Proceedings of the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World

November 3–6, 2014
Visalia Convention Center, Visalia, CA
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Richard B. Standiford and Kathryn L. Purcell, Technical Coordinators

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Abstract


Beginning in 1979, there have been a series of symposia held every 5 to 7 years addressing the state of our knowledge about science, policy and management factors affecting California’s oak resource. This program represents the seventh symposium in the series. California’s oak woodlands cover 10 percent of the state, and in addition, are a key ecological component of conifer forests. Oak woodlands are the most biologically diverse broad habitat in the state, making conservation of their ecosystem values an important policy and management priority. The meeting location in the San Joaquin Valley was conveniently situated for both northern and southern California oak scientists, managers, policy makers and interest groups. These proceedings have 56 papers in a broad array of subject areas, including: wildlife and oaks; oak ecosystem services; oak restoration; oak conservation, management and utilization; and the gold-spotted oak borer and sudden oak death.

Keywords: California oak woodlands, oak conservation, oak wildlife, oak range management, sudden oak death, goldspotted oak borer, oak restoration, oak genetics.
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Frederick D. Euphrat
General Session
People and Oaks

Paul F. Starrs

Abstract
While technical knowledge of oaks, acorns, habitat, wildlife, and woodland environments is evolving and a sought-after field of study, there are profound linkages, at once humanistic and artistic, where it comes to people and oaks. Looking at six distinct facets of humans and oak woodlands, this essay suggests that the bonds of people to place can be mediated by the trees in our immediate surroundings. And as human companions in a living biogeography, oaks are especially recognized and significant.

Key words: art, human impacts, humanities, working woodlands

And what’s an oak worth to you?
What is a given oak worth to a respectful audience? That question is one for the ages, and certainly there are oaks of such formidable maturity and productivity that many an answer is plausible. While the varieties of *Quercus* singled out for attention vary with locale, examples are notable, and often they are historic: The huge Whistler Tree in Águas de Moura in Portugal’s Alentejo is a cork oak said to have yielded a million bottle corks; the King Oak of Charleville Forest, Ireland, may be 800 years old; a Portuguese ilex oak visited in 1916 by the geographer J. Russell Smith dropped a yearly average of 720 liters of acorns (Smith 1916); the Major Oak in Sherwood Forest, Nottinghamshire, England, is, according to legend, where Robin Hood and his outlaw band slept; the Angel Oak has its own park on Johns Island near Charleston, South Carolina. And although the 14 trees that once made up the grove of Council Oaks in Austin, Texas, are whittled down now to just one exemplar, the Treaty Oak, that is still a respected feature from Comanche and Tonkawa Tribal history. Long-living and tending toward the spectacular, oaks command respect, especially when they stand solitary and unapologetic. Botanists, arborists, wildlife biologists—practicing scientists, in short—tend to brusqueness in discussing their subjects, but the public at large is given to the emphatic when describing trees they admire. The territory where arts and humanities meet ascetic science can be fertile ground, if that intersection is recognized and respected. This discussion is about such a dovetailing of people and oaks (fig. 1).

Oaks can be tricky to work with, however. In October 2014 the University of Michigan, relentlessly expanding its top-ten rated law school, acted on a galling concern: What was to be done with a 300-year-old, 19.8 m (65 foot) tall, burr oak (*Quercus macrocarpa*, for sticklers among you) that stood squarely in the expanded footprint of the new building? Bringing together a brain trust comprising the university’s landscape architects, a passel of engineers, gardeners, the University President, and for all we will ever know, the entire staff and student body of Hogworts School for Witchcraft and Wizardry, they elected to uproot the oak to move it. Hassles? Heinous. Cost? A neat $400,000. Return? Beyond a dollar figure, a better answer is likely priceless good will (Householder 2014, Phillips 2014).

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1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3–6, 2014, Visalia, California.
2 Regents and Foundation Professor of Geography, Mail Stop 0154; Department of Geography, University of Nevada, Reno, NV 89557–0048. (starrs@unr.edu).
My theme, as it was solicited, is “People and Oaks.” Later contributors to this symposium build on this theme with history and paleoecology, wildlife, cost-benefit analysis, genomics, wildlife effects and pests, ecosystem services, international perspectives, and much else that is value-added. My goal, however, is to suggest something else, that the working landscapes embodied by oak woodlands, wherever they grow, are deserving of the attention that poets, arborists, sawyers, graziers-with-livestock, planners and polemicists have lavished on the genus *Quercus* and the places they grow. I could do this in any number of ways, as indeed I once did a dozen years ago (Starrs 2002). But no doubt like all of you, I much appreciate how our perspectives on oaks and their landscapes change with time. And where oaks are concerned, that element of time carries weight. I’m going to encapsulate my narrative in six short accounts, each if not a narrative then perhaps a parable of people and their relationship with oaks.

Each story examines a different facet of the human relationship with oaks; these links can be emotional, economic, functional, elemental, aesthetic. The historical geographer Donald Meinig once suggested that “geography represents an age-old and essential strategy for thinking about large and complex matters” and we are hardly in a position to present a contrary argument (Meinig 1996).
Oaks as sustenance and strategic resource

Sustenance and strategic concerns are a longstanding question with oaks. Their products—variously wood, mast, acorns, shelter, aesthetics—are of sizable interest and still greater value. To traditional products—oak planks in the ship’s hull that protected the *USS Constitution* (better known as “Old Ironsides”)—we in 21st century California would add ecosystem services, acorns, grazing land, wildlife habitat, and a bow toward the role played by acorns for wildlife in pre-European California, an importance recognized by California Native Americans who, evidence suggests, were active managers of the woodlands, and certainly drew on tree products: acorns ground for flour; leaves and mast for feed; habitat for wildlife that sustained hunting human populations (Anderson 2005). “People and oaks,” indeed.

Alongside such uses came to be strategic concern about the value of oaks. As a building material, oaks were significant; branches, scrub oaks, and acorns fed livestock in Spanish-Mexican and Anglo times. Exotic oak varieties were introduced to bolster the species found in California (Campos and others 2013). But by the late nineteenth century, and through the 1940s, the products of oaks, whether native and introduced, were a near-obsession (fig. 2).

As an example, one particular concern was the cork oak, native to Spain and Portugal. Cork, an outer bark stripped every 8– to 12–plus years, was a valued oak product, but one found around the Mediterranean Basin, and, though introduced, rarely in North America. Hobbyists during Revolutionary times including Thomas Jefferson sought to establish cork trees (*Quercus suber*) in the United States, but efforts at the land-grant university, the University of California headquartered in Berkeley, were led by foresters, including the prodigious and multitalented Woodbridge Metcalf, an extension forester who...
took up cork oak introduction efforts begun in the 1870s in the Southland, Napa, Sonoma, and in the upper Sacramento Valley, and redoubled efforts, greatly expanding sites. A cadre of test plantings, research done on earlier-established cork oaks, test-stripping of bark, and harvested cork usability tests continued through the 1950s, but efforts were largely abandoned as pines and redwoods took over in the attention of foresters, and apprehensions faded about countries along an unstable Mediterranean fringe peremptorily ceasing cork shipments (Brooks 1997). And to be fair, aside from a crucial role of well-formed cork plugs turned into wine stoppers, there were other insulators, flooring materials, and wall surfaces coming onto the scene, though none with a warmth and intrinsic interest inherent to cork oak bark.

Figure 3—Nineteenth-century photographs can open a startling window into the past, as here where downtown Oakland, California, is seen from the third floor of the Wilcox Hotel, once at the center of the city. (Photograph courtesy of the Society of California Pioneers, Lawrence & Houseworth Collection, date approximately 1865)

Other attributes of the oak, in California and elsewhere, are inevitably linked to the attractive qualities of the Mediterranean-type ecosystem, with its summer-dry, winter-wet (such is the hope) climate. It is no accident that lands fringing the Mediterranean Sea, California, Chile, South Africa, and western Australia have strong proponents, sizable populations, and a serious fan base: they also readily support wine grapes (good ones), olives, sizable food production … and oaks. But *Quercus* are not particularly choosy in their preferred habitat: Mexico retains the world’s highest diversity of oak species, and its climate is more equable year-round than the summer-dry Mediterranean type.
Oaks as aesthetic features

As aesthetic contributions, giving visual contrast, pleasure, high regard, and even wealth to an adopted landscape, oaks are longstanding landscape features. In consideration of that argument now, take a single city: Oakland, California. While the reputation and perhaps even notoriety of Oakland today suggests a benighted history of urban blight, that is unfair and a canard. Oakland, incorporated in 1852, cherished its namesake tree, even as the Central Pacific Railroad, the ferry moles pointing precariously toward San Francisco and the South Bay, and a booming distribution network from city center to streetcar suburbs made the city a vital hub (fig. 3).

Photographs from the Lawrence & Houseworth Collection, housed at the Society of California Pioneers, showed the place of the hardwood trees in the Oakland city firmament and sense of place. Much the same could be said of adjoining valleys and agricultural endeavors: it was no accident that oaks appear in movies made by the Essanay Film Manufacturing Company, based in Niles Canyon (Alameda County), with films for a time starring Charlie Chaplin and “Broncho Billy” Anderson.

The language associated with these photographs of Oakland from 100 to 150 years ago speaks to permanence, an embrace of variety, and enthusiasm for an indigenous landscape where the Mediterranean was an object of respect.

Oaks as cultural objects

Figure 4—Oaks provide identity, in city names, for streets and byways, and here, for a small ranch along Highway 1 in Monterey County, California. The “rancho” is an evocation of the Hispanic heritage of California; “encina” is the Castillian Spanish term for the holm oak (Q. ilex) but can be used with less specificity to describe any oak or oak woodland (an encinar). (Photograph by Paul F. Starrs, 2011)

As cultural artifacts, oaks are nicely rooted in poetry, literature, wayfinding systems, landscape architecture, art, and a sense of self. A durable fashionability goes without
saying, as does the lasting power of oak wood, and its vexing qualities when worked with, especially where furniture-makers, arborists, and scientists attempting to extract useful tree-cores are concerned. Are trees and their enveloping landscapes “cultural objects”? Certainly Jared Farmer argues exactly that, in his recent book “Trees in Paradise,” all about California and its representative trees, which pointedly and dismissively fails to include oaks from species in any way emblematic of California and its human history (fig. 4).

Place names say otherwise: “oaks” are among our most common street names; ranches and features often have a Spanish take on oaks (encina or Encino, for instance, or “robles” or Thousand Oaks or Live Oak, or Oakland, for that matter). In the GNIS database are well over 1,000 place names sporting the word “oak.” Until 2009, the minor league baseball team for Visalia, California, was the “Oaks.” Art, too, is replete with oaks, and clearly, that aspect of California life—whether lavishing praise upon California as—so one booster put it—“a better Mediterranean,” presumably because English was spoken there (at least after a fashion), or because California was held to have immense value on its own merits (Starrs 1988, 11).

Pictorial art, whether in photography (think of the mid-nineteenth century city of Oakland photographs, or the Chaplin films) or in painting was much sought after. Pictorial art captures a critical era in California life and times while exotic species were arriving willy-nilly and changing the look and feel of Alta California. Through a crucial 100-year period from mid-1800s to mid-1900s, oaks were a prevalent landscape feature, and often included in works of art. The oak woodland was a staple of nineteenth and twentieth-century plein air artists, and is still. Work by California painters such as Granville Redmond (1871–1935), William Wendt (1865–1946), Maynard Dixon (1875–1946), Richard Diebenkorn (1922–1993), Eyvind Earle (1916–2000), and Wayne Thiebaud (1920–present). And talented artist-ecologists such as Laura Cunningham, in A State of Change: Forgotten Landscapes of California (2010), reach even farther back into the historic past of landscape evolution.

At about mid-twentieth century, an aggressive spread of irrigated agriculture in the Sacramento-San Joaquin Valley and through the Coast Ranges began to disrupt what Spanish-Mexican culture and agriculture had not quite undone, removing oaks to permit cropping without the annoyance of mid-field trees (Starrs and Goin 2010). Nor were ambiguous utterances from range managers, who at time proposed removing oaks to spur grass production, particularly helpful. Oaks do not find machinery to be particularly good “friends,” so there is sufficient blame to spread around, in the saga of California oaks as landscape objects.

**Oaks as working landscape**

Which brings us to a modern and complicated pass: today and oaks. There is nothing wrong with a well-maintained oak woodland landscape, and, in fact, land and life in the lower Iberian Peninsula, in southeastern Portugal and Spain, and equally parts of France, Italy, Greece, and elsewhere, are home to an established and cherished low-intensity—but assuredly multi-product—agrosilvopastoral management system, the *dehesa* and *montado*, which have attracted no small attention. A so-called “permanent agriculture” of tree crops often centers on a mast of chestnuts, acorns, or other tree bounty that have, with human encouragement, fed livestock and wildlife at least since Roman times, and likely for centuries before that. The legacy and bounty is considerable, but did not transfer directly to California, and others will write of the contrast in systems, so on that theme I touch lightly for now.
The reality is, a “working landscape” attempts foremost to use resources already present, without making vast or irreversible alterations. So the lessons of Spain and Portugal are notable, especially in Visalia, where traditions from those lands were implanted and endured, perhaps even through today.

**Oaks as imperative and scold**

Before we grow too self-congratulatory, it bears noting that the work of the Integrated Hardwood Range Management Program (IHRMP) and of range managers and foresters at Berkeley, UC Davis, and from the scattered corners of California, have worked toward, but not prevented, a contemporary crisis in oak regeneration, management, and (Heaven forefend) proliferation. If mighty oaks from little acorns grow, they do not grow quickly or easily. In a state of 38 million residents, some with obscene amounts of cash, oaks are not safeguarded by public opinion (fig. 5).

![Subdivisions with names such as “Live Oak Ranch” predictably excised the live oaks, and obliterated any semblance of a working “ranch” some time ago, and the housing crash of 2008 took care of anything like replanting efforts—leaving a void of terraformed earth, neatly scraped clean to bare mineral soil by the same Caterpillars and other tracked vehicles invented by California’s geniuses of industrial agriculture, which were turned to other purposes: prepping places for people and pretentious](image-url)
manses, dropped like Dorothy and Toto on what used to be a grassland dotted with rather elegant if dispersed oaks.

Planners, ranchers, researchers, stand around and regard a radically revised landscape, and promoters of heritage tree ordinances are left mouth agape in protest, with not much beyond little fines to be issued as a rejoinder and punishment for oak removal.

**Oak woodlands as researchable features**

On the theme of oaks and research, anyone curious about what’s been done can consult the proceedings of the last six symposia—and, as a kind of culmination, this seventh symposium, which struck many attendees as offering a particularly effective summary and extension of recent work. For me to dwell at length on current trends in research and the practical advice being distributed to landowners and oak fanciers would reduplicate the bibliographies of later essays in this volume, and those will have the freshest material (fig. 6).

What deserves particular mention is that there is increasing attention in the literature on owners and managers of working oak woodlands studying the practices of other oak-rich regions, and, rather pointedly, learning from their successes and failures. A 500-some-page volume edited by Campos and others (2013) compares management, ecological issues, and ecosystem services derived from the woodlands of Spain and California, and follows on work originally presented at the 2001 fifth oak symposium in San Diego (Campos and others 2002). The 2013 book concludes with an observation weighing the value of comparative inquiry: “it pays to acknowledge how much can be learned from comparative research that matches physical, cultural, historical, economic, and geographical features, and then carefully
places likenesses and departures side-by-side, in a deliberate attempt to learn across oceans, landscapes, economies, and societies” (Starrs and others 2013, 493).

That argument for acknowledging and sustaining multiple-product landscapes and the people who inhabit them ties into a debate that weighs existence value at any cost against contrasting arguments that favor a utilitarian approach to the preservation of places and people. If there is a debate there (and even the most secular researcher can be stricken with an attack of honesty which suggests that maybe taking one side or another comes down to a matter of faith), then words from a recent op-ed column published in the New York Times seem especially apt: “So what should we do? Should we continue to invest in keeping ecosystems in historical configurations? Should we attempt to engineer landscapes to be resilient to tomorrow’s conditions? Or should we just let nature adapt on its own?” (Marris and Aplet 2014).

Those are questions that woodland managers and their scientific advisors will forever have in the back of their minds. That is precisely what good questions are for: nagging and, on occasion, producing answers both practical and practicable.

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How Oaks Respond to Water Limitation

Michael F. Allen

Abstract
Oaks are extremely resilient trees. They have persisted since the mid-Cretaceous, with life forms ranging from shrubs to large trees, from evergreen to deciduous. They have two distinct, but critical, adaptations to drought that make this “mesic” taxon adaptable to dry hot environments. First, they form both arbuscular and ectotrophic mycorrhizae, with a high diversity of fungi that independently evolved many times. This means that a single tree forms mycorrhizal symbioses with partners adapting to different conditions and accessing many different resources. Oaks also have deep roots. This allows access to water resources deep in the groundwater, and with hyphae that extend into the granite matrix. Thus, water can be accessed even during drought periods when surface soils are extremely dry. Fine roots and mycorrhizal hyphae persist utilizing hydraulically-lifted water, and can even take up nutrients during these extremely dry conditions. These mycorrhizal hyphae remain viable during drought periods allowing them to rapidly utilize surface precipitation from summer monsoonal events. Together, these adaptations should allow oaks to persist and even thrive under the projected climate change, unless conditions become too harsh. That remains a critical task of future research and monitoring.

Key words: anthropocene, drought, mycorrhiza, nitrogen, nutrient, oak, root

Introduction
Oaks represent one of the most adaptable and resilient trees present on earth. They occupy multiple continents and environments ranging from tropical cloud forests to desert woodlands. They have persisted since sometime in the mid-Cretaceous. Their life forms range from shrubs to majestic trees, from drought-tolerant “live oak” evergreens, to cold-tolerant deciduous trees. All of these lifeforms thrive in California, and create the well-known image of the classical California ecoregion.

California is largely arid, and even where mesic, subject to seasonal and extended drought. To survive, oaks have undergone many evolutionary adaptations to deal with drought and to persist. Among the 18 species and 30-some varieties of oaks in California, taxa range from lowland coastal and inland valleys, up hillsides and foothills, to higher elevation mountain plant communities. Although there is a plethora of adaptations to drought stress, in this treatise, I focus on belowground characteristics that allow oaks to access water deep into the profile, and nutrients and water in the surface soils even during drought. I will also focus on the work from my laboratory and colleagues in southern California. Although there is excellent work throughout the state, the mechanisms responsible for oak survival in southern California are reflective of those that work throughout the state and across oaks in general.

I focus on two mechanisms in particular that give oaks a distinct advantage in the Mediterranean-type climate that characterizes California. First, oaks form mycorrhizae, a mutualistic symbiosis with fungi, with a large diversity of fungi.

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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These include arbuscular mycorrhizae (AM) with Glomeromycota, an ancient monophyletic group of fungi, and ectomycorrhizae (EM) with a high diversity of Ascomycetous and Basidiomycetous fungi. Oaks are able to switch between these two mycorrhizal types both developmentally and environmentally (for example, Egerton-Warburton and Allen 2001). This provides oaks with the ability to form a symbiosis with a large diversity of fungi that have independently evolved multiple times, with many different structural and physiological characteristics. Second, oaks have very deep roots. Oak roots emerging in Texas caves have been found as deep as 25 m (Jackson and others 1999). This allows oaks to tap groundwater resources or water pockets deep in the regolith, characteristic of California geomorphology.

In our studies, we have developed an understanding of both deciduous and evergreen oaks from three sites. These are stands of evergreen coast live oak (*Quercus agrifolia*) in riparian woodlands extending up the hillside at the Shipley Reserve (Querejeta and others 2009) and in the Santa Margarita Ecological Reserve (Borynasz others 2005), and a mixed stand of coast live oak and deciduous California black oak (*Q. kelloggii*) located within a mixed evergreen forest at the James Reserve NRS (Kitajima and others 2013).

**Belowground architecture of California’s oaks**

Oaks form both surface and deep roots. This variation allows them to tap both the surface moisture from individual storms, and deeper water that is either stored in the regolith or is flowing in groundwater. Without the ability of oaks to tap stored or flowing deep water, it is unlikely that oak stands would survive extended, dry summers (for example, Kitajima and others 2013).

Mycorrhizae are mutualistic symbioses formed between plant roots and fungi. The fungi radiate out from roots into the soil accessing nutrients in forms and in spatial locations inaccessible to the plant roots. In tapping those nutrient resources, the fungal hyphae also provide a continuous network whereby water can flow from areas of higher to lower moisture. By including mycorrhizae in the soil-plant-atmosphere continuum, I have previously advocated the concept of the SMPAC (soil-mycorrhiza-plant-atmosphere continuum) that provides both nutrients and water to the plant (Allen 2007). Hyphae can either form a dense network around individual roots or can be more diffuse but extend several meters outward. These fungi also release enzymes and organic acids into soil that mineralizes both organic and inorganic forms of nutrients making N and P, and even Fe and Ca available for uptake (for example, Allen and others 2003). Mycorrhizae also alter carbon balance. The plant provides carbon to the fungus in exchange for nutrients, wherein the fungus forms compounds resistant to decomposition. Mycorrhizal fungi form compounds that are relatively resistant to degradation (Treseder and others 2005), including glomalin, a glycoprotein (Rillig and others 1999) that binds soil aggregates, and chitin, a long-chain polymer of N-acetylglucosamine (Treseder and Allen 2000) that can bind with CaCO₃ forming hard rhizomorphs and even large mats (Allen and others 1996). Thus, mycorrhizal fungi are important in sequestering carbon directly. Our estimates of carbon allocation to mycorrhizal fungi in California mixed forests range from 20 to 35 percent of the net primary production based upon hyphal production and turnover, and N isotopic fractionation (Allen and Kitajima 2014, Allen and others 2014).

Oaks are among a select group of trees that form both arbuscular mycorrhizae (AM) and ectomycorrhizae (EM) (Egerton-Warburton and Allen 2001). Members of the Fagaceae are among the most ancient of plants that formed EM, between 100 and
200 million years ago. But oaks also retained their ability to form the original, primitive AM that evolved with the invasion of the land, somewhere between the Ordovician and Silurian Periods (Redecker and others 2000). This means that oaks are able to take advantage of a wide range of mycorrhizal fungi that have a multitude of different strategies for dealing with environmental variability. Oaks form AM during drought years and up hillsides, in largely inorganic soils, and when their roots extend into grasslands where AM predominate (Querejeta and others 2007). In stands where large amounts of organic matter accumulate and N is largely immobilized, oaks will form EM with a high diversity of fungi, including many with the ability to break down organic N and transfer it to the plant (Bledsoe and others 2014). Oaks will switch between AM and EM mycorrhizae depending upon the location, season and yearly precipitation (for example, Querejeta and others 2009).

Finally, as oak roots grow through fractures in the bedrock, their mycorrhizae grow with them. The roots remain within the fractures, but if the bedrock is weathered, the mycelial network actually grows into the granite matrix (Bornyasz and others 2005).

Temporal and spatial variation in water availability for oaks

In California, precipitation varies in extremes by amount and form. Annual rainfall for oak stands can vary from a few centimeters to a meter or more, depending upon the location and the year. During wet years, precipitation can come as snowfall from northern fronts or from the “pineapple express” bringing heavy tropical rains. Monsoonal events, even occasional hurricanes, can bring moderate to heavy local rains during the summer drought. These different storm types have different signals that can be identified using δ¹⁸O and δD. Groundwater isotopic signatures can reflect those different storms and the plants that tap these water sources can be identified by analyzing xylem water as a marker.

As precipitation falls on the soil surface, it penetrates the soil in nearly random “wetting fronts”. Water from an individual storm may penetrate only a few millimeters, or may saturate the soil down to groundwater, depending upon the form (snow melt or rain), duration, amount, and intensity. Importantly, water penetration follows channels downward, including along roots or rock fractures. Although precipitation varies greatly, that variation may not be reflected in the soil moisture. During years of high precipitation, or following heavy snowfall, the soil becomes saturated, and the groundwater is recharged. But during moderate, and even low precipitation years, the surface soils generally still saturate (Kitajima and others 2013). During these years groundwater recharge is reduced.

Adaptations to drought by southern California oaks

Seedling establishment is dependent upon microsites with sufficient moisture for germination. If seedlings emerge in the grassland or hillside away from mature trees, they become AM (Lindahl 2002). AM fungal hyphae provide nutrients and water by increasing access to soil resources. However, a seedling that emerges within a stand of mature trees taps a network largely of EM fungi (Bledsoe and others 2014). Once the seedling receives full sunlight (either in an open canopy, or with a gap formation in a previously closed canopy), the taproot extends vertically through the shallow soils and into the regolith and the secondary roots extend horizontally through the
soil. In the surface soils, these secondary roots utilize most of the soil that can flow into roots and root hairs. However, the mycorrhizal hyphae can cross soil gaps and tap soil water found either in small soil pores (Allen 2007) or across air gaps (fig. 1). These hyphae, from both EM and AM fungi, allow the plant to access both moisture in the saturated soils, but also importantly, soil moisture provided by monsoonal events during the summer droughts when there are air gaps in soil pores.

During drought, the mycelial network can provide access to water, drawn from deep in the profile and transported to hyphae via hydraulic lift (for example, Allen 2007, Egerton-Warburton and others 2007, Querejeta and others 2003). At night, a negative gradient in water potential develops from plant to the surface soils. As stomata close, water moves back through roots, fine roots, and into the mycorrhizal fungal hyphae (Querejeta and others 2003). Mycorrhizal fungal hyphae are sustained well into the dry season when it should be too dry for the hyphae to survive (Kitajima and others 2013). Further, even nutrients such as N, can be tapped by this hydraulic lift during the dry season. The hyphae near the roots are hydrophobic, so water remains within the hyphae. The hyphal tips, however, are hydrophilic, and permeable to water. Droplets emerge from the hyphal tips, absorb N (experimentally added in the form of $^{15}$N). When the stomata re-open the next morning, the SMPAC gradient is re-established, and the $^{15}$N dissolved in the drop is transported to the plant (Egerton-Warburton and others 2008).

Mature trees tap deep water, and this water is especially critical during the dry season (Kitajima and others 2013). During the winter and early spring, when temperatures are cool and often before leaf out by deciduous oaks, soil water is recharged and water enters the deeper layers, and can even flow laterally through the groundwater (Kitajima and others 2013). During the summer drought, there is a greater use of water than can be provided by soils, so that deeper water is tapped by mature oak roots. During the driest part of the year, the deep roots transport deep water to the tree. At night, some of that water is transported to the mycorrhizal fungi via hydraulic lift (Querejeta and others 2003) and, once in the network, on to adjacent seedlings that have tapped the mycorrhizal mycelial network (Egerton-Warburton

Figure 1—Arbuscular mycorrhizal fungal hyphae crossing air gaps. The water droplets have been absorbed by root hairs and fine roots (right), but AM fungal hyphae extend across air gaps accessing water droplets on the other side of the gaps. Those droplets adjacent to the hyphae were gone by the next day. Images were collected in situ using the Soil Observatory System (Allen and Kitajima 2013).
and others 2007). This process is especially notable in the valley riparian stands where deep water is available during the summer dry season (Querejeta and others 2009).

As the taproot extends vertically, it may find fractures in the granite matrix, often created by earthquakes (Bornyasz and others 2005). If the granite has weathered sufficiently, hyphae from mycorrhizal fungi extend into the matrix providing a large water source to the deeper-rooted plants (Bornyasz and others 2005). Isotopic analyses show that both uptake of water from the granite matrix and hydraulic redistribution contribute to a seedling’s water balance (Allen 2006, Kitajima and others 2013).

Projections of future impacts: intersections of perturbations

Evolutionarily, oaks are physiologically adapted to mesic conditions with summer precipitation (Mensing 2005). That they have been able to persist, even thrive during the drier periods in California’s paleo-past, provides important clues to their current capability to adapt to the expected stressors of the future. As we peer into the 21st century, we can envision a suite of interacting perturbations affecting oak woodlands, presenting challenges to managing this critical element of California’s landscape (table 1).

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<th>Impacts</th>
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<td>Direct</td>
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<td>Increased C sequestration due to greater allocation to roots and mycorrhizae</td>
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<td>N deposition</td>
<td>Decreased water-use efficiency</td>
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<td>Decreased C sequestration due to reduced allocation to fine roots and mycorrhizae</td>
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<td></td>
<td>Invasive grasses</td>
<td>Increased fire frequency</td>
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<td>Indirect</td>
<td>Rising temperatures</td>
<td>Greater water stress</td>
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<td>Increased drought stress</td>
<td>Greater seedling mortality</td>
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<td>Decreased groundwater</td>
<td>Reduced deep water sustaining plants during drought</td>
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<td>Reduced hydraulic lift, reducing fungal persistence during summer drought and reduced water allocation from deep-rooted mature trees to seedlings within the fungal network</td>
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There are both direct and indirect anthropogenic impacts on vegetation. Both can affect the water uptake and allocation in oaks that will impact their growth, reproduction and survival. The direct human impacts that will alter water uptake and utilization by oaks include elevated atmospheric CO₂ due to fossil fuel consumption. Elevated CO₂ would not, in itself, be detrimental to plants. Increased atmospheric CO₂ increases water use efficiency because the higher partial pressure means a higher CO₂:H₂O exchange rate. It also means that nutrients become more limiting, thereby resulting in increased mycorrhizal activity (see Allen and others 2003). But along
with elevated CO₂, the use of fossil fuel results in greater N deposition. The NOx deposition results in a net fertilization of a site. This deposition reduces the root:leaf ratio and the relative amount of EM activity in some obligately EM plants (Allen and others 2010). Interestingly, AM plants may adjust to the added CO₂ and N by increasing root and mycorrhizal activity to match aboveground productivity (Allen and others 2003, 2010). Since oaks are switchers, they may readily adapt to both elevated CO₂ and NOx deposition (fig. 2). They have previously lived through periods of both higher CO₂ (creating conditions of N limitations), and low CO₂ (creating conditions where N becomes more available).

Invasive grasses have a mixed impact on oaks. The presence of the grasses themselves reduces EM activity (Allen and Karen, unpublished data) and the oak roots that extend beyond the canopy into a grassland or seedlings that establish in the adjacent grasslands tend to be AM, not EM. While oaks form AM, this mycorrhizal association is not as effective for oak seedling growth as EM associations (Egerton-Warburton and Allen 2001). In addition, grasses carry fire more extensively and frequently than do widely-spaced shrubs. But, the fire is not as hot as in dense shrub stands, potentially resulting in lesser injury to mature oak trees. In the past, California Indian tribes burned the understory of oak stands, in part to sustain the harvest of mushrooms. Most of the mushrooms produced under these conditions are EM fungal sporocarps (Anderson and Lake 2013).

The major indirect concern to oaks is global-to-regional climate change resulting from elevated CO₂. That atmospheric CO₂ increases global temperatures has been known for over a century. But how it plays out at regional scales and the implications for greater water loss with increasing atmospheric temperatures, and groundwater extraction by both native plants and human needs becomes a critical topic for further research. If the increased water demand, due to greater temperatures, is coupled to less groundwater (Famiglietta 2014), a longer summer drought could become limiting to oak survival.

Alternatively, oaks have tended to become more dominant during the warmer, drier periods since the Pleistocene (Mensing 2005). Fagaceae likely arose and began forming EM during the late Jurassic, when atmospheric CO₂ levels were far higher than today (Allen 1996). Higher atmospheric CO₂ drives not only global
temperatures, but also results in higher carbon:nutrient ratios (Allen 1996). This forcing factor could well be a driver to develop ectomycorrhizal associations in which the fungi mineralize and transport organic N to the host. In fact, using isotopic fractionation between sporocarps, soil, and leaves, we estimate that oaks receive between 50 and 90 percent of their N via this mechanism (Allen and Cario, unpublished data). Oaks appear to have arisen during the Miocene (Mensing 2005), an interesting geological period with low CO2 but high temperatures (Knorr and others 2011). AM systems are more tolerant of a broader temperature and moisture range than EM systems (for example, Vargas and others 2010). One could hypothesize that oaks kept their AM affinities even while other Fagaceae from mesic climates became almost exclusively EM. This allowed oaks, generally mesic taxa, to utilize both EM and AM to survive especially well in relatively mesic patches during arid periods in California’s geological record.

These evolutionary adaptations could prove especially valuable as we move into the Anthropocene. Climate projections show warming conditions between 3 and 5 °C across the next century. Precipitation projections are inconclusive, but in any case, warming temperatures will increase evaporative demands on plants, inducing drought stress. Further, greater variability is likely, again resulting in increasing drought periods. But oaks have an incredible ability to form deep roots and switch mycorrhizae as dictated by conditions. Based on past climate history (Mensing, The paleohistory of California oaks, these proceedings), we should expect an increase in oak stands, unless the extremes are too large. That is a question for future monitoring and research.

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Acorns and Acorn Woodpeckers: Ups and Downs in a Long-Term Relationship

Walter D. Koenig, Eric L. Walters, Johannes M.H. Knops, and William J. Carmen

Abstract
Acorn woodpeckers are one of the most conspicuous and abundant birds in California oak forests due to their unique dependence on acorns, a food resource eaten directly and stored in specialized structures on their territories for later use when acorns are no longer present on trees. Parallel long-term studies of the demography and behavior of this species and of patterns of acorn production by oaks at Hastings Reservation in central coastal California have revealed many ways that acorn crops influence the ecology and behavior of acorn woodpeckers. We present results focusing on the large-scale effects of oaks on the geographical ecology of acorn woodpeckers and how the acorn crop influences woodpecker demography, including the probability that young remain as helpers and the corresponding fitness consequences of this decision.

Key words: acorns, acorn woodpeckers, masting, Melanerpes formicivorus, oaks

Introduction
One need not study acorn woodpeckers (Melanerpes formicivorus), a common avian resident and by far the most common woodpecker in California, for very long before it becomes apparent that their dependence on acorns, as suggested by their common name, is far more appropriate than their proclivity to eat ants, as suggested by their scientific name. Indeed, except perhaps for a brief period during late summer, it is difficult to not be struck by the degree to which the lives of acorn woodpeckers revolve around oak trees and their acorns, as much of their time involves harvesting acorns, storing them in unique structures known as ‘storage trees’, or ‘granaries’, located on their territories, defending granaries from both conspecifics and other species, and eating acorns when conditions are unsuitable for flycatching or obtaining otherwise more nutritious food.

Early in our long-term study of the social behavior of acorn woodpeckers, which we began in 1974 by continuing a study initiated in 1968 by Michael and Barbara MacRoberts (1976), it became obvious that many aspects of acorn woodpecker population ecology were dependent on what was clearly a highly variable acorn crop. This was not surprising; not only had Carl and Jane Bock demonstrated that the geographical ecology of acorn woodpeckers was dependent on oak species richness (Bock and Bock 1974), but numerous studies dating back at least 30 years had reported data suggesting that oaks frequently produced highly variable acorn crops (Burns and others 1954, Downs and McQuilkin 1944, Tryon and Carvell 1962).
Despite these prior studies, including ongoing work examining oak regeneration at our study site by Jim Griffin that involved work quantifying acorn fall under a number of valley oaks (*Quercus lobata*, Griffin 1971), we soon decided that more detailed investigation of the acorn crop and its effects on the acorn woodpecker population were warranted.

Here we briefly summarize some of those effects, extracted from what has become parallel long-term studies of the social behavior and population ecology of acorn woodpeckers and variable seed production in California oaks (Koenig and Mumme 1987, Koenig and others 1994b, Koenig and others 2011, Koenig and others 2015). We present results illustrating the effects of the acorn crop on the demography of the acorn woodpecker population, summarize some of the large-scale biogeographical effects of oaks on acorn woodpeckers, and briefly discuss effects the acorn crop has on their social behavior.

**Methods**

Our study site is Hastings Natural History Reservation in central coastal California, a field station run by the Museum of Vertebrate Zoology, University of California Berkeley. Acorn woodpeckers are cooperative breeders, living in family groups of 2 to 16 individuals generally consisting of both multiple breeders of both sexes and offspring that remain in their natal group as nonbreeding helpers, often for many years (Koenig and others 1984). Acorn woodpeckers at Hastings have been individually color-banded and monitored continuously since 1971; studies quantifying the acorn crop were initiated in October 1980 (Koenig and others 1994a). Thus, most of our analyses include bird data from 1981 (the first year for which we had acorn data from the prior fall) through 2012 or 2013. Weather data are from Hastings Reservation headquarters (36° 23’ N, 121°, 33’ W).

Our measure of the acorn crop is based on a modified version of the visual survey technique introduced by Graves (1980). Each autumn two observers counted as many acorns in 15 seconds as they could on each tree using binoculars; counts were then combined (N30) and ln-transformed ($ln[N30+1] = LN30$) for subsequent analysis. Surveys were performed on an initial sample of 250 marked trees (several of which have since died) spread throughout the field site and divided among the five tree oak species present in at least part of the study site (currently 86 *Q. lobata*, 56 *Q. douglasii*, 63 *Q. agrifolia*, 21 *Q. chrysolepis*, and 20 *Q. kelloggii*). Trees were located near established acorn woodpecker territories, and although unequally divided among the species, provide a reasonably unbiased sample of the importance of not only the acorn crop for the different species but the relative importance of the species to the acorn woodpecker population. Thus, we took the mean of LN30 values in year $x$ for all individuals of the same species for an estimate of that species’ acorn crop, and the mean of LN30 values for all 250 individuals in year $x$ for an estimate of the overall size of the acorn crop in a given year. For a few analyses, we divided trees based on where they were located within the study site; we were particularly interested in differences in areas where only three of the oak species were generally present (*Q. lobata*, *Q. douglasii*, and *Q. agrifolia*; all “1-year” species that mature acorns in a single year) compared to sites where four species were present (the prior three plus *Q. chrysolepis*, a “2-year” species that matures acorns in 2 years) and those where all five were common (the prior four plus *Q. kelloggii*, also a 2-year species).

In order to keep track of timing, we refer to the calendar year of an event as taking place in ‘year $x$’, where $x$ ranges from -1 to +1. The primary effects of the acorn crop in the fall of one year (typically ‘year -1’) are manifested on the woodpecker
population the following spring (typically ‘year 0’). Lagged effects are referenced similarly.

Statistical analyses, described in the text, were conducted in R 3.0.3 (R Core Team 2014).

Results

Variability in the acorn crop

As expected, the acorn crop varied considerably from year to year; the mean acorn crop for *Q. lobata* as estimated by our annual survey is graphed in fig. 1a. Variability as measured by the coefficient of variation (CV = standard deviation x 100 / mean) for the five species individually at Hastings between 1980 and 2013 ranged from 55.3 percent for *Q. douglasii* to 74.5 percent for *Q. kelloggii*. Acorn production is typically asynchronous among species, however, particularly among those that require different number of years to mature crops (Koenig and Haydock 1999, Koenig and others 1994b). Consequently, the overall variability in the number of available acorns from any of the five species in the oak community (‘community variability’), although still variable from year to year (fig. 1b), was considerably less so than that of any one of the species by itself. The mean CV for the five individual species at Hastings was 62.7 percent, nearly 50 percent greater than the community variability as estimated by considering all five species together (fig. 1b).

Acorn woodpeckers exhibit little to no preference for different species of acorns (Koenig and Benedict 2002, Koenig and others 2008a) and territories in our study have access to between three and five species of oaks. As a result, years when few acorns of any species are available to groups are rare. Three to four such years are evident from fig. 1b; when sufficiently bad, poor years resulted in the disintegration of many groups, with the proportion of birds of different classes disappearing being inversely related to their status in the dominance hierarchy (Hannon and others 1987). Conversely, when the overall acorn crop was very good, some groups were able to produce a fall nest. Such nests, which start in August or September and fledge young as late as early November, occurred in about one-third of years and contributed only 4.3 percent of the population’s total productivity overall. In 1984,
however, following the bad acorn crop of 1983 and a poor 1984 spring acorn woodpecker breeding season, 50 percent of the calendar-year’s productivity of fledglings was attributed to fall nests (Koenig and Stahl 2007).

**Long-term effects of the acorn crop**

Good acorn crops were not only accompanied by occasional fall nests but were followed by early and highly productive breeding seasons the following spring, including significantly larger clutch sizes ($r = 0.37$, $P < 0.05$), significantly more groups having successful second nests ($r = 0.64$, $P < 0.001$), and significantly more young fledged per group ($r = 0.76$, $P < 0.001$; fig. 2b).

When high productivity in year 0 followed a good acorn crop in year -1, groups had more helpers the following spring in year +1 ($r = 0.59$, $P < 0.001$) and larger mean group size ($r = 0.61$, $P < 0.001$; fig. 2c). Thus, the effects of a good acorn crop were detectable in the population over 2 years later. It is likely that such effects might be felt even longer, but the negative lag-1 correlation between annual acorn crops (the correlation between the overall mean acorn crop in year 0 and year +1 = -0.49, $P = 0.005$) resulted in a significant inverse correlation between the acorn crop in year -1 and fledging success 2 years later (fig. 2d). Going backwards in time, however, the overall mean acorn crop, which was strongly weighted in our sample by the productivity of *Q. lobata*, a 1-year species, was significantly correlated with mean maximum temperature the prior April (fig. 2a), apparently due to a complex relationship linking mean temperature to phenological synchrony, pollen availability, and fertilization success (Koenig and others 2015). Thus, based on mean maximum temperature during a particular April, it was possible to predict the overall acorn crop that fall (fig. 2a), fledging success of the acorn woodpecker population the following year ($r = 0.42$, $P = 0.01$), and mean group size 2 years later ($r = 0.35$, $P = 0.05$).
Figure 2—Scattergrams of (a) the mean acorn crop in year -1 vs. maximum April temperature in year -1; (b) the mean number of young fledged per group in year 0 vs. the mean acorn crop in year -1; (c) mean group size in year 1 vs. the mean acorn crop in year -1 and; (d) the mean number of young fledged per group in year 1 vs. the mean acorn crop in year -1. Pearson correlations (all $P < 0.001$) listed.

**Role of oak richness**

A reanalysis and updating of Bock and Bock’s (1974) study of the relationship between acorn woodpeckers reported on the Audubon Christmas Bird Counts confirmed that the distributional limit of the species along the Pacific Coast is set not by the limit of oaks, but by sites where oak richness drops to a single species (Koenig and Haydock 1999). Moreover, results supported the intuitively pleasing conclusion that mean woodpecker population size is determined by the extent of oak woodland in an area (resource abundance), while annual variability in population size is inversely correlated with oak species richness (resource variability). The rationale for this finding is that annual variability in the overall acorn crop decreases as the number of oak species increases due to asynchrony in acorn production, as illustrated in fig. 1. No such relationship was detected by either study among sites in the southwestern United States. Although the reasons for this difference are unclear, it is possibly related to the relatively rare co-occurrence of 1-year and 2-year species of oaks in the Southwest. With a high proportion of sites containing only species of oaks that mature acorns in the same number of years, there is quite possibly greater synchrony of acorn production, and thus higher overall acorn variability, in the Southwest compared to the Pacific Coast (Koenig and Haydock 1999).

There is similar evidence that variability associated with oak species richness may be detectable even within a limited geographic scale such as our Hastings study site. By dividing the study area into regions within which different numbers of oak species (three, four, or five) were common, we tested their effects on woodpecker productivity. Among the three categories of oak richness, mean woodpecker group
size increased with increasing oak richness (Kruskal-Wallis test, $\chi^2 = 8.8$, df = 2, $P = 0.01$) whereas annual variability in group size decreased significantly (Kruskal-Wallis test, $\chi^2 = 12.3$, df = 2, $P = 0.002$) with oak richness (fig. 3). The latter result was due to a sharp decrease in CV among sites with access to four or more oak species, the areas that included both 1-year and 2-year species of oaks.

Figure 3—Mean and coefficient of variation in the size of acorn woodpecker groups at Hastings Reservation, 1975 to 2013, depending on the number of oak species to which they had ready access. The three oak species in the first category are all ‘1-year’ species that mature acorns in a single year; additional species are ‘2-year’ species requiring 2 years to mature acorns.

**Crop size and helping behavior**

Young acorn woodpeckers typically delay dispersal as a ‘best of a bad job’ strategy when they are unable to fill a reproductive vacancy in the population (Koenig and Mumme 1987). The availability of such vacancies, and thus the proportion of helpers able to become breeders in any one year, was influenced by the acorn crop. Specifically, when the acorn crop was good (year -1), a higher proportion of helpers survived the subsequent winter to become helpers the next spring (fig. 4a). This was presumably because the high reproductive success in spring of year 0 resulted in more offspring being produced, and with a limited number of territories, a higher proportion of birds were forced to remain as helpers in year +1. This relationship remained significant even after controlling for the acorn crop in year 0. In contrast, the proportion of helpers that remained as helpers into the next breeding season decreased with larger acorn crops in the same year (year 0) (fig. 4b). This relationship may once again be a side-effect of the lag-1 correlation in the acorn crop, since it was not significant in an analysis that included both the acorn crop in year -1 and in year 0, but to the extent it is real it was possibly the result of favorable food conditions resulting in an increased number of vacancies in otherwise poor-quality territories that were then colonized by older helpers. In any case, the acorn crop clearly had important effects on the probability of helpers obtaining reproductive vacancies and, conversely, continuing to help in their natal group.

The acorn crop also influenced the degree to which helpers influenced the reproductive success of groups. Prior work in other cooperative breeding species has suggested that in many cases, helpers are most important when conditions are poor, allowing pairs to breed successfully when they otherwise would be unable to acquire sufficient resources for themselves and their offspring (Covas and others 2008, Magrath 2001). In contrast, in acorn woodpeckers, evidence indicates that helpers
significantly increase survivorship and reproductive success of breeders when conditions are good—that is, following large acorn crops—rather than when conditions are poor (Koenig and others 2011). Perplexingly, this effect was only observed for helper males (fig. 5a); the statistical effect of a helper female on reproductive success was nonsignificantly positive and independent of the acorn crop.

This result becomes even more difficult to explain when looked at in greater detail. First, assuming that the different effects of helpers are due to differences in their provisioning behavior, we would expect to see feeding rates that parallel the above patterns. In contrast, there was no relationship between provisioning rates of helpers and environmental conditions—that is, the prior fall’s acorn crop—for either male (fig. 5b) or female helpers. How, then, did helper males benefit their group? If we restrict the analysis to first spring nests only, the strong positive relationship between the effect size of a helper male and the acorn crop disappears (fig. 5c). The probability of having two successful nests in a season, however, increased significantly among breeding pairs when they had helper males (fig. 5d).

Figure 4—Scattergrams of (a) the percent of helpers that remained as helpers from year 0 to year +1 versus the mean acorn crop in year -1, and (b) the percent of helpers that remained as helpers from year 0 to year +1 versus the mean acorn crop in the fall of year 0; Pearson correlations and significance (*$P <0.05$; ***$P <0.001$) listed.
Discussion

Acorns, which can be high in lipids but are generally low in available protein, are in general a supplementary food resource for acorn woodpeckers that provide a relatively small, but still extremely important, fraction of the energetic requirements of their populations in central coastal California (Koenig 1991, Koenig and Mumme 1987). Acorn availability allows acorn woodpeckers to remain resident in all but the worst acorn years (Hannon and others 1987) and provides them with the flexibility to feed more nutritionally valuable insects to their nestlings (Koenig and others 2008b). It is thus not surprising that acorn woodpecker dependence on this resource is manifested in a variety of ways, both demographically and behaviorally.

When the acorn crop fails, the effects are immediately evident in terms of the breakdown of group structure and the disintegration of many woodpecker groups (Hannon and others 1987). Conversely, when the acorn crop in the fall is good, birds can have fall nests (Koenig and Stahl 2007). Because the acorn crop of different species of oaks are to some extent asynchronous, the probability of territory abandonment in a poor year is mitigated by oak richness, especially in areas of sympathy between ‘1-year’ and ‘2-year’ species that mature acorns in different years. Such effects are manifested in acorn woodpecker populations along the Pacific Coast by reduced annual population variability in sites with greater oak species richness,
but are even expressed on a smaller scale within our study site by groups with access to more species of oaks exhibiting higher mean group size and lower annual variability.

The size of the acorn crop has longer-term effects by driving high woodpecker productivity the following spring and resulting in relatively large groups 2 years later. Because of the correlation between mean maximum temperatures in the spring and the subsequent acorn crop, apparently driven by effects on phenology and pollen availability, it is possible to predict, at least to some extent, not only the acorn crop but the reproductive success and subsequent group size of acorn woodpeckers in the population 2 years later based on environmental conditions during the spring.

The acorn crop also affects the competitive environment faced by acorn woodpecker helpers and thus the probability that they will obtain a reproductive vacancy rather than remain as nonbreeders in their natal group. More dramatically, the presence of helper males, but not helper females, enhances the reproductive success of groups, not by their provisioning behavior, but by increasing the probability that the group will successfully fledge more than one nest in a season. What helper males are doing is currently under study, as is the even more perplexing reason for why helper males, but not helper females, exhibit these effects.

In contrast to some superficially comparable systems, such as that of Clark’s nutcrackers (*Nucifraga columbiana*) and piñon pines (*Pinus edulis*) (Vander Wall and Balda 1977), the evolutionary dependence of the acorn woodpecker—oak system is apparently mostly one-way. That is, although acorn woodpeckers are highly dependent on acorns and oaks, no species of oak is dependent, as far as is known, on acorn woodpeckers for dispersal or regeneration. Indeed, given the relative efficiency with which acorn woodpeckers are able to recover acorns stored above ground in their granaries as opposed to western scrub-jays (*Aphelocoma californica*) that store acorns in the ground where subsequent germination is potentially enhanced (Carmen 2004), it is unsurprising that oaks exhibit no obvious adaptation facilitating their use or harvesting by acorn woodpeckers. Acorn woodpeckers are, nonetheless, one of the most characteristic denizens of California oak woodlands, and continue to provide endless surprises with their unique and surprising behavior.

**Acknowledgments**

We thank our colleagues who have helped with the acorn woodpecker and oak studies over the years and the many field assistants who collected much of the data. We particularly thank Vince Voegeli and the Museum of Vertebrate Zoology, University of California, Berkeley, for their assistance. Our work has been supported by the National Science Foundation, most recently by grants IOS-0918944 and DEB-1256394, and the UC Integrated Hardwood Range Management Program.

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The Paleohistory of California Oaks

Scott Mensing

Abstract
Oak woodlands are a fixture of California geography, yet as recently as 10,000 years ago oaks were only a minor element in the landscape. The first fossil evidence for California’s oaks is in the early Miocene (~20 million years ago) when oaks were present across the west, intermixed with deciduous trees typical of eastern North America. As climate became drier, species dependent upon summer precipitation went locally extinct and oaks retreated west of the Sierra Nevada. During the Pleistocene (the last 2 million years) oak abundance declined during cool glacial periods and expanded during warm interglacials. After the last glacial maximum (~18,000 years ago), oaks expanded rapidly to become the dominant trees in the Coast Ranges, Sierra Nevada foothills, and Peninsular Ranges. During the Holocene (the last 10,000 years) oaks in the Sierra Nevada were most abundant during a warm dry period between 8000 and 6000 years ago. Native American use of fire to manipulate plants for food, basketry, tools, and other uses helped maintain oak woodlands and reduce expansion of conifers where these forest types overlapped. Fire suppression, initiated by the Spanish and reinforced during the American period has allowed oak woodland density to increase in some areas in the Coast Range, but has decreased oaks where pines are dominant. Extensive cutting of oaks has reduced their populations throughout much of the state.

Key words: California, oak woodlands, paleoecology, Quercus, vegetation history

Introduction
Oak woodlands characterize much of the California landscape, but widespread oak communities are of relatively recent origin in the state. During most of California’s geologic history, oaks were absent or much more limited in their distribution. Fossil evidence shows that species conforming to modern California oaks were present in western North America by about 10 million years ago, but their range shifted into the state within the last few million years as the summer-dry Mediterranean climate developed and strengthened. During the last 100,000 years, oaks were only a minor element of the landscape, most likely persisting as isolated refugia. At the end of the last ice age, about 10,000 years ago, oaks rapidly expanded creating the woodlands of today. Even during this time period, climate change has influenced the range and distribution patterns of oak woodlands, such that in some locations, woodlands have only been in place for the last few thousand years. Evidence of the first appearance of humans in California also dates to about 10,000 years ago, so that the expansion of oak woodlands after ice ages coincides with a period of human land use. Native Californians lived throughout the oak woodlands and evidence suggests that their practice of frequently burning the landscape influenced the development of the open oak savannas commonly described in the earliest European accounts. Within just the last 2 centuries, intensive resource use has extensively altered the distribution and abundance of oak woodlands throughout most of their range in California.

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
2 Department of Geography, University of Nevada at Reno, 1664 N. Virginia Street, Reno, NV 89557. (smensing@unr.edu).
Early Miocene (20-16 Ma)

California oaks were not originally part of a summer dry Mediterranean climate, but appear to have evolved under a summer rainfall regime. California oak history begins in the Pacific Northwest in the Early Miocene, between 20 and 16 million years ago (Ma), with the first fossils that can be compared with modern oaks (Wolfe 1980). The presumed ancestors for black oak (\textit{Q. pseudolyrata} - \textit{Q. kelloggi}) and valley oak (\textit{Q. prelobata} - \textit{Q. lobata}) are found in Oregon (fig. 1), not California (Chaney 1920).

These oaks grew with a diverse mix of species within genera now commonly found in either east Asia: ginko (\textit{Ginkgo}), zelkova (\textit{Zelkova}); the eastern United States hickory (\textit{Carya}), tulip tree (\textit{Liriodendron}), sweet gum (\textit{Liquidambar}), elm (\textit{Ulmus}) and magnolia (\textit{Magnolia}); or now confined to riparian habitats in the west, such as maple (\textit{Acer}) and beech (\textit{Fagus}) (Axelrod 1983). As summer rainfall disappeared through the late Cenozoic, most deciduous broadleaf species went locally extinct, but California’s oaks survived (Axelrod 1973). Today’s native species must have been pre-adapted to summer drought and were able to persist in the region as summer rainfall diminished and the climate became more Mediterranean (Blumler 1991).
### Table 1—Middle Miocene (M Mio) and Early Miocene (E Mio) floras mentioned in the text with the best known age in millions of years. Chronology follows Woodburne and Swisher (1995), and Schorn (unpublished data)

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*Site# refers to site identification numbers in figures 1 and 2.
Species are: Qa = Q. agrifolia, Qk = Q. kellogii, Qw = Q. wislizeni, Qc = Q. chrysolepis, Qe = Q. engelmannii, Ql = Q. lobata, Qd = Q. douglasii, Quercus agrifolia, Q. douglasii, and Q. engelmannii are not mapped.
X = fossil present that conforms to the modern species.
x = identification determined ambiguous by the author.
Unpublished floras examined at the University of California Museum of Paleontology paleobotany collection.

### Middle Miocene (16 – 10 Ma)

By the beginning of the Middle Miocene ~16 Ma, two additional oaks comparable to modern species are found in the fossil record (fig. 2), canyon live oak (Q. hannibali – Q. chrysolepis) and interior live oak (Q. wislizenoides – Q. wislizeni). The vast majority of oak woodlands were still outside of the present area of California, in

**Figure 2**—Distribution maps of the fossil localities and modern ranges of canyon live oak (*Q. chrysolepis*) and interior live oak (*Q. wislizeni*). Filled symbols represent sites where there is greatest confidence in the fossil identification and open symbols are sites with the least confidence following table 1.

Only two species were confidently present in California during the Middle Miocene, black oak found in the southern Coast Range and north of Lake Tahoe, and canyon live oak near the Tehachapi (Axelrod 1939, Renny 1972) in southern California (table 1, figs. 1 and 2). In the Tehachapi, oaks grew alongside laurels (*Persea*), suggesting a wetter climate than now. These two species had the widest distribution pattern of all the oaks, also being found in Nevada, Oregon, Idaho and in the case of black oak, southern Washington (Smiley 1963).

In Oregon, black oak, valley oak and canyon live oak grew with eastern deciduous species as well as redwoods, indicating mild temperatures with wet summers (Axelrod 1973, Chaney 1959). Fossils with lobed oak leaf morphology resemble both valley oak and Oregon white oak. These two species may have had similar progenitors in the Pacific Northwest that diverged sometime after the Middle Miocene, with valley oak becoming restricted to California.

Interior live oak fossils were restricted to Nevada during the Middle Miocene (fig. 2) where they co-occurred with canyon live oak and black oak along with deciduous species indicative of a summer wet climate, including ancestors of madrone (*Arbutus*), walnut (*Juglans*), *Eugenia* (extinct), birch (*Betula*), maple (*Acer*), buckeye (*Aesculus*), persimmon (*Diospyros*) hickory (*Carya*), elm (*Ulmus*) and zelkova (*Zelkova*) (Axelrod 1956, 1973, 1985).

**Late Miocene (11 – 5 Ma)**

By the late Miocene, California oaks became restricted within the present boundaries of the state. Reliable fossil evidence for each species can be found within or near
some portion of the species present boundaries (table 2; figs. 1 and 2), indicating that the mild and humid climate of the Early Miocene had begun to give way to a more seasonal Mediterranean climate.

Table 2—Pleistocene (Pleist), Pliocene (Plio) and Late Miocene (L Mio) floras mentioned in the text with the best known age in millions of years. Chronology follows Woodburne and Swisher (1995), and Schorn (unpublished data)

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a Site# refers to site identification numbers in figures 1 and 2.
b Species are: Qa = Q. agrifolia, Qk = Q. kellogii, Qw = Q. wislizeni, Qc = Q. chrysolepis, Qe = Q. engelmannii, Ql = Q. lobata, Qd = Q. douglasii, Quercus agrifolia, Q. douglasii, and Q. engelmannii are not mapped.
c X = fossil present that conforms to the modern species.
d x = identification determined ambiguous by the author.
e Unpublished floras examined at the University of California Museum of Paleontology paleobotany collection.

The Remington flora (Condit 1944) and adjacent Burlington flora in the west central Sierra Nevada held five species of oak, including canyon live oak, black oak, interior live oak, valley oak and the first appearance of blue oak (Q. douglasoides – Q. douglasii) (table 1). Chaparral species from several genera were present, including manzanita (Arctostaphylos) and buckbrush (Ceanothus), providing the first evidence of a diverse oak woodland associated with chaparral shrubs. Summer rainfall types present included maple (Acer), buckeye (Aesculus), sweetgum (Liquidambar), laurel (Persea), and elm (Ulmus), indicating that although oaks and chaparral were present, the landscape was still not comparable to modern oak woodlands (Axelrod 1973).

The first fossils that have been attributed to coast live oak (Q. lakevillensis – Q. agrifolia) appeared about 5 to 6 Ma on the northwest slopes of the San Jacinto Mountains in southern California (Axelrod 1937, 1950a, 1950b). Coast live oak was only found at its southern limit, although this species is uncommon in the fossil record indicating that it was either rare, or difficult to differentiate.

**Pliocene (5 – 2 Ma)**

The major Pliocene sites are located within the modern distribution of the species today. The Central Valley was a large inland sea in the early Pliocene (Johnson and
others 1993) that would have modified temperature and precipitation patterns but prevented colonization of the Central Valley and created a barrier to dispersal. Mixed oak woodland appears to be well developed at the Sonoma and Napa localities (Axelrod 1944, 1950c) with blue oak associated with interior live oak, coast live oak, canyon live oak and valley oak. Most of the fossils suggest a modern forest typical of the Coast Range with redwood (*Sequoia*), Douglas fir (*Pseudotsuga*), alder (*Alnus*), tan oak (*Lithocarpus*), sycamore (*Platanus*) and shrubs such as mountain mahogany (*Cercocarpus*), buckbrush (*Ceanothus*) and manzanita (*Arctostaphylos*). Several fossils stand out as exotic, including elm (*Ulmus*) and laurel (*Persea*), suggesting persistence of a climate wetter than today.

**Pleistocene (2 Ma – 10,000 yr B.P.)**

Evidence for oak woodland abundance and distribution during the Pleistocene comes from pollen data. Oak pollen percentages are lowest during glacial maxima and stadials (cool periods) and highest during warm interglacials and interstadials (fig. 3).

![Figure 3—Pleistocene age pollen diagrams for sites in California recording oak. Filled circles represent packrat midden samples with oak pollen and open circles represent samples with no oak pollen. Time series are based on independent age models. Marine oxygen isotope stages (1-6) follow Bradley (1999). Gray bands identify cold periods (stadials and glacial maxima).](image)

Along the northern California coast, oak pollen is most abundant during the Holocene and the last interglacial (about 125 Ka – thousand years ago; Heusser and others 2000). During glacial maxima, oak pollen abundance is very low. Although
glacial cycles include a great deal of climate variability, the duration of cool/wetter phases is longer than warm/dry phases. Interglacials persist for 10,000 to 15,000 years while glacials last 90,000 to 100,000 years. Oak woodlands were regionally important during interglacials, but nearly disappear from the landscape for long periods of time during periods of glacial advance.

The Clear Lake (404 m elevation) record in the northern Coast Ranges supports this interpretation (Adam 1998). During colder conditions pines, sagebrush and juniper dominated the landscape. Shifts from oak dominance to oak absence were abrupt (Adam and West 1983) suggesting that when the climate became wet and cold, oak woodlands were quickly replaced by pine forest, but when climate became warm and dry, oaks rapidly reestablished. Similar evidence has been presented from the southern Coast Ranges (Heusser 1978, 1995; Poore and others 2000).

If oak woodlands were largely absent from their present range during glacial epochs, it is natural to ask where they were. The most likely answer is in isolated refugia such as rocky south facing slopes. There is no clear evidence of refugia, but wood rat middens *Neotoma* (packrat) in Kings Canyon in the Sierra Nevada foothills (920 to 1270 m elevation) had oak pollen during warmer interstadials which was then absent during the coldest period of the glacial maximum (Cole 1983). After the glacial maximum, oaks recolonized the area, suggesting migration from a source area not too far away. The pattern of nearly continuous expanses of oak woodlands in the Coast Ranges and around the Central Valley is a recent phenomenon. During ice ages low elevation California would have been characterized by coniferous forest. The characteristic Mediterranean climate of California with its oak covered rolling hills has only existed for brief periods during interglacial cycles like the one we enjoy today.

**Holocene (10,000 years ago to historic)**

The earliest evidence of human occupation in California suggests an arrival date of ~11,500 years ago. (Aikens 1978), though direct Native Californian influence on oak woodlands is largely restricted to the last few thousand years. Studies from the modern day upper elevational limit of black oak in the Sierra Nevada provide a consistent story of vegetation change (Davis and Moratto 1988, Edlund 1996, Smith and Anderson 1992). The late Pleistocene was dominated by juniper and/or incense cedar, sagebrush and pine with very little oak, suggesting an open landscape with a cooler drier climate than today. Beginning about 10,000 years ago oak began to increase (fig. 4), reaching a maximum between 8,000 to 6,000 years ago, then slowly declining while pine and fir increased. Oaks remained a minor component in the montane forests of the Sierra Nevada until the late Holocene when evidence suggests that burning by native Californians once again favored an increase in oak woodlands at the expense of conifers (Anderson and Carpenter 1991).
Coastal sites show a steady increase in importance of oak following the end of the ice age, reaching maximum levels about 8,000 – 7,000 years ago, remaining high throughout the Holocene (Byrne and others 1991). While low elevation oak woodlands (blue oak, valley oak, coast live oak and interior live oak) became well established in the mid-Holocene, higher elevation oak populations (black oak and canyon live oak) became a minor component of the lower montane forests (fig. 5).
The Influence of native Californians on oak woodlands

Although new studies are being made to quantify the role of Native Americans on forest structure, at this time their influence on oak woodlands must largely be inferred from observations made at the time of initial contact, oral histories of elders, and landscape changes that have been documented since the demise of the native populations. California Indians set fires for the purpose of clearing ground to gather acorns, promoting secondary growth used for basketry materials, clearing brush for hunting, and facilitating collection of seeds (Anderson 2005, Blackburn and Anderson 1993). Acorns are the most abundant plant food found in archaeological sites throughout central California (Anderson 2005), confirming that oaks have been important to California Indians for a long time. Fires, set by California Indians, are believed to have been the major factor in determining the type of vegetation found by Europeans when they arrived in California (Stewart 2002).

Pollen studies of Woski Pond in Yosemite National Park provide some of the clearest physical evidence that anthropogenic influences were important in maintaining oak woodlands in the Sierra Nevada (Anderson and Carpenter 1991). This record shows an increase in oaks and decrease in pine beginning about 650
years ago coinciding with a shift from the Tamarak complex to the Mariposa complex, characterized by a larger population and greater reliance on acorns. Forest clearance through burning would have favored expansion of oaks and improved conditions for gathering acorns. Open oak woodlands increased during a cool wet climate period (referred to as the Little Ice Age) when pines and firs would have typically been favored. Oak woodlands predominated in Yosemite Valley as a result of Indian-set fires rather than climate change (Reynolds 1959).

In the absence of periodic burning, ponderosa pine (*Pinus ponderosa*) is successional to black oak, and within the lower montane forest, the typical forest structure today is one of young, tall ponderosa pine and white fir (*Abies concolor*) overtopping old black oak. Young black oaks are uncommon. Large complexes of bedrock mortars at 2100 m elevation (Bennyoff 1956) near the upper treeline of black oak today suggest the montane forest included many more oaks in the past.

Frequent burning by California Indians to manipulate the landscape was not confined to the Sierra Nevada, but has been documented throughout the state (Anderson 2005). At least 35 tribes in California used fire to increase the yield of desired seeds, drive game, and stimulate growth of specific plants (Reynolds 1959). More studies are needed to determine the extent to which Native American use of fire may have expanded oak woodlands in the recent past.

### The Impact of European settlement on oak woodlands

Franciscan missionaries constructed a chain of 21 missions and nine settlements in Alta California between 1769 and 1821 A.D. (Gerhard 1982). The distribution of Franciscan missions between 1769 and 1821 A.D followed the distribution of coast live oak, termed *encina* (*Q. agrifolia*) and valley oak (*Q. lobata*) termed *robles* (Rossi 1980). Although the Spanish introduced many herbaceous weedy species that completely transformed the understory layer in oak woodlands, there is no clear evidence that the mission period, or the subsequent period of Mexican control, had any significant impact on the distribution or abundance of California oak woodlands (Mensing 1998). The Spanish introduced laws to prevent setting fires (Timbrook and others 1982), which may have benefitted oak recruitment and survival in coastal environments where frequent fires set by California Indians would have regularly killed seedlings.

Following the Gold Rush in 1849, impacts on oak woodlands intensified. First, along all major river corridors in the Central Valley where valley oaks dominated riparian woodlands, oaks were nearly completely removed for use as fuel and clearing for agricultural land. Second, oak woodlands were extensively cleared for agriculture and range improvement in rich agricultural lands of the Coast Ranges, southern California, the Sacramento and San Joaquin Valleys. Third, in wildland settings, forests and woodlands increased in density with improved fire suppression efforts. In some communities, oaks increased with the absence of fires, whereas in others oaks have been out competed by conifers. Finally, urbanization has expanded into oak woodlands fragmenting wildland habitat. Changes in land use practices have led to poor oak regeneration in many but not all woodlands, but the factors that result in low regeneration rates are not fully understood.

Despite challenges with recruitment, clearing, and changes in fire, oak woodlands remain the iconic California landscape. The long-term history of oak woodlands in California illustrates that they have persisted through millions of years of climate change and thousands of years of human impacts.
Acknowledgments
Howard Schorn played a critical role in providing me with an up to date chronology of the fossil flora data and helping guide me through the fossil material. Pollen data were obtained from the North American Pollen database. I appreciate the guidance early in my career on oak research provided by Roger Byrne, Joe McBride, Jamie Bartolome, Frank Davis and Tom Scott. The California Geographical Society graciously provided permission to reprint the figures and tables previously published in a longer version of this paper as a two-part article in the California Geographer (Mensing 2005 and 2006).

References


Abstract
The development of goals and policies for Californian oak woodlands is reviewed; then some important considerations for future policy development are highlighted. California and Spain share long and illuminating histories of human interaction with oak woodlands. The Integrated Hardwood Range Management Program, initiated about 1985, was a focal point for Californian research and policy, but also created connections among researchers, advisors, conservation organizations, and agencies. As the program’s funding ran out, those constituencies continued to strengthen relationships through grassroots organizations like the California Rangeland Conservation Coalition. We highlight four aspects of conservation policy and management for oak woodlands that are important as we move forward. These include thinking about the impact of policies and management initiatives at multiple spatial and temporal scales, avoiding policy conflicts and acknowledging tradeoffs, having awareness that most ecosystem services are really social-ecological services, and managing for multiple functions and processes instead of drifting back into single purpose management thereby reducing production of other important services.

Key words: conservation, dehesa, hardwoods, landscape, range

Cross oceanic connections and Mediterranean woodlands
Human interactions with oaks in Mediterranean California and Spain have a long history. Oaks dominate Mediterranean-type landscapes in the northern temperate world (Campos and others 2013). In California, oaks expand their ranges during interglacials, as they have over the past 10,000 years. During the glacial periods that comprised up to 90 percent of the Pleistocene period, oaks were confined to small refugia. People showed up in coastal California 14,000 years ago and by 6,000 years ago there is ample evidence that they were actively utilizing and engineering oak woodlands. Evidence supporting similar human influence on the Spanish oak woodlands also dates back about 7,000 years. Cave art shows that humans interacted with a diverse megafauna in Europe that included large deer, wild sheep, mammoths, cave bears, and lions. A similar diverse megafauna persisted in California up until a few thousand years post-Ice Age and well after human contact. In both instances people used acorns as their most important energy source but used animals to balance this diet with protein. An argument can be made that acorns were the most important source of human energy until the rise and spread of small grain agriculture. Even after cropping was common in Europe, acorns were eaten as a famine food well into the twentieth century. Although the evidence of human activity in California comes much later than in Spain, by 5,000 years ago they were managing and utilizing oak

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1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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European contact dramatically changed California but also forged closer links to Spanish woodlands, which by about 1200 had evolved a system of oak woodland grazing and cultivation called dehesa that produced multiple products and relied on plentiful available labor. Spanish colonial systems of land allocation, and rangeland grazing traditions, were brought to California’s oak woodlands in the 18th century (Alagona and others 2013). This caused displacement of native people and introduction of now ubiquitous species of plants and animals, including the grasses and forbs that today characterize the oak woodland understory. Some of the oaks in today’s woodland are older than European settlement. An important difference between Spain and California is that the Californian oak woodland is relatively stable without intensive human intervention, while the dehesa quickly turns into thick scrub without cultivation.

Gold discovery in 1848 and the accompanying California population growth and inland expansion increased pressure on oak landscapes. The more fertile valley oak dominated sites were mostly cleared for cultivation, moving the center of oak distribution into the foothills. Demand for meat led to near extinction of the Tule elk. Conflicts with livestock and resultant predator control led to extinction of the wolf in California and the grizzly. Initial efforts to increase crop agriculture and livestock production led to policies and practices that built on Spanish traditions, including both deliberate burning and prohibitions against burning. The legacy of Native American fire use, coupled with the introduction of livestock and plants, makes it possible to argue that the late 19th century was the period when Californian and Spanish oak woodlands looked most alike: scattered oaks and grass. However, the Spanish achieved a grassy dehesa understory through intensive management of brush with cultivation, in order to produce grains, cork, charcoal, cheese, and meats in a relatively small space for local markets and family consumption. California’s woodlands were managed by the Spanish primarily for an export market of dried meats, tallow, and hides, requiring little management aside from branding animals to keep track of ownership and capturing them for skinning and rendering at the appropriate times.

The Spanish and later Mexican colonization process, which first allocated land for missions and the military, then to individuals on a merit basis in large ranchos, had historically supported extensive livestock grazing as the major use (de Dios Vargas and others 2013). As crop agriculture spread after statehood in 1850, most valley oak woodlands and many upland types were cleared, for more intensive grazing and for crops. The ranchos and mission lands (already almost completely secularized during the Mexican period) were mostly broken up and transferred to new owners, while other lands were allocated to United States citizens for farming and reclamation projects. Non-arable forests and deserts remained in federal hands, leading to the approximate 50-50 split in today’s land ownership for Alta California. Oak woodlands are now primarily (90 percent) privately owned.

Oak woodlands did not initially attract the scientific attention of the higher elevation national forests, because most range research in the first half of the 20th century was conducted by the U.S. Department of Agriculture, Forest Service (USDA FS) in order to better manage public, rather than private, land. However, by the 1930s the University of California (UC) and the USDA FS had established collaborative range research enterprises in Lassen and in Madera Counties. The San Joaquin Experimental Range near Fresno became a center for research on foothill range. Later, UC established the Hopland and Sierra Foothill field stations. All three of these facilities included significant oak woodlands; testing grazing practices, and
range improvements including oak canopy management primarily through tree clearing. At this time it was assumed that as the oak woodlands were primarily owned privately for livestock production, so research and extension should focus on increasing the profitability of grazing practices with little attention to other values, including those of the landowner. This situation changed in California by the 1980s.

The integrated hardwood range management program
In 1985, primarily due to concerns about the impacts of wood harvest as biofuel on deer habitat and resulting pressure for state regulations, the UC proposed a cooperative program of research and education with the Departments of Forestry and Fish and Game focused on oak woodlands (Passof and Bartolome 1985). The primary threats facing hardwood rangelands were viewed as unregulated firedwood harvesting in northern California, poor natural regeneration of blue and valley oaks, and the conversion of woodlands to housing and other uses. The Integrated Hardwood Range Management Program (IHRMP) funded basic and applied research, initiating work on ranch economics, woodland regeneration/restoration, and wildlife habitat-relationships. Five Cooperative Extension Specialist positions were hired and strategically placed throughout the state.

Over its more than 20 year history, the IHRMP addressed many basic and applied problems, initially focused on issues of best management practices for the classic multiple use quadrad of forage, firewood, wildlife habitat, and water. It also made an investment in learning about landowner goals and values for their oak woodland—at the time a major step for professions like range management, incubated by public agencies for public lands. This effort translated into research and outreach targeting landowners needs and concerns. The pay off was in documented changes in the acceptance and application of conservation-based practices by oak woodland landowners on ranches. By the end of the IHRMP, emphasis had shifted to broader issues of land use policy and planning and ways to work more closely with local governments and quasi-governmental conservation groups. Much of the effort turned to understanding and promoting sustainability and non-market values including ecosystem services.

The IHRMP had a strong international effect, exemplified by a long-term collaboration and exchange agreement between UC and Spanish academics working on oak woodlands, which culminated in a recent book comparing conservation and management of California oak woodlands and Spanish dehesa (Campos and others 2013).

Quantitative comparisons of Californian (oak woodlands) and Spanish (dehesa) landscapes show that important differences underlie the superficial similarities. Although both the dehesa and oak woodland occur on acidic soils, the dominant landform is a very old and relatively level peneplain in Spain in contrast to the Californian oak woodland’s foothill landforms. The need for intensive management to maintain the dehesa, the wide adoption of diverse economic land uses including hunting, and the prevalence of absentee ownership distinguish Spain from California and strongly affect policy.

The IHRMP’s 2006 Strategic Plan (IHRMP 2006) reflected a strong shift in program emphasis, listing three broadly defined goals and supporting activities.

Goal I. Ecosystem goal: Promote healthy and sustainable woodland ecosystems.
- Develop and evaluate recommendations for sustainable management.
- Develop monitoring protocols.
- Conduct woodland ecology research.
- Monitor the status of oak woodlands.

Goal II. Policy goal: Provide leadership and promote policies to foster oak woodland conservation.
- Develop planning information.
- Promote collaboration with new clientele.
- Balance conflicting demands.

Goal III. Economic goal: Maintain hardwood rangelands as working landscapes with sustainable economies.
- Demonstrate benefits of working landscapes.
- Develop estate-planning alternatives.
- Develop diversification strategies.
- Change the acreage of functional hardwood rangelands
- Change public attitudes
- Promote oak positive management practices among woodland owners and managers.
- Evaluate the use of IHRMP educational materials.

The “integration” component of the IHRMP (It was comprised of the State Department of Forestry and Fire Protection, the Department of Fish and Game, and the UC Division of Agriculture and Natural Resources) was affected by state budget constraints almost at the inception of the program that reduced the scope of non-UC funded research, although demonstrated accomplishments in oak conservation were still considerable (Standiford and Bartolome 1997). The program benefitted enormously from international collaboration, especially in the developments related to economics (Goal III above). The last official IHRMP components were folded into other state programs in 2009, with the UC specialists and affiliated advisors continuing work on hardwood rangelands, but now more loosely affiliated primarily as members of the UC Oak Woodland Conservation Workgroup. Some of the goals in the 2006 IHRMP Strategic Plan have been addressed but the approach still needs updating.

Coalitions and collaboration
From the start, IHRMP research found that oak woodland landowners tend to have strong stewardship values, and a desire to promote wildlife habitat and natural beauty, as part of making a living off of the land. Today, oak woodland managers and owners remain a fascinating topic of study, but now they have broken the shackles of objectification as research subjects, and have taken a leadership role in promoting conservation of oak woodlands and rangelands on what we now call “working landscapes.” Through grassroots organizations like the California Rangeland Conservation Coalition (CRCC), the California Central Coast Rangeland Coalition, and the California Rangeland Trust they speak for themselves, and are building upon landowner values of land stewardship to conserve lands and the spectrum of values of “working landscapes.” As non-profit land trusts like the Nature Conservancy have come to understand the value of the landowner stewardship, conservation initiatives that draw on that ethic, like conservation easements, have become more prominent. These groups have a strong interest in research, and Cooperative Extension, with a long history of working with private landowners, is a valued participant and at times a facilitator of these kinds of collaborative research and conservation efforts. Policies
that promote landowner stewardship and management for market and non-market products, such as EQIP are a very important economic benefit and have made the Natural Resources Conservation Service (NRCS) an increasingly important player in oak management and policy. Tax incentives like the Williamson Act, which reduces the tax rate on agricultural land, are sought. Interestingly, the Nature Conservancy is active in Spain as well, and among landowners, there is today an interest in learning about some of the value-added products from the dehesa and their transferability. The famous acorn-fed ham of Spain is one such product that a few California landowners are exploring.

Four directions
Next we call attention to four important considerations for future policy development. No doubt there are others.

Multi-scalar, cross boundary conservation for working landscapes
As we have shown, there has been a continued diversification of tools and actors involved in oak woodland conservation, and increased reliance on the landowner. For this approach to work, conservation policies must consider the connections between pastures, landowners, and landscapes (fig. 1). Landowner stewardship goals are vital to management of rangelands at the ground level; ranch sustainability is critical to oak woodland conservation at the landscape level. It is important that policies at any scale contribute to strengthening positive connections among scales, rather than weakening any level in this nested hierarchy. For example, the Williamson Act promoted landscape level conservation, by helping to support ranch enterprises—and most oak woodlands belong to ranchers today. Policies like EQIP influence pasture level management, but also help strengthen the ranch enterprise. Funding provided by NRCS for conservation easements works at the landscape scale, and could be linked to programs at the pasture and ranch scale. While regulation is important and has a critical role protecting natural resources, draconian regulations that add costs, make landowners believe they are being treated unfairly, or take away from their ability to enjoy ranching, weaken ranch sustainability, and ultimately weaken both pasture and landscape level conservation. In 2001, a majority of ranchers surveyed in northern and central California reported that “Society’s hostility to ranching” was an important reason they might quit ranching altogether. Organizations like the CCRC, on the other hand, by promoting the value of ranching to California’s environmental health, reinforce the positive aspects of ranching for ranchers.
Figure 1—Conservation strategies must consider the interdependence and feedback among scales in the oak woodland, such as landscape, ranch, and pasture. Changes at any one level will affect the others.

The oak woodland landscape is a complex of interdependent private and public lands. Ranch lands may buffer public lands, ranch cattle may reduce fire hazard and increase biodiversity, meat produced on nearby rangelands may find a market of nearby urban dwellers looking for local products. In some areas, public lands may provide the grazing lands that ranches need to survive. How do we best maintain the mosaic of private and public, urban and rural lands that will support communities and woodlands? Individual oaks are valuable, but do not offer the rich ecosystem services of a woodland. The current emphasis by the NRCS on Ecological Site Descriptions, predictive State-and-Transition models and associated recommended management practices has much potential for assisting oak woodland management decisions at the scale of a ranch enterprise (Spiegal and others 2014).

The landscape of landowners is changing, as numerous studies have shown (Ferranto and others 2011, Huntsinger and others 2010). This is a function of changing demographics and is not new to either Spain or California. The dehesa is protected by stringent land use controls, but absentee ownership, scarcity of available labor, and an even lower ratio of cash income to land value put it at risk. In both places growing numbers of landowners own their lands primarily for amenities, including the enjoyment of recreational opportunities, living in the countryside, and even working with livestock. What does this mean for oak conservation policy? Research has shown that these landowners are not as active managers, in fact some have a hands off ethic, assuming the land will take care of itself. Others are very interested in wildlife habitat and reducing fire hazard, but they don’t have the tools or information they need to achieve those goals, especially in an oak positive manner. Future policy and research needs to consider the needs of these landowners, and to explore the possibility of boundary-crossing alliances for oak conservation. A recent study found that such landowners were most interested in collaborating with others.
on goals that were directly important to them, such as fire prevention (Ferranto and others 2013).

**Policy tradeoffs: The baby and the bathwater**

A recent USDA series of townhall meetings with agriculturalists around the state found that conflicting policies and management initiatives are a serious problem for rural landowners. For example, in the case of the endangered California tiger salamander (CTS, *Ambystoma californiense*), half of the habitat in the San Francisco Bay Area is now in stockponds created and managed by livestock producers. Fencing the ponds to keep out livestock was once commonly recommended and even required by agencies, reducing the usefulness of the ponds and resulting in costs for fencing and trough installation. Research has shown that salamanders are more common in grazed stockponds because of the effects on the surrounding vegetation (DiDonato 2007). In another example, the rare California black rail (*Laterallus jamaicensis coturniculus*) is often found in small wetlands created by irrigation system leaks in the foothill oak woodlands of Yuba and Nevada counties. Efforts at water conservation, while a needed and important goal, could incidentally result in the loss of significant habitat.

With the federal listing of the California tiger salamander as endangered, the Endangered Species Act (ESA) could have been a burden to the ranching enterprises that maintain open grasslands and stockponds, but this was prevented by Section 4(d), which allows special rules that ease take prohibitions for certain activities. Because of an exemption for normal ranching activities, salamanders can continue to benefit from habitat created and maintained by ranchers. The ESA can offer pathways to additional funding through mitigation easements that can provide income to livestock producers, helping them to continue to manage their stockponds and maintain the ranches that support the whole relationship. This mutually beneficial relationship that is crucial to the persistence of the species (USDI-FWS 2004).

Habitat Conservation Plans required by the ESA work at the landscape scale to mitigate negative impacts to listed species. However, as per the lack of recognition of the “social-ecological” nature of some of this habitat, the needs of rangeland graziers in terms of connectivity and continuity of rangelands at the landscape scale are generally not considered, despite the positive role that grazing has been found have for numerous rare species. Failure to consider scale, goal, and policy conflicts can have negative outcomes; the flexibility to consider multiple goals and consider tradeoffs is needed.

**Oak woodlands are social ecological systems**

We have described the long-term impact of humans on oak woodlands, and how thousands of years of management have shaped these systems. Yet when we talk about ecosystem services, we tend to forget the human role in how they are and have been produced. In fact, most of what we call “ecosystem services” are social ecological system services” (Huntsinger and Oviedo 2013). Humans have engineered the landscape, and human activity can support desirable ecosystem services. For example, in addition to the cases of the rail and the salamander above, grazing has been shown to improve the ecosystem service of habitat provision for several rare species in vernal pools and grasslands (Marty 2005, Weiss 1999). We have tools for conserving things like land and particular oaks, but how do we conserve the ongoing
practices and activities that contribute to a sustained flow of ecosystem services?

In Spain and the rest of the European Union, direct payment for ecosystem services in the form of payments for particular agricultural practices are common but have not always been directed at needed sustainable and integrated management for dehesa systems. It has also been pointed out that unless such practices fit the landowner culture or become part of landowner culture, they are only ephemera supported by budget allocations (de Snoo and others 2013). Overall, the amount of available subsidies payment to dehesa owners for various practices, and cost-sharing for the Californian oak woodlands, are probably about the same and substantial for the average landowner. One of us asked an Italian cowherd why he said he was going to adopt rotational grazing, although one could see nothing that needed to change in his fantastic alpine rangelands. He said, “well I will get 10 euros a head for that”. Compare that to the wonderfully rich and diverse reasons a California rancher will give you for adopting a particular practice. It is vital that management policies build on, link to, and become part of the landowner value system, and that the reasons are incorporated into or draw on rancher knowledge.

**Back to the future**

Our woodlands are multifunctional. Over time, the community of those who care about, own, and manage the woodlands has become more and more aware of the multiple benefits these lands are capable of providing to each of us and to society. Wildlife habitat, food, watershed, beauty, all of these will be illustrated in our meeting today. Considerable progress has been made in helping agencies and the public understand the value of working oak woodlands, and even in reaching owners of smaller properties with information about how to manage for some of the things they care about. Unfortunately, at times, when an opportunity arises to manage for something as important as carbon sequestration, increased forage production, or native plant restoration, we may focus single-mindedly on that and fail to consider the impacts on other resources. In Spain, it was found that maximizing carbon sequestration in woodlands reduced biodiversity and water production. Fertilizing rangelands may increase invasive species, eventually negating any benefit. We need to understand the full impacts of our management decisions before we launch into them whole (Spanish) hog.

**Conclusions**

Can Californians learn anything about policy from Spain? We believe there is a lot to learn about incentives and marketing—there is a well developed labeling system in Spain that helps landowners capture the benefits of environmentally and culturally beneficial management. At the same time, we believe that the Californian education and outreach work is second to none, and might prove useful in Spain. But because of our different land use change systems—in Spain land fragmentation is highly restricted—we are alone in struggling with how to serve the needs of a growing exurban population with oak woodlands to steward. How can we best attract this group into the oak conservation tent?
References


Wildlife and Oaks
Coarse Woody Debris Metrics in a California Oak Woodland

William D. Tietje, Michael A. Hardy, and Christopher C. Yim

Abstract
Little information is available on the metrics of coarse woody debris (CWD) in California oak woodland, most notably at the scale of the stand and woodland type. In a remote part of the National Guard Post, Camp Roberts, that has not burned in over a half century, we tallied 314 pieces of CWD in a blue oak (Quercus douglasii)-coast live oak (Q. agrifolia) woodland with patches of tree-sized bigberry manzanita (Arctostaphylos glauca). Compared to its representation in the live tree community, blue oak trees produced only half of the pieces of CWD expected. In contrast, coast live oak trees produced somewhat more pieces than expected, and in sharp contrast, manzanita produced four times more than expected. Among the three species of CWD that we tallied, coast live oak was the most abundant and comprised nearly half (43 percent) of all logs on the study area. Blue oak and manzanita comprised 35 percent and 22 percent of logs, respectively. Although coast live oak logs were more abundant, the largest volume of CWD was blue oak, and the largest logs were blue oak. The largest log measured 0.9 m in diameter, 12.8 m in length, and 3.6 m$^3$ in volume. Relatively more blue oak logs were hollow than logs of live oak or manzanita, by two times and three times, respectively. Two-thirds of all CWD was found in more advanced stages of decay. This effect was most pronounced for coast live oak and least for manzanita. Information on CWD from remote and relatively unmanaged blue oak-coast live oak woodland that has not burned for >50 years will assist the management and maintenance of this important habitat element.

Keywords: California oak woodland, coarse woody debris, CWD, dead and down wood, downed wood, Quercus spp.

Introduction
Coarse woody debris (hereafter, CWD, log, or downed wood) is a key structural component that influences a variety of ecological processes in temperate hardwood and coniferous forests (Harmon and others 1986, McComb and Lindenmayer 1999). In California oak woodland, CWD provides habitat for invertebrates, plants, and fungi and is known to be an important habitat component for a diverse assemblage of vertebrate species (Block and Morrison 1990, Tietje and others 1997b). The California Wildlife Habitat Relationships System (CIWTG 2005) predicts that 56 amphibians, 9 reptiles, 116 birds, and 49 mammals (46 percent of terrestrial vertebrates) use CWD for nesting sites, protective cover, travel lanes, and latrine and viewing sites. Large logs that are hollow are especially valuable for wildlife.

Although studies have examined CWD in hardwood forests elsewhere in North America (for example, McCarthy and Bailey 1994, Muller and Liu 1991, Rubino and McCarthy 2003), baseline data on the abundance, distribution, and characteristics of CWD in California oak woodland are needed to inform management and conservation efforts.
CWD in California oak (*Quercus* spp.) woodlands are relatively scarce. In the one broad-scale study, Tietje and others (2002), using data collected by the U.S. Department of Agriculture, Forest Service (USDA FS) in 1994 on 495 forest inventory and analysis (FIA) plots located throughout California oak woodland (see Waddell 2002), reported that CWD from blue oak (*Quercus douglasii*) occurred over the largest area of California oak woodland. Coast live oak (*Q. agrifolia*), however, produced the largest per-hectare volume. Over half the CWD (67 percent) was relatively small (<31 cm large end diameter) and three quarters (74 percent) was moderately decayed, suggesting that even the current amounts of CWD are not being sustained. This study suggested that CWD was mostly lacking over as much as half of the California oak woodland. The authors concluded that more detailed information was needed on the metrics of CWD by California oak woodland type at the stand scale.

Here, we present baseline data on the amount, size, species composition and characteristics, and decay class of CWD, and the relationship of these metrics to standing live trees. Our study area was located in Central Coastal California in a relatively undisturbed oak woodland that has not burned in >50 years.

**Study area**

We conducted our study on Camp Roberts, a training facility of the California Army National Guard, located 18 km north of Paso Robles, California. This study is part of a long-term project conducted in California oak woodland (1993 to 2014) that examines the effects of experimental manipulations of habitat elements on the small terrestrial vertebrate community and longer-term environmental effects, including predicted climate change (see Hardy and others 2013, Lee and Tietje 2005, Tietje and others 1997a). We conducted the study reported here on 11 of our 22 1.1 ha study plots, each with a permanent 8 x 8 sampling grid with 15 m intersections (fig. 1).

![Figure 1—Camp Roberts study area, coastal-central California, showing the 11 1.1 ha study plots on which live trees and CWD was inventoried in 2007. An experimental burn was conducted in 1997 over 203 ha (stippled areas) that enclosed 11 additional 1.1 ha study plots (see Discussion).](image)

Our study area is characterized by cool, wet winters and warm, dry summers. Total annual precipitation, falling as rain mostly between November and March, averages approximately 38 cm (66 year range = 10.8 cm to 74.1 cm; Western
Regional Climate Center 2001). Topography varies from nearly flat to steep hills (>40°). This area is referred to as the ‘back country’. Use by military personnel is limited to occasional nighttime reconnaissance training. No military activity or management has altered the amount of CWD and, at the time of the study (2007), fire had not occurred in the ‘back country’ for 54 years (W. Tietje, personal communication).

The study area is covered by mixed blue oak-coast live oak woodlands (Camp Roberts EMAP 1989). Our 11 study plots are located in open to dense patches of woodland that represent a range of tree stand characteristics. The more dense woodland patches have a well-developed shrub layer composed primarily of toyon (Heteromeles arbutifolia), redberry (Rhamnus crocea), poison oak (Toxicodendron diversilobum), and bigberry manzanita (Arctostaphylos glauca). Manzanita often attains tree size on the study area (that is, >10 cm diameter at 1.37 m above ground; DBH) and >10 m in height). Common forbs include deerweed (Lotus scoparius), filaree (Erodium spp.), fiddleneck (Amsinckia spp.), and hummingbird sage (Salvia spathacea). The more open woodland patches are dominated by annual grasses, including wild oats (Avena spp.), bromes (Bromus spp.), and fescues (Festuca spp.).

**Materials and methods**

**CWD measurements**

Using a modification of the ‘numerous shorter transects on a grid system’ first tested by Howard and Ward (1972) and further described and applied by Waddell (2002), we measured CWD in January 2007 on each of our 11 study plots at alternate intersections of the 8 × 8 grid (32 points per plot). At each of the 32 sampling points, we recorded logs that were intersected by four 10 m transects (therefore, 1 280 m of transect per plot) laid out in the cardinal directions from the grid point. Recorded logs were at least 7.6 cm in diameter at the point of intersection and ≥1 m in length. We recorded the length of each piece from the 7.6 cm diameter point to the larger end or its junction with a larger piece of downed wood, and the diameter at the small and large ends. Any piece was counted twice that either intersected two lines or that was curved such that it intersected the same line twice. From these measurements, we calculated the number of pieces, percent cover, and the volume (m³) for each study plot (see Waddell 2002).

**Decay class and wildlife sign**

For each piece of CWD, we recorded whether it was hollow (in other words, cavity ≥1 m long and ≥¼ the length of the end diameter of the log; Waddell 2002) and we collapsed the five decay classes described by Waddell into the following four:

- **1 = Sound Throughout**: bark covering >50 percent, sound sapwood and heartwood; fine limbs present; big limbs not pull out.
- **2 = Mostly Sound**: bark covering <50 percent, sound sapwood, heartwood soft; most fine limbs gone; big limbs not pull out easily.
- **3 = Mostly Decay**: little or no bark; soft sapwood, heartwood mostly missing, big limbs lost or pull out easily; piece will support its weight.
- **4 = Soft Throughout**: integrity, sapwood very soft, heartwood missing; no big limbs; piece will not support its weight.
As measures of animal use of CWD, we recorded the following:

- Wildlife food (for example, acorns or berry seeds) or scat on the logs.
- Whether a big-eared woodrat (*Neotoma macrotis*; see Matocq 2002) house was incorporated into the CWD or the house was within the hollow of a log. Woodrat dwellings are conspicuous piles of sticks, twigs, leaves, and herbs collected by the woodrats from the surrounding area.

**Live tree sampling**

To describe select features of stand structure, we sampled live trees on our 11 study plots using the point-center-quarter method (PCQ Method; Cottam and Curtis 1956) in June and July 2007. We randomly selected two non-adjacent intersections on alternate grid lines on each of the 11, 8 x 8 study plots (n = eight sampling points per study plot). Within a 10 m radius about each intersection, we measured the distance to the nearest live tree ≥10 cm DBH and ≥1.5 m tall in each of the four quadrants (NE, SE, SW, NW), and recorded DBH and species. To account for quarters in which we did not detect a live tree (136 of 704 quarters were treeless; 19 percent of total), we used the correction described by Warde and Petranka (1981). We standardized each measure as the number of live trees per hectare.

**Statistical analyses**

We wanted to explore two questions. First, what is the relationship between live tree attributes and several attributes of CWD on our study area at Camp Roberts? Second, how do CWD metrics differ among the species of CWD? For the first question, we ran an ANOVA to compare the DBH of the live trees to the large-end diameter of the downed wood. To determine differences between species of downed wood, we ran several tests. Using a likelihood ratio test, we compared the proportion of logs to live trees for the three species of CWD (blue oak, coast live oak, and bigberry manzanita). We also compared decay classifications among CWD species using likelihood ratio tests. We compared size (length, large-end diameter, and volume) of CWD by species using one-way ANOVAs. When ANOVA results were significant (p ≤0.05), we used Tukey multiple comparison HSD tests to identify important interspecific differences and report the *p* value we computed for each comparison (Wright 1992). We performed tests at α = 0.05 using R version 2.12.1 (The R Foundation for Statistical Computing 2010) and SAS JMP, Version 11 (JMP® Pro 11, SAS Institute Inc., Cary, NC).

**Results**

**CWD metrics**

We tallied a total of 314 logs comprised of three species (coast live oak, blue oak, and bigberry manzanita). Coast live oak logs comprised 43 percent (134/314) of all logs tallied. Blue oak and manzanita comprised 35 percent (109/314) and 22 percent (71/314) of logs, respectively. Due to small sample size (n = 11), we did not conduct statistical analyses on our calculations of the mean density or the mean volume of CWD. Combined log density on the 11 study plots ranged from 58.24 to 325.96 logs per ha and combined log volume across the plots ranged from 2.82 to 21.02 m³ per
ha. By species (data from the 11 study plots combined; table 1), coast live oak logs were the most common (71.73 logs per ha), but blue oak logs comprised the most volume (3.77 m³ per ha). Although the density of manzanita CWD pieces was higher than blue oak, the volume of manzanita (1.66 m³ per ha) on our study area was less than half that of either blue oak (3.77 m³/ha) or coast live oak (3.59 m³ per ha). With the three species of logs combined, mean log density was 155.16 logs per ha and mean volume of logs was 8.24 m³ per ha (n = 11; table 1).

Table 1—Mean and standard deviation (sd) of the density (logs per ha) and volume (m³ per ha) of coarse woody debris (CWD) by species and overall on eleven 1.1 ha study plots (n) in blue oak-coast live oak woodland with patches of tree-sized manzanita at Camp Roberts, California, 2007

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>mean (logs per ha)</th>
<th>sd</th>
<th>mean (m³ per ha)</th>
<th>sd</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coast live oak (Quercus agrifolia)</td>
<td>11</td>
<td>71.73</td>
<td>47.18</td>
<td>3.59</td>
<td>2.96</td>
</tr>
<tr>
<td>Blue oak (Quercus douglasii)</td>
<td>11</td>
<td>46.42</td>
<td>21.13</td>
<td>3.77</td>
<td>3.39</td>
</tr>
<tr>
<td>Manzanita (Arctostaphylos glauca)</td>
<td>11</td>
<td>59.85</td>
<td>49.17</td>
<td>1.66</td>
<td>1.79</td>
</tr>
<tr>
<td>Overall (species combined)</td>
<td>11</td>
<td>155.16</td>
<td>75.18</td>
<td>8.24</td>
<td>5.36</td>
</tr>
</tbody>
</table>

We found numerous significant differences among CWD species in the characteristics of the individual logs that we inventoried (n = 314; table 2). First, large-end diameter varied by species (F = 7.773, p < 0.001). Blue oak logs were significantly larger in diameter (21.85 cm) than both manzanita (15.65 cm, p < 0.001) and coast live oak (18.53 cm, p = 0.038). The two latter species were similar in diameter (p = 0.151). Log length also varied appreciably among species (F = 15.01, p < 0.001). Blue oak logs were significantly longer (3.80 m) than coast live oak (3.12 m, p = 0.018) and manzanita logs (2.19 m, p < 0.001). Coast live oak logs were significantly longer than manzanita logs (p = 0.003). Finally, the mean volume of individual logs differed among species (F = 7.012, p = 0.001), with blue oak logs being larger (0.18 m³) than coast live oak (0.09 m³, p = 0.028) and manzanita logs (0.04 m³, p = 0.001). Coast live oak and manzanita logs were similar in volume (p = 0.305). With species combined, logs on our study area averaged 19.03 cm in diameter at the large end, 3.15 m in length, and 0.11 m³ in volume (table 2).

Table 2—Mean and standard deviation (sd) of the large end diameter (cm), length (m), and volume (m³) of 314 pieces (logs) of coarse woody debris (CWD), by species and overall, inventoried on eleven 1.1-ha study plots in blue oak-coast live oak woodland with patches of tree-sized manzanita at Camp Roberts, California, 2007

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>mean (diameter)</th>
<th>sd</th>
<th>mean (length)</th>
<th>sd</th>
<th>mean (volume)</th>
<th>sd</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coast live oak (Quercus agrifolia)</td>
<td>134</td>
<td>18.53</td>
<td>8.75</td>
<td>3.12</td>
<td>1.93</td>
<td>0.09</td>
<td>0.17</td>
</tr>
<tr>
<td>Blue oak (Quercus douglasii)</td>
<td>109</td>
<td>21.85</td>
<td>13.65</td>
<td>3.80</td>
<td>2.32</td>
<td>0.18</td>
<td>0.40</td>
</tr>
<tr>
<td>Manzanita (Arctostaphylos glauca)</td>
<td>71</td>
<td>15.65</td>
<td>7.56</td>
<td>2.19</td>
<td>1.06</td>
<td>0.04</td>
<td>0.04</td>
</tr>
<tr>
<td>Overall (species combined)</td>
<td>314</td>
<td>19.03</td>
<td>10.73</td>
<td>3.15</td>
<td>2.01</td>
<td>0.11</td>
<td>0.26</td>
</tr>
</tbody>
</table>
Approximately 27 percent (29/109) of blue oak logs, 15 percent (20/134) of coast live oak logs, and 10 percent (7/71) of manzanita logs were hollow. Relative to availability, hollow blue oak logs were more numerous than hollow logs of other species (Fisher’s exact test, $p = 0.009$). Two-thirds (67 percent) of all CWD was found in more advanced stages of decay. Decay classification differed among species (Chi-square = 16.88, $p = 0.0002$). In general, coast live oak was the most decayed and manzanita the least decayed of the three species (fig. 2).

![Decay class distribution histograms for blue oak, coast live oak, and manzanita.](image)

**Figure 2**—Decay class distribution histograms for blue oak, coast live oak, and manzanita tallied at Camp Roberts, California, 2007.

**Live tree and snag metrics vs. CWD metrics**

Live tree density on our 11 study plots ranged from 84.43 to 361.71 trees per ha (n = 11 plots, mean = 248.16, sd = 89.81) and mean tree DBH ranged from 18.33 – 28.26 cm (n = 11 plots), mean = 22.27, sd = 3.23). The ratio of the count of live trees to the number of CWD pieces was significantly different among species (Chi-square = 122.71, $p <0.001$; fig 3). Specifically, we found that the live tree to CWD ratio for blue oak was different than live tree to CWD ratios for both manzanita and coast live oak (Chi-square = 106.43, $p <0.001$; fig. 3). Blue oak produced only half (35 percent) of the pieces of CWD expected based on its representation in the live tree community (66 percent of live trees). In contrast, coast live oak produced 1.7 times more than expected (43 percent of the pieces) compared to its live tree representation (28 percent). In sharp contrast, manzanita produced nearly four times more CWD (23 percent of the pieces) than expected based on its presence in the live tree community (6 percent of trees). The volume of CWD produced by the three tree species followed this same pattern (fig. 3).
Wildlife use and woodrats

Approximately a third (32 percent) of the CWD logs showed signs of wildlife use, mostly remains of scat (28 percent) or food (5 percent, seed or nut fragments). Woodrat houses were associated with 15 percent of the CWD pieces. The piece provided a support for the house or in a few cases a house was entirely within the hollow of the piece. The remaining pieces of CWD (68 percent) had no visible signs of wildlife use. (The sum of the percentages is >100 percent due to multiple associations for some logs.)

Discussion

Our study results are likely representative of the maximum amount of coarse woody debris (CWD) that can occur in remote, mostly unmanaged, and therefore relatively natural blue-coast live oak woodland with abiotic and biotic factors, tree and stand characteristics, and land-use activities similar to those described here. Livestock grazing or land use that would alter the amount or distribution of CWD has not occurred since the California Army National Guard Post, Camp Roberts, was established in 1941, and the area has not burned for >50 years (see fig. 1). We therefore suspect that the CWD metrics we describe are somewhat higher than the unknown amounts of CWD that occurred historically when burning by Native Americans was a common management activity (Agee 1996, Anderson and Moratto 1996, Keeley 2002). How do the CWD metrics from blue oak-coast live oak woodland at Camp Roberts compare to inventories conducted in woodlands in San Luis Obispo and nearby counties, statewide, and elsewhere?

On a relatively xeric study area dominated by chaparral and blue oak woodland in south San Luis Obispo County and northern Santa Barbara County, Borchert and others (1993) reported a density of 15 logs per ha, far fewer than at Camp Roberts. In contrast, on relatively mesic study sites dominated by coast live oak and California
Bay (Umbellularia californica) with small amounts of tan oak (Lithocarpus densiflorus) and Pacific madrone (Arbutus menziesii) in coastal San Luis Obispo County west of Camp Roberts, the volume of CWD was 1.4 times more than at Camp Roberts (Tempel and others 2006). Identical sampling techniques were used on both study areas, thereby increasing the likelihood that the more CWD near the coast can be attributed to the environmental factors that produced a more diverse and dense tree community with total basal area over three times that at Camp Roberts.

Of eight species of oak (Quercus spp.) tallied in California by the USDA FS forest inventory and assessment (FIA) in 1994, the greatest volume of CWD was in coast live oak (11.49 m\(^3\) per ha), followed by canyon live oak (Quercus chrysolepis) (10.62 m\(^3\) per ha), Oregon white oak (Q. garryana) (7.98 m\(^3\) per ha), and blue oak (7.44 m\(^3\) per ha) (Tietje and others 2002). The statewide average volume of coast live oak was over three times the volume tallied at Camp Roberts (11.49 m\(^3\) per ha vs. 3.59 m\(^3\) per ha, respectively) and blue oak volume was twice the volume observed at Camp Roberts (7.44 m\(^3\) per ha vs. 3.77 m\(^3\) per ha, respectively). Coast live oak logs and blue oak logs were also somewhat larger on the FIA plots. Differences in CWD tallied in the California assessments can be attributed in part to the different sampling methodologies and different geographic scales, but the differences are probably due largely to natural variation among geographic locations and the management histories of the areas sampled.

Finally, the studies we reviewed from other areas of the United States (for example, McCarthy and Bailey 1994, Muller and Liu 1991, Rubino and McCarthy 2003) reported more CWD than we tallied at Camp Roberts. Coniferous forests generally have greater accumulations of CWD than temperate hardwood woodlands (see, for example, Gora and others 2014, Harmon and Hui 1991), oftentimes an order of magnitude greater (Harmon and others 1986), for several reasons. Compared to hardwood woodlands, there are relatively more snags in coniferous forests (Chave and others 2009) and conifer logs are generally larger and more decay resistant than oak logs. Also, coniferous forests most often occur in a climate less favorable to decay organisms than do most hardwood woodlands (Harmon and others 1986). Harmon and others (1986) provide further examples of CWD from temperate hardwood and coniferous forests in the United States and from other parts of the world (see especially table 1, pages 138 and 139).

In our study at Camp Roberts, the ratios of live trees to the amount of CWD contributed by the trees differed substantially among the three species we inventoried. The occurrence of blue oak logs was relatively low compared to its representation in the live tree community. Nonetheless, several factors underscore the importance of blue oak downed wood in woodland habitats. Blue oak is the most widely distributed oak (Quercus spp.) in California (Griffin and Critchfield 1972) and is a predominant contributor of CWD throughout California oak woodland (Tietje and others 2002). In our study, blue oak contributed the greatest overall volume of CWD. Individual blue oak logs had larger average diameter, length, and volume than coast live oak or manzanita logs, and a greater proportion of blue oak logs were hollow. Hollow logs provide key habitat structures that are used by many kinds of wildlife for denning and refuge, as evidenced in this study by woodrat utilization of hollow logs for their houses and for escape cover. Also, because of their generally larger size, and because they predominate in drier areas less favorable to decomposer fungi, blue oak logs decay more slowly and therefore last longer than coast live oak logs. Collectively, these factors demonstrate the importance of blue oak logs in the oak woodland community.
Coast live oak, which made up approximately a third of the live tree community, contributed relatively more CWD and, of the three species, the most logs to our inventory. CWD pieces were also more numerous within 6 m of the trunks of coast live oak trees than were logs under blue oak trees on 11 ranches surveyed in 1995 in four central coast counties (Tietje and others 1997a). Although coast live oak CWD was used more than other species by woodrats as support for their houses, this observed ‘preference’ may simply be an artifact of coast live oaks’ greater occurrence in preferred woodrat habitat, that is, in the more mesic areas of the woodlands with a well-developed shrub understory (see Lee and Tietje 2005). The more moist microclimate they prefer may have been the reason that coast live oak logs were in a more advanced state of decay than the other species of logs, but a complex interplay of factors, including the heavier bark that tends to slough sooner and the level of extractives in coast live oak (compared to blue oak or manzanita), may also have been involved (Harmon and others 1986). Highly decayed logs cannot support a cavity and therefore may be of less value for vertebrate wildlife. Fauteux and others (2013), however, reported that several species of boreal small mammals benefit from ‘late-decay CWD’ due to the protective cover and nesting sites it provides, and the food (mushrooms, insects) it oftentimes offers.

Manzanita, the third of the ‘tree’ species inventoried at Camp Roberts, comprised a small proportion of the live trees, but provided well over half as many pieces of CWD (71 pieces) as did both blue oak (109) and coast live oak (134). As indicated by its generally less advanced decay, manzanita persists on the ground longer than either coast live oak or blue oak. Although pieces accumulate and are available to wildlife for a long time, they are relatively small and rarely hollow, providing comparatively little value other than as latrine, travel, and lookout sites. Furthermore, manzanita is not usually a dominant species in oak woodland.

Most California oak woodland is privately owned and used primarily for livestock production (Tietje and Schmidt 1988). Active ranch management may remove CWD incidental to livestock management priorities. In California, prescribed fire is often the tool of choice for enhancing livestock forage production and limiting fuel (that is, downed wood) accumulation (California Department of Forestry and Fire Protection 1996, Griffin and Muick 1984). The experimental burn conducted on some of our study plots at Camp Roberts in 1997 removed 35 percent of the CWD (Vreeland and Tietje 2002). Our inventory of CWD in a blue oak-coast live oak woodland, largely unaltered by fire or land use for more than half a century, provides a measure with which to compare future research on the effects of land-use and fire on CWD in California oak woodland of the stand characteristics that we describe. As expressed by Harmon and others (1986; p. 275), “In some cases, human influences have been so pervasive that natural conditions are difficult to define”. CWD is an integral component of California oak woodland that is essential for the maintenance of the full complement of invertebrate and vertebrate wildlife. Information from this study can assist in the prudent management and retention of this important resource.

Acknowledgments

We thank National Guard Post Camp Roberts for permitting access to study sites and Camp Roberts Environmental Office and the Camp Roberts Fire Department personnel for their support of our research and for historical information they provided on prescribed and wild fires that have occurred over the Camp Roberts ‘back country’. We gratefully acknowledge R. Cooper and C. Tietje for their assistance with data collection in 2007. A.Y. Polyakov provided valuable comments and editorial suggestions on an earlier version of the manuscript.
Discussion with J. Shelly and materials he provided improved the manuscript. The University of California Cooperative Extension Office, San Luis Obispo County provided logistical support.

References


Foraging Behavior of European Starlings: Implications for Mitigating Their Impact on Native Species

Kathryn L. Purcell

Abstract
European starlings (*Sturnus vulgaris*) are a remarkably successful invasive species known to compete with native bird species for nest sites. The objective of this study was to understand why starlings avoid ungrazed pastures and provide recommendations to help mitigate the impacts of starlings on native bird species. I used aviary trials to examine the effects of grazing and mowing practices on starling foraging behavior. In experiment 1, I examined the effects of grass height and litter. Starlings preferred to forage in short grass without litter. In experiment 2, I modified the treatments to more closely simulate actual grazing and mowing practices. Results further confirmed avoidance of areas with tall grasses. Starlings entered all three of the mowed treatments more than the control treatment. No preference was found for the treatment representing long-term exclusion of grazing, therefore a single year of exclusion from grazing or mowing appears sufficient to deter foraging by starlings. Short grass and lack of litter likely facilitate increased mobility, increased ability to detect and capture prey, and increased visibility to see potential predators. Recommendations include leaving moderate or high levels of forage in areas where starlings prefer to forage, such as moist swales and level, open woodlands. Because distance to foraging sites has been found to be negatively correlated with nest density, competition with native species for nest cavities may be decreased by reducing the quality of foraging habitat. Rotational grazing that creates a mosaic of varying grass heights might offer opportunities for reducing starling densities. In exurban areas, avoidance of extensive mowed and watered lawns that attract starlings is recommended. Further research is needed to investigate thresholds of grass height at which starlings are discouraged from foraging. A species as numerous as the starling almost certainly has impacts beyond the guild of cavity-nesting birds. Interspecific relationships among ground-foraging insectivores should be investigated in areas where native bird species co-occur with starlings.

Key words: birds, European starlings, grazing, invasive species, mowing, wildlife

Introduction
Invasive species are one of the largest threats to native wildlife around the world. They have caused dramatic changes in ecological systems and have profoundly altered communities and ecosystems. Approximately 42 percent of threatened and endangered species are placed at an increased risk by non-native, invasive species (Pimentel and others 2005). In addition, economic losses associated with invasive species and their control total approximately $120 billion each year in the United States (Pimentel and others 2005). Solutions to the invasive species problem based on sound science are needed.

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The European starling (Sturnus vulgaris) is one of the world’s most numerous and successful birds. It is a species of temperate regions and has a wide breeding range extending from Western Europe to central Asia, and from Iceland to northern India (Feare 1984). In addition, starlings have been introduced and established populations in North America, South Africa, Australia, New Zealand, and several West Indies and Pacific islands (Feare 1984, Lever 2005). In North America, starlings have been remarkably successful. About 100 individuals were released in New York’s Central Park in 1890 by the American Acclimatization Society, whose chairman Eugene Schieffelin had determined that every bird species mentioned in Shakespeare’s work should be introduced to North America (Lever 2005). From there, starlings spread rapidly and their range now extends from the east to the west coasts and from the Arctic in Alaska to the tropics in Mexico. Starlings in North America now comprise about a third of the world’s total population of starlings and are among the most abundant species of birds in North America (Feare 1984). Starlings first appeared in California in 1942 (Jewett 1942) and are now likely the most abundant bird in the state (Small 1994).

Starlings are aggressive competitors and are known to usurp cavities of native cavity-nesting birds, whose nest sites are commonly assumed to be limiting (Short 1979, Troetschler 1976, Weitzel 1988). Cavity-nesting birds, and particularly secondary cavity nesters, comprise a high proportion of the bird species found in oak woodland bird communities (Purcell 2011, Verner and others 1997). Starlings use nest cavities similar in size and shape to those used by native species, raising concerns about nest site availability for these species (Purcell 2011) and behavioral experiments have confirmed that native bird species recognize the presence of starlings at their nest sites as a threat (Olsen and others 2008).

Starlings are often associated with livestock and are often found foraging in grazed pastures. Research has shown that starlings nesting in the foothill oak woodlands of the Sierra Nevada avoid ungrazed areas (Verner and others 1997). Starlings forage on the ground on soil arthropods found in moist soil. Tall grass in ungrazed areas presumably limits maneuverability and therefore foraging efficiency, but results also suggest that plant litter depth may also explain the avoidance of ungrazed areas (Purcell and others 2002). Mowed and watered lawns are also attractive foraging areas. Residents of foothill oak woodlands are encouraged to remove biomass around their homes to reduce fire risk, and often modify the landscape by planting lawns that require watering, providing ideal foraging habitat for starlings.

Starlings have the potential to affect the diversity and resilience of oak woodlands, yet we have a poor understanding of their habitat needs in this ecosystem. The aim of this study was to provide insights into how starlings have been able to successfully invade oak woodlands and to understand why starlings avoid ungrazed pastures, with the goal of providing recommendations for grazing management and mowing practices on rangelands that may help reduce the impacts of starlings on native bird species. In an effort to achieve these objectives, I used aviary trials to study the foraging behavior of starlings in relation to grass height and litter depth.

In the first set of experiments, I attempted to tease out whether grass height, litter, or both were important in foraging habitat selection. If poor mobility is the reason ungrazed pastures are avoided, this could be due to either tall grass or litter impeding movement. The second set of experiments was designed to more closely simulate actual grazing and mowing practices with the goal of providing recommendations for ranchers and rural homeowners interested in reducing starling nesting density on their land. In these experiments, treatments involved mowing plots and leaving or
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removing the clippings to simulate grazing and weedeating or mowing, and mowing and raking all dead biomass from plots to simulate multiple years of grazing.

**Study area**

This research was done at the San Joaquin Experimental Range (SJER) in Madera County, California in the foothills of the western Sierra Nevada. The SJER is 1875 ha in size and ranges in elevation from 215 to 520 m. Vegetation consists of a sparse woodland overstory of blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus sabiniana*). An understory of scattered shrubs includes wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucoderma*), Mariposa manzanita (*Arctostaphylos viscida mariposa*), holly-leaf redberry (*Rhamnus ilicifolia*), and coffeeberry (*R. tomentella cuspidata*). In some areas the overstory is primarily blue oak with an open understory. Soft chess (*Bromus hordeaceus*), ripgut brome (*Bromus diandrus*), Mediterranean barley (*Hordeum geniculatum*), wild oat (*Avena barbata*), annual blue grass (*Poa annua*), broadleaf filaree (*Erodium botrys*), popcorn flower, (*Plagiobothrys nothofulvus*), common fiddleneck (*Amsinckia menziesii intermedia*), and others dominate the annual grassland understory. The SJER has been moderately grazed by cattle since about 1900 except for a 29 ha Research Natural Area and a few smaller ungrazed pastures that have been ungrazed since 1935. The climate at SJER is characterized as Mediterranean with cool, wet winters and hot, dry summers. Most precipitation falls as rain.

Starlings were first recorded at SJER in the late 1960s and by 1970 SJER several nesting pairs occupied cavities around the buildings. They have been abundant breeders throughout SJER since around the mid-1980s (Purcell and others 2007). Abundance appears to have stabilized since 1995 (Purcell and others 2002).

**Methods**

Starlings were captured at nests (Stanback and Koenig 1994) or in drop-in traps using decoy birds as attractants (Zajanc and Cummings 1965). Birds were aged and sexed and each bird received an aluminum U.S. Geological Survey leg band and three colored plastic bands (two bands per leg), creating a unique color combination to allow identification of birds in the field to ensure they were tested only once. The research complied with all U.S. Department of Agriculture, Forest Service requirements for animal welfare. Housing for birds retained in captivity adhered to appropriate standards of care and provided for their safety, health, and well-being (Fair and others 2010). Birds were fed crushed dog food, poultry mash, or other high protein feed, along with meal worms and fruit, and provided water ad libitum. Birds were released following trials. Research was done under U.S. Fish and Wildlife Service banding permit 21859 and California Department of Fish and Wildlife Scientific Collecting Permit 5479.

In Experiment 1, done in 2006, three treatments and a control were tested: 1) mowed to simulate short grass, 2) raked to simulate tall grass without accumulated litter, 3) mowed and raked grass to simulate short grass without litter, and 4) a control treatment that was unmowed and unraked. Raking removed both the current year’s growth that was dead and unrooted (which would become residual dry matter) and previous or accumulated growth (litter). Fifteen trials were completed.

Experiment 2 was done in 2010 and 2011. The treatments tested were: 1) mowed, with clippings removed to simulate grazing or mowing with a grass catcher, 2)
mowed, with clippings left on the ground to simulate weedeating or mowing without a grass catcher, and 3) mowed and raked, with clippings removed to simulate consecutive years of grazing or mowing with a grass catcher, and 4) control. Eighteen trials were completed in 2010 and 20 in 2011, for a total of 38 trials.

Experiments were done in sites that had been ungrazed for several years to ensure the presence of accumulated plant litter. We used an open-bottom enclosure constructed of PVC painted green and chicken wire with a central perch, assembled by connecting the sides and top with zip ties. Side length of the enclosure was 1.87 m, area of each treatment within the enclosure was 0.88 m², and total volume was 6.77 m³. Ropes were placed on the ground to delineate the quadrants, treatments were randomly assigned to each quadrant, and the treatments were applied. We recorded average grass height in each quadrant and then placed the enclosure on the experimental plot.

Starlings were placed one at a time in the enclosure. A video camera (JVC digital camcorder) on a tripod was set up to achieve a downward view of the four treatment plots and on one side and slightly off center. We always selected a side opposite the control plot so the foraging bird would not be blocked from view by tall grass. After the bird was placed in the enclosure we left the area. We returned after 25 to 30 minutes and removed the bird from the enclosure. Up to three starlings were tested in a morning, all using the same experimental setup. All trials were done in May except for one trial in 2010 that was done in late April.

We recorded each bird’s foraging behavior by viewing the video tape. After allowing 5 minutes from the time researchers were out of the area to allow the bird time to acclimate to the enclosure and for the initiation of normal foraging behavior, we recorded two response variables during the following 20 minutes: the number of times a starling landed in or walked into a quadrant (number of entries), and the total number of seconds a starling spent in a quadrant (seconds).

**Statistical analysis**

For both experiments, differences in the number of seconds starlings spent in each treatment were tested using Proc Mixed (SAS Institute Inc. 2012), with individual included as a block (random effect) as each individual was subjected to each of the four treatments. The mean time (seconds) starlings spent in each quadrant was square-root transformed, which resulted in residuals being approximately normally distributed. Differences in the number of times a starling entered a treatment were tested using GLIMMIX (SAS Institute Inc. 2012), using a negative binomial distribution with a log link function. Individual was again included as a random effect. Tukey’s studentized range test was used to control for Type I experimentwise error rates, with an overall significance level of 0.05.

**Results**

Results from Experiment 1 showed that starlings preferred to forage in short grass without litter. The overall tests for total seconds spent in each treatment and the number of entries into each treatment were both significant ($P < 0.001$ for both) and the adjusted $P$ values for comparisons revealed that the rankings of the treatments for both variables were $\text{MR} > \text{M} > \text{R} = \text{C}$, where $\text{MR} =$ mowed and raked, $\text{M} =$ mowed, $\text{C} =$ control and $\text{R} =$ raked (figs. 1a and b). The mowed and raked treatment was preferred and both of the tall grass treatments were avoided.
Results from Experiment 2 further confirmed avoidance of areas with tall grasses. The overall tests for both time spent in treatments and the number of times starlings entered a treatment were again significant ($P = 0.03$ for square root of seconds and $P < 0.001$ for number of entries). Starlings spent more time in the mowed treatment with the clippings left on the ground compared to the control treatment (ML > C; adj. $P = 0.038$; fig. 2a). None of the other comparisons was significant. Starlings entered all three of the mowed treatments more than the control treatment (ML = MR = MRD > C; adj. $P$ values all $<0.004$. fig. 2b). The treatment simulating long-term exclusion of grazing (MRD) did not differ from the other mowed treatments.

The inability to distinguish among the treatments in Experiment 2 as finely as in Experiment 1 may have been due to the relative differences in grass heights among treatments. Average differences in grass heights between the mowed and unmowed treatments was 44.7 cm in Experiment 1 compared to only 36.0 cm in Experiment 2 (for Experiment 1, average grass height for mowed treatments was 8.8 cm and for control plot was 53.5 cm; for Experiment 2, average grass height for mowed

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Figure 1—Results of European starling foraging experiments done in May 2006 at the San Joaquin Experimental Range, CA. a) Mean time (square root seconds) that starlings spent in each treatment. b) Mean number of times a starling landed in or walked into a quadrant with each treatment type. Treatments were MR = mowed and raked, M = mowed only, R = raked only, C = control. Error bars represent one standard error.

Figure 2—Results of European starling foraging experiments done in 2010 and 2011 and the San Joaquin Experimental Range. a) Mean time (square root transformed) that starlings spent in each treatment. b) Mean number of times a starling landed in or walked into a quadrant with each treatment type. Treatments were ML = mowed with clippings left, MR = mowed with clippings removed, MRD = mowed with clippings removed, then raked, C = control. Error bars represent one standard error.
treatments was 12.4 cm and for unmowed plots was 48.4 cm). Starlings entered and spent more time in control plots in Experiment 2, perhaps as a result of the lesser relative differences between mowed and control treatments.

Discussion

Our study adds to a growing list of studies that have shown that pastures with shorter grass are preferred by starlings (Atkinson and others 2005, Buckingham and others 2006, Devereux and others 2004, Whitehead and others 1995, Whittingham and Devereux 2008, Williamson and Gray 1975). Interestingly, the majority of these studies were spurred by concerns over decreases in farmland birds, and specifically starlings, in northern and western Europe.

Prey abundance is not believed to be the factor driving foraging choices for short grass (Atkinson and others 2005, Devereux and others 2004) and tall grasses have been shown to have greater abundance and diversity of arthropods (Morris 2000). Habitat structure was clearly important, and clearly more important than botanical composition (Buckingham and others 2006). Several studies have suggested the functional explanation for this response is that tall grass impedes movement and that prey is easier to detect and capture in short grass. Starlings moved more rapidly and walked more steps in short grass (Brownsmith 1977, Devereux and others 2004), allowing them to search more efficiently. I found that both tall grass and litter were avoided, suggesting that litter may also impede movement.

Shorter grass may also provide lower perceived predation risk for foraging birds. Short grass likely provides increased visibility to detect potential predators approaching. Starlings feeding on invertebrates in tall grass were more vigilant, had reduced feeding rates, and were slower to respond to a model hawk compared to those feeding on short grass (Brownsmith 1977, Devereux and others 2004, Whittingham and Devereux 2008). Starling densities were also higher in fields with feeding areas further from hedges where predators may lurk (Whitehead and others 1995).

No studies have directly addressed questions related to biomass removal vs. grass clippings left on the ground. In experiment 1, starlings preferred the raked plots where the previous year’s biomass was removed. In experiment 2, although I found no significant differences between plots with clipped leavings and treatments other than controls, starlings clearly didn’t avoid these treatments (fig. 2) and they appeared to be attractive to starlings, perhaps offering interesting foraging opportunities that did not inhibit their mobility. Previous studies have shown that starlings prefer recently mown pastures (Devereux and others 2006, Whittingham and Devereux 2008), suggesting the effect of clippings left on the ground may be ephemeral.

I detected no effects of long-term grazing, as measured by starling response to the mowed and raked plots with clippings removed (fig. 2, MRD compared to MRD and MR). A single year without grazing is apparently sufficient to deter starlings from foraging. I know of no other studies that have directly addressed long-term grazing. Buckingham and others (2006) found that recent grazing was a strong predictor of field usage, but no studies to date have suggested that removing pastures from grazing for multiple years has any lasting effect on starling foraging behavior once they are returned to grazing.

Eradication of starlings is clearly not feasible, but with improved knowledge of starling habitat requirements, starling numbers may be reduced, minimizing their impacts on native bird species in California’s oak woodlands. The distribution of
foraging habitat relative to nest sites could be useful in limiting starling numbers and their impacts. Starling breeding density is limited by nest site availability where foraging habitat is readily available, maximizing nest-site competition with native cavity-nesting species. Bruun and Smith (2003) found that when high quality foraging habitat was limited, starlings flew longer distances to forage, thereby enlarging their home ranges and reducing density. When starling density is reduced, competition for nest sites will be relaxed.

Recommendations to reduce the impact of starlings on cavity-nesting birds for rangelands include leaving moderate or high levels of residual dry matter when possible, especially in the areas where starlings prefer to forage. Purcell and others (2002) found that starlings were found in level, open woodlands with fairly well-developed soils such as the moist swales also preferred by grazing livestock. Rotational grazing, where pastures with both short and tall grass occur simultaneously, may be a useful tool for reducing starling densities but this needs to be tested experimentally. Rotations that create a mosaic of different grass heights will require some starlings to fly longer distances to forage and result in lower starling density. The spatial scale of this heterogeneity requires consideration; patch sizes should probably be fairly extensive, as small-scale heterogeneity could benefit starlings by providing both beneficial conditions for starling foraging and reservoirs for their prey (Devereux and others 2004). Where starlings are present in suburban and exurban areas, avoiding extensive mown and watered lawns will help avoid attracting starlings. Urban environments likely serve as habitat reservoirs in the drier months when starlings leave the oak woodlands in search of moist soils for foraging, and there are important opportunities to reduce starling numbers there as well.

Further research is needed to investigate thresholds of grass height at which starlings are discouraged from foraging. We collected data on grass height and biomass for each of our experiments but results were confounded by application of the experimental treatments. Our goal was to test responses to treatments, not responses to specific grass heights. Grass heights tested have varied widely among studies, with ‘short’ grass treatments ranging from 3 to 9 cm and ‘long’ grass treatments from 6 to 19 cm. Future experiments should refine the specific grass heights at which starlings hesitate to forage in order to identify less attractive foraging habitat. Recommendations from such studies would be useful not only for livestock management, but understanding on how best to protect rural households from fire risk.

Differences between mowing and grazing treatments as they relate to foraging habitat for starlings and other ground-foraging birds also need a more thorough examination. Grazing differs from mowing in that livestock are selective in the species and locations they graze, and grazing occurs over a longer time period. Cattle also compact the soil, and dung has its own rich invertebrate fauna, which starlings are known to exploit (Morris 2000). While starlings are known to associate with livestock, the relationships are not clearly understood.

From the first sightings of starlings in California in 1942 to becoming one of the most abundant, if not the most abundant, bird species in California (Small 1994), concerns have been raised about competition with native species for nesting cavities. However a species so numerous has almost certainly also affected other ground-foraging species, particularly those that feed on soil arthropods. Western meadowlarks (Sturnella neglecta) have decreased over the last 27 years at SJER (Purcell and Mori, n.d.) and Breeding Bird Survey (BBS) data show declines in both California and the Western BBS region (Sauer and others 2014). Causes for declines are unknown. Meadowlarks feed on the ground in open areas and eat soil
invertebrates (Davis and Lanyon 2008) and overlap with starlings in feeding habits. As a group, grassland bird species show consistent declines across North America (Brennan and Kuvlesky 2005, Knopf 1994, Vickery and Herkert 2001). Inter-specific relationships among the guild of ground-foraging insectivores should be investigated in areas where native species co-occur with starlings.

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Literature Cited


Role of Oaks in Fisher Habitat Quality in the Sierra Nevada Mountains at Multiple Spatial Scales

Craig M. Thompson, Kathryn Purcell, Rebecca Green, and Richard Sweitzer

Abstract
Fishers (Pekania pennanti) occur in ponderosa pine, mixed conifer, and mixed hardwood conifer habitats in the southern Sierra Nevada at elevations from approximately 1400 to 2300 m. They are a candidate species for listing under both the Federal and California Endangered Species Acts. Since 2007, the U.S. Department of Agriculture, Forest Service (USDA FS) Pacific Southwest Research Station has been investigating fisher habitat selection in the mixed hardwood conifer landscape of the Sierra National Forest. California black oaks (Quercus kelloggii) occur in the forest types fishers occupy and are important habitat elements at multiple spatial scales. In the Kings River Fisher Project study area, black oaks were the most common species used for denning and the second most common species used for resting (52 percent and 24 percent respectively). At larger spatial scales, occupancy models indicate that hardwoods, in association with structural characteristics, such as stem diameter diversity and the presence of large snags, are important components of fisher habitat. Although little is known of fisher foraging habitat, black oaks are also associated with many important prey species of fishers. Shade-intolerant California black oaks are less abundant than they were historically; the creation of small openings to promote recruitment of young trees would therefore aid in the long-term maintenance of Sierra Nevada fisher habitat.

Key words: cavity, California black oak, fisher, habitat use, Pekania pennanti

Introduction

Oaks are known to be a vital resource for numerous wildlife species throughout the United States. In 1940, W.R. Van Dersal wrote “few treatises on birds or mammals fail to mention acorns as the food of some animal or another, if any foods at all are listed. The records are widely scattered, but in accumulating data with respect to the utilization of woody plants by wildlife for another purpose (Van Dersal 1938b), those for oaks were found to surpass the records for most other genera of woody plants” (Van Dersal 1940). The author went on to list 186 different species known to use either acorns or oak leaves as a primary food source. Oaks provide other resources as well, readily forming cavities that are used as den or nest sites for numerous bird and mammal species (McDonald 1990).

The importance of oaks to ecological systems includes indirect effects as well. Ostfeld and others (1996) presented a conceptual model outlining the direct and indirect relationships between oak trees, birds and herbivorous mammals, carnivores, raptors, insects, and humans. They highlighted the positive relationships between mast production, small mammal densities, and predators. Changes in forest composition nationwide, particularly the loss of oaks due to altered disturbance

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regimes, has been identified as potential trophic cascade resulting in the loss of native biodiversity (Gillen and Hellgren 2013).

Fishers (*Pekani pennanti*) are a species of conservation concern in the western United States, currently proposed for listing under the Endangered Species Act. Once distributed widely across North America, their western range is now restricted to isolated populations in the Cascade, Klamath, and Sierra Nevada regions. Recently reintroduced populations in Olympic National Park and the central Sierra Nevada represent an effort to connect isolated populations and reestablish populations in historic habitat.

Fishers maintain large home ranges to meet their life functions. Rather than occupying a fixed den site, they move constantly and select new resting sites when necessary. This behavior necessitates the presence of numerous suitable resting sites scattered throughout the animal’s home range. Fishers can use a variety of structures for resting, including tree cavities, stick nests, mistletoe brooms, large branches, hollow logs, rock piles, and underground burrows.

Female fishers typically give birth in late March to early April. At this point they cease the typical nomadic behavior of moving to a new rest site each day and localize to a single tree cavity. This cavity, referred to as the natal den, is where the female gives birth to one to three kits (fig. 1). The family remains in this cavity for a period of weeks, after which she begins moving the kits to new structures referred to as maternal dens. This behavior continues for several months during which the females use anywhere from zero to six maternal dens. While tree cavities are the predominant structure used, as the kits get older hollow logs and underground burrows may be used as well.

Throughout California, fisher habitat is frequently associated with the presence of hardwoods, particularly California black oaks (*Quercus kelloggii*). Oaks provide fishers a variety of resources, including resting and denning sites. Oaks also help to support rodent and sciurid populations, which are an important prey source for fishers. Our objective in this paper is to summarize fisher use of oaks as resting and denning sites, and to explore the ecological relationship between fishers and hardwoods at larger spatial scales.
Study area

The Kings River Fisher Project study area is located in the High Sierra District of the Sierra National Forest, approximately 50 km east-northeast of Fresno, California (fig. 2). Elevation ranges from 1100 m to 2282 m. Dominant forest types include montane hardwood-conifer, Sierran mixed conifer, and ponderosa pine (*Pinus ponderosa*; http://www.dfg.ca.gov/biogeodata/cwhr/). Dominant tree species at the lower elevations include ponderosa pine, incense cedar (*Libocedrus decurrens*), and California black oak. At higher elevations the vegetation is dominated by incense cedar, white fir (*Abies concolor*), and ponderosa pine with infrequent sugar pine (*Pinus lambertiana*) and giant sequoia (*Sequoiadendron giganteum*). The climate is Mediterranean, with the majority of precipitation falling in the winter months as rain and snow.

Methods

**Microsite**

We used radio telemetry to follow fishers to resting sites from 2007 through 2014 in the Sierra National Forest. Fishers were captured using Tomahawk box traps equipped with an attached cubby for the animal’s comfort and security. Traplines were laid out along secondary or tertiary roads, with traps spaced approximately 500 to 1000 m apart. Traps were placed in the most suitable habitat available: dense forest drainages, along large logs, or in areas of complex understory. Traps were checked daily; captured fishers were transferred into a metal handling cone and anesthetized using a combination of Ketamine hydrochloride and Diazepam (200 mg Ketamine /1 mg Diazepam). Animals were weighed, sexed, and aged using a combination of tooth wear and sagittal crest development. Body measurements recorded included body length, tail length, girth, zygomatic arch width, footpad dimensions, and canine length. Biological samples collected included up to 6 cc blood for epidemiological analysis, tissue and hair for genetic identification, and any ectoparasites observed.
Animals were permanently marked using passive integrated transponder (PIT) tags inserted subcutaneously at the nape of the neck and equipped with radio collars weighing no more than 3 percent of the animals total body weight. Animals were placed back in the trap cubby, then released at the trap site when fully recovered.

Ground telemetry was used to locate the animals as frequently as possible (typically every 3 to 5 days). Once an animal’s telemetry signal was detected, technicians attempted to estimate the animal’s location using triangulation. If the animal appeared stationary, the technician attempted to follow the radio signal and locate the exact structure in which the animal was resting. Once located, the structure was tagged, UTM coordinates were collected, and basic data were recorded (e.g., structure type, tree species, forest conditions). More detailed data such as tree diameter at breast height (DBH), tree height, and slope position were recorded on subsequent visits after the animal had left the area.

Adult female fishers were carefully monitored during late winter and spring to document reproduction and den site selection. Once an adult female was located in the same location for 3 consecutive days, the structure was labelled a natal den and motion-sensitive cameras were placed around the structure to verify use and document litter size. When the female moved the kits to a new maternal den, the process was repeated. By mid-June, when the family was again moving on a near-daily basis, structures were considered rest sites, not dens.

**Mid-scale**

To quantify fisher use of different forest types within the study area, we conducted semi-annual scat detector dog surveys between 2007 and 2012. Detector dogs, provided by the University of Washington’s Center for Conservation Biology, are trained to locate the scat of a focal species. Surveys were conducted in May and October of each year, and scats collected were genetically verified by the U.S. Department of Agriculture, Forest Service (USDA FS) Rocky Mountain Research Station’s Wildlife Genetics Laboratory. Surveys consisted of two dogs alternating visits to a 14 km² sampling unit. Each unit was surveyed three times during each semi-annual survey. Confirmed fisher scat locations were overlaid on a 1-km-square grid of the study area. Because detector dog surveys are an unstructured survey method, each dog had a GPS logger attached to its collar to document the survey path. The survey route for a particular day would cover a number of grid cells, and we developed an effort covariate for each cell based on the amount of time spent surveying that grid cell. This process resulted in a binary detection matrix with 234 sampled 1 km² cells and 12 sampling occasions (Spring 2007 – Fall 2012).

We quantified forest type and structure within each grid cell using global nearest neighbor (GNN) data developed by the Landscape Ecology, Modeling, Mapping, and Analysis (LEMA) team at Oregon State University (http://lemma.forestry.oregonstate.edu/data/structure-maps). GNN data are 30 m resolution ArcGIS grids created by extrapolating plot-level data to remote imagery. We used 2012 imagery, the most recent data available. While LEMMA GNN data provide a variety of structural attributes, to better understand the importance of oak habitat to fishers, we focused on 15 variables known to be important to fishers (table 1).
Table 1—Forest structure variables selected for use in evaluating fisher use of hardwood habitat with the Sierra National Forest, California; data generated by the Landscape Ecology, Modeling, Mapping, and Analysis group at Oregon State University

<table>
<thead>
<tr>
<th>Variable Name</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>BA</td>
<td>Basal area of live trees &gt;=2.5 cm dbh</td>
</tr>
<tr>
<td>BA_con</td>
<td>Basal area of live conifers &gt;=2.5 cm dbh</td>
</tr>
<tr>
<td>BA_hdwd</td>
<td>Basal area of live hardwoods &gt;=2.5 cm dbh</td>
</tr>
<tr>
<td>CANCOV</td>
<td>Canopy cover of all live trees</td>
</tr>
<tr>
<td>CC_con</td>
<td>Canopy cover of all conifers</td>
</tr>
<tr>
<td>CC_hdwd</td>
<td>Canopy cover of all hardwoods</td>
</tr>
<tr>
<td>OGSi</td>
<td>Regionalized old-growth structure index for plots within NWFP. Calculated from abundance of large live trees, snags and down wood, and diversity of tree sizes</td>
</tr>
<tr>
<td>DDI</td>
<td>Diameter diversity index. DDI is a measure of the structural diversity of a forest stand, based on tree densities in different DBH classes</td>
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<tr>
<td>COVCL</td>
<td>Categorical cover class: 1 = sparse (CANCOV &lt; 10), 2 = open (CANCOV &gt;=10 and &lt; 40), 3 = moderate (CANCOV &gt;=40 and &lt;70), and 4 = closed (CANCOV &gt;=70)</td>
</tr>
<tr>
<td>SIZECL</td>
<td>Categorical size class, based on dominant quadratic mean diameter and canopy cover. 1 = shrub/seedling (QMD &lt; 2.5 or CANCOV &lt; 10), 2 = sapling (QMD &gt;= 2.5 and &lt; 25), 3 = small tree (QMD &gt;=25 and &lt;37.5), 4 = medium tree (QMD &gt;=37.5 and &lt;50), 5 = large tree (QMD &gt;=50 and &lt;75), 6 = giant tree (QMD &gt; 75)</td>
</tr>
<tr>
<td>SNAGDEN</td>
<td>Density of snags &gt;=25 cm dbh and &gt;=2 m tall</td>
</tr>
<tr>
<td>DWbio</td>
<td>Biomass of down wood &gt;=25 cm diameter at large end and &gt;=3m long</td>
</tr>
</tbody>
</table>

To evaluate fisher use of each grid cell, we created an occupancy model using Program PRESENCE (Hines 2006). We assumed constant probability of cell colonization and extinction across the study period, in part due to the small size of a grid cell compared to a fisher home range. Colonization and extinction rates refer to the probability that a grid cell will go from unoccupied to occupied, or occupied to unoccupied, respectively, between survey efforts. We assumed that detection rates varied according to both the season of the survey and the amount time spent surveying a particular cell.

We examined the influence of habitat variables on fisher occupancy using two approaches. First, we evaluated the influence of hardwood and conifer structure by comparing univariate models of canopy cover and basal area. Differences in performance among models were assessed using log-likelihood ratio tests. Second, we used an all model approach, retained models with non-zero AIC weights, and calculated evidence ratios for individual variables (Arnold 2010).

Statewide

Statewide, we collected information on den use from three other large-scale fisher monitoring projects. The Sierra Nevada Adaptive Management Project (SNAMP) was a large-scale investigation, led by the University of California at Berkeley, into the ecological impacts of fuel reduction and forest restoration in the Sierra National Forest. Between 2007 and 2014, SNAMP captured and monitored fishers in an area between Oakhurst, California and the south entrance of Yosemite National Park.
SNAMP researchers identified 125 fisher dens over 7 seasons. In northwestern California, the Hoopa Valley Tribe and the Wildlife Conservation Society has monitored fisher density and reproduction on the Hoopa Valley Reservation since the mid-1990s. The study began collecting detailed information on den structures in 2005, and over 4 seasons, provided descriptions of 111 dens. Finally, on industrial timberland in north-central California, Sierra Pacific Industries (SPI) has been monitoring fisher reproduction on two study areas since 2006. In Sacramento Canyon outside Weaverville, SPI recorded 55 denning structures used by fishers in 2006 and 2007. Then from 2010 through 2013, SPI monitored reproductive activity of reintroduced fishers on their Stirling Tract, northeast of Chico, and identified 63 dens.

Results

Microsite scale
We located 260 fisher den sites between 2007 and 2014. California black oaks accounted for 52 percent of den sites (n = 135), followed by white fir (25 percent, n = 64) and incense cedar (13 percent, n = 34) (fig. 3). The dens located in oaks were exclusively in cavities, with the overwhelming majority occurring in live trees (95 percent, n = 248). Oaks used for denning were generally large, averaging 75.9 cm DBH and 17.6 m tall. However, a variety of sizes of trees were used, ranging from 15.8 to 134.5 cm DBH (fig. 4).

Figure 3—Use of different tree species by fishers for (A) den sites, and (B) rest sites in the Kings River Fisher Project study area of the Sierra National Forest, 2007-2014. (C) Distribution of basal area by species across the study area for comparison.
During the same period, we located 853 rest sites, with California black oaks accounting for 28 percent (n = 234) (fig. 3). Other dominant species used included white fir (31 percent, n = 259), sugar pine (7 percent, n = 59), ponderosa pine (19 percent, n = 148), and incense cedar (15 percent, n = 117) (fig. 3). Oaks used as rest sites tended to be large, averaging 78.4 cm DBH (SD = 22.4 cm) and 18.2 m tall (SD = 8 m). Comparatively, conifers used as rest sites averaged 101.9 cm DBH (SD = 36.1 cm) and 28.3 m tall (SD = 16.0 m). Of the rest sites located in black oaks, 196 (84 percent) were located in cavities typically formed by heartrot and accessed through a branch scar. The remaining 16 percent were platforms created by either a large limb or a broken top.

**Mid-scale**

Over the 12 sampling periods, we located 877 genetically-verified fisher scats. We calculated univariate occupancy models for six hardwood or conifer canopy cover and basal area variables, and a null model. Influence of season on detection rate of scats was dropped as a covariate because in all cases it reduced model performance. Log Likelihood ratio tests indicated that while overall canopy cover was the best fitting model (table 2), it was not significantly different than the second best fit, basal area of hardwoods (P = 0.09). Basal area of hardwoods was a significantly better fitting model than either total basal area (P <0.0001) and basal area of conifers (P <0.0001) (table 2).
Table 2—Univariate fisher occupancy models for forest structural variables in the Sierra National Forest, CA. Symbols indicate occupancy (ѱ), colonization (ʮ), extinction (ԑ), and detection probability (p). In all models, colonization and extinction rates were assumed to be constant, detection probability varied by survey effort, and occupancy was related to structural variables. Variable descriptions are listed in Table 1.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>wgt</th>
<th>-2*LogLike</th>
</tr>
</thead>
<tbody>
<tr>
<td>ψ (CANCOV), ѱ, ϵ, p (effort)</td>
<td>1170.71</td>
<td>0</td>
<td>0.742</td>
<td>1158.71</td>
</tr>
<tr>
<td>ψ (BA_hdwd), ѱ, ϵ, p (effort)</td>
<td>1173.62</td>
<td>2.91</td>
<td>0.173</td>
<td>1161.62</td>
</tr>
<tr>
<td>ψ (CC_hdwd), ѱ, ϵ, p (effort)</td>
<td>1175.05</td>
<td>4.34</td>
<td>0.084</td>
<td>1163.05</td>
</tr>
<tr>
<td>ψ (BA), ѱ, ϵ, p (effort)</td>
<td>1190.47</td>
<td>19.76</td>
<td>0</td>
<td>1178.47</td>
</tr>
<tr>
<td>ψ (CC_con), ѱ, ϵ, p (effort)</td>
<td>1197.56</td>
<td>26.85</td>
<td>0</td>
<td>1185.56</td>
</tr>
<tr>
<td>ψ (BA_con), ѱ, ϵ, p (effort)</td>
<td>1199.49</td>
<td>28.78</td>
<td>0</td>
<td>1187.49</td>
</tr>
<tr>
<td>ψ, ѱ, ϵ, p (effort)</td>
<td>1201.86</td>
<td>31.15</td>
<td>0</td>
<td>1191.86</td>
</tr>
</tbody>
</table>

The all model approach, utilizing multivariate models to quantify evidence ratios for each variable, resulted in 34 models with non-zero AIC model weights. No one model dominated, the highest ranked model, [ѱ (BA_con, DDI, SNAGDEN)] received an AIC weight of only 0.215. Instead, the top 10 models all included various combinations of hardwood and conifer canopy cover or basal area, stem diversity, and snag density (table 3). Biomass of downed wood, old-growth structure index, cover class, and size class were dropped from consideration because they failed to appear in any of the top 25 models. Evidence ratios indicated that the strongest contributing variables were stem diameter diversity and snag density, which appeared in nearly all the top 10 models (table 4). However it should be noted that neither of these variables, when considered singly, was among the top models. In fact, a univariate snag density model received an AIC value of 1200.96 (ΔAIC = 50.86) and was not significantly different than a null model (P = 0.09). A univariate stem diameter diversity model performed slightly better, with an AIC = 1181.73, ΔAIC = 31.63. Therefore while these variables are important to fishers, evidence indicates that they must be present in combination with other variables to be useful.

Table 3—Top 10 multivariate models relating forest structure to fisher occupancy in the Sierra National Forest, CA. Symbols indicate occupancy (ѱ), colonization (ʮ), extinction (ԑ), and detection probability (p). In all models, colonization and extinction rates were assumed to be constant, detection probability varied by survey effort, and occupancy was related to structural variables. Variable descriptions are listed in Table 1.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>wgt</th>
<th>-2*LogLike</th>
</tr>
</thead>
<tbody>
<tr>
<td>ψ (BA_con + DDI + SNAGDEN), ѱ, ϵ, p (effort)</td>
<td>1150.1</td>
<td>0</td>
<td>0.2155</td>
<td></td>
</tr>
<tr>
<td>ψ (CC_hdwd, BA_hdwd + DDI + SNAGDEN), ѱ, ϵ, p (effort)</td>
<td>1150.86</td>
<td>0.76</td>
<td>0.1474</td>
<td></td>
</tr>
<tr>
<td>ψ (cancover + BA_con + DDI + SNAGDEN), ѱ, ϵ, p (effort)</td>
<td>1151.83</td>
<td>1.73</td>
<td>0.0907</td>
<td></td>
</tr>
<tr>
<td>ψ (CC_hdwd + BA_con + DDI + SNAGDEN), ѱ, ϵ, p (effort))</td>
<td>1151.88</td>
<td>1.78</td>
<td>0.0885</td>
<td></td>
</tr>
<tr>
<td>ψ (CC_con + BA_con + DDI + SNAGDEN), ѱ, ϵ, p (effort)</td>
<td>1152.1</td>
<td>2</td>
<td>0.0793</td>
<td></td>
</tr>
<tr>
<td>ψ (BA_hdwd + DDI + SNAGDEN), ѱ, ϵ, p (effort)</td>
<td>1152.19</td>
<td>2.09</td>
<td>0.0758</td>
<td></td>
</tr>
<tr>
<td>ψ (cancover + BA_hdwd + DDI + SNAGDEN), ѱ, ϵ, p (effort)</td>
<td>1152.99</td>
<td>2.89</td>
<td>0.0508</td>
<td></td>
</tr>
<tr>
<td>ψ (BA_con + DDI), ѱ, ϵ, p (effort)</td>
<td>1153.6</td>
<td>3.5</td>
<td>0.0374</td>
<td></td>
</tr>
<tr>
<td>ψ (CC_hdwd + BA + DDI + SNAGDEN), ѱ, ϵ, p (effort)</td>
<td>1153.62</td>
<td>3.52</td>
<td>0.0371</td>
<td></td>
</tr>
</tbody>
</table>
ψ (CC_con+BA_hdwd + DDI + SNAGDEN), ψ , r, p (effort) 1154.19 4.09 0.0279

Table 4—Weight of evidence ratios supporting the importance of individual forest characteristics in fisher occupancy models. Values range from -1 (low importance) to 1 (high importance)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Summed model weight</th>
<th>Evidence ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>DDI</td>
<td>0.979</td>
<td>0.957</td>
</tr>
<tr>
<td>STPH</td>
<td>0.818</td>
<td>0.635</td>
</tr>
<tr>
<td>BA_con</td>
<td>0.571</td>
<td>0.141</td>
</tr>
<tr>
<td>BA_hdwd</td>
<td>0.361</td>
<td>-0.278</td>
</tr>
<tr>
<td>CC_hdwd</td>
<td>0.316</td>
<td>-0.368</td>
</tr>
<tr>
<td>Cancover</td>
<td>0.184</td>
<td>-0.631</td>
</tr>
<tr>
<td>CC_con</td>
<td>0.154</td>
<td>-0.692</td>
</tr>
<tr>
<td>BA</td>
<td>0.058</td>
<td>-0.884</td>
</tr>
</tbody>
</table>

**Statewide**

Statewide we collected information on a total of 614 dens used by fishers between 2006 and 2014 (table 5). Overall, use of hardwoods versus conifers was fairly evenly divided; 53 percent hardwood versus 47 percent conifer. However the dominant species used was California black oak, accounting for 39 percent of all den sites. In three of the four studies providing data, an oak species was the most common den site.

Table 5—Documented den use of tree/snag species by female fishers at four research projects throughout California

<table>
<thead>
<tr>
<th></th>
<th>Kings River Project, USFS</th>
<th>UC Berkeley, Sierra Nevada Adaptive Management Project</th>
<th>Hoopa Monitoring Program</th>
<th>Sierra Pacific Industries</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA black oak</td>
<td>52% 27% 13% 46%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White oak</td>
<td>- - 2% -</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tanoak</td>
<td>- - 48% 3%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chinquapin oak</td>
<td>- - 6% -</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Live oak</td>
<td>&lt; 1% - - 7%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White fir</td>
<td>25% 26% - 6%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>7% 3% - 3%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Incense cedar</td>
<td>13% 35% 1% 6%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>- - 25% 19%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sugar pine</td>
<td>3% 7% 3% 3%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>other</td>
<td>- 2% 2% 8%</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Discussion

Oaks provide essential resources and habitat elements for fishers and related species worldwide. In Portugal, hardwood cavities accounted for 65 percent of the rest sites used by genets (*Genetta genetta*), with the majority of these located in cork oak (*Quercus suber*) and holm oak (*Q. ilex*) (Carvalho and others 2014). In Poland, cavities accounted for 60 percent of the rest sites selected by pine marten (*Martes martes*), with 20 percent of those located in oaks (Zaleweski 1997). In the United States, hardwoods comprised 40 percent of maternal dens in the northeast United States (Powell and others 1997), 94 percent of natal dens in Maine (Paragi and others 1996) and 90 percent of rest sites in Wisconsin (Kohn and others 1993). In California, Zielinski and others (2006) identified mean DBH of hardwoods as a significant predictor of fisher rest site suitability and Yaeger (2005) identified California black oak as the only tree species used more than expected by fishers for resting on two study sites in Northern California; the Hoopa Valley Reservation and the Shasta-Trinity National Forest.

Den site selection

In California, large oaks appear to be the dominant source of den structures for fishers. In a comprehensive review of fisher denning habitat in the western United States, Raley and others (2012) reported that the cavities used for natal and maternal were most often created by heartwood decay, and that the presence of heartrot is greater in older trees than younger (Manion 1991). It has also been shown that the number of dead limbs in California black oak, potential avenues for heartrot entry, increases exponentially with age (Garrison and others 2002). Another potential benefit to the use of cavities in live hardwood trees for denning is security. During the spring breeding season, males wait outside the natal den for the opportunity to breed when the female leaves the cavity. Females often select cavities with an opening too small for the larger male to enter, thereby protecting her newborn kits from potential harm. When formed via heartrot, cavities in oaks form scar tissue around the entrance. This woody tissue is extremely dense, and neither aggressive male fishers nor potential predators are capable of expanding the entrance to gain access. Conifers and snags do not form this scar tissue, and cavities are therefore more vulnerable to aggressive intrusion.

Thermoregulation

Fishers’ selection of resting and denning structures is influenced by a variety of factors, including thermoregulatory properties. Tree size is clearly important. Large trees modulate temperature better than smaller trees and cool less at night (Coombs and others 2010, Wiebe 2001). Entrance size also influences temperatures in cavities (Rhodes and others 2009). In British Columbia, fishers shifted from platforms to cavities to subterranean rest sites as the ambient temperature dropped (Weir and others 2005). In the Sierra Nevada, at the southern extent of the fishers’ range, the relationship appears inverted; fishers use cavities more often for resting when minimum temperatures are colder (Purcell and Thompson, unpublished data). Similar behavior and consequences have been observed in other species as well; pine marten in Poland select resting sites in relation to ambient temperature (Zaleweski 1997) and black bears (*Ursus americanus*) in the eastern United States suffered 15 percent
greater heat loss during winter hibernation in subterranean dens as opposed to tree cavities (Pelton 1996).

Oak cavities also appear to be more stable thermal environments than conifer cavities. In a study examining the interior conditions of tree cavities during prescribed fire, internal temperatures in cavities in live California black oak trees were more stable than within either snags or conifer trees (C. Thompson, unpublished data). While this observation needs to be explored in greater detail, it may help explain the frequent use of oak cavities as dens. Fisher kits are born with limited thermoregulatory capacity, and temperature stability may therefore be a critical consideration in den selection and thermoregulation (Raley and others 2012).

**Association with prey**

Numerous small mammal and sciurid species are known to rely on oak mast as a primary food source. For example, Innes and others (2007) found that dusky-footed woodrat (*Neotoma fuscipes*) density was positively associated with the presence of large oaks and Steinecker and Browning (1970) highlighted the importance of acorn availability to overwintering by western gray squirrels (*Sciurus griseus*). The population density of these species often fluctuates strongly in relation to mast production (Wolff 1996), and both fishers and martens respond numerically to these fluctuations (Jensen and others 2012). Therefore, the role of black oaks in supporting healthy prey populations for fishers in the state appears well established.

Our results also indicate that oaks play an important role in the suitability of California fisher habitat at larger spatial scales. Both hardwood basal area and hardwood canopy cover univariate occupancy models performed better than their conifer counterparts. The better performance of the hardwood basal area model compared to hardwood canopy cover may be associated with the value of having large oaks distributed throughout a fisher’s territory, as opposed to denser stands of smaller trees. Given the tendency of larger, older oaks to produce greater mast crops (McDonald 1990), the larger oaks would support a more stable and diversified prey base for fishers.

Furthermore, Purcell and others (2009) reported that while structures selected for resting were large, they were often surrounded by smaller trees, making the standard diversity of tree DBH an important predictor of rest site habitat. The authors concluded that this pattern may reflect the fact that historical logging and management has transformed the Sierra Nevada mixed conifer forest from a forest dominated by large trees and snags to one having fewer large trees surrounded by a matrix of smaller trees (Goforth and Minnich 2008, Vankat and Major 1978). Our finding that the diameter diversity index, in association with closed forest conditions, is strongly associated with occupancy at the home range scale may indicate a resource benefit from a complex forest structure as well.

**Management implications**

California black oaks provide a wealth of resources to fishers and help to maintain a stable prey base. Altered disturbance regimes have resulted in the loss of oaks throughout California. In the Sierra Nevada, decades of fire suppression have resulted in the shade-intolerant oaks being outcompeted by shade-tolerant species such as incense-cedar and white fir. While fishers do use these shade-intolerant species for resting and denning, they clearly select hardwood species when available. Furthermore, the shade-tolerant conifer species do not support the diverse prey
assemblage associated with oak mast. Therefore to promote fisher habitat throughout the state, land managers should not only promote the retention of large oaks wherever they occur, but also promote the recruitment and growth of young oaks through the creation of small gaps within the forest and the reduction of shade-tolerant conifers.

References


Bat Activity at Remnant Oak Trees in California Central Coast Vineyards

William D. Tietje, Theodore J. Weller, and Christopher C. Yim

Abstract
During 1990 to 2013, the area planted with wine grapes increased nearly 4.5 times in San Luis Obispo County. Much of this development occurred on open oak savanna with scattered oak (Quercus spp.) trees. Remnant trees are retained in some vineyards, but their value to biodiversity retention has not been quantified. During April to September 2014, at six vineyards in San Luis Obispo County, we compared echolocation activity of bats and the abundance of insects at remnant trees to locations without trees in the vineyards. The mean number of insects per night was over two times greater at vineyard trees. We recorded 3,677 bat calls at vineyard trees compared to 1,070 bat calls at open vineyard sites. Calls characteristic of bats that forage around trees were almost exclusive to trees (97 percent of high frequency calls), compared to calls of open-space bats, which were similar at both site types (57 percent of low frequency calls at trees vs. 43 percent in open vineyard). These findings indicate that large remnant oak trees in vineyards not only support higher levels of bat activity, but also increase the diversity of bats that occur and forage in the vineyard. This small-scale study lays the framework for addressing larger, more complex questions surrounding the benefits of remnant trees for bats and the ecosystem services they provide to grape growers.

Key words: bats, California, ecosystem services, echolocation, oak woodland, remnant tree, vineyard

Introduction
Over the past two decades, vineyards have become a predominant feature on the California Central Coast landscape. During 1990 to 2013, the area in vineyards increased from 3300 ha to 14 675 ha in San Luis Obispo County alone (San Luis Obispo County Annual Crop Reports 1990-2013), a 4.5-times increase. Much of this land conversion has occurred, and continues today, on former oak savanna with scattered oak trees. Despite lower production levels, many grape growers choose to retain these trees. However, we know of only one study that has examined the contribution of remnant trees in vineyards toward the maintenance of ecological functions and biodiversity of the native oak savanna. Michael and Tietje (2008) concluded that passerine bird diversity and numbers were similar at large valley oak (Quercus lobata) trees in vineyards and valley oak trees of similar architecture in adjacent oak savanna. However, the habitat value of these trees in vineyards to biodiversity more generally remains unquantified.

In other settings, large remnant trees are considered keystone structures, providing a wide range of ecosystem services (Lumsden and Bennett 2005, Manning and others 2006, Tews and others 2004). It is becoming increasingly clear that managing and

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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3 Ecologist, USDA Forest Service, Pacific Southwest Research Station, Arcata, CA. (tweller@fs.fed.us).
4 Statistics student, California Polytechnic State University, San Luis Obispo, CA. (yimcunechris@gmail.com).
maintaining these structures may be an economically and ecologically prudent way to retain many of the ecological functions of the native woodland habitat and thereby maintain biodiversity in the agricultural matrix. The trees may also provide important ecosystem services and economic benefits that may not be apparent to grape growers, land managers, or the public (Kunz and others 2011).

Insectivorous bats (Microchiropteran spp.) are of increasing importance because of their role in the provision of ecosystem services in the agricultural matrix. Nationwide, bats are credited with saving the agricultural industry nearly 24 billion dollars annually in chemical pest control services (Boyles and others 2011). Recent studies demonstrate that the maintenance of even scattered trees in highly modified landscapes makes a major difference in the use of an area by bats. For example, bat activity and richness increased significantly with the presence of only one to several scattered trees compared to bat activity in treeless areas. (Fischer and Law 2010, Lumsden and Bennett 2000). Where there are scattered trees, bat foraging areas tend to be centered on the trees (Lumsden and Bennett 2000, Threlfall and others 2012). Furthermore, Lumsden and Bennett (2000) observed that not only did bat activity drop off appreciably in the treeless areas of their study, but the community composition of bats was different. Arthropod abundance also increased with the presence of scattered trees and had a positive relationship with foraging activity of insectivorous bats (Lumsden and Bennett 2005, Threlfall and others 2012).

Hence, we predicted increased bat activity around remnant trees in vineyards. Remnant trees in vineyards may provide the heterogeneity and resources needed to meet the roosting and foraging requirements of bats adapted for foraging in woodland. To our knowledge, no study has documented the effect remnant trees within a vineyard setting have on the occurrence and foraging activity of bats.

**Study objective**

Our objective was to evaluate use of remnant trees by bats in vineyards of central-coastal California. We compared bat activity and insect abundance at trees within vineyards to paired locations without trees in the same vineyard. We evaluated the null hypotheses of no difference in bat activity or insect abundance between the tree and the paired location without a tree.

**Methods**

**Study area**

We conducted our study in the Central Coast region of California within the northern half of San Luis Obispo County, east of the Highway 101 corridor. The area is characterized by a Mediterranean climate with hot summers and mild-to-cool winters. Nearly all rainfall occurs between October and May, and average annual rainfall varies widely by geographic location in the study area, from as little as 13 cm to 97 cm.

**Tree site and no-tree site selection**

We created a list of potential sites using Google Earth, and then selected study sites based on land owner access permission and on-the-ground evaluations. Our six study vineyards were more than 3 years old (in other words, producing fruit), ≥50 ha in
area, and had at least one widely separated oak tree. Candidate trees were either valley oak or blue oak (*Q. douglasii*), >50 cm diameter at 1.37 m above ground (DBH) with large spreading canopy, and at least 100 m from another tree, vineyard edge, and anthropogenic features such as a building, open water, or highway. The same spatial criteria were used to select the non-tree site, which we placed 100 m from the paired tree and >100 m from any other tree or anthropogenic feature. We chose to study single remnant trees rather than small groups of trees to reduce ambiguity in our assessment of a tree effect. We selected the 100 m distance between tree sites and no-tree sites to balance the need to be close enough such that habitat, aspect, topography, and microclimate were similar, but far enough apart to minimize recording the same individual bats using both sites sequentially. This distance (100 m) was also used by Frey-Ehrenbold and others (2013) to define control areas for their study of bat activity around habitat structures. Finally, we measured tree DBH (cm), tree height (m), and canopy radius as the mean of four distances (m) in the N, S, E, W directions from the base of the trunk to the drip line (outermost edge of the tree’s canopy).

**Bat sampling**

We recorded echolocation activity during the summer active season (April to 21 September 2014) using Anabat II echolocation detector microphones (Titley Electronics Ballina, NSW, Australia) that were housed in weatherproof casings (‘bat hats’; EME System, Berkeley, California) and directed straight down (fig 1). Polycarbonate sound reflector plates on the microphone enclosures were positioned at 45 degrees below horizontal so that the angle of call reception was upward at 45 degrees. All microphones were placed at the top of 3-m-long by 1.9 cm diameter conduit. Detectors were connected via Canare LE5-C microphone cable to bat detectors and ANABAT storage Zero-Crossings Analysis Interface Modules (Z-CAIMs) housed in weather proof and dust proof containers which we hung from a carabiner attached to the conduit. We affixed a 10 watt, 30 cm by 40 cm, solar panel to the conduit between the microphone and dust proof container. Because the echolocation recorders were operated using solar power, we attached the conduit by hand clamps to a vine post on the south side of the remnant tree and oriented the echolocation recorder system south. This location provided both maximum solar exposure during the daytime and unobstructed vertical exposure to bat calls at night. At the no-tree site, in the same manner as at the tree, we secured an echolocation recorder system to a vine post and oriented the recorder south.
Echolocation recorders were activated from sunset to sunrise. To control for night-to-night variation in bat activity (Hayes 1997) resulting from factors such as weather or insect emergences, we used a paired design. That is, we deployed echolocation detection systems concurrently and for equal time at the tree site and no-tree site within a vineyard. During April to mid-July, we sampled at only one vineyard. After mid-July and until the end of fieldwork on 21 September, we moved our echolocation detection systems every 5 to 9 days and repeated paired sampling among six replicate vineyards. During the study (1 April to 21 September 2014), we accumulated 122 nights of paired sampling.

**Insect sampling**

During August to 21 September, 2014, we sampled flying insects at the tree and no-tree sites with 15 cm by 30 cm insect trap cards (yellow sticky card; Gempler’s, Inc.). We adhered a card to a 20 cm by 35 cm piece of cardboard and then clamped a card along a telescoping fiberglass painter’s pole at each of 2 m and 5 m heights. We then clamped the pole to the same vineyard post that supported an echolocation recorder system. Insect cards were deployed and collected on the same schedule as were the bat echolocation recorders (5 to 9 days). During this time, the four insect trap cards in a vineyard were up day and night. We therefore designated each full day (24 hr) a ‘trap day’ for each of the four cards; therefore, four insect trap card days were accumulated for one 24-hr day.

Using a home photo lab and camera stand, we photographed each card with a Nikon D3200 SLR camera. Jeffrey T. Drake, an independent researcher, counted the insects using computer image processing. The insect trap card photographs were processed on a PC using algorithms to separate possible insects from background and other non-insect material (Drake 2009).
Data summary and analyses

We viewed time vs. frequency displays of recordings using the program ANALOOKW (version 3.8c). Potential bat echolocations were separated from non-bat ultrasound via use of two filters. The first filter identified sounds with frequencies $\geq 20$ kHz and durations $>2$ ms (millisecond). The second filter identified sounds $\geq 7$ kHz and duration $\geq 5$ ms. This second filter was designed to identify potential echolocation calls of California bat species (in the family Mollosidae) that echolocate at low frequencies as they fly in open space. Each file that passed either filter was visually inspected to determine whether it was a bat call. We defined a bat call as either a series of $\geq 2$ echolocation calls each with duration $\geq 2$ ms or a single echolocation call with duration $\geq 5$ ms. Bat calls were then categorized as to whether they were produced by high frequency ($\geq 35$ kHz; hereafter HiF) or low frequency ($<35$ kHz; LoF) echolocating bats, based on minimum frequency. Finally, we used a set of filters designed for use with the Anabat system to identify echolocation calls of species of bats in California (C. Corben, personal communication). Because one bat can produce multiple call records during one night, we could not equate number of calls to the number of bats at a particular site. Instead, we let the number of bat calls be an index of bat activity at the site, as typically done by others (Hayes 1997). Due to an unusually high number of bat calls on several nights, the distributions of bat activity recordings per night were heavily skewed. To achieve normality, we transformed the data using a square root function.

To compare the number of echolocation recordings between tree sites and no-tree sites, we used paired t-tests, one for HiF calls and one for LoF calls. We tested insect counts with ANOVA. For all statistical analyses we used SAS JMP, Version 11 (JMP® Pro 11, SAS Institute Inc., Cary, NC). Differences were considered significant at $\alpha = 0.05$.

Results

Trees

Mean measurements of the six vineyard trees (five valley oak and one blue oak): DBH, 104.7 cm (83.8 to 142.2 cm); height, 19.5 m (12.2 to 29.3 m); canopy radius, 9.8 m (8.1 to 16.0 m).

Bat Activity

During 122 nights, we recorded 4,747 bat calls, 3,677 at tree sites and 1,070 at no-tree sites. Of the bat calls recorded at trees, 2,449 were HiF and 1,228 were LoF. Of the bat calls in open vineyard (no-tree sites), 119 were HiF and 951 were LoF. We recorded significantly more HiF bat calls at trees than in the open vineyard ($t = 5.113$, $p <0.0001$). In contrast, the number of recordings of LoF bat calls was similar at trees and in the open vineyard ($t = 1.026$, $p = 0.3063$; fig. 2).
Bat species

Of the 2,568 HiF recordings at the tree sites (2,449 HiF calls) and no-tree sites (119 HiF calls), 1,213 were assigned to the 50 kHz frequency class and 53 were assigned to the 40 kHz frequency class. The remainder, based on the filters we used, was not assigned to a frequency class. Species comprising the 50 kHz frequency class likely included the California myotis (*Myotis californicus*), Yuma myotis (*Myotis yumanensis*), canyon bat (*Parastrellus hesperus*), and possibly the Western red bat (*Lasiurus blossevillii*). Among these species, it is likely that the majority of the 50 kHz activity was produced by California myotis, as they specialize on foraging near the canopy of trees (Simpson 1993). Other species that may have contributed to HiF bat activity include long-legged myotis (*M. volans*), little brown bat (*M. lucifugus*), and western small-footed myotis (*M. ciliolabrum*). Of the LoF echolocating species, we were able to identify the Mexican free-tailed bat (*Tadarida brasiliensis*) and the hoary bat (*Lasiurus cinereus*). LoF bat species could also have been pallid bat (*Antrozous pallidus*), big brown bat (*Eptesicus fuscus*), silver-haired bat (*Lasionycteris noctivagans*), fringed myotis (*M. thysanodes*), and Townsend’s big-eared bat (*Corynorhinus townsendii*). Mexican free-tailed bats and hoary bats are open-space bats (*sensu* Schnitzler and Kalko 2001) and were identified from similar numbers of calls recorded at tree sites and no-tree sites.

Insects

Over an accumulation of 180 trap card days, we captured 393 insects on 24 insect trap cards, 273 at tree sites and 120 at the no-tree sites. More than twice as many insects were captured in vineyards at trees than at no-tree sites (mean = 3.0 insects/trap day at trees vs. 1.3 insects/trap day at no-tree sites, a significant difference (*t* = –2.9, *p* < 0.01; fig. 3). At the 2-m card height, 2.7 insects per trap day and 1.4 insects per trap day were collected at tree and no tree sites, respectively, and
3.4 insects and 1.2 insects, respectively, at 5 m. There was no difference in number of insects captured between the 2 m card and 5 m card heights \((t = -0.35, p = 0.73)\). Furthermore, similar proportions of insects were collected at both heights at tree sites and no-tree sites; that is, card height did not interact with the presence of the tree \((t = 0.83, p = 0.42)\).

![Figure 3—Histogram showing the average number of insects per night collected at tree sites and no-tree sites in six vineyards in San Luis Obispo County, California, 2014.](image)

**Discussion**

Our study results support our alternative hypothesis that large remnant trees enhance biodiversity within vineyards. We recorded more bat activity and higher insect abundance at trees than at the no-tree locations within vineyards. We found that large-bodied, low-frequency echolocating bats (25 kHz, Mexican free-tailed bats and hoary bats) dominate activity in those areas of the vineyard that lack trees. By contrast, the majority of bat activity we recorded around trees was produced by small-bodied, high frequency echolocators in the 50 kHz frequency group. We expect that most of this activity was by California myotis. This provides compelling evidence that the habitat heterogeneity created by large remnant oak trees may create foraging opportunities in the producing vineyard for another guild of bats. Bats may have been using the oak trees as roosting habitat or foraging habitat, but we strongly suspect the latter. Large oak trees provide rugose bark, hollows, and foliage surfaces that the open vineyard cannot provide to the woodland-dependent suite of bats. The trees also create a microhabitat and wind break that may allow insect prey to move beyond the tree canopy where they become available to open-space (aerial hawking) bats. We do not mean to suggest that the vineyard with trees provides a suitable surrogate for the native oak savanna it perhaps replaced. Our results indicate only that scattered large oak trees may add the structural diversity and prey necessary to support a broader community of bats than would be supported by the comparatively homogenous structure of a treeless vineyard.

Our results are not particularly surprising. Recent studies conducted in other landscape contexts and other parts of the world acknowledge the importance to foraging bats of legacy trees and large remnant trees. For example, Mazurek and
Zielinski (2004) recorded more bat activity at individual old growth legacy trees (Sequoia sempervirens), especially those with basal hollows used by the bats for roosting, than at nearby commercially-mature trees. Fuentes-Montemayor and others (2013) working in agricultural areas in Scotland and Lumsden and Bennett (2005) in Australia, showed that, although bat foraging activity was notably higher in more heavily treed habitats, the occurrence of foraging bats in areas with only scattered trees was much greater than in non-treed locations. Fischer and others (2010) reported that with the addition of one or two trees, bat species richness more than doubled and bat activity increased by as much as 10 times. Our study results provide evidence that the large remnant oak tree within a vineyard serves bats’ habitat needs in like manner as the scattered tree has been shown to do in other landscape contexts.

Oak trees in vineyards may become increasingly important as vineyard size increases. DeMars and others (2010) concluded that this was the situation for passerine birds in crop fields in the agricultural matrix of the Willamette Valley, Oregon. Those Oregon white oak (Quercus garryana) trees that were most isolated had more visits and more species of birds than did trees that occurred in groups. A commercial vineyard on the California Central Coast may be >240 ha in size and devoid of trees. It is likely that use of such a vineyard will be limited to large-bodied, low-frequency echolocating bats. While these bats are voracious predators, particularly where they occur in large numbers (Boyles and others 2011), their prey is limited to large-bodied insects. Lumsden and Bennett (2000) surmised that those bats in the open treeless parts of their study area were only passing through en route to foraging areas. Maintenance of a broader suite of bat species within vineyards may lead to a more diverse set of ecosystem services provided, particularly in the form of insect reduction.

In the Okanagan Valley, British Columbia, open vineyard does not replace the habitat value for bats of nearby native habitat (Rambaldini and Brigham 2011), at least not for the pallid bat (Antrozous pallidus). Is it possible that by the retention and maintenance of remnant oak trees within the vineyard, many of the ecological functions of the native oak savanna can be retained? If so, might there be unrecognized benefits to the grape grower? The retention and maintenance of oak trees in the vineyard incur a cost to the grape grower: pruning, water uptake, irrigation system modification, additional end posts, altering of tractor passes, less land in production. Without value to the grower, many of the trees will likely be lost. If bats can be shown to benefit their operations, grape growers may be more willing to maintain oak trees within their vineyards.

To document the ecosystem services provided by bats in vineyards, some important questions need to be answered. Do the bats benefit the grower? For example, do bats eat Lepidopteran grape pests such as cutworm (Agrotis spp.) moths and nocturnal leafhoppers (family Cicadellidae) in great enough quantity to make a difference in grape production? Do they prey on the recently introduced light brown apple moth (Epiphyas postvittana) and orange tortrix moth (Argyrotaenia franciscana)? If these two grape pests become well-established in Central Coast vineyards, could bats make a difference? If so, can grape growers reap the benefits in terms of lower pest loads or reduced use of pesticides? Perhaps, yes. The two most frequently identified bat species in this study, hoary bat and Mexican free-tailed bat, prey on moths. In walnut orchards in the California Central Valley, codling moths (Cydia pomonella) parasitize the walnut kernel, causing millions of dollars of damage annually in lost crop and the cost of increased application of insecticides. Long and others (2014) concluded that Mexican free-tailed bats consume enough codling moths to save more than $17,000 in crop loss at an average-sized walnut
orchard. If bats can provide similar benefits in vineyards, grape growers will have greater incentive to maintain the remnant trees.

The value of this small-scale study is twofold. It demonstrates that remnant oak trees within the vineyard provide foraging foci for insectivorous bats, due perhaps in part to the larger number of insects that occur at the trees than in the open vineyard. Second, it lays a framework to address larger, more complex questions. How do we conserve biodiversity in the agricultural matrix and how do we document the economic benefits that can accrue to the grape grower? For the scientist, the concern is whether trees in a vineyard enhance the distribution, abundance, survival, reproductive success and diversity of bats in the agricultural matrix. For the grape grower, a foremost concern is whether trees and bats help to provide an integrated pest management program without excessive cost to operations. Addressing these concerns is necessary to inform management guidelines that not only maintain the trees, but that also advance the livelihood of the grape farmer.

Many of the oak trees in vineyards are aging. If not valued in the eyes of the grape grower, most of these trees will be lost. The ecological and economic values of remnant oak trees for insectivorous bats, and for the ecosystem services the bats provide, need to be further documented and, importantly, articulated to growers.

Acknowledgments

We thank the owners of our study vineyards for permitting access to their properties for field data collection. M. Battany assisted with initial contacts with vineyard owners and S. Giordano and B. Fahey provided valuable assistance with deployment of bat echolocation recorders and the processing and organization of the echolocation data. D. Headrick provided helpful suggestions on the insect sampling methodology. J. Drake conducted the Computer Image Processing of the insect trap cards. A.Y. Polyakov and R.F. Long provided helpful comments on an earlier draft of the manuscript. The University of California Cooperative Extension Office, County of San Luis Obispo, provided logistical support.

References


Oak Tree Selection by Nesting Turkey Vultures (Cathartes aura)¹

Gregory A. Giusti,² R.J. Keiffer,³ Shane Feirer,³ and R.F. Keiffer⁴

Abstract

Turkey vultures (Cathartes aura) are a ubiquitous component of California’s oak woodland faunal assemblage. Though obvious, they are one of the least studied vertebrates found in our hardwood forests. This study attempts to define the role of oak trees as nesting sites for this large avian species. Verified nest trees are evaluated to determine tree structure and morphology, tree size, cavity size and cavity volumes. Nest trees need to be large and old to develop the nest characteristics being utilized by turkey vultures. Nest trees tend to be erect with large trunk cavities that extend to the ground. The entrance location and aspect of the nest cavity does not appear to be a limiting factor in selection. Internal nest cavity volumes vary between 0.80 m$^3$ and 1.55 m$^3$. External tree sizes (DBH) vary between 91.4 cm to 165.1 cm. Selected trees were both alive and standing snags. The project is currently conducting transect surveys across the ownership to determine the relative abundance of potential nest trees based on the information gathered from known nest trees.

Key words: Cathartes, nest cavities, turkey vultures

Introduction

Long-term quantitative life history studies of turkey vultures (Cathartes aura) are sporadic in different parts of the breeding range across North America, but rare in California. Such studies are needed to evaluate the factors affecting the status and health of turkey vulture populations (Kirk and Mossman 1998) particularly in a state like California where oak woodlands are under various pressures from development and conversion. Limited information exists for western populations nesting habits except in generalized format such as “typically roosts in large trees”—for example, cottonwood (Populus deltoides) – or on rock outcrops (Davis 1983, Thomaides and others 1989) and on saguaro cactus (Carnegiea gigantea) in southern Arizona (Bennett and Kunzmann 1994).

This study surveys known oak trees used by turkey vultures on the 2144 ha (5,300 ac) University of California’s Hopland Research and Extension Center (HREC) in southern Mendocino County, California. The purpose of the HREC study is to identify, catalog, analyze and characterize existing turkey vulture nest trees and nest tree cavities. Data collection included: 1) tree characteristics (species, diameter at breast height [1.37 m, DBH]); 2) nest characteristics (cavity volume, entrance dimensions, cavity height, tree structure characteristics); and 3) site characteristics (slope, aspect, elevation). The study also includes a property-wide transects/assessment of existing trees that meet the physical parameters of currently occupied nest trees to better understand the availability of suitable nest sites. The paucity of information regarding tree selection by these large cavity nesters in

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California’s oak woodlands puts this ubiquitous species at risk of losing suitable nesting habitat through benign neglect and lack of instructional information for resource managers and planners who have the jurisdiction to protect habitats.

Methodology

Historically, known nest trees have been archived at HREC during the past 20 years. Not all known nest trees are still standing as many of them have fallen due to age and decay and are no longer available for use. Those remaining trees have been cataloged using GPS technology and overlaid on existing property maps.

Once identified, tree metrics were collected including 1) tree species identification; 2) trunk DBH; 3) height of cavity entrance; 4) cavity entrance opening (including radius for volumetric estimates); and 4) length or depth of nest cavity.

Surrounding stand characteristics (trees per acre, distance to closest neighboring tree, percent canopy cover, and proximate distance to road) were also collected at the time. Those nest site characteristics are not included in this assessment as no linear relationship was evident relative to nest tree selection and surrounding oak woodland structure or composition.

Additionally, 30-m belt transect surveys are underway to assess the presence of potential trees that have both the size and cavity characteristics that may suit turkey vulture nesting. Trees over 50.8 cm (20 inches) DBH along these transects are tallied and assessed for nesting potential. If present, cavities are measured, cataloged and mapped.

Results

During the past 20 years 12 known nest sites have been cataloged and verified as turkey vulture nest sites. In every case, the discovery of the nest tree was a matter of chance as the adult birds exhibit no obvious signs of nest presence such as aggressive behavior, calls, agitated behavior, and so forth. Even when chicks are present, the adults exhibit no obvious evidence of nest presence.

One of the nest sites included a large black oak (Quercus kelloggii) that had fallen over and a nest with nestlings was found. The nest was located within the root ball of the fallen tree and the eggs and later young were on the ground. Two young were hatched and raised until one day the site was visited and found to have been raided by a predator. Only fledging feathers were found spread across the area and both the young and adults were gone. It is assumed that this nesting attempt ended in failure.

During this study five of the historic nest sites were verified to be active. Each nest was found within an existing cavity. Four of the five nests were in living trees and one was in a snag. The snag was so decadent that it was not possible to determine the tree species. The other cavities are within Q. lobata or Q. garryana, or hybrids of the two. The trees are found along active roads, a skid trail, or within a stand of trees. There appears to be no linear relationship between tree location, stand density, level of human activity or other measurable metric that could aid in nest site predictions.

All of the nest trees shared similar characteristics in that each tree was erect, had relatively large cavity openings the result of limb failure with accompanying internal decay that extended the cavity to the ground. Nest cavity entrance ordinal direction does not appear to be a factor as each cavity has a different orientation.

Trees tend to be relatively large relative to other surrounding trees in the matrix. Tree height is variable as is the cavity entrance from the ground. Each tree provides structure for the birds to land and roost to aid in attending the nest (table 1).
In each case none of the nest sites had any tangible evidence of occupancy including discarded feathers, down, food remnants or detectable smell. In other words, there were no external factors that would alert a passerby that a nest was active. In every case, the nest cavity extended from the entrance to the ground. In essence the birds are ground nesters encircled by a tree.

### Table 1—Nest characteristics, including tree DBH, length of the cavity, cavity entrance radius, and cavity volumes expressed in standard and metric values

<table>
<thead>
<tr>
<th>Tree Number</th>
<th>DBH (cm)</th>
<th>Length (m)</th>
<th>Radius (cm)</th>
<th>Volume (ft³)</th>
<th>Volume (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>66</td>
<td>38&quot; (96.5 cm)</td>
<td>10'11&quot; (3.3 m)</td>
<td>12.5&quot; (31.75 cm)</td>
<td>37.03</td>
<td>1.05</td>
</tr>
<tr>
<td>67</td>
<td>44&quot; (111.76 cm)</td>
<td>13' (3.9 m)</td>
<td>14&quot; (35.56 cm)</td>
<td>54.9</td>
<td>1.55</td>
</tr>
<tr>
<td>68</td>
<td>42&quot; (106.7 cm)</td>
<td>4’10&quot; (1.4 m)</td>
<td>16.6&quot; (41.9 cm)</td>
<td>28.5</td>
<td>.80</td>
</tr>
<tr>
<td>69</td>
<td>65&quot; (165.1 cm)</td>
<td>6’3&quot; (1.9 m)</td>
<td>18&quot; (45.7 cm)</td>
<td>44.7</td>
<td>1.26</td>
</tr>
<tr>
<td>68-A</td>
<td>36&quot; (91.4 cm)</td>
<td>7’0&quot; (2.1 m)</td>
<td>17&quot; (43.1 cm)</td>
<td>49.5</td>
<td>1.40</td>
</tr>
<tr>
<td>Mean</td>
<td>45&quot; (36-65&quot;)</td>
<td>4’10&quot;-13 (1.4-3.9)</td>
<td>12.5-18&quot; (31.75-45.7)</td>
<td>42.7</td>
<td>1.20</td>
</tr>
<tr>
<td>Range</td>
<td></td>
<td></td>
<td></td>
<td>(28-54)</td>
<td>(.80-1.55)</td>
</tr>
</tbody>
</table>

### Discussion

The scope of previous work in California evaluating tree use for both roosts and nest sites is extremely limited to the works of Looney (2006) and Harris (1996). Looney (a senior project paper) is the only known work that has addressed this topic in oak woodlands. Others have studied turkey vulture roosts and nest sites in Texas (Buckley 1996), Florida (Stolen and Taylor 2003), and Pennsylvania (Thompson and others 1990). Most of these studies have linked communal roost sites to adjacent animal damage related problems and did not necessarily address the ecological or dendrological aspects of tree selection. Coleman and Fraser (1989) describes in broad terms habitat use of turkey vultures in Pennsylvania while Kelly and others (2007) used evaluated regurgitated pellets at nest sites in South Carolina as a basis of determining adult food selection to juveniles. In each of these citations, the authors simply referred to roost or tree selection in general terms such as “large conifer” or “large hardwood” and did not provide quantitative assessments of diameters, height, nest cavity volume, or other tree characteristics.

The project raises obvious questions about turkey vulture behavior in nest selection. To date there is no obvious preference for tree location, size or juxtaposition to areas of human activity. There appears to be an obvious selection criteria based on nest cavity volume and extent. In each case the cavity size is relatively large and extends to the ground implying that not only size but “extent” of the cavity is an important determinant factor.

Another obvious question raised focuses on ingress and egress in and out of the cavity. Obviously adults must enter and exit the cavity several times a day to feed their young. Motion sensitive video used as part of this project has not detected any audible communications taking place between adults and nestlings. We assume that birds simply arrive at the nest and enter and exit without a great deal of fanfare. The young are quite while in the nest and only exhibit a loud hissing sound when
disturbed by the researchers. We further assume that the young exhibit innate exiting behavior when it’s time to fledge.

As for policy implications for this study, Giusti and others (2005a, 2005b) have written extensively on the threats and risks to oak woodlands throughout California. In their works they have attempted to provide guidance to land managers and decision-makers on the aspects of oak woodland ecology, ecological services and biological functionality in their decision matrices insure the sustainability of this forest type across the landscape. Similarly in coniferous forests, oak woodlands provide critical habitat elements to a myriad of vertebrate and invertebrate species. Some species, like turkey vultures, require unique habitat elements to insure viable populations. Large nest trees with suitable cavities is a unique habitat element that has heretofore not been addressed in management guidelines and lacks any credible field testing to assist in the development of such guidelines at this time.

References


Oak Management
Restoring California Black Oak to Support Tribal Values and Wildlife

Jonathan W. Long, Lenya Quinn-Davidson, Ron W. Goode, Frank K. Lake, and Carl N. Skinner

Abstract
Mature California black oak (Quercus kelloggii) trees are a keystone for many Native American cultures and support important ecological values. Black oaks depend on low-intensity, relatively frequent fires to reduce competition from conifers, yet they are also vulnerable to intense fires. Restoring mature, large canopy oaks that produce high quality acorns for tribal gatherers will depend upon reestablishing a more frequent fire regime. However, in many areas that have become overly dense, thinning treatments, out-of-season burns, and/or relatively severe fires may be needed to reopen the forest and reduce fuel levels before more traditional use of fire can achieve desired outcomes. Treatments that enhance acorn production may conflict with policies to maintain high forest canopy cover and decadent structures that support some sensitive wildlife species. However, both acorn gathering and habitat for sensitive species can be supported by adopting a landscape-scale strategy that sustains black oaks in a variety of conditions and plans for gaps and decadent areas based upon their relative suitability. Restoration of California black oak would not only sustain tribal values and wildlife habitat, but it would also promote greater ecological resilience in dry, frequent-fire forest types in the Sierra Nevada and throughout its range.

Key words: California black oak, cultural burn, ecosystem services, landscape restoration, prescribed burning, resilience, traditional ecological knowledge

Introduction
California black oak (Quercus kelloggii) is a cultural keystone species, according to the definition proposed by Garibaldi and Turner (2004) as “culturally salient species that shape in a major way the cultural identity of a people, as reflected in the fundamental roles these species have in diet, materials, medicine, and/or spiritual practice” (p. 4). Black oak clearly meets the criteria for this distinction based upon its multiplicity of uses; significance in names, stories, and ceremonies; value for trade; and lack of substitutability for California Native Americans who live in the heart of its range, such as the North Fork Mono (Aginsky 1943, Anderson 2007). Much information has been published about California black oak ecology (McDonald 1969, 1990) as well as its importance to Native Americans (Anderson 1993, 2005). This paper builds upon that foundation by laying out a strategy to restore desired

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1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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conditions for black oaks within the range where Native peoples have traditionally used fire to tend this keystone species.

Acorns have long been central to indigenous cultures in California (Baumhoff 1963), serving as both a direct food source and an indirect food source by sustaining game animals. Desirable properties of black oak acorns include a large nut that is easier to deshell, pound, and grind than other nuts; a distinctive taste and texture that yields excellent acorn soup or porridge (Figure 1); a high oil content; and storability (Anderson 1993).

Figure 1—Black oak acorn porridge, a traditional food prepared by Lois Conner, North Fork Mono, in a basket made by her grandmother, Lilly Harris, circa 1920. (Photo by Jonathan Long)

Black oaks also support a wide array of animal species. A study of ponderosa pine forests on the Sierra National Forest identified 19 bird species that nested in California black oak, with a greater use of live trees than snags (Purcell and Drynan 2008). The acorn woodpecker depends on black oak acorns, and good crops demonstrate potential to expand the bird’s breeding season (Koenig and Knops 1995). Band-tailed pigeons may be an important indicator of the condition of black oaks because of their strong association with those trees for roosting and acorns (Bottorff 2007, McDonald 1969). California black oak is also an important habitat element for sensitive species, including the California spotted owl and the fisher (Long and others 2014). Acorns play a foundational role by supporting black bears, small mammals, and other animals in the fall and winter when other food sources are not available (Mazur and others 2013, McShea and Healy 2002, Tevis 1952). Black oaks continue to provide great economic value through their association with successful deer hunting enterprises in California (Loomis and others 1995). Black oaks also have relationships to various fungi, including mycorrhizal species that help to exchange carbon, nitrogen, and water within soils and among plants, and species that produce truffles and mushrooms that support both wildlife and tribal subsistence (Anderson and Lake 2013, Southworth and others 2011).

**Desired conditions**

Tribal acorn gatherers emphasize the importance of the productivity and health of black oaks for the larger ecosystem, including the multitude of wildlife species that
utilize acorns. However, they particularly emphasize the importance of black oak trees that produce large quantities of good quality acorns (those that are not infested with weevils or worms) (Anderson 2005). The mere presence of oaks is not sufficient because black oaks take 80 to 100 years before they become mature enough to produce large quantities of acorns (McDonald 1969). The current condition of California black oak in the Sierra Nevada appears characterized by declining quality and dominance, as fire exclusion has caused old-growth, open ponderosa pine-California black oak woodlands to become rare (Taylor 2010). Fire suppression has helped shade-tolerant conifers invade and outcompete black oak, causing the remnant mature oaks to have reduced vigor (Cocking and others 2012, Skinner and others 2006).

Trees that are desired for acorn harvest have full crowns (high canopy volume) with few broken limbs and low rates of mistletoe infection (Figure 2). Cavities, which are important for wildlife, are common in both wild and tended oak trees, and gatherers do not consider cavities to be detrimental to acorn production. Gatherers do desire low branches (Figure 2) that facilitate use of beater sticks for gathering. Wildfires do not promote this architecture, but instead promote taller and narrower growth forms (see Crotteau and others, these proceedings), as can be found in the Beaver Creek Pinery (Figure 3).
Impacts of fires and tending practices

Available fire history indicates a strong association between black oak and frequent, regular fires in the southern and central Sierra Nevada and throughout its range on south aspects, ridges, and lower elevations (Van Wagtendonk and Fites-Kaufman 2006). At a more northerly site in the Klamath Mountains, black oak appears more common on mesic, north-facing slopes at lower elevations with a median fire return interval of about 11 years (Taylor and Skinner 2003). Frequent fires create openings that give shade-intolerant black oak the space and resources needed to thrive within conifer-dominated forests. Traditional practitioners and researchers have both shared the perspective that large oaks (specifically trees >20 cm diameter at 1.37 m above ground) tolerated frequent, low-intensity fires that maintained low fuel levels (Jack 1916, Skinner 1995, Skinner and others 2006). However, because of their relatively thin bark, black oaks are more sensitive to fire than the mature forms of associated conifers, such as Douglas-fir, ponderosa pine, sugar pine, and white fir (Skinner and others 2006). For that reason, McDonald (1969) described fire as “black oak’s worst enemy” (p. 15), reflecting a concern that black oaks are highly vulnerable to fire damage, even from prescribed fires. That black oak both needs fire and is threatened by it suggests that fuels and structural conditions need to fall within particular margins for fire to favor large trees and their associated benefits. This complex relationship with fire helps explain why the pros and cons of fire in forests with black oak have been debated for at least a century (for example, Jack 1916).

Fires may kill the stems of black oaks (top-kill) or the entire tree. Research at Blodgett Forest in the mid-1980s showed that tree-sized (>3 m tall) black oaks survived fall and spring prescribed burns without top-kill (Kauffman and Martin 1990). However, a more recent study found that burning not only killed small trees, but also induced mortality of larger trees after several years (Kobziar and others...
Oaks underneath overtopping conifers may demonstrate greater sensitivity to fire than would otherwise be expected due to compromised vigor and increased fuel loading (Cocking and others 2014). Although black oaks that are top-killed by fire do not disappear from a site, the ecological services that they provide may be lost for many years or even longer if conditions do not facilitate regrowth of mature trees. McDonald (1969), who documented that oaks need many decades to mature, noted that nearly all trees he had seen were resprouts, which can grow much faster than ones from seeds (McCreary and Nader 2011) and competing conifers (Skinner and others 2006). Consequently, where oaks are merely top-killed they will reestablish mature trees much more rapidly than in areas where acorns must germinate or seedlings are planted following severe fires.

**Cultural burns**

Goode (2014) described cultural burning as a traditional use of fire intended to stimulate desired conditions for targeted cultural resource species, including California black oak. He noted that traditional cultural burning in the North Fork Mono area would have been conducted about three times in 10 years, with another two to three burns in the following 2 decades. Consistent with these observations, Anderson (1993) noted that indigenous fires were set annually in the Sierra Nevada wherever the land “needed it,” as indicated by abundant growth of brush, with the result that tended areas were customarily burned every 2 to 10 years.

**Season of burning**

The typical season of burning reported by tribal practitioners from the central and southern Sierra Nevada was autumn or early winter (October through December, typically after or before rains) (Anderson 1993, Appendix R). Burning during the fall prior to gathering of the new acorn crop was beneficial for clearing the forest floor and controlling pest incidence, as well as limiting the density of competing conifers. However, Anderson (1993) pointed out one account of late winter burning by Hazel Hutchins, Mono, who reported that, “The Mono women set the fires in January, February, or March before the leaves sprouted and the mushrooms grew” (p. 39).

In a review of season of burning research, Knapp and others (2009) noted that black oak-dominated forests below the snowline are well suited to burning during tree dormancy, when leaves are available as flashy fuels and leafless canopies allow sufficient sunlight to dry the forest floor. Burning in the dormant season when the trees do not have their canopy also results in less scorch (Knapp and others 2009). Concerns associated with spring burning include impacts to wildlife and plants. The primary denning time for fisher is mid-March to mid-April, which can coincide with budburst in oaks. Pups in dens may be vulnerable to smoke, leading to concerns over prescribed burning during that period (Long and others 2014). These natural cycles and traditional practices suggest the need to consider potential negative effects when burning during early spring.

**Effects on acorn production and other values**

California black oaks and native peoples represent a mutualism where the oaks benefit humans and human tending benefits trees. Anderson (2005) explained that burning treatments can provide a very effective biological control on filbert worms and weevils. In addition to increasing production of high quality acorns, other benefits of burning and other tending cited by practitioners include producing
charcoal for wildlife, reducing mistletoe infection, and encouraging growth of grasses, forbs, and mushrooms (Anderson 2005, Anderson and Lake 2013). In the 1970s, U.S. Department of Agriculture, Forest Service managers at Shasta Lake sought to mimic the historical burning by local Wintu and Pit River people to improve acorn production, with a goal of enhancing deer and elk populations (Skinner 1995). They found that by burning the stands in January, there would be a large increase in that year’s fall acorn crop even while surrounding unburned areas experienced a poor crop (Skinner 1995).

**Intersections with broader restoration issues**

Restoration of California black oak lies at the heart of broader discussions of how to promote socioecological resilience in the Sierra Nevada (Long and others 2014). The species has suffered long-standing declines due to fire suppression and other historical activities, including widespread efforts to systematically replace it with conifers favored for timber production. But today, the many values of California black oak as wildlife habitat and a source of forest products position it as a centerpiece for demonstrating the potential benefits of fire-centric restoration of forests in California (Long and others 2014). Challenges associated with this type of approach include balancing concerns for sustaining old-forest wildlife species as well as limiting fire-induced losses of mature black oaks, whether through wildfire or prescribed fire.

Black oak has a particularly important role in the evolving approach toward restoration forestry in the Sierra Nevada, which emphasizes the importance of retaining hardwoods, restoring heterogeneity, and designing treatments according to topography (North and others 2009). Treatments to increase sunlight to black oak trees may conflict with policies intended to conserve the California spotted owl and fisher, both of which have been associated with maintaining high forest canopy cover (Long and others 2014). However, treatments may promote high variability at the landscape scale, which would allow society to retain decadent conditions to support those wildlife species in the near term while also maintaining healthy oaks that can provide food resources and habitat for the long term. Restoration treatments may promote openings in areas that are more valued for acorn gathering and are closer to roads and in flatter areas. Locations of historically tended “orchards” identified by gatherers or in historical records would provide a useful starting point. At a finer scale, expanding gaps around mature oaks may encourage both acorn production and recruitment of young trees that can take off when mature trees fall (Purcell and others 2012). Meanwhile, tree clusters with high canopy cover and desirable structures for wildlife, including resting platforms (Figure 4), may be preserved for their short-term habitat value (North and others 2009).
Restorative burning and other treatment strategies

The strategies to reclaim degraded forests may entail practices that differ from those typically employed in actively maintained forests. Black oak groves that have been overgrown with conifers due to fire exclusion may have changed so dramatically in terms of fuels and structure that restoring their condition may not be feasible simply by reintroducing fire. Under indigenous regimes, burns were so frequent and fuel levels so low that they did not pose a hazard to the forest, according to elders’ accounts (Anderson 1993, 2005). For example, burning from the bottom of a slope was reported as a common practice (Anderson 1993), although that practice tends to be hazardous in contemporary forests with extensive areas of high fuel loads. Reclamation of degraded stands may require multiple reentry burns before the resource is set up for intensive use and frequent fall burning, and burning outside of the historical fall-winter seasons may realign the system to the point where in-season burning can occur more safely (see Knapp and others 2009).

Treatments that kill and remove invading conifers are important for restoring desired conditions for black oaks. Various researchers have studied how thinning conifers can promote acorn production and other values in black oak (McDonald and Vaughn 2007) as well as white oak (Devine and Harrington 2013). Such treatments may be particularly important in the short term for reducing the threat from fire and promoting renewed growth of suppressed black oaks. However, for the long term, tribal practitioners highlight the importance of reintroducing fire to promote desired understory plants and reduce the incidence of undesirable pests and pathogens.

The potential use of managed wildfire or more intense prescribed fire as a forest restoration strategy becomes very complex when considering black oaks. Cocking and others (2014) suggested that fires may need to be relatively severe in order to curtail dominance by conifers, at least in stands where conifers are already well established and mechanical thinning is not practical. This idea recalls the “corrective burning” used by aborigines in Australia and described by Lewis (1994) as a way to reclaim forests that had gone too far from their desired condition; those more severe burns would effectively reset the system, then be followed up with maintenance.

Figure 4—A large legacy black oak used by a fisher for a rest site. (Photo by Rebecca Green)
burning at intervals that promote desired conditions. However, if such burns were to occur over a wide area, they might reduce the flow of ecological services provided by mature black oaks for decades. Therefore, strategies may need to be tailored to reduce the potential for unusually large and severe wildfires and to safeguard particularly sensitive, high-value legacy trees.

**Conclusion**

Treatment strategies to enhance California black oaks for acorn gathering should increase resilience of forests to drought, disease, and wildfires by reducing the likelihood of losing mature trees for extended periods, promoting more open stands with fewer conifers, and enhancing structural diversity, pyrodiversity, and biodiversity. Research at the scale of large landscape demonstration areas, as well as smaller experimental plot studies, will help to understand the benefits of more active caretaking of mature black oaks. Useful indicators for evaluating trends in black oak conditions include the abundance of trees with large, full canopies, and the availability of high quality acorns for gathering. Continuing research partnerships among scientists, land managers, and tribal gatherers will improve adaptive management systems for forests with black oak and sustain the many benefits from these “trees of life.”

**References**


Restoring Indigenous Prescribed Fires to California Oak Woodlands

Don L. Hankins

Abstract
It is recognized that California Indians have stewarded the landscape for millennia. As such, the coupling of fire and culture are interrelated and interdependent in many California ecosystems including oak woodlands. Colonization and subsequent governmental fire policy mandates have disrupted the cultural use of fire, which in turn has disrupted ecological functions where those fires are absent. As society grapples with the devastating impacts of wildfires and the loss of biological diversity, many Indigenous people see traditional fire use as a key to mitigation of devastating losses while retaining traditional livelihoods associated with burning. Indigenous burning in California is a keystone process, which creates heterogeneity of species and habitats while also promoting many culturally significant foods, materials and other resources of value to Indigenous communities and society. This research focuses on the restoration of Indigenous burning to oak woodlands and the ecological and cultural effects thereof. Preliminary findings and community perspectives of this research will be discussed.

Key words: biodiversity, blue oak, Indigenous prescribed fire, valley oak

Introduction
Fire plays an integral role in maintaining many ecosystems globally, and in many of those ecosystems the fire regimes established by Indigenous and local people have become a keystone process. As a keystone process, the decoupling of natural processes may facilitate the existence of such ecosystems, buffer them from environmental change, and contribute to coevolution of process and composition within these systems. Mensing (2005) states that the contemporary biogeography of California’s oak woodlands has been established since the last glacial period, and was enhanced and maintained by California Indians (Jepson 1923, Mensing 2006).

Valley oak (Quercus lobata) and blue oak (Quercus douglasii) represent two species with relatively broad distributions, and are two species of importance to Tribes within their ranges. It is well documented that California Indians burned within oak woodlands for a variety of purposes and spatial and temporal scales (Anderson 1999, 2005; Bean and Lawton 1973, Hankins 2013, Lewis 1973) largely linked to subsistence activities, including production of acorns, grasses, and other cultural resources. Jepson (1923) believed the distribution and structure of valley oak woodlands was tied to regular burning by Indigenous populations.

The spatial-temporal arrangement of fire created heterogeneity within the landscape (Martin and Sapsis 1992) typically at a fine scale. Drawing from Jepson (1923) and Mensing (2006) we can deduce that Indigenous prescribed fires were an integral process in oak woodlands of California. These fires have been applied through past environmental change (in other words, climate change) events (Eriksen 1

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1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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and Hankins 2013), and have contributed to ecosystem resiliency and would vary spatially and temporally with respect to environmental parameters.

Due to concomitant effects of colonization, traditional Indigenous burning has been displaced from the landscape. As we look to reinstate Indigenous processes into oak woodlands, we can draw from existing knowledge that both valley oaks and blue oaks are relatively tolerant of fire (Bartolome and others 2002, Holmes and others 2011, Standiford and others 2012, Swieki and Bernhardt 2002), but life stage and fire severity are key factors for survivorship. High severity fire events can cause complete overstory mortality and limited response of sprouting trees (Wills 2006). Van de Water and Safford (2011) summarized pre-contact fire histories and suggest that California oak woodlands had a mean minimum of 5 years and mean maximum of 45 years with a median of 12 years between fires. Standiford and others (2012) found fire return intervals between 5 to 25 years in blue oak woodlands in the southern Sierra Nevada. Given the limited occurrence of lightning ignitions at lower elevations (such as the Sierra Nevada foothills and Central Valley) in California (van Wagendonk and Cayan 2008), the fire regime in valley oak and blue oak woodlands is likely one dominated by human ignitions partly due to the greater population densities in these areas. Purcell and Stephens (2005) suggest these fires were likely of lower intensity due to their frequency, but intensity increased as shifts in fire management (in other words, fire suppression) lengthened return intervals and increased fuel loads. Indigenous burning in valley and blue oak woodlands was noted in early explorer accounts (Belcher 1843). In the time since European arrival to California, oak woodlands have undergone changes including invasive species introductions, habitat loss and fragmentation, and altered ecosystem processes (Mensing 2006).

**Declines and conservation**

Valley oak and blue oak woodlands have undergone many changes following European colonization. Historically, expansive valley oak woodlands extended for miles across the broad floodplains of the Central Valley, and blue oaks occurred as a nearly contiguous belt in the foothills surrounding the Central Valley. Today these woodlands persist in disjunct patches. While still widely distributed, the reduction of valley oak woodlands is cause to consider the remaining woodlands an endangered ecosystem. To a lesser extent blue oaks have also been subjected to land use changes and resulting loss and fragmentation of habitat. Current threats to the valley and blue oak woodlands include invasive species, limited recruitment and altered fire regimes including fire suppression. These woodlands support a tremendous diversity of native species. One conservation concern is for native grasses and forbs, which are largely displaced by non-native species (see Lulow and Young 2011). The relationship between plant associations is complex, but as Roche and others (2012) describe, oak woodlands harbor native grasses, which are less prevalent when oaks are absent.

Given the decline of valley and blue oak woodlands, it is particularly important to address the role of fire in achieving conservation and management objectives through future environmental change. Hobbs and others (2011) discuss restoring process, inclusive of Indigenous stewardship practices, as a means to manage ecosystems. While it is recognized the past environment cannot be achieved as a restoration goal, it is possible to direct the future potential of these systems by restoring Indigenous prescribed fire as process, thus making them more resilient. This research implements the management goals held in common by land managers and Indigenous populations
working to conserve and perpetuate oak woodlands for ecological and cultural purposes.

**Methodology**

The goals of this project were to: 1) measure the effects of Indigenous prescribed fire on biodiversity and culturally important species associated with valley oak and blue oak woodlands; and, 2) to implement and share traditional fire knowledge of Indigenous communities. The framework for implementation of this project integrates the use of Indigenous prescribed fire to enhance and conserve native species. Indigenous prescribed fire was achieved through working with local members of the Native American community in the areas surrounding each project site to implement burning according to traditional ecological knowledge. At the Big Chico Creek Ecological Reserve members of the Mechoopda and Konkow Valley Bands of Maidu were involved in burn implementation. At the Cosumnes River Preserve members of the Ione and Wilton Bands of Miwok, unaffiliated Miwok descendants and members of the California Indian Water Commission were involved in burn implementation alongside Tribal, state and local fire crews. The implementation of each burn coincided with the onset of the first fall rains followed by the initial growth of non-native annual grasses and forbs (between 2 to 5 weeks following the first rains). Burns at the Big Chico Creek Ecological Reserve (BCCER) occurred during fall 2011 and 2012, while burns at the Cosumnes River Preserve (CRP) occurred during fall 2013. Ecotones and microtopography along with existing roads and ditches were used as boundaries to confine burning. In areas lacking these features, black lines were established prior to the primary burn day. Ignitions involved strip and spot firing depending upon field conditions and site-specific considerations.

Fire effects monitoring and research outcomes were monitored on 20 x 20 m plots established at each study site. A modified relevé sampling method was utilized to document cover, species composition, structure and fuels in established plots. Additional data was collected on culturally significant species occurring on these plots. Counts or population estimates for select cultural resources were made on each plot, and tribal practitioners determined resource quality. Here I will report on cover, species composition and summarize data on culturally significant species.

At BCCER, nine plots were sampled in spring 2013 according to treatment categories of fire history; specifically 1 or 2 years following burns or on sites that had not been burned. A total of three plots were assigned to each treatment category. At CRP, 15 plots established for ongoing monitoring were sampled in spring 2013 pre-fire and resampled in spring 2014 post-fire on burned and unburned plots. Three of these plots were excluded from burning for comparative purposes.

Statistical analysis of data was completed in JMP 7.0.2© (SAS Institute, Inc. Cary, NC) focusing on ground cover and species richness. Data was analyzed with a standard least squares model with an emphasis on effects leveraging for treatment (fire history). Due to the unbalanced sampling between controls and burn plots at CRP the model was adjusted with a restricted least squares (REML) method whereby the random affect of treatment was nested by year.

**Results**

At BCCER, 91 species of vascular plants were identified across all plots with 59 of those being native. Amongst the native species there are many culturally important
species including at least 31 traditionally utilized for food, 6 for medicine, and 12 for fiber. Some of the representative native species include blue wild rye (*Elymus glaucus*), Lithurie’s spear (*Trityleia laxa*), blue dick (*Dichlostema sp.*) and foothill clover (*Trifolium ciliolatum*). Representative non-native species include red brome (*Bromus madritensis*), common hedge parsley (*Torilis arvensis*), rose clover (*Trifolium hirtum*) and yellow star thistle (*Centaurium solstitialis*).

Cover data from BCCER was averaged by treatment for analysis. Least squares fit for total species richness, native species richness and total cover were not found to differ significantly between treatments. By contrast, the proportion of native cover was found to differ significantly (see table 1). The average total cover on control plots was 53 percent, where plots burned 1 year prior had a reduced cover of 48 percent and plots burned 2 years prior increased cover to percent. In comparison, the average proportion native cover for controls was 13.7 percent, plots burned 1 year prior had increased cover to 20.8 percent, and plots burned 2 years prior had increased cover to 42.9 percent. This suggests that burns promoted native species cover, with a noted increase in cover 2 years following the burns. While native species collectively benefitted from the burns, there are no cultural species that stand out individually as being significantly different in terms of cover.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Analysis of Variance Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness</td>
<td>$F = 0.922, p = 0.4475$</td>
</tr>
<tr>
<td>Native species richness</td>
<td>$F = 1.662, p = 0.2664$</td>
</tr>
<tr>
<td>Total cover</td>
<td>$F = 2.846, p = 0.1352$</td>
</tr>
<tr>
<td>Proportion native cover</td>
<td>$F = 11.449, p = 0.009^*$</td>
</tr>
</tbody>
</table>

At CRP, 49 species of vascular plants were identified across all plots with 23 being native species. At least 11 of the native species are traditionally utilized for food, 10 for medicine, and 11 for fiber; some species fall into more than one category. Amongst representative native species were creeping wild rye (*Leymus triticoides*), white root sedge (*Carex barbarae*) and goose grass (*Galium aparine*). Representative non-native species include ripgut brome (*Bromus diandrus*), wild radish (*Raphinus sativus*) and Italian thistle (*Carduus pycnocephalus*).

Changes in cover were not significant across treatments. The average pre-burn cover for control plots was 58 percent, whereas burn plots had 68.4 percent. Following the burn cover on control plots was 56.2 percent, but burn plot cover was reduced to 52 percent. Total cover following burn treatment was significantly lower on burned plots (see table 2). However, the change in proportional cover for native species was not significant. Changes in species richness and native species richness were also not significant. Although, some of the culturally important species were observed to increase. For instance, across all plots the pre-treatment culm count of creeping wild rye yielded a mean of 26.5 culms, whereas the post-treatment count yielded a mean of 76.7 culms; most substantial gains were on burned plots, but the difference between burned and control plots was not significant.
Table 2—Least squares fit random effects predictions. Valley oak woodland at the Cosumnes River Preserve

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Burn</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness</td>
<td>$t = 1.29, p = 0.3116$</td>
<td>$t = 0.09, p = 0.9409$</td>
</tr>
<tr>
<td>Native species richness</td>
<td>$t = -0.43, p = 0.7429$</td>
<td>$t = 0.15, p = 0.9049$</td>
</tr>
<tr>
<td>Total cover</td>
<td>$t = -2.46, p = 0.0250^*$</td>
<td>$t = 0.11, p = 0.9190$</td>
</tr>
<tr>
<td>Proportion native cover</td>
<td>$t = -2.07, p = 0.0606$</td>
<td>$t = 0.36, p = 0.7435$</td>
</tr>
<tr>
<td>Creeping wild rye abundance</td>
<td>$t = 1.05, p = 0.4791$</td>
<td>$t = -0.01, p = 0.9935$</td>
</tr>
</tbody>
</table>

**Discussion**

The data suggests that fire may play an important role in maintaining and enhancing native vegetation in blue oak and valley oak woodlands, but more monitoring time may yield stronger conclusions. Based on the results, it appears that the reduced cover 1 year following burns may provide an opportunity for native species establishment by the second year following burns. This data suggests that fires may temporally facilitate the prevalence of native species, which has been previously observed in other vegetation communities (see Hankins 2013). Although analysis did not demonstrate a significant relationship between treatment and the proportion native cover or richness within the valley oak woodland, presumably, the observed temporal lag in cover response amongst blue oak woodlands is an indicator for what could occur in valley oak woodland. In consideration of the observed response differences, it is possible that this difference between cover responses may be attributed to variability in precipitation during the years under analysis. Specifically, the valley oak woodland was burned during a period with no subsequent precipitation for months following the burn, and thus little moisture was available to facilitate response by native perennial grasses and forbs. By contrast, more typical precipitation patterns followed the burns in blue oak woodland. Under normal conditions, the periodic precipitation would provide moisture to enable native vegetation to recover. As stated previously, the timing of the burns coincided with the onset of the rainy season. Plant phenology, mostly germination of non-native grasses and forbs, was a key indicator for implementation of burns at both sites, but the outcomes of these burns yielded somewhat differing results. One critical consideration that has yet to be analyzed is the role of climate parameters on the outcomes of these burns. Specifically, a persistent dry period followed the valley oak burn, and lasted several months. Based on observations of many of the same native species in other burned environments, there is usually a rapid regeneration of vegetation, particularly amongst perennials. Following the valley oak burn there was little regeneration until precipitation resumed months later. This late precipitation was observed to enable another germination period for non-native grasses and forbs, which may have been outcompeted by natives under normal rainfall.

Another factor to consider in the management of these oak woodlands is the relationship of patch size to species richness and the composition thereof. From a conservation biogeography perspective, it is likely that blue oak woodlands would be more resilient to non-native species due to the spatial extent and configuration of these woodlands within the landscape (in other words, they often occur in extensive and contiguous belts), whereas valley oak woodlands largely exist in relatively small remnant patches which are more susceptible to invasion. This particular valley oak woodland was bordered on two sides by annual grasslands with a dominance of invasive species, a highway, and an agricultural field. Thus the invasion potential is high. Furthermore, the numbers of species observed within blue oak versus valley

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oak woodlands represent the additive phenomenon of increased richness relative to increased habitat area.

This data represents preliminary work in the restoration of Indigenous prescribed fire to oak woodlands. Given changes to the landscape and the ubiquity of non-native species, achievement of management objectives may require mixed approaches. For instance, it was observed that areas subject to higher burn intensity (such as where coarse debris had burned) recovered mostly to native species. Based on previous research by Lewis (1994) and Fulé and others (2004) and field observations (personal notes), this begs the question of whether alternative prescriptions such as high intensity or higher severity may be a potential management approach in the short term. Future research should investigate this further.

Acknowledgments
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References


The Value of Oak Woodland Habitats as Control for Medusahead (*Taeniatherum caput-medusae*)

Elise S. Gornish, Jeremy J. James, and Emilio A. Laca

Abstract

Although medusahead (*Taeniatherum caput-medusae*) is one of the most dominant invasive rangeland grasses in the West, we know surprisingly little about the environmental factors that drive medusahead abundance. Understanding the conditions that influence spread dynamics is central for developing effective monitoring, prevention and control programs.

We established grassland plant communities and added medusahead seed across a range of five densities (from 0 to 50,000 seeds per m²) in open grassland and oak savannah habitat. We followed plants throughout the season to understand how habitat and seedbank dynamics affect underlying vital rates and overall density.

Oak woodlands reduced medusahead abundance by almost 300 percent, and this effect was greater later in the growing season. The negative effect of oak woodlands was almost an order of magnitude less for common competitive annual species. We also found that reproductive spike production was lower in the oak habitat than the open habitat; and that seeding rate had a negative relationship with seed produced per spikelet. These effects ultimately contributed to a reduction in medusahead reproductive output between habitats, across seeding rates. This work highlights the value of oak woodland habitats as an effective and sustainable way to control medusahead density and recruitment.

Key words: annual grass, conservation, grassland management, invasive plant, restoration

Introduction

The winter annual grass medusahead (*Taeniatherum caput-medusae*), is one of the dominant invasive range species in the West. Originating in the Mediterranean, medusahead has already invaded 17 western states since it was first identified in Oregon in 1887 (McKell and others 1962). A variety of methods have been tested to control the noxious weed, including grazing, herbicide, and controlled burning (DiTomaso and others 2007). The continued aggressive spread of medusahead, however, suggests that current control efforts, even in the presence of an initial decline in weed density, are largely unsuccessful. A recent meta-analysis (J. James and others, in press) suggests that high variation of medusahead cover in response to control treatments is likely due in, large part, to underlying environmental factors such as habitat type or seedbank dynamics.

Indeed, several environmental factors have been identified as being particularly important filters for medusahead dominance and control. For example, as little as 5 percent tree cover can significantly reduce medusahead cover (Shlisky 2001). Certain soil characteristics can also play a role as well (for example, Nafus and Davies 2014),

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since medusahead has been shown to respond to soil fertility (Bovey 1959), and soil water content (Bansal and others 2014). Having an understanding of the relationship between environmental factors and medusahead dominance would be useful for developing more effective control techniques for the weed.

In order to understand how environmental factors might affect the underlying vital rates and overall density of medusahead, we investigated how seeding density (to simulate differences in the seedbank) and habitat type (open vs. oak) affect medusahead recruitment. Since the oak habitat provides less ideal conditions for medusahead through shading and precipitation interception, we expected medusahead density to be considerably lower in the oak habitat compared to the open habitat (Shlisky 2001). We also expected interactions among habitat type and seeding density since density dependence has been shown to operate within medusahead populations (Bovey 1959). Specifically, we expected that individuals experiencing less intraspecific competition (in other words, lower seeding densities) would respond to the comparatively higher resource open grassland habitat with a larger reproductive output (Archer and Detling 1984, Lee and Bazzaz 1980) compared to individuals experiencing less intraspecific competition because of reduced density stress (for example, Banyikwa 1988).

Methods

Species description and site preparation

Medusahead has rapid germination embedded in thatch or at the soil surface in the early winter after autumn rains. Seedlings (approximately 7 cm tall) emerge after late winter rains. As the plant grows, it produces several internodes, and can attain a full of height of 20 to 60 cm (Parish 1956). In May, after the production of four to five tillers, individuals will flower. Individual plants can produce between 15 to 23 spikelets, with each spike producing about 12 seeds.

In early fall of 2013, paired permanent plots (1 m²) were installed in two habitat types (open grassland and oak woodland). Canopy cover was approximately 50 percent higher in the oak woodland habitat (mostly blue oak, *Quercus douglasii*, and interior live oak, *Q. wislizeni*) compared to the open habitat. In the oak woodland habitat, leaf litter was also substantial (mean = 501.8 grams, SD = 176.2 grams per m²). Existing vegetation at all sites was initially removed by mowing and standing thatch was removed. The soil was solarized in an attempt to equalize soil conditions and reduce the seed bank. We applied soil solarization via clear 4 mm thick polyethylene tarps that covered the plots at the soil surface for approximately 14 days to encourage seed germination (depletion of the seed bank). Glyphosate (Roundup) was then applied to kill germinated plants.

Plots were hand seeded with one of five densities of field-collected medusahead (0, 100, 1000, 10,000, and 50,000 seeds per m²; see Marañón and Bartolome 1989 for seed bank values), mixed in with 500 grams of medusahead thatch. Immediately following the addition of medusahead seed, we added 6,000 seeds each of neighboring grass species (annual rye, and brome) and 4,000 seeds of a clover mix (for a total of 16,000 neighbor seeds added) to maintain a realistic competitive environment (Marañón 1998; E. Gornish, unpublished data). Treatments were randomly assigned to plots within habitat level quadrats. Main factors were replicated four times for a total of 40 plots (two habitats × five seeding densities × four replicates = 40 plots).
**Data collection**

We censused the plant density frequently during the growing season. Census periods coincided with important transitions in the life cycle of the medusahead plant. These included: germination in December 2013; emergence in April 2014; establishment in May 2014; and flowering culm production in June 2014. During each census period, the density of medusahead tillers as well as the density of all other live plants was estimated by counting live tillers within the 0.25 m² center subplot and multiplying by four.

In June 2014, we counted the total number of flowering spikes in each plot. At this time, we also bagged the spikes of 10 individuals in each plot with drawstring organza germination bags (7.6 x 10 cm). Three months later, we collected the bags and counted total seed number for each spike, and assessed percent germination by plating out all captured seeds.

**Analysis**

We first analyzed the effect of habitat, seeding rate, census month (fixed factors), and replicate (random factor) on medusahead density with a multivariate model that included a Poisson error structure to accommodate count data. We then created a separate multivariate model for each demographic component of recruitment (spike number per plot, seed number per spike, percent germination, and finally, total reproductive output per plot [spike number per plot x seed number per spike x percent germination per spike]). These models included the explanatory variables of habitat and seeding rate (fixed factors), and replicate (random factors). The models describing spike number per plot and seed number per spike included a Poisson error structure to accommodate count data.

**Results**

Medusahead density was significantly lower in the oak habitat (mean density = 82.3 tillers per m²) than in the open habitat (mean density = 267.7 tillers per m²) (p < 0.001), and this negative effect became more pronounced throughout the growing season (p < 0.001). Although the density of the common annual competitors was also slightly smaller in the oak habitat (mean density = 169.5 tillers per m²) compared to the open habitat (mean density = 200 tillers per m²) early in the growing season, this pattern disappeared by April 2014.

Medusahead reproductive spike production was five times greater in open grassland habitats (estimate = 2.22, SE = 0.08, z = 28.4, p < 0.001). There was also a small, but significant positive relationship between spike production and seeding rate (estimate = 0.0003, SE = 0.0001, z = 26.7, p < 0.001; fig. 1A). However, there was no interaction between habitat and seeding rate. Habitat did not appear to affect average seed number per spikelet (fig. 1B), but there was a small, negative relationship between seeding rate and seed number per spikelet (estimate = -0.0001, SE = 0.0004, z = -2.78, p = 0.007; fig. 1B). There was no effect of habitat, or seeding rate on percent germination of seeds produced across plots (fig. 1C). When these three factors are multiplied together to identify total reproductive output per m², we found that as main effects, habitat and seeding rate were not important drivers of recruitment. However, the interaction of habitat and seeding rate was important for driving differences in total reproductive output (estimate = 0.08, SE = 0.02, z = 4.2, p < 0.001; fig. 1D).
**Discussion**

Although environmental variables are important drivers of population growth rate (for example, Jacquemyn and others 2010, Lehtila and others 2006), there is a surprising lack of research that investigates the relationship between habitat characteristics, vital rates and invasion (Ramula 2014). In order to clarify if habitat type and seedbank dynamics in fact play a role in mediating the dominance of medusahead, we investigated how medusahead density and recruitment are affected by oak habitats and different seeding rates.

To our knowledge, this is the first time a study has formally quantified the negative effect of oak woodland habitat on medusahead dynamics. As expected, we found that oak habitats provide a less ideal environment for medusahead, resulting in lower densities and lower reproductive spike production, compared to open habitats. We expect that one or more of the environmental factors associated with the high heterogeneity of resources associated with oak canopies (Marañón and Bartolome 1994), such as leaf litter and soil moisture (for example, Callaway and others 1991) indirectly reduced the competitive dominance of medusahead. Explicitly documenting the identity of the factors that mediate negative effects of oak habitat on medusahead would be helpful for developing a more nuanced understanding of variables that might contribute to variation in the success of medusahead control efforts.

We also found that seeding rate (a proxy for the seedbed) is an important driver of per spikelet seed production. This was not entirely unexpected as demographic factors are often driven by underlying seed or population size (for example, Ramula...
2014). Although previous studies have also documented the effects of density on medusahead spike production (for example, Murphy and Turner 1959), studies investigating how the interactive effects of seed density and environmental factors operate across the life cycle of an invasive species are uncommon (Ramula and Buckley 2009). And, this type of information is needed for making predictions of future invasions of the weed (for example, Mangla and others 2011, Wallace and Prather 2013), as well as developing adequate control methods.

We found that medusahead recruitment ultimately responded to an interaction between seeding rate and habitat type where there was a relatively linear, positive relationship between seeding rate and total reproductive output in the oak habitat, but not in the open habitat. This suggests that the role of the seedbank in mediating medusahead dominance oak habitats is even more pronounced, in terms of recruitment, than in the open grassland habitat. This work demonstrates the integral role of oak woodlands for effective, continued management of medusahead, providing yet another piece of support for the continued development and maintenance of oak conservation strategies.

Acknowledgments
The authors thank Brittany Forer and Lauren Connell for field help.

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Thinning Interior Live Oak in California’s Southern Sierra Nevada

Richard B. Standiford and Neil K. McDougald

Abstract
This study describes a thinning and resprout control study in Madera County. The study site was a dense, 40-year old interior live oak stand (*Quercus wislizeni*) that originated from resprouting, with 100 percent canopy cover. Tree thinning was initiated in 1998 in cooperation with the local Resource Conservation District to evaluate thinning treatment to reduce first risk and to increase forage production. Three thinning treatments were evaluated: (1) thin one-third of the standing tree basal area (resulting in a post-thin basal area of 46 square feet per acre); (2) thin two-thirds of the standing tree basal area (resulting in a post-thin basal area of 27 square feet per acre); and (3) control/no thin (basal area of 73 square feet per acre). Because interior live oak is such a prolific sprouter, half of the thinned plots were treated with herbicides to prevent resprouting and to retain the open canopy structure. Canopy cover, diameter and height growth, and acorn production were monitored over a 13-year period. Periodic annual increment for basal area and volume was not significantly affected by the thinning treatment. Individual tree DBH growth was significantly increased with the thinning. 13 years after the thinning, the 1/3 treatment had virtually identical volume to the control, although the 2/3 thinning treatment had significantly less volume per acre. The sprout control treatment had no significant effect on the overstory tree growth, although a more open understory was maintained by controlling resprouting. Individual tree acorn production was significantly increased as a result of the thinning treatments. Thinning appears to be a promising management tool to diversify stand structure in dense live oak stands in the Southern Sierra, increasing economic value for livestock use and reducing wildfire risk.

Key words: interior live oak, oak thinning

Introduction
Interior live oak (*Quercus wislizeni*) is widespread in California, occurring on 16 percent of California’s oak woodlands (Waddell and Barret 2005). It is characterized by a vigorous sprouting capacity (Fryer 2012, Plumb and McDonald 1981). It is well-adapted to fire, and shows a rapid response to top-killed fire damage (Plumb and Gomez 1983).

The rapid regrowth of interior live oak results in very high density canopy cover classes following wildfire, which has a negative effect on forage production, water yield, and some wildlife species (Fryer 2012). Interior live oak is predominantly found on private lands (78 percent of the total cover type), making multiple use management and economic livelihood of private owners a key component of long term conservation (Waddell and Barrett 2005).

Dense stands of interior live oak are widespread throughout the Sierra Nevada foothills. To date, there have been no investigations of the effects of thinning on interior live oak stand characteristics. Bonner and other (2008) have shown promising results with thinning of coast live oak (*Quercus agrifolia*), a coastal live

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1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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oak with similar silvical characteristics to interior live oak. This suggests that there could be positive effects on stand structure from thinning treatments.

Methods

The Coarsegold Resource Conservation District (RCD) has had an active program to reduce impacts from catastrophic wildfires on a diverse array of wildland vegetation types, and provides technical assistance and support for cost-share payments to landowners with appropriate silvicultural and restoration strategies. They requested the assistance of the University of California to develop thinning recommendations on interior live oak to guide landowner actions.

A study site on a private ranch was selected near the town of North Fork, California in Madera County. The study site was at an elevation of 579.12 m (1900 ft), and was seasonally grazed as part of a cow-calf operation. The study site had developed from a rangeland clearing 40 years earlier. The overstory interior live oak canopy cover was close to 100 percent. The stand has a very high fire risk, and had no forage production due to the heavy shading of the understory. The area was representative of large acreages of similar, dense interior live oak stands in the Southern Sierra.

The study was designed with two thinning levels (thin one-third, and two-thirds of the basal area), and an unthinned control. There were 6 replications of each thinning level. Each replication was 0.1 acres in size. On half of the replications, the stumps were treated with herbicides (glyphosate), to prevent resprouting of the cut stumps. The trees were harvested in the winter of 1998. Trees were selected for harvest to accomplish the basal area retention goals for each treatment. The herbicide treatments were applied at the time of harvesting. Rings of the harvested trees were counted, and the stand age of 40 years was confirmed. Table 1 below shows the summary statistics of the study site.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Basal area (sq. ft./ac)</th>
<th>Volume (cu. ft./ac)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>95.3 (5.6)</td>
<td>1876 (306)</td>
</tr>
<tr>
<td>Thin 1/3</td>
<td>48.5 (2.5)</td>
<td>1387 (167)</td>
</tr>
<tr>
<td>Thin 2/3</td>
<td>26.8 (1.5)</td>
<td>769 (103)</td>
</tr>
</tbody>
</table>

Data was collected on all residual trees in the study area in 1998, 2002 and 2010. At each measurement, diameter at breast height (1.37 m, DBH) and total height was calculated. From these figures, merchantable volume to a 5.08 cm (2 inch) small end diameter was calculated, using the volume equations in Pillsbury and Kirkley (1984).

Crown radius of all residual trees was taken in two directions in 2010 to calculate overstory canopy cover percent. The canopy radius of the resprouting cut stumps was also measured in two directions in 2010 to calculate the understory canopy cover percent.

Acorn production was evaluated in 2000, 2001 and 2003 on all residual trees using the visual estimation methodology described by Graves (1980). All trees were placed into one of the four classes described by Graves (Class 1 = no acorns; Class 2 = acorns visible on close exam; Class 3 = acorns readily visible, don't cover entire tree; Class 4 = acorns readily visible, cover entire tree).
Results

**Volume and basal area growth**

Figures 1 and 2 show the 13-year total volume and basal area per acre for the three treatments. The one-third thinning treatment had virtually the same volume as the unthinned control after 13 years. Both the one-third and two-thirds thinning treatments were growing at an increasing rate in both volume and basal area, while the control growth was decreasing over the study period. The replications with stump sprout control were combined with those without herbicide treatment, since understory treatment had no significant effect on volume or basal area. Expressed as a compound annual growth percent, the two-thirds thinned treatment grew at 5.1 percent, the one-third thinned treatment grew at 3.8 percent, and the unthinned control grew at 1.7 percent.

Table 2 compares the 13-year periodic growth per acre and for individual trees. There was no significant difference in per acre volume or basal area periodic annual growth, although the one-third treatment had the highest numerical growth rate. Individual tree DBH growth was significantly higher in the two-thirds thinning treatment, growing over 4.5 times faster than the unthinned control.

![Figure 1](image-url)  
*Figure 1—Volume per acre for interior live oak thinning treatments from 1998 through 2010.*
Table 2—13-year changes in periodic annual increment and per tree measurements (means with different letters are significantly different at the 0.05 level)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Vol. growth (cu.ft./ac/yr.)</th>
<th>BA growth (sq.ft./ac/yr.)</th>
<th>DBH growth (inches/tree/yr.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>59.9</td>
<td>1.3</td>
<td>0.03 A</td>
</tr>
<tr>
<td>Thin 1/3</td>
<td>78.5</td>
<td>1.4</td>
<td>0.08 AB</td>
</tr>
<tr>
<td>Thin 2/3</td>
<td>51.7</td>
<td>1.2</td>
<td>0.14 B</td>
</tr>
<tr>
<td>Significance</td>
<td>N.S.</td>
<td>N.S.</td>
<td>Sign. 0.05</td>
</tr>
</tbody>
</table>

**Overstory and understory crown cover and sprout growth**

Figure 3 shows the overstory and understory crown cover after 13 years. The overstory cover was significantly affected by thinning intensity, and the understory cover was significantly affected by the stump herbicide treatment. Stump herbicide treatment did not affect the overstory cover, except for the two-thirds thinning, which had a 20 percent greater canopy cover when the stump were treated. The amount of understory cover was not affected by the thinning intensity. Table 3 shows the effect of thinning on sprout height and cover. The treated stumps had smaller canopy cover and very short sprout heights. The untreated stumps had sprouts of 1.83 to 2.44 m (6 to 8 ft) in height, and a cover of 12 to 16 percent, showing that thinning without stump treatment results in a significant ladder fuel and high fire risk, while thinning with sprout control had reduced fire risk.
Figure 3—Overstory and understory canopy cover in 2010 by thinning and stump treatments.

Table 3—13-year sprout height and understory canopy cover by thinning treatment

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Sprout height (ft.)</th>
<th>Sprout cover (pct.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thin 2/3 basal area</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No sprout control</td>
<td>8.4</td>
<td>16 pct.</td>
</tr>
<tr>
<td>Sprout control</td>
<td>&lt;1</td>
<td>4 pct.</td>
</tr>
<tr>
<td>Thin 1/3 basal area</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No sprout control</td>
<td>6.1</td>
<td>12 pct.</td>
</tr>
<tr>
<td>Sprout control</td>
<td>&lt;1</td>
<td>4 pct.</td>
</tr>
<tr>
<td>Significance</td>
<td>Sprout control sign. at 0.01;</td>
<td>Sprout control sign. at 0.01;</td>
</tr>
<tr>
<td></td>
<td>thin intensity N.S.</td>
<td>thin intensity N.S.</td>
</tr>
</tbody>
</table>

**Acorn production**

Figure 4 shows the probability of acorn production for the unthinned control and the two thinning intensities. For the 3 years sampled (2, 3 and 4 years after the thinning), there was a significant treatment effect from the thinning on the probability that a tree would have acorns (Class 2, 3 or 4). It will be necessary in future studies to determine if this has an impact on per acre acorn production, since thinning reduces the number of trees per acre and canopy cover.
Discussion
This study was useful in describing changes in interior live oak stand structure after thinning and sprout control. Over the 13 years in the study, there were no significant stand level growth differences from the thinning treatments, although the one-third thinning level had reached the same per acre volume level as the unthinned control.

The most significant stand level thinning impact is in individual tree growth. The two-thirds thinned stands were growing on average over four times greater than the unthinned stand. Over time, we would expect the thinned stands to have larger individual trees, that approach the unthinned stand in canopy cover and per acre volume. The thinning also significantly increased the probability of acorn production.

This study was designed to evaluate if thinning reduced the fire risk for landowners with interior live oak. This showed that thinning alone resulted in significant resprouting of the residual stumps, causing high risk of catastrophic wildfire from fuel ladders. Herbicide treatment of the residual stumps maintained a very low level of understory fuel ladders. It will be important for any fuel thinning to reduce the overstory crown cover, as well as treating the stumps in order to reduce fire risk.

Acknowledgments
We wish to thank the owners of the Wyle Ranch in North Fork, and the Coarsegold RCD for cooperating in this study.
References
Using Avian Focal Species to Inform Rangeland Management in California Oak Woodland

Alicia D. Young, Breanna Owens, Melissa Odell, Corey Shake, Wendell Gilgert, and Geoffrey R. Geupel

Abstract

Biological knowledge about bird focal species may be used to inform planning, habitat management, and restoration efforts, with the assumption that the implementation of these species-based recommendations will maintain and enhance healthy functioning habitats and the ecosystems services they provide. Point Blue Conservation Science in collaboration with the Natural Resources Conservation Service (NRCS) state office in California recently formed the Rangeland Watershed Initiative (RWI) to restore ecosystem function by working with ranchers on privately held hardwood rangelands in the foothill regions that surround California’s Great Central Valley. An integral component of RWI is to place partner biologists in NRCS offices in key communities to assist in the planning, monitoring and evaluation of farm bill conservation practices. Partner biologists use the Oak Woodland Bird Conservation Plan and the focal species described within to assist ranchers in developing NRCS conservation plans and evaluating the prescribed practices in an adaptive management context. We present examples of how bird focal species are used to prescribe and evaluate rangeland conservation practices in California’s Oak woodland.

Key words: adaptive management, bird conservation plan, effectiveness monitoring, focal species, rangeland health

Introduction

Among terrestrial wildlife, birds are recognized as an excellent indicators of habitat condition (Askins 2000, Koskimies 1989, Martin 1995). Because they are diverse, found in almost every habitat type, are high on the trophic system, sensitive to environmental change, and relatively cost-effective to monitor, California Partners in Flight (PIF) has used suites of bird focal species to developed habitat-based conservation plans for seven major habitat types in California (Chase and Geupel 2005). Each suite of species’ habitat requirements defines a spectrum of spatial attributes, habitat characteristics, and management regimes representative of a healthy habitat.

Oak woodlands cover 13 percent of California (approximately 2.8 million hectares, or 7 million acres). Over eighty percent of these lands are privately owned and primarily managed as working ranches (CDF 2003). California’s oak woodlands are a vital landscape providing habitat for over 330 species of birds, mammals, reptiles and amphibians during some stage of their life-cycle (Barrett 1980, Block and Morrison 1998, Verner 1980). With rapid land conversion to orchards (primarily almonds), vineyards, and housing, oak woodlands are one of the most threatened habitats in California. Recent collaborations between ranchers, conservation groups,
and public agencies seek to conserve oak woodlands for wildlife, people and the ecosystem services they provide (for example, California Rangeland Conservation Coalition).

The California Oak Woodland Bird Conservation Plan was developed to promote the conservation and restoration of oak woodland habitat to support long-term viability and recovery of both bird and other native populations of wildlife (CalPIF 2002). The focal species in the plan were identified to guide and prescribe specific habitat management recommendations for use by landowners, managers and practitioners to help maintain and improve the health of hardwood rangelands.

Point Blue Conservation Science’s (Point Blue) Working Lands Program recognizes agriculture’s significant role in long-term environmental stewardship and is making efforts to increase direct engagement with farmers and ranchers to better understand their needs and challenges while improving overall landscape productivity and health. Ecologically functional rangelands provide for water storage and stable nutrient cycles, in addition to supporting livestock and wildlife.

In this paper we focus on adaptive management decision-making in hardwood rangelands based on data collected on breeding oak woodland focal bird species. We provide examples of how this information can be used for planning and evaluation in a NRCS planning context on hardwood rangelands in California.

Rangeland watershed initiative

Point Blue formally partnered with the U.S. Department of Agriculture’s Natural Resource Conservation Service (NRCS) in 2011 to implement the Rangeland Watershed Initiative (RWI), with the goal of increasing the NRCS’s biological technical capacity and implementation of conservation and wildlife related practices. NRCS works primarily with farmers, ranchers, and forestland owners to voluntarily address resource concerns on privately held land using Farm Bill conservation programs to provide monetary incentives. To date, Point Blue has placed nine cost-shared (public—and privately funded) RWI partner biologists in NRCS field offices throughout California’s Great Central Valley and beyond. The biologists provide “value-added” assistance to the NRCS interdisciplinary conservation planning team, by adding specialized fish and wildlife knowledge and habitat management skills to the conservation planning process. In addition, partner biologists provide the monitoring and evaluation component of the NRCS planning process, which is critical for effective adaptive management. Partner biologists are based in NRCS field offices and live in the surrounding communities that the field offices serve; building community relations and landowner trust.

Partner biologists spend, on average, 25 percent of their time in the collection of bird, soil and vegetation data as part of the RWI integrated monitoring program. This program has been designed to evaluate conservation practice effectiveness, inform landowner decision-making and measure ecological function. Participation by ranchers is voluntary and thus far includes 34 properties in the Great Central Valley foothills region. Partner biologists make regular visits to the property using relatively easy and transparent monitoring protocols.

The main objectives of the RWI monitoring and evaluation program include:

- Understanding of the ranch operation, wildlife, and ecosystem through repeated observations.
- Provide ranchers and other stewards of the land with information and tools to monitor ecological function and evaluate prescribed practices.
• Evaluate spatial variation in ecological function within and across rangelands and the relationship to historic and current management practices.
• Establish a baseline that can be used to understand how ecological function on rangelands changes over time in relation to conservation management implementation.

In order to meet these objectives, five key metrics were identified related to ecological function:

1. Wildlife use and habitat condition. Bird richness and abundance will be used as indicators.
2. Vegetation. Plants convert sunlight into the energy for people, wildlife, and animal agricultural production. We will conduct both qualitative and quantitative assessments of vegetation cover and composition of species and functional groups across the rangelands.
3. Water infiltration. Water infiltration is the process of water entering the soil, and is integral to the ability of rangelands to support life.
4. Soil compaction. Soil compaction is a measure of how tightly soil particles are packed together. Compacted soils have reduced pore space for water infiltration, water retention, root growth, soil aeration, and seedling germination.
5. Soil carbon. Soil organic matter is a primary organic source of carbon in soil, has a high capacity for storing water, and plays a key role in soil stabilization.

Using knowledge of oak woodland focal species habitat and life history requirements paired with inventories and/or results from point count surveys, partner biologists contribute to the development of conservation plans throughout the NRCS nine-step planning process (table 1). The planning process is a collaborative effort that includes NRCS staff, and landowner (or lessee) input and management goals.

<table>
<thead>
<tr>
<th>NRCS conservation planning process</th>
<th>RWI partner biologist contribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Step 1. Identify problem and opportunities</td>
<td>Bird presence/absence from current surveys or online resources</td>
</tr>
<tr>
<td>Step 2. Determine goals and objectives</td>
<td>Landowner/lessee interview</td>
</tr>
<tr>
<td>Step 3. Inventory resources</td>
<td>Current bird surveys</td>
</tr>
<tr>
<td>Step 4. Analyze resource data</td>
<td></td>
</tr>
<tr>
<td>Step 5. Formulate alternatives</td>
<td>Prescribe practices based on multi-species benefits and desired future outcomes, using California PIF Bird Conservation Plans, focal species accounts, and other current resources</td>
</tr>
<tr>
<td>Step 6. Evaluate alternatives</td>
<td></td>
</tr>
<tr>
<td>Step 7. Implement the plan</td>
<td></td>
</tr>
<tr>
<td>Step 8. Monitor and evaluate</td>
<td>Effectiveness monitoring: future bird surveys, including focal species presence/absence, to evaluate the plan and modify as needed</td>
</tr>
<tr>
<td>Step 9. Re-plan or adjust the plan</td>
<td></td>
</tr>
</tbody>
</table>
Study area

The RWI core focus is on hardwood rangeland habitats in the Central Valley foothills of California. While these rangelands are comprised of multiple habitat types, including riparian, grassland, and oak savannah, the vast majority is blue oak (Quercus douglasii) woodland. The RWI partner biologists are located strategically in NRCS offices to work with those ranchers and producers that own or manage lands in the Sierra Nevada and Coastal Range foothills surrounding the Central Valley (fig. 1). Participants in the RWI through 2014 included ranches in eight valley foothill counties, representing 34 properties and 29 landowners/lessees. Size of properties ranged from 89 to 5260 hectares, and ranged from properties surrounded by intensive non-agriculture to those that form part of an extensive oak woodland habitat.

Figure 1—NRCS field office location of Point Blue Rangeland Watershed Initiative partner biologists.

While blue oak woodlands currently cover over 1.2 million hectares (3 million acres) in California, they are facing increasing threats by conversion and regeneration problems (Bolsinger 1988, Muick and Bartolome 1987). There is no one clear answer as to why regeneration rates are poor. Numerous causes have been cited, including increased depredation by animals and insects, associated vegetation changes, incompatible livestock grazing, fire suppression, and climate change. No matter the cause, private blue oak woodland owners will need to be part of the solution for improving oak regeneration and rangeland habitat health. The RWI objectives, aimed at the ultimate goal of improved rangeland health, simultaneously promote economic sustainability of current and future generations of ranchers while continuing to provide valuable contiguous habitat for wildlife.
Oak woodland focal species

The California PIF approach to focal species selection for the each of the seven habitat-based Bird Conservation Plans was to select a suite of species whose requirement, as a group, “define different spatial attributes, habitat characteristics and management regimes representative of a healthy system” (Chase and Geupel 2005). In order to include species with different vegetative and habitat element requirements to complete their life cycle, species were chosen to include as many of the following criteria as possible:

- Use a given habitat type as their primary breeding habitat.
- Breeding requirements represent a full range of successional stages.
- Have a special management status or have experienced a reduction from their historical breeding range.
- Commonly breed throughout a given habitat type, allowing adequate sample size for statistical comparisons, and therefore, the ability to assess response to management or habitat changes.

Following these criteria, the various habitat focal species groups tend to include species at risk, those species considered umbrella or keystone, and species that are common and abundant for a given habitat.

The California PIF Oak Woodland Bird Conservation Plan (CalPIF 2002) recognizes 22 bird species as focal species. These species represent an array of life cycle requirements (table 2), and require a variety of habitat elements within oak woodlands (table 3). Bioregionally-based population targets have been developed for several of the oak woodland focal species. These numerical targets were based on all available data and use the highest recorded densities for that species for the bioregion. As part of the RWI, subsets of these species are used—based on geographic location, specificity to blue oak woodlands, and conformity to standardized monitoring protocols—to evaluate the health of hardwood rangelands and guide habitat management recommendations.
Table 2—Oak woodland focal species in California, with information on their use of acorns, nesting substrate, general foraging habitat in oak woodlands, and whether the species is endemic to California (reproduced from CalPIF 2002)

<table>
<thead>
<tr>
<th>Species</th>
<th>Consumes acorns?</th>
<th>Caches acorns?</th>
<th>Nest</th>
<th>Foraging habitat in oak woodlands</th>
<th>Migratory status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood Duck (Aix sponsa)</td>
<td>Yes</td>
<td></td>
<td>2°</td>
<td>Cavity</td>
<td>Wooded Streams</td>
</tr>
<tr>
<td>Red-shouldered Hawk (Buteo lineatus)</td>
<td></td>
<td></td>
<td></td>
<td>Platform</td>
<td>Woodlands</td>
</tr>
<tr>
<td>Wild Turkey (Meleagris gallopavo)</td>
<td></td>
<td></td>
<td></td>
<td>Ground</td>
<td>Woodlands</td>
</tr>
<tr>
<td>Band-tailed Pigeon (Columbia fasciata)</td>
<td>Yes</td>
<td></td>
<td></td>
<td>Ground</td>
<td>Woodlands</td>
</tr>
<tr>
<td>California Quail (Callipepla californica)</td>
<td>Yes</td>
<td></td>
<td></td>
<td>Ground</td>
<td>Woodland-shrub</td>
</tr>
<tr>
<td>Northern Pygmy Owl (Glaucidium gnoma)</td>
<td></td>
<td></td>
<td>2°</td>
<td>Cavity</td>
<td>Woodlands</td>
</tr>
<tr>
<td>Acorn Woodpecker (Melanerpes lewis)</td>
<td>Yes</td>
<td>Tree, many</td>
<td>1°</td>
<td>Cavity</td>
<td>Woodlands</td>
</tr>
<tr>
<td>Lewis’s Woodpecker (Melanerpes lewis)</td>
<td>Yes</td>
<td></td>
<td>1°</td>
<td>Cavity</td>
<td>Woodlands</td>
</tr>
<tr>
<td>Nuttall’s Woodpecker (Picoides nuttallii)</td>
<td>Yes</td>
<td></td>
<td>1°</td>
<td>Cavity</td>
<td>Woodlands</td>
</tr>
<tr>
<td>Ash-throated Flycatcher (Myiarchus cinerascens)</td>
<td>Yes</td>
<td></td>
<td>2°</td>
<td>Cavity</td>
<td>Open Woodlands</td>
</tr>
<tr>
<td>Western Scrub-Jay (Aphelocoma californica)</td>
<td>Yes</td>
<td>Ground, many</td>
<td></td>
<td>Cup</td>
<td>Woodland-Scrub</td>
</tr>
<tr>
<td>Yellow-billed Magpie (Pica nuttalli)</td>
<td>Yes</td>
<td>Ground, few</td>
<td></td>
<td>Cup</td>
<td>Woodlands</td>
</tr>
<tr>
<td>Oak Titmouse (Baeolophus inornatus)</td>
<td>Yes</td>
<td>Tree, few</td>
<td>2°</td>
<td>Cavity</td>
<td>Woodlands</td>
</tr>
<tr>
<td>White-breasted Nuthatch (Sitta carolinensis)</td>
<td>Yes</td>
<td>Tree, few</td>
<td>2°</td>
<td>Cavity</td>
<td>Woodlands</td>
</tr>
<tr>
<td>Bewick’s Wren (Thryomanes bewickii)</td>
<td></td>
<td></td>
<td></td>
<td>2° Cavity</td>
<td>Woodland-Scrub</td>
</tr>
<tr>
<td>Blue-gray Gnatcatcher (Polioptila caerulea)</td>
<td></td>
<td></td>
<td></td>
<td>Cup</td>
<td>Woodlands</td>
</tr>
<tr>
<td>Western Bluebird (Sialia Mexicana)</td>
<td></td>
<td></td>
<td>2°</td>
<td>Cavity</td>
<td>Open Woodlands</td>
</tr>
<tr>
<td>California Thrasher (Toxostoma redivivum)</td>
<td></td>
<td></td>
<td></td>
<td>Cup</td>
<td>Woodland-Scrub</td>
</tr>
<tr>
<td>European Starling (Sturnus vulgaris) (I)</td>
<td></td>
<td></td>
<td>2°</td>
<td>Cavity</td>
<td>Agriculture edge</td>
</tr>
<tr>
<td>Hutton’s Vireo (Vireo huttoni)</td>
<td></td>
<td></td>
<td></td>
<td>Cup</td>
<td>Woodlands</td>
</tr>
<tr>
<td>California Towhee (Pipilo crissalis)</td>
<td></td>
<td></td>
<td></td>
<td>Cup</td>
<td>Woodland-Scrub</td>
</tr>
<tr>
<td>Lark Sparrow (Chondestes grammacus)</td>
<td></td>
<td></td>
<td></td>
<td>Ground</td>
<td>Grass-Woodland</td>
</tr>
</tbody>
</table>

* Cavity-nesting species differ as to whether they excavate their own cavities (1° cavity nester) or they take over disused nests or naturally occurring cavities (2° cavity nester).

b (I) denotes an introduced, nonnative species.

c Also occurs in Baja California, Mexico.
d Also occurs in Baja California, Mexico, and extreme southern Oregon.
**Table 3— Essential habitat elements for focal species, based on California Wildlife habitat Relationships System Version 7.0 (reproduced from CalPIF 2002)**

<table>
<thead>
<tr>
<th>Focal Species</th>
<th>Acorns</th>
<th>Cavities</th>
<th>Trees</th>
<th>Shrub</th>
<th>Grass/ herb</th>
<th>Snags</th>
<th>Brush piles</th>
<th>Water/ riparian</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood Duck (<em>Aix sponsa</em>)</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>California Quail (<em>Callipepla californica</em>)</td>
<td>X</td>
<td>X</td>
<td></td>
<td>XX</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red-shouldered Hawk (<em>Buteo lineatus</em>)</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern Pygmy Owl (<em>Glaucidium gnoma</em>)</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Band-tailed Pigeon (<em>Columbia fasciata</em>)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acorn Woodpecker (<em>Melanerpes lewis</em>)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lewis’s Woodpecker (<em>Melanerpes lewis</em>)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nuttall’s Woodpecker (<em>Picoides nuttallii</em>)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ash-throated Flycatcher (<em>Myiarchus cinerascens</em>)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Western Scrub-Jay (<em>Aphelocoma californica</em>)</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow-billed Magpie (<em>Pica nuttali</em>)</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oak Titmouse (<em>Baeolophus inornatus</em>)</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-breasted Nuthatch (<em>Sitta carolinensis</em>)</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bewick’s Wren (<em>Thryomanes bewickii</em>)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue-gray Gnatcatcher (<em>Polioptila caerulea</em>)</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>California Thrasher (<em>Toxostoma redivivum</em>)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Western Bluebird (<em>Sialia Mexicana</em>)</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hutton’s Vireo (<em>Vireo huttoni</em>)</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lark Sparrow (<em>Chondestes grammacus</em>)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>California Towhee (<em>Pipilo crissalis</em>)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*a* Includes selected elements classified by CWHR as “essential” or “secondary essential”.
Methods

The RWI follows standardized avian survey protocols to collect information on ranch-specific bird populations (Ralph and others 1993). The most commonly utilized method was variable radius point counts. Point counts can used to detect changes in local (and regional) bird populations from year to year, including species composition differences among habitat types, species abundance, and local habitat relationships.

Point count surveys

Point count surveys followed guidelines described in Ralph and others (1995). In summary, we sampled each point count location for 5 minutes, and placed detections within one of six bins based on the distance from the observer to the initial detection of that bird. The distance bins were defined in meters as follows: 0 to 10, 10 to 20, 20 to 30, 30 to 50, 50 to 100, and greater than 100. All birds detected were recorded and initial detection cue (song, visual, call or wing noise) for each individual was also recorded. Counts were conducted from local sunrise until approximately 3 hours after sunrise (in other words, peak singing hours), and did not occur in inclement weather. All point count stations were located at least 200 m apart and were surveyed at least twice during the peak months of the breeding season (April to early July). Timing of surveys varied by elevation, latitude, and seasonal conditions throughout the RWI study area.

Analysis: point count data

Data analysis was restricted to the subset of California PIF oak woodland focal species encountered. In addition, we excluded all birds detected at greater than 50 m from the observer (to avoid observer biases), and species flying over the sampling locations but not actively using the habitat. The indices of bird species richness were defined as the total number of species detected per point across visits in one year. The indices of bird abundance were defined as the mean number of individuals detected per point per visit in one year – the same as the California PIF definition of species population targets (CalPIF 2002).

Results

Point Blue has developed several tools and products to help determine likelihood of focal species presence and communicate rangeland habitat management recommendations to landowners and managers. The California Avian Data Center (CADC) (http://data.prbo.org/cadc2/) is the online regional node of the Avian Knowledge Network (http://www.avianknowledge.net/). CADC integrates data on birds and ecosystems to improve conservation outcomes today and in the future. Online tools and information include links to the California PIF Bird Conservation Plans, and interactive maps to explore: avian data summaries, modeling of bird distribution response to climate change, and predicted current bird focal species occupancy in the Central Valley region.
Another tool available to landowners and land managers is the Oak Woodland Healthy Habitat Guide (fig. 2). This guide provides a brief overview of the focal species concept, photographs and descriptions of oak woodland bird species, and tips for improving or maintaining habitat features and vegetative layers. These habitat recommendations are not ranch-specific, but widely accepted as beneficial habitat improvements and management activities and can be used for planning as required by NRCS farm bill program implementation. They include:

- Retain dead or decaying trees and snags to provide cavity and granary tree locations.
- Restore understory vegetative layers and habitat elements by retaining downed woody material, creating brush piles, and encouraging shrub regeneration.
- Foster the regeneration of blue oaks by protecting oak seedlings and being cognizant of grazing timing and intensity in areas of dense seedlings.
- Adjust grazing scheme from year to year to avoid grazing the same field at the same time of year over and over.
- Control noxious and invasive weeds and encourage the distribution of native perennial grasses.
- Manage for a mosaic of tree canopy cover, including patches of over 40% canopy.
- Limit tree thinning to those oaks that are undersized and poor acorn producers.

![Oak Woodland Healthy Habitat Guide](image-url)
For those rangelands where we have collected focal species point count data, we can provide ranch-specific information on focal species presence, abundance, and distribution across the property. Habitat recommendations are tailored to the goals and needs of the land manager and specific attributes of the rangeland.

Figure 3 is an example of a subset of focal species abundance results from a ranch in the Sacramento Valley. It includes, when available, the focal species population targets provided by the California PIF Oak Woodland Bird Conservation Plan. In this example, the species associated with the canopy, mid-canopy, and understory layer are present, and for the most part, similar in abundance to the PIF population targets. However, focal species associated with the shrub layer are in very low numbers or absent—a strong indication that the shrub layer is a limiting factor for birds at this ranch. While this summary of ranch-wide bird populations is informative, stratified results (often by field) of species richness, overlaid on a distribution map, allowed us to identify specific areas to focus upon (fig. 4). For example, areas or fields where focal species richness was low were given habitat improvement recommendations, based on the habitat-specific focal species that were missing from survey results (in other words, shrub associated species). Conversely, habitat maintenance was encouraged in areas where focal species richness was high. By using a distribution map, additional factors such as soil type, slope, aspect, and adjacent habitats, were also taken into account when management recommendations were suggested, and habitat improvements could be better prioritized and visualized by the ranch manager.

4-letter bird species codes: YBMA = Yellow-billed Magpie, NUWO = Nuttall’s Woodpecker, ACWO = Acorn Woodpecker, OATI = Oak Titmouse, WEBL = Western Bluebird, HUVI = Hutton’s Vireo, BGGN = Blue-gray Gnatcatcher, WESJ = Western Scrub Jay, LASP = Lark Sparrow, CAQU = California Quail.

1 No California PIF population target available.
2 No detections at XXX Ranch.

Figure 3—Oak Woodland bird focal species average bird abundance index (± 1 SE) with nesting layer at a ranch participating in the Rangeland Watershed Initiative and California PIF population targets.
Conclusions

California Partner in Flight focal species were selected to represent species whose requirements define different spatial attributes, habitat characteristics, and management regimes representative of a healthy oak woodland ecosystem. Biological knowledge about the life characteristics and habitat requirements of focal species can be used to inform habitat management and restoration efforts, while maintaining and enhancing the overall ecological community. As an integral part of the RWI, avian focal species surveys are used to inform range management in oak woodlands. Point Blue’s partnership with the Natural Resource Conservation Service allows partner biologists located in NRCS field offices to effectively interact with managers of privately-held oak woodlands throughout California on a regular basis, as well as provide technical assistance, and monitor progress of habitat improvement projects. By incorporating the goals of the land managers and property-specific attributes and limitations, these recommendations are geographically unique to the property and help to achieve sustainability for the future of ranching, oak woodland habitats and the species that inhabit them.
References


Growth and Management of a Remnant Stand of Engelmann Oak at Los Angeles County Arboretum & Botanic Garden

James E. Henrich

Abstract
Commercial, residential and ranch development combined with pressures from grazing, foraging and pests have decimated Engelmann oak (Quercus engelmannii) populations, resulting in this species being designated as vulnerable by the International Union for Conservation of Nature Red List of Threatened Species. Los Angeles County Arboretum and Botanic Garden has the largest population of Engelmann oak in Los Angeles County and therefore has a responsibility to conserve and manage it, ensuring the grove’s long-term survival. To achieve this goal, the arboretum has adopted a four-phase management program that includes the following: weed abatement; fostering successful establishment of natural recruits; supplementing natural recruits with nursery-grown saplings from field-collected acorns; and using precipitation and temperature data to guide the frequency and quantity of supplemental irrigation during winter, spring and late summer months. History of the plight of Engelmann oaks, observations about the natural history of the arboretum’s population, an overview of our management program, and conservation progress to date are presented.

Key words: conservation, Engelmann oak, management, natural recruits, Quercus engelmannii

Introduction
Geological data indicates the historical distribution of Engelmann oak (Quercus engelmannii) was from western Arizona to the Pacific Coast south to northern Mexico and west to northern Baja California. Desertification resulting in the Mojave and Sonoran deserts restricted populations to western California south of the San Gabriel Mountains. Current populations exist in the Black Mountains of San Diego County (93 percent), the Santa Rosa Plateau of Riverside County (6 percent), Orange County (0.5 percent), and Los Angeles County (less than 0.1 percent). (Scott 1991).

This species typically occurs on 0 to 10 degree south-facing slopes where water drains rapidly from the topsoil/hardpan interface. The soil can be deep loamy-clay or shallow and rocky, often associated with a source of summer water from springs or streams. They perform best with a minimum of 38.1 cm (15 inches) of annual precipitation, and limited exposure to frost and extreme summer heat. It often occurs as a co-dominant species with coast live oak (Q. agrifolia).

Several factors have been responsible for declining populations of Engelmann oak (Pavlik and others 1991). The climate of southern California has changed substantially during the last 2 centuries. It has been conjectured that “our” climate was historically much more moderate with summer monsoonal events and lower summer temperatures, all conducive to a healthier environment for this species. Concurrent with expansion of civilization, predation from domesticated ungulates,
rodents and insects have further reduced the reproductive potential. Over-grazing has contributed to soil compaction and changes in understory vegetation. Expansion of farmland, residential, and commercial development has resulted in loss of individuals and entire populations, as well as, population fragmentation. Although wind pollinated, the ever increasing distance between fragmented populations reduces successful pollination.

Dwindling populations of Engelmann oaks in the state of California have warranted the designation of vulnerable for Engelmann oak on the IUCN Red List (Nixon and others 1998). Throughout most of its range, it is at best, only secondarily protected, especially on military sites in the Black Mountains of San Diego County. The Santa Rosa Plateau in Riverside County is the only large site that is actively managed, by The Nature Conservancy. This species is virtually unprotected or managed elsewhere throughout the state, except for the small population located at Los Angeles County Arboretum.

Harvesting viable Engelmann oak acorns is challenging at best. Engelmann oak is a masting species on a 3-year cycle. This means acorns are produced in abundance every 3 years with limited numbers produced during the 2 other years. Typical predators include squirrels and at least three species of beetles. The current cycle for our trees is 2010, 2013 and should be again in 2016. It is easy to find viable acorns during mast years because of the abundance of acorns, more than can be predated. However, nearly all acorns are predated during non-mast years. Acorns typically mature and begin falling from the trees in mid-September, continuing into December. It is possible to harvest some viable acorns for ex situ production each year, but the greatest probability for natural recruit germination occurs only during mast years.

The greatest concentration of natural recruits occurs within the drip line of mature trees. This zone would typically contain the greatest amount of moisture and provides protection from full sun. Greater rodent predation is reported within the canopy zone of trees. Areas outside of the drip line typically have greater exposure to sun; soils are drier and result in increased attrition. Saplings growing in the nursery and those planted in the landscape tolerate full sun if planted in winter to early spring, allowing time for root establishment, and provided with adequate water.

Conservation management plan

The arboretum’s conservation management plan emphasizes the following goals: manage the exotic grasses and forbs; establish a replacement population of trees by preserving natural recruits and planting nursery-grown saplings; use temperature and precipitation data from within the grove to guide frequency and quantity of supplemental irrigation during winter, spring, and late summer. Additional goals include: enhancing the overall health of the mature trees by monitoring environmental factors and pathogens and taking corrective action as needed; introduce sympatric native shrubs, grasses, and forbs to restore the habitat to a natural ecosystem; and educate the public about the plight of Engelmann oaks and the arboretum’s effort to preserve its population of trees.

Methodology

One facet of our program entails identifying locations of natural recruits with irrigation flags that act as a visual cue during mechanical control of exotic ground-plane vegetation. The second facet involves harvesting viable acorns, typically during mast years and propagating them in our nursery. The highest probability of
distinguishing viable from nonviable acorns is ascertained by performing the float test—acorns that float are discarded and those that sink are planted (immature endosperm or predation by insect larvae result in air spaces within the acorns making they buoyant). Saplings are planted in March and April after sowing acorns in November or the following late fall and winter after temperatures have dropped and the ground has become saturated by rain or irrigation. Each seedling is provided with an open-mesh poultry wire cage, an accession label (accession number links the lineage of the seedling with the parent tree), three wire stakes to secure the cage in place and a band of colorful flagging tape on the top of the cage. Cages provide protection from mechanical damage from foot traffic and line trimmers used to control ground-plane exotic weeds. Irrigate monthly if in open areas or on the scheme for mature trees when planted within the grove and abate weeds immediately around the cages.

The minimum precipitation for healthy Engelmann oak tree growth is 381 mm (15 inches), an annual amount that is now atypical for this species throughout most of southern California. The conservation management plan mandates supplemental monthly, deep, thorough irrigation from December through May to ultimately achieve more than the minimum annual precipitation needs. Winter precipitation is monitored, in addition to visible stress to the trees (change in leaf color, drooping branches, or defoliation) to determine when supplemental irrigation is needed. The goal is 508 to 635 mm (20 to 25 inches) of cumulative precipitation and supplemental irrigation. This greater volume of “precipitation” is sought because the soil depth is in general shallow, resting on a clay hardpan. All irrigation applications are many hours long, encouraging penetration through leaf litter and mulch to achieve thorough soil saturation. Extreme summer temperatures without monsoonal rains require one additional application of water in mid-August, coinciding with monsoonal rains in Riverside and San Diego Counties.

**In situ vs. ex situ management**

Management of saplings in situ is simple and straightforward. Irrigation flags are inserted into the ground next to each sapling, acting as a visual cue for inventory and weed abatement (fig. 1). The best time to spot seedlings is late winter into early spring when new leaves are most visible and weeds don’t yet obstruct them. Natural recruits collectively receive a single accession number with unique qualifier to distinguish each sapling. Irrigation follows the regime for mature trees. Weeds are manually removed from a 61 cm (24-inch) diameter circle around each sapling. String trimmers are used between seedlings to reduce weed growth to about 15.2 cm (6 inches).
2010 was a mast-year for the arboretum’s Engelmann oak population, resulting in an abundance of acorns. Approximately 3,600 natural recruits were identified and flagged in the grove between March and May of 2011. Only about 400 natural recruits remained in late 2013, an 88.9 percent attrition.

*Ex situ* management is more complex. Acorns are preferably collected directly from the parent tree. They are collected from the ground only under isolated trees. Each acorn lot is placed in a paper bag labeled with the female parent accession number and collection date. All acorns are subjected to the float test; only those that sink are dried and retained in the original bag; the ratio of sinkers to floaters is recorded on the paper bag and on a spreadsheet. Each lot is assigned a new accession number that references the parent tree accession. The paper bags are stored in a cooler at 4.4 °C (40 °F) until sowing in late November to early December.

Acorns are planted 2.5 cm (1 inch) deep in 17.8 cm (7 inch) single-cell cone-tainers™ provided with artificial medium (fig. 2). Each Cone-tainer™ is marked with a plastic label bearing the lot’s accession number, genus, and species, as well as female parentage (fig. 3). All trays are thoroughly watered and covered with a wire cage to exclude rodents. Germinated seedlings are counted monthly through June.
Figure 2—Nine-month-old seedlings in the nursery growing in Ray Leach “Cone-container”™ single cells.

Figure 3—Each sown acorn is marked with a plastic label bearing the lot’s accession number, genus, and species, as well as female parentage.
Germination occurs rapidly after sowing. Radicle development is the first growth activity, developing to pencil-dimensions and elongating to 12.7 to 15.2 cm (5 to 6 inches) (fig. 4). Few secondary roots are formed during the first growing season but become more abundant in ensuing months. Shoot development and emergence occurs as rapidly as 4 to 6 weeks, and will continue throughout an acorn population for up to 6 months when given adequate irrigation. Vegetative growth reaches 2.5 to 7.6 cm (1 to 3 inches) tall the first growing season before summer dormancy. Multiple shoots are common and damage to shoots or natural dieback often results in initiation of new shoots.

Figure 4—Radicle development is the first growth activity, developing to pencil-dimensions and elongating to 12.7 to 15.2 cm (5 to 6 inches).

Percent germination across all acorn lots from our site was recorded in 2014 after sowing in November 2013: 26.7 percent in February; 28.7 percent in March (55.4 percent cumulative); 11.5 percent in April (66.9 percent cumulative); 5.9 percent in May (72.8 percent cumulative); 0.5 percent from June to September (73.3 cumulative).

Each sapling is planted with a small metal tag bearing the following information: accession number (for example, 20130425*X; where “2013” represents the collection year, “0425” represents the seed lot designation and “X” is a unique qualifier number assigned to each sapling beginning with “1”), female parent tree (for example, LACA235), genus, species, common name, family, and natural distribution.

Saplings should be planted soon after germination, beginning as soon as 2 months, continuing through March or April. Resume planting the following rainfall season, from December through February and continue through March or April if necessary.
Resume planting the following December after first rainfall or irrigation, continuing as above. Saplings more than 18 months old typically have elongated tap roots or stunted tap roots, less than desirable for planting but definitely worth experimenting with to determine survivability.

The cultural program provided for *ex situ* saplings is critical for their establishment and survival to maturity. Holes are dug in moist soil to a depth that will accommodate the taproot. A sapling is inserted into the hole to a depth that matches both single-cell Cone-tainer™ planting mix and soil surfaces and held in place with one hand. The other hand is used to fill the planting hole halfway and water is poured into the hole to settle the soil. Soil is backfilled to the rim of the planting hole and water is applied at least two more times to completely saturate the new planting. Loosened soil around the sapling is compacted using fingertip pressure and the disturbed area is watered one more time. The wire-staked accession label is inserted into the ground adjacent to the seedling. A 7.6 cm (3 inch) diameter by 45.7 cm (18 inch) tall poultry-wire cage is placed over the seedling and label. Cages are secured with three 40.6 cm (16 inch) wire stakes (fig. 5). Six seedlings are planted per accession with the goal to establish one seedling per parent tree. Seedlings are planted in the vicinity of the female parent tree to simulate natural acorn dispersal. They are watered according to the regime for the mature trees unless planted outside the grove where there is no canopy. These exposed seedlings are watered monthly through the first two summer dormant seasons.

Weeds are removed primarily by hand from within the cages and out to a radius of 30.5 cm (12 inches). String trimmers are used to reduce weed growth to 15.2 cm (6 inches) tall between seedlings. Cutting weeds shorter than 15.2 cm can result in
damaging non-flagged seedlings. Cages are removed when the saplings are 0.6 to 0.9 m (2 to 3 ft) tall. Established saplings are mapped with typical survey equipment using geo-relational monuments that allows their exact placement within the landscape, from which maps can be generated.

**Conclusion**

Environmental, ecological, and human-influenced pressures have and continue to diminish and fragment *Q. engelmannii* populations. The greatly diminished distribution of Engelmann oaks in southern California prompted the IUCN to assign it a vulnerable status. The arboretum is fortunate to have the largest grove of Engelmann oaks in Los Angeles County and therefore has a responsibility to conserve and manage it, ensuring the grove’s long-term survival. A conservation management program has been implemented to guide the process. Results of this program include: concluding that supplemental irrigation is necessary to reduce leaf drop, and maintain health and vigor in the greater Los Angeles area; protecting natural recruits from mechanical damage increases survival rates; *ex situ* sapling production is very successful; and, vegetating with *ex situ* saplings is successful when planted during winter/spring precipitation periods, supplemental irrigation is applied, and protection is provided to prevent mechanical damage.

**References**


Thinning – a Tool for Restoration of California’s Southern Sierra Nevada Blue Oak Woodlands

Richard B. Standiford, Ralph L. Phillips, and Neil K. McDougald

Abstract
Fire frequency on a blue oak (Quercus douglasii) dominated rangeland in California’s southern Sierra Nevada foothills was approximately every 10 years until 1965, followed by a 30 year period of fire exclusion. This resulted in a dense tree overstory with small diameters, high crown cover, poor acorn and forage production, and limited complexity in vertical habitat structure. Tree thinning was evaluated as a treatment to restore pre-fire stand structure to these rangeland areas. Three thinning treatments were evaluated: (1) thin one-third of the standing tree basal area (resulting in a post-thin crown cover of 33 percent, 66 square feet per acre of tree basal area, and 160 trees per acre); (2) thin two-thirds of the standing tree basal area (resulting in a post-thin crown cover of 12 percent, 35 square feet per acre of basal area, and 100 trees per acre); and (3) control/no thin (crown cover of 55 percent, 97 square feet per acre of basal area, and 247 trees per acre). Acorn production was monitored annually since 1995, and showed that both thinning levels significantly increased the proportion of trees with acorns, although per acre acorn yields were not affected. Significant increases in forage production were documented with the heavier thinning intensity. Over 50 percent of the stumps in the thinned areas resprouted. There was significantly higher height growth in the two-thirds thinned area than the one-third thinned area. Periodic annual increment for the stands was not affected by thinning, although individual tree diameter growth was positively affected by the heaviest thinning. Crown cover of the heaviest thinning had grown back to the same level as the moderately thinned treatment after thirteen years. Thinning results in more open stands, with larger average tree size, larger individual crowns, and a larger proportion with acorns compared to unthinned controls.

Key words: blue oak, oak thinning

Introduction
Blue oak (Quercus douglasii) woodlands are widespread in California, occurring on 1.2 million hectares (3 million acres), representing the state’s largest oak woodland cover type (Waddell and Barrett 2005). Blue oak is found in California’s Sierra foothills, the southern Cascades, and the Coast range. The overstory tree canopy is predominantly in the oak genus (Quercus spp.) with an understory of exotic annual grasses and forbs, and occasional native perennial grasses (Bartolome 1987).

Since European settlement of California, blue oak woodlands have been managed primarily for livestock production (Huntsinger and others 1997). They also have high levels of biodiversity (Garrison 1996), and provide water, outdoor recreation and aesthetics. Over 90 percent of California’s blue oak woodlands are privately owned (Waddell and Barrett 2005).
At the landscape scale, oaks have been subject to land use change from land clearing, urbanization, and conversion to agriculture (Standiford 2001). At the stand level, blue oak had a trend of increasing canopy cover and basal area over the past 60 years (Holzman and Allen-Diaz 1991).

Fire has been part of California’s oak woodland ecosystem for the past several thousand years (Byrne and others 1991). It has been used as a management tool by Native Americans to improve game habitat and enhance desirable vegetation types (Anderson 2007). Ranchers also used fire to enhance forage production and maintain an open stand structure (Allen-Diaz and others 2007). McClaren and Bartolome (1989) showed a mean fire interval for central Sierra Nevada blue oak woodlands of 25.2 years between 1681 and 1848, 7.1 years from 1849 to 1948, and no fires from 1949 to the present. Standiford and others (2012) also showed a mean fire interval of 12.8 years from 1850 to 1965 in blue oak woodlands, with no fires since.

Increases in blue oak density from fire exclusion partially explains poor recruitment of the relatively shade intolerant blue oak (Bartolome and others 1987). Increasing density also impedes forage production for the silvopastoral management system practiced on blue oak woodlands (Frost and others 1997).

To date, there have been no studies on thinning in blue oak woodlands. There is a long-term study on thinning coastal oak woodlands (Bonner and others 2008). An individual tree growth model for blue oak has been developed from a statewide assessment, allowing thinning level impacts to be modeled (Standiford 1997).

This study was designed to evaluate a controlled thinning experiment to restore pre-fire stand structure in blue oak woodlands by evaluating the effect of different canopy densities on a range of vegetation variables over time.

**Methods**

The study area chosen was a relatively dense blue oak stand on a private ranch in the southern Sierra Nevada foothills near the town of California Hot Springs in Tulare County, California. The elevation averaged 838 m (2750 ft). The slopes ranged from 8 to 18 percent, with a northwest aspect. The area was seasonally grazed as part of a cow-calf livestock operation. The area averaged 90 square feet of basal area and 45 percent overstory canopy percent.

The study was designed to investigate two different thinning intensities (one-third and two-thirds of the basal area removed) against an untreated control. Nine 404.7 m² (one-tenth ac) plots were established in the study area and complete data was taken on tree cover, basal area, volume and number of stems. The three thinning treatments were assigned to the nine plots in a randomized, complete plot design.

Three plots were thinned to one-third of their original basal area, three plots were thinned to two-thirds of their original basal area, and the remaining three plots were untreated controls. As part of the thinning design, trees were felled with a stump height of 15.24 cm (0.5 ft) in the six plots with thinning treatments. The trees were randomly selected to meet the post-thinning basal area goals. Table 1 gives the summary statistics for the nine thinning blocks immediately following treatment in the fall of 1995.
Acorn production, stump sprouts, forage composition, and forage yields were evaluated in each study block. Individual tree height, diameter at breast height (1.37 m, DBH) and crown radius in two directions were measured. Merchantable wood volumes were calculated (Pillsbury and Kirkley 1984), as well as crown cover percent. The study area excluded livestock with electric fencing for the duration of the study. It was accessible to deer and rodents.

**Results**

**Forage production and composition**

Forage yields in total pounds per acre were sampled in the summer of 1997, 1998 and 1999 (2, 3 and 4 years after the thinning). Figure 1 shows the trend of higher forage yield as thinning intensity increased for each year sampled. The two-thirds thinning treatment had significantly higher production than the control in two of the three years. The one-third thinning level was not significantly different than the control.

Point counts were taken to evaluate understory vegetation cover at the genus level. The only significant treatment effect was the percent of bare soil the year after thinning (12 percent bare soil in the two-thirds treatment, versus 3 percent in the one-third treatment and 0 in the control). This effect disappeared by the second year after thinning. There were no significant thinning effects on forage composition.
Stump sprouting

Figures 2 and 3 show the percent of stumps with living sprouts and average sprout height. There was a significant sprouting percent difference by treatment in only 1 year out of 9. After 7 years, the proportion of stumps with living sprouts decreased dramatically due to the high levels of stem girdling by rodents, resulting from the high thatch levels in the study area because of grazing exclusion.

The two-thirds thinning treatment has a general trend of increased sprout height that was significant in 4 of the first 6 years after thinning. High mortality rates from rodent girdling resulted in non-significance in the last three measurements.

Acorn production

Acorn production was evaluated on all residual trees using the visual estimation methodology described by Graves (1980). All trees were placed into one of the four classes described by Graves (Class 1 = no acorns; Class 2 = acorns visible on close exam; Class 3 = acorns readily visible, don't cover entire tree; Class 4 = acorns readily visible, cover entire tree). Figure 4 shows the proportion of trees with acorns (Classes 2, 3 or 4). There was a significant effect from the thinning treatment on the proportion of trees with acorns in 5 of the 7 years surveyed.

To test if there was a significant effect on the total production of acorns from the thinning treatments, the expansion factor described by Graves (1980) was applied to each tree (Class 1 = 0 pounds; Class 2 = 0.1 pounds of acorns per 10 sq. ft. canopy; Class 3 = 0.7 pounds per 10 sq. ft. canopy; Class 4 = 2.3 pounds per 10 sq. ft. canopy). Figure 5 shows that per acre acorn production was not significantly affected by the thinning treatment.
Figure 2—Proportion of stumps with living sprouts for two thinning treatments. N.S. indicates not significant at 0.05 level, and Sign. indicates significant at 0.05 level.

Figure 3—Sprout height for two thinning treatments. N.S. indicates not significant at 0.05 level, and Sign. indicates significant at either the 0.01 or 0.05 level.
Stand and tree growth and development

Crown cover, merchantable wood volume per acre, and individual tree growth was evaluated over the 13 years of the study. Table 2 below shows the general results.
Periodic volume and crown growth at the stand level was not significantly affected by the thinning treatment. Only individual tree diameter growth showed a significant increase.

Table 2—13-year changes in periodic annual increment and per tree measurements (means with different letters are significantly different at the 0.05 level)

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Volume (cu. ft./ac/yr.)</th>
<th>Crown cover incr. (pct./yr.)</th>
<th>Mean DBH incr. (in./tree/yr.)</th>
<th>Mean ht. incr. (ft./tree/yr.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>14.7</td>
<td>1.02</td>
<td>0.03 A</td>
<td>0.11</td>
</tr>
<tr>
<td>Thin 1/3</td>
<td>22.3</td>
<td>1.02</td>
<td>0.06 A,B</td>
<td>0.26</td>
</tr>
<tr>
<td>Thin 2/3</td>
<td>18.8</td>
<td>1.58</td>
<td>0.09 B</td>
<td>0.32</td>
</tr>
<tr>
<td>Significance</td>
<td>N.S.</td>
<td>N.S.</td>
<td>Sign. at 0.05</td>
<td>N.S.</td>
</tr>
</tbody>
</table>

Figure 6 shows the 13-year growth in oak canopy cover percent after thinning. There was no significant difference in the two-thirds and the one-third thinning level, showing the rapid capacity of the heavily thinned blue oak crowns to occupy the site.

Discussion

This first ever study of blue oak thinning was developed to determine the effects of two thinning levels (one-third and two-thirds reduction of basal area). With the observation that blue oak in large parts of their range may be denser as result of fire suppression, the thinning was intended to be applied as a restoration tool to mimic the effects of a more regular fire return interval that has been disrupted for the last 50 plus years.
Thinning did increase the forage production levels for the heaviest thinning, although there was no change in forage composition at the levels investigated. Thinning also increased the vertical canopy diversity due to the resprouts. However, heavy rodent damage to resprouts in these areas with no cattle grazing, had a significant negative effect on the success of coppice management. A study of coppice management of blue oak in the northern Sierra showed that livestock grazing had a positive effect on sprouting success and height growth (Standiford and others 2010).

Thinning did increase the probability of acorn production of residual trees in the stand. In several years, over 80 percent of the trees in the heavily thinned stands had acorns. This did not change the per acre production of acorns, due to the lower density of trees, but it will be useful to continue to monitor this effect to see if the enhanced per tree production has longer term impacts.

Although thinning did not have a significant effect on stand level growth, it did enhance individual tree growth. The effect of the thinning over time will be fewer, large trees as compared to the untreated controls. It is also important to note that the canopy cover of the most heavily thinned stand increased from 12 percent to over 30 percent in 13 years, and was statistically the same as the less heavily thinned treatments in canopy cover.

Acknowledgments

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References


Influence of Fire on Engelmann Oak Survival – Patterns Following Prescribed Fires and Wildfires

Zachary Principe

Abstract
Engelmann oaks (*Quercus engelmannii*) are restricted to extreme southern California and northern Baja, California. Their entire range falls within a landscape increasingly prone to human induced wildfires. The influence of fire on seedlings and saplings has been well studied, but there is less information available on its effects on mature trees. Two monitoring programs tracked *Q. engelmannii* for 13 years in areas experiencing fires and adjacent unburned areas.

At the Santa Rosa Plateau Ecological Reserve, management fires were initiated in 1988. Management units have been subjected to grass-layer fires from one to three times. Damage at the base of the trunk was present in roughly half of the surveyed trees. During the survey period, 4 percent of the trees died in 4 categories; (1) killed directly by fire (46 percent), (2) obtained trunk damage that may have led to mortality 3 to 6 years after fire (15 percent), (3) had no visible fire damage (23 percent), or (4) had fire scars, but died more than 8 years after the most recent fire (15 percent).

An Engelmann oak monitoring program was initiated in 2000 on the Santa Ysabel Open Space Preserve (SY). The 2003 Cedar Fire burned portions of SY and the oak monitoring sites. Sites were surveyed after the fire to assess trees for damage and again in 2008 and 2013. On SY, *Q. engelmannii* grow in three matrix vegetation communities, grassland (with cattle grazing), sage scrub, and chaparral. Fire damage differed among communities. Trees in grasslands received the least amount of damage, those in sage scrub received intermediate damage, and those in chaparral the greatest damage. Survival was inversely related to damage which resulted in large difference in survival among the three communities. In surviving trees, sprouting type appeared dependent on the amount of damage trees received. Basal sprouting was common in highly damaged trees while crown sprouting was most common in trees with low levels of damage.

Engelmann oak trees appear resistant to grass-layer fires which generally result in low levels of damage and mortality rates similar to adjacent unburned areas. Trees are sensitive to higher levels of damage associated with greater fuel loads in sage scrub and chaparral. Although, basal sprouting is uncommon in mature trees following damage, trees able to survive high levels of damage can persist as shrubs for at least a decade. As a result, the structure of the vegetation community is simplified with the loss of the tree canopy.

Key words: Engelmann oak, prescribed fire, *Quercus engelmannii*, wildfire

Introduction
Engelmann oak (*Quercus engelmannii*) is the rarest oak tree species in California, as a result of its very narrow distribution within one of the most urbanized areas of California (Pavlik and others 1991, Scott 1990). Multiple threats, including direct habitat loss and the increased potential for exposure to wildfires, exist to the species as a consequence of its proximity to large human population centers. Wildfires,
including two of the largest in California since 1932, burned large portions of this species’ range in 2003 and 2007 (CalFire 2014). Continued human population growth in southern California will likely increase wildfire ignitions, especially near the wildland-urban interface (Keeley and Fotheringham 2001, Syphard and others 2007). As the climate of southern California is predicted to become hotter (Cayan and others 2008, Loarie and others 2008, Shaw and others 2012), more wildfires could occur if the amount of precipitation remains unchanged or increases (Westerling and Bryant 2008). With multiple factors pointing to the potential for a greater number of wildfires throughout the range of *Q. engelmannii*, it is important to better understand the influence of fire on various life stages.

*Quercus engelmannii* faces another challenge as a result of altered understory composition. Engelmann oak woodlands and savanna typically contain understory vegetation dominated by non-native annual grasses. These woodlands are often adjacent to grasslands that are also dominated by non-native annual grasses, which include brome grasses (*Bromus* sp.), wild oats (*Avena* sp.), wild barley (*Hordeum* sp.) and rattle fescue (*Festuca myuros*). As a result, management of these areas is generally considered necessary to enhance populations of native grassland and understory species. Management of the non-native grasses at locations with Engelmann oak woodlands and savanna includes prescribed fire and cattle grazing.

In the face of climate change, increased anthropogenic fire ignitions, use of fire as a management tool, and very large recent wildfires, there is a need to increase the understanding of how the role of fire shapes the population structure of this narrowly distributed species. The results of a long-term *Q. engelmannii* monitoring program, from two locations experiencing wildfires and/or prescribed fires over the last 30 years, are examined to better understand the influence of fire on *Q. engelmannii* trees.

**Methods**

The study was conducted at two locations in southern California. Santa Rosa Plateau Ecological Reserve (SRP) is located at the southern end of the Santa Ana Mountains, in Riverside County, in what is now the northern portion of ecologically intact range of *Q. engelmannii*. Santa Ysabel Open Space Preserve (SY), located in central San Diego County, is in the foothills of the Volcan Mountains in the central portion of its range. The topography of SRP is dominated by mesas and rolling hills with elevations ranging from 380 to 625 m. The SY is split into two non-contiguous units, SY East and SY West, which are separated by approximately 1.5 km. The SY West topography is dominated by the steep Santa Ysabel Creek canyon and the surrounding gently sloping hills with elevation ranging from 870 to 945 m. The SY East topography is dominated by the west-facing slope of the base of the Volcan Mountains with elevation ranging from 915 to 1160 m. The climate at all sites is Mediterranean, with hot, dry summers and cool, wet winters. Approximately 90 percent of the annual precipitation occurs between November and April.

The SRP, SY West and portions of the SY East locations support Engelmann oak savanna and woodland, with a contiguous grass understory and scattered stands of *Q. engelmannii*. The grassland and savanna understory vegetation is dominated by non-native annual grasses and forbs including ripgut brome (*Bromus diandrus*), soft-chess brome (*B. hordeaceus*), wild oat (*Avena* sp.), shortfruit filaree (*Erodium brachycarpum*), and foxtail fescue (*Festuca myuros*). These areas also contain a relatively high abundance of the native purple needlegrass (*Stipa pulchra*). The remaining woodlands at SY East have understories of sage scrub or chaparral. The
sage scrub understory is characterized by 0.5 to 1.5 m tall semi-woody shrubs—white sage (*Salvia apiana*) and California buckwheat (*Erigonum fasciculatum*)—with non-native annual grasses growing between shrubs. The chaparral understory is comprised of 2 m-tall dense woody shrubs dominated by ceanothus (*Ceanothus* sp.), growing with scrub oak (*Q. berberidifolia*), toyon (*Heteromeles arbutifolia*) and manzanita (*Arctostaphylos* sp.).

A prescribed burn program was initiated at SRP in 1988 within the grasslands and oak woodlands. Management goals for the program concentrated on the manipulation of the herbaceous plant community following the removal of cattle grazing between 1984 and 1996 from different areas as they were added to the protected lands at SRP. Trees monitored for this study are located in nine management units. Two management units have been burned once and five units have burned three times under prescription since 1988. Two management units act as untreated controls and have not been burned under prescription. The last large wildfires occurred in 1980 and 1981, with each burning opposite thirds of SRP, including the untreated control units. Additional wildfires burned portions of the monitoring location in 1945, 1962, 1968, and 1979.

There is an active year-round cow-calf operation at both SY units and no prescribed burn program. Wildfire history differs by unit. During the time that reliable fire records have been kept, SY East has burned relatively infrequently, with fires burning portions of the Engelmann oak long-term monitoring sites only in 1940 and 2003. Portions of the long-term monitoring sites at SY West have burned in 1956, 1981, 2006 and 2007.

Monitoring was completed using the tree as the sampling unit. A total of 540 permanently tagged oak trees (>10 cm diameter at breast height [1.37 m, DBH]) were monitored from 2000 to 2013. Size was measured using DBH. Survival was documented at each survey date. The presence and size of basal fire scars on the trunk was recorded. The number of sapling in the understory and in an area extending 3 m from the edge of the canopy were counted. If the canopy of a tree intersected another tree, the count ended where the canopies intersect. Based on the long-term data set, individuals ≥20 cm are well-established and had low mortality rates prior to the recent drought. As a result, saplings were defined as individuals ≥20 cm in height.

The 2003 Cedar Fire burned a portion of the long-term monitoring sites at SY East, including roughly half of the grassland and sage scrub sites and all of the chaparral sites. Indices of damage and fire severity were recorded for trees within the Cedar Fire’s perimeter immediately after the fire. The area burned under each tree was recorded as percent of the understory burned. Fire severity was ranked based on the completeness of understory fuel consumption and ash deposition (0 to 9, with 0 being the least severe and 9 being the most severe). Damage to the canopy was estimated using maximum and average height of leaves consumed by the fire, maximum and average height of leaves scorched by the fire, and percent of canopy indirectly killed by the fire. Damage to the trunk was estimated based on the area of the trunk with bark scorched (bole charred - outer surface burned, but fire did not penetrate the entire thickness of the bark), bark consumed (bark completely burned to the cambium layer), and wood and cambium consumed.

All analyses conducted were univariate with a single independent variable. For continuously measured response variables, comparisons were made using general linear models (ANOVA and regression). For measurements made using binary scales or categorical rankings contingency table analysis (chi square), a form of the generalized linear model was used. All analyses were conducted in JMP 11.0.
As the last large wildfires, prior to the initiation of the monitoring program at both SRP and SY, occurred in 1981, the year of 1982 will be used as the starting date for the number of fires to which the monitoring trees have been exposed.

Results

Santa Ysabel East

Roughly 53 percent of monitored trees at SY East burned in the 2003 Cedar Fire. Prior to 2003, none of the trees had burned since at least 1940. All indices of fire damage were significantly correlated. Area of bark scorched (bole charred) was selected as the damage index to be used to investigate the influence of vegetation community on damage and damage on performance of oaks following the fires. For a majority of analyses, the area of bark scorched was converted to a categorical variable (high, medium, and low) to allow for easier graphical display and interpretation. For the remainder of this paper, fire damage will refer to area of the bark scorched.

Fire damage

Fire damage differed significantly among vegetation communities following the Cedar Fire ($F = 46.9; p < 0.0001$). Trees in chaparral received the highest levels of damage, sage scrub had intermediate levels of damage, and grasslands experienced the lowest levels of damage. The distribution of trees within fire damage classes varied significantly by community ($X^2 = 38.3; p < 0.0001$; fig. 1). Most trees in chaparral were in the high damage class. Trees in the sage scrub were fairly evenly distributed among damage classes and a majority of trees in the grasslands were in the low damage class.

Figure 1—The percent of trees within each of the three fire damage classes in response to the 2003 Cedar Fire at SY West; high (black), intermediate (light grey), and low (dark grey) by vegetation community; chaparral, sage scrub (CSS), and grassland.
Survival

Survival decreased from 2004 to 2008 for trees damaged by the Cedar Fire. Trees dying between 2004 and 2008 occurred only in shrublands, but included trees in all damage classes. Survival did not change between 2008 and 2013.

Survival in 2008 was inversely related to damage class ($X^2 = 30.0; p < 0.0001$). A very high percentage of trees with low levels of damage survived compared to a low percentage of highly damaged trees (fig. 2). As damage varied by vegetation community, a similar pattern was observed across the vegetation communities with trees in grasslands surviving at high rates and trees in chaparral surviving at low rates ($X^2 = 18.5; p < 0.0001$).

![Figure 2—Percent survival of trees at SY West in response to the 2003 Cedar Fire by damage class.](image)

Overall, survival through 2013, for trees damaged by the Cedar Fire, was 75 percent, while survival for trees in areas of SY East outside of the Cedar Fire was 95 percent.

Growth type following damage

For trees damaged by the Cedar Fire, growth type significantly differed by damage class ($X^2 = 29.0; 0.001$). Trees receiving low levels of damage were most likely to sprout from the canopy, while trees with high levels of damage were most likely to basal sprout (fig. 3). Trees receiving intermediate levels of fire damage had a fairly even distribution of growth types, with trees that both basal and canopy sprouted.
Figure 3—The percent of trees with different growth types following receiving damage in the 2003 Cedar Fire; canopy/crown sprouts (black), basal sprouts (dark grey), and both canopy/crown and basal sprouts (light grey) by fire damage class; low, intermediate and high.

**Santa Ysabel West**

**Survival**

Roughly 72 percent of the trees at SY West monitoring sites burned in the 2006 and/or 2007 wildfires. No wildfires had burned any of the sites since 1981. The understory is largely herbaceous and dominated by non-native annual grasses. Survival of trees outside the 2006 and/or 2007 fires was 100 percent at SY West between 2003 and 2013. Survival of trees burned by one or both of these fires was 99 percent between 2003 and 2009. Survival of trees burned by one or both fires dropped to 95 percent by 2013. Two of the three trees that died between 2009 and 2013 had visible fire damage and may have died as a result of that damage. At SY East, for trees exposed to fire and with herbaceous understory, survival through 2013 was also 95 percent.

**Santa Rosa Plateau**

**Survival**

A total of 21 prescribed fires and 2 small wildfires have burned long-term monitoring trees at SRP since 1982. Approximately 19 percent of the trees burned once, 63 percent burned three times, and 17 percent have not burned since 1982. Survival of trees not exposed to fire was 100 percent between 2003 and 2013. Survival between 2003 and 2013 of trees burned one or three times was identical at 95 percent. Dead trees occurred in 4 categories; (1) killed directly by fire (46 percent), (2) obtained damage to the base of the trunk that may have precipitated mortality 3-6 years following a fire (15 percent), (3) had no visible fire damage over the course of the survey period (23 percent), or (4) had old fire scars, but died eight or more years after the most recent fire making it impractical to classify cause of mortality (15 percent).

**Scars**

**Santa Ysabel**

Basal fire scar data is available for both 2002 and 2013 for trees with herbaceous and sage scrub understories. The presence of basal scars was independent of vegetation community in both 2002 ($X^2 = 0.38; p = 0.83$) and 2013 ($X^2 = 0.92; p = 0.63$).
presence of basal scars in 2013 was significantly related to the number of fires trees were exposed from 2003 to 2013 ($X^2 = 48.9; p < 0.0001$). Roughly 10 percent of trees not exposed to fires had scars compared to 63 percent of trees exposed to one fire and 26 percent of trees exposed to two fires between 2003 and 2013. As a result, the percent of trees with scars increased from 5 percent in 2002 to 29 percent in 2013. The increase is due to new scars from trees exposed to the 2003, 2006, and 2007 fires. In the footprint of these fires, the percent of trees with scars increased from 5 to 44 percent.

Survival of trees with herbaceous and sage scrub understories exposed to fire from 2003 to 2007 with scars in 2002 was significantly lower than trees without scars ($X^2 = 7.7; p = 0.0055$). Survival was 75 percent for trees with scars in 2002 and 97 percent for trees without scars.

**Santa Rosa Plateau**

Basal fire scar data is only available for 2002 from SRP. As a result, the presence of scars was investigated with respect to the number of fires trees were exposed to between 1982 and 2002. The presence of basal fire scars in 2002 was significantly related to the number of fires trees were exposed ($X^2 = 30.1; p < 0.0001$; fig 4). For trees burned from 2003 to 2012, trees with scars in 2002 were more likely to be dead in 2013 than trees without scars ($X^2 = 3.9; p = 0.047$). Survival between 2003 and 2013 was 90 percent for trees with scars in 2002 and 98 percent without scars in 2002.

![Figure 4—Percent of trees with basal scars at SRP in 2002 based on the number of fires trees were exposed between 1982 and 2002.](image)

**Saplings**

The percentage of trees with saplings was significantly higher at SRP than SY in both 2003 ($X^2 = 9.5; p = 0.0021$) and 2013 ($X^2 = 15.2; p < 0.0001$). However, the percentage of trees with saplings at SY East and SY West was higher than some management units at SRP, indicating the distribution of saplings varies at multiple scales on the landscape. With the recent drought, the percentage of trees with saplings at both locations decreased between 2003 and 2013. In 2003, 43 percent of trees at SRP contained saplings compared to 38 percent in 2013. In 2003, 30 percent of trees at SY contained saplings compared to 22 percent in 2013.
With SRP and SY data combined, the percentage of trees with saplings in 2013 was 24 percent for trees not exposed to fire since 1982 and 34 percent for those exposed to fire ($X^2 = 4.1; p = 0.04$). The number of fires trees were exposed since 1982 had a significant influence on the percentage of trees with saplings ($X^2 = 42.1; p < 0.0001$). The pattern of trees with saplings compared to number of fires is not straightforward with 24 percent of trees exposed to no fires, 23 percent exposed to one fire, 11 percent exposed to two fires, and 48 percent exposed to three fires supporting saplings.

**Santa Ysabel**
The percentage of trees with saplings in 2013 was identical (22 percent) for trees exposed to fire or not exposed to fire since 1982. The percentage of trees with saplings in 2013 varied based on the number of fires to which the trees were exposed. However, the differences were not significant ($X^2 = 4.5; p = 0.11$). Approximately 22 percent of trees exposed to no fires, 27 percent exposed to one fire, and 11 percent exposed to two fires supported saplings in 2013.

**Santa Rosa Plateau**
The percentage of trees with saplings in 2003 was 34 percent for trees not exposed to fire between 1982 and 2003 and 46 percent for those exposed to fire, but this was not found to be a significant difference ($X^2 = 2.6; p = 0.10$). The number of fires trees were exposed to between 1982 and 2003 did have a significant influence on the percentage of trees with saplings ($X^2 = 35.0; p < 0.0001$). Approximately 34 percent of trees exposed to no fires, 14 percent exposed to one fire, 52 percent exposed to two fires, and 75 percent exposed to three fires supported saplings in 2003.

The percentage of trees with saplings in 2013 was 28 percent for trees not exposed to fire since 1982 and 40 percent for those exposed to fire, but this was not found to be a significant difference ($X^2 = 2.5; p = 0.11$). The number of fires trees were exposed to since 1982 did have a significant influence on the percentage of trees with saplings ($X^2 = 23.6; p < 0.0001$). Approximately 28 percent of trees exposed to no fires, 15 percent exposed to one fire, and 48 percent exposed to three fires supported saplings in 2013.

**Discussion**
Engelmann oak trees appear resistant to grass-layer fires, moderately sensitive to sage scrub fires, and sensitive to chaparral fires. The difference in survival among trees growing in the different vegetation communities is very likely due to differences in fuel loads. The difference in fuel loads, although not measured for this study, was easily observed. Grasslands have the lowest fuel loads due to both the absence of shrubs and, at SY, the presence of cattle grazing. Sage scrub has intermediate fuel loads due to the presence of short-stature semi-woody shrubs with a grass understory. Chaparral has high fuel loads due to dense tall-stature woody shrubs. The difference in fuel amount and structure was evident on the damage trees received in each community. Very low levels of damage in grassland trees were characterized by minor damage to the base of the trunk and canopy damage only close to the ground. Intermediate levels of damage in sage scrub trees were characterized by minor to intermediate trunk damage and damage to larger areas of the canopy. High levels of damage in chaparral trees were characterized by
intermediate and high levels of trunk damage and damage to all or a majority of the canopy. These differences in damage were inversely related to survival. As a result, the greatest change to the *Q. engelmannii* population occurred within the chaparral where mortality was very high. Additionally, the chaparral trees able to survive are generally very different in structure even a decade after the fire. This has resulted in the loss of the tree canopy in this community as most *Q. engelmannii* are multi-stemmed, only slightly taller than the surrounding chaparral shrubs, and appear many years away from regaining tree height or structure.

Although *Q. engelmannii* trees appear resistant to grass-layer fires, there appears to be a trend toward increased mortality for trees with basal scars when they are exposed to subsequent fires. At SY, trees with scars increased five-fold following the 2003, 2006 and 2007 fires, excluding trees growing in the chaparral. As a result, nearly 30 percent of the monitored population now has unhealed basal scars. Overall, mortality was found to be nearly 10 percent higher for trees with scars exposed to fire compared to trees without scars. This is consistent with results found by Fry (2002) where preexisting scars appeared to be responsible for fire-induced mortality of two of the three oak trees killed in response to a prescribed fire in Santa Clara County. The increase in the number of trees with scars and their higher mortality rate lead to the potential for even higher mortality rates in response to future fires at SY. At SRP where nearly 50 percent of trees had scars by 2002, mortality was found to be about 10 percent higher for trees with scars in 2002 that were burned between 2003 and 2012. The mortality rate for trees at SRP, in response to prescribed fires, may be lower than areas burned in wildfires due to pre-burn management actions. At SRP fire crews often clear fuels away from trees near the control lines in order to minimize fuel loads and smoldering adjacent to unburned fuels. Additionally, trees near the control lines are generally burned in back fires, which exhibit less extreme fire behavior. As a result, mortality rates of trees observed at SRP may be lower than they would be in response to wildfires. As the trunk appears to be most susceptible to damage that leads to mortality, relatively simple management actions, such as removing fuels from around the base of the trunk, could be taken to protect trees.

The annual survival from 2002 to 2013 was 0.993 for all trees monitored. If trees growing in the chaparral are removed from the analysis, annual survival increases to 0.995. This survival rate is similar to the 1943 to 2006 survival rate (0.996) of the valley oak (*Q. lobata*) (Davis and others 2011). Annual survival was 0.99 or greater (annual mortality less than 1 percent) for all management units except SY East due to the high mortality of trees in the chaparral in response to the Cedar Fire.

The population growth rate cannot be directly estimated as the recruitment rate into the tree size class is unknown. The sapling data associated with this monitoring may help us calculate that rate in the future. Currently, the percent of trees with saplings has decreased, from 38 to 31 percent, in the last decade as a result of the recent drought. A similar decline in the total number of saplings from 1,700 to 1,150 was also observed. Even following the decline of saplings in the last decade there was an average of 2 saplings per adult tree in 2013, down from 3 saplings per tree in 2003. These are similar to the numbers of late stage seedlings and saplings per adult tree recently found for *Q. lobata* and *Q. douglasii*, in Santa Barbara County, California, which ranged from roughly 2 to 57 per tree (Pearse and others 2014). As the definition of sapling used in this study includes both saplings and a portion of their larger late stage seedlings, it is likely that the estimates of saplings per tree would be closer if similar definitions had been applied. As saplings occur clustered around 31 percent of the trees at SY and SRP, a shift in the distribution of adult oaks may occur within individual woodlands. The trees with saplings contained an average
of 6.8 saplings per adult tree, providing each with a good opportunity to at least replace itself.

Based on the pattern of saplings present in 2003 and 2013, with respect to the number of recent fires, it does not appear fires greatly decrease their presence on the landscape. At SRP, in both 2003 and 2013, the percentage of trees with saplings was highest in areas exposed to more than one fire. At SY, the percentage of trees with saplings was higher in areas burned once compared to unburned areas. It is likely that much of the variability in the distribution of saplings is unrelated to fire and it is more likely that areas with the greatest density of saplings are, by chance, the areas that have burned most frequently. The relatively high survival rates of *Q. engelmannii* saplings exposed to fire would allow saplings to persist following these fires. Depending on fire damage, survival rates of saplings exposed to fire range from 60 to 95 percent, while survival rates for saplings receiving low levels of fire damage (which are likely typical of saplings with grass understories) were found to be >80 percent (Lawson 1993, Principe 2002). In this study, the persistence of saplings in areas exposed to the highest frequency of fires demonstrate that these areas support capacity to maintain *Q. engelmannii* woodlands in the future.

In conclusion, both wildfire and prescribed burns reduce the survival of all size classes of *Q. engelmannii*. Fires also increase the occurrence of basal scars, which appear to increase mortality when trees are exposed to subsequent fires. The overall impact of fires on the long-term viability of *Q. engelmannii* populations is, however, unknown and would require demographic modeling to help tease out its influence. For areas where there is concern over the viability of the population, the use of prescribed fire should be considered carefully as mortality of all size classes will likely be increased unless protective measures are taken. Based on observations made following prescribed fires at SRP and large wildfires in San Diego County in 2003 and 2007, the influence of fire appears site specific. At many locations in San Diego County, following wildfires, there appears to be high tree mortality, similar to that observed in the chaparral and sage scrub at SY, but limited numbers of saplings. As a result, some stands appear to have been substantially reduced in spatial extent. This is in contrast to most areas of SRP where, even after repeated fires, tree mortality is low and saplings are relatively abundant. At SRP, it is also common to observe multiple saplings being released from the sapling bank with rapid growth following the fire-induced death of their nurse/parent tree. More information is needed to gain a better understanding if the indirect effects of fire on the environment of *Q. engelmannii* (decreased abundance of non-native annual grasses following fires on seedlings and sapling recruitment and growth rates) outweigh the increase in mortality.

**References**


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Oak Ecosystem Services
Landowner Total Income From Oak Woodland Working Landscapes in Spain and California

Jose L. Oviedo, Lynn Huntsinger, and Pablo Campos

Abstract
Conventional accounting of agricultural income focuses on the commercial operating income from oak woodland ranches, omitting the value of amenities to the landowner and real capital gains, which includes land revaluation (appreciation). These accounting exercises also mix income earned through self-employed (landowner and household) labor with ranch operating income, making it difficult to estimate separately how capital investment and landowner labor time are remunerated. In this paper we estimate the total landowner income and profitability rates from six oak woodland case studies in Spain and California. We use data from commercial operations, private amenity values from two contingent valuation surveys and average land revaluation rates. Self-employed labor returns are estimated for each economic activity. We find that when private amenity values and capital gains are considered, profitability rates range from 9.7 to 12.6 percent in California, and 6.3 to 8.7 percent in Spanish case studies, rates that are competitive with alternative investments. Self-employed labor is present in two California and in two Spanish case studies, providing positive returns in the former, though below the average wage rate from an alternative employment, and no returns in the latter. Our results provide a more complete economic valuation of these oak woodlands and a better understanding of landowner decisions and motivations for current and future land investment.

Key words: income accounting, private amenities, rangeland economics

Introduction
It is well-recognized that private amenities (environmental and lifestyle values enjoyed by landowners) have a significant influence on the price of rangelands and that land appreciation also influences these prices and the owner’s long-term financial status (Campos and others 2009, Torell and others 2005). It is also acknowledged that the landowner and household (self-employed) labor is often present in ranching operations (Huntsinger and others 2010) and a return is desired from this labor. When these factors are not considered in economic analysis, it is hard to understand land prices and why landowners so often persist in ranching, instead of making other investments with their financial resources.

Such is the case for oak woodlands in Spain and California. Apart from commercial operating income, the conventional profit associated with commodity production, these working landscapes have three additional income streams for the
landowner. These are often not factored into applications of the System of National Accounts (SNA), the internationally agreed upon standard set of recommendations for how to compile measures of economic activity, and are identified as: (i) private amenity income, because the SNA is generally limited to market commodities; (ii) income from self-employed (landowner and household) labor, which in the SNA is mixed with operating income; and (iii) capital gains from land revaluation (appreciation) and other assets, which is acknowledged as part of total income (BEA 2009, Eisner 1989) but not measured in current applications of the SNA. This leads to an incomplete valuation of landowner returns, and therefore of full economic activity, in oak woodlands. Accounting systems that include these three income sources can help correct this failing, and better understand the decisions of ranchers about their lands.

In this paper we measure the total landowner income and profitability rates from six oak woodland case studies in Spain (named dehesas) and California. We apply at the farm scale the Agroforestry Accounting System (AAS), which is designed specifically to overcome the limitations of the SNA for total income measurement when applied to agroforestry systems (Campos 2000). We integrate the value of market commodities, costs and capital investment, private amenities consumed by the landowner, and capital gains. To that end, we use landowner records from the case studies, private amenity values from two contingent valuation surveys, and average land revaluation rates from official statistical sources. Income from self-employed labor is estimated for each economic activity.

Methods

Total income from an economic activity is defined as: “that which can be consumed while keeping real wealth intact, saving (= investment) is the difference between this measure of income and actual (final) consumption. Both income and saving will then include real capital gains. To preserve the saving-investment identity, investment would also have to include these capital gains. Failure to include them causes a disparity between income statements and balance sheets that reflect market values” (Eisner 1989: 17). According to this definition, total income is the aggregated value of final consumption and investment, and the two components of total income from an oak woodland ranch are the net value added and capital gains. The AAS departs from this definition and extends the concept of production to include in income measurement the amenities consumed by the landowner.

Net value added and capital gains are obtained from the two accounts used by the AAS: the production account and the capital balance account, respectively. The production account measures output and cost flows from current production, including gross capital formation (gross investment) as output and work in progress (ongoing work on products not yet finished) used as cost. The net value added is estimated as net operating margin (the net surplus from the operation before taxes and subsidies on production) plus labor. The net operating margin is the balance between outputs and costs (similar to a typical enterprise budget). Labor includes employee and self-employee compensation. The capital account incorporates entries, withdrawals and revaluation (changes in the value) of fixed capital and stored work in progress. Capital gains are measured from capital revaluation less capital destruction plus normal depreciation during the accounting period. The production and capital accounts provide the information needed to estimate the immobilized capital (IMC), which is the average annual capital investment in a woodland operation, including in land, infrastructure, equipment and animals.
The total income from the oak woodland to the landowner is the sum of capital income plus landowner self-employee compensation. Capital income is the sum of net operating margin and capital gain, and represents the return to capital investment obtained annually both as an actual monetary and expected return. Self-employee compensation represents the income returns to the labor devoted by the landowner and household in the operation.

Outputs and durable goods sales are valued at producer prices and costs and durable goods bought are valued at purchase prices. Both prices exclude operating subsidies and taxes. We do not consider subsidies and taxes, and nor does the SNA, because they are economic transfers between sectors. In addition, taxes and subsidies regimes are different between countries and would partly distort our results. While in Spain dehesa owners mostly receive subsidies from the European Union, in California ranchers are more likely to benefit from tax breaks.

Profitability rates are measured on the basis of capital income related with IMC over the accounting period in order to be consistently comparable to alternative investments. The estimation of profitability refers to the ratios of net operating margin, capital gain and capital income to IMC, which offers the operating, capital gain and total profitability rates, respectively. Operating and capital gain profitability are expressed in nominal terms. Total profitability is presented both at nominal and real terms, the latter being a nominal rate deflated by consumer price index.

Data
Data taken from the case studies refer to commercial operating activities in the woodland and capital (asset) values except land. These data were collected from account books, in-depth interviews and field data in 2010 for the Spanish case studies and in 2007 for the California case studies. Private amenity output, land price and land price revaluation were obtained from other sources as explained below. We also detail the criteria to estimate the part of mixed operating income corresponding to self-employed labor compensation.

Private amenity values
The missing measurement of privately consumed (non-market) amenities in income accounting is a relevant gap because these are “a significant part of the real income of many individuals” (Krutilla 1967: 779). To obtain a monetary value for the non-market production of private amenities in Spanish and California oak woodlands, we used a contingent valuation study applied in the two oak woodland areas.

For the Spanish case studies, the landowner willingness to pay (WTP) for private amenities is estimated from a 2010 contingent valuation study of 765 privately-owned oak woodlands and forests in Andalucia (Oviedo and others, n.d.). The authors use a logit regression to estimate a WTP function from the analysis of a single-bounded question. For the California case studies, the landowner WTP for private amenities is estimated from a 2004 contingent valuation study of 115 privately-owned oak woodlands in California (Campos and others 2009). The authors use a weighted least square regression to obtain a WTP function from the analysis of an open-ended question.

Substituting the values of the corresponding explanatory variables from our case studies into these functions, we obtain the WTP for each case study. This WTP corresponds to the output amenity value we integrated into the AAS. The estimated values were transformed to United States dollars in the Spanish cases and updated to
2010 United States dollars in the California cases.

**Land prices and land revaluation**

The same surveys that included the contingent valuation questions also included a question about what landowners thought the current sale price of their woodland was. They were also asked to allocate (in percent) how this land price was explained by the commercial and amenity benefits from the woodland. Based on this, we constructed two functions in each study area, one for the land price and one for the percentage of land price explained by private amenities. Using the values of the corresponding explanatory variables we obtained the land price and the percentage of the land price explained by private amenities for each case study.

The capital account also requires an estimation of how much land price changes during the year (land revaluation), as part of the capital gain figure. However, land revaluation is a highly variable figure and using the one from a single year would not represent a long-term trend. Instead, we employ an average value for a longer period by using statistical data for rangeland price variation in the studied areas of the case studies. For the dehesa, we calculated the average nominal cumulative land revaluation rate for dry natural grassland in Spain for the period 1994-2010 from MARM (2011), resulting in a 6.7 percent rate. For the California ranches we calculated the average nominal cumulative land revaluation rate for rangelands in California for the period 1999-2010 from CASFMRA (2012), resulting in a 7.9 percent rate.

We also distinguish the share of land revaluation from commercial and private amenity activities. As in both areas we observe decreasing real commercial operating income (Ovando and others, n.d.; Torell and others 2001) and increasing values of amenities to landowners (Huntsinger and others 2010; Oviedo and others, n.d), we assume that all land revaluation is explained by an expected increase in future private amenity values and is entirely attributed to the capital gains of this activity. This is open to re-assessment if trends change.

**Self-employed labor**

Many landowners and their households work the land themselves, obtaining income that is a mix of returns from self-employed labor and capital investment. This mixed income is an integration of net operating margin, including both returns to manufactured net operating margin and resource rent and self-employee compensation, and is obtained from the production account. We propose here an *ad hoc* criterion of separating the components of this mixed income (net operating income and self-employed labor).

For each woodland activity, we estimate the value of this mixed income and the hours of self-employed labor devoted to it. The resource rent is known from the local market (we estimate it from our case studies). When there is no self-employed labor, the remaining income (once resource rent is subtracted) corresponds to the manufactured net operating margin. When there is self-employed labor devoted to an activity, three situations could arise: (i) if the mixed operating income is negative, we attribute all of it to the manufactured net operating margin (self-employed labor is unpaid); (ii) if the mixed operating income is positive and on a per hour basis is lower or equal than 80 percent of the employee hourly wage in the area, all is attributed to self-employed labor; (iii) if the mixed operating income is positive and on a per hour basis higher than 80 percent of the employee hourly wage, self-
Case study description

The dehesa is an ancient land use system in the oak woodlands of Spain, largely in the southwest of the country. Cork, acorns, pigs, sheep, goats, cattle (including fighting bulls), mushrooms and other products are marketed from woodlands with well-spaced oaks and a grass understory grass in a dry-summer, frost-free Mediterranean climate.

We analyze three dehesa case studies: Dehesas A, B and C. Dehesa A is a flat property of 179 ha, located in Córdoba province. Holm oak (*Quercus Ilex*) occupies almost the entire property. Firewood is harvested for landowner use and silvopastoral practices are carried out to improve pasture productivity. Cattle are crossbred meat breeds, and purebred Iberian pigs graze on acorns and grass. Wild boar and small game are hunted. Dehesa B is a moderately sloped sierra property of 1336 ha, located in Sevilla province. Holm and cork oaks (*Q. suber*) cover 87 percent of the land. Cork and firewood harvesting is carried out, and silvopastoral management aims to improve grass and acorn yields. Purebred retinta cattle are the only livestock breed raised. The property includes an enclosed commercial hunting reserve (coto). Dehesa C is a property of 1260 ha on a moderate to highly sloped sierra located in Córdoba province. Pure stands of holm oak cover 43 percent of the property. There is no timber or firewood harvest. Iberian pigs and merino sheep are reared, and segureña sheep graze on the property. This dehesa has a partially enclosed commercial hunting reserve (coto).

On the California side we also have three case studies: Ranches A, B and C. Ranch A is located in Shasta County and covers 2671 ha. Oak woodland and annual grassland are 34 and 55 percent of the property, respectively. English crossbreeds graze dryland range and irrigated pasture. Firewood is sold by the ranch owner as stumpage and a fee is collected annually from hunters who are allowed access. Ranch B is located in Tehama County and covers 1358 ha. Oak woodlands occupy 65 percent of the property. Hunting is the main commercial activity and firewood is harvested. The landowner maintains a small herd of English crossbred cattle that are used to help meet vegetation management goals. The rancher also leases winter pasture to a local livestock producer and cultivates crops for cattle and big game. Ranch C is located in Mendocino County and covers 2656 ha. Oak woodlands cover 38 percent of the property. It is family-operated ranch and the main activity is livestock production.
Table 1—Income, capital and profitability indicators in three dehesa case studies ($ per hectare of useful agrarian land except for profitability rates which are in percent)

<table>
<thead>
<tr>
<th>Class</th>
<th>Dehesa A</th>
<th>Dehesa B</th>
<th>Dehesa C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>COM</td>
<td>PA</td>
<td>TOT</td>
</tr>
<tr>
<td>1. Labor (L)</td>
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<td>179.4</td>
</tr>
<tr>
<td>1.1 Employee compensation</td>
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<td>179.4</td>
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<tr>
<td>1.2 Self-employed compensation a</td>
<td>0.0</td>
<td>-</td>
<td>0.0</td>
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<tr>
<td>2. Net operating margin (NOM)</td>
<td>-117.8</td>
<td>642.1</td>
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<td>3. Net value added (NVA=NOM + L)</td>
<td>61.5</td>
<td>642.1</td>
<td>703.6</td>
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<tr>
<td>4. Capital gain (CG)</td>
<td>-91.1</td>
<td>377.1</td>
<td>286.0</td>
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<tr>
<td>5. Capital income (CI=NOM + CG)</td>
<td>-208.9</td>
<td>1,019.2</td>
<td>810.2</td>
</tr>
<tr>
<td>6. Total income (TI=CI + L)</td>
<td>-29.5</td>
<td>1,019.2</td>
<td>989.6</td>
</tr>
<tr>
<td>7. Land price b</td>
<td>5,020.2</td>
<td>3,787.2</td>
<td>8,807.4</td>
</tr>
<tr>
<td>8. Immobilized capital (INC)</td>
<td>9,113.3</td>
<td>3,787.2</td>
<td>12,900.5</td>
</tr>
<tr>
<td>9. Operating profitability (NOM/CIN) (%)</td>
<td>-0.9</td>
<td>5.0</td>
<td>4.1</td>
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<tr>
<td>10. Capital gain profitability (CG/CIN) (%)</td>
<td>-0.7</td>
<td>2.9</td>
<td>2.2</td>
</tr>
<tr>
<td>11. Total profitability (CI/CIN) (%)</td>
<td>-1.6</td>
<td>7.9</td>
<td>6.3</td>
</tr>
</tbody>
</table>

COM: Commercial activities; PA: Private amenity activity; TOT: Total.

a As value is quantity (hours of work) times price (wage rate), we prefer to maintain the self-employed item when its value is zero to denote real unpaid labor in the commercial activity. A dash implies that there is no self-employed labor time devoted to ranch operations in the case study.

b Land price at the beginning of the year.
Results

In tables 1 and 2 we present a set of income, capital and profitability indicators from our case studies. As the AAS classifies economic activities according to types of production, we differentiate between commercial and private amenity activities. All results are in 2010 United States dollars per hectare and represent nominal values (they are not adjusted by inflation).

In the three dehesa cases, private amenity activities contribute more than commercial activities to all income indicators except for income resulting from labor, which is completely derived from paid employment (table 1). Commercial activities have negative values in the net operating margin in all cases. Capital gains from private amenities are high as all land revaluation is attributed to this activity. Capital gains from commercial activities come from manufactured investments and are negative for Dehesas A and C, and positive for B. Capital income from commercial activities is negative for the three dehesas. The main contribution to total capital income comes from the net operating margin in Dehesa A (65 percent) and from capital gains in Dehesa B and C (75 and 90 percent respectively).

According to the functions elaborated from the Oviedo and others (n.d.) data, 43, 54 and 57 percent of total land price is explained by private amenities in Dehesas A, B and C, respectively (table 1). The contribution of manufactured capital to immobilized capital in the accounting period represents 32 percent for Dehesa A, 17 percent for Dehesa B and 11 percent for Dehesa C.

The profitability indicators also show differences between commercial and private amenity activities, with negative or low values for the former and positive values for the latter (table 1). Total profitability ranges from 6.3 to 8.7 percent (table 1). If capital gains were not considered the total profitability would be reduced around 5 percent (ranging from 0.6 to 4.1 percent); and if private amenities were ignored the total profitability would be reduced by 4 percent (becoming negative in all cases). The real total profitability, which considers the inflation rate in the period 1994 to 2010, is 3.2, 5.6 and 3.5 percent for Dehesas A, B and C, respectively. These rates do not include net subsidies on livestock production, which have been important in dehesa management in the past decades, and increase landowner profitability.

For the ranch cases, private amenity activities contribute more than commercial activities to all income indicators except for labor in all cases and for net value added in Ranch A. For Ranches B and C, landowner self-employment contributes 19 and 79 percent to labor income, respectively (table 2). Commercial activities offer positive values for the net operating margin in the three cases, although it is very low or even close to zero in ranch B and C. Capital gains are contributed mainly by private amenity activities, being low or negative for commercial activities (table 2). Capital income from commercial activities offers positive values for the three cases, although it is particularly low for Ranches B and C. The main contribution to total capital income comes from capital gains in the three ranches.
Table 2—Income, capital and profitability indicators in three ranch case studies ($ per hectare of useful agrarian land except for profitability rates which are in percent)

<table>
<thead>
<tr>
<th>Class</th>
<th>Ranch A</th>
<th>Ranch B</th>
<th>Ranch C</th>
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<td>1.1 Employee compensation</td>
<td>35.3</td>
<td>-</td>
<td>35.3</td>
</tr>
<tr>
<td>1.2 Self-employed compensation</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2. Net operating margin (NOM)</td>
<td>104.1</td>
<td>114.9</td>
<td>219.0</td>
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<tr>
<td>3. Net value added (NVA=NOM + L)</td>
<td>139.4</td>
<td>114.9</td>
<td>254.3</td>
</tr>
<tr>
<td>4. Capital gain (CG)</td>
<td>4.1</td>
<td>279.5</td>
<td>283.5</td>
</tr>
<tr>
<td>5. Capital income (CI=NOM + CG)</td>
<td>108.2</td>
<td>394.4</td>
<td>502.5</td>
</tr>
<tr>
<td>6. Total income (TI=CI + L)</td>
<td>143.5</td>
<td>394.4</td>
<td>537.8</td>
</tr>
<tr>
<td>7. Land price&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1,293.2</td>
<td>2,201.9</td>
<td>3,495.1</td>
</tr>
<tr>
<td>8. Immobilized capital (INC)</td>
<td>1,774.9</td>
<td>2,201.9</td>
<td>3,976.8</td>
</tr>
<tr>
<td>9. Operating profitability (NOM/CIN) (%)</td>
<td>2.6</td>
<td>2.9</td>
<td>5.3</td>
</tr>
<tr>
<td>10. Capital gain profitability (CG/CIN) (%)</td>
<td>0.1</td>
<td>7.0</td>
<td>7.1</td>
</tr>
<tr>
<td>11. Total profitability (CI/CIN) (%)</td>
<td>2.7</td>
<td>9.9</td>
<td>12.6</td>
</tr>
</tbody>
</table>

COM: Commercial activities; PA: Private amenity activity; TOT: Total.

<sup>a</sup>As value is quantity (hours of work) times price (wage rate), we prefer to maintain the self-employed item when its value is zero to denote real unpaid labor in the commercial activity. A dash implies that there is no self-employed labor time devoted to ranch operations in the case study.

<sup>b</sup>Land price at the beginning of the year.
According to the functions elaborated from the Campos and others (2009) data, 63, 63 and 61 percent of the total land price is explained by private amenities in Ranches A, B and C, respectively (table 2). The contribution of manufactured capital to immobilized capital in the accounting period represents 12 percent for Ranch A, 21 percent for Ranch B and 15 percent for Ranch C.

The three profitability rates show higher values for private amenity activities (table 2). Total profitability ranges from 9.7 to 12.6 percent (table 2). If capital gains were not considered the total profitability would be reduced by around 6 percent, ranging from 3.2 to 5.5 percent; and if private amenities were ignored the total profitability would be reduced by around 3 percent, to 2.6 percent in Ranch A and near zero percent in the other two cases. If we consider the inflation rate in the period 1999 to 2010, we find that the real total profitability is 9.9, 9.1 and 7.0 percent for Ranches A, B and C, respectively. United States subsidies in the form of tax relief and crop production subsidies are not included in the capital income indicators and profitability rates, which would be slightly increased if taken into account.

**Concluding remarks**

We have quantified the income and profitability from oak woodlands to landowners in Spanish dehesa and California ranches in a standardized framework that includes market and (non-market) private amenity values, capital gains, and returns from household labor. Our analysis shows that private amenities add about 3 percent to total profitability while integrating capital gain based on historical land revaluation trends adds about an additional 6 percent in an average year. In real terms, dehesa and ranch total profitability is in the 3 to 5 percent and 7 to 9 percent ranges, respectively. Both capital gains and private amenities are important for explaining landowner income and land prices in our case studies, and create profitability rates that can compete with alternative investments of similar risks and time horizon.

We also find that in some case studies there is unpaid or low-paid self-employed labor, showing that landowners substitute hired labor with their own labor and that they work for a low remuneration to maintain their operating activities. This willingness to keep their operations with unpaid or self-employed labor returns can be attributed to their desire to enjoy land and work-related amenities. In other words, self-employed labor returns could be embedded in the amenity income value. In addition, we recognize that our private amenity income estimate could be overvalued if the private amenity activities were using as inputs intermediate services from other ranch activities.

Important economic values associated with the activities of these working woodlands are missed, or not accounted for, in the income measurement by national accounts and related economic analysis. The amenity component of ranching enterprises is becoming more important with as yet not fully understood outcomes for these ecosystems (Huntsinger and others 2010). If we want to progress in ecosystem accounting and in the integration of the market and non-market values into economic and policy decisions, the proposed method in this paper can be a departing point for larger scale application to these working woodlands. This could support conservation programs based on a better understanding of landowner decisions and potential responses to natural resource conservation policy.

**Acknowledgments**

The authors thank Alejandro Álvarez, Cristina Fernández, Larry Forero, John Harper, Bruno...
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References


Effects of Nitrogen Deposition on Multiple Ecosystem Services of the California Oak Savanna

Elise M. Tulloss and Mary L. Cadenasso

Abstract
The influence of enhanced nitrogen (N) deposition on key ecosystem services provided by oak woodlands was experimentally investigated. Fertilizer was applied for 2 years to paired plots in the oak understory and adjacent open grassland. Treatments simulated four N deposition levels and effects on forage productivity, biodiversity, and soil N supply were measured. At each treatment level, understory plots received twice the N fertilizer of paired open plots to simulate a deposition hotspot effect of the oak canopy. Soils in the open had lower inorganic N concentrations than the understory regardless of fertilizer level. Productivity largely did not respond to fertilization except at the highest level, where it declined by 34 percent and 25 percent relative to control plots in understory and open areas, respectively. Understory and open plots lost an average of two and one species under high N, respectively. These results indicate oak woodlands are resistant to the effects of N deposition on these ecosystem services up to 100 to 200 kg/ha/yr, which is a much higher level than currently received or expected. The different contributions by understory and open areas to these ecosystem services highlight the need to consider both habitats when predicting response to environmental change.

Key words: biodiversity, ecosystem services, nitrogen deposition, oak woodland, productivity, understory

Introduction
Oak woodlands provide many ecosystem services that benefit California, but understanding how these services may be altered in the face of environmental change is a challenge. Of particular importance are supporting services such as forage production and biodiversity. Forage production supports ranching operations, which is the primary use of oak woodlands (Huntsinger and others 2004). Biodiversity can support additional ecosystem functions such as decomposition, primary production, and nutrient cycling as well as support aesthetic or other cultural services in oak woodlands (Havstad and others 2007).

Nitrogen (N) deposition is one element of global change that may impact forage production, species diversity, and N cycling, in California oak woodlands. As agricultural land use intensifies and urban areas expand, N deposition to the adjacent oak woodlands is likely to increase (Grimm and others 2008). Nitrogen is often the limiting nutrient in oak woodland ecosystems (Harpole and others 2007a). Thus, N deposition may improve certain ecosystem services such as soil nutrient supply and productivity (Jones 1963). However, there may be tradeoffs as increasing levels of N deposition may negatively affect soils via nutrient loss and soil acidification (Likens

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1 An abbreviated version of this paper was presented at the Seventh Symposium on Oak Woodlands: Managing Oak Woodlands in a Dynamic World, Nov 3-6, 2014, Visalia, California.
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and others 1996, Vitousek and others 1997). Diversity may also suffer as excess N has also been shown to lead to species loss and increased dominance of invasive species (Harpole and others 2007b). It is important to determine critical levels of N deposition in oak woodlands beyond which the system can no longer absorb additional inputs without negative consequences to ecosystem services (Fenn and others 2010).

Nitrogen deposition levels are low in California compared to areas in the eastern United States and Europe. Oak woodlands are exposed to N deposition rates ranging from two to seven kg/ha/yr, but with hotspots of 30 to 90 kg/ha/yr in areas near intensive agriculture or the Los Angeles air basin (Fenn and others 2003). About 40 percent of California oak woodlands may be in exceedance of a critical level of N deposition based on lichen indicator species (Fenn and others 2010). Despite successful efforts to curtail N emissions (McDonald and others 2012), oak woodlands remain susceptible to increasing N deposition because of the concentration of new urban and agricultural developments in the oak woodland range (Ferranto and others 2014).

In oak woodlands, the tree-grass mosaic vegetation structure introduces spatial heterogeneity to the ground layer ecosystem. Oak understory and open grassland areas make important, and unique, contributions to ecosystem functions at the landscape scale. Particularly in low canopy cover oak savannas, tree canopies are hotspots of atmospheric deposition compared to the adjacent open grassland and understories are recognized as islands of soil fertility in the landscape (Dahlgren and others 1997; Tulloss and Cadenasso, n.d.). Understory soils have greater nutrient and organic matter concentrations and the plant community is distinct from the open (Jackson and others 1990). Changes in forage productivity, plant community diversity and ecosystem N supply, in response to N deposition, may vary between understory and open areas in the savanna.

We focus on three oak woodland ecosystem services—forage productivity, plant species diversity and soil N supply—to investigate how N deposition will affect these heterogeneous landscapes. Specific objectives were to 1) quantify the effect of N deposition on the ecosystem services of forage productivity, plant species richness, and N supply and 2) compare those effects in understory and open environments. We expected productivity and diversity to increase with N deposition as more N resources become available to support more plants. We also expected N deposition to correlate with N supply. However, at high levels of N deposition the ecosystem will likely be N saturated leading to a saturation in productivity and diversity or a possible decrease in those functions. Because understory soils have greater N cycling rates, they will likely have the capacity to absorb excess N, and thus, we further expected the understory to reach a saturation point at a higher level of N deposition.

Methods

We simulated a range of N deposition rates using fertilizer treatments in a field experiment at Hopland Research and Extension Center (HREC) in Mendocino County. Hopland has low ambient N deposition rates of 2 to 5 kg/ha/yr (NADP 2014); the understory receives approximately twice the deposition of the open (Tulloss and Cadenasso, n.d.). The study site had a savanna-type vegetation structure where oak canopy cover was about 30 percent. Fertilizer levels simulated four different deposition scenarios: 1) “Low,” a deposition level that occurs in much of the California oak woodland region (equivalent to a doubling of HREC ambient levels), 2) “Medium-Low,” the highest level found across the California oak
woodland, 3) “Medium-High,” a potential increase above the highest level under increased N emissions, and 4) “High,” a very high level that corresponds to agricultural fertilization rates and is not anticipated (table 1). The treatments maintained the natural deposition hotspot effect beneath oaks meaning that within a single fertilizer treatment, the understory plots received double the fertilizer of the plots in the adjacent open.

### Table 1—Application rates of ammonium nitrate fertilizer applied to open and understory plots. Each treatment level was divided into monthly applications. The division was unequal to mimic seasonal variation in inputs. To achieve the experimental deposition level, fertilizer was added assuming ambient deposition of two kg/ha in the open and four kg/ha in the understory based on previous site measurements (Tulloss and Cadenasso, n.d.)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Position</th>
<th>Deposition (kg/ha/yr)</th>
<th>Monthly application rate (g/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Sep-Nov, Dec Jan- Feb Mar Apr-Jun</td>
</tr>
<tr>
<td>Low</td>
<td>Open</td>
<td>5</td>
<td>0.22 0.13 0.25 0.09</td>
</tr>
<tr>
<td></td>
<td>Understory</td>
<td>10</td>
<td>0.43 0.25 0.50 0.19</td>
</tr>
<tr>
<td>Med-Low</td>
<td>Open</td>
<td>10</td>
<td>0.57 0.34 0.67 0.25</td>
</tr>
<tr>
<td></td>
<td>Understory</td>
<td>20</td>
<td>1.15 1.33 1.33 0.5</td>
</tr>
<tr>
<td>Med-High</td>
<td>Open</td>
<td>50</td>
<td>3.43 2.05 3.97 1.50</td>
</tr>
<tr>
<td></td>
<td>Understory</td>
<td>100</td>
<td>6.93 4.16 8.03 3.05</td>
</tr>
<tr>
<td>High</td>
<td>Open</td>
<td>100</td>
<td>6.93 4.16 8.03 3.05</td>
</tr>
<tr>
<td></td>
<td>Understory</td>
<td>200</td>
<td>14.00 8.40 16.23 6.16</td>
</tr>
</tbody>
</table>

### Experimental design

Paired 2 x 2 m² fertilizer and control plots were established in the understory and adjacent open of 20 trees (fig. 1). The oak trees selected for the experiment were Blue oaks (*Quercus douglasii*) and Valley oaks (*Q. lobata*) with a canopy diameter of at least 10 m. Each tree/open area was randomly assigned to one of the four fertilizer treatments. Ammonium nitrate was mixed into 500 ml of water and sprayed onto fertilized plots starting in fall 2010 and continuing monthly until spring 2012. Equivalent water volume was sprayed onto control plots. To avoid both surface effects of the fertilizer and irrigation effects, application date was coordinated with rain events as much as possible so that fertilizer would quickly be washed into soil by rain. Plots were fenced to prevent grazing.
Data collection and analysis

Productivity was determined by clipping plants at the soil surface from a 10 cm diameter ring randomly located in the outer 0.5 m of the plots. Plant biomass and litter were separated, dried, and weighed. Soil N supply was quantified by collecting 0 to 30 cm depth soil cores below each clipped ring and extracting inorganic N from soil cores with potassium chloride. Soil and plant biomass collections were made in the fall immediately following the first significant rains of the season and in the spring at peak biomass during the 2010-11 and 2011-12 seasons. To quantify diversity, a modified Daubenmire method was used to determine percent cover of all species present in the central m² of each plot in the spring of 2011 and 2012. From percent cover data, species richness was calculated for all plots (alpha diversity, \( \alpha \)). Beta diversity was also calculated. Beta diversity, specifically Whittaker’s \( \beta \), measures the turnover, or differences in species richness among plots of each habitat type (i.e., understory and open). It was calculated as \( \beta = \gamma / \alpha - 1 \), where \( \gamma_i \) is the total species pool for the habitat type \( i \) (understory or open).

To analyze the data, we fit linear mixed effects models predicting forage productivity, alpha diversity, or soil N supply using N fertilizer level and landscape position (open versus understory) as fixed effects and plot and tree as nested random effects to account for spatial autocorrelation. Individual models were run for each sample date. Data was log transformed to meet homogeneity of variance assumptions except for species richness data from spring 2011. All analyses were performed in JMP 11 (SAS Institute Inc. 2013).

Results

Soil N

Soil inorganic N concentrations exhibited high variation from tree to tree. A significant positive effect of fertilizer on soil N concentration appeared to be driven by differences between paired control and fertilized plots at the highest treatment level (table 2, fig. 2). Soil N was significantly higher in the understory compared to
the open (fig. 2). With one exception in spring 2012, soil N in the open did not increase over understory levels, even when comparing across treatments. Fall 2011 soil N concentrations were higher than fall 2010 and 2011 and 2012 spring samples, indicating a potential year effect. The significant interaction between fertilizer level and position was due to a stronger positive response to N in open plots compared to the open.

Table 2—P-values for linear mixed effects models testing the effect of N fertilization and landscape position (open versus understory) on ecosystem services

<table>
<thead>
<tr>
<th>Ecosystem Service</th>
<th>Season</th>
<th>Position (P)</th>
<th>N Level (N)</th>
<th>P x N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forage productivity&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Fall 2010</td>
<td>0.889</td>
<td>0.647</td>
<td>0.743</td>
</tr>
<tr>
<td></td>
<td>Spring 2011</td>
<td>0.023*</td>
<td>0.014*</td>
<td>0.0005**</td>
</tr>
<tr>
<td></td>
<td>Fall 2011</td>
<td>0.017*</td>
<td>0.086</td>
<td>0.887</td>
</tr>
<tr>
<td></td>
<td>Spring 2012</td>
<td>0.067</td>
<td>0.004*</td>
<td>0.961</td>
</tr>
<tr>
<td>Plant species diversity&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Spring 2011</td>
<td>&lt;0.0001**</td>
<td>0.4093</td>
<td>0.2430</td>
</tr>
<tr>
<td></td>
<td>Spring 2012</td>
<td>0.0005**</td>
<td>0.0307*</td>
<td>0.2524</td>
</tr>
<tr>
<td>Soil N supply&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Fall 2010</td>
<td>&lt;0.0001**</td>
<td>0.0004**</td>
<td>0.2703</td>
</tr>
<tr>
<td></td>
<td>Spring 2011</td>
<td>0.0002**</td>
<td>0.2195</td>
<td>0.8728</td>
</tr>
<tr>
<td></td>
<td>Fall 2011</td>
<td>&lt;0.0001**</td>
<td>&lt;0.0001**</td>
<td>0.0220*</td>
</tr>
<tr>
<td></td>
<td>Spring 2012</td>
<td>&lt;0.0001**</td>
<td>&lt;0.0001**</td>
<td>&lt;0.0001**</td>
</tr>
</tbody>
</table>

<sup>a</sup> aboveground productivity (g/m²), <sup>b</sup> species richness (i.e., alpha diversity), <sup>c</sup> Total inorganic N availability (ug/g)

*P < 0.05, **P < 0.001
Productivity

Similar to soil inorganic N concentrations, there was high variation in forage productivity among replicates. Productivity differed between understory and open only in spring 2011 and fall 2011. In both seasons, productivity was slightly greater in the understory compared to the open. In spring 2011, fertilization had a positive effect on productivity at low levels, but at the highest level productivity was reduced. At 100 kg/ha of fertilizer, productivity increased relative to control plots by 90 percent in the open and 65 percent in the understory, but decreased 30 percent in the understory at 200 kg/ha of fertilizer, giving an overall hump-shaped relationship between productivity and fertilization (fig. 3). In spring 2012, there were no positive effects of fertilizer on productivity. 2011-12 was a drought year, which may explain the lack of response to fertilizer in the spring compared with the previous year (fig 3, table 2). A significant interaction between fertilizer and landscape position in spring 2011 reflects the negative response to fertilizer in the understory at 200 kg/ha, while the open had a positive response up to 100 kg/ha. In spring 2012, plant productivity in both understory and open plots negatively responded to high fertilizer. Fall productivity showed no response to fertilizer (table 2).
Figure 3—Productivity response (mean +/- se) to N deposition level. Nitrogen deposition level is presented as categorical treatment. Understory plots are triangles and open grassland plots are circles. Fertilized plots are filled symbols and paired control plots are open symbols. Note differences in y-axes between Fall and Spring.

**Diversity**

Species richness at the plot level (alpha diversity) was lower in the understory compared to the open. The understory was characterized by higher beta diversity, or in other words, greater species turnover among plots (table 3). In spring 2011, fertilizer treatments had no effect on species richness, but in spring 2012, fertilizer reduced species richness significantly (table 2). The high N treatment lost on average two species from understory plots and one from open plots compared to control plots (fig. 4).
Table 3—Alpha and beta diversity mean and standard error in understory and open landscape position

<table>
<thead>
<tr>
<th>Position</th>
<th>Alpha diversity**</th>
<th>SE</th>
<th>Beta diversity*</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>9.3</td>
<td>0.4</td>
<td>4.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Understory</td>
<td>5.5</td>
<td>0.2</td>
<td>5.7</td>
<td>0.3</td>
</tr>
</tbody>
</table>

*P<0.05, **P<0.001; asterisks indicate significant differences in those diversity measures between open and understory positions.

Discussion and conclusions

At N deposition levels simulated here, little reduction to the key ecosystem services of forage productivity, biodiversity, and soil N supply was found. Some reduction in services was found when a rate of N deposition that is unrealistically high was applied. Therefore, California oak savannas may be resistant to N deposition. Soil N supply, which is logically a service expected to change under increased deposition, maintained levels comparable to control plots over a wide range of simulated deposition rates. In addition, N supply was consistently lower in the open than understory even where fertilizer in the open exceeded the rate in the understory. This could be due to higher plant uptake and microbial immobilization or to increased rates of N loss through leaching or volatilization and denitrification. The lack of a productivity response at low N levels supports the latter explanation and suggests N deposition in oak woodlands may have stronger impacts on downstream ecosystems than internal ecosystem functions. We are currently analyzing ion-exchange resin bags for evidence of N loss through leaching that would corroborate this.

Forage productivity and diversity services in the understory were more sensitive to the effects of N fertilization than open grasslands. Under a scenario where the understory continues to act as a deposition hotspot in the landscape, negative effects on these ecosystem services may appear first and be more severe in the understory than in the adjacent open within the same site. Understory and open grassland each make distinct contributions to the larger species pool and ecosystem N budget. A loss of productivity and especially of understory specialist species could represent an
important loss of resilience in the larger ecosystem. Fortunately, N deposition rates are much lower than the high fertilization rates that impacted ecosystem services and not expected to increase to those high levels in the future.

The results of this experiment emphasize the need to understand the effects of environmental changes on ecosystem services in spatially and temporally heterogeneous landscapes. Oak under stories are important reservoirs of soil nitrogen, forage productivity, and species diversity in the landscape. They may be more susceptible to the effects of high N deposition. In addition, the seasonal and year effects we observed suggest that long-term N deposition may affect the ecosystem in ways that our two year experiment was not able to capture. In particular, the 2011-2012 drought may have reduced the positive productivity response to low fertilizer levels because plants were primarily water limited instead of N limited. The drought may also have exacerbated the negative effects of high fertilizer on productivity by increasing the amount of time fertilizer was exposed to dry plant surfaces and increased foliar scorching. Ecosystem services of the California oak woodland are expected to change in response to trends in N deposition, climate, and land use changes. Monitoring deposition and its effects at relevant spatial and temporal scales may be crucial for anticipating a critical deposition level that will disrupt ecosystem services. In particular, we suggest that capturing variation between understory and open environments will be important for predicting the effects of N deposition on oak woodlands.

References


Developing Ecological Site and State-and-Transition Models for Grazed Riparian Pastures at Tejon Ranch, California

Felix P. Ratcliff, James Bartolome, Michele Hammond, Sheri Spiegal, and Michael White

Abstract
Ecological site descriptions and associated state-and-transition models are useful tools for understanding the variable effects of management and environment on range resources. Models for woody riparian sites have yet to be fully developed. At Tejon Ranch, in the southern San Joaquin Valley of California, we are using ecological site theory to investigate the role of two managed ungulate populations, cattle and feral pigs, on riparian woodland communities. Responses in plant species composition, woody plant recruitment, and vegetation structure will be measured by comparing cattle and feral pig management treatments among and between areas with similar abiotic conditions (ecological sites). Results from the second year of this project highlight the spatial variability of riparian woodland vegetation communities as well as temporally and spatially variable abundances of cattle and feral pigs. Development of riparian ecological site descriptions and state-and-transition models provide both a generalizable framework for evaluating management alternatives in riparian areas, and also specific direction for managing cattle and feral pigs.

Key words: cattle, ecological site descriptions, feral pigs, riparian area management, state-and-transition models

Introduction
Ecological site concepts and state-and-transition models have been widely developed to model spatial and temporal vegetation dynamics in arid rangelands. An ‘Ecological Site’ as defined by the Natural Resources Conservation Service is “a distinctive kind of land with specific physical characteristics that differs from other kinds of land in its ability to produce a distinctive kind and amount of vegetation, and in its ability to respond to management actions and natural disturbances” (Bestelmeyer and Brown 2010, Caudle and others 2013). Describing ecological sites allows land managers to prioritize management and conservation objectives and fine-tune management practices in heterogeneous landscapes by classifying the management area into discreet units with different potential vegetation dynamics and different responses to management actions (Bestelmeyer and Brown 2010).

State-and-transition models are typically organized as box and arrow diagrams showing what the potential vegetation states are for a given ecological site and what conditions cause transitions between states. States may be quantitatively or qualitatively described, but essentially represent a plant community within a range of variation which is of ecological or management interest (Westoby and others 1989). Dynamic soil properties such as erosion and sedimentation may also be used to distinguish between states (Duniway and others 2010). Most often these models are
used to display transitions due to temporal drivers on a given area such as: changes due to management, fire, or precipitation; however they can also be used to catalog spatial transitions occurring within an ecological site as a result of past conditions (Bestelmeyer and others 2011, Petersen and others 2009).

Development of ecological sites and state-and-transition models in the United States has been almost entirely limited to upland sites and has largely ignored riparian areas (Stringham and others 2001). Riparian systems along creeks in California’s semi-arid San Joaquin Valley have the underlying spatial and temporal variability in environmental factors which make them good candidates for non-linear plant community succession.

In addition to the physical factors responsible for spatial variability in upland systems (differences in soils, climate, and landscape position) spatial variation in riparian areas is also largely driven by differences in fluvial processes and hydrologic cycles between sites (Caudle and others 2013, Repp 2011, Stringham and Repp 2010). Processes governing temporal variation within riparian ecological sites differ somewhat from those in uplands as well. In addition to climatic and management drivers associated with inter-annual variation in uplands, intra and inter-annual fluvial processes and changes in soil hydrology may drive temporal variation in vegetation composition (Stringham and others 2001, Stringham and Repp 2010).

Some management practices that have limited effects on species composition in California’s upland rangelands may have amplified effects in riparian areas. Livestock grazing is thought to be responsible for little of the inter-annual variation seen in California’s upland grasslands (Jackson and Bartolome 2002), but even in lightly-stocked pastures grazing may have large effects on riparian vegetation as cattle tend to prefer these areas to surrounding uplands (George and others 2011). The effects of livestock grazing, however, are likely contingent on physical attributes of the system and characteristics of the plant species present (Kauffman and Krueger 1984).

Tejon Ranch, located in Southern California, contains 97 124 ha (240 000 ac) of conserved lands which are jointly managed by the Tejon Ranch Company, Tejon Ranch Conservancy (Conservancy), and two grazing lessees. Riparian area management was highlighted in the 2013 Ranch-Wide Management Plan, and the Conservancy’s riparian goals and objectives primarily revolve around managing vegetation structure to benefit a suite of nesting birds, but also include increasing native plant species cover and elimination of non-native species such as tamarisk (Tamarix ramosissima). Cattle grazing is the most widespread management action affecting riparian areas on the ranch, but recently concern has grown around a large population of feral pigs which appear to disproportionately favor riparian areas. In 2013, this study was initiated to investigate whether an ecological site and state-and-transition approach could identify baseline characteristics in riparian vegetation and demonstrate the effect of cattle and feral pig management on riparian resources.

Methods

Project location
The Tejon Ranch is located in southern California, encompassing areas of the San Joaquin Valley, Sierra Nevada, Mojave Desert, Tehachapi Mountains, and South Coast Ranges. The study takes place in the San Joaquin Valley portion of the Tejon
Vegetation sampling

Vegetation sampling occurred at each of the plots in late May and early June of 2013 and 2014. A “greenline” transect followed the foot of the creek bank and sampled vegetation growing near the water’s edge. This sampling method was adapted from the greenline sampling technique developed by Alma Winward (2000). Winward defines the greenline as “The first perennial vegetation that forms a lineal grouping of community types on or near the water’s edge. Most often it occurs at or slightly below the bankfull stage” (Winward 2000). We decided to move the greenline from the top of bank to the toe of the bank for the following reasons:

- The herbaceous vegetation at the top of bank was typically composed of the same annual grass species that dominate the adjacent uplands. In order to sample the herbaceous species composition most influenced by the stream we needed to sample in the wetter soils found at the toe of the bank.
- The first perennial species to form a continuous or semi-continuous line of vegetation was either a shrub (typically *Baccharis salicifolia*) or tree (typically *Salix* sp. or *Populus fremontii*). These woody plants were recorded in the sampling transects regardless of whether they were performed at the toe of the bank or the top of bank.

At each plot, greenline vegetation composition was measured along 50 m of the creek in three different strata: herbaceous, shrub, tree. To measure herbaceous vegetation, a line-point transect was performed whereby a point was extended every half-meter along the transect tape and the first hit within the first one-meter above the ground was recorded. A line-intercept transect was used to record shrub and tree composition along the greenline and perpendicular transects. This method records the lineal distance occupied by each species overhanging the transect tape within each canopy. Any plant overhanging the tape between one and three meters of height was recorded in the “shrub” category, and any plant overhanging the tape above three meters in height was recorded as a “tree”. It is important to note that the canopy categories were distinguished only by height. For example, the vining California grape (*Vitis californica*) could occur in the herbaceous, shrub, or tree category even though it is not technically an herb, shrub or tree.

Cattle and feral pig monitoring

In July 2013, a Moultrie M-880 camera trap was deployed at each study location to monitor feral pig and cattle activity at each study location, and to develop estimates of their activity on each plot. The camera traps were deployed within 25 m of the plot center. They were positioned to maximize detections of pigs, cattle, and other wildlife. Cameras were typically put along game trails or along creeks in areas with wide fields of view and few obstructions or branches which could trigger the camera in the wind.

The cameras were set to record a 30 second video each time they were triggered by movement, with a 15 second time lapse between videos. Videos were chosen
instead of still photographs because we wanted to more accurately assess the number of feral pigs, which often occur as large groups of unidentifiable individuals. Videos also enable the collection of behavioral data.

Prior to analysis, camera trap data were seasonally adjusted per plot. The seasonal adjustment corrected for missing data due to camera malfunction by estimating the number of cattle and pig detections in the missing period. We assumed these were proportional to the detection rate of the remainder of the season. For example, if a camera malfunctioned for 1 week out of the 12-week winter season, we assumed the missing week contained $1/11$ the number of detections of pigs and cattle as seen over the remainder of that season.

**Statistical methods**

Hierarchical cluster analysis of plot-level plant species composition can be used as a quantitative method of defining states and transitions for state-and-transition models (Spiegal and others 2014). A state can be defined as a grouping of plots with similar vegetation characteristics and close linkage distances between plots (close distances between plots in the cluster dendrogram). A temporal transition, then, is when a plot moves in cluster space between years (when the vegetation on a given plot changes from that characteristic of one cluster to another) (Spiegal and others 2014). Spatial transitions would then occur when different vegetation clusters occur in different areas within the same ecological site.

A cluster analysis was performed on the greenline vegetation data to investigate patterns of riparian plant community structure within the 15 study plots over 2 years. For this analysis the 30 unique plot*year combinations were clustered based on absolute cover of all live plant hits. Data were square-root transformed so that dominant species did not overly-influence the cluster assignments (McCune and Grace 2002). Similarly, all species occurring on less than 2 plot*years were removed from the analysis so that very rare species did not disproportionately influence the analysis. Species were entered for each canopy class separately. For example, the tree *Salix laevigata* occurring in both the shrub and tree canopies would be included twice: SALA_S and SALA_T. This allowed us to determine when differences between clusters were due to vegetation structure as well as composition. The cluster analysis was performed using Bray-Curtis distance which calculates similarity based on species found to be present on plots, not based on mutual absences (Zuur and others 2007).

Following Dufrene and Legrendre (1997), the cluster dendrogram was pruned to the number of groups which contained the most significant indicator species. Indicator species analysis also describes which species best characterize a cluster-based on the presence and abundance of species within and between groups (Dufrene and Legrendre 1997). Cluster analysis and indicator species analysis were performed in PC-ORD (McCune and Mefford 2011).

**Results**

The cluster analysis and subsequent dendrogram pruning using indicator species analysis revealed that four clusters was the optimal number to describe the variation seen among the 30 plot*years. These clusters are composed of anywhere from 4 to 12 plot*years, and include plots from one to three stream segments (table 1).
Table 1—Cluster assignments among the 30 plot*years

<table>
<thead>
<tr>
<th>Cluster Number</th>
<th>Plots included</th>
<th>Total plot*years in cluster</th>
<th>Stream segments included</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>UT2<em>2013, UT2</em>2014, UT3<em>2013, UT3</em>2014</td>
<td>4</td>
<td>Upper Tejon Creek</td>
</tr>
</tbody>
</table>

When looking at all three canopies together (table 1), there are strong spatial patterns to the cluster assignments. The Tunis Creek plots all form one exclusive cluster (cluster 4), and the indicator species analysis suggests that this cluster is distinguished from others by the occurrence of *Salix laevigata* in the herbaceous, shrub, and tree canopies; and by the high cover of *Hordeum murinum*, *Nasturtium officinale*, *Polypogon monspeliensis*, and *Rumex* sp. in the herbaceous canopy (table 2). The plots along Lower Tejon Creek cluster together as well (cluster 3), and one plot (Chanac 2) is included in the cluster too. This cluster is distinguished by *Salix goodingii* in the shrub and tree canopies, high cover of *Populus fremontii* in the shrub and tree canopies, high cover of *Baccharis salicifolia* in the shrub canopy, and high cover of *Xanthium strumarium*, *Apium graveolens*, and *Cynodon dactylon* in the herbaceous canopy. The plots along El Paso Creek cluster together and are joined in the cluster by plots from Chanac and Upper Tejon Creeks (cluster 1). This cluster is distinguished by having high cover of *Vitis californica* in all canopies and high cover of *Carduus pycnocephalus* in the herbaceous canopy. Finally, one cluster contains two dry plots on Upper Tejon Creek which are characterized by upland vegetation along the greenline (cluster 2). Significant indicator species for these plots are: *Bromus diandrus*, *Bromus rubens*, and *Brassica nigra*. 
Table 2. Significant indicator species for each cluster

<table>
<thead>
<tr>
<th>Cluster</th>
<th>Species</th>
<th>Canopy layer</th>
<th>Indicator value&lt;sup&gt;a&lt;/sup&gt;</th>
<th>p-value&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Carduus pycnocephalus</em></td>
<td>Herbaceous</td>
<td>50</td>
<td>0.0186</td>
</tr>
<tr>
<td></td>
<td><em>Vitis californica</em></td>
<td>Herbaceous</td>
<td>83.3</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td><em>Vitis californica</em></td>
<td>Shrub</td>
<td>100</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td><em>Vitis californica</em></td>
<td>Tree</td>
<td>100</td>
<td>0.0002</td>
</tr>
<tr>
<td>2</td>
<td><em>Bromus diandrus</em></td>
<td>Herbaceous</td>
<td>45.5</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td><em>Brassica nigra</em></td>
<td>Herbaceous</td>
<td>50</td>
<td>0.0126</td>
</tr>
<tr>
<td></td>
<td><em>Bromus rubens</em></td>
<td>Herbaceous</td>
<td>100</td>
<td>0.0004</td>
</tr>
<tr>
<td>3</td>
<td><em>Apium graveolens</em></td>
<td>Herbaceous</td>
<td>46.5</td>
<td>0.0166</td>
</tr>
<tr>
<td></td>
<td><em>Cynodon dactylyon</em></td>
<td>Herbaceous</td>
<td>37.5</td>
<td>0.0476</td>
</tr>
<tr>
<td></td>
<td><em>Xanthium strumarium</em></td>
<td>Herbaceous</td>
<td>37.5</td>
<td>0.0452</td>
</tr>
<tr>
<td></td>
<td><em>Baccharis salicifolia</em></td>
<td>Shrub</td>
<td>44.8</td>
<td>0.0034</td>
</tr>
<tr>
<td></td>
<td><em>Populus fremontii</em></td>
<td>Shrub</td>
<td>47</td>
<td>0.0196</td>
</tr>
<tr>
<td></td>
<td><em>Salix goodingii</em></td>
<td>Shrub</td>
<td>62.5</td>
<td>0.0026</td>
</tr>
<tr>
<td></td>
<td><em>Populus fremontii</em></td>
<td>Tree</td>
<td>47.4</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td><em>Salix goodingii</em></td>
<td>Tree</td>
<td>75</td>
<td>0.0008</td>
</tr>
<tr>
<td>4</td>
<td><em>Hordeum murinum</em></td>
<td>Herbaceous</td>
<td>47.2</td>
<td>0.0226</td>
</tr>
<tr>
<td></td>
<td><em>Nasturtium officinale</em></td>
<td>Herbaceous</td>
<td>54.6</td>
<td>0.0082</td>
</tr>
<tr>
<td></td>
<td><em>Polypogon monspeliensis</em></td>
<td>Herbaceous</td>
<td>77.4</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td><em>Rumex sp.</em></td>
<td>Herbaceous</td>
<td>52.8</td>
<td>0.0086</td>
</tr>
<tr>
<td></td>
<td><em>Salix laevigata</em></td>
<td>Herbaceous</td>
<td>50</td>
<td>0.0086</td>
</tr>
<tr>
<td></td>
<td><em>Salix laevigata</em></td>
<td>Shrub</td>
<td>49</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td><em>Salix laevigata</em></td>
<td>Tree</td>
<td>43.2</td>
<td>0.0002</td>
</tr>
</tbody>
</table>

<sup>a</sup> Indicator value is a measure of how well each species characterizes the cluster it is in. It is maximized (with a value of 100) when a species is only found in one cluster, and when it is found to occur in all plots within that cluster (Dufrene and Legrande 1997).

<sup>b</sup> The p-value tests the null hypothesis that the indicator value is actually 0 (McCune and Grace 2002).

There were no transitions observed between years for any of the 15 plots. For each of the plot*years, the plot*year with the closest linkage distance (distance in the cluster dendrogram) was the same plot in the alternate year, indicating that vegetation composition was very stable between years. This compositional stability between years also held when the tree layer was removed and the analysis was performed on the shrub and herbaceous canopies together. In this analysis, the closest plot*years in cluster space were always the same plot in an alternate year (with the exception of two plots in Lower Tejon Creek), and no transitions between clusters were observed between years. When both tree and shrub layers were removed from the analysis, the plots comprising each cluster changed significantly, and one transition was observed. In this subset of the analysis, Tunis Creek Plot #3 (TU3) transitioned from a cluster containing only Tunis Creek plots to one with a variety of other creeks. The indicator species analysis suggests that this transition is driven by a decrease in cover of *Hordeum murinum*, *Nasturtium officinale*, and *Rumex* sp.; and a subsequent increase in *Bromus diandrus*.
**Abundances of pigs and cows**

More than 27,000 videos were reviewed from the 15 plots between late July 2013 and the first week of June 2014. Of these, 9,540 videos contained cattle and 4,173 videos contained pigs. An index of activity was built for each species. The index is simply the sum of the seasonally adjusted number of individuals of each species observed in all the videos reviewed. This activity index was then separated by season and plot to show seasonal as well as spatial heterogeneity in cattle and pig activity (figs. 1 and 2).

Seasonal cattle activity declined in the riparian plots from summer 2013 to spring 2014, likely reflecting cattle preference for these areas in the summer and fall when they offer thermal cover, green forage, and water. This decline may also reflect operational decisions by grazing lessees to remove cattle in response to the severe 2013-2014 drought. In contrast, feral pig activity was relatively stable over the course of the year (fig. 1). Spatial variation in pig and cattle activity was high when looking across the entire sampling period. Even plots within the same pasture (such as CH1, CH2, and CH3) had cattle and pig activity that varied by more than a factor of 2 (fig. 2).

![Cow Activity Index--By Season](image1)

![Pig Activity Index--By Season](image2)

*Figure 1—Cattle and pig activity among the 15 plots by season, starting in summer 2013 and continuing through spring 2014.*
Discussion

The cluster analysis showed that there is strong spatial grouping of vegetation states on the landscape; however, this is expressed differently among the stream segments. Sometimes a cluster is exclusive to a stream segment (for example cluster 4 on Tunis Creek). This might indicate that the creek segment constitutes a unique ecological site and that the physical differences which distinguish this site are responsible for the observed variation in vegetation. Other times clusters occur alongside other clusters on multiple stream segments (for example clusters 1, 2, and 3 on Chanac, El Paso, and Upper Tejon Creeks). This means either that different ecological sites are present within a single stream segment, or that there are different states found in the same ecological site across space. An important future step for this project will be defining the ecological sites so that we can better understand the drivers governing spatial variation.

When looking at the indicator species associated with transitions, it is evident that differing cover of widespread species (not just presence/absence) often plays a big role in differentiating between clusters. For example, *Bromus diandrus* and *Salix laevigata* are found on many sites, yet they are indicative of clusters 2 and 4 respectively. Therefore it is feasible that these represent alternate states within an ecological site and transitions could occur over time within a plot if the abundances of these species were to change. Furthermore, if cattle and pigs affect woody plant recruitment or survival then it is possible for them to drive transitions on a plot.

The high degree of stability between years on all plots indicates that when considering all vegetation canopies together, transitions are unlikely to occur on any given year and may take many years to transpire. This is largely due to the perennial nature of the species in the shrub and tree canopies. One strategy for observing transitions in such a system is to observe study plots over many years. A second strategy will be available to us after we define ecological sites among all the plots. If there are multiple states occurring on different plots within an ecological site, then we can infer that these represent alternate states and that there may be transitions between them. These ‘spatial transitions’ could result from different historical factors causing different transitions over time on each plot and could provide useful information about the range of potential vegetation states within an ecological site. Short-term studies could show what potential effects of management are by looking
at the effects of temporal drivers including cattle and feral pig activity, annual variation in precipitation, fluvial disturbances such as floods and sediment deposition on woody plant recruitment, vegetation composition, and changes in fluvial geomorphology.

The camera trapping results show that cattle activity is greatly influenced by season; spending much more time in riparian areas in the summer and fall when these areas provide shade, water, and green forage. Pig activity increased over the course of a one-year period despite high hunting pressure from Tejon Ranch operations which took more than 1000 pigs between September 2013 and July 2014 (roughly the same window as the camera trapping). The spatial variability of cattle activity within a single pasture shows that pasture-scale grazing intensity along riparian corridors is difficult to control in large pastures; even in pastures with low grazing pressure. The pasture containing all three Chanac Creek plots is 4016 ha (9926 ac) and had cattle activity which varied by a factor of two within the three plots. While this heterogeneity in grazing intensity might have desirable outcomes such as increased vegetation heterogeneity (Fuhlendorf and Engle 2001), it poses challenges for management seeking to achieve uniform control or striving to avoid patches of intensive use. Some desired management outcomes may therefore be better achieved by limiting timing of riparian grazing rather than attempting to control intensity through stocking rates in large pastures.

The vegetation cluster analysis showed that there is significant variation in vegetation composition between the 15 study plots. Future work to define ecological sites will help determine when this variation is due to underlying physical factors at each plot and when it is due to historical transitions that brought about the states observed today. The stability of vegetation clusters between years points to the need to look at factors which could precipitate transitions over time, rather than expecting to see transitions on an inter-annual basis. These investigations will focus on the effects of temporal drivers including cattle and feral pig activity, annual variation in precipitation, and fluvial disturbances such as floods and sediment deposition on woody plant recruitment, vegetation composition, and changes in fluvial geomorphology. Finally, we plan on building cattle and pig exclosures to better understand the role of cattle and pig activity in these systems.

References


Soil Organic Carbon Stability Across a Mediterranean Oak Agroecosystem

Leslie M. Roche, James F. Chang, Johan Six, Anthony T. O’Geen, and Kenneth W. Tate

Abstract
Rangelands are estimated to cover 30 to 50 percent of the world’s land surface and have significant belowground carbon (C) storage potential. Given their geographical extent, many have suggested that even modest changes in C storage via management practices could alter the global C cycle, creating climate change mitigation opportunities. Our objective was to investigate soil organic carbon (SOC) stability across a managed annual grassland, savanna, and oak woodland landscape. We sampled A and AB horizons from 20 soil profiles to assess long-term SOC stabilization pathways using combined physical and chemical SOC laboratory fractionation techniques. We found that although total SOC was positively correlated with woody plant cover, the SOC stabilization mechanisms differed only slightly across this gradient of woody cover (0 to 100 percent)—for all practical purposes, the relative proportions of physically protected C, biochemically protected C, and unprotected C were largely non-responsive to woody cover. Therefore, we found woodland and savanna soil carbon stores were not more resilient to disturbances than grassland carbon stores, and so can be quickly degraded and lost upon removal of woody cover.

Key words: carbon sequestration, hardwood rangeland, soil organic carbon stabilization

Introduction
Soil organic matter (SOM) is the largest carbon (C) reservoir in the terrestrial biosphere (~1,550 Gt C), and contains over two-fold the C found in the atmospheric pool (~750 Gt C) (Schlesinger 1997). Over the last decade, there has been substantial concern regarding the impacts of land management practices and associated land-use changes on terrestrial C stocks (Follett and Reed 2010). Land-use and land-cover influence SOM pools, and thus exert strong controls over the mean residence time of soil organic C (SOC) (Houghton and others 1999, Schimel 1995). Understanding the relationship between land management practices and SOC stability is critical. Land management potentially impacts SOC stability via impacts to dynamic soil properties such as soil structure and aggregate stability, which determine soil’s capacity to retain C (Six and others 2000a). Management practices can also alter dominant vegetation classes, which control both organic C inputs and inherent biochemical resistance to decomposition (Guo and Gifford 2002, Post and Kwon 2000).

Rangelands span diverse land resources—including uncultivated grasslands, shrublands, and forested lands—and are estimated to cover approximately 30 to 50 percent of the world’s terrestrial surface and store 10 to 30 percent of the world’s SOC (Conant and others 2001, Derner and Schuman 2007, Ojima and others 1993,
Schlesinger 1997, Watson and others 2000). Current global estimates for rangelands put SOC sequestration rates as high as 0.3-0.5 Pg C/yr (Lal 2004, Schlesinger 1997, Scurlock and Hall 1998), positioning rangelands as a major terrestrial C reservoir. Given the large geographical extent of rangelands, many have suggested that even modest increases in C storage via management practices could alter the global C cycle—providing opportunities for climate change mitigation (Dahlgren and others 2003, Derner and Schuman 2007, Laca and others 2010).

Previous research on rangeland ecosystems has largely focused on total SOC pools, with limited attention to the principal drivers affecting SOC dynamics and C sequestration. Total SOC alone is not a sensitive measure of SOC dynamics and may not accurately predict SOC stabilization over longer time scales in response to land management practices or environmental conditions. Previous efforts in more intensive cropping systems have utilized physical and chemical fractionation techniques to isolate functional SOC fractions, which are defined by stabilization mechanisms and can therefore be related to SOC stability (Denef and others 2004, Jagadamma and Lal 2010, Six and others 2000a). The two major pathways of SOC stabilization are 1) physical protection of SOC in soil microaggregates, and 2) biochemical protection of SOC via inherent recalcitrance (Six and others 2000a). Together, these pathways create a complex protection stratum that potentially grades SOC stability on a spectrum of labile to stable SOC pools.

Oak woodland-savanna-grassland rangelands in Mediterranean regions around the world cover approximately 7 million hectares, and receive substantial management and removal of oak and other woody species to enhance forage and livestock production goals (Roche and others 2012). In California’s oak rangelands, loss of relatively high total SOC levels has been documented within two decades of woody species removal (Dahlgren and others 1997). The objective of this study was to investigate pathways of SOC stability across a landscape mosaic spanning open savanna to oak forest in an attempt to identify underlying mechanisms for SOC loss.

**Methods**

**Study area**

This study was conducted at the University of California Sierra Foothill Research and Extension Center (SFREC) in Yuba County, CA (39°14’22”N, 121°17’46”W). Located in the northern Sierra Nevada foothills, SFREC has a Mediterranean climate with hot, dry summers and cool, wet winters—mean annual precipitation is 740 mm and mean annual air temperature is 15 °C. Soils were formed on basic metavolcanic (greenstone) bedrock and are classified as Typic or Mollic Haploxeralfs. The clay mineralogy consists of vermiculite-chlorite, vermiculite, chlorite, kaolinite, and some smectite (Dahlgren and others 2003).

The landscape is a mosaic of open grassland and oak canopy, producing patches of open grassland, savanna, woodland, and forest. This hardwood rangeland is dominated by Quercus douglasii (blue oak), a deciduous oak, with Q. wislizenii (live oak) and Pinus sabiniana (foothill pine) also present. Understory vegetation is dominated by annual grasses such as Avena fatua (wild oats) and Bromus spp. Common forbs include Erodium spp. (filaree) and Trifolium spp. (annual clovers).
**Field sampling and bulk soil analysis**

We excavated 20 soil profiles across a woody plant canopy cover gradient from open savanna to closed forest. Soil profiles were excavated at one to two subplots prior to onset of the rainfall season. Soils were sampled from A and AB horizons as intact clods. At each soil profile sampling site, we used a modified convex spherical densitometer to calculate percent canopy cover (Mulvey and others 1992). Sampling sites were classified as open savanna (<25 percent), oak woodland (25 to 80 percent), or oak forest (>80 percent).

Total C/N analysis using a dry combustion elemental analyzer (ECS 4010, Costech Analytical Technologies Inc., Valencia, CA) and standard chemical and physical soil analyses were performed on bulk soil samples (fig. 1). Bulk density was determined using the 3D scanner method (NextEngine DeskTop 3D Scanner Model 2020i, NextEngine, Inc., Santa Monica, CA) (Rossi and others 2008). Soil texture and pH were analyzed using the pipette method (Jackson 2005) and a 1:1 soil to water ratio (Soil Survey Staff 2004), respectively.

![Soil analysis scheme](image)

Figure 1—Soil analysis scheme. Letters indicate the soil separation procedure: A) aggregate size class separation, B) microaggregate separation, C) intra-microaggregate particulate organic matter separation. Superscript numbers denote treatments and analyses: 1) total C/N, 2) hot water carbon extraction, and 3) wet oxidation treatment, and 4) selective dissolution of Fe. LMA = large macroaggregates, SMA = small macroaggregates, micro = free microaggregates, s+c = free silt plus clay. cPOM = coarse particulate organic matter, Tmicro = total microaggregates, Ts+c = total silt plus clay not occluded in microaggregates, imPOM = particulate organic matter inside total microaggregate, s+cm = silt plus clay inside total microaggregates.

Selective dissolution of extractable Fe was also performed to assess potential effects of soil mineralogy on SOC stability (O'Geen and others 2010). We acquired quantitative mineralogical properties by performing selective dissolution of extractable Fe on bulk soil samples adapted from standard methods (Soil Survey Staff 2004). Selective dissolution procedures were conducted to yield three forms of extractable Fe, which were measured via atomic adsorption (AAnalyst 200, PerkinElmer Instruments, Shelton, CT) 1) dithionite-citrate extractable Fe (Fe$_{d@}$), considered as total extractable Fe; 2) sodium pyrophosphate extractable Fe (Fe$_{pyr}$), considered as total organo-metal complexed Fe; and 3) ammonium oxalate extractable Fe (Fe$_{ox}$).
**Physical and chemical SOC fractionation**

SOC fractions were acquired in order of microbial accessibility by first physically fractionating bulk soil into aggregate size classes, followed by sequential hot water extractions and wet oxidation treatments (fig. 1).

**Aggregate size class separation and microaggregate isolation**

To assess soil aggregate stability, four aggregate size classes were first isolated via wet sieving of bulk soil (Benchfly 2013b) (fig. 1, procedure A). Each aggregate size class was then forced-air dried at 60 °C and prepared for total C/N analysis.

An additional 20 g soil subsample separated into three additional fractions (Benchfly 2013a, Gentile and others 2011, Six and others 2000b): particulate organic matter plus sand (cPOM, >250 μm), total microaggregates (free microaggregates and microaggregates protected within macroaggregates; Tmicro, 53 to 250 μm), and total silt plus clay outside of Tmicros (Ts+c, <53 μm) (fig. 1, procedure B). Fine POM occluded in Tmicros (imPOM, >53 μm) were separated from silt plus clay inside total microaggregates (s+cm, <53 μm) (fig. 1, procedure C) according to Zotarelli and others (2005). All fractions were forced-air dried at 60 °C and stored at room temperature for subsequent analyses, including total C/N analysis.

**Hot-water extraction and wet chemical oxidation treatments**

Hot water extractable SOC (HWC) was obtained from Ts+c (HWC-Ts+c) and s+cm (HWC-s+cm) size classes with methods modified from Haynes and Francis (Haynes and Francis 1993) (fig. 1, procedure 2). Total dissolved organic C in water extracts were analyzed with a Shimadzu TOC Analyzer (Model TOC-VCSH, Japan).

Following hot water extraction, Ts+c and s+cm subsamples underwent wet chemical oxidation treatments according to Siregar and others (2005) (fig. 1, treatment 3), and then prepared for total C/N analysis.

**Physical and biochemical SOC protection pathways**

Using results from physical and chemical fractionation techniques, we integrated the measured fractions into three functional SOC pools:

Unprotected SOC = cPOM + HWC-Ts+c + NaOCl-Ts+c

Physically Protected SOC = imPOM + HWC-s+cm + NaOCl-s+cm

Biochemically Protected SOC = NaOCl-Ts+c + NaOCl-s+cm

We standardized functional SOC values by total SOC (cPOM + Tmicro + Ts+c) to produce relative values for each pool.

**Statistical analysis**

Given that the samples sites were located across a hardwood gradient, we first examined potential relationships between woody plant canopy cover and total SOC. For this initial analysis only, we combined A and AB horizon data and constructed multiple linear mixed effects (LME) regression models (Pinheiro and Bates 2000, Rabe-Hesketh and Skrondal 2008) to test effects of woody plant canopy cover.

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5 XB represents SOC oxidized during NaOCl treatment.
(continuous, fixed effect) on total soil organic carbon (response variables). To account for hierarchical nesting of multiple soil profiles within a single vegetation plot, plot ID was designated as a grouping variable (random effect).

To investigate pathways of SOC stability across woody plant canopy cover classes, we examined differences in 1) aggregate size class distributions, 2) SOC fractions, and 3) the three functional SOC pools (unprotected, physically protected, and biochemically protected C pools) for the A and AB soil horizons. To account for hierarchical nesting of multiple soil profiles within a single vegetation plot, we designated plot ID as a grouping variable (random effect).

We also examined biochemically labile and stable SOC fractions. We constructed separate LME regression models for each woody plant canopy cover class and soil horizon combination to compare mean SOC concentrations between 1) HWC-Ts+c and HWC-s+cm, and 2) NaOCl-Ts+c and NaOCl-s+cm. For these models, vegetation plot identity remained the grouping variable (random effect), and the HWC and NaOCl treatment IDs were fixed effects (in other words HWC-Ts+c/HWC-s+cm and NaOCl-Ts+c/NaOCl-s+cm). Standard diagnostic analyses were utilized, and all models were estimated in Stata/SE 13.0 (StataCorp 2013).

**Results and discussion**

**Soil characteristics and total SOC patterns**

Tables 1 and 2 summarize general study site soil characteristics across the woody plant canopy cover classes. Mean total SOC and total N concentrations were consistently greater in A horizons than AB horizons for all woody plant canopy cover classes (table 2). O horizons were most prevalent in oak forest soil profile sites—O horizons were observed in five of six oak forest sites, two of six oak woodland sites, and no O horizons were observed at open savanna sites.

Preliminary analyses of Total SOC contents showed significant ($P = 0.037$) increases in SOC along a gradient (0 to 100 percent) of woody plant canopy cover. This pattern of increasing total SOC with woody cover is consistent with previous research demonstrating enhanced soil fertility under tree canopy relative to adjacent open grassland (Dahlgren and others 2003, Dahlgren and others 1997, Kay 1987).

The high concentration of Fe in these soils (table 2) potentially facilitates the formation of stable organo-mineral complexes and Fe hydr(oxides) that enhance resilience of aggregates, where organic C can be physically protected from microbial attack (Barthes and others 2008, Panayiotopoulos and others 2004). The high mineral surface area of poorly crystalline Fe-(hydr)oxides likely further enhances SOC stability through greater aggregation (Six and others 2000b) and adsorption sites for polyvalent organic materials (Duiker and others 2003).
## Table 1—Mean bulk soil properties (± 1 SE) of the fine earth fraction in A and AB soil horizons for each woody plant canopy cover class

<table>
<thead>
<tr>
<th></th>
<th>Texture</th>
<th>Bulk density (g cm⁻³)</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thickness (cm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A Horizon</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open savanna</td>
<td>5.3 ± 0.5</td>
<td>40.9 ± 1.9</td>
<td>18.1 ± 1.3</td>
</tr>
<tr>
<td>Oak woodland</td>
<td>5.8 ± 0.7</td>
<td>35.1 ± 1.8</td>
<td>44.4 ± 0.9</td>
</tr>
<tr>
<td>Oak forest</td>
<td>6.2 ± 0.7</td>
<td>37.7 ± 1.0</td>
<td>44.5 ± 1.1</td>
</tr>
<tr>
<td>AB Horizon</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open savanna</td>
<td>17.0 ± 1.3</td>
<td>39.0 ± 2.3</td>
<td>41.2 ± 1.1</td>
</tr>
<tr>
<td>Oak woodland</td>
<td>14.5 ± 1.6</td>
<td>33.6 ± 2.5</td>
<td>45.0 ± 1.2</td>
</tr>
<tr>
<td>Oak forest</td>
<td>14.0 ± 2.0</td>
<td>35.1 ± 1.1</td>
<td>44.5 ± 1.2</td>
</tr>
</tbody>
</table>

## Table 2—Mean concentrations (g C/kg soil) (± 1 SE) of total SOC¹, total N, Fe₉ₑ (total extractable Fe), Fe₉ₓ (poorly crystalline + organo-metal complexed Fe), and Feₓᵧᵧoxy (organo-metal complexed Fe) and mean C/N of A and AB soil horizons for each woody plant canopy cover class

<table>
<thead>
<tr>
<th></th>
<th>Total SOC a (g/kg soil)</th>
<th>Total N (g/kg soil)</th>
<th>C:N</th>
<th>Fe₉ₑ (g/kg soil)</th>
<th>Fe₉ₓ (g/kg soil)</th>
<th>Feₓᵧᵧoxy (g/kg soil)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A Horizon</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open savanna</td>
<td>30.5 ± 2.6</td>
<td>2.9 ± 0.4</td>
<td>11.7 ± 1.7</td>
<td>20.2 ± 1.0</td>
<td>2.7 ± 0.21</td>
<td>2.2 ± 0.13</td>
</tr>
<tr>
<td>Oak woodland</td>
<td>42.0 ± 8.3</td>
<td>3.1 ± 0.6</td>
<td>13.8 ± 1.3</td>
<td>32.0 ± 5.4</td>
<td>2.6 ± 0.34</td>
<td>2.4 ± 0.17</td>
</tr>
<tr>
<td>Oak forest</td>
<td>36.0 ± 4.1</td>
<td>3.8 ± 1.0</td>
<td>12.1 ± 2.0</td>
<td>25.8 ± 3.4</td>
<td>3.2 ± 0.39</td>
<td>2.1 ± 0.32</td>
</tr>
<tr>
<td>AB Horizon</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open savanna</td>
<td>12.6 ± 1.9</td>
<td>0.9 ± 0.1</td>
<td>14.6 ± 2.2</td>
<td>21.8 ± 1.2</td>
<td>2.2 ± 0.11</td>
<td>2.7 ± 0.30</td>
</tr>
<tr>
<td>Oak woodland</td>
<td>13.0 ± 2.4</td>
<td>0.7 ± 0.04</td>
<td>17.8 ± 3.3</td>
<td>31.6 ± 7.2</td>
<td>2.3 ± 0.14</td>
<td>3.1 ± 0.14</td>
</tr>
<tr>
<td>Oak forest</td>
<td>15.4 ± 1.9</td>
<td>1.0 ± 0.1</td>
<td>16.4 ± 2.3</td>
<td>28.9 ± 3.2</td>
<td>3.1 ± 0.27</td>
<td>3.2 ± 0.31</td>
</tr>
</tbody>
</table>

¹ Total SOC calculated as cPOM + Tmicro + Ts+c

### Aggregate stability and SOC fractions

Proportions of large and small macroaggregate (LMA and SMA) size classes were not significantly different among vegetation classes (fig. 2), which suggests soil stability and resistance to disturbances is similar for open savanna, oak woodland, and oak forest soils. Size class distributions were generally skewed toward larger classes in A soil horizons, while the LMA, SMA, and macroaggregate size classes were more evenly distributed in AB soil horizons (fig. 2). It is well known that more stable C pools are found with increasing soil depth (Rumpel and Kogel-Knabner
2011), and so the increase in proportion of microaggregates with depth is not surprising. Microaggregates are more stable than the larger macroaggregate size classes (LMA and SMA), and therefore represent a longer term pool for soil carbon storage (Six and others 2000a).

Figure 2—Mean (± 1 SE) weight distribution (percent size class of bulk soil) of aggregate size classes across woody plant canopy cover classes for A (A) and AB (B) horizons. LMA=large macroaggregates (> 2000 μm), SMA=small macroaggregates (2000-250 μm), micro=micromacgregates (25-53 μm), and s+c=silt plus clay (<53 μm). For each size class, different successive letters indicate significant differences (p <0.05).

Overall, the larger aggregate size classes appeared to store more SOC than smaller aggregate size classes, and SOC concentrations in macroaggregates (LMA and SMA) and microaggregates (micro) generally decreased with depth (fig. 3). For the cPOM, Tmico, Ts+c, s+cm, and imPOM fractions, SOC concentrations also generally decreased with depth. There were no significant differences in SOC between vegetation classes for the Ts+c, s+cm, or imPOM fractions (table 3); however, Tmico-SOC significantly increased with woody plant cover for A horizons, and cPOM-SOC significantly increased with woody plant cover for AB horizons.

For hot-water extraction and wet chemical oxidation treatments, only HWC-s+cm (considered biochemically labile) significantly differed between vegetation classes (table 4). The concentration of HWC characterizes the relative availability of “active” SOC, which is energetically preferred for microbial assimilation (Ghani and others 2003, Haynes and Francis 1993). The overall apparent accumulation of HWC Ts+c and s+cm with greater canopy cover may be attributed to inputs of fresh residue-C from degradation of organic materials in overlying O horizons observed at oak forest and woodland sites.
Table 3—Mean (± 1 SE) concentration (g C/kg soil) of SOC fractions across woody plant canopy cover classes for A and AB horizons. For each size class within a horizon, means with different letters are significantly different (P < 0.05)

<table>
<thead>
<tr>
<th>SOC Fraction</th>
<th>A Horizon</th>
<th>AB Horizon</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>cPOM (g/kg soil)</td>
<td>Tmicro (g/kg soil)</td>
</tr>
<tr>
<td>A Horizon</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open savanna</td>
<td>7.9 ± 0.6</td>
<td>12.6 ± 1.6</td>
</tr>
<tr>
<td>Oak woodland</td>
<td>10.3 ± 3.4</td>
<td>18.8 ± 3.9</td>
</tr>
<tr>
<td>Oak forest</td>
<td>8.4 ± 1.7</td>
<td>16.3 ± 1.8</td>
</tr>
<tr>
<td>AB Horizon</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open savanna</td>
<td>1.1 ± 0.3</td>
<td>5.3 ± 0.9</td>
</tr>
<tr>
<td>Oak woodland</td>
<td>1.3 ± 0.2</td>
<td>5.8 ± 1.6</td>
</tr>
<tr>
<td>Oak forest</td>
<td>2.4 ± 0.5</td>
<td>6.6 ± 1.1</td>
</tr>
</tbody>
</table>

For the A soil horizon, mean HWC concentrations were significantly (P <0.05) lower in the s+cm than in the Ts+c fractions across all vegetation classes; for the AB soil horizon, mean HWC concentrations were significantly (P <0.05) lower in the s+cm than in the Ts+c fractions for the oak savanna and oak woodland classes (table 4, statistical test results not shown in table). This suggests a strong microbial influence on the Ts+c fraction, where mucilages produced during SOM decomposition become binding agents for macroaggregation.
Table 4—Mean (± 1 SE) concentration (g C/kg soil) of hot water extractable C (HWC-) and sodium hypochlorite resistant C (NaOCl-) associated with total silt plus clay outside (Ts+c < 53) and inside (s+cm) microaggregate size classes in the A and AB horizons for each woody plant canopy cover class. For each size class within a horizon, means with different letters are significantly different (P <0.05).

<table>
<thead>
<tr>
<th></th>
<th>HWC-Ts+c (g/kg soil)</th>
<th>HWC-s+cm (g/kg soil)</th>
<th>NaOCl-Ts+c (g/kg soil)</th>
<th>NaOCl-s+cm (g/kg soil)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A Horizon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open savanna</td>
<td>0.52 ± 0.06</td>
<td>0.25 ± 0.01 a</td>
<td>2.5 ± 0.3</td>
<td>2.0 ± 0.3</td>
</tr>
<tr>
<td>Oak woodland</td>
<td>0.49 ± 0.09</td>
<td>0.29 ± 0.03 ab</td>
<td>3.9 ± 0.8</td>
<td>2.2 ± 0.8</td>
</tr>
<tr>
<td>Oak forest</td>
<td>0.63 ± 0.12</td>
<td>0.36 ± 0.05 b</td>
<td>3.0 ± 0.6</td>
<td>2.3 ± 0.3</td>
</tr>
<tr>
<td>AB Horizon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open savanna</td>
<td>0.19 ± 0.02</td>
<td>0.15 ± 0.03</td>
<td>1.3 ± 0.2</td>
<td>1.0 ± 0.2</td>
</tr>
<tr>
<td>Oak woodland</td>
<td>0.26 ± 0.06</td>
<td>0.13 ± 0.01</td>
<td>1.2 ± 0.2</td>
<td>1.0 ± 0.2</td>
</tr>
<tr>
<td>Oak forest</td>
<td>0.21 ± 0.02</td>
<td>0.15 ± 0.04</td>
<td>1.5 ± 0.4</td>
<td>1.1 ± 0.1</td>
</tr>
</tbody>
</table>

SOC remaining after a NaOCl treatment represents C that is biochemically protected via complex organic assemblages inherent in plant tissues (Siregar and others 2005). NaOCl-resistant SOC in s+cm represents SOC that is further protected by physical occlusion in microaggregates. NaOCl-resistant SOC concentrations were significantly lower in the s+cm than in the Ts+c fractions for open savanna and oak woodland A horizons (table 4, statistical results not show in table)—suggesting a stronger biotic control. In contrast, NaOCl-resistant SOC concentrations found in the AB horizon were relatively similar across Ts+c and s+cm, suggesting a stronger abiotic control. The observed high concentrations of poorly crystalline Fe (hydr)oxides in these soils (table 1) potentially enhances SOC stability (Kleber and others 2005, Mikutta and others 2006).

**Pathways of SOC stabilization**

Canopy cover had limited influence on the proportions of unprotected, physically protected, and biochemically protected SOC pools. The percent unprotected and percent physically protected C were significantly (P <0.05) different between vegetation classes for A soil horizons; however the difference in mean responses between the open savanna and oak forest classes was only 6 to 7 percent (fig. 4). Additionally, the percent biochemically protected C pool was not significantly (P >0.10) related to woody plant canopy cover.

An unexpected and important finding was that the unprotected carbon pool was >44 percent for all vegetation classes. That is, the dominant fraction of the total carbon pool is determined by abiotic and biotic controls (for example, moisture, temperature, intrinsic biodegradability of inputs, and N availability) on microbial activity (Six and others 2002). Although there is considerable potential for carbon sequestration with woodland conservation and restoration, these carbon stores are not more resilient to disturbances than grassland carbon pools and can be quickly degraded and lost upon oak removal. These findings provide evidence for the underlying mechanisms driving
documented losses of total SOC levels with oak removal on hardwood rangelands (Dahlgren and others 1997).

Figure 4—Carbon pool values (fraction of total carbon ± 1 SE) for the three functional SOC pools for A (A) and AB (B) horizons for each woody plant canopy cover class. For each functional SOC pool, different successive letters indicate significant differences (p < 0.05).

Acknowledgments
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Tracy V. Hruska,² Lynn Huntsinger,² and Jose L. Oviedo,³

Abstract
An ongoing study of the small wetlands in the northern Sierra Nevada foothill oak woodlands that provide habitat for the state-threatened California black rail (Laterallus jamaicensis coturniculus) offers an example of the way that the social ecological systems (SES) framework can be used to analyze a natural resource problem. At the outset, it was hypothesized that the area’s hydrology, West Nile Virus from wetland mosquitoes, the population ecology of the bird, and the decisions of landowners would have important impacts on the wetlands and birds. A SES framework was applied to identify and understand the interactions among ecological and human factors. The case of irrigated wetlands in Sierra foothill woodlands turns out to be an example of a fractured SES. Actions within the social system are having profound impacts on the natural system, but these resulting changes in the natural system appear to have little or no feedback to the social system. Intervention points identified include education of landowners, influencing water districts, and incentivizing conservation.

Key words: California black rail, irrigation, pasture, water conservation, wildlife

Introduction: social ecological systems
Small wetlands in the northern Sierra Nevada foothill oak woodlands provide habitat for the state-threatened California black rail (Laterallus jamaicensis coturniculus). One ongoing study of the sustainability of the wetlands offers an example of the way that the social ecological systems (SES) framework can be used to analyze a natural resource problem. Fundamentally, a “social ecological system” is composed of an ecosystem and the people that interact with it. Such systems are complex and adaptive—society and environment are considered to “co-evolve” (Glaser and others 2008). Here we use the SES concept to assess the dimensions of sustainability for the rail and its wetlands, and at least some of the drivers that influence it.

The SES concept is most often used where society derives a stream of benefits from the natural system. The fact that society is dependent upon and in turn affects the surrounding environment has probably been known at least since early humans learned how to make fire. Despite this lengthy history, strategies in the academic literature for successfully managing SES and applying the SES framework have generally remained vague. Specific management recommendations are hindered by the diversity and complexity of the systems, and authors stress that there is no universal formula.

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Scientific understanding of the interaction between society and the environment has often been hampered by the fact that neither social nor ecological systems occur at only one spatial or temporal scale. Interactions between scales are common and may cause either gradual or sudden transitions across multiple scales (Gunderson and Holling 2002, Levin 1992). Studies or monitoring efforts focusing on only one scale, typical in natural resource management, are prone to failure.

Although the simultaneous interaction of processes at multiple scales is often included in the definition of SES as “nested, multilevel systems” (Binder and others 2013), monitoring or evaluating systems across scales is often beyond the budget and knowledge of natural resource managers or scientific researchers. For this reason, some authors have recommended concentrating analysis on interactions of specific sub-components (Roe 1998), while others have suggested that social-ecological interactions are typically determined by a small number of “controlling processes” that should be the analytic focal point (Holling 2001). In either case, the spatial or temporal scale of management is inadequate to address the scale of ecological processes, leading to bad, ineffectual, or no management (Cumming and others 2006). However, there are still a number of general guidelines and hazards to be aware of when thinking about how to apply the SES concept to management.

One strategy is adaptive management, which is a response to the realization that previous command-and-control-style management made unrealistic assumptions about the degree to which ecological systems could be understood and predicted (Walters and Hilborn 1978). In simplified form, adaptive management consists of establishing a goal, conducting management activities designed to achieve that goal, monitoring and evaluating the effects of those activities, and altering the management plan in response. The challenge with adaptive management is that, not only is it difficult to establish institutionally (Jacobson and others 2006), but adaptive management plans tend to focus on the ecological system without adequate consideration of the social system, including the limitations of the manager.

Adaptive management to achieve the sustainability of a SES, as opposed to a natural resource system, would be sensitive to the different tiers of social actors, ranging from individuals to organizations and government agencies, as well as the governance structures that limit their behavior and the social and economic trends that motivate them (Folke and others 2005). Some authors have highlighted land tenure regimes and legal structures that enable resource users to self-organize as key components of successful ecosystem management, where organized groups can effectively and collaboratively manage a resource they all depend on (Adger and Luttrell 2000, Folke and others 2005, Ostrom 1990). Collective adaptive management is often difficult or impossible, however, in cases where social conflict (Galaz 2005), domineering government regulation, or tenure configurations or other institutions prevent resource users from collaboration and adaptation (Ostrom 1990). Collaboration between multiple tiers of stakeholders, combined with ongoing monitoring of the natural system, is the best way to ensure sustainability of a SES. While the sustainability of small wetlands may seem like a simple case of turning on some water, the SES framework gives us a fuller picture of how sustainability might work, and the management initiatives needed, in the situation of the black rail in foothill oak woodlands.
Case study: wetlands in a working landscape

The goal of the overall research on the rails and wetlands is to evaluate the sustainability of small wetlands within the bird’s foothill distribution, given the potential impact of climate change on water accessibility and management. At the outset, it was hypothesized that the area’s hydrology, West Nile Virus from wetland mosquitos, the population ecology of the bird, and the decisions of landowners would have important impacts on the wetlands and birds. A SES framework was applied to identify and understand the interactions among ecological and human factors. In this summation we focus on the results of a survey and interviews with landowners and water managers aimed at understanding management decisions affecting wetlands within the study area.

Wetlands in a social-ecological system

The secretive California black rail is a small ground-dwelling marsh bird, and was known only from large marshes in San Francisco Bay and along the lower Colorado River until it was “discovered” in the Sierra foothills of Yuba, Nevada, Placer and Butte Counties 20 years ago (Richmond and others 2008). First detected in 1994 at Sierra Foothill Research and Extension Center in Yuba County, the bird persists in small wetlands of 0.1 to 14 ha, where livestock grazing is a common use of local woodlands. Wetlands suitable for rails have shallow flowing water and short vegetation—open water is not of use to the birds. Wetlands used by rails may include densely vegetated marshes produced by springs, purposefully created wetlands, accidental leaks along canals and irrigation pipes, tailwater from irrigated pasture, and the marshy fringes of artificial ponds. Even apparently native springs in the area are likely influenced by extensive and leaky water transport systems that date from the Gold Rush. Water district managers have reported that the dirt-floored canals may lose 30 to 70 percent of their water through evaporation and seepage. An isotope study in Colorado found that ponds as far as 2 km from irrigation canals were fed primarily by irrigation water (Sueltenfuss and others 2013).

The SES framework allowed recognition that ecosystem services like the provision of rail habitat are a product of the interaction of humans and environment, rather than arising from the ecosystem alone (Huntsinger and Oviedo 2014). More than three-fourths of the bird’s wetland habitat was found in recent studies to be created or influenced by irrigation and water use related to ranching and, to a lesser extent, other forms of agriculture (Richmond and others 2010). To better understand the “social ecological ecosystem service” of rail habitat provision, in 2013, landowners and water managers within the bird’s habitat distribution were interviewed about their use of water. Based on these interviews, a mail survey was developed and administered in 2014 to a random selection of landowners stratified by property size in the study area using the Dillman Tailored Design Method with a multi-wave technique that included a cash incentive of two dollars in the first mailing (Dillman 1978, Dillman and others 2009). Results were analyzed with SPSS with weighting to match property size distribution in the study area (Atlas Support 2014, Holt and Smith 1979). About 55 percent of the surveys sent to valid addresses were returned, resulting in a sample of 470 respondents with property sizes ranging from 1.2 to 3237.5 ha.

Results showed that about half the landowners purchased irrigation water from a water district and approximately a third have a canal or ditch on the property. About 40 percent had irrigated pasture for livestock production, found in previous studies to
provide the most consistently used rail habitat through runoff (tailwater). Almost a third of respondents reported having a “wet area”, indicating that they might have rail habitat on the property. Few survey respondents reported any management of the wetlands, with 9 percent reporting draining some of them in the last 5 years, and 8 percent reporting that they created some during the last 5 years. About half said that they valued wetlands for wildlife, about a quarter thought the green forage was useful for livestock, but about a quarter reported not doing any management because the ponds simply did not “bother” them.

**Water use and management by landowners**

The most important reason to manage water for landowners in the study were was to reduce wildfire hazard, while of all the things asked about, concern about West Nile Virus was the least important reason. Interviewees, even those that had lost an animal to the disease, explained that they used vaccination to protect their horses and thought the risk to them was low. Enjoyment of the property, water saving, and water price were all relatively important to people in making decisions about water.

The most important reasons for creating or maintaining ponds for half or more of owners were wildlife watching, aesthetics, bird watching, and watering livestock. When respondents were asked what it would take to get them to create a wetland on their property, approximately a quarter said they would “do it for free if it benefitted birds and wildlife.” More than a third of landowners said they would do it in exchange for free water, and about a fifth said they would do it if it provided livestock forage in summer. Another third said they would “never create a wetland.” Property size made no difference in their responses.

Using a bivariate logistic regression analysis considering the relationship of water features with property size and purchasing water district water, the occurrence of springs on a property was found to be strongly related only to acreage (p<.003), while ponds were strongly related only to having water district water (p<.000). In contrast, the occurrence of wetlands like those used by the rail was found to be strongly related to property size (p<.037) and irrigation water purchases (p<.003). Both of these characteristics are strongly related to ranching.

Having water district water apparently changes the relationship of a landowner to water and the feedbacks from drought. Despite the fact that California is in the 3rd year of severe drought, irrigation water purchasers agreed at a higher rate than other landowners that they had plenty of water for their property. In fact, water districts have buffered the impacts of drought on their customers, maintaining existing flow without reductions until very recently, after the completion of the survey. Those purchasing water district water were more likely to agree that drought could have a big impact on their property, and that having less water would reduce their ability to use water. They also more strongly disagreed that they could adapt to a water shortage. Results indicate that while water is important to most respondents, those who purchase irrigation water from water districts are more dependent on the water they purchase (table 1) than are those using other sources, or not irrigating at all. About 80 percent of the land is owned by those purchasing irrigation water, and 63 percent of those landowners reported having irrigated pasture for livestock (p < .000).

Incorporating water districts into the SES hypothesized at the outset makes it clear that the feedbacks to water district decisions about water need further research. Water districts earn their funds through selling water—this makes them reluctant to cut back. It is also no doubt the case that landowners put political pressure on water districts to maintain water supplies. Other than that, water districts seem to operate
independently from any consideration of small wetlands like those studied. At the state level, there is a strong push to conserve water, pushing water districts into efforts to line and pipe canals, and to fix leaks. The SES framework made clear the “weak links” (water districts and landowners have no reason to consider impacts on wetlands) and the “wetland-negative links” (pressure to conserve water) in the sustainability of the wetlands.

Table 1—Percent of landowners purchasing and not purchasing water district irrigation water within foothill California black rail habitat that agree with the following statements about water availability in 2013

<table>
<thead>
<tr>
<th>Statement</th>
<th>% Agree or strongly agree</th>
<th>P ((\chi^2))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irrigation water purchaser</td>
<td></td>
<td></td>
</tr>
<tr>
<td>I have plenty of water for my property</td>
<td>80</td>
<td>64</td>
</tr>
<tr>
<td>Drought can have a big impact on my ability to make a living</td>
<td>50</td>
<td>34</td>
</tr>
<tr>
<td>Having less water will reduce my ability to use my property</td>
<td>94</td>
<td>85</td>
</tr>
<tr>
<td>I can easily adapt to a water shortage</td>
<td>17</td>
<td>31</td>
</tr>
<tr>
<td>No irrigation water purchased</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Scale and feedbacks

Research on the black rail illustrates the importance of scale when looking at ecosystem service production from a social-ecological systems perspective. At the pasture scale, grazing can reduce the suitability of rail breeding habitat in spring if vegetation height and density are greatly reduced (Richmond and others 2012). At the regional scale, water districts have impacts. Focusing on the landscape, the persistence of the working landscapes that foster rail habitat is critical, including maintenance of the livestock enterprises that support semi-natural grasslands, and the use of water for irrigation and stockponds. One important feedback to consider is that if protecting rail habitat is costly to the landowner, the ranching operation may be less profitable and less able to sustain itself. Instead, the land may be sold and parcelized, or placed into alternative land uses that are less rail-friendly. On the other hand, landowners reported that knowing that they were benefiting wildlife, or provision of the needed water for free, would motivate them to create a wetland. This willingness indicates that creation of wetlands on private land could be initiated through the right education or incentive programs.

Learning from irrigated wetlands

It was initially hypothesized that the specific factors likely to influence management of wetlands included landowner concerns about the recently-arrived West Nile Virus (as mosquitoes live in wetlands), drought and/or rising water costs, water conservation initiatives, changes in landowner management practices, the land ethic of the landowner, and land use change. A series of interviews revealed the following as important factors supporting habitat persistence and led to changes in our hypotheses and survey questions: availability of inexpensive water, the need to maintain a water district water allocation by using the allocation each year, the high cost of labor and
repairs for irrigation and water transport systems, owner indifference to grassy hillside or sloping wetlands, and the limited funds for water districts to implement water conservation technologies and to improve water transport. The central importance of water districts to the future of small wetlands was not anticipated in the original hypotheses, nor was landowner indifference to West Nile Virus (though the impact of West Nile on rail populations has now been documented).

The landowner survey revealed that landowners have limited direct effect on either rails or wetlands, either positive or negative. Far more important to wetlands, and thus to rails, are the actions of water districts. The continued provision of abundant water at relatively low prices will probably ensure that landowners will continue to spread water on their land in patterns similar to present. Severe hikes in water prices or decreases in supplies would likely result in less irrigation, with negative implications for wetlands. Perhaps even more important, water seepage from unlined irrigation canals appears critical to the maintenance of rail habitat. If water districts continue to line irrigation ditches with concrete or convert them to pipes, the amount of persistent water on the landscape will decline, in turn decreasing the size and number of wetlands. Current concerns over water shortages and efficiency in California suggest that pressure to decrease canal leaks and seepage will continue. Preliminary interviews with water districts suggested that there is little regulation to protect existing wetlands from being dried up by improvements to irrigation canal infrastructure. It is possible that such regulations might either be enforced or created in the future, however.

Studying the case of irrigated wetlands in an SES framework reveals several challenges for sustainability of the system. First and foremost, key components of the natural system are functionally invisible to key components of the social system. Water districts neither monitor wetlands or rails, nor do they make any attempt to manage them (except to dry them up if an irrigation leak is found to be the cause). Landowners rarely manage wetlands directly either, and many seem unaware that small, shallow wetlands offer wildlife benefits.

Secondly, linkages between tiers of the social system are missing, leading to little communication or collaboration. Wetlands typically occur on private lands but are fed by water from irrigation canals. Water districts line or pipe irrigation canals regardless of whose land is affected by the decline of water seepage, and landowners have little or no input in this process. State water regulators, if they are aware of the relation between irrigation water and wetland habitat at all, have so far made no mention of this connection when pushing for water conservation efforts and curtailing some legal rights held by water districts to collect surface water for later distribution.

In essence, the case of irrigated wetlands in the Sierra foothills is an example of a fractured SES. Actions within the social system are having profound impacts on the natural system, but these resulting changes in the natural system appear to have little or no feedback to the social system. This disconnect is due at least in part to the fact that irrigated wetlands are a largely unintended consequence of a different resource system, that of irrigation water, which is being actively managed on all tiers of social organization. Completing the feedback circuit for irrigated wetlands is not impossible, but education of the social actors about their presence and cause is a necessary first step. Shoring up connections between landowners, water districts, and state/federal regulators will be necessary if these wetlands are to be sustained into the future.
References


Ranching and Utilization of Oak Woodlands
Private and Public Incomes in Dehesas and Coniferous Forests in Andalusia, Spain

Paola Ovando\textsuperscript{2,3}, Pablo Campos\textsuperscript{3}, Jose L. Oviedo\textsuperscript{3}, and Alejandro Caparrós\textsuperscript{3}

Abstract

We apply an ecosystem accounting system to estimate the total social income accrued from private and public products in a group of agroforestry farms in Andalusia (Spain). We provide bio-physical and economic indicators for two contrasting farm types, a sub-group of 15 publicly owned coniferous forests and a sub-group of 24 privately owned dehesa farms. Total social income attained, in 2010, an average value of €140 per hectare in public forests and €352 per hectare in private dehesas. In public forests, social and environmental targets prevail over the demand for revenues from agroforestry private uses. Public landowners are willing to transfer the potential incomes from agroforestry uses to other economic agents including the consumers of public products. In private dehesas landowners are willing to accept cash losses from traditional agroforestry uses such as livestock breeding and game in return for the enjoyment of private amenities attached to land and animal’s tenancy. Both farm types provide diverse public non-market products that display higher aggregated values in the areas where public forests are located.

Key words: ecosystem accounting, environmental income, multiple-use, private amenities, public non-market products

Introduction

The quantification and integration of economic and physical environmental indicators to support decision making could play a key role for targeting policies and incentives to conserve the natural variety of ecosystems. Nonetheless, most ecosystem conservation strategies are underpinned by the circumstance that the value of many public environmental services is not captured in final market products, and, consequently it is not reflected in economic accounts.

This research applies the Agroforestry Accounting Systems (AAS) (Campos and others 2001, Caparrós and others 2003) to estimate the total social income accrued from a large selection of market and non-market products delivered by agroforestry ecosystems (table 1). This AAS ecosystem accounting approach is applied to 39 large agroforestry farms in Andalusia (Spain). Technical and economic data collected at farm level focus on market outputs and costs for different private agroforestry products (Ovando and others, in press). This information is then completed using the results of larger

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\textsuperscript{3} Institute of Public Goods and Policies (IPP), Consejo Superior de Investigaciones Científicas (CSIC), Madrid, Spain. (pablo.campos@csic.es; jose.oviedo@csic.es; alejandro.caparros@csic.es).
scale studies that provide simulated or imputed exchanges values for private and public non-market products and government expenditures in Andalusian forest, shrubs and rough grasslands (hereinafter jointly referred to as montes). The technical and economic study at farm level and the investigations that model the production and simulate the exchange value of different non-market products were developed in the frame of a large scale forest accounting project in Andalusia (RECAMAN) (Campos and others 2014).

Our research provides a set of detailed biophysical and economic indicators, in order to characterize private dehesas and public forests management. The results derived from this study allow us to examine the main factors that contribute to private and social incomes in public forests and private dehesas and how they could affect agroforestry management decisions.

Methods

Case studies
The economic unit of analysis is an agroforestry farm, in which the Monte covers more than 50 percent of its total surface. This study focuses on 24 privately owned dehesas and 15 publicly owned coniferous forests that are distributed across Andalusia (fig.1). Private dehesas average a useful agricultural surface (UAL) of 674 ha; with 88 percent of the farms larger than 200 ha and 46 percent larger than 500 ha. Close to 78 percent of the dehesa surface is covered by open oak and wild olive woodlands, 4 percent by softwood forests, 3 percent by other woodlands, 10 percent by treeless shrubland, 3 percent by rough grasslands and 2 percent by crops. Public forests are much larger, with an average size of 3647 ha of UAL, having all the farms a surface bigger than 500 ha. In this case softwood forests cover 60 percent of the farm surface, meanwhile open oak woodlands scarcely a 5 percent of this surface, other woodlands 16 percent (mainly gallery forests), treeless shrubland 14 percent, and similarly to private dehesas, rough grasslands and crops occupy 3 percent and 2 percent of UAL, respectively.
**Total social income estimation**

Total social income (TI) is estimated using the AAS’ production and capital accounts (Caparrós and others 2003). The production account records the flow of market and non-market outputs (TO) and costs (TC) associated to single and aggregated agroforestry products over the accounting year, and gives, as a balancing item, the net operating margin (NOM = TO - TC). The capital account depicts the values and variations borne by work-in-progress (growing trees and animal inventories) and fixed assets (breeders, land, trees yielding repeated outputs and manufactured assets) over the period. Those variations are taken into account for the estimation of capital gains (CG).

<table>
<thead>
<tr>
<th>Concept</th>
<th>Definition and valuation criteria</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>TIMBER, CORK, FIREWOOD</strong></td>
<td>Growth, work in progress used (harvest), sales, investments and capital gains borne from woody products revaluation. Growth and stock estimations depart from forest inventories at farm level, and are valued following Caparrós and others (2003).</td>
</tr>
<tr>
<td><strong>CONSERVATIONIST FORESTRY</strong></td>
<td>Direct government payments to landowners for applying concerted forestry treatments that enhance the production of public ecosystem services. Those payments generate an intermediate output in the private forestry account that is consumed in the production process of public landscape and biodiversity services.</td>
</tr>
<tr>
<td><strong>GRAZING RESOURCES</strong></td>
<td>Acorns, herbs, browses and fruits produced in forest, grass and crop lands and that are consumed by livestock, game and other wild species. Game species grazing has an economic value only if there is an opportunity cost for these resources that is when the hunting ground is fenced, irrespective of the presence of livestock.</td>
</tr>
<tr>
<td><strong>LIVESTOCK</strong></td>
<td>Extensive breeding of cattle, fighting bulls, sheep, goat and equines. Livestock activity also includes fat stockbreeding (mainly montanera pigs) and apiculture.</td>
</tr>
<tr>
<td><strong>GAME</strong></td>
<td>Game breeding and hunting. This activity considers species with information on their population dynamics (Iberian red deer, wild boar, partridge and rabbits) and species for which we lack of this dynamic (turtledove, quail, hare). Game environmental prices are taken from a survey of 741 hunting grounds in Andalusia.</td>
</tr>
<tr>
<td><strong>PRIVATE AMENITIES</strong></td>
<td>The economic value of private amenities comes out of the exclusive enjoyment by private non-industrial landowners of recreational opportunities, legacy options and other non-market services attached to the tenancy of land (Campos and others 2009). Private amenities’ value is taken from a survey of private monte owners in Andalusia (765 questionnaires).</td>
</tr>
<tr>
<td><strong>OTHER PRIVATE PRODUCTS</strong></td>
<td>Other private products include crops, housing services for both the landowner and farm workers, and the production and sale of industrial nuts.</td>
</tr>
<tr>
<td><strong>MUSHROOMS</strong></td>
<td>The quantity of edible mushrooms that could be collected in the monte was obtained from a telephone survey (8,076 interviews) of adult residents in Andalusia. Mushrooms are valued at the farm gate using market prices net of manufactured costs.</td>
</tr>
<tr>
<td><strong>PUBLIC RECREATION</strong></td>
<td>Public recreation values are taken from a regional study in Andalusia. The monetary value of this product is estimated using two structured non-market valuation surveys with face-to-face interviews of adults. First, a survey of open access visitors in different natural areas of Andalusia (4,030 questionnaires), that provides the willingness to pay (WTP) for a visit to those areas. Second a survey</td>
</tr>
<tr>
<td>LANDSCAPE &amp; THREATENED BIODIVERSITY</td>
<td>Landscape and threatened biodiversity are taken from a regional study in Andalusia that carried out a choice experiment conducted with adults by face-to-face interviews (3,214 questionnaires). The survey provides information on the WTP of Andalusian residents to warrant the future provision of those services, in the same quantity and quality as they are supplied today, thought an additional tax during the next 30 years. The individual landscape WTP value is assigned to 10 natural protected areas in Andalusia. The biodiversity WTP value is distributed equally between 235 endangered species.</td>
</tr>
</tbody>
</table>
Table 1—Methods and data sources for estimating market and non-market output and cost (continued)

<table>
<thead>
<tr>
<th>Concept</th>
<th>Definition and valuation criteria</th>
</tr>
</thead>
<tbody>
<tr>
<td>NET CARBON SEQUESTRATION</td>
<td>Gross carbon dioxide (CO₂) sequestration considers tree and shrub annual biomass growth. CO₂ release, as result of tree or shrub felling, burning or death is assumed to be instantaneous. Carbon is valued using the EU Emissions Trading Scheme prices.</td>
</tr>
<tr>
<td>NATURAL WATER YIELD</td>
<td>Natural regulated water accounts for the hydrological flows of precipitation water (and superficial springs) which constitute the input that is transformed by forestland into the output “forest water”. Natural regulated water with economic value is made up of the superficial water run-off that reaches a regulated reservoir in Andalusia, and it is valued using the results of a hedonic land price model in Andalusia.</td>
</tr>
<tr>
<td>OTHER PUBLIC PRODUCTS</td>
<td>Gross fixed investment and intermediate services delivered by government expenditures on fighting against forest fires and drove ways management.</td>
</tr>
</tbody>
</table>

Source: Own elaboration based on Ovando and others (in press), and Campos and others (2014).

On the other hand, the aggregation of NOM and CG gives the capital income (CI) or the return to capital as a production factor. TI is then quantified by adding CI to labor compensations (LC), and it is estimated at producer prices; that is without accounting for subsidies and taxes on production.

We single out the contribution of environmental (EI) and manufactured assets (MCI) to capital income (CI = EI+MCI). The return to environmental assets or environmental income (EI) is estimated as a residual value from the total social income after labor and other manufactured costs are covered, including the opportunity cost of manufactured capital (Campos 2015).

**Market and non-market agroforestry products**

Private accounts involve those activities that are under the direct control of the landowner, and include six uses: forestry, livestock, game, crops, market services and the consumption of private amenities as the only non-market product. Public non-market uses include carbon sequestration, natural water regulation, open access mushroom gathering and recreation, and landscape and threatened biodiversity conservation services. Table 1 offers a brief description of the single products that our AAS application considers. Public account records as part of forestry activity the outputs and costs for fighting against forest fires and drove ways management, which are two sub-activities controlled directly by the government. This account also considers the government investment and ordinary expenditures for providing landscape, biodiversity, recreation and mushroom public products.

**Results**

The results display weighted average values according to the UAL surface that each farm has in the group of private dehesas and public forests. Those average results are not statistically representative of private dehesas and public forest farms in Andalusia, if we consider the relatively small number of case studies, albeit, these outcomes are suitable to illustrate the economic
rationality and trends that drive private dehesa and public forest management in this region, considering that most of its dehesas are private properties and most of its softwood forests are publicly owned.

**Biophysical indicators**

Cork is the main forestry product in the group of private dehesas, and it is missing in public forests, whereas timber is the chief forestry product. Cork had an extraction ratio of 73 percent over its growth in private dehesas in 2010, while timber an extraction ratio of 46 percent over its growth in public forest over the same period. Livestock and game species in private dehesas consume more than 6.5 times the amount of grazing resources as in public forests. Even so, livestock and game species account for a similar share of total grazing resources consumed in both types of farms (table 2).

Private non-market amenities attain a final output of € 247/ha in private dehesas, while in public forests the consumption of this service cannot be realized (its NOM equals 0 €/ha) due to the public nature of land tenancy. Dehesa and forest case studies have similar biophysical yields for mushroom and net carbon sequestration; meanwhile the yield associated to biodiversity and recreation is higher for public forests and the value of natural water is bigger in dehesa case studies. Public forests are located in natural areas that received double the amount of visits to areas in which private dehesas are to be found. In addition, the simulated exchange value for a visit to the areas where the public forests are located is 45 percent higher than the price associated to a visit to the dehesa farms’ areas. Similarly, the number of species and the final output associated to threatened biodiversity is 37 percent higher for public forests in comparison to dehesas (table 2).
Table 2—Selected biophysical indicators (year 2010)

<table>
<thead>
<tr>
<th>Concept</th>
<th>Unita</th>
<th>Private dehesa</th>
<th>Public forest</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Quantity (u)</td>
<td>Priceb (€/u)</td>
</tr>
<tr>
<td>TIMBER HARVEST</td>
<td>m³</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>TIMBER GROWTH</td>
<td>m³</td>
<td>0.1</td>
<td>1.1</td>
</tr>
<tr>
<td>CORK HARVEST</td>
<td>kg</td>
<td>76.2</td>
<td>1.3</td>
</tr>
<tr>
<td>CORK GROWTH</td>
<td>kg</td>
<td>103.7</td>
<td>0.2</td>
</tr>
<tr>
<td>GRAZING RESOURCES</td>
<td>FU</td>
<td>571.5</td>
<td>0.04</td>
</tr>
<tr>
<td>LIVESTOCK</td>
<td>FU</td>
<td>274.7</td>
<td>0.07</td>
</tr>
<tr>
<td>GAME</td>
<td>FU</td>
<td>296.8</td>
<td>0.01</td>
</tr>
<tr>
<td>LABOR</td>
<td>h</td>
<td>16.1</td>
<td>9.4</td>
</tr>
<tr>
<td>PRIVATE EMPLOYEES</td>
<td>h</td>
<td>12.3</td>
<td>8.9</td>
</tr>
<tr>
<td>PRIVATE SELF-EMPLOYED LABOR</td>
<td>h</td>
<td>0.1</td>
<td>6.6</td>
</tr>
<tr>
<td>PUBLIC EMPLOYEES</td>
<td>h</td>
<td>2</td>
<td>21.2</td>
</tr>
<tr>
<td>PRIVATE AMENITIES</td>
<td>ha</td>
<td>1</td>
<td>247.1</td>
</tr>
<tr>
<td>MUSHROOMS</td>
<td>kg</td>
<td>2.3</td>
<td>6.1</td>
</tr>
<tr>
<td>NATURAL WATER YIELD</td>
<td>m³</td>
<td>8,418</td>
<td>0.01</td>
</tr>
<tr>
<td>Regulated</td>
<td>m³</td>
<td>1,035</td>
<td>0.06</td>
</tr>
<tr>
<td>Non-regulated (free)</td>
<td>m³</td>
<td>7,383</td>
<td>0</td>
</tr>
<tr>
<td>NET CARBON SEQUESTRATION</td>
<td>tCO₂</td>
<td>2.8</td>
<td>13.7</td>
</tr>
<tr>
<td>PUBLIC RECREATION</td>
<td>visit</td>
<td>2.5</td>
<td>10.4</td>
</tr>
<tr>
<td>LANDSCAPE</td>
<td>ha</td>
<td>1</td>
<td>92.1</td>
</tr>
<tr>
<td>BIODIVERSITY</td>
<td>Nº</td>
<td>47.1</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Source: Own elaboration based on Ovando and others, in press.
a FU: Forage unit (1 kg of barley with an energy content of 2,723 kcal); h: hour; ha: hectare of useful agricultural land (UAL); N°: average number of threatened species; t: metric ton.
b Average exchange rate in 2010 1 € (euro) = 1.327 US$ (http://www.ine.es).
c Values lower than 0.05.

Total social income distribution

Our analysis focuses on the single contribution of private and public products to total social income (TI) over the accounting year, and on how this income is broken-down into labor compensations and the partial returns to environmental and manufactured assets.

In 2010, an average private dehesa generated a total social income of €352/ha, whereas a public forest produced a social income of €140/ha. Private products contributed to 33 percent of TI in private dehesas and public products to the remaining 67 percent. In the case of public forests, private products delivered a negative total social income in 2010, which was offset by the income of public products (table 3). The factors that contributed positively or negatively to explain total social income in both types of agroforestry farms are diverse and complex.

Private income is being severely affected by the negative capital gain assigned to private amenities owing to a devaluation of −3.4 percent on land market prices in 2010 (MARM, 2011). The option for enjoying private amenities in dehesas lessens the influence of this capital loss, the contribution of private amenities to TI being €25/ha. In public forests, the consumption of private amenities could not be realized. Although, the variations of land
market prices in the accounting period have an effect on the estimation of the capital gain/loss of private amenities. Indeed, the income of private amenities in public forest is equal to the capital loss associated to land depreciation (table 3).

Another factor that affects total private income in dehesa case studies is the negative manufactured capital income of livestock, which indicates that the production costs of this activity are not covered in 2010 by its outputs. Game activity also displays a negative manufactured capital income in private dehesas and public forests, while the environmental income associated to this activity represents the value of animals (female breeders and other individuals). This environmental income does not offset the manufactured capital income losses of game in private dehesas, in contrast to public forests in which game delivers positive private capital and total incomes (table 3). In any case, the extent of income losses from livestock and game activities is significantly higher in private dehesas.

### Table 3—Total social income distribution by single agroforestry product (year 2010, €/ha)

<table>
<thead>
<tr>
<th>Class</th>
<th>Private dehesa</th>
<th>Public forest</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Environ.</td>
<td>Manuf.</td>
</tr>
<tr>
<td></td>
<td>mental income</td>
<td>capital income</td>
</tr>
<tr>
<td>Private</td>
<td>234</td>
<td>-227</td>
</tr>
<tr>
<td>Timber</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Cork</td>
<td>175</td>
<td>-25</td>
</tr>
<tr>
<td>Firewood</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Grazing resources</td>
<td>17</td>
<td>-39</td>
</tr>
<tr>
<td>Game</td>
<td>11</td>
<td>-39</td>
</tr>
<tr>
<td>Livestock</td>
<td>-99</td>
<td>42</td>
</tr>
<tr>
<td>Crops</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Private amenities</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>Other private</td>
<td>0</td>
<td>-30</td>
</tr>
<tr>
<td>Public</td>
<td>197</td>
<td>-4</td>
</tr>
<tr>
<td>Recreation</td>
<td>20</td>
<td>-1</td>
</tr>
<tr>
<td>Mushrooms</td>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td>Carbon</td>
<td>37</td>
<td>37</td>
</tr>
<tr>
<td>Landscape</td>
<td>49</td>
<td>-1</td>
</tr>
<tr>
<td>Biodiversity</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>Natural water</td>
<td>67</td>
<td>67</td>
</tr>
<tr>
<td>Others public</td>
<td>0</td>
<td>-4</td>
</tr>
<tr>
<td>Total</td>
<td>431</td>
<td>-231</td>
</tr>
</tbody>
</table>

Source: Own elaboration based on Ovando and others (in press).

*Average exchange rate in 2010 1 € (euro) = 1.327 US$ (http://www.ine.es).*

The environmental income associated to public products is 21 percent higher in public forests with respect to private dehesas. The EIs for public uses referred to in table 3 depict lower values than those of public products referred to in table 2, after covering their respective public production costs (mainly government expenditures for the provision of public non-market products). The main differences between dehesas and forests are due to higher environmental income values for public recreation, carbon sequestration and biodiversity in the public farms. The negative manufactured capital income of public products is, in part, a result of the devaluation of the manufactured
assets used to provide public products in 2010. This outcome is also related to the preferences of the Spanish households for assigning no additional landscape values in sites different to the ten areas mentioned in table 1 and, given that the government spends money in these areas to boost landscape conservation, the resulting negative income is assigned to manufactured investment.

Discussion and conclusions
This study examined differences and similarities in the contribution of single and aggregated private and public products to total social income in a group of private dehesas and public forests. Biophysical yields delivered by both type of farms are affected by their spatial extent, vegetation structure and other specific botanical or geographic characteristics, which also affect the quantity and quality of agroforestry products, as well as their prices and production costs. The management aims and strategies of private dehesas and public forests respond to the property rights that can be attributed to different products, but also to legal, institutional and social commitments attached to private or public tenancy of land.

Land tenants at private dehesas stand for non-industrial owners of large private farms whose management strategies are frequently attached to a mixed investor–amenity consumer rationality. This rationality typifies a landowner that demands, simultaneously, market revenues from her/his investment and the exclusive enjoyment of private amenities attached to land tenure (Campos and others 2009). Our results showed that livestock and game activities diminish private income in dehesas, although those activities are maintained in such farms. This outcome suggests that the mixed investor-amenities consumer rationality also stands for livestock and game management, to which amenities values have not been measured but seem to be internalized into the value of private amenities stated by private monte owners.

In public forests, environmental and social targets prevail over the demand of profits from market products (timber, game, livestock, and others). Timber is the main market product supplied in these farms. Game and livestock activities are marginal, although they do not embrace large income losses for the agents (different from the landowner) that lease the land out for breeding livestock and hunting. This outcome suggests that public forest landowners transfer the potential environmental and manufactured incomes from these agroforestry uses to other economic agents. The provision of non-market public services is also relevant for public landowners, since their management integrates environmental criteria. Indeed, two thirds of private labor costs are due to conservationist forestry practices intended to enhance biodiversity and landscape conservation in those public forests.

Ecosystems conservation policies should ideally consider different conservation strategies for public forests and private dehesas. Public forest managers seemed to have internalized the provision of environmental services into their strategies, which may lead to monetary losses. Total social income function in private dehesas depends partially on traditional forestry, livestock and game uses, and it is also reasonable to suggest that social preferences are affected by the resulting cultural landscape. This hypothesis supports the legitimacy of government compensation to landowners as a means of translating non-market values of the environment into real financial
incentives for maintaining and even increasing the provision of public non-market services that the society demands, while keeping multiple agroforestry uses.

Acknowledgments

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References


Ranching Sustainability Analysis

Royce Larsen, William Tietje, and Karl Striby

Abstract
California oak woodland creates a landscape of renowned beauty, providing the public with essential natural resource services and economic values through ranching. Ranchers however, come under intense pressure and scrutiny from the public to demonstrate stewardship of the land they manage. The solution often chosen to address these concerns is, simply, more regulations. Regulations impose a financial and philosophical burden on California ranchers; in fact, they threaten the very existence of ranching. This paper discusses the development and on-going implementation of the Ranching Sustainability Analysis System (RSA). The RSA is a self-assessment process that guides the rancher through a series of questions that cover social, economic, and natural resource aspects of 11 ranch-management categories. Ranch scores can be submitted to a confidential database. Anonymous summary scores allow ranchers to compare the operation to their peers and to track sustainability progress over time. Essential components for the ongoing implementation of the RSA have been the strong support of an ad hoc committee of ranchers, delivery through a series of workshops, San Luis Obispo County Cattlemen's Association support, and voluntary participation. Although in the early stages of implementation, the RSA has potential to aid private landowners throughout California in implementing and demonstrating sustainable ranching practices.

Key words: oak woodland, land stewardship, ranching sustainability analysis

Introduction
Ranchers continue to come under intense pressure and scrutiny from environmentalists and the public in general to demonstrate their stewardship of the land and natural resources they manage. However, ranchers feel that the solution often chosen to address the public’s natural resource concerns is simply more regulations which imposes a financial and philosophical burden on ranchers; in fact, they threaten their very existence. As Jack Varian, owner of V6 Ranch, in Parkfield, California puts it: “Eventually the pinpricks (regulations) to the elephant (ranching) will bring it down. If we can teach the public what ranchers do, why they do it, and how ranching benefits the larger community, we can increase public acceptance of ranching. Ranchers own 80 percent of the oak woodland in San Luis Obispo County. If the Ranch Sustainability Analysis System can assist in enhancing the social, economic, and natural resource sustainability of ranches such that the ranches can stay in the family, so will the oaks stay on the land.”

It is vital for ranchers to be able to demonstrate that they are good stewards of the land and yet be able to earn a living from the land they own. A Ranching Sustainability Analysis (RSA) system was developed by the Integrated Hardwood Range Management Program (IHRMP) and area ranchers on the central coast as one way to show that ranchers are managing properly.

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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The mission of the RSA is to create and implement a voluntary self-assessment program in which ranchers can evaluate all aspects of their operations to ensure the sustainability of their production, lands, and families; to determine what they do well and find ways to ensure proper stewardship of themselves, their animals, and their natural resources.

How does it work?
The Ranching Sustainability Analysis is a self-assessment process that guides the rancher in asking a series of questions within 11 subject categories about the social, economic, and natural resource management practices he or she is using. These categories are: livestock management, soil management, forage management, biodiversity/wildlife, regulations, relationships, economics, energy, monitoring, pest management, and water quality.

Ranching does not lend itself easily to a “one size fits all” approach, so the expertise of the ranchers, their in-depth and long-term knowledge of their own lands, is vital to this process. There are up to nine questions per category. Users score their practices from 1 to 7 (poor to excellent). Please see the whole RSA document at: http://cesanluisobispo.ucanr.edu/Custom_Program743/Ranching_Sustainability_Self-Assessment_Project/.

The following are three examples selected from the RSA demonstrating how the scoring works. The photos are only used to demonstrate a potential low versus high score. All scoring is done by the rancher based on their understanding of his ranch. Different members of the same family, or employee’s on the same ranch, may score each question differently, which then allows for a discussion as to why they scored it differently. This allows for the family and employees to be more unified in their management practices. Photos in figures 1 through 3 provide an example of how this scoring works.

Figure 1—A question from the category of Wildlife/Biodiversity: How well do you meet the habitat needs of game species? The photo on the left represents poor wildlife habitat and would receive a score of two. The photo on the right represents healthy wildlife habitat and would receive a score of six.
Figure 2—A question from category of Relationships: Family, Employee, Community, and Land: How well have you and your family established written goals that are clearly defined and inclusive of everyone in your operation? The photo on the left has no written goals and would receive a score of one. The photo on the right represents strong written goals and would receive a score of six.

Figure 3—A Question from the category of Economics: How diversified is your income, e.g., multi-species operation, rental property, hunting, and agritourism? The photo on the left represents having livestock only and would receive a score of three, while the photo on the right represents additional income from other resources and would receive a score of six.

Once a rancher, or family, has gone through the whole document, ranch scores can be submitted to a confidential database, or kept by the individual. Individual ranch, and industry summaries, allows ranchers to compare their individual operation over time, and to compare with their peers. Therefore the industry would be able to track sustainability progress over time. This process will help individuals and families to identify specific “action items” that they wish to pursue to improve their operations. There are at least seven good reasons that a rancher may want to complete this self-assessment. These reasons are:

- Presents a fast and easy way to create their written record.
- Fosters communication among family, employees, and agencies.
- Demonstrates their dedication to stewardship.
- Stimulates creative thinking about good ranching practices.
- Acts as a non-regulatory tool that may help them with regulators.
- Provides a new way to measure their practices leading to additional profitability.
- Developed by ranchers who understand the needs of ranchers and land managers.
Results to date

The past several years, using a grant from the Wildlife Conservation Board’s Oak Woodland Conservation Act of 2001, the project has focused on connecting with the agricultural and environmental communities. Great progress has been made through the efforts of an impressive committee of local private landowners and ranch managers who are recognized locally and nationally as outstanding land stewards. The Rancher Committee believes that the RSA can be a powerful tool to guide private landowners through everyday decision-making processes. The Committee is fully committed to seeing this effort through to completion. Importantly, this tool could be adapted for use throughout California. Supporting the RSA, the Integrated Hardwood Management Program (IHRMP) has held workshops and tailgate meetings to stimulate discussion and interest in sustainable ranching among people with diverse experiences and backgrounds. We feel that a win-win situation is in the making. That is, if ranching is sustained, so also will working landscapes (oak woodlands) continue to provide a diversity of livestock and other agricultural products; high quality water supplies; wildlife habitat; recreational opportunities; and aesthetic values.

The RSA will also provide a means for the academic community to assess the needs of the ranchers. For example, some results obtained during recent workshops presented on the Central Coast show some management topics that UC Cooperative Extension, or other agencies, could focus on workshops and provide more information to land owners and managers. Figure 4 shows results from a workshop showing that the percentage of ranchers considering a conservation easement is highly varied, suggesting that a workshop may be needed to provide technical information of what a conservation easement is and how it could be a useful tool to help keep ranches solvent. Results from fig. 5 show that most of the ranchers have not established written goals for their ranch, suggesting that a workshop on how to do establish written goals would be a priority topic for a workshop. At the same time, the results from fig. 6 suggest that most ranchers are very good at following the labels for vaccine, medicine and chemical use, suggesting that it may not be necessary at this time to do a workshop on how to use vaccines, medicines, or chemicals.

Figure 4—Results of responses from the category Biodiversity/Wildlife Conservation: “To what extent have you considered a conservation easement?”
Future directions

The Ranching Sustainability Analysis will evolve to meet the needs of the California ranching community and to reflect increasing understanding of rangeland sustainability and good stewardship practices. The written components of the RSA may be considered a “living document” that develops and matures over time. Our plans include the following:
• Pilot the RSA, including the development of a confidential database.
• A workbook with state-of-the-art educational materials on rangeland practices.
• A website with Interactive Model Ranch to illustrate some of the social, economic, and natural resource sustainable practices used by California ranchers.
• Third-party certification that would provide unbiased confirmation of the sustainability of ranch practices for peers, regulatory agencies, the environmental community, and the general public.
• Develop partnerships with ranching associations and other organizations.
Evaluating Recreational Hunting as an Incentive for Habitat Conservation on Private Land in California

Luke T. Macaulay

Abstract
Private land plays a crucial role in the conservation of biodiversity in California, yet these lands are the least protected and most prone to environmental degradation. In 1930, Aldo Leopold recognized the potential to better conserve private land by an incentive scheme where recreational users would pay landowners for access to conserved wildlife habitat. While research has shown that significant funds are spent to utilize large areas of private land for wildlife-associated recreation, this study seeks to specifically understand whether this recreational use actually results in improved conservation practices. I use interviews with private landowners and private land managers in California who owned >404 ha (1000 ac) to evaluate whether those landowners with recreational utilization are more likely to perform habitat conservation practices. Interviews revealed that while not widely adopted, hunting was the primary recreational use on many private lands surveyed, and that some conservation practices were performed to enhance the hunting enterprise. There appears to be an important role for extension and outreach efforts to better inform landowners of the earning potential from recreational hunting as well as the conservation practices that could enhance both wildlife habitat and revenue for a hunting enterprise.

Key words: biodiversity, management, ranching, rangelands, recreation, wildlife

Introduction
Wildlife-associated recreational use on private land has been shown to be a significant source of income for many landowners in the United States, but its conservation impact is poorly understood (Bagi and Reeder 2012, Brown and Reeder 2007, Carpio and others 2008, George and others 2011; Macaulay, n.d.; Nickerson and others 2001). Many studies have hypothesized that recreational use creates an incentive to perform conservation practices and maintain habitat, but many of these studies rely on theory or anecdotal accounts (Benson 2001a, Rasker and others 1992). Empirical research on conservation practices associated with recreational use has been equivocal, with some authors finding conservation benefits (Butler and Workman 1993, Oldfield and others 2003, Standiford and Howitt 1993), and others finding few differences in practices (Benson 2001b). Furthermore, some practices designed to maximize returns from recreational use may resort to activities that result in short-term gains for particular species of interest, but may degrade habitat for other species (for example, planting food plots, introductions of non-native species) (Macaulay and others 2013). Models evaluating economic drivers of land use change have not explicitly considered the role of income or benefits from recreation as motivating land use decisions (Lubowski and others 2008, Rashford and others 2011). This research seeks to provide 1) a better understanding of the economics of

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recreational use and the type of recreational activities pursued and 2) whether landowners with recreational benefits on their land implement more conservation practices that those without.

To better inform this issue, this study is gathering detailed information from private landowners and managers to specifically determine how recreational use may influence decisions regarding land-use and conservation practices. This information will help to inform how policy, government programs, and Cooperative Extension efforts may be used to encourage practices that not only help to conserve natural resources, but also provide increased recreational benefits on private land.

Methods
A semi-structured interview questionnaire was developed and tested in a classroom and in a focus group of experts and students in rangeland management. Thirty-seven semi-structured interviews were conducted with 27 private landowners or land managers, five commercial hunting operators, three real estate appraisers, and two regulatory personnel in the spring and summer of 2012. The majority of private landowners interviewed were randomly sampled from all individuals owning more than 404 ha (1000 ac) in the Central Coast mountain range of California between Santa Clara County in the north and San Luis Obispo County in the south. I interviewed several landowners who owned or managed land in the southern San Joaquin Valley and in Mendocino County. I acquired regional ownership information from county assessors from the area from which to randomly sample landowners.

Due to the wide-ranging nature of semi-structured interviews, not all questions in the interview questionnaire were fully answered due to either time constraints, lack of immediate knowledge of the answer by the interviewee, or unwillingness of interviewees to answer certain questions. As a result, much of the results presented here are of a qualitative nature and do not constitute a generalizable knowledge of landowners in California. The results have served to inform future survey and interview efforts, which are currently ongoing.

The questionnaire requested information from landowners about revenue earned from their property by various uses, and asked about management practices performed on the property for various business enterprises. Interviews revealed that most landowners did not keep detailed accounting records on the operations of their property. As such, information about net revenue of the property was difficult to assess primarily due to challenges of quantifying expenses such as labor, fuel or depreciation associated with the ranch operation. As such, interviews did not reveal whether land management efforts resulted in net revenue improvements in coming years. The estimates cited in this manuscript are assessments of gross revenue estimates unless expenses are specifically noted. The interview guide also requested information on common rangeland management practices such as planting food plots (usually agricultural crops planted specifically for wildlife to feed on), predator control, brush management, game species introductions, and habitat improvement practices (such as planting oaks or maintaining riparian zones). For a condensed list of questions asked during interviews, please refer to the following questionnaire.
Research Questionnaire (Luke Macaulay)

What are the main activities on your ranch and percentage of effort / economic activity from each?
Do you have a fee hunting operation: why or why not?
What land area of the property is engaged in each productive activity?
What management activities do you perform on your property?
What government programs do you participate in?
What is your stocking rate for livestock?
Do you perform wildlife census surveys?
Do you perform predator control?
Do you track harvest of wildlife on the property?
Do you set harvest guidelines and rules?
If you have a hunting operation, what is its organizational arrangement? Guided, yearlong, multi-year?
What is the number of paying hunters?
How many people are allowed to hunt for free?
What services and amenities are provided for the hunting operation?
What are your motivations for owning/managing this land?
How do the various operations on the property affect the stability of revenues?

Results

Economics of recreational use and the type of recreational activities pursued

In general, the interviews found that much of the recreational activity on private lands greater than 404 ha (1000 ac) was for hunting, although many of those properties, in particular those less than 2023 ha (5000 ac) oftentimes only allowed friends and family on the property for hunting. Overall, 87 percent of randomly sampled landowners had some recreational hunting on their property, with half of those landowners reserving hunting for personal or family use, 31 percent having hunting clubs, and 6 percent with guided operations (fig. 1).

Figure 1—Types of hunting use (or no hunting) on 16 randomly selected properties greater than 404 ha (1000 ac) in the Central Coast of California.
Results from interviews found large variation in earnings from hunting. Several landowners were primarily oriented towards livestock operations and had hunting clubs that earned marginal amounts of money (oftentimes just enough to pay for annual hay expenses or property taxes). Two properties were oriented towards hunting as a primary use, with relatively small or no income from livestock. One operation ran a simple hunting club with yearlong access, and earned gross income of $10/0.4 ha (1 ac), with minimal expenses that resulted in profitable operations, while the other maintained employees and facilities for the hunting club, which resulted in higher gross income on the property, but also substantial costs which led this property to operate at a loss. One property in particular operated both livestock and hunting operations at high efficiency, using a guide service for hunting, and as a result appeared to earn higher levels of revenue than any other properties. I did not encounter properties earning money from fishing or wildlife watching, although one large property was oriented primarily towards personal horseback-riding recreation.

The availability of habitat in the form of shrub cover, oak trees and grassland was an important need for the availability of hunting operations. Properties composed of almost entirely of grasslands had little wildlife availability for hunting operations, and generally viewed feral pigs as pests that they sometimes would pay others to help manage. This suggests an interesting shift in perspective about pigs, with some landowners viewing them as a cost to a primarily livestock operation, while those seeking income from all available streams found a source of income from the presence of pigs.

In keeping with rangeland research (Huntsinger and others 1997), many landowners were not focused on earning income from their land and instead utilized the property for personal enjoyment. Others seemed content with their income as it stood from livestock operations alone and did not want to invest the time it would take to set up a hunting operation. The most common reason that landowners did not have hunting on the property was that they did not want hunters disturbing other aspects of their livestock operation.

Interviews confirmed that rangelands were marginal income generating operations when considering the cost of capital that is invested in the land. Operations trying to make income from the property grossed from $10 to $30 per 0.4 ha (1 ac), not including costs of labor and management. Land prices for rangelands in the Central Coast region oftentimes range from $1000 to $2000 per 0.4 ha (1 ac). Dividing annual gross income by land value only (the primary capital cost for these operations) results in estimated gross returns from operations in the range of 0.5 percent to 3 percent, not including the cost of labor and other expenses. These estimates should be viewed as rough approximations given that interviews did not gather detailed accounting records, but instead relied on landowner’s general estimates at the time of the interview. Furthermore, these estimates do not include capital appreciation of land over time. Nonetheless, the results show the relatively small returns that can be expected in annual cash flow from rangelands in the central coast of California.

Are conservation practices incentivized by recreational use?

Interviews found that in many cases landowners were managing for wildlife-associated recreation, but at times utilized practices that could have some negative repercussions for other aspects of the ecosystem. Although some landowners utilized practices that conservation professionals recommend, such as leaving cover for wildlife and minimizing risks of invasive species, many others were interested in attaining benefits for desired wildlife species through more intensive management
actions such as the planting of food plots or introducing or maintaining non-native game animals such as feral pigs and wild turkeys.

I found that most landowners maintained water resources, such as stock ponds and water troughs, which were utilized for both livestock and wildlife populations. It appeared as though the primary motivation for installing and maintaining water sources was for livestock operations, although several of these landowners had implemented wildlife escape ramps into troughs, which helped reduce mortality of wildlife that fell into troughs. At least one landowner implemented water sources at ground level, designed specifically for wildlife access.

Several landowners implemented practices to maintain habitat for wildlife, such as creating and maintaining brush piles for wildlife as well as leaving cover for wildlife by reducing grazing in certain areas. Several landowners conducted some level of brush management as a means of increasing grass and forb production; although, areas where brush was cleared tended to represent very small percentages of property ownership. There did not appear to be a sufficient benefit to justify the expense of widespread clearing of brush. I did not encounter landowners who had implemented any planting of oaks, nor did I find many landowners managing grazing to protect riparian areas.

I found evidence that two landowners purposefully either introduced or maintained exotic game species to improve hunting opportunities as part of the recreational use of the property. In one case, landowners introduced wild turkey (Meleagris gallopavo) to their property to establish a population for hunting, and several other properties benefitted from the regular occurrence of wild pigs (Sus scrofa) on the property, sometimes taking actions such as planting food plots or limiting harvest to help maintain high populations for the hunting operation.

In several cases, the landowner planted agricultural crops as food plots for wildlife. The most common species planted was barley, which was oftentimes planted to support or enhance feral pig populations. In at least one case, areas that were previously planted had converted to dense infestations of the invasive species, yellow starthistle (Centaurea solstitialis), and one patch was planted over a small remnant patch of relatively rare native grassland. At the same time, one landowner was familiar with the risks of invasion of weeds following food plot planting, and as a result carefully selected locations for such plot and restricted these areas to previously cultivated areas.

Most landowners had a lack of knowledge of current harvest ecology recommendations for hunting, which oftentimes recommend the harvest of female deer to enhance production and increase the buck to doe ratio of the deer population. Doe harvest can result in increased deer production through increasing fawn survival due to reduction in competition by other does (known as a density-dependent response) (Macaulay and others 2013). The main exception to this trend was found in landowners and land managers of property enrolled in the Private Lands Management (PLM; see discussion) program, who had a much better understanding of harvest ecology, and at the same time implemented various habitat improvement practices that benefited wildlife. One PLM land manager safeguarded fawning areas from overly intensive grazing and implemented regular deer surveys on his property, allowing him to document changes in deer populations over the years as well as population parameters such as fawn survival rates. Others implemented re-vegetation of riparian zones, reduced grazing intensity on certain pastures, and removed old, unused barbed wire fences from the landscape.

Most landowners practiced some form of predator control, and several complained that government regulation had hampered their ability to control
predators. Much concern was directed towards state laws implemented since 1972 that have significantly limited the ability of landowners to use lethal control of mountain lions, culminating in the passage of Proposition 117 in 1990 (CDFW 2007). Predator control can be a controversial practice, and landowners noted that many state Department of Fish and Wildlife biologists advocated that game species populations were only minimally affected by predation. However, at least one landowner performed regular November deer census surveys and documented an improved fawn survival rate from .28 fawns per doe to 1.1 fawns per doe as a result of an intensive 2-year effort to reduce coyote populations, which is consistent with studies of coyote control on white-tailed deer fawn survival (Beasom 1974). Although the practice of predator control of coyotes is opposed by various environmental groups (Project Coyote 2014), no landowners were able to eliminate coyote populations on their property despite years of intensive efforts in control. As such, it appears that the persistence of coyotes on the landscape is not threatened, and that control efforts serve to temporarily reduce the density of coyotes on the landscape.

**Discussion and conclusion**

Interviews with landowners and land managers in California, uncovered large variation in earnings from recreational hunting operations, which suggests that there is an inefficient market where the value of recreational hunting rights is not well established or known. Although some landowners were implementing habitat improvement practices on their property, I found that most did little habitat improvement and instead either harvested game that was already occurring on the property, or focused on planting food plots and performing predator control. This suggests a high potential for government efforts through Cooperative Extension to inform and educate landowners about the market potential as well as best practices for wildlife management for recreational hunting enterprises. Because the most often cited reason for not allowing hunting on the property was concern about hunters disturbing livestock operations, there appears to be a significant opportunity to educate hunters about how to minimize disturbances to ongoing ranching operations.

With the exception of properties enrolled in the PLM program, there appeared to be a lack of knowledge of many wildlife management practices that are currently recommended, such as deer census counts, estimation of fawn survival, and collection of information about age of harvested deer. The PLM program, administered by the California Department of Fish and Wildlife (CDFW), is a government program that has the potential to improve conservation outcomes associated with recreational use. This program was developed in the 1980s and allows landowners greater flexibility over seasons and harvest in return for improved conservation practices. Yet, despite the potential for benefits for both landowners and natural resources, it has relatively low adoption rates with 101 landowners currently enrolled in the program statewide, representing just over 404 686 ha (1 million acres) of private land (approximately 2 percent of private land in California) (CDFW 2014). Although participation has increased over the years, (in 1988, 54 landowners covering 284 494 ha (703,000 ac) were enrolled) there appears to be a large potential to expand this program, which appears to result in increased implementation of conservation practices. One concern for future expansion that may need to be addressed is the cap on elk tags, which is currently set at 250 tags per year. Expanded adoption of the PLM program could also result in increased ability of ranchers to
maintain their livestock operation by diversifying income streams (Huntsinger and others 2014)

In addition, results confirm the findings of Smith and Martin (1972), which showed that land prices for rangelands are far higher than would be expected given the income that can be made from ranching operations. This is likely due to the non-monetary enjoyment and benefits that landowners gain from the property, as well as anticipated capital appreciation in the value of the land in the future. The lack of detailed accounting by land managers of the expenses associated with management practices and the difficulty in attributing revenue benefits from particular management practices makes an economic analysis of management practices difficult. Furthermore, the time lag between the implementation of management practices and the potential for increased returns to recreation further complicates making direct connections between management practices and recreation benefits.

In conclusion, while landowners and managers implemented some conservation practices to enhance the recreational values on their properties, there appeared to be many opportunities to enhance this work. There also appeared to be a lack of knowledge about the income-earning potential of hunting, as well as significant distrust of hunters by landowners. Ongoing outreach efforts could serve to improve relationships between hunters and landowners and increase the conservation practices performed on properties, which could improve the potential to earn revenue from recreational use.

References


Acorn Production and Utilization in the Republic of Korea

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Abstract

Oak acorns have historically provided food for humans and animals in cultures across Asia, North Africa, Europe, and North America. The advent of the twentieth-century saw acorns become marginalized as a food crop in the United States and most of the world, but they have remained a constant part of the cuisine of the Korean Peninsula. Consequently, Korea is often cited when discussing the potential of a commercial acorn industry in California, yet little is actually known about acorn production in Korea.

This is a report of preliminary results from a project conducting interviews across the Republic of Korea and mining government statistical archives. Statistics from 2003 to 2012 show net acorn consumption in South Korea of approximately 14,000,000 kg/year with domestic production declining to approximately 400,000 kg/year as imports from China grew to make up 94 percent of consumption. Domestic production is entirely foraged by hand from the wild, primarily by older women. Processing of acorns consists of soaking, drying, shelling, leaching, and milling, and can take place at the family, community, or factory scale. Ultimate consumption takes the form of a variety of human foodstuffs, chiefly acorn tofu, but also dried acorn pasta, fresh acorn pasta, and acorn pancakes.

Key words: acorn, exports, food, imports, Korea, oaks, production, Quercus

Introduction

Oak acorns have historically provided food for humans and fodder for animals in cultures across Asia, North Africa, Europe, and North America (Bainbridge 2006). Today, this starchy nut of long-lived trees also offers potential benefits for mitigating long-term climate change through oak tree carbon sequestration. Because acorns can be used to replace a portion of the grain in animal feed (Bouderoua and others 2009, Keddam and others 2010, Rodriguez-Estevez and others 2011) in addition to serving as a human food, the potential exists to complement the millions of hectares planted to annual cereal grains with perennial hardwood oak groves that produce food and simultaneously sequester atmospheric carbon, provide wildlife habitat, create windbreaks, protect watersheds, and conserve soil.

Because of this great potential, it is important to understand existing acorn production and use in cultures that still utilize them. Although once widely used throughout the northern hemisphere, the Korean peninsula is one of the few remaining regions where acorns are still harvested in large quantities on a regular basis for human consumption (Bainbridge 1986). Traditionally, oak groves served as
a backup source of carbohydrates for rural villages in years when the rice harvest was poor (Lee and others 2007). Acorns continue to this day to play a role in Korean cuisine, with certain towns being known for their production of acorn specialties (Lee 2013), but little else is known in the West about the Korean acorn industry. This research project aims to document traditional production and utilization practices as well as the current state of affairs of acorn production and use in the Republic of Korea.

Methods
Traditional production and processing practices were documented through fifteen structured interviews conducted across the Republic of Korea. In order to capture any differences in practices due to environmental or regional factors, interviews were split equally across the five ecological provinces of the country (Shin and Kim 1996), so that three interviews were conducted in each ecological province. Care was also taken so that all political provinces of the country were represented. Suitable locations were identified by looking for regions noted for production of acorns or acorn foods. Sources of information used to identify these regions included the online INVIL database (Information Network Village 2002), which is a rural economic development program serving 400 villages. Additionally, local experts were consulted and the scientific literature was combed for geographic references to acorn production or consumption in the Republic of Korea.

Once a list of suitable locations was established, appropriate intermediaries were contacted to arrange the interviews. These intermediaries were usually a county official, the local village INVIL coordinator, or the village mayor. If a county official, they were asked to provide information as to which village in their county was best known for acorn production, and to provide a local village contact. Once a local village contact was established, they were asked to identify an elder in their village that was very knowledgeable in acorn production and processing. An interview was then scheduled with that village elder. The structured interview covered oak tree establishment and management, acorn harvesting, and postharvest processing and use. Interviews were conducted in English with simultaneous Korean language translation and responses were recorded in writing in addition to audio recording. When possible, photographic documentation was also taken of acorn harvesting/processing tools, equipment, and procedures.

In addition to the structured interviews, an in depth search of the Republic of Korea government archives was performed to determine if statistics could be found documenting domestic production of acorns as well as import and export figures.

Results
Interview data has not yet been analyzed, so these are preliminary results documenting the current state of affairs of acorn production and use based on data from the government archives and general observations made during the interview process.

Extensive mining of the government archives uncovered excellent documentation of current acorn production (Korea Forest Service 2014a), and imports and exports (Korea Forest Service 2014b). The original data was broken out separately for whole acorns and acorn powder. Domestic production was exclusively whole acorns, which also dominated the import category, while the export category was dominated by acorn powder. For the purposes of this report, quantities of whole acorns and acorn
powder have been combined into a single number. Whenever a statistic about acorns is encountered in this report, it is referring to the combined amounts of whole and powdered acorns.

The most recent 10 years of complete data, 2003 to 2012, were analyzed, and domestic acorn production, acorn imports, and acorn exports were plotted (fig. 1). Net acorn consumption was computed as: net consumption = [(domestic production + imports) – exports], and plotted as well. Net consumption varied over the ten to year period, averaging 13,701,412 kg/year. In the last year of complete data, 2012, net consumption was comprised of 3 percent domestic production, 3 percent South African imports, and 94 percent Chinese imports. Domestic production declined steadily over the ten years from a peak of 1,378,221 kg/year and 9 percent of net consumption in 2003, to a low of 392,567 kg/year and 3 percent of net consumption in 2012. Imports as a percentage of net consumption rose as domestic consumption fell, rising from 91 percent in 2003 to 97 percent in 2012. Exports were very limited, averaging 0.07 percent of net consumption over the ten year period.

China dominated the imports (fig. 2), comprising 96 percent of all imports over the 10-year period, followed by South Africa with 3 percent of imports, and Kyrgyzstan with 0.3 percent of imports over the same period. In decreasing order, Iran, Vietnam, Saudi Arabia, Uzbekistan, Myanmar, Turkey, and Argentina also provided small amounts of imports.
Tiny in comparison to imports, exports from the Republic of Korea over the 10-year period (fig. 3) were primarily to North America, with 44.6 percent going to Canada and 32.2 percent going to the United States. Malaysia received 12.9 percent of exports, followed by (in decreasing order) China, Japan, Sri Lanka, Algeria, Libya, Saudi Arabia, Australia, the United Arab Emirates, Singapore, Germany, Great Britain, and Qatar.
It was generally observed from the interviews that all of the domestic acorn production is collected from the wild by hand and is mostly harvested by older women. Steps in acorn processing can occur in different order, but usually include soaking the whole acorns to kill pests and cause the shells to swell, drying the nuts causing the shells to shrink and crack, shelling the nuts, soaking the nuts in multiple changes of water to leach out the tannins and grinding the nuts while still wet into a slurry that is either used to make acorn foods directly, or drying the slurry into powder for future use.

Processing of acorns can take place at the family scale, a larger community scale, or at the factory scale. At the family scale, individuals collect acorns and process them at home, using them to make food primarily for their family. At the community scale, individuals collect acorns in larger quantities and process them mostly at home, but may also send them to a community mill for grinding, finally making acorn food not just for their family, but also to sell to friends and neighbors, or, as is sometimes the case, to sell in their restaurant. At the factory scale, acorns are still collected by individuals, but they are sold to a local wholesale merchant. These merchants consolidate acorns from many collectors into larger quantities that they then supply to factories. The factories then process the acorns using industrial-scale equipment for eventual sale to grocery stores and restaurants as acorn-based foods.

Overwhelmingly, the primary acorn food consumed in South Korea is dotorimuk, usually translated as ‘acorn jelly’ but more descriptively translated as ‘acorn tofu’. It is made from acorn starch and has the consistency and appearance of soybean tofu except that it is medium brown in color. It is very mild in taste, and is usually taken on the flavor of the sauce with which it is served. Some cooks, however, prefer a mild residual astringency in the dotirmuk and will purposely leave some of the tannins in the acorn for this purpose. Dotorimuk can also be cut into slices and dried in a dehydrator. This is called dotorimuk malengi or ‘dried acorn tofu’. When reconstituted in water, these strips very closely resemble chewy pasta cooked al dente. Dotori guksu or ‘acorn noodles’ are a form of pasta resembling Japanese soba that are made from acorn powder mixed with wheat or buckwheat flour. A form of fresh pasta is made from acorn powder mixed with potato and/or glutinous rice flour and is called dotori sujebi or ‘hand-torn acorn noodle’. These pasta dumplings are most common in soup but are sometimes used in salads as well. One sometimes sees dotori jeon, which are savory acorn pancakes made using a mix of acorn powder and wheat or other flour. Acorns are also distilled to make a drink known as dotori sul or ‘acorn liquor’ that has an alcohol content around 40 percent and is primarily manufactured in the Democratic People’s Republic of Korea.

Discussion
The steady increase in the proportion of net consumption comprised by imports mirrors the steady decline in domestic production. It is unclear why domestic production has been declining steadily over the last 10 years, but it may be related to the steadily increasing household income over that same period (Korean Statistical Information Service 2014) which might mean a declining need to collect acorns for income in the presence of available imports from other countries.

Most notable about the import statistics, is the geographic breadth of countries supplying acorns, from China to South Africa to Argentina. With the overwhelming majority coming from China, questions arise as to the nature of acorn production in that country. Are they also all wild-collected, or have managed acorn orchards been established? It is worth pointing out, too, that oaks are not native to South Africa, and
the approximately 400 000 kg exported to the Republic of Korea in 2012 must either be the result of wild collection from large stands of naturalized oaks or of production from managed acorn orchards. Much remains to be understood about current world commercial acorn production.

As with the import statistics, the export statistics are notable for their geographic breadth, spanning the continents from Canada to Malaysia to Algeria to Australia to Germany. Most notable, however, is that over 75 percent of all exports go to North America. It is expected that these export patterns are driven by demand from temporary or permanent ex-patriot Korean communities in these countries.

Acorn foods are not at all uncommon in the Republic of Korea. With a 2003 to 2012 average net consumption of 13 701 412 kg/year and a population of 48,580,293 in 2010 (Korean Statistical Information Service 2014), the average in-shell equivalent acorn consumption in the Republic of Korea is 0.28 kg/person, which compares favorably to the 2003 to 2012 average United States consumption rate of 0.18 kg/person of in-shell equivalent pistachios (USDA Economic Research Service 2014). The 13.7 million kg/year net consumption of acorns also compares favorably with the 11.4 million kg/year of black walnuts processed annually in the United States (Wax 2013).

Recognizing that North America is the major importer of acorn products from Korea, and that acorns are a globally traded crop exceeding black walnuts in volume, it is curious that California, with its bounty of oak trees, and long history as a global leader in nut production, does not have even a small commercial acorn industry. Sue Chin, however, may be pointing the way to the future. She is a Korean-American businesswoman who collects and processes acorns into flour and baked goods that she sells not only in her small cafe in Martinez, California, but also nationwide through sales over the internet (Sue's Acorn Mill and Cafe 2013).

If Sue Chin is a harbinger for the future, perhaps the United States black walnut industry can provide an idea as to what a commercial acorn industry might look like in California. There is one major black walnut processor in the United States, Hammons Products, which is supplied almost entirely by individuals wild-collecting nuts across 16 states in the Midwest. These nuts are purchased from collectors at one of 250 temporary hulling stations that are set up across the heartland each season, after which they are transported to a central plant in Missouri where they are processed and packed (Wax 2013). If a commercial industry like this could be built around utilization of the acorn in California, it could add value to existing oak rangeland and woodland, thereby helping to protect these landscapes from development and preserving them for future generations.

**Acknowledgments**

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References


Fourteen Years of Forage Monitoring on the California Central Coast Shows Tremendous Variation

Royce Larsen, Karl Striby, and Marc Horney

Abstract
To better understand forage production (above ground biomass) and precipitation patterns in the Central Coast region of California, the first in a growing network of primary production monitoring sites were established in 2001. The California Central Coast has a Mediterranean climate with cool, moist winters and hot, dry summers, and is dominated by annual grasslands and oak woodlands. By 2010, 12 sites were established across San Luis Obispo County, stratified by different rainfall zones, greater than 635 mm (coastal) to less than 200 mm (inland) for an average year. Forage production was measured each spring. The amount of rainfall varied from site to site, as well as from year to year. Annual rainfall ranged from less than 51 mm to over 1016 mm depending on the site and year. Both annual rainfall and its monthly distribution varied significantly. Total production ranged from a high of 11 201 kg/ha (coastal) to a low of 33 kg/ha (inland). Total annual rainfall and monthly distribution was a major driver of forage production. In addition, residual dry matter (RDM) seemed associated with plant species composition. The percentage of forbs observed at the sites was inversely related to RDM level. This data has helped local ranchers, agricultural commissioners, resource conservation districts and others in making management decisions for rangelands on the Central Coast, ranchers being particularly interested. This data set will also be useful for comparing changes in forage production that may occur due to variation in amount and timing of rainfall in the coming years.

Key words: California annual grasslands, forage production

Introduction
Most of California has a Mediterranean-type climate which is characterized with cool moist winters and hot dry summers. Topographic variation yields a great many ecological sites and associated plant communities across California. One broad division is between the annual grassland type, which commonly exists below 365 m in elevation and consists mostly of naturalized species, and many introduced species from the Mediterranean region of southern Europe (George 2014). These annual grasslands are often co-dominant with oak woodlands or savannas, which in many areas are vestiges of their former extent (George 2014). In addition to climate and topographic variation, California is at the confluence of several tectonic plates which have a diverse geology leading to a mixed assortment of soils that vary in their ability to support vegetation (O’Geen and Arroues 2014).

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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Annual forage productivity has been monitored at the San Joaquin Experimental Range since 1935, the Hopland Research and Extension Center since 1952, and the Sierra Foothill Research and Extension Center since 1978 (George and others 2014a). At these locations, total forage production varied greatly from year to year. George and others (2001) provided a summary of the data showing how annual rangelands grow, and the effects that rainfall and temperature have on forage production at these stations.

Though these long-term data sets are very important in understanding production of annual grasslands, they are limited to three locations around the state and have not illuminated much about variations among range sites within those experimental stations rangelands.

Our objective was to develop an additional long-term dataset, one which samples forage production by range sites on the Central Coast of California. This data will also be useful as ecological sites are completed in San Luis Obispo County.

Methods

Study area

San Luis Obispo County is dominated by coastal prairies, annual grasslands, oak-woodlands and chaparral vegetation types (George and others 2014b). Average annual precipitation ranges from 1,067 mm to less than 152 mm (fig. 1). Average annual rainfall is recorded on a water-year, July 1 through June 30, following San Luis Obispo County’s format for recording annual precipitation. The coastal mountain range near the coast rises over 762 m creating a rain shadow effect significantly reducing precipitation east of the range.

![Figure 1—Average annual precipitation across San Luis Obispo County. The county is divided into three zones based on average annual rainfall. The locations of each site monitored, the zone they are in, and the year they were established are shown as follows: Adelaida (1), Camatta (2), Cambria (3), Carrizo (4), Huasna (5), and Morro Bay (6), were established in 2001; Shandon (7) was established in 2003; Bitter water (8) and Soda Lake (9) were established in 2004. Cal Poly (12), Creston (10), and Pozo (11) were established in 2010. The name corresponds to the number in the figure.](image-url)
Forage sampling

As early as 1975, range managers divided San Luis Obispo County into three rainfall zones, >508 mm, between 305 and 508 mm, and <305 mm, to facilitate range management (Weitkamp 1975). Twelve representative sites, between the years 2001 and 2010, were established across San Luis Obispo County in these different rainfall zones. Figure 1 shows the distribution of sampling sites and the average annual rainfall across the county. Sites representing the coastal zone included Cambria, Morro Bay, Huasna, and Cal Poly. Sites representing the central zone included Adelaida, Shandon, Creston, and Pozo. Sites representing the eastern zone included Camatta, Bitterwater, Soda Lake and Carrizo. The characteristics of each site, including soil type, range site, elevation, and distance from the coast are shown in table 1.

Table 1—Information on the soil series, soil name, range site, elevation and distance from the coast for each site in San Luis Obispo County that was monitored

<table>
<thead>
<tr>
<th>Site name</th>
<th>Precipitation zone</th>
<th>Year started</th>
<th>Soil unit</th>
<th>Soil name</th>
<th>Range site</th>
<th>Elevation (m)</th>
<th>Distance from coast (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cambria</td>
<td>Coastal</td>
<td>2001</td>
<td>191</td>
<td>Tierra</td>
<td>Course Loamy Claypan</td>
<td>134</td>
<td>4</td>
</tr>
<tr>
<td>CalPoly (W5)</td>
<td>Coastal</td>
<td>2010</td>
<td>127</td>
<td>Cropley Clay</td>
<td>Clayey</td>
<td>103</td>
<td>11</td>
</tr>
<tr>
<td>Huasna</td>
<td>Coastal</td>
<td>2001</td>
<td>165</td>
<td>Los Osos-Diablo Complex</td>
<td>Loamy Claypan</td>
<td>159</td>
<td>15</td>
</tr>
<tr>
<td>Morro Bay</td>
<td>Coastal</td>
<td>2001</td>
<td>128</td>
<td>Cropley Clay</td>
<td>Clayey</td>
<td>27</td>
<td>4</td>
</tr>
<tr>
<td>Adelaida</td>
<td>Central</td>
<td>2001</td>
<td>134</td>
<td>Dibble</td>
<td>Clay Loam</td>
<td>323</td>
<td>31</td>
</tr>
<tr>
<td>Creston</td>
<td>Central</td>
<td>2010</td>
<td>103</td>
<td>Arbuckle-Positas Xerofluvent- Xerorthents Nacimiento-Los Osos Choice Silty Clay</td>
<td>Clay Loam</td>
<td>363</td>
<td>35</td>
</tr>
<tr>
<td>Pozo</td>
<td>Central</td>
<td>2010</td>
<td>50</td>
<td>Not Available Fine Loamy Clay</td>
<td>Clay Loam</td>
<td>482</td>
<td>37</td>
</tr>
<tr>
<td>Shandon</td>
<td>Central</td>
<td>2003</td>
<td>179</td>
<td>Nacimiento-Los Osos</td>
<td>Fine Loamy Clay</td>
<td>585</td>
<td>61</td>
</tr>
<tr>
<td>Bitterwater</td>
<td>Eastern</td>
<td>2004</td>
<td>140</td>
<td>Choice Silty Clay</td>
<td>Clay Loam</td>
<td>628</td>
<td>71</td>
</tr>
<tr>
<td>Camatta</td>
<td>Eastern</td>
<td>2001</td>
<td>101</td>
<td>Balcom-Nacimiento</td>
<td>Loamy</td>
<td>508</td>
<td>56</td>
</tr>
<tr>
<td>Carrizo</td>
<td>Eastern</td>
<td>2001</td>
<td>440</td>
<td>Belly Spring Panoza</td>
<td>Loamy</td>
<td>793</td>
<td>81</td>
</tr>
<tr>
<td>Soda Lake</td>
<td>Eastern</td>
<td>2004</td>
<td>240</td>
<td>Panoza-Beam Complex</td>
<td>Coarse Sandy Loam, Limy Upland</td>
<td>808</td>
<td>77</td>
</tr>
</tbody>
</table>

Since these sites were on private rangeland where grazing could not be controlled, three temporary exclosures were erected at each site. Total forage production was measured each spring by clipping vegetation from two 0.093 m$^2$ plots within each exclosure at the time of peak growth, for six samples per site. Total forage included plant species that were palatable, but excluded non-palatable species such as
fiddleneck (*Amsinckia* spp.), lupin (*Lupinus* spp.), turkey mullen (*Eremocarpus setigerus*), and tar weed (*Hemizonia* spp.). Samples were oven dried and weighed. Measurements were made at the time of peak growth. This usually occurred in late April, but there were yearly and site differences based on rainfall timing and amounts. Rainfall records were obtained from the ranch headquarters, or the nearest weather station operated by the County of San Luis Obispo or Bureau of Land Management’s remote automated weather stations (RAWS). Each fall, the exclosures were moved in a random distance (between 7 to 21 m) and direction to a grazed location, but remained on the same soil type, slope and aspect. This was done to avoid affects from old residual dry matter (RDM) accumulations and to be representative of the current grazing levels. Old RDM influences both the amount of production and the species composition (Bartolome and others 2006). A visual estimation of species composition was recorded at each site at the time of peak growth.

**Data summary**

This case study is meant to provide descriptive data representing the first 14 years of a project to improve the representation of variability in rangeland forage production across the Central Coast. Subsequently, greater provision of funding and increased interest and participation by ranchers and range managers in the region has allowed the expansion of the monitoring network in ways which is beginning to allow replications of measurements across range sites (and ecological sites as they are developed), precipitation zones, slope/aspect, soil moisture and temperature gradients. It is our intention to make use of the sampling improvements to investigate how patterns in precipitation timing and amounts and temperature impact production/species composition across these areas.

**Results**

The rainfall was highly variable by both year and site. The high was recorded at the Cambria site (coastal zone) at 1022 mm during the 2004-2005 growing season, and the low was 43 mm at the Soda Lake site (eastern zone) during 2013-2014. Figure 2 shows the distribution of rainfall by zones and year. Not only did the amount vary from year to year, and across precipitation zones, but the timing of that precipitation also varied. The average year consisted of rainfall beginning in October, with the heaviest rainfall during December, January, and February, then tapering off in March, April and May (fig. 3). Some years, like 2012-2013, water-year started when expected, but ended early (fig. 3). In contrast the 2013-2014 water-year did not start until very late (fig. 3), without a germinating rain until February, 4 months later than normal.
Rainfall, especially total amount, seemed to be the dominant factor in forage production. This pattern was clearly shown when averaged over all sites and years (fig. 4). Even though rainfall was the dominant factor, forage production still varied considerably from year to year and there were large differences from coastal, central to eastern zones during any given year (fig. 5). However, as expected the coastal zone...
always had the highest forage production, and the eastern zone was always the lowest (fig. 6). During this study, the site with maximum production was at Cambria (2005-2006 growing season) and had 11,503 kg/ha while the site with the minimum production was at Soda Lake (2006-2007 growing season) and had 33 kg/ha. Overall the average was 3,934 kg/ha across all years and sites.

Figure 4—Average forage production and precipitation for all sites.

Figure 5—Total forage production for each site monitored in San Luis Obispo County. Production was measured at time of peak growth, late April or early May depending on the year.
Our data suggests a pattern of grass dominance over forbs when RDM was highest (fig. 7). Forbs seemed to increase, and sometimes even exceed grass cover, for a couple of years when RDM was low (fig. 7). This pattern was observed more so in the eastern side of the county where low productivity generally resulted in lower RDM levels.

Figure 7—Dominant forage type, grass versus forb, relative to residual dry matter (RDM). RDM was measured during the fall prior to germination and growth of forage.

Discussion
The interannual variability in total forage production makes land-use planning difficult. What is worse is that in many years, it may not be clear how productive a year it will be until most of the growing season has passed. Our data indicates a
larger interannual variation than George and others (2014a) reported for the three experimental ranges in Northern and Central California. The Central Coast often receives less precipitation than Northern California making management much more difficult for ranchers or range managers (George and others 2010). Such variation makes it difficult to maintain persistent numbers of breeding females in livestock herds. Since mother cows in a cow/calf operation have to be kept for the whole year, stocking should be kept light to moderate in order to ensure adequate feed during the leaner years. Stocker cattle are a good option for many to utilize extra feed during the wetter years. This can be helpful because the stockers can be removed (sold, or grazing leases closed) when the feed runs out.

We hope that by continuing to record fall RDM levels and subsequent peak production on the same sites, we may learn more about whether, or how much, low RDM levels impact recovery of production levels following periods of drought. We also anticipate learning about the magnitude of real drought impacts, and how best to express them to government policy makers.

Acknowledgments

We thank the owners of our study sites for permitting access to their properties for field data collection and their cooperation throughout this study period.

References


Goldspotted Oak Borer
The Goldspotted Oak Borer: Revisiting the Status of an Invasive Pest Six Years After Its Discovery

Steven J. Seybold and Tom W. Coleman

Abstract
The goldspotted oak borer, *Agrilus auroguttatus* (Coleoptera: Buprestidae), was first associated with oak mortality in San Diego County, California in May of 2008. Since that time, a research and survey program has outlined the biology of this flatheaded borer in the invaded and native habitats; delimited the invaded range; and developed the components of an integrated pest management (IPM) program. Significant advances have been made in the understanding of its host range, feeding habits, life cycle, and natural enemies in Arizona and California. Some research progress has also been made on the evaluation of techniques for the detection of the pest and treatments to ameliorate its damage. Since the original discovery, we have learned that *A. auroguttatus* feeds primarily on red oaks in the section *Lobatae* and that although its landscape-level impacts unfold slowly, it appears to be capable of killing these trees without the aid of abiotic or other biotic factors. The biology, behavior, and impact of *A. auroguttatus* have also been contrasted with a less well understood sibling species, the Mexican goldspotted oak borer, *Agrilus coxalis*. The key questions remaining about *A. auroguttatus* are: 1) Has sufficient progress been made to facilitate a functional IPM program should the expanding distribution of *A. auroguttatus* reach the urban oaks of the Los Angeles basin or woodland oaks in the foothills of the Sierra Nevada? and 2) Can we assess the risk and predict the population expansion to these lands?

Key words: *Agrilus auroguttatus*, California black oak, canyon live oak, coast live oak, goldspotted oak borer, mortality agent

Introduction
The goldspotted oak borer (GSOB), *Agrilus auroguttatus* (Coleoptera: Buprestidae) (fig. 1), is a flatheaded borer of the phloem and outer xylem that was first collected and described in the early 1900s from specimens from the Huachuca Mountains in southeastern Arizona (Schaeffer 1905). It was not noted as an economically or ecologically important associate of oaks (Brown and Eads 1965, Cibrian and others 1995, Furniss and Carolin 1977) until it was collected in survey traps in southern California in 2004 (table 1) and associated with dying oaks in eastern San Diego County in 2008 (Coleman and Seybold 2008a, b). Thus, this beetle is an indigenous exotic species (Dodds and others 2010, Seybold and Downing 2009) that has expanded its range in a discrete fashion from one native North American ecosystem to another with rather dramatic consequences to non-co-evolved oaks in the new habitat. In comparison to its pines (*Pinus* spp.) and other conifers, California...
has a relatively depauperate guild of insects that colonize the phloem and xylem of oaks and, prior to the advent of *A. auroguttatus*, none of these insect species has had a significant area-wide impact on the health of oaks (table 2).

Figure 1—Dorsal view of an adult female goldspotted oak borer, *Agrilus auroguttatus* (Coleoptera: Buprestidae). (photo: USDA Forest Service, Northeastern Area Forest Health Protection, Durham, NH Office)

Table 1—First collection records of goldspotted oak borer, *Agrilus auroguttatus*, in California

<table>
<thead>
<tr>
<th>Date</th>
<th>County</th>
<th>Location</th>
<th>Collection method</th>
<th>Specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>VI-18-2004</td>
<td>San Diego</td>
<td>Chambers Park Campground, Lake Cuyamca, N of Cuyamaca Rancho State Park</td>
<td>Survey trap</td>
<td>1, CSCA&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>VII-16-30-2004</td>
<td>San Diego</td>
<td>Paso Picacho Campground, Cuyamaca Rancho State Park</td>
<td>Survey trap</td>
<td>2, CSCA&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>VII-24-2006</td>
<td>San Diego</td>
<td>Julian, 4945 Heise Park Road</td>
<td>Funnel trap catch with exotic <em>Ips</em> lure</td>
<td>1, CSCA&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>VI-27-2008</td>
<td>San Diego</td>
<td>Noble Canyon Trailhead, Cleveland National Forest</td>
<td>Purple flight intercept traps near <em>Quercus agrifolia</em></td>
<td>2, CAS&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>X-26-2012</td>
<td>Riverside</td>
<td>Idylwild, along Hwy 243</td>
<td>Beneath the bark of <em>Quercus kelloggii</em></td>
<td>2-3 larvae&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>XII-8-2014</td>
<td>Orange</td>
<td>Weir Canyon</td>
<td>Beneath the bark of <em>Q. agrifolia</em></td>
<td>5 larvae&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup> Coleman and Seybold (2011).
California State Collection of Arthropods, Sacramento, California.
California Academy of Sciences, San Francisco, California.
No vouchered specimens because the larvae were destructively sampled as a consequence of the mtDNA analyses conducted at UC-Riverside for Riverside County specimens (Lopez and others 2014b) and Orange County specimens (Rugman-Jones and others, unpublished data).

Table 2—The entomological context for the goldspotted oak borer, *Agrilus auroguttatus* (Coleoptera: Buprestidae), invasion of California: bark and woodboring insects associated with declining oaks and tanoaks

<table>
<thead>
<tr>
<th>Species</th>
<th>Feeding group</th>
<th>Significance (early vs. late in decline cycle)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agrilus auroguttatus</em> Schaeffer&lt;sup&gt;b&lt;/sup&gt;</td>
<td>flatheaded borer, phloem and outer xylem of stem and largest branches</td>
<td>Highly significant, early</td>
</tr>
<tr>
<td>Coleoptera: Scolytidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pseudopityophthorus pubipennis</em> (LeConte)/ <em>P. agrifoliae</em> Blackman</td>
<td>bark beetles, phloem of stem and branches</td>
<td>Moderately significant, can be early on seriously weakened trees</td>
</tr>
<tr>
<td><em>Monarthrum dentiger</em> (LeConte)/ <em>M. scutellare</em> (LeConte)</td>
<td>ambrosia beetles, xylem of stem and branches</td>
<td>Moderately significant, late— stem breakage of SOD-infected trees</td>
</tr>
<tr>
<td><em>Gnathotrichus pilosus</em> (LeConte)</td>
<td>ambrosia beetle, xylem of stem and branches</td>
<td>Moderately significant, late— stem breakage of SOD-infected trees</td>
</tr>
<tr>
<td><em>Xyleborinus saxeseni</em> (Ratzeburg)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>ambrosia beetle, xylem of stem and branches</td>
<td>Not significant, late, important for wood decomposition</td>
</tr>
<tr>
<td><em>Cyclorhipidion bodoanum</em> (Reitter)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>ambrosia beetle, xylem of stem and branches</td>
<td>Not significant, late, important for wood decomposition</td>
</tr>
<tr>
<td>Coleoptera: Buprestidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chrysobothris femorata</em> (Olivier)/ <em>mali</em> Horn/wintu Wellso and Manley</td>
<td>flatheaded borers, flatheaded appletree borer, Pacific flatheaded borer, bark and outer xylem of stem and branches</td>
<td>Not significant, late, important for wood decomposition</td>
</tr>
<tr>
<td><em>Agrilus angelicus</em> (Horn)</td>
<td>flatheaded borer, Pacific oak twig girdler, xylem of small branches and twigs</td>
<td>Not significant, early, but attacks peripheral portions of tree</td>
</tr>
<tr>
<td>Coleoptera: Bostrichidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Scobicia declivis</em> (LeConte)</td>
<td>false powderpost beetle, lead cable borer, xylem of stems and branches</td>
<td>Not significant, late, important for wood decomposition</td>
</tr>
<tr>
<td>Coleoptera: Cerambycidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Xylotrechus nautilus</em> (Mannerheim)</td>
<td>roundheaded borer, oak cordwood borer, phloem and xylem of stem and branches</td>
<td>Moderately significant, can be early on seriously weakened trees</td>
</tr>
<tr>
<td><em>Phymatodes lecontei</em></td>
<td>roundheaded borers,</td>
<td>Moderately significant, can be...</td>
</tr>
</tbody>
</table>
Research and survey activities since 2008 have established that colonization by larvae of this beetle leads to the mortality of large diameter (>45.7 cm (18 inches) in diameter at breast height, DBH) red oaks (*Quercus*, Section *Lobatae*) and that the feeding activity of the larvae is not always associated with pathogenic fungi or other microorganisms (Lynch and others 2014). The decline of the primary hosts in California (coast live and California black oaks) is a long process (conservatively 3 to 5 years) (Chen and others 2015, Haavik and others 2015), which provides a window of opportunity for management of the pest. The key to limiting future expansion of the invaded range of *A. auroguttatus* is thought to be the prevention of the movement of infested firewood (Jones and others 2013). Based on new biological data collected since 2008, a risk assessment and a map of the projected distribution for *A. auroguttatus* are under development (Venette and others, Assessing the risks posed by goldspotted oak borer to California and beyond, these proceedings).

**Invasion history, feeding habits, host range, and life history**

The awareness that a new pest might be damaging oaks in San Diego County developed slowly in the 1990s and 2000s when anecdotal reports of dying trees were attributed variously to drought; deteriorating air quality; a native flatheaded borer called the Pacific twig girdler, *Agrilus angelicus*; or pathogens in the genus *Phytophthora* (Bohne and Rios 2006, 2007, 2008; Garbelotto and Hüberli 2006, Rizzo and Garbelotto 2003; Pavel Švihra, University of California Cooperative Extension, retired, personal correspondence). Although it was tempting to connect the areawide demise of the coast live oaks, *Quercus agrifolia*, California black oaks, *Q. kelloggii*, and canyon live oaks, *Q. chrysolepis*, in San Diego County to sudden oak death, caused by *Phytophthora ramorum*, which was causing oak mortality further to the north in California (Rizzo and Garbelotto 2003), no evidence of *P. ramorum* was ever detected in the San Diego County zone of oak mortality (P.A. Nolan, County of San Diego, personal communication). Because no cause could be linked to the decline of these oaks, the syndrome was described ambiguously as “oak croak,” and considered to be a drought-related event (Bohne and Rios 2006, 2007, 2008).

In May 2008, larvae of a buprestid in the genus *Agrilus* were recovered from the main stem of declining oaks on the Descanso Ranger District of the Cleveland National Forest (Coleman and Seybold 2008b). Because there were
no records of a main-stem-infesting species of *Agrilus* on California oaks (Furniss and Carolin 1977), we speculated at first amongst ourselves that these might be an introduced population of the twolined chestnut borer, *Agrilus bilineatus*, from the eastern United States (Haack and Benjamin 1982) or of the oak splendour beetle, *Agrilus biguttatus* from central Europe (Moraal and Hilszczański 2000). However, rearing of the larvae and flight trapping at the site revealed that the species that was killing these oaks was a taxon or taxa that had been known to coleopterists for many years as either *Agrilus coxalis* or *A. auroguttatus*. The relatively “ancient” taxonomic literature (Fisher 1928, Schaeffer 1905, Waterhouse 1889) that accompanied these taxa provided the only biological background on these pests in the absence of the traditional forest entomological monographs for western North America (Cibrian and others 1995, Furniss and Carolin 1977). A survey of museum collections established the complete, but sparse, collection history of both taxa (Coleman and Seybold 2011), which provided some limited data on the seasonal activity of the adults. In addition to specimens recovered from declining oaks, the invasive *Agrilus* in California had been trapped in 2004 and 2006 in the vicinity of the infested area of the Cleveland National Forest by survey entomologists with the California Department of Food and Agriculture (table 1). These finds had been reported as a new locality record in the taxonomic literature (Westcott 2005). Following a period of discussion, analysis, and deliberation by morphologists and molecular population geneticists, it became clear that the population of this organism in San Diego County was *A. auroguttatus* and that its introduction into California was consistent with a source population from the Dragoon Mountains (fig. 2) in southeastern Arizona (Coleman and Seybold 2009, Coleman and others 2012b, Hespenheide 1979, Hespenheide and Bellamy 2009, Hespenheide and others 2011, Lopez and others 2014b, Westcott 2005). *Agrilus auroguttatus* had also been collected on one occasion from southern Baja California (Westcott 2005) and is also thought to occur elsewhere in northern Mexico and perhaps in New Mexico (Coleman and Seybold 2011). *Agrilus coxalis*, on the other hand, is only known from the area from the central Mexican mainland south to Guatemala (Coleman and Seybold 2008b, 2011; Coleman and others 2012a,b, 2015a). Although there were unsubstantiated reports of the importation of oak firewood into the general area of eastern San Diego County from Mexico and the high probability of the movement of firewood along the general tourist route from New Mexico and Arizona via Interstate Highway 8 to San Diego, the specific details of where, when, and how *A. auroguttatus* came to be established in and around the rural communities of Descanso, Guatay, and Pine Valley, California have not been ascertained. The two species have been assigned common names: the goldspotted oak borer, *A. auroguttatus*, and the Mexican goldspotted oak borer, *A. coxalis*.
Figure 2—Historical collection records of the goldspotted oak borer, *Agrilus auroguttatus*, from four mountain ranges (Santa Catalina, Santa Rita, Huachuca, and Chiricahua) in the Coronado National Forest in southeastern Arizona (Coleman and Seybold 2011). General collection localities are denoted by an X, whereas specific locations from collection labels are indicated by black dots (•). The putative origin of the population of *A. auroguttatus* that has been introduced into California is circled in red (Lopez and others 2014b).
Adult *A. auroguttatus* feed on oak foliage; larvae feed on the phloem and outer xylem. The adult feeding removes foliar tissue from the periphery of oak leaves, but appears to have little bearing on the health of the crown. Details of the foliage feeding behavior of the adults in the field have not been observed. In contrast, much more is known about the larval feeding habits (Coleman and Seybold 2008b, Haavik and others 2013). Larvae mine initially through the phloem in a general radial direction, ingest this tissue, and create meandering and generally longitudinal galleries filled with boring dust (frass) where the phloem meets the xylem. These subcortical galleries are stained black in color when the outer bark is removed for examination of the larvae. The larvae appear to feed primarily at the interface between the xylem and phloem. Thus, the feeding activity of the larvae damages the nutritive and water-conducting tissue of the tree as well as the morphogenic thin layer of cambium responsible for formation of the xylem and phloem. The feeding activity also elicits oak sap flow, which is manifested as pools of sap around the patches of necrotic tissue below the bark as well as sap staining on the bark surface. In some cases in *Q. agrifolia*, the tree exudes a deep red sap secretion that forms globules on the bark surface in response to the underlying feeding activity. Larval frass is never observed on the bark surface.

The host range has been examined in both the adults and the larvae. In laboratory tests, Chen and others (2013) found that adult *A. auroguttatus* generally had a preference for *Q. kelloggii* foliage when tested in dual choice arrangements with *Q. agrifolia*, *Q. chrysolepis*, and *Q. engelmannii* (a white oak, *Quercus* Section *Quercus*). In a no-choice laboratory study, foliage from white alder, *Alnus rhombifolia*, elicited overall poor performance of adults when compared with oaks (Haavik and others 2014b). Field surveys in Arizona, California, and Mexico (*A. coxalis*) provided initial assessments of the host ranges of the larvae (Coleman and Seybold 2011; Coleman and others 2012a, 2012b, 2015a). In California, larval *A. auroguttatus* have been observed in the field in the phloem of *Q. agrifolia*, *Q. chrysolepis*, and *Q. kelloggii*, and rarely in *Q. engelmannii*. Adult emergence through the outer bark has occurred on all of these species (Coleman and others 2015b). In Arizona, *A. auroguttatus* develops in two red oaks (Section *Lobatae*) Emory oak, *Q. emoryi*, and silverleaf oak, *Q. hypoleucoides*, as hosts (Coleman and Seybold 2011, Haavik and others 2014a), whereas in Mexico, *A. coxalis* develops in a red oak (Section *Lobatae*), *Q. conzatti*, and a white oak (Section *Quercus*), *Q. peduncularis* (Coleman and others 2012b). The complete host range of *A. coxalis* is poorly understood. In laboratory tests with cut oak logs, larvae of *A. auroguttatus* rarely completed development fully (Haavik and others 2014b). However, quantification of partial larval development suggested that larvae of this species would feed on both red and white oaks as well as taxonomically intermediate species, *Q. chrysolepis* (Quercus Section *Protobalanus*) and *Q. suber* (Quercus Section *Cerris*). Of note, phloem of one white oak, valley oak, *Q. lobata*, was fed on by larvae during the laboratory assays, whereas phloem of two other white oaks, Oregon white oak, *Q. garryana*, and *Q. engelmannii* were not fed on by larvae (Haavik and others
2014b). The quantitative differences in preference by *A. auroguttatus* for its various hosts as assessed in the laboratory and in the field could bear more research scrutiny, as could its potential to feed on oak species from eastern North America.

A newly published U.S. Department of Agriculture, Forest Service Forest Insect and Disease Leaflet (Coleman and others 2015b) and a University of California Cooperative Extension Pest Note (Flint and others 2013) provide thorough summaries of the life history (fig. 3) and photographs of the life stages of *A. auroguttatus* in California. These summaries are based largely on the research of L.J. Haavik at University of California Davis (Haavik and others, 2012a, 2012b, 2013, 2014a, 2014b, 2015) and V.M. Lopez at University of California, Riverside (Lopez 2013, Lopez and Hoddle 2013, 2014, Lopez and others 2014a, 2014b). In brief, the eggs are thought to be laid in crevices on the bark surface shortly after the initiation of the adult flight season (middle of May-end of September). By analogy to other *Agrilus* sp., the adults are expected to feed on the foliage in the upper crown after emergence (Rodriguez-Saona and others 2007). Mating also may take place at this location, though *Agrilus* in eastern North America on birch, *Betula*, and poplar, *Populus*, appear to mate on the vertical or prostrate (in other words, fallen) stems of these trees in these genera (Carlson and Knight 1969). Males and females of *A. bilineatus* also have been reported to mate on the branches and trunks of *Quercus* in eastern North America (Haack and Acciaiavatti 1992), whereas males and females of the emerald ash borer, *Agrilus planipennis*, have been reported to mate on the foliage and stems of ash, *Fraxinus*, in China (Wang and others 2010). In North America, male *A. planipennis* have landed and attempted to mate with female decoys on both the stems (Rodriguez-Saona and others 2007) and the foliage (Lelito and others 2007) of ash. Rodriguez-Saona and others (2007) proposed that the “primary mate-finding strategy of *A. planipennis* involves active visual search by males for females on tree trunks.” Nothing further of the location of mating behavior of *A. planipennis* seems to be known from the invasive North American population (Herms and McCullough 2014). Unlike *A. planipennis*, which colonizes ash trees by initiating oviposition in the upper crown before the main stem (Herms and McCullough 2014), female *A. auroguttatus* tend to move to the lower bole (Coleman and others 2014) to oviposit. Males are also found to land on the main stem (Coleman and others 2014), which suggests that mating may occur here too. Under optimal conditions in the laboratory, female adults can survive for 72.1 (±6.3) days. When paired with a single male and water and oak foliage, females become sexually mature after 8 days; have an ovipositional period of 43.6 (±7.4) days; and lay approximately 200 eggs (Lopez and Hoddle 2014). In the field, larvae hatch from the eggs, mine through the outer bark and into and through the phloem. Larval feeding occurs primarily from mid-June to late November and considerable feeding occurs where the phloem meets the xylem. After completing their feeding activity, larvae tunnel back toward the bark surface where they create a small pupal cell about 3.2 to 6.4 mm (1/8 to 1/4 inches) below the bark. This late larval
stage (the pre-pupa) can be found throughout most of the year (mid-October to mid-June) when compared to the other life stages (Haavik and others 2013). There are four larval instars (Haavik and others 2013). The pupa is present from early April to late July after which metamorphosis to the adult occurs followed by emergence through a distinctive D-shaped hole in the bark surface. The life cycle is thought to take a complete year (univoltine), but some individuals may require an additional fraction of a year to complete development (Haavik and others 2013).

![Figure 3—Univoltine life cycle of the goldspotted oak borer, *Agrilus auroguttatus*. Lower right: Pre-pupa or “J-larva” in quiescent repose in a pupal cell near the bark surface of coast live oak, *Quercus agrifolia* (T.W. Coleman, photo). This is the most frequently encountered life stage (Haavik and others 2013).](image)

**Impact on California oaks and landscapes**

As a phloem/cambium/xylem borer of the main stem (Mattson and others 1988), *A. auroguttatus* belongs to a class of pests that ranks amongst the most pernicious of forest insects in terms of its impact to the health of trees. As a newcomer to California’s oak ecosystems, *A. auroguttatus* appears to find itself in a habitat with highly vulnerable host species accompanied by limited biological regulation of its population. The loss of functional phloem as a consequence of the high densities of larval mines on the xylem surface of dead and dying oaks accompanied by a similarly high density of adult emergence holes through the bark surface (Chen and others 2015, Haavik and others 2014a) are together a testament to the impact of *A. auroguttatus* on the trees. Necrosis of the outer xylem and phloem leads to crown decline and loss of photosynthetic capacity. These declines appear to occur gradually. Coast live oaks under more advanced cases of infestation show physiological symptoms of water stress that resemble trees experiencing drought (Coleman
and others 2011). With coast live oak, host colonization by *A. auroguttatus* has been recorded primarily on trees greater than 15 to 20 cm in DBH; trees below this threshold appear to escape colonization (Chen and others 2015, Coleman and others 2012a, Haavik and others 2014a).

In landscape-level surveys throughout the infested area in San Diego County, just over 60 percent of oaks show evidence of colonization by *A. auroguttatus* (Coleman and others 2012a). In the core area where tree mortality appears to have been occurring for about 10 years, this estimate approaches 90 percent (Coleman and others 2012a). At two experimental sites in the core area, the rates of new infestation of *Q. agrifolia* over a 2.5 year study period were 50 percent and 32 percent (Chen and others 2015). Oak mortality throughout the infested area has been assessed at 13 percent, with the estimate climbing to 50 percent in the core area (Coleman and others 2012a). In contrast, mean oak infestation rates for *A. auroguttatus* and *A. coxalis* were approximately 4 percent in their respective native habitats in Arizona and southern Mexico. Mean rates of oak mortality were only 2 percent in these instances (Coleman and others 2012a). Across the landscape in San Diego County, nearly 28,000 trees have been thought to have been killed by *A. auroguttatus* (USDA FS FHM 2014) with aerial detection showing mortality occurring at a generally expanding radial pattern through 2010 and intensification over the infested area with time. Sites at the periphery show new cases of infestation and mortality that occur at a relatively gradual rate (Haavik and others 2015). In the core area the dynamics of decline and mortality also appear to be gradual (Chen and others 2015), but where trees have died and have not been salvaged for firewood, rather dramatic changes in the structure and distribution of fuels are occurring in the canopy, in the understory, and on the surface of the forest floor (Coleman, Influence of the goldspotted oak borer on fuel loading in southern California, these proceedings).

**Management, dispersal, and risk assessment—what can we do and what is the risk of doing nothing?**

Since its discovery on oaks in 2008, considerable research on *A. auroguttatus* has been conducted to provide the foundation for an integrated pest management (IPM) program (table 3). For an IPM program to be efficacious, a certain degree of synthesis must occur between our knowledge of the biology of this pest and our approaches to monitor the organism and control its populations (fig. 4). The techniques to detect and control the pest have to be tested and validated.
Table 3—Developing the elements of an integrated pest management program for the goldspotted oak borer (GSOB), *Agrilus auroguttatus*, in California

<table>
<thead>
<tr>
<th>Element</th>
<th>Key findings</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biology and</td>
<td>Discovery of injury in CA</td>
<td>Chen and others (2013); Coleman and Seybold (2008b, 2009, 2010b); Haavik and others (2013, 2014b); Lopez and Hoddle (2013, 2014); Lopez and others (2014a).</td>
</tr>
<tr>
<td>host range</td>
<td>Adult feeding preference on foliage</td>
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<td></td>
<td>Larval feeding preference on cut logs</td>
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<td></td>
<td>Number, phenology, and feeding location of larval instars</td>
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<td></td>
<td>Distinguishing adult males and females</td>
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<tr>
<td>Quantifying</td>
<td>Adult longevity and flight capacity</td>
<td>Chen and others (2015); Coleman and others (2011, 2012a); Coleman and Seybold (2010a); Haavik and others (2012b, 2014a,b, 2015); Hishinuma and others (2011); Lynch and others (2014); Seybold and Coleman (2010a).</td>
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<td>impact</td>
<td>Injury symptoms and tree health rating system</td>
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<td></td>
<td>Induced water stress as a consequence of larval feeding</td>
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<td></td>
<td>Interaction with other wood borers in CA and AZ</td>
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<td></td>
<td>Infestation and injury rates in CA, AZ, and MX</td>
<td></td>
</tr>
<tr>
<td>Monitoring</td>
<td>Monitoring guidelines and trapping techniques</td>
<td>Coleman and others (2014).</td>
</tr>
<tr>
<td>and detection</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control-</td>
<td>Discovery of GSOB natural enemies in AZ and CA</td>
<td>Coleman and others (2012b, 2015a); Coleman and Seybold (2011); Gibson (2010); Haavik and others (2012a); Lopez (2013); Lopez and others (2014b).</td>
</tr>
<tr>
<td>biological</td>
<td>Description of <em>Calosota elongata</em> from AZ</td>
<td></td>
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<tr>
<td></td>
<td>Distribution of <em>Calosota elongata</em> in CA</td>
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<td></td>
<td>GSOB population genetics and origin of invasive population in CA</td>
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<tr>
<td>Control-</td>
<td>Use of sanitation (tarping, grinding, and debarking) as a management tool</td>
<td>Jones and others, (2013); Seybold and others (2010a).</td>
</tr>
<tr>
<td>mechanical</td>
<td>for infested wood</td>
<td></td>
</tr>
<tr>
<td>Control-</td>
<td>Systemic insecticide options for GSOB</td>
<td>Chen and others (2015); Coleman and others (in preparation).</td>
</tr>
<tr>
<td>chemical</td>
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<td>synthesis</td>
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</table>
Coordination of Life Cycle and Management Activities for GSOB
An IPM Framework

Figure 4—Synthesis of the goldspotted oak borer, Agrilus auroguttatus, life cycle with the monitoring and control steps of an integrated pest management program (Coleman and others 2015b).

With *A. auroguttatus* we have a primitive monitoring tool, which is an unbaited purple-colored sticky trap (Coleman and others 2014, Francese and others 2008). This trap has been used to delimit the invasive population in San Diego County (fig. 5). However, it failed to detect a satellite population in Riverside County because the survey traps there were too distant from the point of introduction. Presently, this trap cannot be used to provide a quantitative estimate of populations of *A. auroguttatus*, but it has been used to outline the period of seasonal flight activity (Coleman and others 2014, Haavik and others 2013). A lure to increase the trap catch is still lacking, and complexity revealed by work on the chemical ecology of *A. planipennis* suggests that developing a powerful olfactory-based lure for *A. auroguttatus* may be difficult (Crook and Mastro 2010). Field assays with potential semiochemicals originating from oak foliage and stem volatiles have not revealed any attractants for *A. auroguttatus*, though some of these prospective behavioral chemicals have elicited electrophysiological responses from the antennae of *A. auroguttatus* (Coleman and others 2014).
Positive (red) and negative (green) trap catches of GSOB in a trapping survey of CA (2009-2012)

Figure 5—Delimited distribution of the goldspotted oak borer, Agrilus auroguttatus, in southern California based on a 4-year flight trapping survey with purple prism sticky traps (right) (Coleman and others 2014). The borer was only trapped in flight in San Diego County during the survey. Since the end of this survey period, the beetle has also been found in Riverside and Orange Counties (not shown).

Control of populations of A. auroguttatus can be approached from three perspectives: biological control; mechanical control; and chemical control. Although considerable effort has been expended to lay the groundwork for biological control (Lopez 2013), it appears that the difficulties encountered in mass rearing A. auroguttatus will preclude our capacity to rear and release its natural enemies. An ensemble of natural enemies has been identified (table 3), and this “alpha-level” effort has also resulted in the description of a new wasp species, Calosota elongata, which appears to specialize on larvae of A. auroguttatus (Coleman and Seybold 2011, Gibson 2010). This exophytic larval parasitoid occurs both in the native (Coleman and Seybold 2011) and invaded (Haavik and others 2012a) habitats of A. auroguttatus. The expansion of the distribution of A. auroguttatus in southern California (Coleman and
others 2014, Haavik and others 2015) and the relatively high levels of oak mortality in the core area of the distribution (Coleman and others 2012a) suggest that none of the natural enemies documented so far appears to have had much of an impact in regulating the population density of the invasive pest. It is possible that the introduction of *C. elongata* to San Diego County is a fairly recent event and that there is a delay in the biological regulation until this parasitoid has increased its own population density. Nonetheless, further exploration may be necessary to reveal additional natural enemies, particularly egg parasitoids that may have greater specificity for *A. auroguttatus*. This exploration might take place in Arizona, New Mexico, and northern Mexico in the native range of *A. auroguttatus* or in southern Mexico and Guatemala in the native range of the sibling species. Conservation of the limited arthropod natural enemies in the invaded habitat through judicious use of insecticides may be an important factor (see below). One obvious class of predators of *A. auroguttatus* are woodpeckers such as the acorn woodpecker, *Melanerpes formicivorus* and Nuttall’s woodpecker, *Picoides nuttallii* (both Piciformes: Picidae) (Coleman and others 2011), but the degree of impact of these birds on the sessile larvae, pre-pupae, and pupae of *A. auroguttatus* has not been quantified.

Sanitation techniques for reducing the population density of *A. auroguttatus* have involved tarping, debarking, or chipping/grinding firewood-sized pieces of oak wood (Jones and others 2013). This research has demonstrated unequivocally that *A. auroguttatus* will develop and emerge from firewood and that tarping the wood and exposure to intense sunlight will not prevent the adults from emerging. Further, care must be taken with chipping the wood in attempts to destroy the larvae. Only grinding the wood to a 7.6 cm (3 inches) chip size is sufficient to prevent adult emergence from the treated firewood pieces (fig. 6). Debarking firewood is also an effective means of separating the beetle life stages from the xylem, but the bark itself must be treated subsequently to kill the remaining insects (Jones and others 2013). Techniques for protecting oaks from *A. auroguttatus* with insecticides have been explored in two studies in San Diego County (Chen and others 2015, Coleman and others, unpublished data). It is likely that only uninfested or newly infested trees (0 to 25 emergence holes on the lower stem) will have a high probability of being protected by these treatments (Coleman and others 2015b). By analogy with the work on *A. planipennis* and ash trees (Herms and others 2014), the focus of this research has been on systemic insecticides based on emamectin benzoate and imidacloprid as active ingredients. Neither of these insecticide trials have provided overwhelming evidence of the efficacy of these materials and one study (Chen and others 2015) is continuing for another 3 years with re-treatment of the test trees in December 2014.

In 2008-2009, a preliminary risk assessment for *A. auroguttatus* (then thought to be *A. coxalis*) was developed to project the distribution based solely on the range of the hosts (Downing and others 2009). A more elaborate risk assessment has been prepared (Venette and others, Assessing the risks posed by goldspotted oak borer to California and beyond, these proceedings),
and this projection of the potential spread of the beetle into suitable habitat is based on biological data related to freeze tolerance, host susceptibility, and dispersal capacity of the adult beetle (table 3), as well as on the temperature/precipitation conditions of the habitat under assessment.

![Figure 6](image)

Figure 6—The most effective sanitation technique for managing the goldspotted oak borer, *Agrilus auroguttatus*, in firewood is grinding to a 3 inch piece size (Jones and others 2013).

**Conclusions**

Since *A. auroguttatus* was first associated with oaks in California in 2008, significant advances have been made in understanding its host range, feeding habits, life cycle, natural enemies, and impact in Arizona and California. A suite of management approaches have been tested individually during this period as well. The outlines of an IPM program are beginning to take shape and these guidelines have been made available to the public in the technology transfer literature (Coleman and others 2015b, Flint and others 2013). Progress in assembling and transferring this information is occurring none-to-soon, as *A. auroguttatus* has moved in the last several years into two counties north of its San Diego County point of establishment (table 1). Our understanding of the risk that *A. auroguttatus* poses to oak resources in California and Oregon is coming into focus as the key biological data are being analyzed and synthesized into a formal assessment (Venette and others, Assessing the risks posed by goldspotted oak borer to California and beyond, these proceedings). However, the specter remains of a calamity for red oaks in a predicted zone of convergence of the invasive distributions of sudden oak death (Rizzo and Garbelotto 2003) and *A. auroguttatus* in the coastal areas north of the Los Angeles Basin.
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Coleman, T.W.; Lopez, V.; Rugman-Jones, P.F.; Stouthamer, R.; Seybold, S.J.; Reardon, R.; Hoddle, M.S. 2012b. Can the destruction of California’s oak woodlands be...


Mapping spread of the Goldspotted Oak Borer (Agrilus auroguttatus)\(^1\)

Thomas A. Scott,\(^{2,3,4}\) Kevin Turner,\(^{3,4}\) Cara Washington,\(^4\) and Kim Corella\(^5\)

Abstract

The earliest signs of goldspotted oak borer (Agrilus auroguttatus, GSOB)-associated oak declines can be found in 1996 aerial photo images from the Descanso area of San Diego County. By 2014, GSOB had spread over a 4000 km\(^2\) area, with a patchy distribution similar to the early spread of the emerald ash borer (Agrilus planipennis). The GSOB occurs over about 26,250 ha (60 percent) of the oak woodlands in its primary range of infestation; with heaviest damage near rural housing and communities. Three GSOB diaspora have occurred 30, 40, and 55 km from closest known infestation areas, implicating human transport rather than adult flight as the agent of dispersal. Sequential aerial photo plots suggest that individual oaks (7916) took a median of 3 years to die after first sign of canopy decline, and 95 percent died within 8 years. Plots with >9 years of GSOB attack lost up to 76 percent of their oak canopies, with up to 25 percent of canopy loss/year in drought years. Oak canopy losses averaged about 3 percent of total area/year, or the equivalent of about four large, mature oak trees/ha/year. Years of high precipitation slowed GSOB mortality, followed by rapid increases in mortality when these years were followed by a drought year.

Key words: Agrilus auroguttatus, forest pest, goldspotted oak borer, GSOB, oak management, oak woodlands, Quercus agrifolia, Quercus chrysolepis, Quercus kelloggii

Introduction

Oak mortality in San Diego County rapidly increased in the fall of 2002, the fourth year of a 5-year drought. Although this increase resembled previous waves of mortality seen in multi-year droughts (1974-1978 and 1988-1990), higher rates of oak mortality did not stop after a season of heavy precipitation in 2005. The extent of this mortality was initially masked by two large wildfires in 2003 and 2007 (CALFIRE 2014); however, by 2008 an unprecedented number of unburned oaks were reported as dead or in irreparable decline across a large section of the county. In that year, Seybold and Coleman (2008) linked this oak mortality to an outbreak of the goldspotted oak borer (Agrilus auroguttatus, hereafter referred to as GSOB), an exotic bark beetle from the Sierra Madre Occidental (Mexico) and the sky islands of southeast Arizona (Lopez 2015). The first adult GSOB was trapped in San Diego County by the California Department of Food and Agriculture in 2004 (Westcott 2005), but increased rates of oak mortality had been observed 2 years before (Heath and others 2008). We began mapping areas where oak mortality exceeded background levels (1 dead/1000 mature per year) in 2007, and extended our mapping

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area to the entire county as the extent of GSOB damage became evident. In 2009 we set up sequential aerial photo plots to reconstruct the early pattern of GSOB spread.

**Methods**

**Mapping susceptible-oak woodlands and GSOB occurrence**

Oak woodlands in San Diego and Riverside Counties have been mapped by Wieslander (1935; see vtm.berkeley.edu), Griffin and Critchfield (1972), Oberbauer (unpublished 1987), Scott (1991), Anon. (1995), California Department of Fish and Game (2005), U.S. Department of Agriculture Forest Service (USDA FS) CALVEG 2002, 2003, 2009 (USDA FS Region 5 2014), and R. Minnich (unpublished MS). These maps identified the distributional range of the woodland types with susceptible oak species, but with classification systems that mixed oaks with other vegetation, at map scales too coarse (>1:24000) to describe spread. We refined the woodland polygons in these maps to produce a map of susceptible oak woodland canopies at a scale of approximately 1:1500, using georeferenced (in ARCGIS©) satellite and aerial photo imagery to draw canopy boundaries (Eagle Aerial Imaging from 2003-2006, 2008, 2009, 2010; Google Earth Imagery 2010, 2012, 2013, 2014; with pixel size from 0.5 to 1 m). We included woodlands with California black oak (*Quercus kelloggii*), coast live oak (*Q. agrifolia*), canyon live oak (*Q. chrysolepis*), interior live oak (*Q. wislizenii*), and Engelmann oak (*Q. engelmannii*). Our goal was to map just the susceptible-oak trees canopies, minimizing the inclusion of non-canopy habitat and other vegetation types. In woodlands with >75 percent canopy cover, we mapped polygons by canopy perimeters; in woodlands with 20 to 75 percent canopy cover we excluded gaps >150 m² (equivalent to canopy of a two mature oaks) from canopy polygons. In woodlands with <10 percent canopy cover, we attempted to map individual oak canopies.

We classified canopy polygons into five mortality levels, based on counts of dead oak canopies per unit area. Categories with known presence of GSOB and mortality were classified as (1) **Heavy**, >10 dead oaks/ha of canopy; (2) **Moderate**, 5 to 10 dead oaks/ha; and (3) **Present**, 2 to 5 dead oaks/ha. Whenever possible, we ground-verified the presence of GSOB in canopy polygons by field surveys (2008-2014). In addition, we mapped GSOB locations identified by professional foresters, resource managers, arborists, scientists, and trained volunteers. We used two additional categories when GSOB presence could not be checked on the ground (private property): (1) **Probable**, with 1 to 2 dead oak/ha and **Possible**, 0.5 to 1 dead oak/ha.

**Describing the onset and rate of GSOB outbreaks**

We estimated the onset and rate of GSOB outbreaks across the infestation area using sequential aerial photo images. Our goal was to use woodland sample units with a median size of 25 ha oaks; to reflect the scale of the outbreaks with a sufficient number of oaks (300 to 500) to describe patterns of GSOB-associated mortality. Oak woodlands in the GSOB infestation area typically occur in distinct patches; we randomly selected 75 of these patches from our oak woodland map to sample oak mortality across the region where GSOB occurred. Sampling was stratified by elevation, drainage basins, woodland type, size, and geographic location (nearest-neighbor distance >2 km). For each woodland sample unit, we digitized all oak canopy areas that could be resolved at a scale of 1:1500, 1m pixel size across a
sequential series of aerial photo images, 2002 through 2013, from Google Earth (2002-2013), Eagle Aerial Imaging (2003-2006, 2008, 2009, 2010), USDA NAIP (2009, 2012), USGS Digital Orthophoto Quadrangles (DOQs, 1996, 2005) coverages of San Diego County. Each year’s image was georeferenced to the 2009 NAIP (NAIP 2010; NAD1983 UTM Zone 11N) image for San Diego County (>five control points; root mean square errors (RMS) of control points <0.5, median of RMS value of 0.2). We mapped canopies of five species: California black oak, coast live oak, canyon live oak, interior live oak, and Engelmann oak. Oak canopies in each year were digitized as polygons in ArcGIS (ESRI versions 9.3 and 10.2.2), decline in the canopies of individual oak tree were detected by recording change in canopy color, pattern and outline; death was recorded when a canopy was reduced to bare branches, trunk, or stump. We scaled canopy change/decline as typical, declining, irreparably declining, or dead. To document the spread of GSOB among plots, we recorded the year when individual canopy areas changed from typical to irreparable decline (>50 percent canopy decline), or from typical, declining, or irreparably declining to dead. To calculate total canopy loss per woodland, we set the canopy area (m²) of individual oaks in 1996 USGS DOQs as the initial condition, subtracting canopy lost/year. We then compared this rate of loss against background mortality calculated from canopy area lost in samples where GSOB did not occur.

Results and discussion

Range and distribution of GSOB

By the fall of 2014, GSOB had been associated with oak mortality on approximately 26,250 ha (66,700 ac) of oak woodlands in San Diego County, with an additional 9600 ha (24,400 ac) in transition to or likely to be affected in the near future. The range of GSOB-affected woodlands extends from the borderlands of Mexico to the southern end of the Palomar Mountains, and from the desert margin to coastal woodlands near sea level (fig. 1).

In total, the primary GSOB infestation area encompasses about 43,500 ha of oak-associated woodlands. This range also includes about 8900 ha of woodlands burned in the 2003 Harris Fire and the 2007 Witch Fire (CALFIRE 2014), where it was impossible to separate GSOB-associated oak mortality from the extensive oak mortality resulting from fire. These fires occurred after GSOB mortality began, removing evidence of an additional 34 percent of GSOB-impacted woodlands. The oldest areas of infestation have the most contiguous outbreak polygons, newer areas of infestation have a far patchier pattern of outbreak with intervening areas where GSOB has not been detected.
Figure 1—Map of San Diego County showing the fall 2014 distribution of goldspotted oak borer (*Agrilus auroguttatus*) (mortality categories defined in the methods section). Extreme examples of isolated outbreaks (circled) were most likely caused by human transport of GSOB. The Idyllwild outbreak area is not included to maximize detail of the map in the primary infestation area.

Three separate diaspora of GSOB have been recorded, where beetles moved further than the adult flight limit estimated by Lopez (2013). These new, isolated points of infestation occurred at Marion Bear Park (40 km, before 2008), Ramona (30 km in 2007), and Idyllwild (55 km around 2009). Surveys for GSOB in these remote infestations initially found about 100 ha of infested coast live oak woodlands at Marion Bear Park, 250 ha of similar woodlands infested in Ramona, and 700 ha of infested California black oak woodlands in the Idyllwild. Large tracts of woodlands free of GSOB infestation occur between these isolated outbreaks and the primary infestation area; leaving human transport as the most parsimonious explanation of these GSOB movements. The Idyllwild outbreak represents a special case because there may have been more than one delivery of GSOB-infested oak firewood, creating a constellation of small outbreaks across that community (Turner 2015). There are about 17 300 ha of unaffected oak woodlands in patches across the GSOB the zone of infestation, reflecting both the duration of the outbreak and the unpredictable nature of GSOB movement in firewood. At present, there is little evidence to suggest that the spread of GSOB varies significantly from the early pattern of spread described by Siegert and others (2014) for the outbreak of emerald ash borer.

Woodlands with California black oaks had the highest proportions of heavily infested woodland areas, while canyon-bottom woodlands had low proportions of GSOB outbreak areas (fig. 2). Heaviest GSOB impacts occur in woodlands types at
higher elevations (fig. 3). Canyon woodlands are dominated by coast live oak, a highly susceptible species; however, a substantial proposition of their distribution is outside of the GSOB-infestation area (fig. 3). Engelmann oak-dominated woodlands have a high percentage (58 percent) of area with GSOB present, but a relatively low percentage of area with heavy GSOB impacts. The presence of GSOB is expected because this woodland type occurs almost entirely within the GSOB-infestation area; however, the lack of commensurate levels of heavy to moderate infestations are function of the low percentage of susceptible species (0 to 25 percent) in Engelmann oak dominated woodlands (Scott 1993).

![Bar chart showing intensity of GSOB damage by woodland type. The greatest GSOB-associated damage has occurred in woodlands with California black oak, *Quercus kelloggi* (first three columns).](image1)

![Graph showing distribution of GSOB across elevational gradients of the two most susceptible species, coast live oak (*Quercus agrifolia*) and California black oak (*Q. kelloggi*). Oaks occur from coastal lowlands (far left) to the trans-montane desert (right).](image2)

There is a strong elevational gradient of GSOB damage, which are concentrated above 930 m (3100 ft) above mean sea level (amsl) (figs. 3 and 4) and uncommon below 870 m (1600 ft) (fig. 4). Lower elevation areas have remained remarkably free of GSOB damage even though they receive less precipitation and should be subject to greater stress and susceptibility to GSOB during droughts. The highest prevalence of GSOB outbreaks occur between from 1020 to 1290 m (3400 to 4300 ft). These
elevations have large areas of oak woodlands, but they also have large number of rural houses and the greatest likelihood of firewood importation for heating (fig. 4).

Figure 4—Cumulative frequency distribution of GSOb-associated oak mortality along an elevational gradient. Ninety percent of woodlands with moderate to heavy GSOb-associated mortality (= Outbreak) were above 1050 m (3100 ft) elevation. The elevational distribution of this outbreak is almost indistinguishable from the elevational distribution of woodlands within 100 m of rural homes. Both of these distributions however differ significantly from the cumulative elevational distribution of woodlands where GSOb is not present (Kolmogorov-Smirnov 2 sample test. P <0.01).

Rural homes are a strong indicator of GSOb outbreaks, and an indirect link to GSOb import of firewood for heating in higher elevation areas of San Diego County. Woodlands next to rural homes have a far greater prevalent of moderate- to heavily-attacked oak woodlands, and have a far lower prevalence of unaffected oaks. About 33 percent of woodlands within 100 m radius of rural houses were heavily impacted by GSOb in 2014 (fig. 5), close to twice the percentage (17.5 percent) of heavily damaged woodlands beyond a 1000 m radius. Woodlands between 100 and 1000 m of rural houses have intermediate percentages of GSOb damage and unaffected woodlands.

Figure 5—Proportion of woodlands by GSOb occurrence of categories, grouped by distance from rural housing. About half of woodlands within 100 m of rural houses (1650 ha) have heavy to moderate GSOb infestation; only 30 percent of woodlands >1000 m (5750 ha) have this level of infestation. The inverse is true for percentages of uninfested woodlands.

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Although we were not able to document oak firewood import by rural homeowners, the intersection of oak woodlands with rural homes appear to be the area where GSOB has had the strongest impact. While it is possible that human activities have led to more GSOB-susceptible trees around rural homes, the most reasonable model is that GSOB was transported to oak trees around these homes and then spread to adjacent woodlands, rather than adult dispersal across the infestation area. This pattern of GSOB dispersal appears similar from the documented spread of the emerald ash borer described by Siegert and others (2014), perhaps at a slightly finer scale of GSOB transport by humans, and presumed dispersal distances by adult beetles.

**Origin and rates of GSOB spread**

Elevated rates of oak mortality (>2 percent per year) were first visible in the 2002 aerial photo of a plot in Descanso (32.855°, -116.255°). This plot had 44 dead oaks in 2002, after having 59 oaks in decline in 1996 (the previous aerial photo). Sixteen plots had substantial numbers of declining oaks (>10) by 2002, but no visible mortality. Eight of these plots had >40 declining oaks in 2002, suggesting that declines began several years earlier. Plots developing abnormal rates of oak mortality peaked in 2006, but continued through 2012. All 75 plots ultimately suffered abnormal rates of mortality, but 12 plots had peak mortality in 2003/2004, where GSOB-impacts could not be separated from damage caused by wildfires in November 2003. The absence of aerial photos between 1996 to 2002 makes it difficult to fully describe the onset of GSOB impacts, but it appears that GSOB-associated oak declines began in the years immediately preceding 2002, and spread to current extent by 2006, 5 to 7 years later. There is no discernable pattern of GSOB spread (fig. 6), except GSOB-impacts first appear near Descanso and stay within about 150 km² area for a short time, and then spread by diaspora across the zone of infestation in less than 5 years. This pattern reinforces the importance of transport, with less support for dispersing flights of GSOB adults.

![Frequency distribution of sequential aerial photo plots](image)

Figure 6—Frequency distribution of sequential aerial photo plots (n = 65) by first year of decline and first year of mortality. The medium year of first decline was 2003. Medium year of first mortality was 3 years later, 2006.
The number of dead oaks grew from 44 canopies in 2002 to approximately 1000 canopies in 2009 across all plots with evidence of GSOB occurrence (n = 63). This rates of dead oaks/year, however, dropped by almost 50 percent in 2010 (to 546), and dropped again by over 50 percent in 2011 (to 246). Precipitation in the infestation area in 2010 was considered typical after 8 low years, and precipitation in 2011 was considered exceptionally high (SDCWA 2014). In 2012, GSOB-associated oak mortality increased again to 2000 trees, in a year when precipitation dropped far below normal. A similar increase in oak mortality occurred in 2006, also a drought year that followed a year (2005) of abnormally high precipitation. Comparisons of oak mortality across these wet and dry cycles are confounded by (1) the increasing area of GSOB infestation, (2) increasing age of GSOB attacks at individual plots, and (3) the declining numbers of remaining susceptible oaks on plots. Nevertheless, it is difficult to ignore the apparent impact of good years of precipitation on oak survivorship.

GSOB-associated oak canopy death ranged up to 74 percent loss on plots with >9 years of GSOB damage, compared to a maximum of 3 percent loss in 12 plots without GSOB present. Plots near the center of the infestation area (Descanso, Pine Valley, and Julian) had a median loss of 36 percent of oak canopy area, while plots on the margin of the infestation area had median loss of 18 percent of canopy. On an annual basis, plots with >9 years of GSOB damage lost an average of 326±58 (SE) m²/ha/year of canopy. This represents an average annual loss of about 3 percent of the canopy, or the equivalent of about four mature oak trees/year on each plot. Rates increased dramatically in the first 3 years of GSOB outbreak; however, the worst mortality was recorded during drought years (2004, 2007, and 2012), with some plots losing up to 25 percent of their oak canopy in a single year. Plots with the longest record of GSOB attack typically had 75 to 100 percent of oaks in some state of decline, basically leaving only the smaller oaks hybrids with interior live oak (Q. wislizenii) unaffected.

Individual oaks on sample plots appeared in decline for up to 11 years before dying (declining 2002 to dead 2013). The median numbers of years in decline was 3 (n = 7916); with 70 percent of oaks dead in 4 years, 87 percent dead in 6 years, and 96 percent dead in 8 years. These estimates of oak decline are commensurate with median number of years (3) between first decline and first mortality observed across plots with GSOB.

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Assessing the Risks Posed by Goldspotted Oak Borer to California and Beyond

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Abstract
Goldspotted oak borer, *Agrilus auroguttatus*, has killed approximately 27,000 mature oaks in southern California. Consequently, the future spread of this insect is a significant concern to many oak woodland managers in California and across the United States. “Risk” reflects the likelihood that *A. auroguttatus* will continue to spread in North America and the magnitude of ecological, economic, or social impacts that this insect may cause.

This research project measured several critical biological parameters to refine spatial risk assessments for this insect. Cold tolerance testing of prepupae, the primary overwintering stage, indicates that this insect should be unable to survive in U.S. Department of Agriculture (USDA) Plant Hardiness Zones 2b – 5b. Some survivorship might occur in Zone 6a, but this outcome depends on the degree of cold acclimation that larvae may achieve. Host range testing with cut logs confirmed expectations that California black oak, *Quercus kelloggii*, and coast live oak, *Q. agrifolia*, are hosts and that Engelmann oak, *Q. engelmannii*, is not a host for *A. auroguttatus*. Our assays suggest that interior live oak, *Q. wislizeni*, and valley oak, *Q. lobata*, could be hosts, whereas Oregon white oak, *Q. garryana*, is unlikely to be a host. More study is needed to determine conclusively the host status of blue oak, *Q. douglasii*, canyon live oak, *Q. chrysolepis*, and cork oak, *Q. suber*, though field observations suggest canyon live oak can be colonized and killed by this insect. Flight mill studies indicate that adult females might fly up to 4 to 5 km/day and 9.3 km in their lifetime.

Collectively, these results suggest that *A. auroguttatus* poses the greatest risk nationally to California and southern Oregon. If dispersal only occurs through flight, the effects from this insect will likely remain concentrated in southern California for the next 5 to 10 years. Potential movement of *A. auroguttatus* via infested firewood or other human-mediated pathways and the unknown host status of oak species from eastern North America introduce considerable uncertainty into these models. This refined risk assessment supports the value of efforts to slow the spread of *A. auroguttatus*.

Key words: cold hardiness, exotic invasive species, goldspotted oak borer, mortality agent, MaxEnt, spread

Introduction
Pest risk analysts face the daunting challenge of forecasting the potential spread and impact of non-native species, frequently in areas that have no historical association with that species (Venette 2015). “Risk,” in this context, refers to (i) the probability that a non-native species will arrive, establish, and spread within an area of concern and (ii) the magnitude of economic, ecological, or social harm caused by the species. Pest risk maps are needed to support strategic and tactical risk management decisions, such as whether

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regulatory actions should be taken to restrict human-mediated spread of the species or where monitoring traps should be placed to detect the species.

Extensive oak mortality in southern California in the early 2000s, at the time known colloquially as “oak croak,” was later attributed to the effects of the goldspotted oak borer, *Agrilus auroguttatus* (Coleoptera: Buprestidae) (Coleman and Seybold 2008). This insect species is native to southeastern Arizona and likely present in southwestern New Mexico, Texas, and northern Mexico; the population in California likely originated from the Dragoon Mountains in Arizona (Lopez and others 2014). As such, *A. auroguttatus* may be considered a domestic invasive species because, although this insect is native to the United States, it is not native to the Californian ecosystems where it now occurs and is causing harm.

Initial field observations suggested that coast live oak, *Quercus agrifolia*, California black oak, *Q. kelloggii*, and canyon live oak, *Q. chrysolepis* were particularly sensitive to feeding damage from *A. auroguttatus* (Coleman and Seybold 2008). Another oak species, Engelmann oak, *Quercus engelmannii*, was also infested, but was not apparently killed by *A. auroguttatus*. Larvae feed beneath the bark in the phloem, cambium, and outer xylem. This feeding disrupts the vasculature of the trees and leads to large areas of necrotic tissue; collectively this damage can ultimately cause crown thinning and tree death. More than 27,000 trees have been killed in an area centered near Julian, California (Coleman and others 2012, Haavik and others 2014a, USDA 2014). The area in southern California with oak mortality attributed to *A. auroguttatus* continues to expand (Coleman and others 2012, 2015).

Field observations and collection records provide strong evidence that Emory oak, *Quercus emoryi*, and silverleaf oak, *Q. hypoleucoides*, are hosts for *A. auroguttatus* in Arizona (Coleman and Seybold 2008, 2011; Haavik and others 2014a) and *Q. kelloggii* and *Q. agrifolia* are hosts in California (Coleman and Seybold 2008, 2011; Coleman and others 2011; Haavik and others 2014a). In both states, the density of emergence holes created by adults, the numbers of adult *A. auroguttatus* that emerged from bark samples, or the proportion of affected trees suggested that these oak species supported positive rates of population growth, the ultimate test of host status. In contrast, *Q. engelmannii* was initially presumed to be a host based on widespread mortality of this species in areas known to be infested with *A. auroguttatus* (Coleman and Seybold 2008); however, subsequent, detailed field observations confirmed that although some *A. auroguttatus* can complete development on this species, it is not preferred and unlikely to support positive population growth (Coleman and others 2012). Similarly, extensive mortality of *Q. chrysolepis* has been observed in areas with *A. auroguttatus*. Coleman and others (2012) reported that although the proportion of living and dead *Q. chrysolepis* with injury from *A. auroguttatus* was 48 percent and 60 percent, neither estimate was different from injury levels on comparable *Q. engelmannii*. This lack of a statistical difference may be due to a small sample size. Field surveys in Arizona failed to detect any evidence of feeding or development on Arizona white oak, *Q. arizonica*, or gray oak, *Q. grisea*, in
areas where *A. auroguttatus* occurs (Coleman and Seybold 2011). The pattern of host utilization suggested a rule of thumb that red oaks (Section *Lobatae*) are more likely to be hosts whereas white oaks (Section *Quercus*) are unlikely to be hosts. This generalization led us inadvertently to characterize interior live oak, *Q. wislizeni*, as a known host (Downing and others 2009) when no direct evidence supported that conclusion.

The objective of this study was to gather additional biological information to better estimate where *A. auroguttatus* might locate suitable climate and hosts and when it might spread into these suitable areas. A previous assessment described the distribution and density of oak species that were thought to be hosts (Downing and others 2009). The current assessment builds from this foundation by using climate suitability models and empirical measures of cold tolerance to determine where temperature and moisture might be appropriate for *A. auroguttatus*. We incorporate new information about the potential host status of several *Quercus* spp. that occur at low densities or do not currently co-occur with *A. auroguttatus*. Lastly, we estimate rates of geographic range expansion (spread rates) by measuring flight distance on flight mills as a function of adult age.

**Materials and methods**

**Climate suitability**

Temperature and moisture frequently dictate the limits to the geographic distribution of invasive alien species. Several models, variously called species distribution models, ecological niche models, or environmental suitability models, are available to characterize the impact of abiotic factors such as climate on species distributions. Deductive models depend on a deep understanding of the impact of temperature or moisture on population growth rates; this understanding comes from appropriately designed experiments. In contrast, inductive models statistically relate species occurrence records to environmental covariates and forecast species occurrence based on those statistical relationships. For *A. auroguttatus*, we relied on a hybrid approach to characterize the suitability of the climate in North America. We measured the cold tolerance of this insect and relied on an inductive model, MaxEnt (Phillips and others 2006), to characterize climate suitability in areas where winter temperatures will not preclude establishment of this insect.

**Empirical measurements of cold tolerance**

For many temperate insects cold temperatures are likely to dictate the northern limits to the distribution of a species. Consequently, we assessed the cold tolerance of *A. auroguttatus* by measuring supercooling points of immature individuals, especially fourth (prepupae, “j-stage”) instars. *Agrilus auroguttatus* and other buprestids typically pass the winter in the j-stage, though the insect may pass the winter in earlier instars (Coleman and Seybold 2008). The supercooling point is the temperature at which insect body fluids
spontaneously begin to freeze. Many temperate and subtropical insects are chill tolerant/freeze intolerant (in other words, individuals can survive exposure to temperatures below 0 °C, but die when fluids begin to freeze), so, the supercooling point represents the lowest temperature at which freeze intolerant insects might survive. Little is known about the cold tolerance of buprestids in general, but *Agrilus planipennis*, emerald ash borer, was found to be predominantly chill tolerant/freeze intolerant (Christianson 2014, Crosthwaite and others 2011). We suspect that this cold tolerance strategy is also true for *A. auroguttatus*.

Prepupae of *A. auroguttatus* were collected monthly in the fall and winter from the Cleveland National Forest in San Diego County, California by removing bark from naturally infested oaks. Extracted prepupae were placed in 24-well plastic plates and covered with cotton plugs. Plates were sealed (triple contained) inside insulated coolers and shipped via overnight courier to St. Paul, Minnesota. In a biosecurity level-2 quarantine laboratory, larval supercooling points were measured within 72 hours of receipt by following protocols from Carrillo and others (2004) with coiled copper-constantan thermocouples (Hanson and Venette 2013). Prepupae were held on the thermocouple with high vacuum grease. Thermocouples inside plastic syringes were placed near the center of 20 x 20 x 20 cm polystyrene cubes. When these cubes were placed in a -80 °C freezer, the insect cooled at a rate of approximately 1 °C/minute. Temperatures were recorded once per second. The supercooling point was the lowest temperature recorded before detection of an exotherm (a sudden increase in temperature as the heat of crystallization was released).

For purposes of the risk assessment, we presumed that larvae would achieve the lowest mean supercooling point recorded (in other words, would always achieve the maximum degree of cold tolerance). We then projected the extent of mortality by comparing the distribution of supercooling points with historical records of low temperatures as summarized in USDA Plant Hardiness Zones. This analysis was used to identify Plant Hardiness Zones where *A. auroguttatus* would be unlikely to establish because temperatures are likely to be too cold. In ArcMap, polygons that represented the unsuitable Plant Hardiness Zones were used to mask portions of the conterminous United States.

**MaxEnt models of climate suitability**

We followed procedures for the development of a MaxEnt model as described by Phillips and others (2006) with modifications proposed by Jarnveich and Young (2015). We began by assembling published distribution records for *A. auroguttatus* (Coleman and Seybold 2008, 2011; Coleman and others 2012; Haavik and others 2014a, 2015). We verified that location records were accurate and corrected latitude or longitude when necessary (for example, when coordinates placed a location in Mexico or the Pacific Ocean but the written description was for southern California or Arizona). This exercise produced a list of 66 presence points for *A. auroguttatus*. We then
downloaded the 19 bioclimatic variables from WorldClim.org at 30 arc-second resolution (Hijmans and others 2005). We limited the extent of the analysis to North America.

A significant concern with inductive distribution models is the potential for overfitting environmental covariates (in other words, suggesting a more restricted distribution for a species than can be supported statistically or biologically). We limited the potential for overfitting by taking four precautionary steps (Jarnévich and Young 2015). First, we limited the geographic area from which background samples could be drawn by creating a minimum convex polygon around all presence points in California and Arizona with an additional 2.5 arc-minute buffer. Second, we restricted the analysis to bioclimatic variables that were not correlated (correlation coefficient, |r| < 0.7). Cross correlation analysis (Proc CORR in SAS 9.13) was performed with climatic records extracted from the area within the minimum convex polygon. Third, we excluded variables that gave a discontinuous (jagged) response. Lastly, we compared the area under the receiver operating characteristic curve (AUC) from a model training set of presence points to the AUC from a model testing set of presence points. Because the AUC is scaled from 0 – 1, a difference greater than 0.1 in AUC provided evidence of overfitting (Jarnévich and Young 2015).

The MaxEnt model was initially run with presence points from California and Arizona, background data points drawn from the buffered minimum convex polygon, and all 19 bioclimatic variables. This run was used to identify the variables with the greatest percentage contribution to the overall model. Of the variables that contributed at least 2 percent to the overall model, variables with discontinuous response functions were removed from further consideration. We identified bio10 (in other words, mean temperature of the warmest quarter) as the variable that contributed the most to the model. We then found bio14 (precipitation of the driest month) to be the only other climatic variable that (i) was not correlated with bio10, (ii) gave a continuous response function, and (iii) contributed more than 2 percent to the overall model. We re-ran the MaxEnt model with this restricted set of bioclimatic variables to generate 25 replicate models. For each model, MaxEnt randomly selected 20 percent of the 66 presence points to train the model, the remaining presence points were used for model testing. Model performance was evaluated by the AUC and a comparison with aerial sketchmaps of oak mortality caused by A. auroguttatus.

MaxEnt generated a surface for North America that described the suitability of the climate in each 30-arc-second grid cell as the mean of the 25 replicate models. Values near 1.0 were considered highly suitable, whereas values near 0 were completely unsuitable.

**Host status of oaks**

The potential suitability of oak species that have not yet been colonized extensively by *A. auroguttatus* was determined through a combination of no-choice host range experiments and Monte Carlo simulation. Haavik and others
(2014b) artificially infested cut logs of known hosts (Q. agrifolia and Q. kelloggii), non-hosts (Q. engelmannii) and several species of unknown host status (Q. chrysolepis, Q. wislizeni, blue oak, Q. douglasii, Oregon white oak, Q. garryana, valley oak, Q. lobata, and cork oak, Q. suber) with neonates of A. auroguttatus and recorded the proportions of larvae that entered the host, established a gallery, and developed to fourth instar. In addition, fecundity was measured for females that were fed foliage from these species. These data were used in Monte Carlo simulations (@Risk 4.5, Palisade Software, Ithaca, NY) to generate a probability density function of the number of adult female daughters produced per mother under the assumption that mothers could only feed on one species. Haavik and others (2014b) reported results for two rounds of host testing. We adopted a risk-averse approach and relied on those results that were most favorable for A. auroguttatus in either year to characterize the host suitability of the species. Fecundity was described by a normal distribution, limited to values $\geq 0$, and proportions were described by beta distributions. The simulation was run 10,000 times. The resulting probability density function allowed us to estimate the probability that A. auroguttatus would produce more than one daughter per mother if the mother only was allowed to feed upon one host species. Geographic distributions of oak species determined to be hosts were obtained from USGS (2013). Geographic areas without suitable hosts were clipped from the MaxEnt map in ArcMap 10.1.

**Spread potential for A. auroguttatus**

An initial attempt was made in 2011 to conduct an in-field mark-release-recapture experiment to determine how far adult A. auroguttatus might fly. Over 300 beetles were marked with fluorescent dust and released in the center of a trapping array, but none was recaptured on a purple prism trap. Because large numbers of adult beetles were difficult to collect and the traps were inefficient at attracting adult A. auroguttatus, we elected not to repeat this study.

We used flight mills to estimate the dispersal potential of A. auroguttatus adults. Adults and pupae were collected from the field, triple contained, and shipped via overnight courier to the biosecurity level-2 laboratory in St. Paul, Minnesota. Adults and pupae were held in individual rearing cups, and adults were provided with freshly cut foliage from Q. lobata for at least 2 days.

The general design and operation of the mill are described in Fahrner and others (2014). The arm of the flight mill was affixed to the pronotum of adults with superglue. Adults were placed on the flight mill for 24 hours and allowed to fly with a photoperiod of 24:0 (L:D) hours or 8:16 hours. The flight period always began in light. Under both conditions, adults flew more than 80 percent of the total flight distance within the first 6 hours of being placed on the mill, so we restricted the analysis to this period, which allowed us to combine data from both photoperiod treatments. Flight distance was measured as a function of age, sex, and mating status. A total of 223 beetles were attached to the mill, of which 179 engaged in flight. Beetles were removed
from the mill and observed daily until death. Age-at-death data were used to construct a life table with age measured in days from adult eclosion.

To estimate flight potential, we focused on results for females. Female dispersal is likely to dictate the unaided rate of range expansion of *A. auroguttatus*. As before, we adopt a risk-averse approach. So, for each age (*x*), the mating status (virgin or mated) that led to the greater mean flight distance was used as the measure of flight distance for that age (*f*). Maximum net lifetime flight distance (*d*) was calculated as the sum of the product of *Lxfx*, where *Lx* is the number of days an average individual lives from age *x* to *x* + 1 (Carey 1993). To calculate the population spread rate, we followed procedures modified from Shigesada and Kawasaki (1997). The diffusion coefficient (*D*) was calculated as \( D = \frac{d^2}{\pi} \). The population spread rate is \( 2\sqrt{\varepsilon D} \), where \( \varepsilon \) is the intrinsic population growth rate, which was estimated to be 0.634 from annual changes in densities of *A. auroguttatus* at three sites reported in Haavik and others (2015).

Shapefiles describing the distribution of oaks killed by *A. auroguttatus* in 2010 were obtained from the Insect and Disease Detection Survey Data Explorer (USDA 2015). These polygons were used as the starting locations. Buffers were created around these polygons to represent potential spread in 3-year increments through 2022 by assuming a constant annual rate of spread.

**Results and discussion**

**The composite risk map**

The updated national risk map for *A. auroguttatus* (fig. 1) illustrates the degree of climatic suitability for this insect within the geographic range of oak species that are known or potential hosts. The radiating rings indicate the maximum expected natural spread of *A. auroguttatus* every 3 years from 2010.
The map illustrates that *Agrilus auroguttatus* has the potential to spread beyond Orange, San Diego, and Riverside Counties, the only three counties in California currently known to be infested (Coleman and others 2015). Each county has large areas with hosts, and these areas are projected to be very suitable climatically for this insect. Indeed, oaks killed by *A. auroguttatus* in San Diego County in 2010 occur in areas of the county that are characterized as among the most climatically suitable for the insect. These observed patches of oak mortality were not explicitly considered during the development of the climate suitability model, so the concurrence of oak mortality in areas projected to be climatically suitable provides some degree of confidence in the underlying model.

The risk map suggests some interesting possibilities about the previous and future course of the invasion by *A. auroguttatus*. In San Diego County, the landscape appears to be heterogeneous with respect to climatic suitability. This heterogeneity is created by the variations in temperature and moisture associated with topographic changes. In some cases, abiotic factors may change dramatically over relatively short distances, especially in canyons and ravines. As a result, areas in southern California that are climatically suitable
tend to be somewhat fragmented. This fragmentation may have helped to slow the natural rate of spread of the insect as it has not yet fully occupied the areas considered to be suitable and within its natural dispersal capacity.

Our risk map suggests large areas with suitable climate and hosts occur near the Pacific coast, along the Sierra Nevada, and in northern California. *Quercus agrifolia* tends to be more widespread along the coast, whereas *Q. wislizeni* and *Q. kelloggii* tend to be more widespread in the lower elevations of the Sierra Nevada Range and in the north. In areas that are highly suitable for *A. auroguttatus*, we might expect more rapid population growth, faster local spread, and shorter intervals between the colonization and death of a tree. Thus, the spread of the insect into these areas is a significant concern.

However, our risk map also suggests that while *Q. douglasii* and *Q. lobata* might be hosts, they tend to grow in areas that are climatically less suitable for *A. auroguttatus*. The areas in and around the Central Valley where these oak species occur tend to be too hot and potentially too dry for *A. auroguttatus* to do well. Careful field monitoring is needed to confirm this projection.

**Biology underlying the map**

The coldest supercooling points for *A. auroguttatus* prepupae, mean of approximately -22 °C, were recorded in October 2010. This temperature typically occurs in USDA Plant Hardiness Zone 6a. In this zone, we would expect about 50 percent mortality of *A. auroguttatus* if it were present in a typical winter. In USDA Plant Hardiness Zones 2b-5b, the mean annual extreme low temperature is <-26.1 °C, so larval mortality would be expected to be much greater than 50 percent in most winters, often approaching 100 percent. Our laboratory measures of the cold tolerance of *A. auroguttatus* are consistent with the known, native distribution of the insect in southeastern Arizona. The annual extreme low temperature in the coldest locations within its native range is about -20.6 °C, and most *A. auroguttatus* larvae are sufficiently cold hardy to survive brief exposures to this temperature.

Two climatological factors contributed to the maximum entropy model for *A. auroguttatus*: the mean temperature during the warmest quarter of the year and precipitation during the driest quarter. The temperature component contributed 94.7 percent and the moisture component contributed 5.3 percent to the overall model. The analysis suggested that *A. auroguttatus* may have some sensitivity to heat, as the probability of it being present declined from 95 percent when the mean temperature during the warmest quarter was 16.0 °C to <10 percent when this temperature was 26.0 °C. The probability of *A. auroguttatus* being present with respect to precipitation in the driest month was more complex. This probability was greatest (65 percent) when precipitation in the driest month was approximately 2.3 mm. The probability of *A. auroguttatus* being present declined with either less or more precipitation.

The maximum entropy model revealed considerable variation in climatic suitability for *A. auroguttatus* across the conterminous United States. In general, the eastern half of the country was considerably less suitable than the
western half. The model suggested that areas of moderately suitable habitat might occur in New England, the mid-Atlantic states, and in the Appalachian Highlands, but most areas would be climatically unsuitable. In contrast, relatively few areas in the western United States were classified as climatically unsuitable. Across the conterminous United States, many suitable sites became climatically unsuitable when the effects of cold were considered.

Simulation models of the number of adult daughters produced per female suggested interesting possibilities about the host range of *A. auroguttatus* (table 1). The simulation results were consistent with prior knowledge of the host status for three oak species. For the known hosts, *Q. kelloggii* and *Q. agrifolia*, the probability that a female would give rise to at least one adult daughter (in other words, the probability of replacement) was >90 percent. For the known non-host, *Q. engelmannii*, this probability was <10 percent. For oak species which *A. auroguttatus* has only rarely encountered or has yet to encounter, the probability of replacement on *Q. wislizeni* and *Q. lobata* was >90 percent, indicating that these species could be hosts. On *Q. suber*, *Q. douglasii*, and *Q. chrysolepis*, this probability was 0.58, 0.48, and 0.34, respectively. For the purposes of this analysis, we considered these probabilities sufficient to classify these three species as hosts, but recognize that additional field observations are needed to confirm these classifications. In contrast, the probability of replacement on *Q. garryana* was <10 percent, so we consider this species not to be a host. Although this analysis provides support for the general rule of thumb that red oaks tend to be hosts while white oaks tend not to be, the results also reveal that this pattern may not be absolute. In this case, the simulations suggested that three of the three red-oak species should be hosts, but so should two of the four white-oak species (table 1). In these instances, additional field observations will be necessary to confirm these classifications as well.

**Table 1—Potential host status of several oaks, *Quercus* spp., for *Agrilus auroguttatus* based on the probability that a female will give rise to an adult daughter (in other words, replace herself in the population)**

<table>
<thead>
<tr>
<th>Species</th>
<th>Expected (adult daughters/mother)</th>
<th>Prob. (replacement)^a</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Section Lobatae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Q. wislizeni</em>, Interior live oak</td>
<td>6.5</td>
<td>0.996</td>
<td>Host</td>
</tr>
<tr>
<td><em>Q. kelloggii</em>, California black oak</td>
<td>8.2</td>
<td>0.958</td>
<td>Host^b</td>
</tr>
<tr>
<td><em>Q. agrifolia</em>, Coast live oak</td>
<td>4.8</td>
<td>0.906</td>
<td>Host^c</td>
</tr>
<tr>
<td><strong>Section Cerris</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Q. suber</em>, Cork oak</td>
<td>2.0</td>
<td>0.579</td>
<td>Host</td>
</tr>
<tr>
<td><strong>Section Protobalanus</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Q. chrysolepis</em>, Canyon live oak</td>
<td>1.2</td>
<td>0.342</td>
<td>Host</td>
</tr>
<tr>
<td><strong>Section Quercus</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Q. lobata</em>, Valley oak</td>
<td>5.6</td>
<td>0.947</td>
<td>Host</td>
</tr>
<tr>
<td><em>Q. douglasii</em>, Blue oak</td>
<td>1.6</td>
<td>0.487</td>
<td>Host</td>
</tr>
<tr>
<td><em>Q. garryana</em>, Oregon white oak</td>
<td>0.3</td>
<td>0.081</td>
<td>Non-host</td>
</tr>
<tr>
<td><em>Q. engelmannii</em>, Engelmann oak</td>
<td>0.3</td>
<td>0.067</td>
<td>Non-host^b</td>
</tr>
</tbody>
</table>

^a Probability of replacement determined through 10,000 runs of a Monte Carlo simulation of *A. auroguttatus* development on artificially-infested, cut logs.

^b Known before this study.
The distance a female can fly in general increases with age, from an average of approximately 0.15 km/day at 3 days after adult eclosion to 2.7 km/day at 26 days after eclosion. Daily survivorship of females remains high (≥90 percent) through 11 days after eclosion and declines steadily thereafter. In this study, the oldest adult female survived for 28 days. The maximum net lifetime displacement was estimated at 10.4 km/generation, which gave a diffusion coefficient of 34.1 km²/generation. Because this species is univoltine, these rates equate to distances moved within a year. This calculation assumed that a female would fly for 6 hours along a linear path that radiated from the center of the population distribution and would feed and re-hydrate on oak foliage for 18 hours; if the female survived, flight would resume the next day with no carryover effects from the previous day’s flight. Mortality is assumed to be independent of flight. Population range expansion is also a function of the intrinsic population growth rate. Thus, with diffusion and reproduction combined, we estimate an annual spread rate of 9.3 km/year. This projected spread rate is similar to the rate at which the area in southern California with oak mortality from *A. auroguttatus* increased from 2008-2010 (Coleman and others 2012).

Conclusions
Relative to other United States states, *A. auroguttatus* appears to pose the greatest threat to oaks in California and Oregon. Large areas within these states have suitable hosts and climate. In Arizona, a combination of natural enemies and host-plant resistance may keep this insect from building to damaging levels (Coleman and others 2015). Our forecasts of the potential geographic range for this insect are based upon the best available scientific information, yet we recognize that significant knowledge gaps remain. Extreme uncertainty in risk assessment as a consequence of poor biological understanding is a frequent circumstance among newly invading species. Empirical observations are essential to support or refute the forecasts made in this map and to provide a basis for its refinement.

More research is needed to evaluate the host status of oak species from eastern North America. If the rule of thumb about the suitability of red oaks continues to hold true for eastern oak species, considerable forested acreage would be at risk. Yet, most red and white oaks of California do not appear to have close relatives outside of the region (Nixon 2002).

We hope the updated risk map will help forest health specialists with their efforts to limit the potential damage from this insect. This map should be of immediate benefit in the design of early detection surveys and to help characterize the total area that might be affected if this insect is not effectively managed. We should emphasize that this map focuses on where *A. auroguttatus* might become established. Different factors may be needed to forecast the rate and extent of tree mortality within these areas. The magnitude of impact remains the most difficult component of any pest risk assessment to forecast (Venette and others 2010).
Acknowledgments

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Population Genetics and Biological Control of Goldspotted Oak Borer, an Invasive Pest of California Oaks¹,*

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Abstract
California’s oak woodlands are threatened by the recent introduction of goldspotted oak borer (Agrilus auroguttatus). This invasive wood-borer is indigenous to mountain ranges in southern Arizona where its low population densities may be due to the presence of co-evolved, host-specific natural enemies. Reuniting A. auroguttatus with these natural enemies can potentially provide permanent control of this pest. To initiate a classical biological control program, our research focused on investigating the genetic variation within and between populations in the native and introduced ranges in attempt to identify the geographic origin of the invasive California population. The area of origin for the invasive population was not determined conclusively, although molecular data suggests the Dragoon Mountains in Cochise County, Arizona as a potential source of this beetle, and its host-specific natural enemies. Native and introduced range surveys for natural enemies were conducted in 2012 and 2013 by deploying more than 30,000 A. auroguttatus sentinel. In 2012, the first known egg parasitoid was collected in Arizona and identified as a generalist Trichogramma sp., but in 2013, no egg parasitoids of A. auroguttatus were found. Despite the lack of success in explorations for host-specific egg parasitoids, classical biological control may still be the most viable long-term management option. However, additional research on the biology, life history, and potential natural enemies of this beetle is needed in order to advance its management in southern California.

Key words: classical biological control, cytochrome C oxidase I, egg parasitoids, foreign exploration, invasive species, phylogeography, wood borers

Introduction
California’s oak woodlands are seriously threatened by the goldspotted oak borer (Agrilus auroguttatus), an invasive woodborer native to southern Arizona and perhaps northern Mexico (based on a single specimen collected in Baja California Sur in 1977) (Coleman and Seybold 2011). In 2004, this beetle was first detected in San Diego County, but was not a known pest of indigenous oaks until 2008 (Coleman and Seybold 2008). Approximately 25,000 coast live oak (Q. agrifolia), California black oak (Q. kelloggii), and canyon live oak (Q. chrysolepis) have been killed due to larval A. auroguttatus feeding in the cambial region (Coleman and others 2012a, USDA FHM 2013). This infestation continues to expand in San Diego and Riverside Counties (Coleman and Seybold 2008, Jones and others 2013). In contrast to the high

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* Information presented in this paper has been previously published by the authors in peer-reviewed journals (Lopez and Hoddle 2013, Lopez and others 2014).
levels of mortality caused by *A. auroguttatus* in California, this beetle has never been considered a pest in its native range, and exhibits behavior similar to other *Agrilus* species that preferentially attack trees already in decline (Coleman and others 2012a). Invasive wood borers are notoriously difficult to manage, especially in natural environments, because they can remain undetected until populations are too large and widespread to control using conventional methods such as pesticides or mechanical removal of infested trees (Cappaert and others 2005, Haack and others 2010, Van Driesche and others 2010). Coleman and Seybold (2008) provided the first reports on *A. auroguttatus* infestation in southern California which spanned 6447 ha and killed an estimated 17,000 trees, indicating that the introduction of this beetle likely occurred (probably via infested oak firewood) several years prior to its initial detection. Due to the widespread infestation of *A. auroguttatus* across federal, state, private, and Native American lands in southern California, classical biological control (the importation of co-evolved, host-specific natural enemies from a pest’s native range) is considered to be a viable and promising long-term management strategy for suppressing damaging populations.

Classical biological control has been an effective tool for lowering populations of non-native forest pests (Hajek 1999, Roland and Embree 1995, Ryan and others 1978, Van Driesche and others 2010). While the role of host plant resistance is suspected to play an important role on *A. auroguttatus* population densities (Coleman and Seybold 2011), the rapid increase of this beetle within the oak woodlands of southern California compared to the low densities observed in Arizona may, in part, be due to an absence of co-evolved natural enemies in California. Reuniting *A. auroguttatus* with these host-specific natural enemies may potentially provide permanent control of this invasive pest.

The implementation of an effective classical biological control program for an invasive species requires the knowledge of several key components such as the pest’s area of origin, natural enemies (in the native and introduced range), and life history traits. However, before 2008, none of this foundational information was available for *A. auroguttatus*. To initiate a classical biological control program for *A. auroguttatus* in southern California, our research focused on the following components: 1) investigation of genetic variation within and between populations in the native and introduced ranges in attempt to identify the geographic origin of the invasive California population, and 2) conduct native and introduced range surveys for natural enemies of this woodborer.

Determining the area of origin for *A. auroguttatus* is a fundamental step in the search for co-evolved natural enemies that may be considered for use in a classical biological control program against this invasive pest (Lopez and others 2014). Collection records indicate that *A. auroguttatus* inhabits several mountain ranges in southern Arizona including the Chiricahua, Huachuca, Santa Catalina, and Santa Rita mountains (Coleman and Seybold 2011), and the most recent collection from the Dragoon mountains in 2011, a new locality record, suggests there are additional mountain ranges within the native range inhabited by this woodborer. These “sky island” mountain ranges are isolated from each other by the surrounding Sonoran Desert, which presents a natural dispersal barrier for *A. auroguttatus* and its natural enemies. Narrowing the geographic source of the invasive California population to a specific mountain range in Arizona would, in theory, allow the collection of host-specific natural enemies which have formed a co-evolutionary relationship with the genotype of the invasive population (Stouthamer 2008).

Natural enemy surveys throughout the introduced and native range of an invasive pest are an essential component of any classical biological control program (Goolsby
and others 2003, Hoddle and others 2002, O’Neil and others 2005, Rosen and DeBach 1992, Toepfer and Kuhlmann 2004). In 2009, *A. auroguttatus* natural enemy surveys were conducted throughout the Santa Rita, Huachuca, Chiricahua, and Santa Catalina Mountain ranges, and on the Descanso Ranger District of the Cleveland National Forest in San Diego County, California (Coleman and Seybold 2011). From these initial surveys, two larval parasitoids were associated with *A. auroguttatus*, along with several generalist predators.

*Calosota elongata*, a gregarious, larval ectoparasitoid was discovered on late-instar larvae within pupal cells inside infested *Q. emoryi* in southeastern Arizona (Coleman and Seybold 2011), and was also collected from *A. auroguttatus* pupal cells found during destructive sampling of *Q. agrifolia* in San Diego County, California (Haavik and others 2012). Little is known about this newly described parasitoid (Gibson 2010), though the much lower parasitism rate observed in California (<1 percent) compared to that recorded in Arizona (15 percent) suggests that this species may have been transported into southern California along with the original population of *A. auroguttatus* (Haavik and others 2012). Molecular analyses could help confirm this assumption. *Atanycolus simplex*, a generalist larval ectoparasitoid, emerged from *A. auroguttatus*-infested *Q. emoryi* and *Q. agrifolia* collected in Arizona and California, respectively (Coleman and Seybold 2011). The remaining natural enemies reared from infested oak material or collected from *A. auroguttatus* life stages were generalist species not suitable as classical biological control agents due to their broad host ranges (Coleman and Seybold 2011).

While the majority of known natural enemies are either generalist parasitoids or predators of *A. auroguttatus*, the newly described *C. elongata* could be host-specific. However, an inability to rear adequate numbers of *A. auroguttatus* larvae in quarantine has precluded basic biology studies on *C. elongata*. In contrast, eggs of *A. auroguttatus* can easily be obtained in the laboratory by providing field-collected adults with water, oak leaves and coffee filter paper as an oviposition substrate (Lopez and Hoddle 2014). Due to the inability to rear, and thus determine the specificity of natural enemies attacking *A. auroguttatus* larvae and pupae, search efforts have focused on natural enemies attacking *A. auroguttatus* eggs. Since the overall structure (for example, topography, thickness, and coloration) of oak bark makes collecting naturally deposited *A. auroguttatus* eggs (typically oviposited inside cracks and crevices of bark) an arduous task, our strategy of locating egg parasitoids using sentinel egg masses on filter paper is a practical though semi-artificial alternative. From 2012 to 2013, surveys for *A. auroguttatus* egg parasitoids were conducted throughout the native (southern Arizona) and introduced (southern California) range by deploying sentinel egg masses on filter paper in an attempt to attract, collect, and identify potential egg parasitoids of this beetle.

**Methods**

**Population genetics of *A. auroguttatus***

We utilized sequences of mitochondrial cytochrome oxidase (COI) and the nuclear ribosomal D2 domain of the 28S gene (28SD2) to investigate connectivity among invasive *A. auroguttatus* populations in San Diego and Riverside Counties in southern California, and native populations inhabiting several mountain ranges in southern Arizona. Specimens of *A. auroguttatus* were collected between May 2009 and November 2012 from infested oak trees in the San Jacinto Mountains and
Cleveland National Forest in southern California, and the Chiricahua, Dragoon, Huachuca, Santa Catalina, and Santa Rita Mountains in southern Arizona (table 1). From these individuals, DNA was extracted, amplified, sequenced, and analyzed as described in Lopez and others (2014).

Table 1—Genetic variation in populations of *A. auroguttatus* collected in Arizona and California, assessed as number of haplotypes, and haplotype diversity

<table>
<thead>
<tr>
<th>Locality</th>
<th>County</th>
<th>State</th>
<th>GPS coordinates</th>
<th>No. of individuals</th>
<th>No. of haplotypes</th>
<th>Haplotype diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chiricahua</td>
<td>Cochise</td>
<td>AZ</td>
<td>31°50′N 109°17′W</td>
<td>20</td>
<td>6</td>
<td>0.763</td>
</tr>
<tr>
<td>Dragoons</td>
<td>Cochise</td>
<td>AZ</td>
<td>31°53′N 109°59′W</td>
<td>23</td>
<td>6</td>
<td>0.684</td>
</tr>
<tr>
<td>Huachuca</td>
<td>Cochise</td>
<td>AZ</td>
<td>31°24′N 110°18′W</td>
<td>25</td>
<td>12</td>
<td>0.917</td>
</tr>
<tr>
<td>Santa Catalina</td>
<td>Pima</td>
<td>AZ</td>
<td>32°26′N 110°47′W</td>
<td>10</td>
<td>3</td>
<td>0.733</td>
</tr>
<tr>
<td>Santa Rita</td>
<td>Santa Cruz</td>
<td>AZ</td>
<td>31°43′N 110°52′W</td>
<td>69</td>
<td>9</td>
<td>0.712</td>
</tr>
<tr>
<td>Cleveland National Forest</td>
<td>San Diego</td>
<td>CA</td>
<td>33°18′N 116°48′W</td>
<td>115</td>
<td>15</td>
<td>0.859</td>
</tr>
<tr>
<td>San Jacinto</td>
<td>Riverside</td>
<td>CA</td>
<td>33°44′N 116°42′W</td>
<td>24</td>
<td>3</td>
<td>0.359</td>
</tr>
</tbody>
</table>

**Surveying for *A. auroguttatus* natural enemies in Arizona and California**

Field surveys for egg parasitoids were conducted in the native and introduced range of *A. auroguttatus*. In 2012, *A. auroguttatus* sentinel eggs were deployed at two oak forest field sites in Arizona and California (table 2). In 2013, a total of eight field sites, six in Arizona and two in California, were selected from counties where this beetle had been previously collected (Coleman and Seybold 2011) (table 2). At each site, six and 10 infested oaks (in 2012, and 2013, respectively) were selected for deployment of *A. auroguttatus* sentinel eggs to survey for potential natural enemies targeting this life stage. Trees were considered infested if symptoms described in Hishinuma and others (2011) such as larval galleries and exit holes were present. At each selected tree, sentinel eggs were deployed into specified treatments which were individually suspended on infested trees. The deployment of *A. auroguttatus* eggs at each site was conducted over an eight week period during July to September 2012, and June to August 2013. Sentinel egg masses were prepared, deployed, retrieved, reared, and examined as described in Lopez and Hoddle (2013).
Table 2—Geographic information for field sites and number of sentinel eggs deployed during *A. auroguttatus* natural enemies surveys in 2012 and 2013

<table>
<thead>
<tr>
<th>Site name</th>
<th>Locality</th>
<th>County</th>
<th>State</th>
<th>GPS coordinates</th>
<th>No. of eggs deployed (2012)</th>
<th>No. of eggs deployed (2013)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gardner Canyon</td>
<td>Santa Rita Mtns</td>
<td>Pima</td>
<td>AZ</td>
<td>31°43'N/110°43'W</td>
<td>7428</td>
<td>2272</td>
</tr>
<tr>
<td>Carr Canyon</td>
<td>Huachuca Mtns</td>
<td>Cochise</td>
<td>AZ</td>
<td>31°26'N/110°17'W</td>
<td>-</td>
<td>2159</td>
</tr>
<tr>
<td>Middle March Pass Cochine</td>
<td>Dragoon Mtns</td>
<td>Cochise</td>
<td>AZ</td>
<td>31°51'N/109°57'W</td>
<td>-</td>
<td>2277</td>
</tr>
<tr>
<td>Stronghold</td>
<td>Dragoon Mtns</td>
<td>Cochise</td>
<td>AZ</td>
<td>31°55'N/109°58'W</td>
<td>-</td>
<td>2720</td>
</tr>
<tr>
<td>Turkey Creek Pinery Canyon</td>
<td>Chiricahua Mtns</td>
<td>Cochise</td>
<td>AZ</td>
<td>31°51'N/109°20'W</td>
<td>-</td>
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<tr>
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<td>Cochise</td>
<td>AZ</td>
<td>31°57'N/109°18'W</td>
<td>-</td>
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<td>William Heise Park</td>
<td>Heise County Park</td>
<td>San Diego</td>
<td>33°02'N/116°35'W</td>
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<td></td>
<td>Cleveland National Forest</td>
<td>San Diego</td>
<td>32°50'N/116°32'W</td>
<td>-</td>
<td>1746</td>
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</tr>
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</table>

**Results and discussion**

**Population genetics of *A. auroguttatus***

A section of the COI gene from 286 *A. auroguttatus* individuals (147 from Arizona and 139 from California) was sequenced in an attempt to delineate the area of origin of the invasive California population, and better understand the genetic variation within and between sampled populations. Haplotype distribution, abundance, and diversity across sample locations are shown in table 1. Additionally, identical sequences of 28SD2 from 23 specimens sampled from the Chiricahua, Huachuca, Santa Catalina, and Santa Rita Mountains in Arizona, and from the Cleveland National Forest, and San Jacinto Mountains in California indicated that the individuals collected were all one species, and not the congener *A. coxalis* or perhaps another ‘unknown’ cryptic species morphologically indistinguishable from *A. auroguttatus* or *A. coxalis* (Coleman and others 2012b).

Among the COI sequences, a total of 39 haplotypes were identified which shows high variability in the COI gene region of this species. However, the geographic distribution of these haplotypes revealed little genetic overlap between the native and introduced regions since only two haplotypes were shared between these areas (37 of 39 haplotypes sampled across California (n = 14) and Arizona (n = 23) populations were distinct to either region). The most common haplotype was shared by 82 specimens and found in every sample location except the Santa Catalina Mountains, Arizona. The second overlapping haplotype was shared only between individuals collected from the Cleveland National Forest in California (n = 4) and the Dragoon Mountains in Arizona (n = 1), highlighting the Dragoon Mountains as a possible source of *A. auroguttatus* in southern California. However, it seems likely that we have not yet sampled the full range of variation in this species (table 1), and larger
samples including collections across additional unsampled mountain ranges in Arizona and northern Mexico could help to further pinpoint the geographic source of the California population of *A. auroguttatus*.

Little genetic overlap was also observed between *A. auroguttatus* populations within the native range. Out of the 23 distinct haplotypes identified from Arizona collections, 17 were unique to either the Chiricahua (*n* = 4), Dragoon (*n* = 1), Huachuca (*n* = 7), Santa Catalina (*n* = 3), or Santa Rita (*n* = 2) Mountains, supporting the idea that populations of *A. auroguttatus* from these "sky islands" in southern Arizona are genetically isolated from one another. The lack of gene flow between native populations of *A. auroguttatus* revealed by our data justifies the use of population genetics to focus the search for co-evolved natural enemies of this woodborer. Consequently, future surveys for *A. auroguttatus* natural enemies should focus on unsurveyed mountain ranges in southern Arizona and northern Mexico, and the Dragoon Mountains in southern Arizona, as a potential source for classical biological control agents.

**Surveying for *A. auroguttatus* natural enemies in Arizona and California**

During the natural enemy surveys conducted in 2012 and 2013, more than 30,000 *A. auroguttatus* sentinel eggs were deployed through the native and introduced range of this insect. In 2012, the first known egg parasitoid of *A. auroguttatus* was collected at very low levels (approximately 0.1 percent) from sentinel eggs deployed in the Santa Rita Mountains, Arizona, and was identified as *Trichogramma* sp. Investigation into the identity of this species (using ITS2 sequences) found a previous collection record of this parasitoid from Lepidoptera eggs collected in Riverside County, California (Richard Stouthamer, unpublished data), indicating that this species is likely a generalist that opportunistically parasitized the sentinel eggs.

In 2013, no egg parasitoids of *A. auroguttatus* were found in the native or introduced range of this woodborer despite the increase in field sites surveyed and number of eggs deployed. Considering the absence of parasitism from >18,000 *A. auroguttatus* eggs deployed throughout infested sites in southern Arizona and California in 2013, and the rarity of parasitism recorded from >12,000 eggs deployed in similar treatments in 2012 (Lopez and Hoddle 2013), it may be reasonable to conclude that host-specific parasitoids of this beetle may not exist within the areas sampled. In addition, the low number of *Trichogramma* sp. collected from 2012 surveys suggests that parasitism from generalist egg parasitoids does not significantly contribute to *A. auroguttatus* egg mortality. However, inadequate surveying techniques, and an insufficient search range or duration could have led to the detection of very few egg parasitoids during our concentrated survey for this particular guild of *A. auroguttatus* natural enemies.

**Future directions for *A. auroguttatus* biological control**

The recent introduction of *A. auroguttatus* has resulted in the mortality of tens of thousands of mature red oaks (section *Lobatae*) in southern California, which is drastically changing the composition of these important and unique oak woodland communities (Allen-Diaz and others 2007, Coleman and others 2012a). The difficulty in managing this wood-boring pest in both urban and natural environments has underscored the importance of developing a classical biological control program. Despite the lack of success in explorations for host-specific egg parasitoids, classical
biological control may still be the most viable long-term management option. However, additional research on the general biology, life history, and potential natural enemies is needed in order to continue making advances in this control program. Research investigating the life history of *A. auroguttatus* within its native range is necessary to increase understanding on the phenology of this insect, which may potentially lead to improved methods for natural enemy surveys, especially detection of egg parasitoids. Lastly, the ability to rear and maintain all life stages of *A. auroguttatus* in the laboratory is needed to dramatically improve the potential success of a classical biological control program as this will increase the number of potential host stages that can be examined from natural enemy surveys, and ultimately will affect the ability to rear natural enemies for study in quarantine and eventual potential release into infested regions in southern California.

**Acknowledgments**

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Influence of the Invasive Goldspotted Oak Borer on Fuel Loading in Southern California

Tom W. Coleman

Abstract
The exotic goldspotted oak borer (GSOB), *Agrilus auroguttatus* (Coleoptera: Buprestidae), continues to cause elevated oak mortality in southern California. Initial GSOB research was directed at developing an integrated pest management program. However, little research has examined the secondary impacts associated with this invasive pest. My primary objective was to compare the fuel loading in severely GSOB-infested woodlands (>10 years of oak mortality) to uninfested woodlands in southern California. Forest stand characteristics, canopy fuels, understory fuels, and surface fuels were recorded from 0.25 ha plots, belt transects, and Brown’s transects, respectively. Following preliminary analyses, 77 percent of oaks were infested with GSOB and 41 percent of the oaks were killed by GSOB in infested plots. Dead oaks were slowly decaying in severely infested woodlands, but greater increases in surface fuels (1-, 10-, 100-, and 1000-hour fuels) were recorded, but these differences were not statistically significant. Oak regeneration was greater in GSOB infested stands than uninfested stands, but highly variable in infested plots. An increase in understory vegetation and a greater abundance of surface fuels can lead to an increase in the rate of fire spread, flame lengths, and fire line intensities.

Key words: Brown’s transects, exotic wood borer, fuel structure, oak mortality

Introduction
In 2008, the exotic goldspotted oak borer (GSOB), *Agrilus auroguttatus* (Coleoptera: Buprestidae), was linked to elevated oak mortality in southern California (Coleman and Seybold 2008). The wood-boring beetle prefers to attack and kill large diameter coast live oak (*Quercus agrifolia*), and California black oak (*Q. kelloggi*), in California (Coleman and others 2012b). The movement of infested firewood likely led to the spread of this invasive insect from its native region of southeastern Arizona to southern California and from San Diego County into the mountain community of Idyllwild (Riverside, California) and the city of Orange (Orange County, California) (Coleman and Seybold 2011, Coleman and others 2012a). Tree injury and mortality associated with GSOB has persisted for greater than a decade in eastern San Diego County. Annual aerial surveys estimate GSOB has killed >27,000 oaks in this part of the county (USDA FHM 2014). Tree mortality spans all landownerships, impacting county, federal, private, state, and tribal lands. The GSOB infestation was recently detected killing California black oak on the Palomar Ranger District, Cleveland National Forest (CNF).

Since 2008, GSOB research was directed at determining its biology, developing monitoring techniques, assessing host susceptibility and responses, assessing insecticide and cultural management options, surveying for natural enemies, and disseminating education and awareness (Coleman and others 2011, 2014; Haavik and

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1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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others 2013, 2014; Jones and others 2013; Lopez and Hoddle 2013, 2014). However, little research has examined the secondary effects associated with this invasive pest, including changes to the fuel structure in impacted stands. The influence of invasive insect species, including the emerald ash borer (Agrilus planipennis), European woodwasp (Sirex noctilio), and Asian longhorned beetle (Anoplophora glabripennis), on changes to the fuel structure and influence on wildfire behavior has been largely overlooked in the United States, which might be due to location of infestations in urban areas, limited distributions, and presence of invasive species in ecosystems not frequently disturbed by wildfire. However, the influence of Phytophthora ramorum, the causal agent of sudden oak death, on fuel structure was assessed in coastal oak woodlands of northern California (Valachovic and others 2011), offering a valuable comparison of the impact exotic species have on wildfire behavior.

Methods

The main objective of this study was to compare the changes in fuel structure in severely GSOB-infested coast live oak woodlands (>10 years of oak mortality) to uninfested coast live oak stands in southern California. Infested GSOB sites were surveyed on the Descanso Ranger District, CNF in San Diego County. Uninfested stands were surveyed on the Palomar and Trabuco Ranger Districts, CNF in San Diego and Riverside Counties, respectively. From 2013 to 2014, the forest composition and fuel loads were recorded from a total of nine coast live oak stands (four infested and five uninfested).

Forest stand characteristics (for example, tree and oak diameter at breast height (1.4 m, DBH), basal area (m²/ha) and stems/ha for trees (>1.4 m tall), percent GSOB infestation, percent oak mortality with and without GSOB injury, and GSOB crown injury ranking (1-5)) were recorded from 50 x 50 m plots. Canopy fuels (for example, tree height (m), base crown height (m), percent canopy cover, decay class of dead oaks (rank 1-5)) were recorded from three 6 m x 50 m belt transects. A hypsometer was used to determine tree and base crown height and a densitometer was used to determine percent canopy cover. Tree injury associated with GSOB was determined by the presence of D-shaped emergence holes along the main stem and crown injury rankings followed the health system developed by Hishinuma and others (2011) and Coleman and others (2011). Understory fuels (for example, count of tree species regeneration (<1.4 m) and height (m)) and surface fuels (for example, 1-, 10-, 100-, and 1000-hour fuels, slash depth (cm), percent ground cover (leaf litter, grass, exposed soil, wood cover, rock, moss, tall shrub, and low shrub cover), leaf litter depth (cm), and duff fuel depth (cm) were recorded from 10 Brown’s transects. Additional detail about the sampling methods can be found in Brown (1974), Simard and others (2011), and Donato and others (2013).

A general linear model was used to detect significant differences in forest stand characteristics, canopy fuels, surface fuels, and understory fuels between the GSOB-infested and uninfested stands (PROC GLM). Statistical significance was defined as $P \leq 0.05$ using SAS 9.2 (SAS Institute, Cary, NC 2008). Assumptions of normality were checked for all data using the Shapiro-Wilk test (PROC UNIVARIATE) and heterogeneity of variances was checked by comparing residuals (PROC UNIVARIATE).
Results

Following preliminary analyses, 77 percent of oaks were infested with GSOB and 41 percent of the oaks were killed by GSOB in infested plots. Crown injury rankings from GSOB was significantly greater in infested stands than uninfested stands ($F_{1,8} = 11.81$, $P = 0.01$). Mean crown injury ranking was $2.33 \pm 0.86$ (mean ± s.e.) in infested stands and $1.21 \pm 0.19$ in uninfested stands. No statistically significant differences were detected for mean stand diameter at breast height (DBH), mean coast live oak DBH, stand basal area ($m^2/ha$), and stem density (ha) between infested and uninfested coast live oak stands. Canopy fuels, including tree height (m), base crown height (m), and percent canopy cover, were not statistically different between the two stand types.

The decay of dead coast live oaks was greater in infested stands than uninfested stands following the initial assessments ($F_{1,8} = 50.33$, $P = 0.0002$). The mean decay rate of the dead oaks was $1.97 \pm 0.36$ and $1 \pm 0$ for uninfested stands, suggesting many dead oaks show minimal decay (only loss of smaller twigs) in infested stands. Coast live oak regeneration was greater ($100 \pm 122$) in GSOB infested stands than uninfested stands ($17 \pm 8.10$), but highly variable in the infested sites.

Surface fuels (1-, 10-, 100-, and 1000-hour fuels) were greater in infested stands than in uninfested stands, but these differences were not statistically significant. Mean slash depth (m), leaf litter depth (cm), and duff litter depth (cm) did not differ between the two stand types. Leaf litter depth was greater in the uninfested stands than the infested stands, but this difference was also not statistically significant.

Percent leaf litter was the highest ground cover surveyed across the two stand types. The second and third highest ground cover type measured were grass and soil cover, respectively. These three cover types did not differ between the two stand types. Grass was the tallest (cm) understory ground cover in both infested (21.7 ± 10.1) and uninfested (20.8 ± 8.15) stands, but these differences were not statistically significant.

Discussion

Preliminary data show high levels of injury and mortality from GSOB in infested stands. Coleman and others (2012) reported similar rates of tree injury and mortality associated with GSOB at the center of the outbreak. Several fuel measurements from the canopy, understory, and surface were highly variable between the two stand types, reducing statistical significance. As additional stands are surveyed for this study, the high levels of variability among these fuel measurements will likely be reduced between the two stand types and also provide greater statistical power for the analyses.

The decay of dead oaks in GSOB-infested stands was greater than uninfested stands. However, these trees showed low rates of decay with most dead oaks still standing in the canopy and possessing many large branches. The slow rates of decay may be attributed to recent tree mortality from GSOB (<10 years) and the dry Mediterranean climate of southern California. Similar rates of decay for dead oaks were recorded in stands impacted by P. ramorum along the central coast of California (Valachovic and others 2011) despite the formation of large cankers on the main stem of oaks and secondary attack from ambrosia beetles. Extensive attack from ambrosia beetles (Coleoptera: Scolytidae) along the main stem, which can lead to stem failure, is not commonly observed in the GSOB system. Oak mortality will continue in these woodlands from this invasive wood borer, leading to continuous changes in the fuel conditions.
loading. This is in contrast to the cyclical outbreaks of bark beetles and other native insects that typically have short bouts (2 to 3 years) of tree mortality. Recent studies assessing changes in fuel loading in the western United States have focused on bark beetle-caused tree mortality (see Donato and others 2013, Simard and others 2011), but the influence of exotic insects on fuel loading is still largely underrepresented. Multiple fuel reduction treatments will likely be necessary to reduce the increase in surface fuels associated with GSOB in southern California. A greater abundance of surface fuels can lead to an increase in the rate of fire spread, flame lengths, and fire line intensities. However, fuel managers in the region were more concerned with an increase and the release of understory vegetation that may carry wildfire from the forest floor into the canopy. Currently, these data do not show an increase in abundance of woody plant species in the understory that may increase the threat of a wildfire crowning. These data provide an initial assessment of the changes in fuel loading in this area and long-term changes to plant community may be evident as plots are resampled in the future.

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Proceedings of the 7th California Oak Symposium: Managing Oak Woodlands in a Dynamic World


Effects of the Goldspotted Oak Borer, *Agrilus auroguttatus*, on the Health of Coast Live Oak, *Quercus agrifolia*, in Southern California Before and After Treatment With Two Systemic Insecticides

Yigen Chen, Mary L. Flint, Tom W. Coleman, Joseph J. Doccola, Donald M. Grosman, David L. Wood, and Steven J. Seybold

Abstract

The invasive goldspotted oak borer, *Agrilus auroguttatus* (Coleoptera: Buprestidae), is threatening the health and survival of oak trees in San Diego County, California (Flint and others 2013). The primary oak species colonized and killed in this area include coast live oak (*Quercus agrifolia*), California black oak (*Quercus kelloggii*), and canyon live oak (*Quercus chrysolepis*). The high amount of damage recorded on these hosts suggests that the association between *A. auroguttatus* and these oaks is recent. Damage by *A. auroguttatus* in its native range in Arizona to Emory oak (*Quercus emoryi*) and silverleaf oak (*Quercus hypoleuroides*), is much less severe (Coleman and others 2012), suggesting a longer co-evolutionary relationship.

Preventive and suppressive chemical treatment techniques have not previously been tested for the control of *A. auroguttatus* in California. Management activities have focused primarily on treatment of infested oak wood (Jones and others 2013). We report on a 3.5-year investigation of the efficacy of two systemic insecticides, emamectin benzoate (EB) and imidacloprid (IC), for controlling *A. auroguttatus* in *Q. agrifolia*, in San Diego County.

Trees at two study sites (Japatul Valley, IC and Deerhorn Valley, EB) were treated in April-May 2011 by tree injection, and over 300 study trees were monitored at the locations between April 2011 and October 2014. These sites (on private lands) were characterized by relatively open stands of *Q. agrifolia* and Engelmann oak (*Q. engelmannii*), the latter of which is not considered a host of *A. auroguttatus*. The key elements of the health of *Q. agrifolia* monitored annually by the project team were the number of D-shaped emergence holes (Figure 1A; Flint and others 2013) and the crown condition of the trees (Figure 1B; Hishinuma and others 2011).

There was no tree mortality through the early stages of the study. However, between October 2013 and 2014, eight trees died in the EB study. No mortality was recorded during the IC study. In the test of EB, uninjected trees had an elevated and sustained level of annual increases in *A. auroguttatus* emergence holes recorded 1.5 years after the initiation of the study, whereas EB treatment yielded annual increases that remained lower and constant. In the test of IC, treated trees had a significantly greater annual increase in *A. auroguttatus*

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.

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emergence holes than untreated trees during the third survey period (October 2012-2013). Annual increases in *A. auroguttatus* emergence holes in the un.injected control group of trees for the IC study did not differ during the three survey periods; treatment with IC resulted in an annual increase in *A. auroguttatus* emergence holes that declined consistently over the survey periods. Crown ratings of most trees at both study sites remained unchanged, regardless of insecticide treatment.

![Image](image_url)

Figure 1—Two elements of assessment of the health of coast live oak (*Quercus agrifolia*) in this study were the number of goldspotted oak borer (*Agrilus auroguttatus*) D-shaped emergence holes (A; Flint and others 2013) through the bark surface, and the condition of the crown (B; Hishinuma and others 2011) based on a 5-part rating system where 1 is a healthy crown and 5 is the crown of a dead tree.

In both tests, a higher cumulative increase in *A. auroguttatus* emergence holes was observed from trees that were more severely infested at the beginning of the study. The greatest cumulative increases in *A. auroguttatus* emergence holes were observed in trees with larger diameters at breast height.

Because of the rather gradual decline in the health of *Q. agrifolia* in both treatment groups at both study sites, we conclude that the impact of *A. auroguttatus* is a relatively slow process. Thus, unlike the situation with pests such as tree-killing conifer bark beetles, land managers
may have more time to respond to evidence of new infestations by *A. auroguttatus* in an area to execute tree removals and proper wood sanitation. Although systemic insecticides such as EB have been shown to be efficacious for the control of other similar species such as the emerald ash borer (*Agrilus planipennis*) in the eastern United States (McCullough and others 2011, Smitley and others 2010), our study does not provide evidence of strong efficacy for these materials in the control of *A. auroguttatus* in California.

**Key words:** coast live oak, emamectin benzoate, goldspotted oak borer, imidacloprid, invasive pest, systemic insecticide

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Outreach and Education Efforts to Counter the Spread and Impact of Goldspotted Oak Borer

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Abstract

The goldspotted oak borer (GSOB) Agrilus auroguttatus (Coleoptera: Buprestidae), has killed over 80,000 oaks across all land ownerships, costing over $8 million in public and private funds for mitigation and response. Linked to oak mortality in San Diego County in 2008, this exotic beetle likely arrived in California through infested firewood from Arizona and attacks three native oak species found through California and southern Oregon: coast live oak (Quercus agrifolia), California black oak (Q. kelloggi), and canyon live oak (Q. chrysolepis). The University of California Division of Agriculture and Natural Resources (UC ANR), the U.S. Department of Agriculture Forest Service (USDA FS), and California Department of Forestry and Fire Protection (CAL FIRE) lead collaborative program development to slow GSOB expansion by educating clientele about GSOB-associated oak mortality and the danger of firewood imports. Over 5,100 stakeholders throughout southern California were identified and contacted utilizing both traditional and digital educational delivery strategies, including outreach and training events, print and online resources and a Citizen Scientist/GSOB Early Warning System for detection and monitoring. While it is impossible to measure the extent of GSOB spread mitigated through this effort, we believe we have dramatically reduced the purchase of GSOB-infested firewood in the communities targeted in our outreach.

Key words: Agrilus auroguttatus, forest pest, goldspotted oak borer, GSOB, invasive insect education and outreach, oak management, oak woodlands, Quercus agrifolia, Quercus chrysolepis, Quercus kelloggi

Introduction

In 2007 it became obvious that red oaks were dying in unprecedented numbers in San Diego County at rates far beyond the mortality seen in recent droughts. By the time the goldspotted oak borer (GSOB) Agrilus auroguttatus (Coleoptera: Buprestidae), was linked to oak mortality in 2008 (Coleman and Seybold 2008), thousands of acres of oak woodlands were already heavily impacted (Scott and others, Mapping the spread of the goldspotted oak borer (Agrilus auroguttatus), an invasive exotic bark beetle, these proceedings). It became obvious that a coordinated, rapid outreach...
response was essential to prevent the spread of GSOB to other woodlands in California. This outreach faced similar problems found with most exotic pest outbreaks—limited understanding of the origin, extent and intensity of the loss. Little scientific data was initially available except that GSOB had never been considered a pest problem for oak populations within its native range of southeast Arizona. However, once introduced into California, the beetle thrived. Research and programming about a closely related exotic beetle, the emerald ash borer (EAB) *Agrilus planipennis*, provided a general framework for response (Herms and McCullough 2014), but the application of EAB management techniques to GSOB was unclear.

GSOB damage appeared to be limited to three species of oak; however, the extent and timing of loss was poorly understood. This uncertainty created an exceptionally large group of affected clientele across the oak woodlands of California. The momentum of the problem was obvious: Every GSOB-infested oak represented an opportunity for the pests’ spread to new locations. With thousands of cords-worth of GSOB-infested trees suddenly available for firewood, there was an urgent need to change the behavior of the firewood market. GSOB larvae readily survive throughout firewood production, pupate and emerge as breeding adults wherever firewood was moved or stored.

Most counties throughout California have at least one to all of the three susceptible oak tree species: coast live oak, *Quercus agrifolia*; California black oak, *Q. kelloggii*; and canyon live oak, *Q. chrysolepis*. Approximately 1.2 million hectares (3 million acres) of susceptible oaks occur from southern California into southern Oregon, with a strong likelihood that eastern red oaks could also be attacked. The distribution of GSOB damage has been patchy at all landscape scales, leaving many individual oaks and even entire woodlands unaffected (Scott and others, Mapping the spread of the goldspotted oak borer (*Agrilus auroguttatus*), an invasive exotic bark beetle, these proceedings). At the onset, clientele ranged from homeowners, arborists, park ecologists, ranch managers, to a wide variety of other individuals interested in oaks. Management units ranged from single oaks in residential landscaping up to thousands of hectares in county parks, state parks and national forests.

To slow the spread of GSOB, a large number of unrelated stakeholders needed to be reached and comprehend the potential threat posed to the environment, public safety, property values, outdoor recreation opportunities, and cultural resources. Initial outreach efforts matched the breadth of the stakeholders and were undertaken by a number of local, state, and federal agencies and organizations based in southern California. A number of these groups had previously collaborated to develop resources and capacity to solve other issues with wildfire, drought, and conifer mortality. These efforts coalesced around the University of California Cooperative Extension (UCCE) and the U.S. Department of Agriculture Forest Service-Forest Health Protection (USDA FS FHP) with a division of labor developing organically and with a remarkable degree of cooperation. This culminated in the education and outreach committee coordinated by the Cleveland National Forest, with representatives from UCCE, USDA FS FHP, California Department of Forestry and Fire Protection (CAL FIRE), San Diego County Agricultural Commissioner, City of San Diego Parks, California State Parks, and the Greater San Diego Resource Conservation District. CAL FIRE staff adapted an existing Incident Action Plan, to match the evolving needs for managing GSOB. The Incident Action Plan identified objectives, tasks and established an organizational structure, which helped to formalize existing ad hoc relationships.

By 2009, the University of California Division of Agriculture and Natural
Resources (UC ANR) began an aggressive program to forewarn oak tree managers in uninfested areas in southern California, including the remaining uninfested communities within the known GSOB infestation area. The goal was to establish a flexible education and outreach program with activities focused on increasing clientele understanding of GSOB impacts, distribution, management and problems posed by the movement of firewood. We utilized workshops, community and local government presentations, interagency meetings, webinars and conference calls to slow and ideally mitigate the import of infested firewood. Clientele were asked to participate in the GSOB early warning detection system, a citizen scientist oak health-monitoring program. Communities were encouraged to prepare a rapid response plan that could be implemented immediately in the event of GSOB discovery.

Funding for GSOB research was limited by the 2008 economic downturn, but by 2010 enough information existed to train woodland managers and landowners about the general nature of GSOB impacts and the possible range of management actions that could be taken. Over the next 3 years, a great deal of field and laboratory observations were made on GSOB life history (Coleman and others 2012, Flint and others 2013, Haavik and others 2012, Haavik and others 2013) so that information could be extended on the nature of GSOB-associated impacts.

Framework development

Our goal was to develop a GSOB public education and outreach program framework that would provide clientele educational opportunities and resources to: (1) learn about GSOB spread and firewood movement; (2) discuss options for management once infestation had occurred; and (3) encourage planning for GSOB outbreaks and preemptive management of oaks and oak woodlands in general. Our target audience included agency staff, tree service professionals, landowners, natural resource managers and the general public. There were three tiers of action: (1) training professionals and agency staff to monitor and manage GSOB; (2) make landowners aware of the GSOB problem to change oak firewood use and production and help them detect and manage GSOB; and (3) raise public awareness in general about the potential loss of oaks and danger of moving infested firewood. Traditional and digital outreach methods were utilized and tools were designed to support multiple tiers of action: web-based and in-person trainings; news media; print materials and regular and electronic mail communications. Additionally, program staff provided relevant input and collaboration for new and existing state, regional and countywide coordinating workgroups and projects. Program content was initially developed from existing insect pest and oak tree management information and ad hoc observations. We capitalized on the extensive research and outreach information developed on the emerald ash borer (Herms and McCullough 2014), oak woodland management (UC ANR Oak Woodland Management web page, http://ucanr.edu/sites/oak_range/) and integrated pest management best practices (UC ANR Integrated Pest Management program, http://www.ipm.ucdavis.edu/) when developing resource materials including links to other sources of information for the management of oak woodlands and GSOB. Our Education and Outreach group developed new content collaboratively. This ad hoc group created a conduit between research and outreach that allowed us to identify research needs and rapidly turn research information into outreach. The diversity of our group gave us the flexibility to reach different clientele as we learned about the extent and pattern of GSOB impacts.

To develop a program that was efficient, effective and sustainable, it was
imperative to collaborate and quickly organize coordinating planning and work groups. In addition to ad hoc cooperators, we were able to get the involvement of local, regional and state resource managers by informing them of the threat posed by GOSB to their management units. Their activities and the involvement of researchers were formalized by a series of meetings organized by USDA FS FHP. This resulted in the formation of the GSOB Steering Committee, which developed an incident action plan; a research needs assessment, project prioritization, and strategies for securing funding. Though Steering Committee collaboration, UC ANR applied for and was awarded 2-year funding (July 2010-June 2012), through the American Recovery and Reinvestment Act, to develop GSOB education and outreach programming. Additional funding was secured from the USDA FS State and Private Forestry and CAL FIRE. The funding established a hub for coordination ultimately evolving into a position for a GSOB program coordinator.

In order to extend our impact beyond committee members, we identified more than 5,100 agency staff and stakeholders to train as a second tier for outreach. The group included land managers, tree care professionals, natural resource educators, community organizations and citizen leaders with interests relating to oak trees. Although there was some representation with statewide interests, most of these stakeholders were professionally active and/or resided in one or more of six southern California counties: San Diego, Riverside, Orange, San Bernardino, Los Angeles and Ventura. This was the target group for primary outreach activities and developing local area collaborative partnerships. An additional group began formation during these initial outreach efforts as an Early Warning System program (EWS) of citizen scientists recruited and developed to assist with monitoring and detection efforts in their communities.

Firewood movement and the transfer of pests and diseases had become an issue in California as well as at the national level. With the GSOB-firewood link identified, UC ANR partnered with public and private organizations to initiate the formation of the California Firewood Task Force through the California Forest Pest Council. Voluntarily self-restricting the movement of GSOB-infested wood was the immediate management strategy encouraged to public and private property owners, firewood vendors and consumers to limit the expansion of the beetle to new locations in the state. Through this group, broader firewood research and public outreach messaging and activities became possible. In fostering a collaborative environment for program development, UC ANR was able to rapidly create and extend a coordinated GSOB education and outreach program utilizing a variety of traditional and digital outreach strategies simultaneously.

Education resources
The Internet is the major communication channel for contemporary society and offers a huge opportunity for knowledge transfer. Several online trainings and program tools were established and utilized during the program development period, including web-based, social media and electronic mail functions. Simultaneously, printed resources were developed for use with more traditional outreach activities such as workshops, community meetings and public information displays.

Website
The GSOB website (www.gsob.org) (fig. 1) was created and has served as the hub of current public information and resources. The website features information on basic
GSOB identification, biology, impacts, threats, and distribution maps; news on pre and post infestation management strategies; firewood concerns; frequently asked questions and answers, training opportunities and links to downloadable print materials, webinar recordings, videos, and other resources. During the first 2 years in operation, there were more than 400,000 unique ‘hits’ on the site. Also incorporated are dedicated social media channels (Facebook, You Tube and Flickr) and a GSOB blog, all linked through the website.

Figure 5—Goldspotted oak borer website, www.gsob.org.

Providing stakeholders and the public a web-based means to stay informed, engaged with GSOB issues and encouraged to take action was an important consideration. Several different online survey tools have been developed for the site. The “Report GSOB Symptoms” survey provided the public a means to report suspected GSOB infestation that would create a follow up inspection by one of several members of the collaborative group. Other surveys developed allowed users to volunteer for the EWS citizen scientist oak monitoring and detection program, register for upcoming events, and subscribe to a group email list for current news and information on GSOB. The survey tools provide user-friendly public interaction while yielding the collaborative group valuable information for research, management, monitoring, and determining the effectiveness of communications efforts.

Outreach publications

The development and distribution of print materials have been important components for GSOB education and outreach. As new research data, clientele information and resource needs were realized, we have worked in collaboration with our GSOB education partners to develop and produce informational publications and GSOB awareness products. Key projects include program logo and branding, outreach packets, two types of GSOB identification cards, community and vendor firewood advisory flyers, the Community Preparedness Planning Guidelines brochure, an expanded GSOB pamphlet, updated versions of the GSOB tri-fold brochure, public service announcements, firewood best management practices pamphlet, tabletop outreach displays, a variety of GSOB awareness promotion items and the coordination of Spanish language adaptations. Print materials have been distributed at outreach events and via cooperators. Although more than 50,000 pieces have been
professionally printed, digital file versions of most print materials are featured on the website allowing for on-demand printing and extended distribution. We also assisted our cooperators by distributing printed materials they had developed and produced related to GSOB, oak woodland management and the danger posed by firewood.

**GSOB identification kits and tabletop displays**

Over 300 GSOB identification kit have been produced and distributed to agencies and individuals for use to educate agency personnel, the tree-care industry and citizen scientists about GSOB. The kits include a CD with publications, posters, a preserved GSOB adult and a piece of bark with GSOB exit holes.

Two professional-grade tabletop displays were produced for use at various venues to help communicate the GSOB threat using large pictures and posters (fig. 2). Members of the GSOB outreach group are allowed to check out a display for use at various events. Along with the displays, samples of GSOB-infested bark and tree trunk cross-sections showing GSOB larval feeding damage to the tree’s cambium also drew the interest of attendees, allowing them hands-on examination.

![Figure 6—Complete tabletop displays are available for outreach events.](image)

**Training and outreach**

During the 2-year initial program development period, clientele understanding of GSOB and related oak woodland management was primarily facilitated through a series of training events including nine in-depth day long workshops, webinars, field trainings and numerous presentations to local community groups. All activities were cooperatively organized and delivered with agency, University, local Native American tribes and community partners. Participant evaluations were solicited from participants at the conclusion of many of these events and responses were overwhelmingly positive.

**Traditional mail outreach**

A mass mailing of information packets were sent to approximately 3,000 property owners in or near GSOB infested areas in San Diego County. With the cooperation from officials in Riverside County, about 5,200 property owners in the mountain
community of Idyllwild received an informational letter warning about GSOB several months prior to its discovery there in 2012. Approximately 120 firewood dealers in southern California were sent an informational letter in late 2010 warning them about the dangers of GSOB in firewood. Additionally, over 100 GSOB information and outreach resource packages were mailed to southern California offices of County Agriculture Commissioners, local county UC Cooperative Extension, Natural Resource Conservation Service, water districts, landscape and tree care professional associations, tourist visitor centers, regional preserves, county parks and Tribal associations.

**Workshops**

Workshops were held throughout southern California: seven during year 1 and two the 2nd year. Information was delivered to resource managers, industry professionals, landowners and other stakeholders through multi-agency presentations, hands-on displays, outreach materials, and, at some venues, short field trips. Presenters for the day-long workshops are coordinated from a cadre of specialists and scientists, who have research and work experience with goldspotted oak borer and related oak woodland issues. The presentations covered topics including: cause and extent of oak mortality; current range of infestation and at-risk areas; identification and assessment; integrated pest management; infested wood utilization and disposal; firewood management; and oak woodland restoration and resiliency. Through evaluation surveys conducted at the end of each workshop, 86 percent participating responded they were ‘very likely’ to share the information with others, potentially reaching more than 23,000 additional people. Six-month post-workshop survey respondents indicated that 98 percent had taken some action to help manage GSOB ranging from sharing the information with others, becoming an oak monitoring volunteer, organizing another GSOB event to changing their firewood movement behavior or subscribing to the GSOB listerserv. Survey results also provided us a clearer understanding of topic interests and information needs, which help future GSOB outreach programming be relevant and timely.

**Webinars**

In addition to workshops, two live webinars were hosted with the recordings of those webinars made available on the website for on-demand viewing. One webinar presented information on the threat of GSOB and the other involved restoration after GSOB attack. Both webinar events featured multiple presenters, active links to resources, interactive question and answer segments and evaluation surveys.

**Agency training and meetings**

There has been a GSOB educational component at most agency meetings we have participated in where GSOB is a key agenda item. In addition to meetings, we have also conducted GSOB-specific training for a number of individual agencies or in joint sessions of several agencies. Audiences have included various local, federal, state and tribal agencies. These events have occurred from San Diego County to as far north as San Luis Obispo County. Certain interagency meetings like the Forest Area Safety Task Force and the GSOB Task Force meetings incorporate a GSOB education component as an important part of organizing for action where the participants are updated on the latest GSOB management and education and outreach.
Local community outreach

Local community outreach events provided a forum for in-person, two-way communication and learning with over 600 professionals and stakeholders. Venues included town hall meetings, homeowner association meetings, focused community events (for example Earth Day), civic clubs, advisory committees, volunteer associations, and other formal and informal community groups.

Field training

Hands-on field training has proven to be one of the most popular and effective methods for teaching agency personnel, industry professionals and private citizens how to identify GSOB attack and give them an appreciation of how devastating a GSOB infestation can be in oak woodlands. William Heise County Park in Julian, San Diego County was a good venue for holding some of these field training sessions because it had all three susceptible species of oak trees within the 398.6 ha (985 ac) oak woodland park. Unfortunately, the park has had to remove over 2,000 large diameter oaks killed by GSOB due to the safety hazard they posed to visitors. Attendees were taught to recognize signs such as GSOB exit holes, thinning crowns, bark staining and woodpecker foraging for GSOB larvae (fig. 3). They also witnessed, first-hand, the challenges the park encountered to manage the wood and slash resulting from the removal of more than 2,000 large oak trees.

Youth education

We worked cooperatively with the Cuyamaca Outdoor School to develop a curriculum and a field exercise that taught students about GSOB and other invasive pests. This program has given students the opportunity to learn about and conduct field surveys of oaks looking for signs of GSOB attack and other tree health problems (fig. 4). Students collected tree information and mapped healthy and
GSOB-infested trees. Nearly 12,000 6th graders from San Diego County go through this program every year. Because Cuyamaca Outdoor School is located near the epicenter of GSOB mortality in San Diego County, messages about the danger of moving infested firewood and the impact of GSOB are visible and well instilled.

Conclusions

To date, there has been no evidence of long-range dispersal of GSOB after the first year of our program. Though GSOB was discovered in two adjacent counties, evidence indicates that the initial Riverside and Orange County infestations date back to 2010 or earlier. While we do not believe we have stopped the movement of all GSOB-infested wood, we are confident that we have dramatically reduced the naïve purchase of GSOB-infested firewood within the communities targeted in outreach.

The GSOB public education and outreach program utilized a combination of traditional, digital, and social communication channels. The collaboration of many diverse partners provided synergy and promoted creativity and a sense of ownership. The use of internal GSOB collaborative communications and file sharing group aided collaboration. The program has been flexible enough to grow as new research information, resources and agency and volunteer participants have joined the effort. Resources were strategically developed as a team and designed to increase outreach effectiveness, encourage adoption, promote program sustainability, and facilitate future program development. This program framework is readily adaptable for new invasive pests such as the polyphagous shot hole borer.

The GSOB website is a robust, cost-effective and sustainable means to deliver and receive GSOB information with a wide range of audiences. Online training resources such as recorded webinars and GSOB attack identification aids contribute to the viability of the program. The online reporting tools, event calendars, links and GSOB expert contact information continue to be one of the primary ways to keep stakeholders engaged and raise awareness amongst new clientele.

The program has received positive feedback about its content, format and quality from a variety of users, including private citizens, tree service professionals, agency personnel and peers working on similar invasive pest issues. Constructive comments have resulted in program modifications and content production. We have successfully
contacted all the large landowners in San Diego County and educated concerned residents in all the communities with susceptible oak woodlands. We know that we have changed the behavior of many arborists, foresters and firewood producers/consumers. The program has provided property owners, businesses, agencies, and elected officials with the latest information on GSOB identification, management and prevention measures as well as outreach resources (fig. 5). It has also brought together diverse interest groups to work for the common purpose of preventing the spread of GSOB and reducing its impact in infested areas. These education and outreach efforts should continue as long as there is a need and support for them.

Figure 9—More than 5,100 stakeholders were contacted through a variety of outreach activities.

References


Evaluating Rapid Response to a Goldspotted Oak Borer Diaspora

Tom Scott and Kevin Turner

Abstract

In 2012, the goldspotted oak borer (Agrilus auroguttatus, GSOB) was discovered in the mountain community of Idyllwild, 56.3 km north of its known area of infestation. This was the third time that a point of outbreak was discovered >32.2 km from the GSOB infestation area, suggesting that human transport of GSOB has substantially expanded the halo of California communities at imminent risk of GSOB-associated oak mortality. Even though this pattern of dispersal puts more communities at risk, the isolated nature of these new points of infestation offer some hope that their damage could be reduced or controlled by a rapid, initial response. Idyllwild suffered a major die-off of conifers in 2003, pre-adapting the community with an organizational structure, a tree removal/disposal infrastructure, and even some funding that was needed for a GSOB rapid response. Federal, state, and local agencies turned these attributes into a GSOB rapid response plan which also included components of detection, management, and education. As of 2014, our ad hoc response group had mapped the extent of oaks in decline in the region around Idyllwild, contacted all landowners and community residents through mailings and public meetings, conducted three training workshops, and surveyed approximately 154 properties. A total of 53 infested oaks have been found at 20 locations in Idyllwild and the adjacent community of Pine Cove, with the majority removed within a month of their discovery. Cross-sections from dead oaks indicate that infestations began in 2009, and that infested oak firewood may have been delivered to multiple locations generating simultaneous outbreaks. Although detections of GSOB-infested oak increased each year, we believe this represents an increased rate of discovery rather than an increased rate of infestation.

Key words: community outreach, goldspotted oak borer, rapid response

Background

The goldspotted oak borer (Agrilus auroguttatus, GSOB) was first detected in California in 2004 (Westcott 2005); by the time it was linked to oak mortality in 2008 (Coleman and Seybold 2008a, 2008b), it had already spread over a 150 km² (60 mi²) area of San Diego County. Its distribution has remained patchy, suggesting multiple, often disjunct, points of infestation rather than generalized spread along the margin of the infestation area (Scott and others, Mapping spread of the goldspotted oak borer (Agrilus auroguttatus), these proceedings). The most notable of these disjunct outbreaks occurred in 2008 in Marion Bear Park, and in 2010 in the town of Ramona, 45 km and 30 km west respectively, of the known infestation areas. The life history of GSOB is ideally suited for transport in firewood, and this human-assisted movement appears to be the most likely reason for these diasporas, and the patchy nature of its distribution in general (Flint and others 2013).

1 An abbreviated version of this paper was presented at the Seventh Symposium on Oak Woodlands: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.

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Idyllwild is a mountain resort community of approximately 6000 properties in the San Jacinto Mountains of southern California, surrounded by the San Bernardino National Forest. The landscape of the community is a combination of mixed conifer with areas of shrub understory, dominated by Jeffrey, ponderosa and coulter pines (Pinus jeffreyi, P. ponderosa, and P. coulteri) in a broad valley between large granite plutons. Idyllwild and the adjacent community of Pine Cove are dominated by residential housing with some organizational camps and schools, and a commercial district of shops, restaurants, and inns. The median priced home in 2014 was $275,000 ($208/ft²) with about 5 percent of properties at >1 million dollars. These structures are built into a second-growth mixed-conifer forest with approximately 60 percent of the homes belonging to absentee owners for use as resort cabins.

Nearly every home and many of the businesses heat partially or completely with firewood. Campgrounds and organizational camps in and around the community all allow campers to bring in firewood for use in fire rings. Firewood is an important commodity to the community but it is not regulated in any way.

The two GSOb-susceptible species, California black oak (Quercus kelloggii) and canyon live oak (Q. chrysolepis), typically contribute from 20 to 100 percent of the forest canopy on each property, in many cases forming dominant components of yards and landscaping.

Both Idyllwild and Pine Cove are unincorporated and therefore under the jurisdiction of the County of Riverside for infrastructure, planning, codes, permits and taxation. They are within State Responsibility Area (SRA) for fire protection provided by the California Department of Forestry and Fire Protection (CAL FIRE) who share concurrent jurisdiction with Riverside County Fire Department. These two agencies collaborate on fuels and forest management projects that benefit all mountain communities, including Idyllwild which has its own fire protection district. Both communities are surrounded by San Bernardino National Forest on three sides and Mount San Jacinto State Park on the other. Having multiple local service districts, an active Fire Safe Council, the U.S. Department of Agriculture, Forest Service (USDA FS) San Jacinto Ranger District office, and a joint CAL FIRE/County Fire field office within its boundaries gives the community a fairly high level of self-governance. Other county and state agencies also have offices or staff in or near Idyllwild.

The San Jacinto Mountains form the north end of the Peninsular Ranges; although there are large areas of contiguous forests along this string of mountains, oaks in Idyllwild are separated from oak stands in San Diego County by approximately 47 km (20 miles) of relatively low elevation mountains in the rain-shadow of the Palomar Mountains. Idyllwild is approximately 60 km north of the northernmost GSOb infestation area in San Diego, with over half of this distance nearly devoid of susceptible oaks.

In 2002, massive numbers of conifers began to die in the San Jacintos as a result of a drought-induced bark beetle outbreak which greatly increased the...
community’s risk to a catastrophic fire. In response, all local, state and federal agencies along with the Mountain Communities Fire Safe Council (MCFSC) and Southern California Edison (SCE) joined together to form the Riverside County Mountain Area Safety Taskforce (MAST). The MAST proceeded to develop an Incident Action Plan (IAP) for reducing the threat through coordinated fuels reduction projects and community emergency preparedness. Large amounts of federal funding became available for removing dead and dying trees both inside and outside the community and a robust infrastructure for removing and disposing of dead trees was developed which included a community tub grinding site.

Prior to the 2012 GSOb discovery, Idyllwild had been part of a regional outreach effort by University of California Cooperative Extension (UCCE), CAL FIRE, and the USDA FS to prevent the importation of GSOb-infested firewood by second-home owners and visitors from San Diego. This initiated a community-based GSOb awareness program spearheaded by Marshall Smith, reporter for the Idyllwild Town Crier newspaper. A 2010 town hall meeting with County Supervisor Jeff Stone provided UC personnel a chance to brief him and interested members of the community about the GSOb threat (Smith 2010). About the same time, a GSOb presentation was given to all the members of MAST.

On the heels of the first town hall meeting, several County of Riverside departments, including the Agricultural Commissioner, County Counsel, and Code Enforcement, were tasked by County Supervisor Stone with determining options to prevent the importation of infested firewood from San Diego County. The County mailed a letter to every property owner in the community warning them about GSOb and the threat posed by importing infested firewood. Public concern became so great that some members of the community began scrutinizing firewood being sold from the backs of trucks in the town square and questioning the seller about the wood’s origin. The Idyllwild Garden Club posted roadside signs warning residents not to purchase non-local oak firewood.

A decade before GSOb was found in Idyllwild, the emerald ash borer (*Agrilus planipennis*) prompted the development of a number of management techniques and rapid response efforts when it began killing record numbers of ash trees in the eastern United States. Research on this closely-related species provided information on pesticides and control methods that could be adapted to GSOb. The identification of GSOb in San Diego County predated its discovery in Riverside County by 4 years, during which time detection, management and education/outreach efforts were begun. Outreach included meeting with to Riverside and other counties adjoining to San Diego to encourage them to be prepared for GSOb. Fortunately, the Riverside County Supervisor representing the Idyllwild area took the warning to heart and directed the County Agricultural Commissioner’s office and other county agencies to be prepared to apply these techniques in case GSOb reached the county.
The initial detection and response to GSOB in Idyllwild

In October of 2012, CAL FIRE Forester Kathleen Edwards found GSOB in a California black oak along the major state highway through Idyllwild. This oak had died earlier that fall and was initially recognized by its failure to drop dead leaves. The find was confirmed by CAL FIRE Pest Management Specialist Kim Corella and genetically linked to the San Diego County GSBO population (T. Coleman and R. Stouthammer, personal communication). The black oak had a relatively high rate (see Haavik and others 2012, Jones and others 2013) of GSBO infestation; triggering the ad hoc development of a rapid response program for detection and management of GSBO.

Members of the ad hoc committee had developed the response to the massive conifer die-off in 2003, which facilitated the coordinated multi-agency response following the initial discovery of GSBO. The group had previously developed working relationships, which allowed them to immediately focus on actions rather than defining agency roles and responsibilities. Although there was no source of funding for outreach efforts for GSBO, many components of the previous program were still in place and could be adapted to GSBO. A key component was the linkage that had been created between management agencies and landowners, including an organizational structure (MAST) to identify and remove dead and dying trees.

With the aid of UC personnel, the Riverside County MAST immediately formulated and implemented an IAP for managing GSBO. The IAP identified objectives, outlined the organizational structure and assigned operational tasks to be performed. Operational tasks included outreach/education, survey/detection, managing infested oaks, disposal plan, and exploring additional IPM options. There were eight components of this plan:

1. Community outreach: extension of basic information on GSBO, its impact on oaks, and its transport in firewood to public at large in Idyllwild and Pine Cove.
2. Community-wide GSBO detection: established a GSBO “Hotline” for Idyllwild and Pine Cove residents to report suspicious oak deaths or declines and get answers to questions.
3. Training for resource managers and professionals: training local foresters, resource professionals, arborists, to recognize and report GSBO infested oaks.
4. Surveys and detection of GSBO damage: develop the capacity of MAST to survey the extent and severity of GSBO damage by incorporating information from trained professionals.
5. Landowner education and action: (a) develop the capacity of MAST agency personnel and volunteer to inform owners of GSBO infested oaks about their management options, and (b) management options to protect uninfested oaks.
6. Management protocols for infested oaks: develop and initiate management protocols for GSBO infested oaks including timely removal and disposal.
(7) Funding: find resources for the removal and disposal of dead and dying oaks.

(8) Preventing transport of GSOB infested wood: develop policies and procedures to prevent importation of additional GSOB-infested wood into the community or export of infested wood to other locations outside the community.

Community outreach

The discovery of GSOB was announced in the local newspaper, providing an outlet for general information and to solicit property owners to report suspect trees. This was followed by a press release from the CAL FIRE regional office to emphasize the significance of this new discovery to the rest of the state. Prompted by the Riverside County Agricultural Commissioner’s office, Supervisor Jeff Stone paid for the mailing of an informational letter to the 5,200 property owners within 2 months of the discovery. The letter was jointly drafted by UCCE, CAL FIRE and the Agricultural Commissioner’s office and mailed under the signature of the County Fire Chief. The letter included a GSOB hotline number, the GSOB website URL and a reporting site for GSOB observations. This represented the first formal action taken by the ad hoc committee. Immediately following the letter, the ad hoc group hosted a town hall meeting in January 2013 to brief the public and answer their questions. The Town Crier continued to run articles to maintain resident’s exposure to GSOB. Members of the ad hoc committee participated in events like Earth Day, distributed information at the local post office and other government offices in Idyllwild and gave GSOB presentations to civic groups and clubs. To educate campers about the dangers of transporting GSOB in firewood, campgrounds in and around Idyllwild were provided with GSOB “Buy It Where You Burn It” posters to display in their campgrounds. The Idyllwild Garden Club paid for and installed roadside signs warning the community about the potential dangers of oak firewood at various points in and around the community.

Outcomes and Observations

The 5,200 private property owners in Idyllwild can be grouped into two target audiences: full-time residents (30 percent) and absentee owners (70 percent). Two methods of outreach were able to reach both groups: mailings and the local newspaper.

The Town Crier, with a circulation of approximately 2,800, has a percentage of out of town subscribers that roughly matches the percentage of absentee owners. This local newspaper was instrumental in getting the public’s attention and boosting attendance at the town hall meeting. The official press release announcing the discovery of GSOB generated both regional and statewide news coverage. The mailing was the only sure way of contacting all of the property owners, but we were unable to document how many owners read or responded to it. Nevertheless, the public meeting was
attended by 130 persons, about twice the normal turnout for a town hall meeting. The benefit of these public outreach activities is that they contacted a fairly large audience and, in the process, solidified the general policy goals of the ad hoc committee.

Despite the concerted effort of the large number of professionals and press, certain members of the community still complained that they had not been contacted about GSOB. Anecdotal evidence contradicts this sentiment; volunteers from the fire safe council indicate that the majority of persons they have contacted have claimed to have already heard about the problem of GSOb, though some have apparently been exposed to inaccurate rumors about GSOb management in this tight knit mountain community. The issue may not be a failure to contact all the public about GSOb, but rather ensuring that all get complete and accurate information about GSOb and its management. Knowledgeable volunteers imbedded in the community have been invaluable in correcting inaccuracies that were created by fear and ignorance.

Public outreach for GSOb has triggered enlightened self-interest to change behaviors regarding firewood, but follow-up is needed to ensure that they have adequate information to make good management decisions about trees on their property.

An inherent problem in rapid response ad hoc actions is that less effort is devoted to measuring effectiveness. While it is critically important to contact the public at large, it was difficult to commit the resources to measure the impact of mass media and general mailings on public response to GSOb.

**Community-wide GSOb detection**

One of the first tasks of the ad hoc group was to determine the extent of the outbreak. The entire Idyllwild community was enlisted to help survey for GSOb by providing them with reporting pathways identified in outreach materials. These included the existing GSOb reporting system at the GSOb.org website and the creation of a dedicated GSOb phone “hotline” specifically for Idyllwild. Property owners were encouraged to use these pathways to report suspect trees or to request tree inspections on their property; the interaction on the hotline also provided an opportunity to answer their questions about GSOb management including the infested-tree removal assistance program. The “landowner letter” also encouraged all property owners to closely examine their oak firewood piles and report wood exhibiting possible signs of GSOb attack. Occasional GSOb articles in the Town Crier combined with some paid ads by the Fire Safe Council urged continued public vigilance and participation in GSOb and infested-firewood detection efforts.

**Outcomes and observations**

The GSOb Hotline and GSOb.org website have generated approximately 150 reports of suspected GSOb infestations. Although this number represents only
3 percent of all the properties in Idyllwild, it may reflect the limited extent of GSOB damage, which has been found on <1 percent of the properties. The GSOB volunteers reported that their site visits typically generated requests from adjacent property owners who asked what they were doing and then also wanted their trees checked. Property owners who had their trees inspected tended to share what they learned about GSOB with their neighbors. One absentee owner from San Diego responded to the public inquiries about firewood and related that he had purchased firewood from San Diego and brought it up to Idyllwild about a year earlier; his wood pile was examined and revealed a few GSOB exit holes and galleries in a few pieces of wood still in the pile. A small group of informed activists took it upon themselves to examine wood sold by street-side firewood sellers and providing the vendors with GSOB brochures.

**Training for resource managers and professionals**

Idyllwild has a disproportionately large number of agency personnel, professional arborists, and passionate volunteers that were eager to be trained to recognize and report GSOB infested oaks. Soon after the initial Idyllwild discovery, UCCE staff partnered with USDA FS Forest Health Protection to conduct training for key personnel from public agencies and Southern California Edison where they taught them how to identify GSOB attack and GSOB management. In addition to the classroom training held in Idyllwild, a subsequent group field trip to San Diego County was organized to visit the heavily-infested and severely impacted areas of San Diego County.

**Outcomes and observations**

The trainees have been responsible for detecting most of the infested trees identified in Idyllwild, many of which were observed during the person’s normal course of regular duties. The field trip to San Diego significantly increased participants’ competence and confidence in identifying GSOB, and let them find and identify GSOB infested oaks at a time when most of Idyllwild fieldwork yielded only negative surveys results. This reinforcement proved to be remarkably important; it not only helped their surveying skills, it rekindled their commitment to keep Idyllwild from suffering the same levels of devastation. Employees from CALTRANS, the county road department and SCE have identified infested trees within their respective rights of way and coordinated subsequent tree removal and disposal. The ultimate value of this training was that the incidental observations of the participants became the primary way of finding GSOB-infested trees.
Survey and detection

The first step in detection was to map susceptible and possibly impacted oak woodlands. UCCE staff used false-infrared bands from the 2012 NAIP imagery of Riverside County overlaid onto parcel maps to map California black oak location and canopy condition to help determine priority areas for survey. All the streets with declining canopies were surveyed by vehicle by UCCE staff within the first 2 months following the initial discovery. USDA FS Forest Health Protection checked for infested trees in the vicinity of newly discovered GSOB trees. At the same time, USDA FS San Jacinto Ranger District personnel began to survey National Forest land near the community interface. SCE arborists, CALTRANS and the Riverside County road department (TLMA) began reporting suspicious trees on their respective rights-of-way. Both state and county park staff surveyed their respective lands in and near the community.

With nearly 5,200 private properties to survey, most of which require property owner permission to make access, surveying all the oaks within the community was a daunting task. Fortunately, the MCFSC and their “Woodies” volunteer group, along with members of the Idyllwild Garden Club offered to help with the task. After receiving GSOB survey training, the volunteers were given maps showing them high-priority survey areas they had been assigned. CAL FIRE and UC personnel co-developed survey protocols and reporting procedures for the volunteers and provided expert confirmation when the volunteers identified a new infested tree. The results of all surveys are tracked in a shared GIS database. Incorporated as part of the inspection, the volunteers provide the property owners or tenants with information and outreach materials.

Outcomes and observations

The map generated from the aerial imagery proved to be relatively inefficient in locating GSOB outbreak areas because it failed to identify the widely-scattered, individual infested trees. At the same time, mapping accurately identified declining oaks, but could not discriminate GSOB-infested oaks from the large number of oaks declining from drought (2012). As a result, surveys based on these maps were also relatively inefficient. Although this technique did not allow close access to check for exit holes, it further refined the set of suspect oaks and did yield approximately five GSOB-infested oaks. The majority of detections resulted from incidental observations made by professionals during the course of their normal duties. Inexperienced volunteers conducting surveys in uninfested areas tend to lose motivation very quickly and drop out of the program. Providing volunteers with frequent feedback, appreciation and direction motivates them to continue. Working within a local organizational structure (like the fire safe council) has made the volunteers feel more effective and appreciated. Coordination and
communication between professionals and volunteers greatly has improved the efficiency and effectiveness of surveys. Approximately 1/3 of all GSOB trees that have been identified and removed have been within SCE, CALTRANS or Riverside County TLMA (the county road department) rights of way; it was very important to include these groups in the survey and detection program as well as teach them about GSOB management.

**Landowner education**

Landowners invariably ask what management is recommended if GSOB is found on their property or in nearby neighborhood trees. In addition to providing them the UC-IPM Guide (Flint and others 2013) and directing them to the gsob.org website, they receive a verbal explanation about management options for infested trees as well as protecting uninfested trees from attack.

By fortuitous chance, members of the ad hoc GSOB management group came into contact with volunteers from the local fire safe council (the Woodies) shortly after the initial discovery of GSOB. The Woodies happened to be conducting chainsaw training across the highway as the first GSOB tree was being removed; they took great interest in the proceedings and offered their help. Their mission had been to help landowners mitigate tree and fire hazards across the community, however they immediately grasped the potential threat GSOB posed to the community and were captured as full participating partners in the rapid response to GSOB. This new partner gave the ad hoc committee greater credibility with the community and dramatically increased access to landowners. In the course of conducting parcel surveys of oaks, these volunteers are able provide landowners with information and educational materials on GSOB. The volunteers have been cautioned not to make specific management recommendations but rather to direct the landowner to the appropriate agency or tree care professional for more detailed information.

Landowners were provided the UC IPM Guide and directed to other literature to find out more information about the use of pesticides as preventative treatments against attack by GSOB to protect high-value oaks on their property. They were also advised that the Riverside County Agricultural Commissioner maintains a list of properly licensed pest control businesses on the gsob.org website. Certain pesticide operators have attended one of the GSOB workshops or participated in a 2013 pesticide operator training meeting conducted by the Riverside Agricultural Commissioner in partnership with UCCE, USDA FS and CAL FIRE. One local pesticide company conducted carbaryl applications on oaks at no charge to the property owners in 2014 with the expectation of a clientele for that service in upcoming years. Property owners are cautioned to check on claims made by pesticide operators about the efficacy of treatments that are proposed, especially in light of the need for proper timing of applications.
Outcomes and observations
The parcel inspections conducted by the volunteer surveyors provided an excellent opportunity to educate the property owner about GSOB. The existence of the Woodies as an organized and recognized group within the community greatly facilitated the organization and management of a volunteer surveyor force. It was difficult to always provide landowners with definitive answers. For instance, there was strong confidence in making recommendations to remove and chip infested trees to kill larvae in those trees, but we lacked data as to its actual effectiveness in preventing or reducing GSOB infestation in surrounding trees. Similarly, until definitive field results about the efficacy of preventative pesticide applications become available, discussions with landowners about pesticide options require us to disclose the limits about our current state of knowledge. This lack of definitive information on pesticide effectiveness has likely contributed to the fact that not many landowners have opted for preventive pesticide treatments yet.

Management protocols for infested oaks
Grinding GSOB-infested woody material with a 3 inch-minus (7.6 cm or less) screen was known to be an effective treatment for preventing the emergence of adults (Jones and others 2013). The last phase of Riverside County Fire’s grant-funded bark beetle tree removal program and the associated community tub grinding site were both still in operation in 2012 when GSOB was discovered. MAST working with UCCE and USDA FS experts, quickly developed protocols for the prompt removal and proper disposal of GSOB-infested oaks. Permission was granted to utilize the existing tree removal program and funds to pay for the removal and disposal of GSOB-infested trees. The community had a built-in advantage in that it had an operating grinding site. The protocols MAST developed called for rapid removal (within 2 weeks) of a GSOB tree that was identified during the GSOB flight season (April through September) and that the tree be hauled to the community grinder where it was to sit no longer than 48 hours before being ground to a 3 inch-minus standard. For infested trees found on public lands, such as state and county road rights of way, they were cut and hauled using a combination of public agency resources. For infested trees discovered on private property, the property owner had to voluntarily agree to the tree removal; in return they were not charged with any of the removal or disposal costs. For infested trees discovered near their power lines, SCE used their own resources to cut and dispose of trees following the protocols.

Removing large oak trees generated a lot of biomass in foliage, branches and trunks. Larger limbs and tree trunks from infested trees required special handling to prevent GSOB spread. Smaller-sized material from the tree was not a threat to spread GSOB, but could increase the fire hazard in this very fire-prone area; just cutting down a tree and leaving it as-is on site is generally not an option. There is an inherent cost for proper disposal. Developing biomass processing options which will facilitate utilization of the material will
help to offset the cost of removal and processing while also reducing the impact on the solid waste stream.

In a mountain community like Idyllwild, oak firewood represents the greatest value of any products that can be produced from GSOB-infested oaks. However, the costs for debarking the wood, or putting it in a containment structure for 2 years seasoning, greatly erodes its net value. The labor, handling and other costs associated with those two methods to make the wood “safe” for sale or transport are currently a significant disincentive for most in the firewood business.

Wood ground to a 7.6 cm or less standard or better can be used for fueling a biomass power plant or used in soil amendment products. The costs of processing, handling and shipping chipped oak wood from the Idyllwild grinding site still exceed revenue generated from the purchase of the chips. Therefore, the grinding operation is subsidized by tipping fees paid at the grinding site.

Finally, owners were given information about systemic and barrier spray pesticides (UC IPM 2013) as a means to prevent possible emergence of adults from GSOB-infested oaks that were not removed after discovery. This technique had proven highly effective in stopping adult emergence in experiments on saw logs (Scott and Turner, unpublished data), and the usage was covered under EPA pesticide labeling. The ad hoc committee and the Riverside County Agricultural Commissioner’s Office provided GSOB training for pesticide applicators, but the costs of these treatments were not supported by grants or other funds.

The MAST agencies in partnership with the tree care industry, with UCCE and the County Agricultural Commissioner’s seek to develop additional IPM options and prescriptions for managing GSOB in this forest community. In addition to providing individual landowners and land managers a matrix of options for GSOB prevention and control, a community-wide plan will be developed; without the cooperation of neighboring property owners, control efforts may be in vain. Mt. San Jacinto State Park has offered to host a GSOB IPM demonstration project for the purpose of educating the community.

**Outcomes and observations**

The Idyllwild community had a distinct advantage in that it had an existing infrastructure, funding and sufficient corporate knowledge about GSOB management to allow them to rapidly develop and implement effective GSOB management protocols. The community readily accepted the new program because it had been forewarned about the threat of GSOB starting in 2010 and was also very familiar with the existing tree removal program. The Idyllwild community grinding site had to unexpectedly close during the peak of the 2014 GSOB flight season because the owner left town on a firefighting contract; fortunately, an alternative grinding site was available but was 40 miles and a 2.5 hour round trip distant.

Nevertheless, the desire to retain the firewood from GSOB infested oaks has proven to be a stumbling block for the citizen reporting program. The
default model was to allow owners to keep only the trunks and branches less than 15.2 cm (6 inches) in diameter, taking most of the firewood away. Small limbs and branches were chipped and scattered on site in most cases. A number of property owners were more concerned about losing the potential source of oak firewood than they were about the infested tree causing the spread of GSOB to their other trees or around the neighborhood. Some community members failed to report suspected oak tree on their property out of fear that they would lose the firewood. This prompted agencies to look for ways to remove infested bark while leaving the GSOB-free wood to property owners. Sawyers tried to remove bark by cutting it away as planks with chainsaws or by using a chainsaw-powered debarker. Both of techniques yielded more wood for property owners, and reduced the hauling costs and tipping fees associated with tub grinding. Unfortunately, the labor costs of debarking still exceed the cost of grinding the whole tree, even when the value of the firewood is taken into consideration. The MAST continues investigating methods of separating GSOB-infested bark from the bulk of the wood to give homeowners an option of paying for debarking infested trees at the home site so they can keep the firewood. Some debarking methods leave intact bark which must be disposed of properly in a timely manner. The details on how to ensure that will happen still have to be worked out.

Several property owners with lightly-infested (but still living trees) refused to participate in the infested tree removal program and those trees were neither cut nor removed. There was a persistent thought among some owners that their trees might recover; they could not be swayed with evidence that contradicted this view. Some owners considered the protection of their uninfested oaks more important than the preservation of an infested tree. However the emotion and inertia associated with leaving a GSOB-infested tree also overwhelmed this consideration. That said, relatively few homeowners have opted for treating their trees with pesticides.

**Funding**

The rapid response to GSOB in Idyllwild has been facilitated by residual funding left over from a State Fire Assistance grant awarded to Riverside County Fire Department. However, these funds have now all been expended. County Fire has subsequently applied for more dollars through the California Greenhouse Gas Reduction Fund in order to maintain the program of assisting private property owners with the disposal of their GSOB-infested oaks. CALTRANS, Riverside County TLMA, and SCE have used their own resources to remove infested trees within their rights of way. The three major land management agencies in the community, San Bernardino National Forest, Mt. San Jacinto State Park and Riverside County Parks Departments, would have to identify funds or other resources in order to remove infested trees on their respective lands if that ever occurs. CAL FIRE does have hand crew resources (conservation camps) that can perform tree felling, bucking, de-limbing, and chipping work on public lands and even private lands as a
result of the California Board of Forestry and Fire Protection’s declaration of a GSOB Zone Of Infestation covering the infested area.

Outcomes and observations
Without a reliable source of funding for direct control activities like removing and grinding of infested trees, it will be difficult for any community to mount a consistent, aggressive rapid response. There are also costs associated with producing and distributing outreach materials. The personnel costs of time spent on conducting surveys, education and outreach activities, control and prevention activities also need to be factored. Collaboration by all interested stakeholders was the key to past success in Idyllwild and may lead to better chances of obtaining funding.

Preventing transport of GSOB infested wood
Aggressive control actions to contain and possibly eradicate a small and isolated GSOB population could be thwarted if additional infested material is imported into the community. Therefore, efforts continue to educate the firewood sellers and their consumers about the danger of buying infested firewood. The County of Riverside does have a roadside vendor ordinance which can exert some control due to the need for a business license, but so far their efforts have had little impact on the sale of firewood from the backs of pickup trucks and stake sides. Due to the infestation, now all oak firewood originating from Idyllwild must be considered potentially infested by GSOB which poses a threat if it is moved within the community or outside to other areas. The MAST agencies are working on a strategy for this problem.

Outcomes and observations
Multiple agencies and a multitude of individual citizens will be potentially affected by policies and regulations that may be developed. It will be very important to get public buy-in and acceptance in order to be effective. An aggressive campaign to prevent additional infested wood from coming to the community would be greatly aided by regulations and enforcement of an imported wood ban. Regulatory control of firewood was explored by Riverside County even prior to the discovery of GSOB in Idyllwild, but determined to be infeasible. However, now that there is a new firewood-borne threat (polyphagous shot hole borer) that poses a threat not only to oaks but other native and agricultural species, there may be movement on the regulation front. Policies, protocols and perhaps even regulations will need to be developed in order to ensure that wood leaving the area has been inspected and deemed free of GSOB.
Evaluating the effectiveness of mounting a rapid response

The rapid response to GSOb in Idyllwild did not substantially deviate from most models of rapid response; it contained elements of preparedness, detection, and response (USDA APHIS PPQ 2015). The ultimate goal was to contain and control the GSOb infestation in Idyllwild. And like most rapid response plans, the ultimate success of these efforts may take years to achieve. However, neither residents nor agencies ever considered a no action alternative, because the initial outbreak was limited in size and severity and they had succeeded with a similar tree mortality problem in the past.

Our initial attempts to prepare the community seem to have come too late to prevent the importation of GSOb-infested firewood. Although preparedness efforts began with outreach meetings 2 years prior to the discovery of the GSOb infestation, the beetle probably arrived in Idyllwild a year prior to our efforts. Following the initial detection, we immediately contacted every property owner by mail, held workshops and public meetings to help everyone recognize the impact GSOb could have on Idyllwild.

In regards to detection, the initial detection of GSOb was not due to a systematic search but occurred as a result of an incidental observation of GSOb damage by trained agency personnel. It has proven difficult to motivate volunteers or find agency resources to survey for GSOb in communities until there is evidence that GSOb is present. Furthermore, we have found it difficult to detect a GSOb infestation until 1 or 2 years after the initial attack. After the initial detection, a more systematic detection program located 52 GSOb-infested oaks, but mostly after the trees displayed signs of decline. Systematic surveys that identified GSOb attacks (exit holes) without signs of canopy decline were rare. The exception occurred when we surveyed all of the trees adjacent to a heavily infested tree. We are reasonably certain that our detection system is locating most of the heavily infested trees, but it is difficult to use the absence of observation to prove the efficiency of our system.

The response included a direct control program, consisting of rapid removal and disposal of infested trees, which was implemented immediately after the discovery of the first infested tree. Direct control seemed reasonable and appropriate given the new, small and isolated nature of the infestation and was facilitated due to the existing infrastructure and funding. We had previously observed in San Diego County that heavily-infested trees could release large quantities of beetles. While this observation may be irrelevant in an area where trees are already under heavy GSOb attack, removing a heavily-infested tree at the onset of an outbreak may remove a substantial proportion of the adult GSOb population. In one infested California black oak discovered in Idyllwild, over 1,000 beetles emerged from a sample of 5.6 m² (60 ft²) of bark; extrapolated to the whole bark surface of the trunk and larger branches, this tree had the potential to produce nearly 8,000 adults. In turn, those adults could have produced over 100,000 eggs (Lopez 2013).
Our experience in Idyllwild suggests that given similar circumstances of a new GSOB outbreak, communities should consider mounting a comparable rapid response effort. Preparedness will be key to a timely rapid response.

References


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Oak Restoration and Genetics
**Quercus kelloggii** (Newb.) Sprout Response to Fire Severity in Northern California

Justin S. Crotteau, Martin W. Ritchie, J. Morgan Varner, and John-Pascal Berrill

**Abstract**
We counted seedlings and assessed crown characteristics and abundance of fire-induced stump sprout regeneration in California black oak (*Quercus kelloggii*) 11 to 12 years after wildfire. Regeneration was examined across three levels of burn severity (low, moderate, and high) according to the Composite Burn Index. Fire severity affected crown width of oak sprout clumps; clumps of a given width were taller in areas of high severity fire. Multi-stemmed, sprouting black oak genets were more common than black oak seedlings. The data illustrate a positive sprout clump density association with increasing fire severity. Black oak densities were 3.6, 21.7, and 66.0 genets ac⁻¹ in low, moderate, and high burn severity stands, respectively. Additionally, stand level crown area of the sprouted oak trees was strongly influenced by summed live and fire-killed mature black oak basal area (R² = 0.83) and density (R² = 0.73).

**Key words:** 2000 Storrie Fire, California black oak, CBI, Sierra Nevada Forest Plan Amendment

**Introduction**
Foresters and ecologists are increasingly appreciating the importance of the California black oak (*Quercus kelloggii*) component in montane ecosystems. Black oak provides significant cover, habitat, and forage that many high-profile avian and mammalian species and their prey require (Innes and others 2007, Zielinski and others 2004). In addition, mature black oak stems can have valuable timber; though historically underutilized, it has potential for developing as a commercial product (McDonald and Huber 1994). Furthermore, black oak promotes and thrives on frequent fire (Cocking and others 2012, Engber and Varner 2012, Odion and others 2010). High frequency fire regimes are characteristic of many black oak ecosystems, promoting black oak by preventing dominance of pervasive shade-tolerant conifer species. In California woodland and montane ecosystems, species such as white fir (*Abies concolor* var. *lowiana*) and Douglas-fir (*Pseudotsuga menziesii*) commonly encroach upon oak individuals and stands, and the threat of ecosystem type conversion increases given long, fire-free periods (Cocking and others 2012, Cocking and others 2014).

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1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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It is no surprise, therefore, that public land management policy has been evolving to facilitate black oak individual and community development. The Sierra Nevada Forest Plan Amendment (SNFPA; USDA 2004) mandates that hardwoods be included in stand examinations. The SNFPA additionally requires that managers clear openings around existing black oak to “stimulate natural regeneration” and even “promote hardwoods after stand-replacing [fire] events” (USDA 2004, “Hardwood Management,” p. 53). In response to fire, black oak’s disturbance-activated sprouting mechanism elicits rapid vegetative recovery (McDonald 1990), a competitive growth characteristic in fire-prone environments. Long term assessment of post-fire black oak sprout response on the landscape in a no-action scenario may serve as a platform from which to base future post-fire recovery.

We hypothesized that black oak sprouts vary in size and distribution because fire stimulates severity-dependent responses. We studied black oak sprout regeneration over a 2-year period, 11 to 12 years after the mixed-severity Storrie Fire that burned 21,044 ha (52,000 ac) in 2000. Our objectives were to (1) examine the effect of burn severity on black oak sprouting characteristics; and (2) assess black oak clump (genet) distribution across the burned landscape. We also compared abundance of black oak seedlings versus sprout regeneration. This note provides a snapshot of natural post-fire vegetation response and highlights the rapid recovery rate of an important oak species in California. Our findings provide useful insight for future post-fire recovery decision-making in montane ecosystems with a black oak presence.

**Methods**

Study sites were located in the 9371 ha (23,156 ac) Lassen National Forest (LNF) portion of the 2000 Storrie Fire, in the southern Cascades of northern California. The climate is a montane Mediterranean with a mean annual precipitation of 189.5 cm (74.6 inches), most of which falls as snow during the winter months. Site elevations were between 899 and 1798 m (2,950 and 5,900 ft). Typical forest cover types are Sierra Nevada Mixed Conifer and White fir (Eyre 1980). *Quercus kelloggii* was often found in stands co-dominated by *Abies concolor*, *Calocedrus decurrens*, *Pinus lambertiana*, *P. ponderosa*, and *Pseudotsuga menziesii*. The most commonly associated shrubs were *Arctostaphylos nevadensis*, *A. patula*, *Ceanothus cordulatus*, *C. integerrimus*, *C. velutinus*, *Chrysolepis sempervirens*, and *Q. vaccinifolia*.

We stratified the landscape into three fire severity classes (low, moderate, and high) by the Composite Burn Index (CBI; Key and Benson 2006), a burn severity metric derived from the one year post-fire Relative differenced Normalized Burn Ratio (RdNBR; Miller and others 2008). Since the RdNBR is most influenced by the effects of severity on the overstory, it follows that burn severity had an inverse relationship with residual live overstory density (of all species). Over the years 2011 and 2012, a cluster of evenly-spaced 40.47 m² (0.01 ac) circular plots was randomly located in each of 25 stands randomly selected from the Storrie Fire (Crotteau and others 2013). Overlaid point samples were used to determine fire-killed overstory characteristics on a
subset of the 482 plots. Black oak seedlings and root-collar sprouts were measured within each plot. Root-collar sprouts were determined by the presence of a fire-killed mature stem. Black oak seedlings (>15.24 cm (6 inches) tall) were tallied and total height was recorded. Four characteristics were recorded for oak sprouts located within plots: (1) total count of stems (ramets) emerging from the base of the clump root collar; (2) crown width of the entire clump (an average of two measurements made at right angles); and, for the tallest (dominant) stem, (3) total height, and (4) diameter at 1.37 m (4.5 ft) above ground (DBH).

To meet our first objective, we examined relationships between fire severity and characteristics of individual stems and sprout clumps. Measured covariates were transformed for normality using the square root function. We used ANOVA to determine if burn severity had an effect on black oak attributes. Since we measured a cluster of plots within each stand, we regarded the stand as a random effect. We examined pooled sprout clump crown allometry by regressing dominant stem height on crown width. To address our second objective, we assessed stand level black oak abundance and cover on the burned landscape. We used a stand-level ANOVA model to test the effect of burn severity on abundance data. Crown area was calculated and summed by stand to determine oak canopy cover on a per acre basis, as an indicator of the extent of black oak recovery on the post-fire landscape. We used linear regression to model the relationship between stand-level crown area and fire-killed overstory characteristics.

Results

We found 119 black oak clumps across all of the study’s plots. We then examined the density of sprouts per clump and the dimensions each clump. The number of stems per black oak clump sampled did not differ by burn severity at 11-12 years since fire (ANOVA, $df = 2/112, p = 0.466$). The average clump was comprised of 18 stems (table 1), with a range of 1 to 25. Dominant stems in the high-severity burn plots were 215 percent of the dbh of stems in low-severity burns (ANOVA; $df = 2/112, p<0.001$).

Sprout clumps were generally taller in high-severity burns (ANOVA, $df = 2/112, p<0.001$) (table 1). Sprout clump heights in stands that experienced high-severity fire were 169 percent and 217 percent of the height of the average sprout clump in stands that experienced moderate and low severity fire, respectively. Similarly, clump crown widths varied according to fire severity (ANOVA, $df = 2/112, p = 0.016$). Black oak sprout clump crown widths after high severity fire were 118 percent and 141 percent of the average sprout clump crown width in stands experiencing moderate and low severity fire, respectively. Fire severity affected sprout clump allometry in terms of height relative to width of the entire crown formed by the clump. Following high severity fire, sprout clumps of any given height had significantly narrower crowns than sprout clumps arising after moderate and low severity fire which were generally shorter in stature and had relatively lower height:width ratio.
Table 1—Counts of California black oak overstory and sprouting genet (stump sprout clump) displaying mean characteristics 11 to 12 years after the 2000 Storrie Fire (values in parentheses are 1 S.E.)

<table>
<thead>
<tr>
<th>Burn severity</th>
<th># Live mature stems</th>
<th># Dead mature stems</th>
<th># Sprouting genets</th>
<th># Ramets</th>
<th>Crown width</th>
<th>Crown height</th>
<th>Dominant dbh</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Per acre</td>
<td>Per genet</td>
<td></td>
<td></td>
<td>feet</td>
<td>feet</td>
<td>inches</td>
</tr>
<tr>
<td>Low</td>
<td>1.01 (0.71)</td>
<td>3.16 (2.24)</td>
<td>3.63 (3.14)</td>
<td>17.04 (2.96)</td>
<td>7.62 (1.44)</td>
<td>6.98 (2.01)</td>
<td>0.96 (0.44)</td>
</tr>
<tr>
<td>Moderate</td>
<td>5.70 (5.70)</td>
<td>9.73 (5.03)</td>
<td>21.67 (12.45)</td>
<td>17.71 (3.23)</td>
<td>9.15 (1.49)</td>
<td>8.95 (2.15)</td>
<td>1.38 (0.42)</td>
</tr>
<tr>
<td>High</td>
<td>0.00 (0.00)</td>
<td>45.46 (21.49)</td>
<td>66.02 (31.37)</td>
<td>19.41 (3.09)</td>
<td>10.75 (1.39)</td>
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</tbody>
</table>
Figure 1—Summed crown area of sprouting *Quercus kelloggii* (QUKE) within stands response to the *Q. kelloggii* component of the live plus fire-killed overstory [A] basal area (BA) and [B] density, 11 to 12 years after the 2000 Storrie Fire.
Black oak seedling and sprout frequency varied across the Storrie Fire landscape. Black oak seedlings were found on 3, 7, and 6 percent of plots in the low-, moderate-, and high-severity burns; in contrast, we observed sprouting clumps on 4, 11, and 29 percent of plots (see labeled data points in fig. 1 for stand-level sprout presence on plots). Across burn severities, we found 8.87 (S.E.: 1.60) seedlings ac\(^{-1}\). Stand-level sprouting clump densities varied by burn severity (ANOVA, \(df = 2/22, p = 0.045\)). Mean sprouting clump densities among stands were 3.6, 21.7, and 66.0 clumps ac\(^{-1}\) with regard to increasing burn-severity classes, which corresponded well to the density of top-killed black oak stems (table 1). Both presence and density of sprouting black oaks in high-severity burns appeared to be approximately three times greater than moderate-severity burns and an average of 13 times the low-severity sites.

Regenerating black oak cover was analyzed in stands with evidence of a pre-fire black oak component in the overstory (\(n = 11\)). Mean summed crown area of resprouting black oak was 4,999 ft\(^2\) ac\(^{-1}\) (SE: 1,762), or equivalently, 11.5 percent of the ground area. Summed crown area of regenerating oak had a strong positive association with both the stands’ summed live plus top-killed black oak overstory basal area and density (Adj. \(R^2 = 0.83\) and 0.73, respectively; table 2; fig. 2). Too few stands (with black oak overstory trees present before the fire) were available to test for relationships between fire severity and pre-fire BA and density of black oak in the overstory. However, the greatest black oak crown areal cover was observed as a result of high-severity burns having high live and top-killed basal areas and densities (fig. 1 and 2).

### Table 2—Linear model coefficients of black oak canopy areal cover 11-12 years after the 2000 Storrie Fire

<table>
<thead>
<tr>
<th>Model</th>
<th>Response</th>
<th>Intercept (SE)</th>
<th>Covariates (in log-space)</th>
<th>P value</th>
<th>Adj. (R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Live + top-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>killed basal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>area (SE)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Live + top-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>killed stem</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>density (SE)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>(\sqrt{\text{oak cover (ft}^2\text{ac}^{-1})})</td>
<td>-28.549 (13.033)</td>
<td>41.521 (5.782)</td>
<td>&lt;0.0001</td>
<td>0.83</td>
</tr>
<tr>
<td>2</td>
<td>(\sqrt{\text{oak cover (ft}^2\text{ac}^{-1})})</td>
<td>-61.373 (23.281)</td>
<td>-</td>
<td>36.713 (6.925)</td>
<td>0.0005</td>
</tr>
</tbody>
</table>
Discussion

We found no effect of fire severity on stem density within clumps, suggesting that severity did not influence sprouted stem retention in black oak 11 to 12 years after the Storrie Fire. We did, however, find a severity-dependent effect on the relationship between height and crown diameter. Overall plant size (height and crown diameter) was positively related to burn severity (as in Cocking and others 2014). Although there was no statistical difference in the height to crown diameter relationship between low- and moderate-severity burns, 95 percent confidence intervals (CIs) on the mean illustrate that the relationship after high-severity burns tends to have a steeper ratio than the lesser severities (greater than 1:1 ratio). It appears that height:crown diameter ratio may decrease from moderate- to low-severity. Our results support observations of sprouting black oak heights and crown diameters in a 1978 silvicultural cutting methods study in the Sierra Nevada (McDonald 1978) that found greater sprout growth in clearcut stands than shelterwood-cut stands. These studies (McDonald 1978, Cocking and others 2014, and the present study) each demonstrate that black oak sprout growth has an inverse relationship with overstory density, which has increased in mixed conifer landscapes due to fire exclusion (Parsons and DeBenedetti 1979).
Black oak establishment 11 to 12 years after fire was more commonly manifested as sprouting clumps than as regeneration directly from acorns. Although sexual reproduction is an integral component of black oak dynamics on this landscape, establishment of seedlings was low (only 3 to 7 percent of plots; mean seedlings per acre = 8.87). Further, seedlings did not vary with fire severity as did regenerative sprouting. The limited presence of post-fire seedlings is at least partially due to the short window of acorn production prior to sampling. Twelve years after top-kill leaves little chance for resprouting individuals to sexually reproduce, despite the observed presence of acorns borne on resprouting clumps (J. Crotteau, personal observation). On the other hand, it is interesting that as much as 6 percent of the plots in high-severity burns had successful acorn regeneration, since typical viable acorn crops are not expected until trees are 30 years of age (McDonald 1990). Our findings suggest further areas for study. For example, can black oak sprouts produce viable acorns at a younger age than acorn-germinated individuals? Does fire severity influence the age of viable acorn production? Further research may elucidate differences in the age-dependency of viable acorn production according to regenerative strategy and burn severity.

Sprouting oak clumps were most frequent in high-severity fire footprints. This observed tendency corroborates that black oak has a synergistic relationship with fire (Cocking and others 2014). Whereas the study area’s historic fire regimes may have maintained vegetation community integrity via frequent, low-severity fire, fire exclusion since the beginning of the 20th century has enabled shade-tolerant conifers to crowd stands and encroach upon oaks (Cocking and others 2014, Skinner and Taylor 2006). Frequent fire positively influences the black oak community by inducing regenerative sprouting and by reducing densities of fire-sensitive conifers that have the competitive advantage during long, fire-free intervals. Stand-replacing wildfire or intensive mechanical treatment in overcrowded conifer-oak overstory assemblages may enhance the black oak community on this landscape by resetting the contemporary successional trajectory (Cocking and others 2012, Odion and others 2010). Stands burned by high-severity fire are frequently replaced by sprouting woody shrubs (Cocking and others 2014, Crotteau and others 2013) and interspersed with black oak clumps (fig. 3), suggesting that conifer-encroached black oak ecosystems may display latent resiliency similar to frequent-fire ponderosa pine ecosystems in the northern Rockies (Larson and others 2013). Little is known about the transition from the adolescent oak/shrub community phase to the restored mature oak overstory state (Cocking and others 2014), which suggests further research and creative management strategies need to be developed to guide restoration in this common intermediate phase. Maintenance of the black oak component in these landscapes must ultimately take the form of fostering, or perhaps mimicking, frequent low-severity fire to inhibit future shade-tolerant conifer crowding and maintain historical landscape composition and structure.

Characteristics of the black oak component in the fire-killed overstory (basal area and stem density) were important predictors of the 12 year post-
fire sprouting cover response. This study’s models affirm a distinct positive trend between mature black oak in stands top-killed by fire and the resultant canopy area re-occupied by the sprout-regenerating clumps. Although an expected phenomenon, these relationships are useful for predicting post-burn vegetation recovery on the landscape. If we assume that the summed live and top-killed black oak overstory basal area (or tree density) approximates pre-fire mature black oak densities, our models are useful for prediction of future post-fire recovery. According to these models, managers with knowledge of the black oak component in stands may expect the square root of oak cover (ft² per ac) to increase by 41.5 for every one unit increase in the natural log of the initial oak overstory basal area (ft² per acre). Similarly, for every one unit increase in the log of initial oak overstory tree density (trees per acre), we predict that the square root of oak cover will increase by 36.7 per acre. Though these predictions ignore burn severity due to lack of sufficient replication, there appears to be a biological effect of high severity fire on the magnitude of sprouting clump areal coverage that must be considered to refine coverage predictions (fig. 1).

Finally, conifer stocking via natural regeneration 10 years after stand-replacing fire in the southern Cascades is often insufficient to meet U.S. Department of Agriculture Forest Service silvicultural goals (Crotteau and others 2014). Planting, therefore, is a typical post-fire management practice in this region. To facilitate black oak (and other hardwoods) given active management, the SNFPA calls for formation of 6.1 m (20 ft) buffers around hardwood crowns, within which planting conifers is to be avoided. This study supports that increased availability of above-ground growing space encourages oak height and crown diameter growth, but enforcing 6.1 m (20 ft) buffers around resprouting oaks may not be appropriate for stands that were previously composed of an admixture of shade-intolerant conifers and black oak. At this level of oak protection, 33 evenly spaced black oaks with 0.3 m (1 ft) crown diameters on an acre practically prohibits any planting of conifers; both the mean and median of black oak clumps ac⁻¹ observed after the Storrie Fire’s high-severity burns are greater than this threshold. Managers should be aware that complete satisfaction of SNFPA guidelines may effectively preclude any conifer planting where oaks are relatively abundant. A density-dependent variable radius buffer or a patchy, systematic application of the crown buffer guidelines may be more appropriate for stands meant to satisfy both oak and shade-intolerant conifer recovery objectives.

References


Detecting the Limits of Northern and Southern Lineages of Tanoak in Northern California

Eduardo Sandoval-Castro and Richard S. Dodd

Abstract

Two chloroplast lineages of tanoak (Notholithocarpus densiflorus) meet between Korbel and Hoopa in the North Coast of California. Our earlier work suggests these lineages arose from southern and northern glacial refugia and this region represents their colonizing fronts. Earlier, we detected only one population of mixed lineages, suggesting that seedling establishment is limited locally, by short distance seed dispersal in tanoak. North western California and southern Oregon is recognized as a region of divergent lineages for a number of taxa, but it has not been confirmed whether the divergence is due to previous restriction in northern and southern refugia, or a colonizing front carrying rare alleles into new populations. Distinguishing the origin of this divergence is important, as the refugial scenario is likely to have greater implications for genetic adaptations to local environments and possibly for differences in disease resistance. Plant collections were made from the Hoopa Reservation for future resistance screening (Cobb and others 2008) and additional populations were sampled over the transitional zone. We use gene coalescence simulations to test among competing evolutionary scenarios. We detected minimal mixing of chloroplast haplotypes and a weak signal of nuclear DNA divergence across the break. Simulations confirmed the northern and southern refugial hypothesis.

Key words: chloroplast DNA, microsatellites, Notholithocarpus densiflorus, refugia, seed dispersal, tanoak

Introduction

Past events in the evolution of populations may lead to gene pools that have evolved independently in response to selective forces and to stochastic divergent processes. Although divergent processes may have occurred in the deep past, they can be detected in phylogeographic patterning among populations of living trees if population admixture is limited. In western North America a north-south divergence has been found in southern Oregon and northern California for a number of different taxonomic groups (Brunsfeld and others 2001, Soltis and others 1997). Soltis and others (1997) attributed this divergence to one of two scenarios: 1) “North-south recolonization” following isolation in at least two Pleistocene refugia. 2) “Leading edge hypothesis” in which populations colonizing northwards underwent founder bottlenecks and a novel haplotype was carried forward on the colonizing front. Shafer and others (2010) extended the simple north-south recolonization hypothesis to take account of the complexity of refugia in the Pacific.
Northwest and emphasized the need to consider the ecological and evolutionary consequences of colonization from multiple refugia. Which of the two hypotheses is true in accounting for a phylogeographic divide within a species is important because long periods of isolation of populations in disjunct refugia would likely result in population groups with distinct gene combinations that could provide differential response to stress such as climate change and disease tolerance.

In previous work with *Notholithocarpus densiflorus*, we detected two major chloroplast lineages in coastal California (Dodd and others 2010, Nettel and others 2009). Spatially, these two lineages were composed of northern, or southern populations with a break occurring in Northern California at about 41 degrees North latitude between Korbel and Hoopa. Interestingly, we found only a single population in which chloroplast lineages were mixed over a distance of about 11 km. The sharp divergence between populations sharing the same chloroplast lineage suggests a single colonization route following mutations in the chloroplast genome given the leading edge hypothesis of Soltis and others (1997), or recent convergence of populations from northern and southern refugia with little opportunity for seed mixture (chloroplasts are maternally inherited in this species and therefore dispersed by seed).

Because nuclear and plastid DNA are differently inherited, the combination of plastid and nuclear molecular markers in DNA studies can provide a powerful complementary approach to detecting ancient to more recent population demographic changes. For heavy-seeded species such as tanoak, seed dispersal is likely to be quite limited, and so chloroplast DNA provides a good indication of ancient fragmentation of the species’ distribution. On the other hand, highly polymorphic, co-dominant markers such as nuclear microsatellites allow for inferences on fluctuations in population size, including founder events and bottlenecks.

Here, we have taken a transect over the north-south chloroplast lineage break, to gain more insights on the transition zone and the degree of seed admixture. We test the hypothesis of northward colonization against the competing hypothesis of northern and southern refugia by comparing demographic simulations with data from nuclear microsatellites sampled across the transition zone.

**Materials and methods**

**Sampling and DNA analysis**

Leaves from mature individuals of *Notholithocarpus densiflorus* subsp. *densiflorus* were obtained from coastal populations situated between Korbel and Hoopa reservation in the North Coast of California. We sampled a total of 258 trees from 14 populations, with an average of 19 trees per population (fig. 1, table 1). Total genomic DNA was extracted from the fresh foliage using a simplified cetyltrimethyl ammonium bromide (CTAB) method (Cullings 1992).
Chloroplast DNA

Four polymorphic cpDNA microsatellite loci previously used in tanoak (ucd2, ccmp4 ccmcs5 and rpoB; Nettel and others 2009) were PCR amplified using a fluorescent-labeled primer. PCR amplifications were performed following protocols described by Nettel and others (2009). To ensure reproducibility and consistency in PCR amplification, a negative and two positive samples were run as a control for each set of PCR reactions and genotyped. PCR cocktails were electrophoresed on an ABI 3730 automated sequencer (Applied Biosystems). Microsatellite alleles were visualized and scored in the program GeneMarker 2.2.0 (Softgenetics).

Nuclear DNA

Eleven nuclear microsatellite loci developed for tanoak (LD1, LD3, LD5, LD7, LD8, LD10, LD12, LD13, LD14, LD17, and LD19; Morris and Dodd 2006) were PCR amplified using fluorescent-labeled primers multiplexed in five different groups: 1) LD1, LD3, LD7, LD10, LD14; 2) LD5, LD17; 3) LD12, LD13; 4) LD19; and 5) LD8. PCR protocols followed those described by Nettel and others (2009). To ensure reproducibility and consistency in PCR amplification, a negative and two positives samples were run as a control for each set of PCR reactions and genotyped. PCR cocktails were electrophoresed on an ABI 3730 automated sequencer (Applied Biosystems). Microsatellite
alleles were visualized and scored in the program GeneMarker 2.2.0 (Softgenetics).

**Data analysis**

We checked data quality for scoring errors in nuclear microsatellites using MICRO-CHECKER (Oosterhout and others 2004) and estimated the probability of null alleles using the same program. Chloroplastic microsatellite alleles were combined into haplotypes, where each amplified locus was considered an independent, but linked, character inherited as a unity.

To ascertain reliability of the estimations based on nuclear microsatellites, we tested deviations from Hardy-Weinberg (HW) equilibrium within each population by the inbreeding fixation index, $F_{IS}$, with the software FSTAT ver. 2.9.3.2 (Goudet 2002). HW equilibrium could not be rejected for any of the populations. We estimated population genetic diversity as allelic richness ($A_R$) and expected heterozygosity ($H_E$) with FSTAT. Population structure was inferred using a Bayesian clustering algorithm implemented in STRUCTURE v2.2.3 (Pritchard and others 2000), assuming no a priori knowledge of population boundaries. STRUCTURE runs were based on 500,000 iterations after a burn-in of length 500,000 and assumed correlated allele frequencies and an admixture model with an estimated proportion $\alpha$ of admixed individuals. To check for Markov chain Monte Carlo (MCMC) convergence, we performed 10 replicates for each $K$ value and checked the consistency of results. The most likely number of clusters ($K$) was considered to be the $K$ value with the highest $Pr(X|K)$ (Pritchard and others 2000). Also, the optimal $K$ value was calculated after the $\Delta K$ method described by Evanno and others (2005). Output from STRUCTURE was post-processed using the programs CLUMP (Jakobsson and Rosenberg 2007) and DISTRUCT (Rosenberg 2004).

**Demographic history models**

We employed Approximate Bayesian Computations (ABC) to test the relative likelihood of a northward migration (leading edge hypothesis) against colonization from northern and southern refugia (north-south recolonization hypothesis). ABC tests were performed in DIYABC v. 2.0.3 (Cornuet and others 2013). In preliminary analyses, we ran a simple northward colonization scenario in which a northern group of populations (ACR, AFL, BGR, IGA, MCR, PCR, RMO, YCE) defined by the northern chloroplast haplotype (see table 1) colonized from admixed populations (Pop4 and Pop5) that in turn colonized from southern populations (Pop1, Pop2, Pop3 and TTA). This scenario was tested against two competing scenarios; 1) Colonization of the northern group of populations directly from the southern group followed by an admixture event to produce Pop4 and Pop5 and, 2) an admixed group (Pop4 and Pop5) that arose after contact of northern and southern groups expanding from northern and southern refugia. Parameter (two-population summary statistics: allele size variance, pairwise $F_{ST}$, Goldstein's $\delta\mu^2$ and shared allele distance) estimation was from a reference table, which consisted of 1,000,000
simulated datasets. We used the default generalized stepwise mutation model with a mean mutation rate across loci set at \(10^{-3}\) to \(10^{-4}\) per locus per generation. Uniform priors were used for current and past population sizes and for the timing of demographic events.

**Results**

**Chloroplast diversity and structure**

We detected two alleles each at loci ccmcs5 and rpol. Loci ccmp4 and ucd2 were monomorphic in all populations analyzed. Interestingly, alternate alleles at these two latter loci were fixed in northern and southern populations giving the same two divergent chloroplast haplotypes reported earlier by (Dodd and others 2010, Nettel and others 2009). The resulting two haplotypes were detected admixed in only two populations, within a latitudinal band of about 7 km. Both populations were dominated by the haplotype of southern origin (table 1, fig. 1). This finding supported previous studies on tanoak (Dodd and others 2010, Nettel and others 2009), suggesting this area as a recent contact zone between north and south haplotypes.

**Table 1—Characterization of the 14 tanoak populations sampled in Northern California**

<table>
<thead>
<tr>
<th>Population</th>
<th>Code</th>
<th>Latitude</th>
<th>Longitude</th>
<th>N</th>
<th>Nuclear AR</th>
<th>Nuclear H_e</th>
<th>Chloroplast Haplotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>100 Acre</td>
<td>ACR</td>
<td>41°06'</td>
<td>-123°46'</td>
<td>18</td>
<td>3.8</td>
<td>0.55</td>
<td>A</td>
</tr>
<tr>
<td>Acorn Flat</td>
<td>AFL</td>
<td>41°17'</td>
<td>-123°50'</td>
<td>15</td>
<td>4.5</td>
<td>0.66</td>
<td>A</td>
</tr>
<tr>
<td>Bear Grass</td>
<td>BGR</td>
<td>41°18'</td>
<td>-123°50'</td>
<td>33</td>
<td>4.0</td>
<td>0.62</td>
<td>A</td>
</tr>
<tr>
<td>Iron Gate</td>
<td>IGA</td>
<td>41°11'</td>
<td>-123°44'</td>
<td>10</td>
<td>4.0</td>
<td>0.56</td>
<td>A</td>
</tr>
<tr>
<td>Mill Creek</td>
<td>MCR</td>
<td>41°08'</td>
<td>-123°38'</td>
<td>18</td>
<td>3.9</td>
<td>0.56</td>
<td>A</td>
</tr>
<tr>
<td>Pine Creek</td>
<td>PCR</td>
<td>41°09'</td>
<td>-123°47'</td>
<td>20</td>
<td>3.9</td>
<td>0.57</td>
<td>A</td>
</tr>
<tr>
<td>Ranger Mountain</td>
<td>RMO</td>
<td>41°07'</td>
<td>-123°47'</td>
<td>18</td>
<td>3.8</td>
<td>0.55</td>
<td>A</td>
</tr>
<tr>
<td>Yurok Cemetery</td>
<td>YCE</td>
<td>41°11'</td>
<td>-123°46'</td>
<td>17</td>
<td>4.0</td>
<td>0.62</td>
<td>A</td>
</tr>
<tr>
<td>Tish Tang</td>
<td>TTA</td>
<td>41°03'</td>
<td>-123°35'</td>
<td>17</td>
<td>4.0</td>
<td>0.57</td>
<td>B</td>
</tr>
<tr>
<td>POP1</td>
<td>Pop1</td>
<td>40°52'</td>
<td>-123°52'</td>
<td>20</td>
<td>4.0</td>
<td>0.58</td>
<td>B</td>
</tr>
<tr>
<td>POP2</td>
<td>Pop2</td>
<td>40°56'</td>
<td>-123°51'</td>
<td>20</td>
<td>3.9</td>
<td>0.58</td>
<td>B</td>
</tr>
<tr>
<td>POP3</td>
<td>Pop3</td>
<td>40°58'</td>
<td>-123°47'</td>
<td>20</td>
<td>4.5</td>
<td>0.63</td>
<td>B(19), A(1)</td>
</tr>
<tr>
<td>POP4</td>
<td>Pop4</td>
<td>41°00'</td>
<td>-123°44'</td>
<td>20</td>
<td>4.3</td>
<td>0.61</td>
<td>B(12), A(8)</td>
</tr>
<tr>
<td>POP5</td>
<td>Pop5</td>
<td>41°01'</td>
<td>-123°43'</td>
<td>12</td>
<td>4.2</td>
<td>0.62</td>
<td>B(9), A(3)</td>
</tr>
</tbody>
</table>

N = sample size; H_e = expected heterozygosity; AR = allelic richness detected with nuclear microsatellites; Haplotype A and B detected with Chloroplast microsatellites. Number in parenthesis is the number of individuals with corresponding haplotype A or B.

**Nuclear diversity and structure**

Genetic diversity, measured as allelic richness ranged from an average of 3.8 alleles per locus in ACR and RMO to 4.5 in AFL and Pop3. Expected heterozygosity ranged from 0.55 in ACR and RMO to 0.66 in AFL (table 1). Using the same groupings detected by chloroplast DNA, we tested for
differences in genetic diversity among selected groups. Overall, genetic diversity estimates showed that admixed populations had slightly higher diversity than northern and southern groups (table 2), with differences at or close to the 5 percent level of significance in the contrast between northern and admixed groups.

Table 2—Genetic diversity measured by allelic richness (AR) and observed heterozygosity (HO) for major clusters of populations of tanoak. Overall, one-sided probabilities after 10,000 permutations were AR = 0.05 and HO = 0.07 for North vs Admixed and AR = 0.20 HO = 0.19 for South vs Admixed

<table>
<thead>
<tr>
<th>Genetic Diversity</th>
<th>North group</th>
<th>South group</th>
<th>Admixed group</th>
</tr>
</thead>
<tbody>
<tr>
<td>AR</td>
<td>3.98</td>
<td>4.10</td>
<td>4.28</td>
</tr>
<tr>
<td>HO</td>
<td>0.58</td>
<td>0.59</td>
<td>0.62</td>
</tr>
</tbody>
</table>

Nuclear microsatellites showed high levels of admixture among populations and the STRUCTURE analysis was unable to detect any signal of clustering (fig. 2). However, a chi-square test found a significant (p>0.001) proportion of individuals from northern and southern chlorotypes had greater than 90 percent assignment to the alternate nuclear microsatellite clusters. This is seen as a subtle difference in fig. 2.

Demographic history in tanoaks

Among the competing scenarios that could account for colonization of this region of northern California, our DIYABC analyses found the refugial expansion model, with admixture to be the best fit to our nuclear microsatellite data (fig. 3).
Figure 3—Posterior probabilities for three competing evolutionary scenarios: Scenario 1 simple northward colonization; Scenario 2 secondary contact from northern and southern refugia; Scenario 3 northward colonization from southern haplotype to northern haplotype groups, followed by admixture in region of mixed haplotypes. $n\delta$ is number of closest datasets.

**Discussion**

The distribution of tanoak today is discontinuous from the Sierra Nevada through the Klamath Mountains to coastal California, and so seed dispersal across these breaks is unlikely. However, the divergence of chloroplast haplotypes near to Arcata, Humboldt County, separating central and northern coastal California from extreme north coastal California and Oregon, is interesting. The significance of this break is supported by divergence in nuclear microsatellite diversity (Dodd and others 2010, Nettel and others 2009), indicating that gene flow by pollen has not been sufficiently invasive to fully break down the divergence between these two coastal chloroplast lineages. This would suggest that the northern and southern lineages have only relatively recently met, or that there are partial barriers to mating.

Here we analyzed populations of tanoaks situated in the area where previous studies have found a mixture of haplotypes from the Northern and Southern Coast of California (Dodd and others 2010, Nettel and others 2009). We found higher levels of genetic diversity in the sampling sites where both cpDNA haplotypes were detected. This finding supports our results from Bayesian modeling that these populations of mixed chloroplast haplotypes are a result of secondary contact between divergent groups rather than a stage in the northward colonization of tanoak.

We found very low levels of diversity and high differentiation in cpDNA compared with nuclear microsatellites. Since the chloroplast genome is maternally inherited, the apparent limitation of polymorphic populations to a
narrow band of about 7 km suggests that the distance of seed dispersal is very limited, or that the northern and southern refugial groups have only very recently come into secondary contact. Our earlier work detected a long-term demographic decline in tanoak, probably dating to the mid Holocene. Therefore, it seems most likely that the timing of secondary contact occurred only shortly before the onset of population decline.

In conclusion, our results showed an abrupt transition in cpDNA haplotypes, with the break occurring between Korbel and Hoopa. Nuclear microsatellites showed more genetic diversity with higher levels observed in sampling locations where both cpDNA haplotypes were found together, consistent with expectations in a zone of admixture among divergent lineages. The Bayesian modeling confirmed that the chloroplast divergence was most likely a result of northern and southern refugial populations. The results underline the importance of treating coastal California tanoak as two lineages with divergent evolution that could have important consequences for adaptive traits and must be taken into consideration in any restoration and conservation efforts.

References


Long-Term Performance of Minimum-Input Oak Restoration Plantings

Elizabeth Bernhardt and Tedmund J. Swiecki

Abstract
Starting in 1989, we used minimum-input methods to restore native oaks to parts of their former ranges in Vacaville, California. Each restoration site was analyzed, and only those inputs deemed necessary to overcome expected limiting factors for oak establishment were used. We avoided unnecessary inputs that added to cost and could have unintended negative consequences. All projects were direct-seeded by volunteers using locally collected acorns of valley oak (Quercus lobata) and other native oaks. Other inputs included mulch and protection from herbivores (cattle, voles) or mowing crews. Plantings received sporadic maintenance after planting. None of the plantings were irrigated or fertilized. Growth rates and survival show spatial variation at all locations. Multiple project locations now have stands of oaks that have been established at very low cost, validating the minimum input approach. Some very low input plantings had high mortality due to unanticipated impacts from fire and vole outbreaks that greatly exceeded levels previously observed. Lessons learned from the long-term performance of these plantings can be applied in an adaptive management system to accomplish low cost, ecologically sound oak restoration projects in other locations.

Key words: acorns, direct seeding, herbivore protection, interior live oak, Quercus lobata, Quercus wislizeni, valley oak

Introduction
Valley oak (Quercus lobata) was removed from much of its former range to make way for agricultural and urban development, especially in the late 19th and early to mid 20th centuries. Regulatory protections now in place usually require some form of mitigation if valley oaks or other native oaks are removed for development. Restoration plantings in degraded or non-occupied habitat are a common mitigation requirement.

Under optimal soil and water conditions, valley oak is easy to grow, but it is more difficult to establish valley oak in suboptimal sites. In 1989, we began a project to examine low-input methods for restocking valley oaks on formerly forested parcels that were being used for cattle grazing (Bernhardt and Swiecki 1991, 1997). After visiting previous plantings and reviewing the literature, we developed a model to guide the selection of low input cultural methods needed for successful planting at a given site. Demonstration projects established at that time were designed to show whether valley oaks could be established in rangeland settings from acorns without supplemental irrigation. Based on initial success of low input techniques, the model was used to select inputs for additional restoration plantings that occurred from 1993 through 2000 in Vacaville, California. In this paper, we present long-term survival and growth data and discuss the effectiveness of the minimum input techniques employed for Vacaville plantings conducted between 1989 and 2000.
Methods

All sites were direct seeded using valley oak acorns collected in Vacaville. Acorns were refrigerated in plastic bags between collection and planting. Planting was conducted by volunteers from late October through December after the first soaking rains. Except as noted below, planting sites were prepared by turning over and breaking up the soil with a shovel. Volunteers selected acorns by hand that were free of insect emergence holes, decay, or other obvious defects. At each site, four acorns were planted on their sides at a depth of about 5 cm, spaced 15 cm apart in a square pattern. Planting sites were mulched with wood chips (about 0.8 to 1 m circle) obtained from local arborists, except as noted below. Planting sites were premarked to avoid potentially poor microsites for the 1989, 1993, 1999 and 2000 plantings.

On grazed parcels, planting sites were protected from browsing with protective Vaca cages (Bernhardt and Swiecki 1991). The cages were 122 cm tall, about 45 cm in diameter, and made of galvanized 12-gauge wire mesh (5 by 10 cm) fencing fabric. Each cage was secured on one side to a T-post and on the opposite side by a 86 cm length of 9.5 to 12.7 mm diameter steel reinforcing bar (rebar) driven into the soil at least 30 cm. As the oaks grew beyond the cages and showed browsing damage, in many instances cages were extended to 180 cm tall by wiring on additional fence fabric. Installation of cage extensions was sometimes delayed, so some trees were suppressed by browsing for several years. Cages were removed after trees grew well above browse height, though cage removal has been delayed beyond this point for many trees.

For areas maintained by mowing, we used 3 m lengths of 16 mm diameter steel reinforcing bar (rebar) bent into U-shaped pins. The straight ends of the rebar were driven into the ground to straddle the planting site, with the top of the pin standing about 1 m above ground level. The pins marked the sites and were intended to deter accidental mowing of the trees and were difficult to vandalize.

Height and survival data were collected in August and September 2014. Height data were collected with the aid of a telescoping measuring pole. Trunk diameter 1.37 m above grade (DBH) was measured with a caliper. Canopy diameter was measured along two perpendicular axes, using either a measuring tape or laser rangefinder. The canopy area was calculated using the formula for an ellipse. Data were analyzed using, JMP® 9.0.3 statistical software (SAS Inc., Cary NC). Tukey-Kramer HSD was used to separate means following a significant analysis of variance.

1989 planting

The planted area (east and west) was on two generally south facing hillsides divided by a residential street in north Vacaville. The hillsides were commonly grazed for several weeks or longer between December and June. Grazing duration and intensity has varied widely from year to year, and did not occur in some years. At the start of the project, we anticipated browsing by cattle, moisture stress due to weed competition, soil depth and compaction, and vandalism would be the most likely factors to limit restocking success. As part of a study, we tested five treatments, described in detail in Bernhardt and Swiecki 1991. The lowest input treatment had no protection from cattle grazing. The 2014 assessments did not include relocating the planting sites for this treatment; almost all of these were vacant after the first few years. The other four treatments were protected by Vaca cages. These treatments included augering with a 10-cm diameter bit to a depth of 45 to 60 cm and mulching with landscape fabric covered with woodchips; landscape fabric and wood chip mulch without augering; and preselection of planting sites based on penetrability by a
steel probe (30 cm vs. 45 to 60 cm depth) with only dry grass mulch. We planted 30 sites per treatment per hillside. The planted area was about 1.4 ha on the east side and 1.2 ha on the west side.

1993 planting
The planted area was 2.1 ha on hill slopes and wide drainages along a watershed in a cattle-grazed area in Lagoon Valley. Soils were relatively deep and loamy, with some areas of slippage near the main drainage. Grazing typically began in late December and continued into late April or May. We anticipated that browsing by cattle and rodent chewing would be limiting factors at this location. In addition to valley oak, interior live oak (*Quercus wislizeni*) and California buckeye (*Aesculus californica*) were direct-seeded at this location. We planted 113 sites, all of which were protected with Vaca cages and mulched with wood chips. We used 61 cm tall, 15 cm diameter aluminum window screen cylinders buried to a depth of 15 cm for 82 of the planting sites to protect against rodent herbivory. Screens were folded closed at the top and open below ground. Screens were opened as soon as the plant inside reached the top of the cylinder, and were eventually removed. Empty planting sites were replanted through 1996.

1999 planting
This planting consisted of 94 planting sites over 1.2 ha in a nearly level valley floor area. Sites were along the west side of a 0.9 km long section of abandoned railroad right of way, bordered by residential and commercial development. We anticipated vandalism and accidental mowing of seedlings would be limiting factors. Sites were mulched with wood chips and rebar U-pins were installed after planting, but before seedling emergence.

2000 planting
This planting consisted of 98 planting sites over 1.2 ha along the east side of the same right of way described above for the 1999 planting. We anticipated vandalism, accidental mowing, and soil compaction would be limiting factors. A paved biking trail was constructed on the railroad bed after the 1999 planting but before the 2000 planting. Soil on the east side appeared to be more compacted than on the west side. To mitigate surface compaction, prior to planting, each premarked planting site was excavated to a depth of about 60 cm and refilled using a backhoe. Rebar U-pins were installed prior to planting. Otherwise, sites were planted and maintained as described for the 1999 planting.

Other plantings
Other plantings took place in 1994, 1996, 1997, and 1998 on hillside open-space in Lagoon Valley that was formerly grazed. Planting sites were not premarked or protected in any way and no followup maintenance was conducted. We anticipated that rodents and weed competition for soil moisture would be limiting factors. Sites were mulched with wood chips.
**Calculation of canopy cover**

For each location, the canopy area of trees with DBH >0 was summed and divided by the total area of the planting. Canopy spread was not recorded for some trees; for those, canopy area was calculated from DBH using the formula based on a regression (fig. 2). Canopy spread of existing mature trees was measured from digital images using Google Earth®.

**Results**

**Survival**

Emergence and survival for valley oaks was initially high (> 95 percent of planting sites) for all planting years. Surviving tree densities for locations shown in table 1 vary from 37 to 77 trees per ha. In the oldest (1989) plantings, survival of planting sites protected by Vaca cages (70 percent west, 74 percent east) did not change between the 2014 and 1995 censuses (Bernhardt and Swiecki 1997). No significant differences in survival were seen between the four planting treatments in Vaca cages. We did not attempt to relocate the unprotected planting treatment, but 13 unprotected oaks, all less than 1 m tall, were observed. Most of these were originally planted in Vaca cages that were subsequently lost due to vandalism; no more than two or three may be survivors from the unprotected treatment.

<table>
<thead>
<tr>
<th>Planting</th>
<th>Age in 2014, years</th>
<th>survival</th>
<th>DBH&gt;0 one trunk</th>
<th>two trunks</th>
<th>multiple trunks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989-east</td>
<td>25</td>
<td>74</td>
<td>72</td>
<td>60</td>
<td>31</td>
</tr>
<tr>
<td>1989-west</td>
<td>25</td>
<td>70</td>
<td>58</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>1993</td>
<td>21</td>
<td>84</td>
<td>69</td>
<td>64</td>
<td>28</td>
</tr>
<tr>
<td>1999</td>
<td>15</td>
<td>91</td>
<td>83</td>
<td>40</td>
<td>44</td>
</tr>
<tr>
<td>2000</td>
<td>14</td>
<td>94</td>
<td>84</td>
<td>43</td>
<td>27</td>
</tr>
</tbody>
</table>

*Sites in Vaca cages only.

In May 2007, a grass fire burned most of the 1989 west planting, affecting 77 percent of the planting sites. Trees in the burned area were either topkilled and have since resprouted from ground level (65 percent of all surviving trees) or were at the edge of the burned area and scorched but not topkilled (7 percent of all surviving trees). The remainder appear unaffected by the fire. Due to prolific sprouting of topkilled trees, fire did not decrease survival compared with 1995 census data.

Survival of the 1993 planting (table 1) was affected by both cattle and voles (presumably Microtus californicus). Within the first year of planting, four sites had to be abandoned because cattle had pushed over and mangled the Vaca cages. Because of the heavier cattle use at this location, we reinforced cages by wiring them to the T-posts and adding additional T-posts and rebar to the most impacted sites. Wire screens afforded very short-lived protection; within a year or two, we had to open the screen cylinders because oaks and buckeyes had reached the closed tops. This planting was affected by a surge in the local vole population in 1999. Vole populations and associated damage attained levels we had not previously seen locally. Scattered vole damage have been observed sporadically in the planting after
1999. To date, 16 valley oaks with DBH values ranging up to 12 cm have been girdled and topkilled by voles, and other trees have been partially girdled. Survival of the 15 sites planted with California buckeyes is 100 percent. Eight of 18 sites planted with interior live oak acorns contain surviving trees.

Survival was highest overall at the two youngest plantings (table 1). The 1999 and 2000 plantings are mowed once or twice annually by city crews in May and late summer. In early May 2000, 46 sites in the 1999 planting were mowed by inmate crews using string trimmers while the city coordinator for the site was on vacation. Plants were mowed to heights as low as 5 cm. The mowed seedlings resprouted, and although they were significantly shorter than the unmowed seedlings by August 1999 (8.5 cm vs 15.7 cm), survival on a planting site basis (at least one seedling per site) did not differ. Accidental mowing of marked sites with rebar pins has been an ongoing problem for trees that are shorter than 1 m. Some rebar pins have been rolled over and destroyed by mowing equipment and some sites than have not had the pins replaced (six in 1999 planting, seven in 2000 planting) have been mowed down annually.

Unprotected and unmaintained planting sites on nongrazed grassy upland sites showed good initial emergence but had low long-term survival. For example, the 1994 hillside planting had 95 percent initial survival of valley oak sites the August after planting. By 3 years after planting, survival of valley oak planting sites was 57 percent. In 1999, 5 years after planting, high vole populations in the Lagoon Valley area caused severe damage to this and other unprotected plantings (1996, 1997, 1998), as well as established natural regeneration in nongrazed areas. Some established natural oak saplings with basal diameters greater than 7 cm were killed by girdling of the stem above and below the soil line. Less intense vole population outbreaks have occurred at several times since 1999, mainly in grassy, nongrazed sites. In addition to vole herbivory, large portions of the 1996, 1997, and 1998 plantings were burned in several successive years. Consequently, only a few surviving valley oaks remain from these plantings. Most of the survivors are in mid- to lower-slope positions where oaks unaffected by voles have grown well. The maximum DBH among these survivors is 35 cm. Although deer frequent the area, we have not observed height growth being suppressed by deer browsing at these sites.

**Growth**

Tree size parameters showed relatively wide distributions for all plantings (table 2, fig. 1). The largest trees were in the oldest plantings (fig. 1) but all sites contained small trees that were less than 1.4 m tall and had no DBH. At each location, trees of similar sizes tended to be spatially clustered, indicating the strong role of underlying soil conditions, such as depth and available moisture, as primary determinants of tree size. Tree DBH, height, and canopy spread in the different plantings overlapped substantially (figs. 1, 2) despite the difference in ages for the plantings. Across all plantings, DBH was highly correlated with height and canopy spread (fig. 2).
Table 2—Comparison of size attributes (mean ± standard deviation), and calculated canopy cover of valley oaks at 5 planting locations. Means followed by the same letters are not statistically different from one another according to Tukey-Kramer HSD

<table>
<thead>
<tr>
<th>Planting</th>
<th>DBH, cm</th>
<th>Height, m</th>
<th>Canopy spread, m²</th>
<th>Canopy cover, pct</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989-east</td>
<td>13.2a ± 8.6</td>
<td>5.0a ± 3.2</td>
<td>12.1b ± 13.9</td>
<td>10.0</td>
</tr>
<tr>
<td>1989-west</td>
<td>11.9ab ± 6.6</td>
<td>4.5a ± 2.1b</td>
<td>13.5b ± 9.0b</td>
<td>3.6</td>
</tr>
<tr>
<td>1993</td>
<td>14.3a ± 10.8</td>
<td>5.3a ± 3.1</td>
<td>31.2a ± 25</td>
<td>10.5c</td>
</tr>
<tr>
<td>1999</td>
<td>11.0ab ± 6.7</td>
<td>5.4a ± 2.6</td>
<td>15.6b ± 12.6</td>
<td>9.6</td>
</tr>
<tr>
<td>2000</td>
<td>8.7b ± 6.0</td>
<td>4.8a ± 2.6</td>
<td>11.4b ± 9.9</td>
<td>7.0</td>
</tr>
</tbody>
</table>

*Sites in Vaca cages only.
*Unburned trees only.
Includes canopy contributions of interior live oaks and protected natural trees.

In the 1989-east planting, the largest trees were located at the bottom of the slope along an alluvial fan. Vaca cages have been removed from these large trees, so initial treatment assignments, which were marked on the T-posts, were not available. However, all initial treatments were represented among these uniformly large trees. About one third of the remaining trees in the 1989-east had treatment codes still visible. For these trees, the original treatment did not significantly affect DBH, height, or canopy spread.
Unlike the 1989-east planting, the largest trees in the 1989-west planting were along the hill crest and on a southeast-facing slope. In the 1993 planting, the largest trees were mostly on a north-facing slope and in broad drainages, and were more common in the lower elevations of the planting, which spanned about 85 m of elevation change. Spatial clustering of tree sizes was also evident on the level planting sites used for the 1999 and 2000 plantings, with poorer growth occurring in the more compacted and poorly-drained soils near the center portion of the linear area.

All 55 trees topkilled by the 2007 fire in the 1989-west planting resprouted prolifically. Nine of these had not yet attained a DBH. For the remaining resprouts, the mean DBH of the largest live stem was 3.9 cm (range 0.6 to 10.1 cm, n = 46), significantly smaller (t test P <0.0001) than the DBH of trees outside the burned area shown in Table 2. We were able to measure DBH of the fire-killed trunk at 42 of the burned sites, these averaged 4.2 cm (range 1 to 10.8 cm). The original planting treatments did not significantly affect DBH, canopy area, or height of either nonburned or resprouted topkilled trees in the 1989-west planting. The non-burned trees in the 1989-west planting did not differ significantly from trees in the 1989-east planting with respect to DBH, height, or canopy area (table 2).

As part of the 1993 planting, we installed Vaca cages around browse-suppressed (less than 1 m tall) natural regeneration that was near a mature valley oak in the lower portion of the planting area. We protected six valley oaks that were well beyond the canopy of the existing oak, leaving some adjacent and nearby oaks unprotected. These oaks grew rapidly when protected from winter-spring cattle browsing and most required extended cages within a few years. In 2014, DBH of these trees ranged from 17 to 49 cm. Unprotected regeneration in the same area has remained less than 1 m tall.

Among the interior live oaks in the 1993 planting, seven trees had DBH values ranging from 4.2 to 47 cm, heights from 2.6 to 9 m, and canopy spreads from 3 to 98 m². One interior live oak tree had been topkilled by voles and had resprouted prolifically. Its largest sprout was 1.5 m tall with a DBH of 3 mm.

At most planting spots more than one of the four planted acorns emerged, but we did not thin multiple seedlings. By 2014, the number of planting spots with multiple
oaks varied from location to location (table 1). We excluded the burned, topkilled plants from further analysis. There was no correlation between the DBH of the largest stem at each planting spot and the number of stems at each spot. One seedling usually became dominant and the additional seedlings were suppressed. Among multiple-tree sites where at least one tree had attained a DBH, 54 percent had a second tree that was at least 1.37 m tall. The average DBH of the largest stem was significantly greater than the average of the second stem that was at least 1.37 m tall. Codominant stems were most common in the 1999 and 2000 plantings. The trunks of these trees appear to fuse at the base where they come in contact, though it is not clear whether the appressed trunks actually become grafted together or remain separated by included bark.

The larger oaks at all planting sites have been producing acorns for a number of years. Some small seedlings arising from these were observed in the 1989 and 1993 plantings, although they have been suppressed by grazing.

Removing protective hardware

Removal of protective Vaca cages from large trees was generally delayed beyond the optimum timing and has only been completed to the degree needed for the 1989-east and 1993 plantings in the past 4 years. In a number of instances, especially where the height of the Vaca cage had been extended, branches had grown through the wire mesh. Branches and trunks generally grow around the wire, which can become completely embedded in the tree and can only be cut away at the bark surface. In some cases, straight sections of wire could be cut off and pulled out of the stems, but removal of the Vaca cage at this late stage was time consuming and sometimes difficult. Rebar used to anchor the cages also became embedded at the base of the largest tree trunks and had to be cut off in some instances. Similarly, tops of T-posts were cut off at or below grade with a portable reciprocating saw in instances where roots had grown over the anchor plates and the posts could not be pulled. Rebar U-pins have not yet been removed from most of the 1999 and 2000 plantings. Removal of the pins is overdue for many trees that have begun to grow around rebar that is against the trunk.

Discussion

Results from these plantings show that restoration of valley oaks from direct seeded acorns without irrigation can be successful, even in rangeland settings. These observations confirm earlier results showing that cattle strongly inhibit natural or artificial valley oak regeneration by browsing seedlings and saplings (Bernhardt and Swiecki 1997). No more than a few of the 60 original unprotected sites from the 1989 plantings have survived, and these and other unprotected seedlings at this lightly grazed site are less than 1 m tall. Natural browse-suppressed oak regeneration that was protected from grazing in the 1993 planting grew as well as the planted acorns, whereas short unprotected oaks also failed to grow above 1 m. In contrast, the few surviving oaks in the unprotected plantings in nongrazed areas nearby have grown into small trees, even though deer are common in this area. Protecting browse-suppressed natural regeneration in cattle-grazed areas can be used to recruit valley oak (Bernhardt and Swiecki 1997) and blue oak (McCreary and others 2011), but opportunities are limited where mature trees are very sparse or absent.

By controlling the growth of herbaceous vegetation, grazing can indirectly promote growth and survival of protected oak seedlings by making the habitat less
favorable for voles (Bernhardt and Siewcki 1997, McCreary 2001, McCreary and others 2011). Valley oak seedlings planted in nongrazed grassy areas suffered much more attrition from vole herbivory than seedlings in the nearby grazed parcel, although relatively large saplings were damage even in the grazed parcel. Although voles have been reported to seriously limit oak survival and growth at other sites (Tecklin and McCreary 1993), vole herbivory was not a problem at all Vacaville locations. Significant damage from voles or other rodents has not been observed in the 1989 plantings, which appear to have habitat suitable for voles, or in the 1999 and 2000 urban plantings where habitat is not suitable for voles. Because vole damage can occur when trees are well beyond the size that shelters or screens are useful, habitat modification and other population control measures may be worthwhile inputs.

Although Vaca cages, U-pins, and other protective devices may be necessary to recruit trees, additional labor and cost is required to remove these devices. Timely removal can minimize the work required and allow for easier reuse of materials while avoiding potential damage to trees. Monitoring and an available source of labor are needed to optimize the removal of cages and other devices. Because oaks can grow at widely different rates, hardware removal may need to extend over many years.

The spring grass fire that burned the 1989-west 18 years after the planting did not affect survival of this planting, but the topkill of trees by fire set the growth of these trees back many years. In contrast, repeated grass fires in much younger plantings (1 to several years old) along with vole activity resulted in high attrition rates in several unmaintained plantings in nongrazed areas. We previously showed strong negative effects of fire on growth and survival of natural blue oak seedlings in this same general area (Siewcki and Bernhardt 2002).

Because continued tree attrition due to fire, vole damage, or other factors can continue for many years after initial establishment, we have avoided thinning planting sites to a single tree per site. The presence of multiple seedlings per site has not shown a negative effect on tree growth up to 25 years after planting. Similar results have been seen by Tyler and Moritz (Quercus lobata seedlings and conspecific neighbors: Competitors or allies? these proceedings). In most sites, a single tree becomes dominant even though suppressed additional trees persist for many years. However, these suppressed trees may still be capable of being released if the dominant tree is killed or severely damaged.

Canopy cover after 14 to 25 years was still relatively low at all locations (table 2). Nevertheless, projections based on likely mature canopy spreads show current tree densities are adequate to result in moderate to high canopy cover when trees reach mature sizes. For example, the average canopy area of mature oaks near the 1993 planting site is about 250 m². If all of the surviving valley and interior live oaks in this planting (37 oaks/ha, lowest density of the sites) attained typical mature canopy spread, canopy cover would be about 93 percent. This argues against planting at initially dense rates to increase canopy cover in the short term and instead suggests a strategy of phased planting over time if needed to increase cover. Furthermore, because soil variations strongly influence tree growth over the long term, increasing density in areas with inherently slow growth is a poor strategy for increasing canopy cover.

Acknowledgments

We thank the many volunteers who have assisted with data collection, tree planting, or cage removal over the years, most recently Steve Edmundson, Daniel Garcia, Pam Muick, and
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References


The Effect of Seed Size Variation in *Quercus pacifica* on Seedling Establishment and Growth

Mario B. Pesendorfer

Abstract

*Quercus pacifica*, the island scrub-oak, is the dominant species in oak chaparral on the three largest California Channel Islands. While the population on Santa Cruz Island has experienced a strong recovery, the populations on Santa Rosa and Santa Catalina islands are of conservation concern, and managers are actively restoring oak habitat by planting acorns. Previous work shows that acorn size, a factor that is known to affect planting success, varies significantly across the range of the species. To determine whether acorn size in *Q. pacifica* affects early seedling growth, I planted over 600 acorns from Santa Cruz Island in a greenhouse. Our results show that larger acorns are more likely to germinate, and that acorn mass had strong effects on root mass, shoot mass, seedling height and leaf surface area. Assuming that acorn size may have a similar effect on Santa Rosa and Santa Catalina, I suggest that managers plant larger acorns to maximize the effect of restoration efforts.

Key words: acorns, Channel Islands National Park, *Quercus pacifica*, restoration, seed size, seedling establishment

Introduction

In restoration ecology, understanding the reproductive limitations of target species is essential for the formulation of effective management strategies. When restoring oaks by seeding, for example, variation in seed size can determine the proportion of seeds that successfully establish seedlings, and affect biomass production below and above ground (Navarro and others 2006, Quero and others 2007). Alternatively, seed dispersers providing ecosystem services often show seed size preferences (Wenny and others 2011), and preferentially disperse smaller seeds that show reduced survival (for example, Gómez, 2004). Therefore, managers must be able to identify plant traits that affect the success of restoration efforts, and to consider within-species variation of those traits before deploying seeds (Pywell and others 2003). Here, I investigate the functional consequences of variation in seed size in an oak species of conservation concern.

*Quercus pacifica*, a keystone species of California Channel Islands’ oak chaparral, has been the focus of extensive conservation efforts (Knapp 2010a). On Santa Catalina Island, the oak has experienced 35 percent dieback within the last 60 years (Knapp 2010b). On the other large islands in its range, Santa Cruz and Santa Rosa, *Q. pacifica* populations were long reduced by ranching activity and herbivory by feral non-native livestock (Lombardo and Faulkner 1999, Morrison 2011). The removal of sheep (*Ovis aries*) and pigs (*Sus scrofa*) over the last 25 years has led to a strong rebound of the Santa Cruz Island population, and raised hopes that the recent removal of non-native vertebrates from a second island would result in similar recovery (Morrison 2011). Only Santa Cruz Island has a mutualist, avian disperser of acorns,
the island scrub-jay (*Aphelocoma insularis*). The recovery of the Santa Rosa and Santa Catalina populations will thus initially rely on active seed planting by managers (Stratton 2009). The current study aims to inform management efforts on these islands, but the inference is limited as I only used acorns from Santa Cruz Island.

![Acorn Volume Histograms](image)

Figure 10—Variation of acorn volume in three island populations of *Quercus pacifica*. Histograms depicting the frequency of mean acorn volume per tree. Original data in Pesendorfer and others 2014.

Acorn size is thought to be important for seedling establishment and growth in oaks. In greenhouse grown Holm oak (*Q. ilex*) seedlings, acorn size determined total biomass, and biomass of different parts of the seedlings, but the partitioning among those parts was mostly determined by the parent tree (Leiva and Fernández-Alés 1998, Navarro and others 2006). The effect of acorn size on seedling growth is often strongest in sub-optimal conditions. For example, in low-light areas larger acorns are more competitive than in full-light (Quero and others 2007). The root/shoot ratio, an important predictor of drought tolerance, does not seem to be affected by acorn size, and is likely determined by genetic variation in populations (Leiva and Fernández-Alés 1998). To determine if this relationship holds for *Q. pacifica*, I conducted a greenhouse experiment under optimal growth conditions. I predicted that total
seedling mass, as well as below- and above-ground growth would correlate positively with acorn size.

Methods
In October 2009, I collected 619 Q. pacifica acorns from 77 trees on the annual Santa Cruz Island oak survey (Pesendorfer and others 2014). The acorns were assessed for visual damage from insect activity (for example, oviposition and exit holes), weighed, and length and width at widest point recorded using digital calipers. Until planting, I stored the acorns in a refrigerator at 4 °C, a common technique to keep acorns viable (Navarro and others 2006).

In December 2009, I planted the acorns in a mixture of pyrulite growth mix and sand, homogeneously distributed among 20 propagation trays with 32 round cells of 6 cm diameter and 5 cm depth. The trays were watered daily and maintained on a 14-10 light-dark cycle for the whole study period. After 25 weeks, the seedlings were harvested, dried at 60 °C for 48 hours, and processed. I measured the mass of dry above- and below-ground growth to the nearest 0.1 g using a digital scale (Mettler Toledo MS105), seedling height, number of leaves, and leaf surface area (LiCor LI 3000-A).

I used a set of linear mixed models to test the relationship between acorn mass, seedling emergence and growth parameters. I did not model the interaction between tree identity and acorn mass. All models contained the fixed effect “acorn mass” and the random effect “tree” to account for the repeated sampling (in other words, multiple acorns) on the same individual. To determine the effect of acorn mass on germination, a binary variable, I constructed a general linear mixed model with a binomial error distribution, again using “tree” as a random effect. All analyses were performed in R version 3.01 (R Development Core Team 2013). I used the package “lme4” (Bates and others 2013) for model construction and significance testing of LMMs, and I report the model coefficient $B$, as well associated $t$-values, degrees of freedom and $P$-values. For the GLMM, I used Wald Type II tests in the package “car” (Fox and Weisberg 2011) that estimate $\chi^2$ values and associated $P$-values.

Results
Mass was an important predictor of acorn germination (figs. 2, 3). The mean mass of the 619 viable acorns was 1.49 g ± 0.05 g (± s.e.) and mean acorn mass per tree ranged from 0.23 g to 10.32 g. After 25 weeks, 188 acorns (30.4 percent) germinated, while 431 (69.6 percent) did not show any signs of growth. Acorns that germinated were significantly heavier than non-germinating acorns (fig. 2; GLMM, $\chi^2 = 56.13$, df = 1, $P < 0.001$). Acorns that germinated weighed an average of 2.14 g ± 0.09 g (± s.e.), while unsuccessful acorns weighed 1.21 g ± 0.06 g. The smallest acorn to germinate weighed 0.33 g, which was heavier than the bottom 7 percent of all planted acorns. Of the 188 acorns that germinated, 40 (21.3 percent) produced only a root, but no seedling. Therefore, only 148 of 619 (23 percent) of all collected acorns produced a seedling.

For the acorns that germinated, mass correlated with the growth of seedling parts, but not the root/shoot ratio. Acorn mass explained more variation in root mass, than in shoot mass or leaf surface area (fig. 3 A-D). In contrast, the root/shoot ratio did not correlate with acorn mass (LMM; $B = 0.044$, $t = 0.727$, $P = 0.467$).
Figure 2—The effect of acorn mass on germination. Bold line indicates median, boxes span interquartile range (IQR) and whiskers extend to 1.5 x IQR.

Figure 3—The effect of acorn mass on seedling growth. Acorn mass was significantly correlated with (A) root mass (n = 188), (B) shoot mass, (C) height and (D) leaf surface area of seedlings (all n = 148). For each dependent variable, model coefficient, t-statistic and associate P-value are reported for linear mixed models with individual tree as random effect and acorn mass as fixed effect.
Discussion

The data from this greenhouse experiment suggest an important role of acorn size in germination and early seedling growth of *Q. pacifica*. Under optimal conditions, larger acorns were more likely to germinate, and acorn size was also positively correlated with seedling growth above and below ground. However, the root/shoot ratio of the seedlings was not associated with acorn size, despite considerable variation, suggesting that seed size does not affect the allocation of growth to different plant organs.

Our results largely echo the findings from other studies on the role of seed size in the early development of Mediterranean oaks. Gómez (2004) found in a field study that the mass of Holm oak acorns in Spain was positively correlated with germination rate, seedling height growth and survival over the first 2 years. Similarly, larger blue oak (*Q. douglasii*) and valley oak (*Q. lobata*) acorns had greater emergence rates, survival throughout the first year and increased seedling height (Tecklin and McCreary 1991, Sage and others 2011). The role of acorn size may, however, be diminished under field conditions. When planting *Q. ilex* acorns in the greenhouse and in the field, Navarro and others (2006) found that after 32 months of development, acorn size only explained variation of seedling growth in the greenhouse, but not under natural conditions. The positive effect of seed mass may thus be limited to early phases of seedling development. Nonetheless, I suggest that managers preferentially select large acorns when restoring oak habitat on the Channel Islands, as the combined effect of increased germinability and early growth could still provide a crucial advantage for seedlings.

In addition to selecting seed size, several other management actions may affect the success of seedlings growing from planted *Q. pacifica* acorns. Restoration efforts on Santa Catalina Island suggest that microhabitat variation, post-dispersal seed predation and seedling herbivory play an important role in seedling survival (Stratton 2009). Experiments using exclosures and tree tubes show that *Q. pacifica* seedlings perform best in tree tubes, at least where large herbivores still decimate a large proportion of young oaks (Stratton 2009). In addition to preventing herbivory, tree tubes may also provide seedlings with more water from fog precipitation, a factor that was not assessed previously. In future research, I aim to examine how tree tubes, as well as microhabitat variation and habitat-specific seed placement affect recruitment success of planted acorns.

Acknowledgments

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Establishing a Range-Wide Provenance Test in Valley Oak (*Quercus lobata* Née) at Two California Sites

Annette Delfino Mix, Jessica W. Wright, Paul F. Gugger, Christina Liang, and Victoria L. Sork

Abstract

We present the methods used to establish a provenance test in valley oak, *Quercus lobata*. Nearly 11,000 acorns were planted and 88 percent of those germinated. The resulting seedlings were measured after 1 and 2 years of growth, and were outplanted in the field in the winter of 2014-2015. This test represents a long-term resource for both research and conservation.

**Key words:** Provenance tests, *Quercus lobata*, valley oak

Introduction

We set out to establish a long-term provenance test of valley oak (*Quercus lobata*) collected from across the species range. Provenance tests are designed to compare survival and growth (plus other morphological and phenological traits) among trees sampled from different parts of the species range (Mátyás 1996). By having different sources grown in a common environment, we are able to look at how different sources perform in a novel climate, and how they might respond to climate change (Aitken and others 2008). This study has a multitude of goals, from very practical management questions on how to source seeds for ecological restoration projects involving oaks, to very detailed ecological genomic studies. Our collecting and plant propagating methods were developed with a standard quantitative genetic analysis in mind (with plans for genomic analyses as well in the future).

Here we outline the methods used to establish a provenance test of *Quercus lobata* trees in California, and we present some very early results from the study.

Methods

We attempted to initiate this study in the fall of 2011; however, it was not a mast year, and acorns were difficult to find. We decided to collect from 10 field sites and use those acorns to establish a pilot study, with plans for the larger acorn collection in 2012. It turned out that 2012 had a massive acorn crop, and we were able to collect from 95 different sites from across California.

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Overview

Acorns were collected and brought to the U.S. Department of Agriculture Forest Service (USDA FS), Institute of Forest Genetics (IFG), Placerville, California, where they were sown and then grown in the greenhouse for approximately 1 year. They were then stepped up to larger containers. On November 7, 2014, these trees were growing in two lath houses at the sites where they were to be outplanted in the winter of 2015: one at IFG, the other at the USDA FS Genetic Resource and Conservation Center (GRCC), Chico, California.

Acorn collection

Acorns were collected from across the species range in the fall of 2012, from October 9 to November 7. Sites were selected based on previous research, records of previous collections, and the species distribution across California with a goal to sample as broad an area of the species range as possible. Sites were separated by at least 30 km. There was a set of special collections done in three elevational transects: one at Mt. Hamilton, Santa Clara County, one outside of Madera into the Sierra Nevada foothills, and a third at Tejon Ranch in the Tehachapi mountains. These transects involved sampling trees along the elevational gradient at each of these sites.

At each of the 95 collecting sites, 20 acorns were collected from eight maternal trees (fewer if eight trees with acorns could not be found). The GPS location of each tree was taken, and a brief description of the site was written. A leaf sample for DNA extraction was taken from each tree. In addition, a herbarium sample was collected from each tree, consisting of a small branch with flowers and leaves. The DNA sample was kept cool until it could be placed in a -80 °C freezer. The herbarium sample was pressed in the field. The DNA and herbarium samples were returned to the Sork Lab at the University of California, Los Angeles (UCLA). The acorns were transported to IFG.

After collection, the acorns were stored in a walk-in cold box at 1.1 °C in paper bags inside unsealed zip lock plastic bags to keep the acorns moist, but to allow air flow to prevent rot.

Acorn planting

On November 14 and 15, 2012, 10,326 acorns were planted into Stuewe and Sons D40 containers, 6.4 cm diameter, 25.0 cm depth, 656 ml volume, 20 cells per rack. This container was selected because it had adequate volume for the first year growth and we were able to fit the amount of racks needed to sow the approximately 10,000 acorns into our greenhouse. We used Sunshine #4 aggregate plus soil mix. This mix contained Canadian sphagnum peat moss, coarse perlite, starter nutrient charge (with gypsum), dolomitic limestone, and long-lasting wetting agent. This soil was selected because it is an aggregate mix and, unlike vermiculite mixes, the soil holds its form when plants dry down, giving more flexibility with watering. The aggregate is preferred when growing a large number of plants to alleviate the slower growing plants from being too wet. The acorns were germinated under a 50 percent shade cloth.

With such a large amount of acorns to plant, we balanced our sowing layout between experimental design and practical culturing. Each family (here family = a collection from a single maternal tree) was given an accession number to simplify the
identification of each tree and to lessen the amount of error. The planting of the eight families (accessions) from each of the 95 collection sites was randomized throughout the greenhouse, but the 16 acorns planted within each family were sown in the same rack. This balance was made to reduce the error factor as we progressed with this study.

All collections were then randomized for sowing. There are distinct differences of growing conditions in the greenhouse and the location of each family was mapped within the greenhouse to allow for future data analyses to take that location information into account.

Each seed lot of acorns was surface sterilized with a 10 percent bleach solution to remove any molds or contaminants. The acorns were submerged in the bleach solution for one minute then rinsed in clean water before planting. The bleach solution was changed periodically during the planting process (fig. 1a). Acorns that floated were removed from the experiment. Acorns for each family were bulked weighed, and the number of acorns planted per family was recorded, allowing for the calculation of an average seed weight for each accession.

At planting, the acorns were embedded in the soil sideways but not covered; this prevented the acorns from being planted upside down and mimicked what happens in nature (fig. 1b).
It was determined in the 2011 pilot study that the soil and container were appropriate. In the pilot study, however, the greenhouse was kept at warmer growing temperatures which resulted in erratic germination, making it difficult to properly culture the growing plants among the non-germinated ones. We also felt that the unnatural germination time could influence our growth measurements. Therefore, for the study, the greenhouse was kept cool in the daylight hours (approximately 16 °C) and cold at night (approximately 3 °C). This was done to mimic what would be happening in nature and to achieve more uniform germination. It was observed that the acorns put down a tap root but did not put out any leaves. The greenhouse was kept cold through the winter months and warmed up with the ambient outside temperatures when the acorns started to naturally put on top growth. This worked very well for achieving uniform germination throughout the greenhouse. Acorns were germinated under a 50 percent shade cloth.

The soil moisture level was closely monitored and soil was kept moist but not wet. Until the leaves started to appear, the tubes were kept at the proper moisture level with mist sprinklers, set to mist twice a week. When leaves started to appear the
tubes were hand watered and adjustments were made in amount of water depending on the dryness of the soil in each rack. Where there were dry spots, those racks were watered twice; each container was filled with water, allowed to drain, and filled again.

Mildew was a problem, despite reducing humidity by watering in the early hours and opening the 50 percent shade cloth, giving the plants full sunlight for the majority of the day. The mildew level was unacceptable and the plants were sprayed with Eagle® 20EW fungicide at a rate of 35.5 ml per 99.2 m² (1.2 fl oz per 1000 sq ft) containing Activator 90®, 5 ml /3.78 l (1 tsp/gal) as the surfactant. This was done twice (May 17, 2013 and May 16, 2014). The only other pest was aphids, which appeared at the end of the growing season when the trees where shutting down and the leaves where starting to senesce. The IFG greenhouse practice is to limit the application of chemicals, especially insecticides. To achieve an acceptable balance of beneficial insects and aphids, a certain amount of insects must be tolerated. The protocol of removing infected leaves and keeping the greenhouse tidy of leaf debris is our common practice and was effective at keeping the aphids at an acceptable level.

**Germination**

Germination data was taken weekly using printed pot stakes starting January 2, 2013 and continuing to April 29, 2013. The number of days until germination was calculated on the Monday of each week. We recorded all the germination data from the printed tags when the growth measurements were taken. Germination was scored as above-ground emergence, since the tap root germination was impossible to monitor. As more germination occurred the ability to observe new germinants was difficult, so a flag was put into each tube with an acorn that had not begun to put on leaves to aid in detecting the later germination (fig. 1c). When the majority of germination was achieved, weekly monitoring of germination was discontinued and all new seedlings were put into the category of “late germination” (after 182 days). At this point the trees within a family (accession) were given individual identification numbers becoming individuals within each family.

There was an observed greenhouse location effect on germination. To ensure those effects were captured in data analysis, the greenhouse location of each accession was mapped and recorded. The greenhouse areas were as follows: Bay one-South window, South aisle, North window, North aisle; Bay two- North window North aisle.

**Mutants**

When growing a large number of individuals of one species it is common to see a number of mutations and other odd growing forms manifest in the phenotypes (fig. 2). We observed a number of albinos, and tissue was collected from each albino for future genetic analyses. There were other mutations as well and some of these plants died. Other phenotypes were temporary, and the plants later developed normal appearing leaves. These plants were taken out of the study but kept for observation. Some of the surviving mutants will be planted at the IFG site for future observation.
Figure 2—A set of mutant plants observed in this study.

Selection of 12 best plants
The best 12 of the 16 plants were selected to continue growing for the study. The culled trees were removed from the greenhouse beginning in July of 2013. Their germination date was recorded, and they were measured for height and diameter shortly after culling, a few months before the rest of the trees were measured. Therefore their height data was not compared directly with the main experimental trees. However, the change in basal diameter in that time was expected to be minimal.

First year measurements
Growth measurements were taken on all experimental seedlings in September and October of 2013. A total of 9,129 seedlings were measured. Measurements were disrupted by the government shutdown of 2013; however, temperatures were fairly cold at that point and only minimal additional growth was observed. Three leaves were collected from each seedling for further morphological analyses. We took height and diameter measurements for each plant using a meter stick and calipers.
Stepping up into larger pots for second year growth

To allow for more root growth, seedlings were repotted into larger pots in the winter of 2013-2014 (fig. 1d). We selected Stuewe and Sons TP414 pots—10.0 cm wide, 36.0 cm high, volume 2.83 liters. The same soil that was used in the germination phase was again used. We added Osmocote® 14-14-14 at a rate of 0.45 kg per 0.1 m³ (1 lb per 3.8 cu ft), mixed into the soil when filling the pots.

When the plants were stepped up to the larger pots, they were also moved into their complete randomized block design, as they will be planted into in the field. This was done to help with the organization and logistics of planting into the ground and will help account for the lath house location effects in the second year of growth. The field planting design consists of each maternal tree being represented once in each block, with the maternal trees from a site grouped together in a row-plot. This is a traditional design for provenance tests (Conkle 1973, Kitzmiller 2004) and allows for easier and more effective maintenance of the test over time. The trees will need to be thinned in the next 5 to 10 years, and this design facilitates that process. The position of each of the row-plots is also randomized between the blocks.

At this point the trees were separated into two groups, one for each of the planting sites, IFG and GRCC. The trees to be planted at the GRCC in Chico were then moved to a lath house at the planting site (fig. 3a, c). The trees remaining at IFG were moved to a lath house at the site (fig. 3b). This was done so the plants would acclimate to their eventual planting location. The plants where placed outside on benches that we are able to forklift out to the field. Figure 4 shows a Principal Component Analysis (PCA) of climate data derived from each of the collecting sites using the USDA FS climate estimates from Crookston and Rehfeldt (2008). The two planting sites are shown in white. The figure illustrates two points. First, it shows that the two planting sites both fall within the range of climate variation observed across all of our collecting sites. Second, the two planting sites are in fact quite different in terms of climate.
Figure 3—Photos from the lath house phase of the study. A. Moving the trees to the GRCC in Chico. B. The IFG lath house. C. The GRCC lath house.
Collecting Sites

IFG

Chico

PC 2 explains 20% of variation

PC 1 explains 51% of variation

Figure 4—A graph showing the results of a PCA of climate data derived for each of the acorn collecting sites and the two planting sites.

At the end of their second growing season, total height and basal diameter were again recorded for each plant in the experiment, and the extra plants that will be part of the field boarder rows.

Results

Germination

Despite keeping the greenhouse cool, some above-ground germination started in the winter months. We began taking germination records to capture this early germination at 49 days after sowing, but the majority of the germinations happened between 61 and 103 days after sowing (fig 5). Overall, we observed an 88 percent germination rate.
Figure 5—Chart showing the observed germination date for all 9110 individuals that germinated in this experiment.

First year measurements

Analysis of genetic correlations (correlations using the family mean values) among the measured traits showed that germination date was negatively correlated with all of the other measured traits (germination rate, acorn weight, basal diameter and height) (fig. 6a). Acorn weight was positively correlated with all measured traits except germination date (heavier acorns germinated earlier) (fig. 6a).

Comparing performance between benches, we did observe variation across the greenhouse in the growth of trees (fig. 6b). This suggests that indeed we need to keep track of the trees first planting location in future analyses. We will also be able to track this effect over time. We expect it to be random with respect to the future planting of the experiment because the planting location was randomized with respect to where the seedlings were growing in the greenhouse.
Figure 6—a. Correlations among the first year growth traits. Solid lines show positive correlations, dashed lines show negative ones. The thinner lines are significant at $p < 0.05$. The thicker lines are significant at $p < 0.0001$. b. Differences among the eight greenhouse benches where the seedlings were growing when they were measured after 1 year of growth.
Discussion

Valley oaks are under threat due to land conversion, and more recently, climate change. Information is lacking on the ecological genetics of this species, information that could be key to our understanding of how to manage this species as climate changes.

Here, we show that there are genetic correlations among traits and that there was variation in the timing of germination among these acorns collected across the species range. These early results are not appropriate to use for management decisions; however, they do indicate that this study is poised to produce results that will inform future management of oak woodlands.

This study represents a long-term investment to gain knowledge of the ecological genetics of this species. Once out-planted in the winter of 2014-2015, we will continue to collect survival and growth data for the next 20 to 50 years. In addition, we plan to collect additional morphological data on leaf traits as well as phenological data—recording the date when buds start to expand in the spring.

References


**Quercus lobata** Seedlings and Conspecific Neighbors: Competitors or Allies?¹

Claudia Tyler² and Shelly Cole Moritz²

**Abstract**

In conducting oak restoration, it is common to plant at least two acorns per location to increase the probability that at least one will germinate and produce a seedling. If both seedlings successfully establish, one is generally removed to reduce possible competition. To test the assumption that the near neighbors are competing, we examined several cohorts of valley oak (*Quercus lobata*) seedlings established from acorns planted at the University of California Sedgwick Reserve in Santa Barbara County. We assessed correlations between presence/absence of neighbors and individual performance, hypothesizing that seedlings that emerged without a near neighbor (only one of the two acorns produced a seedling) would have better survival and growth than those with both acorns producing seedlings within one planting location. However, over a 7 to 10 year period, we found that survival rates and mean height of *Q. lobata* with neighbors did not differ significantly from those that emerged and grew without a near neighbor. We also conducted removal experiments in which pairs of established near neighbor seedlings were randomly assigned to one of two treatments: control (both seedlings remain intact) and removal (one seedling in the pair is removed and the target remains). Growth (height, stem diameter at base, absolute and relative growth rates) was not significantly different between control and removals for any year (2011–2014). We also measured access to water via pre-dawn xylem pressure potentials (PDXPPs) in early fall. Contrary to predictions, PDXPPs were not significantly different between the treatments for any year (2011-2014). Both our observational and experimental findings indicate that near neighbors do not have negative impacts on performance for early life stages in *Q. lobata*. We also suggest that there may be advantages to allowing near neighbors to coexist in restoration plantings, where survival of the target individual is still uncertain.

**Key words:** competition, neighbor, predawn xylem pressure potential, seedling growth, seedling survival, water availability

**Introduction**

Ecological theory predicts that when resources are limited, intraspecific competition may be particularly strong since members of the same species are likely to be using the same resources in the same way (Connell 1983). Thus, it is reasonable to assume that an oak seedling with a “near neighbor”—a seedling emerging from an acorn deposited in the same microsite—will face competition and have reduced access to resources resulting in reduced growth and/or survival.

Oak seedlings may establish with near neighbors under natural or artificial circumstances. Acorn “planters” such as jays, magpies, or ground squirrels may cache or scatter-hoard multiple acorns per location (Carmen 1988) and some of those acorns may survive to germinate. Humans conducting oak restoration also disperse acorns in clusters, generally planting at least two acorns per location to increase the probability that at least one will germinate and produce a seedling (Bernhardt and Swiecki 1991). If both seedlings successfully establish, one is generally removed to

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reduce competition (McCreary 2001); that is, we assume that near neighbors in such close proximity are competing. In Mediterranean climates such as southern California, water availability is low during the summer drought and can limit growth of young oaks (Mahall and others 2009). However the interactions of oak seedlings as near neighbors and their effects have not been previously investigated.

To test the hypothesis that there is competition between near neighbors, we examined several cohorts of valley oak (*Quercus lobata*) seedlings established from acorns planted at UC Sedgwick Reserve, employing both observational and experimental approaches. *Q. lobata* is a California endemic species that has been severely impacted by human activities (reviewed in Tyler and others 2006) and even in remnant stands is generally in decline, with continued future declines likely (Davis and others 2011). These trends have contributed to interest in public and private conservation and restoration planting of this species (Alagona 2008, Giusti and others 2004). Thus, understanding the interactions of restored seedlings may be useful in guiding this effort.

## Methods

Research was conducted at the University of California Santa Barbara’s Sedgwick Reserve, located in central Santa Barbara County, California. The climate is Mediterranean, with hot dry summers and cool wet winters. Mean annual rainfall (calculated for the period 1950-2014) is 404 mm.

As part of large-scale field experiments related to oak restoration, acorns of coast live oak (*Q. agrifolia*) and valley oak have been planted at the reserve across a range of savanna and open woodland sites, starting in 1997 (Tyler and others 2002). For the present study we examined a subset of those plantings, specifically several different cohorts of valley oak seedlings established from acorns. In all cases, two acorns per planting location were sown in planting holes that were approximately 15 cm wide. Thus, acorns were placed within 5 cm from each other. Plantings were carried out in January-February of the given year. Here we only include seedlings that had been caged to exclude herbivores and seed predators, in order to examine interactions of seedlings in the absence of other potentially confounding factors. Protection from vertebrate animals was achieved with 1 cm mesh hardware cloth cylinders (diameter 10 cm, height 1.2 m). No supplemental water was provided to seedlings at any stage. Detailed methods described in Tyler and others (2002).

### Observational study

In two cohorts (planted in 1998 and 2003) we assessed correlations between presence/absence of neighbors and individual performance, comparing survival and growth of seedlings that emerged without a near neighbor (only one of the two acorns produced a seedling) to those with both acorns producing seedlings within one planting location. Measurements of survival (presence or absence) and growth (stem height, diameter at base and absolute and relative growth rates) were made annually in late spring to early summer.

### Experimental study

We established removal experiments in 2010 using seedling pairs that had been planted as acorns in 2003, and remained with both neighbors surviving to 2010. As above, all seedlings had established within cages to exclude herbivores. These
plantings were distributed across two different sites at the reserve (Lisque and Figueroa). Within each site, seedling pairs were stratified by size and then randomly assigned to either the control treatment (both seedlings left intact) or removal treatment, in which the smaller of the two seedlings was removed. Growth was measured annually (2010-2014). At one site (Figueroa) we also measured access to water via pre-dawn xylem pressure potentials (PDXPPs) in early fall, 2010-2014.

Results

**Observational study**
Germination and establishment rates were high in all locations in both cohorts. A large proportion of planting locations in both 1998 and 2003 cohorts established with two seedlings (both acorns germinated and emerged). Of the 144 locations planted in 1998, more than half (53 percent) had both acorns germinate and thus two seedlings establish, and 32 percent had one acorn germinate with a seedling established. In 2003, 59 percent of the 100 planting locations had two seedlings establish, and 24 percent had one seedling establish.

In each of these two planting cohorts, we compared survival of seedlings that emerged without a near neighbor (only one of the two acorns produced a seedling) to those with both acorns producing seedlings within one planting location (fig. 1). In neither cohort was survivorship higher for the seedlings growing alone, that is, without a neighbor. For the 1998 cohort, overall survivorship for the 10-year period from 1998 to 2008 was 51 percent for seedlings that started with two per location (with a near neighbor) compared to 45 percent for seedlings that started with one per location. Similarly, for the 2003 cohort, overall survivorship from 2003 to 2010 was 80 percent for seedlings starting with a neighbor, and 71 percent for those starting without a neighbor.

We compared the growth of seedlings that began with two per location and retained a neighbor for the whole study interval, to those that began with one per location (fig. 2). In both cohorts we found that seedling height (fig. 2), growth, and relative growth rates were not significantly different with vs. without a neighbor in any year (independent samples t-tests for each year and parameter, $P > 0.05$).
Figure 1—Number of individuals surviving over time. Plotted separately are the seedlings that started with two individuals per planting location (with a near neighbor) and those that started with only one per location. Data are for two different planting cohorts (1998 and 2003), and are plotted on a log-scale to facilitate comparison of survival rates since starting numbers vary.

Figure 2—Mean seedling height (and one s.e.) over time. Plotted separately are the seedlings that started and ended with two individuals per planting location (with a near neighbor for the entire period) and those that started with only one per location. Data are for two different planting cohorts (1998 and 2003).

**Experimental study**

We compared seedlings heights of target (largest) individuals in controls (neighbor intact) to removals (neighbor removed) (fig. 3). Seedling heights did not differ in 2010 before the removal treatment was initiated (independent samples t-tests, both sites 2010, $P >0.05$). In every subsequent year at both sites, we found no significant difference in mean target seedling height between the treatments (independent samples t-tests, both sites each year, $P >0.05$). We found the same pattern (no statistical difference between treatments) when we examined other measures of growth (diameter at base, annual growth or relative growth rate).
Assessment of predawn xylem pressure potentials of target seedlings in early fall from 2011 to 2014 have revealed no significant differences in water availability between seedlings grown with (controls) vs. those without a neighbor (removals) (independent samples t-tests, each year P > 0.05). (table 1).

Table 1—Mean predawn xylem pressure potentials, bars (1 s.e.). n = 13 for each treatment

<table>
<thead>
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<th>Year</th>
<th>Control</th>
<th>Removal</th>
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<tr>
<td>2011</td>
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<tr>
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<td>(1.8)</td>
<td>(2.1)</td>
</tr>
<tr>
<td>2012</td>
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<tr>
<td>(Oct 2)</td>
<td>(1.4)</td>
<td>(1.6)</td>
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<tr>
<td>2013</td>
<td>-18.3</td>
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<tr>
<td>(Sept 14)</td>
<td>(1.1)</td>
<td>(1.1)</td>
</tr>
<tr>
<td>2014</td>
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<td>-18.5</td>
</tr>
<tr>
<td>(Aug 24)</td>
<td>(1.1)</td>
<td>(1.6)</td>
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</tbody>
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Discussion

Oak seedlings that have emerged from the same microsite and are growing within a few centimeters of each other seem likely to interact in some way. Though light may not be limiting in savanna habitats, water may be (Baldocchi and others 2004, Mahall and others 2009). Valley oak is a winter-deciduous species and grows in spring as well as during the summer drought; therefore it is not unreasonable to suspect that near neighbors might be competing for water. Previous studies on valley oak seedling physiology have found that while valley oak are drought-tolerant, photosynthesis and
growth rates may be correlated positively with access to water in dry years (Mahall and others 2009).

Surprisingly, both our observational and experimental studies found no significant differences in performance of seedlings that are growing in close proximity to a conspecific neighbor to those without a neighbor (potential competitor). In fact, though not statistically significant, our survey of seedlings over a 10 year (1998 cohort) and 7 year (2003 cohort) period revealed that survivorship was slightly higher for seedlings growing with a neighbor. This result suggests that either the planting locations where two acorns germinate and two seedlings establish might be “better” in general, or that there may even be a positive interaction between neighboring seedlings. However, if the latter were true, we would expect to see a negative effect of neighbor removal, which was not the case in our experimental studies.

Rather, our finding of no significant differences in all cases—both observational studies and removal experiments—suggests that there are neither net negative (competitive) nor net positive (facilitative) interactions of these near neighbors in early life stages. It has been stated that “neutralism” should not be considered a type of ecological interaction (Arthur and Mitchell 1989), yet it appears in the present study that “neutralism” is the most appropriate term describing the net intraspecific interaction observed in young oak seedlings.

Our results have restoration implications, in that we found no evidence to advocate removal of neighbors in the seedling or even sapling size classes. We propose that there may in fact be justification for retaining near neighbors in restoration plantings where they are present. The first reason is that even seedlings that start with a neighbor may lose that neighbor eventually to various natural causes of mortality. If those locations had been culled to one seedling artificially, there is no “understudy” to take its place if it dies. A second reason to maintain a neighbor adjacent to the desired or target individual is that a neighbor may protect against or reduce impacts from herbivores. For example, at our study site we have observed large lone saplings become heavily damaged by bark stripping or damaged due to antler rubbing by deer. We suggest that such damage may have been less severe if another (especially a shorter) neighbor had been present. Such predictions warrant further experimental investigation. Based on our studies and additional observation, we propose that a conspecific near neighbor could in fact serve as an ally or at the very least be a neutral companion in the first decade in the life of a valley oak.

Acknowledgments

The seedlings studied in this research were established as part of the Santa Barbara County Oak Restoration Program funded through the Energy Division at Santa Barbara County’s Planning and Development Department, and the Santa Barbara County Agricultural Commissioner’s Office. We thank and acknowledge the contributions of Bruce Mahall and Frank Davis who were co-Principal Investigators on the Santa Barbara County Oak Restoration Program. Many individuals helped with oak plantings especially Bill Kuhn and Peter Slaughter. We thank Mike Williams, Virginia Boucher, Mark Reynolds, and Kate McCurdy for support at Sedgwick Reserve. We are grateful to our many field volunteers, especially our regular early morning assistants – Max Moritz, Stephanie Ma, and Vivienne Vincent.
References


Phenotypic Variation in California Populations of Valley Oak (Quercus lobata Née) Sampled Along Elevational Gradients

Ana L. Albarrán-Lara, Jessica W. Wright, Paul F. Gugger, Annette Delfino-Mix, Juan Manuel Peñaloza-Ramírez, and Victoria L. Sork

Abstract
California oaks exhibit tremendous phenotypic variation throughout their range. This variation reflects phenotypic plasticity in tree response to local environmental conditions as well as genetic differences underlying those phenotypes. In this study, we analyze phenotypic variation in leaf traits for valley oak adults sampled along three elevational transects and in young seedlings grown from their acorns in greenhouse conditions. This project represents the early phase of a long-term provenance study of valley oak (see Delfino Mix and others, Establishing a range-wide provenance test in valley oak (Quercus lobata Née) at two California sites, these proceedings) where we subsample the maternal families sampled along elevation gradients to assess the extent to which selection may be shaping geographical variation in leaf phenotypes of valley oak. We find that leaf thickness is the trait that shows correlations in adult populations in the field and significant variation in the greenhouse. For this trait, we also found significant differentiation across maternal families, providing preliminary evidence that this trait experiences differential selection across natural populations with different environments. This study, part of a large-scale provenance/genomic study of the genetic basis of phenotypic variation, provides an early analysis of leaf traits that may play an important role in local adaptation to climate environments and provide background for management and restoration of California oak forests.

Key words: elevational transect, phenotypic variation, Quercus lobata, valley oak

Introduction
Phenotypic variation, a fundamental attribute of all organisms, is the product of genetic variation and environmental variation, as well as their interactions. This variation reflects the outcome of long-term selection and the response to local environmental conditions. The study of phenotypic variation is one way to investigate the role of natural selection on phenotype due to the effect of local climate on tree populations (Endler 1986, Hedrick 2006). Phenotypic variation can be influenced by both genetic and environmental factors in natural populations, creating patterns of geographic variation in adaptive plant traits (for example, Rehfeldt and others 1999). Elevational gradients offer an opportunity to evaluate the extent of local adaptation in response to climate over small spatial scales. In a classic example, Clausen and others (1948) showed that Achillea phenotypes, such as growth form, size and leaf length, were associated with elevation and populations and that plants

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grew better at their home elevation than in other parts of the range, suggesting local adaptation. Evidence for local adaptation, particularly in response to climate, will be important for understanding species response to climate change. Populations in different parts of a species’ range and in different microhabitats will experience and respond to climate change differently (Davis and others 2005, Rehfeldt and others 2002, Rehfeldt and others 2006). This differential response is due to both the genetic composition of local populations and the magnitude of climate change, which will vary geographically as well (Gugger and others 2013, Sork and others 2010).

In this study, we document gradients in leaf traits in adults sampled along elevational transects in order to observe how phenotypic variation changes along steep climate gradients. Because these phenotypes represent the impacts of genes, environment, and their interaction, we then plant offspring of the adults in a common greenhouse environment to assess the genetic contribution. We present the findings from the first year of a newly established long-term study to gain an initial analysis of what leaf traits may have a strong genetic component and which ones may reflect environmental conditions. Specifically, we have three objectives: (1) identify phenotypic variation in adult leaf morphology that shows significant association along three elevational transects and their corresponding climate gradients; (2) measure phenotypic variation in seedling traits to test whether they differ significantly among transects and among maternal families; and (3) test whether family differences in seedling traits correlate with spatial or climate gradients of maternal tree locations. Recognizing that maternal effects of the seed source may influence the phenotypes young seedlings, findings from the second and third objectives provide initial evidence of whether selection is shaping phenotypic variation in leaf traits and identifies which leaf phenotypic traits may be most affected by long-term selection pressures. We will briefly discuss the implications of this approach for oak management and restoration ecology.

Methods

Valley oak, *Quercus lobata*, is a dominant or co-dominant species in oak savannas, oak woodlands and riparian forests in the foothills of the Sierra Nevada, Coastal Ranges, and Transverse Ranges that surround the Central Valley of California (Griffin and Critchfield 1972). The species inhabits diverse climatic and geographical zones from sea level to 1750 m and local populations support exceptionally diverse animal and plant communities (Pavlik and others 1995). Valley oak is a species of conservation concern because it has lost significant amounts of cover in the last 300 years (Kelly and others 2005) and it currently has recruitment limitations in many areas (Tyler and others 2006). Valley oak is an important resource for acorn woodpeckers (Koenig and Haydock 1999, Scofield and others 2011, Scofield and others 2012, Thompson and others 2014), western scrub jays (Koenig and others 2009), and many rodent species (Jameson and Peeters 2004). Contemporary gene flow through pollen and seed dispersal can be sufficiently restricted to create local genetic structure that would allow local adaptation (Grivet and others 2005, Pluess and others 2009, Smouse and others 2001, Sork and others 2002), while at the same time, pollen movement has a long tail that maintains genetic connectivity among populations (Austerlitz and others 2004, Pluess and others 2009). Historical colonization has created local genetic structure that would have allowed local populations to adapt to local environments (Gugger and others 2013, Sork and others 2010). Analysis of future suitable habitats based on predicted levels of climate change indicate that some populations would have to migrate long distances to track
favorable climate (Sork and others, 2010), which is unlikely in an increasingly fragmented landscape.

During October 2012, we sampled leaves and acorns from trees along three different elevational transects (fig. 1). Leaves were typically collected from lower, sun-exposed branches, but this varied depending on the location and structure of the trees. Sample sizes and elevations, latitude, and longitude of each adult are listed in table 1. We used latitude and longitude to obtain five current climate variables (table 2), based on previous work. The data were obtained by using the custom climate data requests of U.S. Department of Agriculture, Forest Service (USDA FS) (Rehfeldt 2006): http://forest.moscowfsl.wsu.edu/climate/customData/.

![Figure 1—Locations of three elevational transects where leaf samples and acorns were collected from 127 valley oak trees.](image)

**Greenhouse methods**

In the fall of 2012, we selected 59 families derived from the three elevational transects for our study. Acorns from these families were included in large provenance study initiated at the same time (see Delfino Mix and others, Establishing a range-wide provenance test in valley oak (*Quercus lobata* Née) at two California sites, these proceedings). Acorns were planted at the USDA FS, Pacific Southwest Research Station’s Institute of Forest Genetics greenhouse in Placerville, California. The greenhouse is located at 38° 44’ 23” N latitude and 120° 44’ 32” W longitude and 849 m above sea level, at the edge of the species range of valley oak but within its climate range (see fig. 4, Delfino Mix and others, Establishing a range-wide provenance test in valley oak (*Quercus lobata* Née) at two California sites, these proceedings). In total, we planted acorns from 14 trees from Mt. Hamilton, 9 trees from Madera, and 36 trees from Tejon Ranch Transect Transects (table 1).
Table 1—Location and sample size of adult trees of valley oak collected along the three elevational transects and the number of families from those adults grown in greenhouse conditions

<table>
<thead>
<tr>
<th>Transect</th>
<th>Number of Adults</th>
<th>Number of Families</th>
<th>Number of Seedlings</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation (m)</th>
</tr>
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<tbody>
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<td>Madera</td>
<td>2</td>
<td></td>
<td></td>
<td>36.9950</td>
<td>-120.0010</td>
<td>78</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td>37.0269</td>
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<tr>
<td></td>
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<td>Tejon Ranch</td>
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<td>51</td>
<td>36</td>
<td>402</td>
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Acorns were bulk weighed by family before planting. Acorn collecting and planting are described in Delfino Mix and others (Establishing a range-wide provenance test in valley oak (Quercus lobata Née) at two California sites, these proceedings) using acorns collected in October and measured after 1 year of growth (fig. 2).

**Adult and seedling measurements**

From pressed vouchers of adult leaves sampled, we measured the following traits for three leaves per tree: leaf area, leaf thickness, leaf thickness per unit leaf area, leaf dry mass, leaf mass per unit area (LMA), leaf length, perimeter, and leaf perimeter per square root of leaf area as an index of leaf lobedness for each tree. Thickness was measured with digital calipers. Area, length and perimeter were measured in ImageJ (Rasband 2010) using binarized images of leaves from a standard flat bed scanner.

After acorns were planted in November, we recorded days until germination. In fall of 2013, at the end of the first growing season, we recorded the following seedling traits (sample sizes in table 1): diameter of stem base (mm), and height (cm) (see figure 2, bottom). To standardize the developmental states of leaves across seedlings, we selected the three youngest fully emerged leaves from each seedling and then pressed and dried them in paper envelopes. From the pressed vouchers, we measured the same leaf traits measured for adults and listed above. All analyses are based on average across three leaves per seedling.

**Statistical analyses**

For Objective 1, examining adult phenotypic variation, we first describe the environmental differences among the three sites by conducting a canonical discriminant function (CDF) analysis with the five climate variables and then describe morphological differences among the three sites using a discriminant function analysis with six leaf variables using IBM SPSS 20. For each transect, we
used the six leaf measurements as dependent variables and elevation and the five climate variables as independent variables.

For Objective 2, we tested whether days to germination, seedling diameter, and seedling height in the first year were significantly different among transects and across maternal plants within transect, using mixed model nested ANOVAs where transect is a main effect and maternal family nested within transect is a random effect. We used this same model for all morphological measurements of seedlings leaves using the mean values per seedling as the response variable. Resulting $P$-values were adjusted for multiple testing using the false discovery rate (FDR) method of Benjamini and Hochberg (1995).

For Objective 3, we examined the association between seedling types and environmental variables in two ways. First, we estimated the individual correlation coefficients for seedling traits of maternal families and environmental variables associated with the locality of maternal tree. $P$-values were FDR-adjusted as above. Second, we examined the association between phenotype and environment with a redundancy analysis (RDA) multivariate model to identify the most important seedling traits and climate variables taking into account the covariance among variables within each type.

**Results**

**Objective 1**

The CDF analysis of climate environments at the sampling localities of the adult populations yielded two functions (F1 and F2) that explain 85.9 percent and 14.1 percent of total variation, respectively. Highly significant climatic discrimination was found among the three elevational gradients (F1, Wilks’ $\lambda = 0.002$; $\chi^2 = 765.3$; df = 10; $P = 0.0001$; F2, Wilks’ $\lambda = 0.102$; $\chi^2 = 277.9$; df = 4; $P = 0.0001$).

The three transects have very different climate environments, with much less variation within each transect than between (see fig. 3). The standardized canonical discriminant function coefficients indicated that two climate variables, GSDD5 and $T_{\text{min}}$, explain most of the differences among the three transects (table 2). The trends...
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indicate that the Tejon Ranch transect was the coldest and Madera was the warmest. Within each transect, it is interesting to note that the slope of the points for the Tejon Ranch and Madera transects was similar, indicating similar climate variables varied along those transect. The Mt. Hamilton transect points have a very different slope, suggesting a different pattern of climate variation along the transect.

When we examined the CDF of adult leaf traits, we found more variation among individuals within each transect (fig. 4) than we observed for the climate variables (fig. 3). The CDF of adult morphological leaf traits revealed 77.6 percent is significant associated with F1 (Wilks’ $\lambda = 0.46; \chi^2 = 95.28; \text{df} = 12; P = 0.0001$) and 22.4 percent with F2 (Wilks’ $\lambda = 0.82; \chi^2 = 24.8; \text{df} = 5; P = 0.0001$). Leaf thickness and leaf dry mass per unit area had high coefficients on the first F1 and lobedness index and leaf dry mass per unit area on F2 (table 3). The trees sampled along the Madera Transect showed the most variation along the first axis providing an indication of the balance between leaf size and thickness at this drier site.

Table 2—Standardized canonical discriminant function coefficients (F1 and F2) of the five climate variables analyzed to determine climatic differentiation among the three elevational transects of valley oak

<table>
<thead>
<tr>
<th>Climate variables</th>
<th>F1</th>
<th>F2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growing season precipitation from April through September (GSP)</td>
<td>0.176</td>
<td>-0.334</td>
</tr>
<tr>
<td>Mean maximum temperature in the warmest month ($T_{\text{max}}$)</td>
<td>-1.895</td>
<td>-3.897</td>
</tr>
<tr>
<td>Mean minimum temperature in the coldest month ($T_{\text{min}}$)</td>
<td>-4.948</td>
<td>0.012</td>
</tr>
<tr>
<td>Growing season growing degree-days greater than 5 °C (GSDD$5$)</td>
<td>6.883</td>
<td>4.082</td>
</tr>
<tr>
<td>Summer/spring precipitation balance: precipitation of July + August divided by precipitation of April + May (SmSprPB)</td>
<td>0.200</td>
<td>1.114</td>
</tr>
</tbody>
</table>

Table 3—Standardized canonical discriminant function coefficients of six morphological traits of adult leaves analyzed to determine morphological differentiation among the three elevational transects of valley oak

<table>
<thead>
<tr>
<th>Leaf traits (Means per three leaves per adult)</th>
<th>F1</th>
<th>F2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thickness (millimeter)</td>
<td>0.997</td>
<td>0.400</td>
</tr>
<tr>
<td>Thickness per area (millimeter per centimeter$^2$)</td>
<td>0.308</td>
<td>-0.480</td>
</tr>
<tr>
<td>Leaf dry mass per unit area (LMA; grams per centimeter$^3$)</td>
<td>-0.621</td>
<td>0.612</td>
</tr>
<tr>
<td>Mean leaf length (cm)</td>
<td>-0.136</td>
<td>0.577</td>
</tr>
<tr>
<td>Lobedness Index = perimeter (centimeter) per square root of leaf area (centimeter)</td>
<td>-0.367</td>
<td>0.642</td>
</tr>
<tr>
<td>Leaf dry mass (gram)</td>
<td>0.053</td>
<td>-0.533</td>
</tr>
</tbody>
</table>

**Objective 2**

Using separate nested ANOVA for each seedling trait, we find that all families within transect were significantly different using the overall error term (ANOVA, df = 56/603, $P < 0.0001$). Our nested ANOVA model also reveals that many seedling traits were significantly different among transects using family within transect as the error term ($P$-values shown in table 4). We found that leaf thickness showed the strongest differences across transects, with the Madera transect having the thickest and smallest leaves on average (see table 4).
Tables 4—Summary of transect means for first year seedling traits measured in greenhouse at Institute of Forest Genetics, Placerville, California. We tested the significance using separate nested ANOVAs where the main effect of transect was tested over family nested within transect as error term, with false discovery rate (FDR)-adjusted $P$-values associated with degrees of freedom $df = 2, 46$ of numerator and denominator.

<table>
<thead>
<tr>
<th>Seedling trait</th>
<th>$FDR$-adjusted $P$-value</th>
<th>Mt. Hamilton</th>
<th>Madera</th>
<th>Tejon Ranch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Days until germination</td>
<td>NS</td>
<td>87.8</td>
<td>86.2</td>
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<tr>
<td>Mean family seed weight (gram)</td>
<td>NS</td>
<td>7.3</td>
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<tr>
<td>Seedling stem diameter (millimeter)</td>
<td>0.017</td>
<td>2.8</td>
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<td>Seedling height (centimeter)</td>
<td>NS</td>
<td>121.8</td>
<td>161.0</td>
<td>149.7</td>
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<tr>
<td>Mean leaf thickness (millimeter)</td>
<td>0.001</td>
<td>0.131</td>
<td>0.160</td>
<td>0.155</td>
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<tr>
<td>Mean leaf thickness per area (millimeter per centimeter$^2$)</td>
<td>0.007</td>
<td>0.011</td>
<td>0.016</td>
<td>0.012</td>
</tr>
<tr>
<td>Mean leaf length (centimeter)</td>
<td>0.031</td>
<td>6.26</td>
<td>5.84</td>
<td>6.60</td>
</tr>
<tr>
<td>Leaf mass per unit area (g/cm$^2$)</td>
<td>NS</td>
<td>0.009</td>
<td>0.009</td>
<td>0.009</td>
</tr>
<tr>
<td>Lobedness (centimeter per centimeter)</td>
<td>NS</td>
<td>5.8</td>
<td>5.6</td>
<td>5.7</td>
</tr>
<tr>
<td>Mean leaf dry mass (gram)</td>
<td>0.010</td>
<td>0.112</td>
<td>0.092</td>
<td>0.126</td>
</tr>
<tr>
<td>Mean leaf area (centimeter$^2$)</td>
<td>0.015</td>
<td>12.7</td>
<td>10.9</td>
<td>14.3</td>
</tr>
</tbody>
</table>

**Objective 3**

Many seedling leaf traits were correlated with geographical and climate gradients of the maternal plant locations suggesting that these traits may reflect selection on maternal trees. Leaf thickness was most highly correlated with $T_{\text{max}}$ and longitude, but also with latitude and GSDD5 (table 5). Latitude and Sm$\text{SprPB}$ were most frequently correlated with seedling leaf traits (table 5). Elevation was correlated with only two traits—days to germination and seedling leaf area, and longitude was correlated with leaf thickness only.

We also examined the association between leaf traits and environmental variables using a multivariate model, Redundancy Analysis (RDA), which is essentially a multivariate correlation test. We found that the overall models showed a significant association between seedling leaf traits for families sampled at Mt. Hamilton and Tejon Ranch transects, but not Madera Transect, possibly because of a low sample size and only a small section of the gradient represented in the common garden. Based on the scores showing the association between individual traits and the two main axes (RDA1 and RDA2), we find that stem diameter, leaf thickness per area, leaf length, and leaf dry mass were the traits most important for Mt. Hamilton families (table 6.A), while GSDD5, elevation, and $T_{\text{max}}$ were the most important environmental variables. For Tejon Ranch, leaf dry mass, height, leaf length and stem diameter were the traits most important and $T_{\text{max}}$, GSDD5, longitude, and elevation were the important environmental variables. In the Madera transect, most traits had similar associations and longitude, elevation, and $T_{\text{min}}$ were the most important environmental variables. Leaf thickness per area and leaf dry mass were important across the three transects and were correlated with several climate variables in the single correlation tests across all samples. These multivariate tests indicate that leaf morphology is correlated with climate and spatial gradients.
Table 5—Correlations of mean leaf traits per family with spatial and climate variables of localities of maternal plants (top number) with false discovery rate adjusted P-values (bottom number). Significant correlations are in bold. Sample sizes are 59 families, except seed weight with 58 families.

<table>
<thead>
<tr>
<th></th>
<th>Days to germination</th>
<th>Diameter</th>
<th>Leaf thickness</th>
<th>Leaf thickness per area</th>
<th>Leaf length</th>
<th>Leaf dry mass</th>
<th>Leaf area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>-0.302</td>
<td>-0.331</td>
<td>-0.3450</td>
<td>0.087</td>
<td>-0.286</td>
<td>-0.327</td>
<td>-0.328</td>
</tr>
<tr>
<td></td>
<td>0.056</td>
<td>0.044</td>
<td>0.039</td>
<td>0.522</td>
<td>0.060</td>
<td>0.044</td>
<td>0.044</td>
</tr>
<tr>
<td>Longitude</td>
<td>0.238</td>
<td>0.184</td>
<td><strong>0.4760</strong></td>
<td>0.123</td>
<td>0.146</td>
<td>0.153</td>
<td>0.173</td>
</tr>
<tr>
<td></td>
<td>0.115</td>
<td>0.224</td>
<td>&lt;-0.0001</td>
<td>0.378</td>
<td>0.314</td>
<td>0.295</td>
<td>0.241</td>
</tr>
<tr>
<td>Elevation</td>
<td><strong>0.406</strong></td>
<td>0.254</td>
<td>-0.1330</td>
<td>-0.244</td>
<td>0.196</td>
<td>0.236</td>
<td><strong>0.262</strong></td>
</tr>
<tr>
<td></td>
<td>0.019</td>
<td>0.097</td>
<td>0.347</td>
<td>0.107</td>
<td>0.195</td>
<td>0.115</td>
<td>0.087</td>
</tr>
<tr>
<td>GSP</td>
<td>-0.143</td>
<td>-0.316</td>
<td>-0.2470</td>
<td>0.178</td>
<td>-0.304</td>
<td><strong>-0.382</strong></td>
<td><strong>-0.323</strong></td>
</tr>
<tr>
<td></td>
<td>0.319</td>
<td>0.049</td>
<td>0.105</td>
<td>0.236</td>
<td>0.056</td>
<td>0.028</td>
<td>0.046</td>
</tr>
<tr>
<td>T_min</td>
<td><strong>-0.354</strong></td>
<td>-0.276</td>
<td>-0.2470</td>
<td>0.078</td>
<td>-0.232</td>
<td><strong>-0.269</strong></td>
<td><strong>-0.291</strong></td>
</tr>
<tr>
<td></td>
<td>0.037</td>
<td>0.071</td>
<td>0.105</td>
<td>0.556</td>
<td>0.120</td>
<td>0.078</td>
<td>0.060</td>
</tr>
<tr>
<td>T_max</td>
<td>-0.29</td>
<td>-0.134</td>
<td><strong>0.5700</strong></td>
<td><strong>0.403</strong></td>
<td>-0.108</td>
<td>-0.159</td>
<td>-0.175</td>
</tr>
<tr>
<td></td>
<td>0.060</td>
<td>0.347</td>
<td>0.003</td>
<td>0.022</td>
<td>0.437</td>
<td>0.286</td>
<td>0.240</td>
</tr>
<tr>
<td>GSDD5</td>
<td><strong>-0.396</strong></td>
<td>-0.193</td>
<td><strong>0.3210</strong></td>
<td>0.308</td>
<td>-0.157</td>
<td>-0.213</td>
<td>-0.231</td>
</tr>
<tr>
<td></td>
<td>0.022</td>
<td>0.199</td>
<td>0.046</td>
<td>0.056</td>
<td>0.286</td>
<td>0.156</td>
<td>0.120</td>
</tr>
<tr>
<td>SmSprPB</td>
<td><strong>0.358</strong></td>
<td>0.288</td>
<td>0.2880</td>
<td>-0.106</td>
<td>0.286</td>
<td><strong>0.355</strong></td>
<td><strong>0.336</strong></td>
</tr>
<tr>
<td></td>
<td>0.037</td>
<td>0.060</td>
<td>0.060</td>
<td>0.438</td>
<td>0.060</td>
<td>0.037</td>
<td>0.044</td>
</tr>
</tbody>
</table>

Discussion

Natural populations of valley oak contained significant phenotypic variation among three elevational transects that were geographically separated. The trait that differed most strongly in adult trees was leaf thickness. To understand the extent to which phenotypic variation is due to underlying genetic variation, we planted acorns from a subsample of those adult trees in a greenhouse and found that every leaf trait we examined showed significant differentiation in seedlings among maternal families. In particular, when we compared genetic differentiation among transects, the most significant traits were leaf thickness per area and leaf dry mass. On average, the Madera site had the thickest leaves and it also had the warmest temperature. When we looked to see whether leaf thickness showed an association with climate, which would be initial evidence that this trait is under selection, we found a positive correlation with maximum temperature. Given that leaf thickness can be a structural mechanism to reduce evaporative water loss, we suggest that future work looking for locally adaptive traits should pay attention to this character. For example, *Q. ilex* seedlings from the driest provenance, when grown in a common garden from seeds of different provenances, showed higher leaf mass area and total leaf thickness (Gratani and others 2003). These morphological traits were associated with higher water use efficiency, whereas, smaller leaf area was associated with a higher photosynthetic capacity in low air temperature conditions, suggesting potentially adaptive features to provenance climate.
### Table 6—Summary of scores of association of eight morphological seedling leaf traits with two Redundancy Axes (A) and scores of environmental variables with two RDA axes (B)

<table>
<thead>
<tr>
<th>A. Seedlings leaf traits</th>
<th>Madera RDA1</th>
<th>Madera RDA2</th>
<th>Mt. Hamilton RDA1</th>
<th>Mt. Hamilton RDA2</th>
<th>Tejon Ranch RDA1</th>
<th>Tejon Ranch RDA2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem diameter</td>
<td>-0.733</td>
<td>-0.135</td>
<td>-0.957</td>
<td>-0.053</td>
<td>0.923</td>
<td>-0.196</td>
</tr>
<tr>
<td>Height</td>
<td>-0.697</td>
<td>0.327</td>
<td>-0.863</td>
<td>-0.054</td>
<td>1.046</td>
<td>0.109</td>
</tr>
<tr>
<td>Thickness</td>
<td>-0.771</td>
<td>-0.457</td>
<td>0.035</td>
<td>-0.943</td>
<td>0.470</td>
<td>1.222</td>
</tr>
<tr>
<td>Thickness per area</td>
<td>0.639</td>
<td>-0.331</td>
<td>1.022</td>
<td>-0.249</td>
<td>-0.644</td>
<td>0.838</td>
</tr>
<tr>
<td>Length</td>
<td>-0.497</td>
<td>0.327</td>
<td>-1.012</td>
<td>0.053</td>
<td>0.940</td>
<td>-0.162</td>
</tr>
<tr>
<td>LMA</td>
<td>-0.446</td>
<td>-0.589</td>
<td>0.200</td>
<td>-0.713</td>
<td>0.461</td>
<td>0.349</td>
</tr>
<tr>
<td>Lobedness</td>
<td>-0.419</td>
<td>0.274</td>
<td>-0.760</td>
<td>-0.315</td>
<td>0.636</td>
<td>0.154</td>
</tr>
<tr>
<td>Leaf dry mass</td>
<td>-0.741</td>
<td>-0.003</td>
<td>-0.942</td>
<td>-0.157</td>
<td>1.080</td>
<td>-0.068</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>B. Climate and geographical variables</th>
<th>Madera RDA1</th>
<th>Madera RDA2</th>
<th>Mt. Hamilton RDA1</th>
<th>Mt. Hamilton RDA2</th>
<th>Tejon Ranch RDA1</th>
<th>Tejon Ranch RDA2</th>
</tr>
</thead>
<tbody>
<tr>
<td>GSP</td>
<td>0.249</td>
<td>0.832</td>
<td>-0.138</td>
<td>0.407</td>
<td>-0.107</td>
<td>-0.845</td>
</tr>
<tr>
<td>$T_{\text{min}}$</td>
<td>0.263</td>
<td>0.839</td>
<td>0.101</td>
<td>-0.344</td>
<td>0.121</td>
<td>0.612</td>
</tr>
<tr>
<td>$T_{\text{max}}$</td>
<td>0.241</td>
<td>0.035</td>
<td>0.241</td>
<td>0.035</td>
<td>0.279</td>
<td>0.643</td>
</tr>
<tr>
<td>GSDD5</td>
<td>-0.092</td>
<td>0.864</td>
<td>0.212</td>
<td>-0.165</td>
<td>0.285</td>
<td>0.558</td>
</tr>
<tr>
<td>SmrSprPB</td>
<td>0.152</td>
<td>-0.139</td>
<td>0.152</td>
<td>-0.139</td>
<td>-0.166</td>
<td>0.314</td>
</tr>
<tr>
<td>Elevation</td>
<td>0.370</td>
<td>0.672</td>
<td>-0.178</td>
<td>0.252</td>
<td>-0.246</td>
<td>-0.657</td>
</tr>
<tr>
<td>Longitude</td>
<td>0.262</td>
<td>0.840</td>
<td>-0.066</td>
<td>0.586</td>
<td>-0.304</td>
<td>-0.818</td>
</tr>
<tr>
<td>Latitude</td>
<td>-0.122</td>
<td>-0.752</td>
<td>-0.120</td>
<td>-0.879</td>
<td>0.149</td>
<td>0.887</td>
</tr>
</tbody>
</table>

This study suggests that leaf traits are highly differentiated across maternal families and geographical regions, but these findings must be considered cautiously because maternal effects may enhance differentiation among families and possibly overestimate the degree of genetic differentiation. We also found that many leaf traits other than leaf thickness that were related to mass and size, such as leaf dry mass, leaf length and leaf area, were also significantly correlated with geographical and climate gradients, though interestingly seed weight, considered a measure of maternal investment, was correlated only with $T_{\text{max}}$. Again, we caution that these correlations may also be enhanced by maternal effects. Nonetheless, change in morphological traits consistent with a direct response to climate change was observed in *Dodonaea viscosa* subsp. *angustissima*, where leaf width and leaf area were associated with temperature along latitudinal and elevational gradients, respectively (Guerin and others 2012). Thus, other studies have shown a genetic basis for traits such as the ones measured here.

Through the greenhouse experiment, we also found that days until germination showed genetic differentiation among transects and was correlated with latitude and elevation for this trait. The correlation with latitude might suggest that either photoperiod changes or growing season associated with climate might select for more delayed germination. The correlation with elevation as well as several climate variables also indicates that growing season may shape the delay in germination. For example, the number for growing degree-days above 5 °C was negatively correlated
with the days until germination such that provenances from places with a longer growing season germinated faster.

In summary, this study identifies extensive phenotypic variation in leaf morphology in adult populations of valley oak and initial evidence that much of that variation is due to geographical differences and to genetically based differences among families that appears to be under selection. Future analysis of phenotypic traits in these individuals and the full provenance study when they are older and less likely to reflect maternal effects will provide valuable insight about the genetic basis of valley oak phenotypes associated with local climate environments.

**Next steps and implications for oak management and restoration**

This study is part of a large-scale, species-wide provenance study where we will be measuring many phenotypic traits in the future (see Delfino-Mix and others, Establishing a range-wide provenance test in valley oak (*Quercus lobata* Née) at two California sites, these proceedings). The findings, which were based on trees sampled from sharp climate gradients along three elevational transects, demonstrate that at least a portion of the phenotypic variation we observe in natural populations may reflect the impact of natural selection. Using next generation sequencing tools, we are also conducting a parallel genomic study to look for marker genes that are associated with geographical, climate and trait variation in these populations of trees. As plants in the provenance test become older, we will associate phenotypes important to local adaptation with DNA sequence data to find genetic markers for adaptive genetic variation.

**Acknowledgments**

We thank Phoebe Prather and the Tejon Ranch Conservancy for providing access to the Tejon Ranch. For help with planting, we thank Tom Blush, Lisa Crane, Robyn Scibilio, and Paul Hodgskiss. For seedling measurements, we thank Courtney Canning, Daisy Carrillo, Carlene Carvalho, Paul Hodgskiss, Andy Liang, Sarah Ratay, and Mark Taylor. Financial support was provided by the Pacific Southwest Research Station and research seed funding from UCLA.

**References**


Sork, V.L.; Davis, F.W.; Smouse, P.E.; Apsit, V.J.; Dyer, R.J.; Fernandez-M, J.F.; Kuhn, B. 


Urban Sacramento Oak Reforestation: 17 Years and 20,000 Trees

Zarah Wyly\textsuperscript{2} and Erika Teach\textsuperscript{2}

Abstract

The Sacramento Tree Foundation (Tree Foundation), a nonprofit organization operating in the greater Sacramento California region, has been engaged in planting native oak trees in urban and suburban areas since 1998. Through an effort to provide efficient access to tree mitigation services and support compliance with local tree protection ordinances, more than 20,038 trees have been planted, monitored and cared for. Through developing the program and building hyper-local best practices, Tree Foundation staff has achieved a very high rate of success, growing the program to include a broad variety of reforestation, habitat restoration, habitat creation and urban forestry services. As urbanization continues to spread into our oak woodlands, reforestation and habitat enhancement of disturbed open space, urban edges and waterway corridors will support conservation of habitat and species. Successful methods of managing tree establishment issues will increase project sustainability and maximize the cost effectiveness of this work.

Key words: oak reforestation, Sacramento, tree mitigation, urban forestry

History

The Sacramento Tree Foundation (Tree Foundation) is a 501c3 nonprofit organization operating in Sacramento California since 1982. Focused on planting trees and building community, as of 2014 the organization has 25 employees and an annual operating budget of 2.1 million dollars. Though early efforts focused on the urban canopy and city/tree interface issues, today the Tree Foundation operates a variety of programs and services focused on a spectrum of issues from watershed health to public health, energy savings trees to carbon mitigation. In 1998 the Tree Foundation began the operation of the Native Trees in Urban and Rural Environments (NATURE) program, focused on mitigation and planting of native trees. This program has grown and expanded to include a full-service tree mitigation program that operates with a strong commitment to sustainable projects and community involvement.

In 1981 the County of Sacramento California adopted an ordinance to protect and mitigate for the removal of native and landmark trees in circumstances that would otherwise not require action under the California Environmental Quality Act (CEQA). Since its inception, the Tree Preservation Ordinance has required the mitigation of tens of thousands (the total number is unknown as it is not tracked by Sacramento County) of protected trees throughout Sacramento County, with the vast majority of these being native.

\textsuperscript{1} An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia California.

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trees. Many cities within the Sacramento region have adopted the same or similar ordinances and also require mitigation when impacting or removing specific trees. Working with both public agencies and private developers, the Tree Foundation has received 5.1 million dollars of tree mitigation funding to plant, establish and monitor 19,818 trees due to the enforcement of these local ordinances. With these funds, the Tree Foundation has been able to plant and care for 20,038 trees at 115 locations throughout the greater Sacramento area.

In the beginning of this effort, the Tree Foundation followed the best practices currently in use for urban tree planting to meet these obligations. The very first planting projects were located in traditionally landscaped parks or school yards, often directly within areas of turf grass. Large sized planting materials sourced from traditional nurseries were used. The standard planting materials were native valley oak (*Quercus lobata*) trees in #15 size pots and for several projects ball and burlap trees with 5.1 cm (2 inch) caliper trunks were purchased from nurseries as far away as northern Oregon. Planting protocol followed standard urban methods and trees were staked and pruned to meet standard park landscape shape and function. Follow up irrigation and ongoing tree maintenance was delegated to partner land managers to enact with mixed tree establishment results.

Local tree preservation ordinances all require significant ongoing maintenance and monitoring post planting, with annual reporting to local agency officials. Currently the Tree Foundation undertakes official monitoring with reports submitted once a year. The earliest projects were visited and monitored two times yearly with corrective measures taken once a year in late fall or winter. As planting locations within maintained turf became more challenging to find and secure for plantings with large numbers of trees, the program began to look for non-irrigated park edges, wide street sides and medians, bike paths, open space preserves and other similar areas to plant. As plantings moved to non-irrigated spaces on the urban/wild land interface, tree survival dropped drastically and overall project success was compromised. Though the locations and circumstances had changed, the planting methods and care regime had not. The planting of #15 sized or ball and burlap nursery stock into non-irrigated, un-maintained natural spaces with inconsistent follow up care resulted in 50 to 90 percent mortality on some projects, depending on the specific site, project partner and rainfall during that first project year.

The year 2001 was a banner year for the program. For the previous 3 years the program had serviced one to three native tree mitigation contracts and averaged less than 200 mitigation trees planted each year. In the fall of 2001 a contract for the mitigation of 878 native oak trees was received by the program as well as six other contracts for an annual total of 1,278 mitigation trees. These trees were planted in two different locations with the majority of the native oaks being planted at the Haggin Oaks Golf Course, north of downtown Sacramento and adjacent to the Capital City Freeway. From the start, this project was challenging. A mix of planting materials was sourced from a variety of nurseries and in house from the Tree Foundation Seed to Seedling education program for elementary school students. The native oak
species planted included valley oak (*Quercus lobata*), blue oak (*Quercus douglasii*) and interior live oak (*Quercus wislizeni*).

Haggin Oaks golf course was built in 1957 within the oak woodland surrounding Arcade Creek. By the early 2000s, many of the celebrated oaks were experiencing severe decline and death. Replanting was necessary to keep the oaks at Haggin Oaks. Mitigation trees were planted between the greens in irrigated lawn and along a rolling soil berm that separates the course from a walking trail and the Capital City Freeway. For the first several years the oaks within the irrigated turf areas greatly outperformed the trees on the berm due to the fact that no irrigation was provided to the berm trees. This substantially lowered the rate of berm tree survival for this project. In addition to water stress, the berm trees were also impacted by competition from non-native annual grasses and invasive weeds including tree of heaven (*Ailanthus altissima*), scotch broom (*Cytisus scoparius*) and yellow star thistle (*Centaurea solstitialis*). A third challenge was damage caused by voles (*Microtus californicus*). By the third year of the project, survival rates were not high enough to meet agency requirements. Dead and dying trees were replaced with new seedling trees and a temporary irrigation system was installed to water the 800 trees on the berm. These interventions were successful enough to meet project goals and satisfy the mitigation requirements. Today, both the oaks on the berm and within the golf course are well-established and growing well under the continued care and maintenance of the Haggin Oaks staff.

The years 2002 and 2003 returned to a lower level of planting, with less than 500 new mitigation trees each year. This brief break in contract implementation was the beginning of the transition to program operations better informed by restoration best practices and natural resource management theories rather than urban tree planting programs. Over the last decade, the native tree mitigation program has averaged 15 native tree mitigation contracts every year and has planted an average of 1,530 trees each fall/winter planting season.

In 2004, the first full-time field maintenance staff was hired to support the native tree mitigation program. This individual would spend the winter and fall working with community volunteers to plant new projects and the rest of the year performing ongoing maintenance and management including regular irrigation, mulching, weed management, pruning and monitoring. With an influx of new contracts, larger numbers of trees and more project sites, a second field maintenance staff member was hired in 2005. At this time, much of the watering was done by hand using 22.7 l (6 gal) blue jugs or hoses and temporary irrigation systems were built using homeowner grade irrigation materials. The evolution to irrigation standardization using professional grade materials and automatic timers has coincided with significant improvement in annual tree survival and long term tree establishment. The change in program staff coincided with a shift to restoration style planting and maintenance practices. Trial and error with these methods within our unique work areas has resulted in the planting and care methods we use today.
Site specific practices and creative management solutions

Beginning with tree propagation and finishing with final reporting, Tree Foundation staff has found the greatest success by bringing all parts of each project in house and under the careful management of the Director of Urban Ecology. A coequal focus of the Tree Foundation’s work is education, thus community support and maximizing volunteer involvement are as important as providing the best quality tree mitigation. While many of our colleagues work on restoration, reforestation and tree mitigation projects under wild land environments, the Tree Foundation’s Restoration Field Supervisor and her Restoration Field Workers face urban-centric challenges and respond with site specific creative solutions. Planting sites can range from extremely urban including trees in landscaped parks, on school campuses and along roadway planting strips to wild land restoration sites. As project success is measured by our financial supporters and regulating agencies as the number of healthy trees established at the site, this is the primary goal our actions are predicated upon.

All tree planting locations for the program are either publicly owned or managed under some type of easement. This arrangement necessitates a strong partnership with the land manager in order to ensure that tree establishment goals are in line with the long term vision and management strategy of that particular place. After the initial establishment period, land management partners assume the long term responsibility for the trees for the duration of their natural life span. Significant effort is put into developing these strong relationships with schools, parks and open space managers. Due to the history and success of past projects, many of these partners look to the Tree Foundation’s tree mitigation program as potential financial support for projects meeting their management goals. An ideal project is one where the tree mitigation funding can be used to leverage a larger habitat creation or restoration project or allow a project partner to divert funds that would be used to pay for trees and their establishment to other unfunded project components.

The cycle of work begins each fall with the acorn harvest, a project that has received strong community support since the inception of the community based harvesting model in 2010. Each August the Restoration Ecologist and several acorn interns begin the process by applying for harvesting permits throughout the six county Tree Foundation service area and recruiting and training volunteer acorn harvesters to follow the very strict self-imposed harvesting guidelines. By working with many individuals who live throughout the service area, small collections of acorns are made from a large number of locations throughout the greater Sacramento region, thus maximizing potential genetic diversity within the tree nursery. Acorns are then either direct seeded into projects November-February or are potted up in the Tree Foundation nursery or with the help of the Seed to Seedling elementary school program.

The Tree Foundation’s preferred planting stock is deepot seedlings between 12 to 18 months old. When seedlings remain in our nursery past this point, they are transferred to the Rio Cosumnes Correctional Center to be grown into
larger sized trees. These larger trees are used in circumstances where seedlings are not appropriate, such as at school plantings or within park settings. Through experimentation and past failures, we have determined that the planting of seedlings in school and developed park sites do not withstand the pressures of close contact with students and lawn mowers.

The Tree Foundation works with volunteers to plant 100 percent of the native mitigation trees, thus educating and involving the community. As an organization committed to education, the Tree Foundation forges its most lasting connections with citizens through community planting days. However, as an organization that has accepted contracts and funding tied to tree establishment outcomes, it is imperative that the volunteers achieve a high level of quality in their work. Over the last decade, a very controlled method of volunteer planting has evolved that allows all of these goals to be met. Before volunteers are invited out to a planting site, the field crew does significant work to prepare it. This generally includes vegetation management using grazing, mowing, disking or spot clearing with brush cutters, flagging of the site for individual planting locations and species to be planted, and irrigation installation. If conditions are extra dry, the irrigation system may be completely installed and operated prior to planting.

The day of the event, plants and planting materials are staged at each planting site within the field. The amount of work to be done is carefully balanced with the number of volunteers recruited and the number of staff and interns on hand to ensure quality control. Having too few or two many volunteers can greatly impact the quantity and quality of work. In general, we assume each volunteer will plant three seedlings over the course of a 3 hour event. Volunteers arrive, sign waivers, and receive a talk on the project and personal safety before they are split into small groups to work with a planting leader; either a staff member or specially trained intern. In the small groups, every step of the process is demonstrated, from digging the hole to where to put the pot after planting. Following training, volunteers are evaluated on their first attempt and planting leaders spend most of the event checking planting quality and assisting their volunteer team with challenges. Extra equipment is used during volunteer plantings to assist with quality. Squares of burlap are used to deposit and re-apply all soil dug out of a planting spot to ensure seedlings don’t end up planted in a depression. Hammers are handed out to volunteers to avoid the poor quality and danger that occurs when planters try to hammer in the tree shelter stakes using a shovel. Keeping volunteers energized with snacks and fresh fruit as well as having plenty of water and a porta-potty on hand increase the productivity and cheerfulness of the volunteer work crew.

Planting styles used are highly dependent on each unique planting site, though all are a variation of the preferred method. The Tree Foundation prefers to plant native trees as deepot or similar container sized planting materials with 12 to 18 month old stock (from acorns) the preferred age to maximize rooting and shoot growth while minimizing root and shoot overgrowth. A Tubex® brand tree shelter or shrub shelter is used on all
planning materials that it is possible to install one on and pushed into the soil 5.1 to 10.2 cm (2 to 4 inches) deep. A bamboo or similar slender stake is used to secure the tube. Stakes are placed inside the tubes to discourage voles (*Microtus californicus*) from using the stake to gain access to the inside of the tube and are placed on either the north or south side of the tube to best withstand local wind patterns. Insect netting is not used as grasshoppers and other insects do not generally have a significant negative impact on projects in the Sacramento area. On past projects team members have witnessed tube netting tangling the feet of small raptors, becoming dislodged and blowing away as well as disintegrating in the hot summer sun. For Sacramento area projects, the benefit of the netting has not been significant enough to outweigh these negative impacts. In areas with significant mule deer (*Odocoileus hemionus*) or beaver (*Castor canadensis*) populations, a 1.2 m (4 ft) tall hog wire cage secured with t-posts or rebar may also be placed around each tree to provide additional protection. Organic mulch is the preferred ground treatment around new plantings with rice straw most commonly used in open space or wild land settings and wood chip mulch being preferred for developed park and school sites, primarily due to aesthetics and ease of transportation. Irrigation lines and drip emitters are placed on top of the mulch for ease of inspection and repair.

Irrigation is performed on all plantings with the occasional exception for a direct-seeded planting. In open space and wild land settings, drip irrigation lines are placed next to each plant with one or two pressure compensating emitters installed within 30.5 cm (12 inches) of each plant. Irrigation water is obtained in a variety of ways for each site with the most common being a municipal source nearby, use of a trash pump to pull water from a nearby water body, or by way of a fire hydrant hookup nearby. Rarely irrigation may be performed by hand, generally on larger sized trees in park like settings. In these cases, five-gallon “leaky” buckets with holes in the bottom are staged at each tree and filled from a 1,136 l (300 gal) truck bed tank or with hoses and a park facility water connection. In general, trees are irrigated June-October and are given approximately 45.4 to 68.1 l (12 to 18 gal) of water a week the first summer season, 45.4 l (12 gal) ever 2 weeks the second summer season and 45.4 l (12 gal) a month the third summer season. This scheme is altered on a site specific basis depending on soils, infiltration rates and plant growth response. On average to wet water years, third season projects may be irrigated only once or not at all during the third summer. In drier years occasional supplemental water may be provided October through March. Our general observation is that establishing a healthy root system through substantial irrigation during the first growing season leads to trees that are more drought tolerant in future seasons, when compared to trees that did not receive irrigation.

Maintenance is performed at each project site weekly the first season, bi-weekly the second season and on a monthly basis the third season. For project terms of more than three summer seasons, each project is visited and evaluated on a monthly basis. The majority of site maintenance time is spent
on vegetation control, with multiple objectives and benefits. As many Tree Foundation mitigation sites are embedded in highly urban areas, fire is one of the most frequent and costly site impacts to avoid. In certain seasons we have experienced fire at up to 40 percent of our project sites and lost significant irrigation infrastructure and trees. All of the fires at urban interface sites have been started by humans with cigarette butts and other inhalant drug paraphernalia frequently found at the ignition location, with the exception of one fire accidentally started and quickly extinguished by a staff member performing additional late season vegetation control. The Tree Foundation works to minimize fires at sites and the damage caused by fires by evaluating likely areas of fire ignition and mowing or brush-cutting fire breaks. On very high fire potential sites, extra attention is paid to clearing around individual trees and along irrigation transmission areas. With these techniques, trees and irrigation infrastructure can sustain only limited damage even if fire does burn through the project site.

Minimizing herbivory damage is the second main reason intense vegetation control is enacted on project sites, with vole damage being the most destructive in our region. The damage caused by voles fluctuates on a 3 to 5 year cycle with some years being incredibly intense and some years non-problematic. Vole damage also varies within a project site, resulting in different treatments for tree management though a relative small project area. In the most intense cases, all mulch is removed from around the base of the tree and surrounding vegetation is mowed as low to the ground as possible to encourage vole predation and discourage further damage to the tree. Installation of perches in sites experiencing significant herbivory is intended to provide roosting for raptors as most of our sites have little to no surrounding vegetation and no place for visual hunters to perch.

Maintenance within established park sites is focused on protecting trees and preventing damage. Within turf areas, the greatest damage to trees comes from line trimmers and mowers operated by park maintenance staff. It is also challenging to keep mulch in place with weekly mowing coming as close to the edge of the tree establishment area as possible. Greatest success is achieved when turf grass is kept at least 1.2 m (4 ft) from the base of the tree, often with a combination of mechanical removal and maintenance with herbicides. Caging is used to discourage close mowing and square turf-free mulched areas around the tree allow complete mowing more efficiently than circular turf-free zones.

Each individual tree is mapped after planting and monitored on a yearly basis. Mapping and ongoing monitoring are facilitated by a customized ArcGIS database and field crews using Ipads and other handheld technologies. Ongoing maintenance communication is facilitated with smart phone apps such as Trello, which supports message boards for needed actions and materials for each project site, keeping everyone on the same page. Required annual reporting focuses on tree survival rates and informs replanting activities each winter. Projects are generally planned with five percent more
trees than necessary to cover expected losses and avoid replanting activities while still meeting contract requirements.

Recovery and reuse of tree planting materials help leave the planting site in a more natural state and can help make planting projects more cost effective. Many well established Sacramento area mitigation and restoration sites still have irrigation materials, tree tubes and woven plastic landscape fabric, even decades after implementation. Tree Foundation staff has witnessed left behind landscape fabric girdling fast growing trees such as Fremont cottonwood \((Populus fremontii)\). Because of this, landscape fabric is only used on sites where partner agencies require its use and is the first thing removed as project maintenance terms close. Irrigation line is rolled up and reused if possible, aided by a homemade irrigation spooler designed and built by Sarah McKibbin. Tree tubes may be left on if high levels of herbivory are expected on site as they are designed to come apart when trees outgrow them, as has been witnessed on many of the Tree Foundation’s project sites.

**Conclusion**

Filling Sacramento’s urban nooks and crannies with native trees both meets the mitigation intent of local tree protection ordinances and creates valuable habitat for both resident and migratory wildlife. Opportunities to interact with native vegetation; to see the fall acorn crop, to see the spring wildflowers and to experience wildlife, brings our disconnected human population closer to nature while providing local aesthetic, air quality, public health and water quality benefits. Though this approach does not provide complete ecological restoration or necessarily build “natural” habitats, the impacts are significant and positive for people, wildlife and the integrity of the urban forest.

Establishing native trees and vegetation in urban settings is equally challenging when compared to wild land restoration, but with different impacts for which protection is needed. Access to reliable irrigation provides a greater level of success, while the impact of people (sometimes even willfully destructive) can be much harder to control and exceptionally damaging. The Tree Foundation’s success in establishing more than 20,000 native trees is based on three key points that can be replicated anywhere: 1) understanding of site-specific challenges and design to accommodate or avoid them, 2) employment of intelligent, knowledgeable, creative people and management styles that allow them to solve problems creatively, and lastly, 3) to actively schedule flexibility. Many agencies and contracts have timelines that must be followed which do not allow flexibility to accommodate natural variations in timing, vagaries of local weather or other impossible to predict situations that directly impact healthy tree establishment. By accepting the flexibility to work with natural opportunities and accept the unpredictability of nature, great success can be achieved in establishing the next generation of native trees.
Oak Conservation
Economic Incentives for Oak Woodland Preservation and Conservation

Rosi Dagit, Cy Carlberg, Christy Cuba, and Thomas Scott

Abstract
Numerous ordinances and laws recognize the value of oak trees and woodlands, and dictate serious and expensive consequences for removing or harming them. Unfortunately, the methods used to calculate these values are equally numerous and often inconsistent. More important, these ordinances typically lack economic incentives to avoid impacts to oak woodland values because they fail to clearly identify the economic consequences of oak woodland loss; specifically: non-use values (recreation, aesthetics, and so forth), use values (increased real estate value, Council of Tree and Landscape Appraisers’ individual tree valuation) and ecosystem services (carbon sequestration, temperature moderation, air pollution mitigation, stormwater runoff mitigation, and so forth). In this paper, we review the economic methods for valuing oak woodlands that were used to develop fair, equitable and consistent oak woodland values and economic incentives to encourage conservation in Los Angeles County. Economic methods that calculated the true cost of replacing oak values (including ecosystem services and non-use) were found to be more rational and consistent than existing models of simple ratios of replacement by nursery stock. The consensus based decision to move forward with this broader evaluation of oak values represents a major change in Los Angeles County policy, taking 2 years to evolve.

Key words: ecosystem services, economic valuation, non-use values, use values

Introduction
Oak woodlands in Los Angeles County are considered “valuable” for a variety of different reasons. In order to make informed planning decisions, both the costs and benefits of a proposed land use action need to be examined. These valuations should be analyzed in the context of both short and long-term (50 years) impacts, as well as within the context of location. Los Angeles County has over 58 680 ha (145 000 ac) of oak woodlands (Gaman and Firman 2006, Los Angeles County Oak Woodlands Habitat Conservation Strategic Alliance 2011) including 17 species distributed from the coast into the mountains. Although much of these oak woodlands resources are found on publically owned lands, it is estimated that between 12 140 to 17 806 ha (30 000 to 44 000 ac) are privately owned and potentially jeopardized by future development or other impacts such as removal for fuel modification. In terms of biological function, oak woodlands provide habitat for over 300 vertebrate species, thousands of insects, and innumerable associated plants. These trees also provide numerous ecosystem service values to the common good through their aesthetic contributions, abundant recreational opportunities, controlling soil erosion, providing water table management and groundwater recharge, providing carbon sequestration,
filtering air and water pollutants and moderating temperature extremes. Thus, removal of oak woodlands generates a substantial impact to the aesthetic, sustainable and biological diversity of the southern California area and specifically Los Angeles County.

When oak woodlands are removed and replaced by development, it is not simply the trees that are missing, but all the associated functions and habitat are lost as well. The ecosystem services provided by the trees are often replaced with stormwater, carbon, air and temperature management infrastructure which requires long-term investment in maintenance and monitoring. The community assumes the costs to accomplish the services previously provided in perpetuity by the trees.

Oak woodlands are also a repository of genetic variability and biodiversity that can sustain numerous species in times of environmental change. However, it takes 100 years to replace a 100 year-old oak that is removed. In the meantime, the young replacement trees planted as mitigation can only provide a fraction of the benefits lost with the removal of a mature oak, and given the uncertainty of actually recruiting replacement trees into maturity, it takes a very long time, and perhaps never, for any replacement plantings to regain the level of ecosystem services lost with removal of the original woodland trees. Further, replacement trees do not have the provenance of the original trees, which were perfectly suited and adapted to their site.

Beginning in 2001, the state of California began to recognize that county and city oak tree protection ordinances were not achieving the goal of protecting and preserving oak resources throughout the state. For example, Los Angeles County was one of the first counties to enact an Oak Tree Ordinance (1982). This ordinance specifically states, “As one of the most picturesque trees in Los Angeles County, oak trees supply beauty and charm to the natural and manmade landscape. Oak trees add distinct and unique aesthetic character to the areas of Los Angeles County in which they are indigenous. The Oak Tree Permit is established to recognize oak trees as significant and valuable historical, aesthetic and ecological resources.” A number of other values have been defined for natural ecosystems since the Oak Tree Ordinance was written in 1982, including the amenity value of living next to a oak woodland preserve, or the value of ecosystem services like carbon sequestration, slope stability, and flood control. Assessment of implementation of that ordinance over forty years suggests that while individual oak trees may have been preserved, oak woodland resources throughout the county were declining and continue to be threatened by development. The Oak Woodlands Conservation Act (AB 242 2001) set up a process for voluntary conservation and identified oak woodlands as a significant resource throughout the state. This law also requires counties to develop an Oak Woodlands Conservation Management Plan (OWCMP) in order to be eligible for state funds to assist in acquiring oak woodlands for the public trust. Only 21 of the 54 counties statewide had developed plans as of 2010 (California Wildlife Conservation Board 2010).

This initial law was augmented by the passage of SB 1334 (Public Resources Code Section 21083.4) in 2004 (California Public Resources Code 2004), which expanded preservation efforts by requiring that a county, “in determining whether the 1973 California environmental quality act (CEQA) requires an environmental impact report, negative declaration, or mitigated negative declaration, to determine whether a project in its jurisdiction may result in a conversion of oak woodlands that will have a significant effect on the environment, and would require the county, if it determines there may be a significant effect to oak woodlands, to require one or more of specified mitigation alternatives to mitigate the significant effect of the conversion of
oak woodlands.” Counties and cities now were required to develop criteria for impact thresholds and develop tools to encourage conservation.

In July 2009, the California Forest Protocol (CFP) was adopted by the California Air Resources Control Board (CARB) and incorporated into the CEQA Initial Study Checklist by the Natural Resources Agency. This was in response to the requirements of the Global Warming Solutions Act (2006), which required that the state reduce greenhouse gas (GHG) emissions to the 1990 level by 2020. CEQA now requires the analysis and mitigation of potential effects of GHG emissions related to conversion of oak woodlands. Future CEQA documents must include analysis of how biological carbon emissions will change if oak woodlands are converted to other uses. All of these laws acknowledge that oak woodlands have intrinsic values that provide quantifiable benefits.

Finally, many environmental laws grant standing to anyone seeking involvement in an environmental review or management of a resource. Because of SB 1334, anyone can be considered a stakeholder in the oak values of Los Angeles County, and demand that damage to their oak woodland values be calculated and mitigated under CEQA. The Endangered Species Act (ESA 1973) gives anyone the right to challenge or sue to protect habitat for federally listed endangered species, which can include oak woodlands. Hence individuals and groups that are neither landowners nor regulatory agencies can become stakeholders when oak woodland values are calculated. This creates an exceptionally broad pool of individual potential stakeholders, including community, state, federal, and international residents, and they seek an equally broad array of outcomes from existence values to firewood harvest.

**Los Angeles County oak woodlands economic valuation framework**

From 2008 to 2011, a group of concerned arborists, foresters, planners, biologists, and other stakeholders formed the Los Angeles County Oak Woodlands Habitat Conservation Strategic Alliance (Alliance) with the goal of developing an oak conservation plan for Los Angeles County. Starting with the goal of articulating a vision for the future of oak woodlands in the County in 50 years, the Alliance quickly realized that one of the biggest challenges was to clearly, fairly and consistently identify how much it costs the community in perpetuity to replace the various ecosystem services provided by oak woodlands should they be removed. Providing a tool for landowners and decision makers to assess the economic value of oak woodlands became a specific goal of the planning process.

The hope was that by requiring a cost-benefit analysis in the early stages of the planning process, the advantages of conserving and preserving oak woodlands, either through more sensitive development design or outright by fee dedication or easements, would encourage voluntary conservation efforts. Economic valuation would also provide a more realistic framework upon which to base mitigation requirements and address the various requirements of state laws. In order to evaluate these issues and make a determination that balances the preservation of the environment with development, land use changes within designated oak woodlands of Los Angeles County will now be required to:

- Characterize the baseline contribution provided by the existing oak woodlands.
• Analyze how a proposed land use action would change this, either by enhancing the oak woodland ecosystem function or impairing it.
• Examine the proposed land use change within the context of the existing and identified restoration potential of local and regional oak woodlands (mapped zones).
• Calculate the relative costs/benefits to the county.

After reviewing the relevant economic ecosystem service literature, the Alliance initiated a series of workshops inviting numerous economists to contribute their suggestions for how best to establish a protocol for quantifying the economic benefits of oak woodlands. Based on this input, the Alliance developed a valuation equation which is fully described in the Los Angeles County OWCMP (Los Angeles County Oak Woodlands Habitat Conservation Strategic Alliance 2011). The OWCMP articulated the following goals:
• Develop incentives to encourage voluntary oak woodland conservation and balance the regulatory elements of the existing Los Angeles County Oak Tree Ordinance.
• Devise a clear, fair way of assessing and putting value to services provided by oak woodlands.
• Clarify the CEQA process related to oak woodlands and carbon sequestration.
• Facilitate uniform evaluation of land development impacts on oak woodlands.

Voluntary economic incentives to conserve oak woodlands
As part of the effort to encourage voluntary conservation of oak woodlands, the OWCMP documents a variety of economic benefits that can only be realized through preservation. These include:

1. Fee dedication or conservation easements
Both fee dedication (title of the parcel deeded to a public entity such as National Park Service) or conservation easements (legal agreement between landowner and either a land trust or government entity that limits uses of the land to protect its oak resources) are tools that have been used to provide tax deductions as well as opportunities for estate planning that allow landowners to achieve a variety of stewardship goals. Outright purchase (fee simple) acquisition of valuable oak woodland resources is the most direct way to ensure long term protection, however funds for such purchases are always limited. Both county and local land trusts are able to accept dedication of conservation easements that allow the landowner to retain title for the land, but the county or land trust would obtain any development rights. By not exercising those rights, development of that land is prevented. Dedication of a conservation easement “runs with the land,” meaning that the development restrictions will continue in perpetuity, even if the land is sold.

The landowner is thus able to control the future of his land by extinguishing some or all development rights. Many landowners are motivated by personal, ethical or aesthetic reasons and want to ensure the long-term sustainability of their property.
Conservation easements provide a landowner an opportunity to protect a family-owned oak woodland permanently, while still using existing structures or other uses.

2. Avoided permitting, CEQA, mitigation costs

Sensitive development design can often work with and around the oak woodland resources on a parcel rather than removing or degrading that resource. Developments that require any kind of discretionary review undergo a series of evaluations, starting with an Initial Study process, and depending on the level of impacts, may require higher levels of environmental evaluation in accordance with CEQA requirements. Further, permits from regulatory agencies such as California Department of Fish and Wildlife, National Marine Fisheries Service, U.S. Army Corps of Engineers, U.S. Fish and Wildlife Service, and the Regional Water Quality Control Board may also be required. The costs of preparing the necessary environmental studies and documents required to meet these permit application requirements can be substantial, and it can take many years for a project to move from design to implementation, with the potential for lawsuits along the way. Additionally, each of these regulatory entities requires some form of mitigation if impacts are identified as significant. The cost of implementing these mitigations, as well as the cost of identifying, quantifying and mitigating any carbon sequestration impacts can be very expensive and complex to complete.

Mitigation requirements can vary from replacement planting with maintenance of the trees for 10 years, to donating funds to the County Oak Mitigation Fund allowing purchase of twice the amount of oak woodland habitat that is being lost, or to match the Council of Tree and Landscape Appraisers’ (CTLA) value for the trees, whichever is more. A typical individual mature, healthy coast live oak located within an oak woodlands can be valued as much as $100,000. The SB 1334 allows developers to pay into a mitigation fund as part or all of mitigation measures for impacts to oak woodland. In theory, these fees represent the cost of acquiring oak woodland acreage equivalent to the woodland lost, allowing some flexibility where mitigation occurs. This may or may not result in adequate compensation for loss of the oak woodlands in a specific location where there are few opportunities to protect comparable acres of oak woodland.

By contrast, if a development is designed to avoid impacts to sensitive biological resources such as oak woodlands, these costs can be reduced and potentially completely avoided. Such projects would theoretically move through the county planning evaluation and approval process much faster and the resulting overall project cost and timeline reduced.

3. Transfer of development rights

Los Angeles County has a program in small lot subdivisions of the Local Coastal Zone where lots that are limited in allowable square footage can be retired in perpetuity, and the square footage transferred to another parcel. In the case of oak woodlands, transfer of development rights for parcels within Priority Conservation Areas would be obtained in exchange for higher density development in already disturbed locations. This action stops housing developments in woodlands, but does not protect oaks against other uses, such as agriculture or firewood harvest. This gap in protection has led to conflicts in other counties, when landowners undertook an approved use in woodlands that other assumed were protected.
4. Avoided carbon sequestration costs

The recently developed Los Angeles County Climate Action Plan (Los Angeles County 2014) has set the stage for the development of cap and trade systems, and it is anticipated that the fees associated with offsetting the loss of oak woodlands could be substantial. It also provides an opportunity for landowners to become reserves for carbon and provide financial incentives for preserving and expanding their oak woodlands. The evolving process for providing credits or penalties could substantially increase the value of oak woodlands and provide opportunities for restoration.

It thus appears that preservation is the most realistic way to mitigate forest carbon biological emissions to less than significant. Avoiding carbon biological emissions now is probably more effective than relying on future emissions avoidance from still to be implemented mitigation measures.

5. Avoided fuel modification costs

Many of the remaining privately-owned oak woodlands in Los Angeles County are located in designated High Fire Severity Zones. Each year County residents in these areas incur significant costs in order to meet fuel modification requirements. The cost of maintaining required fuel modification within or adjacent to an oak woodland is significantly less than similar fuel modification required for native chaparral or watering and care of non-native tree and landscape plants. Clearing vegetation up to 61 m (200 ft) from all structures can be very costly. The presence of oak woodlands significantly reduces clearance costs because:

- The native understory of oak woodlands typically contains less flammable vegetation.
- Oak trees are harder to ignite and not as prone to rapid combustion, which means they require less pruning and thinning.
- Oak stands that are well maintained (deadwood removed, retaining native leaf litter and perennial native shrubs and forbs) prevent slope failure, reduce erosion and can slow down a wildfire.

In addition to the above existing incentives, the OWCMP identified several other potential incentives to encourage voluntary oak woodland conservation. Both include rewarding landowners who voluntarily either expand existing oak woodlands on their property or plant oaks as part of their landscape.

6. Existing oak woodland expansion credits

This proposed incentive would allow a property owner who has lived on the property for five or more years to document the expansion of their oak woodland. This would provide an opportunity for limited expansion of their developed footprint to encroach into their oak woodland. Using the annual aerial photographs taken by Los Angeles County, an increase of more than 10 percent canopy cover from an identified baseline time would be the threshold for using this option. The goal would be to encourage property owners to allow their oak woodlands to naturally expand, knowing that they could potentially build an addition, such as a garage or pool in the future without penalty. The property owner would need to maintain the remaining oak woodland expansion in perpetuity through either a conservation easement or deed restriction of some kind.
Because any impacts to an oak woodland caused by a discretionary project affecting trees over 12.7 cm (5 inches) in diameter would also be subject to CEQA Section 21083.4 (Conversion of Oak Woodlands) as well as carbon sequestration standards, expansion would need to be sufficient to exceed the level of mitigation measures that would ordinarily have been required (a 2:1 ratio), in order to qualify as “other mitigation measures.” This provision would need to be incorporated into the County Code. To date, this tool is in the development stage and County planners are developing a procedure and process that will hopefully become available in the near future.

7. Exemption for oaks planted or volunteers nurtured by property owners

In order to avoid any possible impediments to future use of their property, property owners routinely cut down volunteer oaks before they reach a diameter of 20.3 cm (8 inches), which is the threshold for protection in Los Angeles County. Local landfills are reluctant to plant oaks, even though many of these sites border publicly owned oak woodlands, because they fear the penalties and mitigation that might be required if they needed to remove the trees at some point in the future. The OWCMP recommends that the County develop a procedure that would allow landowners to map and document the location of oaks they plant by submitting a plan to the appropriate County agency that would be attached to the permanent record for that parcel. Then if at some future time they wished to remove the tree, they could do so without a permit or penalty. Again, Regional Planning is considering this recommendation for implementation. This would be similar to the City of Los Angeles’ Tree Protection Ordinance which currently allows for the removal of protected species that can be proven to have been planted (rather than naturally occurring).

Cost-benefit analysis procedure

Economists examine environmental values from several different perspectives. A few believe that environmental amenities can and should be valued in exactly the same way as any other goods (Baerenklau 2009). However, others such as Salzman (2005) suggests that it is the role of government to pay for achieving ecosystem service protection, because these services cannot be bought or sold and thus function outside of the traditional market system. Others feel that markets reflect individual, rather than community property values in the context of human use only, are volatile and reflect current ideas of value, but don’t reflect enduring or intrinsic values. Typically, the benefits provided by functional oak woodlands have not been incorporated into the cost-benefit equation because they are difficult to assess.

As a result of extensive research and discussion, the Alliance explored a variety of strategies for quantifying the economic values of oak woodlands. Models employed by U.S. Fish and Wildlife Service, National Park Service, the Environmental Protection Agency, the Nature Conservancy and other land trusts were all reviewed. It became clear that oak woodland values are never absolute; they are governed by the situation wherein they occur and the motivations of the persons involved. In the past, these values have been calculated to: (A) estimate compensation for damage; (B) appraise land value in real estate transactions; or (C) estimate non-market values and cost/benefit of management options.
In the first case, oak woodlands are assigned a dollar value to calculate the cost of settlements in tort cases, CEQA mitigation, or post facto penalties/fines when oak trees or woodlands are damaged. In the second case, oak woodlands have a market value in real estate transactions, either as an amenity, because they enhance the landowner’s quality of life; or as a resource attached to the land (firewood, edible mushrooms). In the third case, values present in oak woodlands become independent of the land where they occur, and are used to estimate the relative costs and benefits of management actions or relative value of ecosystem services (wildlife habitat, carbon sequestration, watershed protection).

One of the most direct means of establishing the value of oak woodlands is to calculate the cost of recreating these values after they are lost. Pincetl (2009) suggests that only by examining the costs of restoring impaired or damaged oak woodland, can we determine how much a functional oak woodland is worth. In theory, replacement or restoration costs bypass the need for estimation of abstract or non-market values, by assuming that all these values are restored once the mitigation is carried out. Regulatory agencies and landowners could then forego the complicated process of identifying stakeholders and calculating the values for each instance where an oak tree or oak woodland is damaged. The disadvantage is that the replacement value becomes a general solution to the specific values that are lost when an oak woodland is damaged. There are five models of replacement value: (1) acquisition of oak woodlands that are equivalent to the oak woodlands converted to other land-uses; (2) complete restoration (or creation) of oak woodlands; (3) partial restoration of oak woodland values; (4) planting of oak saplings to replace oak trees removed from the landscape, and; (5) transplanting oak trees that would be lost in a project.

The OWCMP distilled all this information and identified three categories of values: use, non-use and ecosystem services. These were integrated using all of the above considerations into an equation that provides flexibility for users to incorporate whatever tools are most appropriate and applicable to any given situation. Thus the OWCMP quantifies the total oak woodland value as the sum of the use value plus the non-use value plus the ecosystem services values.

**Use values**

The most fundamental use value is the market value of the land upon which the oak woodland resides. Properties with functional oak woodlands offer higher real estate benefits (amenity values) than comparable lands without oaks (Diamond and others 1987, Standiford 1999, Standiford and Scott 2001). Extractive uses such as timber harvesting, firewood production and other uses such as hunting, fishing, providing mast for wildlife, beehives and other harvesting activities also provide a market driven value for a particular oak woodland. Therefore, the market values are more easily compared between the baseline condition of a parcel and any proposed development activity.

Another commonly used tool for valuing individual oak and other landscape trees is the Guide for Plant Appraisal (Guide; Council of Tree and Landscape Appraisers 2000). With a long history of use in calculating the value of tree damage in tort cases, the Guide provides an accepted tool for calculating the value of a tree based on its species, condition, and location. These factors are evaluated either using a Replacement Cost Method, which is applied to smaller trees that could realistically be purchased at a nursery; the Trunk Formula Method, which is used to estimate the value of trees considered too large to be readily available; or the Cost of Cure Method, which is used to identify cost to replace/repair a property to near its natural
condition, and takes into account the cost of maintenance and time needed for re-establishment of the damaged landscape. Each factor can be depreciated by the appraiser if the species is not locally native, is in poor condition, or located where it does not contribute substantially to the overall woodland landscape (Council of Tree and Landscape Appraisers 2000).

However, we recognize that oak woodlands are different from developed landscapes and that the Guide may not be adequate to develop realistic restoration or replacement costs for an oak woodland. The advantage of the CTLA system is that the damaged party is paid at the time of damage, and is not left with a promissory mitigation, which may or may not materialize. A recurring disadvantage with this method is that it is possible to generate a value for the trees that is greater than the real estate value of the land the trees occupy. Another problem is that this method fails to incorporate any ecosystem service values, and instead focuses primarily on the anthropogenic values.

Ecologists include the spatial distribution of oaks when discussing the functional value of an oak woodland (Standiford and Scott 2001). This value resembles the monopolistic value of land, in that the aggregate resources in an oak woodland at one location can never be replicated anywhere else. From a pragmatic perspective, parcels containing oak woodlands in Los Angeles County are as similar or dissimilar as we choose to view them. Nevertheless, the complex climate, geology, soils, and biogeography of the County tend to enhance the unique features of individual oak woodlands.

The value of these woodlands is linked to their scarcity, which in turn is affected by the rate and extent of oak woodland conversions. Location can become critical even when oak woodlands are still abundant: if a linear woodland is permanently severed, then the movement of wildlife along that woodland cannot be restored at a different location. In this sense, the spatial structure and context of a particular oak woodland are integral parts of its value.

Ultimately, the OWCMP recommends that for every 1 acre of oak woodland impacted, at least 2 acres of oak woodland of the same or better quality be placed into the public trust. By using market values associated with the cost of purchasing the two to one replacement ratio, the USE value can be most simply calculated.

Non-use values

Economists define non-use values as those that do not derive from in-situ consumption of the resources (Kopp and Smith 1993). These benefits are described as non-market values, and include those elements of oak woodlands that have no commodity, consumptive or dollar equivalency. Examples would be passive uses such as recreation, open space, watershed protection, or landowner amenity values. Recreational opportunities provided by oak woodlands (hiking, bird watching, and others) result in dollar benefits to local businesses, increase real estate value of adjoining properties, and are considered valuable by both local and long distance stakeholders. Travel costs to access an oak woodland open space, and willingness-to-pay for protecting oak woodlands are examples of methods used to identify how important these resources are in a contingency valuation setting (Baerenklau 2009).

The quantification of these values is an evolving field with multiple procedures that can be utilized, each having a best fit for specific circumstances. The OWCMP provides flexibility for use of the most appropriate model for each circumstance, rather than requiring that any particular tool be employed to calculate the non-use
value for the baseline existing condition of a property and compare that to the value post proposed development.

**Ecosystem service values**

Oak woodlands are critical components of healthy terrestrial and aquatic ecosystems, providing habitat, preventing erosion, moderating water quantity and supporting water infiltration, sequestering carbon, filtering out air and water pollutants, moderating temperatures, and supporting watershed function. These are but a few of the potential ecosystem service values that can be quantified using a variety of tools.

In addition to the quantification of various services provided by oak woodlands, it is important to recognize the role of ecosystem processes and how strongly that influences their value. For example, oak trees survive summer drought because of hydrologic processes that move water through the soils and substrates where oaks occur, and symbiotic processes allow oaks to move water into their roots. However, if the pathway of this process is disrupted, then woodlands are unlikely to remain intact. Recognizing and calculating the cost of replacing this critical landscape scale process should be incorporated into the valuation effort. It is important to note that landscape scale processes like the hydrologic cycle extend far beyond the canopy of oak trees. The relationship between the woodland and its watershed must be considered in defining an oak woodland and hence are important in estimating oak woodland values.

The life history of oaks provides another example of woodland processes that are difficult to detect and quantify in standing trees. Stands of oaks appear remarkably stable; however, individual oak trees eventually succumb to diseases, insect pests, and competition for water, nutrients and light. The process of tree replacement is not necessarily visible in the patterns of trees across a landscape. For instance, coast live oaks have a remarkable ability to expand when conditions are good, and to survive when conditions degrade. In a good year, oaks can rapidly produce thousands of acorns and seedlings, and an established seedling can become trees in a relative short time (5 years). The process however, is dependent on suitable conditions for seedlings to germinate and thrive. The values associated with the individual oak trees can be intact, but the values associated with the ability of the oak woodland to thrive over time can be altered.

The California Air Resources Board (2008) and the California Forest Protocol (SB 812 2002) have designated the conversion of oak woodlands to non-forest use as a biological emission of carbon dioxide that is subject to CEQA analysis and mitigation. The air quality criteria established requires the measurement of oak woodland biological emission by documenting the live tree biomass (including roots), standing dead tree biomass, and woody debris on the ground. With this information in hand, the protocol requires that the potential carbon sequestration over the next 100 years be calculated for all trees over 7.6 cm (3 inches) or greater diameter at breast height, as well as to determine how much sequestered carbon would be released if the live trees, standing dead trees and woody debris were burned. Comparison of the existing condition to the proposed condition following the land use change would then be used to identify the level of significance for this impact.

Additionally, there are several methodologies that are used to document the amount of water run-off reduction, air pollution filtration, temperature moderation (energy use) and erosion control benefits provided by a tree or group of trees. Most are designed for use primarily within the urban forest context, rather than natural
landscapes, however, given the proximity of most oak woodlands in Los Angeles County to the urban edge, these may be applicable.

Existing models that may have applicability for oak woodland service estimation include:

a. Urban Forest Effects (UFORE) is a computer model designed to characterize forest structure (species composition, number of trees, size, density, health, leaf area, biomass, diversity) and use these variables to evaluate primarily air quality parameters like removal of particulate matter, carbon sequestration and storage, temperature effects resulting in energy use benefits and pollen impacts (Nowak and Crane 2000).

b. STRATUM is the street tree management and analysis tool used by many local cities. Using commonly collected inventory data on tree species, size, health and location, the computer model calculates the dollar value of aesthetics, energy conservation, air quality improvement, carbon dioxide reduction, stormwater control and property value increases. The applicability of this model to oak woodland land use conversion is dependent on the location of the proposed development in relation to a more urbanized environment (USDA Forest Service 2009).

c. InVEST (Integrated Valuation for Ecosystem Services and Trade-offs.2) is another computer program designed to “help land managers and government workers assess this wide array of services” (ESA Press Release).

Summary

Ultimately, the Alliance concluded that developing a consistent process for quantifying the existing baseline value of an oak woodland and then comparing that to the value following the proposed development is critical to making informed planning decisions. In order to achieve a goal of no net loss of oak woodlands, the more traditional mitigation measures such as on-site tree preservation and replacement plantings need to be replaced by a more comprehensive and effective mitigation strategy that will not only replace the lost acreage by protecting twice as much acreage of an equivalent stand of comparable size, but also recognizing that replacement plantings will take 30 to 100 years to be effective at sequestering carbon as well as replacing other lost ecosystem services. The costs of such mitigation could be significant.

While the value of oak woodlands is linked directly to the land price (and subsequent management costs) and endowments to manage replacement woodlands, the non-use and ecosystem service values contribute to the overall value of the resource. The structure of woodland acquisitions and the mitigation fee are not fixed; however, the Wildlife Conservation Board has set guidelines to insure consistency in mitigation across counties. In turn, these guidelines can be translated into the price of mitigation and hence the value of oak woodlands. The foremost guideline is that mitigation payments will be used to acquire oak woodlands that are at minimum equivalent to the oak woodlands lost (same species, physical characteristics and site conditions). Ideally the woodlands that are appropriate for mitigation would be identified a priori, through an inventory conducted by the County. This suggests that the amount of compensation should be calculated as the
assessed value of the land that contains the replacement oak woodland or the assessed value of an easement over the replacement woodland. If no replacement woodland can be found, then the value would be based on either the appraised value of the land where the impact to oaks occurs, or the median assessed value of comparable oak woodlands in the vicinity.

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Oak Woodland Conservation Management Planning in Southern CA – Lessons Learned

Rosi Dagit

Abstract
The California Oak Woodlands Conservation Act (AB 242 2001) established requirements for the preservation and protection of oak woodlands and trees, and allocated funding managed by the Wildlife Conservation Board. In order to qualify to use these funds, counties and cities need to adopt an oak conservation management plan. Between 2008 and 2011, a team of concerned arborists, biologists, county foresters, planners, and other stakeholders wrestled with questions such as how to define an oak woodland in southern California, how much oak woodlands are worth, and examined the costs associated with a) losing existing oak woodlands; b) preserving existing oak woodlands; and c) expanding oak woodland habitat to suitable areas in the county. These efforts resulted in adoption of the Los Angeles County Oak Woodland Conservation Management Plan in 2011. However, it took until 2014 to work out the associated implementation plans for regional planning and public work staffs. The pitfalls and successes of developing this plan will be discussed in hopes of sharing the lessons learned with others.

Key words: conservation planning, oak woodlands

Introduction
Many counties and cities throughout California have long protected individual oak trees, and Los Angeles County led the way with the enactment of their Oak Tree Ordinance in 1982. However, these local regulations have had limited scope and success in protecting oak resources. Recognizing that loss of oak woodlands was increasing throughout the state, the legislature enacted the California Oak Woodlands Conservation Act (AB 242 2001), which established requirements for the preservation and protection of oak woodlands and trees, and allocated funding to be managed by the Wildlife Conservation Board that would support a variety of ways to preserve oak woodlands throughout the state. In order to qualify to use these funds, counties were required to adopt an oak woodland conservation management plan. As of 2010, only 21 of 54 counties in the state had adopted such plans (CWCB 2010).

In 2004, SB 1334 (Public Resources Code Section 21083.4) expanded this preservation effort by requiring that a county, “in determining whether CEQA requires an environmental impact report, negative declaration, or mitigated negative declaration, to determine whether a project in its jurisdiction may result in a conversion of oak woodlands that will have a significant effect on the environment, and would require the county, if it determines there may be a significant effect to oak woodlands, to require one or more of specified mitigation alternatives to mitigate the significant effect of the conversion of oak woodlands.” In order to comply with this...
state law, counties and cities need to identify clear criteria for determining thresholds for impacts and develop implementation tools to encourage conservation through the use of easements, replacement plantings, other mitigation efforts.

In 2006, the Global Warming Solutions Act (AB 32, 2006) required that the state reduce greenhouse gas (GHG) emissions to the 1990 level by 2020. In order to accomplish this goal, the Natural Resources Agency and California Air Resources Board expanded the analysis of GHG emissions to include evaluation of any impacts resulting from the conversion of oak woodlands to other uses. Oaks are an important tool for sequestering carbon dioxide, with each mature tree capable of sequestering 9 metric tons of carbon in a 50 year lifespan (Sacramento Municipal Utility District Tree Benefits Estimator 2015), with the current extent of oak woodlands throughout the state sequestering approximately 325 million metric tons of above and below ground carbon (Gaman 2008). Conversion of oak woodlands can result in both direct GHG emissions as well as reduce the potential for sequestration, which has been identified as a key mitigation strategy for reducing emissions. The effort to incorporate biogenic GHG is underway with the development of local Climate Action Plans and through the implementation of the voluntary Urban Forest Project Protocol.

Los Angeles County was in the process of responding to these new requirements by developing their Climate Action Plan concurrently with the revision and update of the county General Plan. This provided an opportunity to incorporate the values, benefits and protection of oak woodlands into the county vision in a variety of important ways.

Between 2008 and 2011, a team of concerned arborists, biologists, county foresters, planners, and other stakeholders including building industry representatives, wrestled with questions such as: what will the oak woodlands of Los Angeles County look like in 50 years, how to define an oak woodland in southern California, how much oak woodlands are worth, and examined the costs associated with a) losing existing oak woodlands; b) preserving existing oak woodlands; and c) expanding oak woodland habitat to suitable areas in the county. These efforts resulted in adoption of the Los Angeles County Oak Woodland Conservation Management Plan (LACOWCMP) in 2011. However, it took until 2014 to work out the associated implementation plans for regional planning and public work divisions, and a few recommended actions remain to be accomplished.

### Getting started

The three critical ingredients for developing an oak woodlands conservation management plan in Los Angeles county included: 1) a dedicated team, 2) political support, and 3) funding. The LACOWCMP was made possible due to the alignment of all these elements at a critical time in county planning efforts.

**1. Dedicated team**

Spearheaded by the Resource Conservation District of the Santa Monica Mountains (RCDSMM), and the Los Angeles County Department of Fire Department Forestry Division (Forestry), the Los Angeles County Oak Woodlands Habitat Conservation Strategic Alliance (Alliance) was formed in 2008. Over 30 people representing arborists, biologists, foresters, city and county planners, UC Cooperative Extension as well as agriculture and natural resources staff, building industry representatives, landscape architects, members of the California Native Plant Society, Audubon, California Oak Foundation, environmental consultants, as well as National Park Service, California Department of Fish and Wildlife and U.S. Fish and Wildlife
Service staff contributed over 6,000 volunteer hours of time, meeting monthly for almost 2 years. Many of these Alliance members contributed text or edits to the document as it evolved.

In order to obtain consensus on definitions of oak woodlands in Los Angeles County, the Western Chapter of the International Society of Arboriculture hosted several workshops on oak woodland conservation, attracting over 150 concerned stakeholders who helped shape the conversation and assist in identifying goals, needs and possible solutions. For these we relied upon a variety of oak planning documents that provided a framework for fine tuning our definitions (Guisti and others 2005, Guisti and others 2008).

We also coordinated a series of workshops on the economic elements of oak woodland conservation, inviting three economists (Dr. Kenneth Baerklau from UC Riverside, Dr. David Sunding from UC Berkeley, Dr. Bowman Cutter from Pomona College) to assist us in identifying possible incentives for oak woodland conservation as well as to develop a formula for calculating oak woodland values, especially ecosystem service values, that would be clear, fair and consistent.

Public stakeholder meetings were held at various locations throughout the county in order to get input on the proposed plan from over 150 community members. It was through these meetings that we were able to hear from local homeowner associations, private landowners and most interestingly, the local landfills. This input allowed us to revise and edit the document to incorporate the ideas for incentives from the public, as well as from the planners and economists. Collectively, over 500 people took the opportunity to help us shape an oak woodland conservation plan that was tailored to the needs of Los Angeles County.

2) Political support

The support of our local county supervisors, Zev Yaroslavsky and Michael Antonovich, was critical to the success of this effort. Without the input and guidance of their field deputies, as well as their direction to county staff to participate in this effort, we would not have been able to integrate this planning effort into the wider county planning process. It was fortuitous that the county General Plan and Climate Action plans were also being developed during the same time frame. This provided a rare opportunity to have the ideas of the oak woodland conservation plan be represented in the larger planning frameworks as well. Finally, it was only through the support of these supervisors that the plan was eventually adopted and county staff directed to develop the implementation tools needed to incorporate the recommendations of the LACOWCMP into county planning processes.

3) Funding

Initial funding was provided by contributions from both supervisors of $25,000 each. We submitted a grant proposal to the Wildlife Conservation Board in 2008, but due to the grant freeze that occurred at that time, we were not successful in obtaining any additional funding. Thus it was only thanks to the contribution of volunteer time that we were able to complete this effort. Although it would have helped our independent consultants to have additional funding, their tax deductible contributions worth over $50,000, as well as the county staff time, and our initial $50,000, was all we had, and so we made it work.
Plan development process
Once we formed the core Alliance planning group, the next challenge was to learn how other counties had approached this effort, to see what might work for us, and to begin articulating our goals and objectives. By inviting a large variety of stakeholders to contribute, the process may have taken a bit longer, but resulted in widespread support from those who felt that their concerns had been heard and addressed. This was particularly important for the Building Industry Association members, who were most concerned that the plan would increase the regulatory burden but who were interested in the possibility of developing a clear road map for developers that would provide more guidance and certainty in the development process.

Identify goals
What do we want oak woodlands to look like in Los Angeles County in 50 years? This question formed the basis of our planning effort. Using consensus based decision-making, the many stakeholders involved in this process were unanimous in agreeing that there should be no further net loss of oak woodland resources in Los Angeles County. A secondary goal was to meet the requirements of all the applicable state laws, particularly the Oak Woodlands Conservation Act (AB 242), so that the county would be eligible for funding to help protect and preserve their oak woodland resources by fee title acquisition. Finally, it was recognized that recovery of degraded or lost woodlands was also an important part of the process for preserving and expanding oak woodlands into the future.

Eventually we determined that the main goal of the LACOWCMP was to articulate a long-term vision for protecting, managing and restoring oak woodlands. Integrating this effort into the concurrent broad scale planning effort provided the opportunity to identify ways to:
- Encourage voluntary conservation of oak woodlands on private property.
- Properly identify the costs to the community when existing oak woodlands are lost to development or conversion to other activities.
- Link mitigation at the project level to the long term conservation plan goals.
- More accurately identify cumulative impacts.
- Attempt to prevent any further loss of oak woodlands in Los Angeles County (no net loss).

From this start, we further refined the plan to include several additional goals:
- Protect existing oak woodland ecosystems.
- Recover degraded or lost oak woodland ecosystems.
- Maintain the benefits provided by oak woodland ecosystems.
- Develop land use regulations and procedures that conserve oak woodland ecosystems.
- Coordinate conservation planning and restoration efforts.
- Comply with the requirements of the California Oak Woodlands Conservation Act.

Establish definitions
The next important step was to agree on the definitions of what constituted an oak woodland, oak stand, and various states of woodland condition (intact, moderately degraded, severely degraded). Given the diversity of 17 oak species and a larger number of community assemblages in Los Angeles County, the definitions had to be
applicable to scrub oaks, as well as scattered valley oak savannah systems. In this effort we relied heavily upon Guisti and others (2005, 2008), the Yolo County Oak Woodland Conservation and Enhancement Plan (2007), as well as input from California Department of Fish and Wildlife staff and documents (CDFG 2007).

We struggled with how to handle the variety of spatial relationships between oak species and woodland types, as well as the complexity of fragmented habitats associated with different stand sizes and integrity. Perhaps the most difficult process was to develop a tool planners could use to consistently map the extent of canopy, and to determine if the property was part of an oak woodland or not. Oak woodlands rarely coincide with property boundaries, but rather extend beyond individual parcels. Since planners are restricted to analyzing a proposed project on a specific parcel, overlaying and examining a landscape level scale can be really challenging. After extensive stakeholder input and discussion, the following definitions were developed (LACOWCMP 2011).

### III.1.1 Definition of an oak tree

All native trees of the genus *Quercus* that meet size and location requirements are protected by the Los Angeles County Oak Tree Ordinance. This includes small shrubby oaks typically clustered on slopes, as well as individual large oaks that are naturally widely distributed across the landscape. Under California state law, oaks greater than 12.6 cm (5 inches) diameter at breast height (DBH) are also protected (%PRC 21083.4(a)).

### III.1.2 Definition of an oak woodland

According to the California Department of Fish and Game (Section 1361), “Oak woodlands” are defined as an oak stand with greater than 10 percent canopy cover, or that may have historically supported greater than 10 percent canopy cover.” Currently the county uses this definition when evaluating planning impacts in most areas (with the exception of within the Local Coastal Plan zone) and this definition is also used for, and by, this OWCMP.

Separately, an oak stand was defined in this document as a group of similar trees growing in a contiguous pattern, having sufficiently diverse age-class distribution, composition and structure, and growing on a site of sufficiently uniform quality that it is distinguishable as a unit. Stands are a basic physical unit of vegetation in the landscape and do not have a set size (Keeler-Wolf and Evans 2006).

### Map historic and existing extent of oak woodlands

With definitions in hand, the next challenge was to map the existing oak woodland resources throughout Los Angeles County, and develop criteria for prioritizing protection, restoration and acquisition. The county extends from the coast to mountains over 3048 m (10,000 ft), and contains representation of all the biomes found in the continental United States within it 12 302 km² (4,750 mile²) boundary. A consequence of this physical diversity is a high biologic diversity of oak alliances and associations.

Determining the historic extent of oak woodlands required examining the original land grant maps (UC Berkeley library) for the county, as well as geo-referencing and digitizing the 1886 Map of Timber and Forests of Los Angeles County (California Department of Forestry Annual Report) and comparing this to the 1935 Wieslander Vegetation Map for Los Angeles County. Although forester A.E. Wieslander did not
complete his goal of mapping all the vegetation throughout the state of California for the U.S. Forest survey, his plot data for Los Angeles provided an important reference point. By mapping 16 ha plots defined on U.S. Geological Survey topographic quadrants and collecting extensive information on the vegetation within those plots, it was possible to return to those locations and compare current conditions.

Existing maps of oak distribution (CALVEG, Gaman and Firman 2006) were broad scale, which made it difficult to definitively create boundaries that accurately included all oak woodlands areas. One of the major limitations of these data sets was that small areas of oak woodlands existing within developed areas might not be included. With that limitation in mind, we developed GIS overlays of the oak vegetation types and added a 61 m (200 ft) buffer around them to include potential oak zones. This was overlaid on the county parcel map data to create a Potential Oak Woodland Conservation Map, which is now available to planners on the county website. Higher resolution versions of these maps were prepared for several high-density oak woodland areas within the county as well. There is still work to be done to refine these maps to incorporate more recent LiDAR data and establish a baseline of oak woodlands coverage throughout the county, but as a start it allows a property owner to identify if their parcel lies within a mapped oak woodland. This is also a helpful tool for planners at the initial study phase of a project to help identify any ecological constraints associated with oaks for a given parcel.

Finally, a mapping exercise completed by Lyle and Safford (1997) examined historic locations of oak woodlands and using a GIS model incorporating soils, slope aspect, elevation and other variables, developed the Oak Woodland Restoration Potential Model. Their maps identify areas within the county that most replicate previous conditions that had supported oak woodlands, and provide a strategy and road map for prioritizing locations for restoring oak woodlands within the developed landscape.

**Identify tools for economic valuation of oak woodlands**

Developing a cost benefit analysis tool for planners and decision makers was by far the most challenging part of the development of the LACOWCMP. Our goal was to not only identify ecosystem services costs and benefits, but provide guidelines on how to develop a baseline that would provide planners and decision makers with a better understanding cumulative impacts and long term costs. The multiple economic benefits provided by existing oak woodlands would have to be calculated, and then compared to the costs associated with avoided permitting and mitigation costs, building and maintaining necessary infrastructure (storm water conveyance, air and water pollution controls, carbon sequestration, and so forth) of equal value. We hoped that by identifying and quantifying these costs, decisions to preserve and avoid impacts, as well as encourage voluntary conservation would be more easily identified and implemented.

**What worked?**

The most significant accomplishment of the Alliance was the extensive effort to build a solid, consensus-based planning process that ultimately allowed all participants to support the final plan. Also, by organizing the plan into two sections, we were able to provide a way for our supervisors to successfully adopt the plan. Part I outlined the voluntary conservation efforts that makes the county eligible for Wildlife Conservation Board funding and was enthusiastically embraced by all stakeholders.
The more technical and potentially controversial recommendations to implement oak woodland conservation were included in Part II. Political support was critical, as it was only by direction of the county supervisors that county staff could undertake the administrative and regulatory changes recommended in Part II. It also provided time for the plan to evolve within the planning and public works department so that it could most effectively influence changes.

The second most significant accomplishment of the LACOWCMP was that the goals and objectives were able to influence the vision and goals for county general plan, climate action plan and local coastal plan. Our timing could not have been better!

Last but not least, the LACOWCMP has resulted in the development of guidance documents that are now on the regional planning web page and in process of being made part of the public works internal guidance efforts. By compiling all the relevant information into one document that is now available on the county web site, property owners can learn how to avoid impacts and develop designs that protect their oak woodlands so that they can move more smoothly and swiftly through the development process. Increasing coordination between county departments, transparency, clarifying the goals and processes, and allowing public works to demonstrate the best management practices in their projects are all major steps towards preserving and expanding the oak woodland resource into the future.

**Challenges remaining**

While we made a significant amount of progress since 2008, there is still much work to be done. We need to update and increase accuracy of oak woodland protected areas maps, and make those maps easily available on the internet, so that landowners can identify the extent of oak woodlands on their properties. There is need for a systematic tracking and reporting of effectiveness that has not yet been fully organized and tested. We need to work with county staff to clarify metrics to be tracked (number of acres preserved, restored, and so forth), funding for the county Oak Mitigation fund, as well as long term monitoring of oak restoration and preservation acres. Working with local partners such as universities and land use consultants, the county could establish a standard protocol for monitoring oak woodland conservation easements, develop and evaluate adaptive management strategies, and identify additional methods to monitor and evaluate the short and long – term success of oak woodland conservation and enhancement projects. Using county GIS information, it should be possible to track changes in oak woodland coverage over time. We also continue to encourage the county to contribute oak woodland data to the Natural Resources Projects Inventory, which is managed by the UC Davis Information Center for the Environment (ICE) and the California Biodiversity Council (CBC). This database tracks restoration project effectiveness throughout the state and could provide a broader perspective to evaluate the effectiveness of the LACOWCMP implementation.

Another challenge is to continue to participate in the development and implementation of the biogenic GHG emissions cap and trade strategies on both the county and state level. The opportunity to preserve and restore oak woodlands through these efforts could be substantial.

We also need to continue to publicize the opportunity and institutionalize the process for documenting voluntary expansion or planting of oak woodlands so that landowners are encouraged to plant oaks or dedicate conservation easements. This is an important element of a larger public outreach effort to encourage long term
stewardship partnerships to recognize and reward landowners who voluntarily conserve and restore their oak woodlands.

Summary
The collaborative effort of many stakeholders from 2008 to 2014 resulted in the development and implementation of the LACOWCMP (Los Angeles County Oak Woodlands Conservation Management Plan 2011), as well as implementation of a revised initial study checklist, standardized mapping of oak canopy extent and outlined strategies for comparing the cost-benefit analysis associated with proposed development/conversion of oak woodlands. It was designed to be a living document, able to accommodate new information and evolve as needed. While much progress was made, several tasks remain to be accomplished in order to protect and preserve oak woodlands in Los Angeles County for the future.

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Oak Woodland Conservation as Mitigation for Roadway Improvement¹

Park Steiner² and Jackson Ford²

Abstract

East Side Potter Valley (ESPV) Road is a heavily used rural collector road running north/south through the unincorporated area of Mendocino County known as Potter Valley. The roadway is significantly deteriorated and in need of repair and upgrade. The Mendocino County Department of Transportation (MCDOT) road project encompasses approximately 6.4 km of roadway that will be rehabilitated, straightened, and widened to bring the road section up to federal highway safety standards. An estimated 144 utility poles and miles of ditches will require relocation to accommodate the widening. New pole installations are required to meet strict fire prevention standards, necessitating relatively complete vegetation clearance near transformer poles and under power lines.

The total number of trees to be removed due to lane widening and pole relocations is estimated to exceed 800. Slightly over half of the trees are valley oak (Quercus lobata), ranging in diameter from 5 cm to greater than 50 cm. Trees to be removed occur in fence lines, under utility lines, and in riparian corridors immediately adjacent to the roadway. Due to the small size of each individual impact site and the already “domesticated” nature of the project landscape, it was felt that site-specific mitigations would be difficult to implement and of limited biological value. As a result, the concept of doing larger, collective mitigation at alternative sites was a more realistic approach.

Departing from more traditional mitigation approaches, MCDOT is providing a three-phase mitigation of 1) restoring approximately 2 ha of valley oak woodland habitat, and 1.2 ha of seasonal wetland/riparian forest habitat within Potter Valley, to be protected in perpetuity through a land trust conservation easement; 2) implementing a Potter Valley oak awareness program, whereby MCDOT sponsored a day-long public oak awareness workshop in September, 2014. This community collaboration provided local residents with information on the benefits of and methods for restoring oaks on private lands. Additionally, in response to community interest, MCDOT is committed to assisting the Potter Valley Unified Community School District (PVUCSD) initiate an environmental education program for their students; and 3) a one-time donation to the existing Redwood Valley Outdoor Education Program (RVOEP) to be utilized for student transportation, staffing, equipment, and for support of ongoing Mendocino County Resource Conservation District habitat rehabilitation efforts at the 18.2 ha RVOEP site.

Some aspects of the mitigation have already been implemented; others are in their final stages of development and/or approval. MCDOT anticipates having all easements, agreements, permits, and MOUs in place with landowners, schools, and regulatory agencies so that tree removal for utility pole relocation can commence in 2015. This unique mitigation program is an example of community and agency collaboration for oak restoration and positive conservation outcomes associated with road construction projects.

Key words: conservation easement, linear transportation, mitigation, roads, valley oak, wetlands

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Introduction

Potter Valley is an unincorporated rural agricultural and residential community located in southern interior Mendocino County. The community is located about 209 km north of San Francisco and has a population of approximately 1,000. Water is plentiful in the valley as the result of an interbasin hydroelectric project that diverts flow from the upper mainstem Eel River into the headwaters of the East Fork Russian River in Potter Valley. Water from the project is distributed for irrigation over most of the valley floor. At this time, grapes, pears, hay, and pasture for livestock dominate the agricultural landscape within the valley. The irrigation water also sustains a shallow water table under much of the valley.

The abundance of water and the shallow water table have resulted in a significant presence of trees in Potter Valley, primarily valley oak (Quercus lobata). Unlike the typical “lollipop” distribution of this species on valley floors prior to development, the current population is much more linear in its presence, growing along fence lines, lining private roadways, grouped in yards, or adjacent to riparian corridors. Valley oak tends to be quite prolific in Potter Valley, but thrive only where trees are protected from grazing, crop cultivation, or other clearance pressures. Trees vary in size and age. There are many groups of densely spaced saplings, especially within fence lines. In other areas, more mature trees are found in small but stately groves that may represent old-growth relics. Other tree and shrub species are interspersed within the valley oak dominance, some native, others not.

While most landowners in Potter Valley conduct some form of agriculture on their lands, many also work and shop elsewhere such as in Ukiah, Willits, Lake County, or more distant destinations. Many students from Potter Valley also commute regularly to attend schools out of the valley. The roads in and out are a vital link for Potter Valley residents, used by most on a frequent if not daily basis.

Between the 1950s and 1990s, Potter Valley supported an active timber industry, utilizing conifers from the National Forest and private lands to the north and east of the valley. The East Side Potter Valley (ESPV) Road was the primary route for moving timber and lumber products to and from two commercial operations in Potter Valley, a large sawmill near the Eel River and a smaller pallet mill located within the valley itself. Decades of heavy truck use took its toll on ESPV Road, especially during winter months when high waters tended to saturate the minimal base layer under the road.

The Mendocino County Department of Transportation (MCDOT) is responsible for maintaining over 1770 km of roads and 137 bridges in Mendocino County, including those in Potter Valley (CSAC 2014). The ESPV Road is the larger and most heavily used of two arterial roads running north/south through Potter Valley. It is also the primary route to the Lake Pillsbury Recreation Area in the Mendocino National Forest. In addition to the degraded condition of its base and bed, ESPV Road is narrow by current standards (AASHTO 2014), lacks adequate shoulders, has abrupt edges into ditches along much of its length, and is lined by many trees and utility poles. There are numerous driveway entrances onto the main road, a series of unsafe curves, and intersections with three smaller rural collector roads. Sight visibility is inadequate at one abrupt rise in the road. ESPV Road is a busy road with an anecdotal history of too many accidents. As a result, MCDOT has pursued the rehabilitation and widening of ESPV Road since 1998, and is now acquiring needed right-of-way in anticipation of initiating utility pole relocation and reconstruction during 2015.
During preliminary environmental studies required to rehabilitate and widen ESPV Road, it became apparent that biological impacts would be significant including the removal of more than 800 trees and the filling of an area of jurisdictional wetland. The road project extends approximately 6.4 m with impact sites distributed the entire length. The challenge for MCDOT staff was creating a mitigation package that would be cost effective and yet would be deemed acceptable by the resource agencies responsible for issuing the various regulatory permits for the project.

Policy environment for transportation projects

Environmental policy for road projects is essentially the same as for any other “project” in California. Environmental impacts resulting from a project must be avoided, minimized, or mitigated (CEQA 2012). The level of compliance required for a project is determined by the funding source(s) for that project. If a county road project is locally funded or funded through a state source such as the California Transportation Commission (CTC), State Transportation Improvement Program (STIP), or local funds, then the level of environmental compliance must meet the requirements of the California Environmental Quality Act (CEQA). Compliance with CEQA is under the jurisdiction of the various state resource agencies such as the California Department of Fish and Wildlife (CDFW) and the Regional Water Quality Control Board (RWQCB); those agencies are responsible to see that the project proponent meet all CEQA obligations as well as their respective permitting responsibilities.

If county road project funds are federal in origin such as from the Federal Highway Administration (FHA) or the Federal Emergency Management Agency (FEMA), then the standard for compliance is to meet the requirements for the National Environmental Policy Act (NEPA) as well as CEQA. The NEPA provides environmental protections similar to CEQA. Compliance with the provisions of NEPA is administered through Caltrans in a process called NEPA Delegation. Federally listed species as defined under the Endangered Species Act (ESA 1972) are the responsibility of the U.S. Department of Fish and Wildlife (USFWS) or the National Marine Fisheries Service (NMFS), depending on the species involved. Also at the federal level, wetland and some water quality issues under the Clean Water Act (CWA 1973) fall under the jurisdiction of the U.S. Army Corps of Engineers (USACOE). Any interactions with these federal departments for a county road project are also administered through Caltrans by means of the Delegation process.

If a project has joint CEQA and NEPA obligations, then both levels of compliance must be met by the project proponent. In addition to the CEQA and NEPA, all required state regulatory permits must also be obtained by the road department. The CDFW is responsible for plants and wildlife while the RWQCB oversees wetland and water quality issues. There can be shared responsibility between federal and state agencies when jurisdictional responsibilities overlap.

It is well past the scope of this paper to indulge in the complexities of policy that have embroiled the ESPV Project over the past years. Funding sources have changed repeatedly as have environmental requirements. Suffice it to say that the project has strived to meet the requirements of both CEQA and NEPA. The permitting to date has been with three primary agencies: CDFW (1600 Lake or Streambed Alteration Agreement), RWQCB (401 Clean Water Certification), and USACOE (404 Clean Water Act – Dredged and/or Filled Waters). The CDFW Agreement was signed on
August 28, 2014. As of October 31, 2014, both other permits applications, also submitted during 2014, await final approvals.

**Study area and proposed project**

The MCDOT proposes to reconstruct, and widen approximately 6.4 km of ESPV. The bounds of the project extend from the bridge crossing the Russian River at mile post (MP) 2.46 northward to the intersection of Main St. and Eel River Road at MP 6.42. The current road structure is severely deteriorated and is in need of reconstruction. The existing road consists of two 2.7 to 3.7 m wide traveled lanes with paved shoulders as narrow as 15.2 cm. The proposed project consists of grinding and recycling the current pavement and base using a process called foamed asphalt. New base material will be added as needed. The lanes will be widened to approximately 4.3 m and will include aggregate base shoulders varying in width from 0.3 to 1.5 m (typically 1.2 to 1.5 m).

![Figure 1—Project location map for the East Side Potter Valley Road Rehabilitation and Widening project.](image)

For the most part, the road alignment will not be changed from its current position, only widened. The exception is a 427 m portion of the road near the northern end of the project that currently contains two sharp switchback curves. The
alignment of this section of road is to be straightened. The radius of the curve at the northern-most end of the 6.4 km straight stretch will be increased to meet current highway speed design criteria (AASHTO 2014).

In another road improvement, the abrupt cresting of the hill near MP 5.5 fails to meet current highway sight visibility requirements. This hill crest is to be brought into specifications by down-cutting the road approximately 3 m as it crests the hill. This will significantly reduce the vertical profile of the road at this site, increasing visibility for traffic in both directions.

An estimated 144 utility poles require relocation to accommodate the widening. The poles support both PG&E power distribution and AT&T communications lines. Some tree and brush removal will be required to complete pole relocation. When any PG&E poles are relocated, the new installations are required to meet current, stricter fire prevention standards, necessitating relatively complete vegetation clearance near transformer poles and under lines (PG&E 2010). Oaks and other native tree species will be affected including a small number of trees in various riparian corridors. A number of non-native fruit and ornamental tree will also require removal.

Most existing roadside drainage ditches and some Potter Valley Irrigation District (PVID) channels will likewise need to be moved outward from their current locations during reconstruction, but will be returned to their original dimensions and function. The PVID will use this replacement opportunity to upgrade some of their aged and undersized culverts, distribution boxes, and gates.

**Methods**

A preliminary Natural Environment Study (NES) was conducted in 2004 by an independent consulting firm, North State Resources (2012). That NES was updated and finalized in 2012 by the same consultant. The intent of these studies was to determine if any special status species or any biologically sensitive habitats were present in the Biological Study Area (BSA). The consultant first reviewed state and federal databases for known occurrences. Following that, field surveys were conducted by qualified professionals at appropriate times of the year to confirm presence/absence for any species of concern along the entire length of the project. Also, a wetland delineation conducted in 2002 was re-evaluated to confirm that the mapping remained accurate in 2012.

Though not classified as species of concern, it became apparent early in the planning process that a significant number of trees would need to be removed as a result of the road widening process. Private property fences are present at the margin of right-of-way along much of the 6.4 km length of the project. Widening the roadway requires the acquisition of a commensurate amount of new right-of-way to accommodate the construction. As a result, existing fences are to be moved back to the bounds of the new right-of-way acquisitions. In Potter Valley, fence lines are one of the most successful regeneration locations for various trees and shrubs; dense vegetation frequently results in fences becoming living hedgerows, especially when the fences are adjacent to pastures and irrigation channels. Moving fences requires the removal of the vegetation, in part, to meet clear zone requirements for vehicles traveling on the roadway. These clear zone requirements apply to new road construction as specified by the American Association of State Highway and Transportation Officials (AASHTO 2014).

The MCDOT conducted a tree survey in 2009 to enumerate losses directly attributable to project grading activities and fence relocation. Trees were categorized by species and by gross grouping based on diameter at breast height (1.37 m; DBH).
classes. The DBH bins were selected somewhat arbitrarily, but seemed appropriate to provide representation of the trees observed along the project corridor. The size bins were <15.2 cm, 15.2 to 30.5 cm, 30.5 to 50.8 cm, and >50.8 cm.

By 2011, PG&E confirmed that they would also be doing a significant amount of tree removal to meet their vegetation clearance requirements. The PG&E conducted their own independent survey in 2011 to document trees that would be removed as a result of their pole relocation activities. Some of these trees were common with trees being removed for grading and fence relocation; other tree removals were independent from the MCDOT identified removals and needed to be added to the project totals.

Both the MCDOT and PG&E surveys have been revisited more recently in an attempt to determine which entity will be financially responsible for removal of which trees. Also, as a result of right-of-way negotiations, some trees slated for removal may now be protected. As a result, the exact number of trees to be removed remains uncertain. Verification of the exact location of each tree has been somewhat problematic given that the DBH’s have been estimated by the surveyors. Also, there has been a differing interpretation of how many “trees” might be emanating from a single “clump” where stump sprouting has occurred. Jointly, both MCDOT and PG&E have agreed to conduct an additional GPS/GIS survey before finalizing the exact numbers. Both entities will participate in this survey that will be necessary prior to the removal of any trees.

Results

Biological surveys

The biological surveys for special status species (NES) indicated no listed species are present within the BSA. Salmonids are not present due to the barrier presented by Coyote Dam which has no fish ladder to allow passage to the East Fork Russian River. No listed amphibians are present due in part to the proliferation of the aggressive, non-native American bullfrog (*Lithobates catesbeianus*) in the numerous ponds and canals around Potter Valley. Though historically there may have been some plants now listed as being of species of concern, the highly disturbed and ruderal nature of the lands adjacent to the project resulted in no occurrences of such species.

Much of the 6.4 km project entails general habitat disruption as defined under CEQA. Most notable is the removal or disturbance of trees, shrubs, and various roadside herbaceous plants. The greatest impact was potentially from tree removal; it was determined independently through the MCDOT and PG&E surveys that more than 800 trees would be removed during utility pole, fence, and ditch relocations. While none of the trees are listed as species of special concern, this vegetation provides food and shelter for a variety of birds and other wildlife species.

Table 1 presents a summation of the combined tree removal for MCDOT and PG&E as it was known in 2011. At that time, it was believed that the number of trees to be removed would be 812. The table breaks out the results by species and size categories. As of September 2014, the total tree count was adjusted to 947, but without the detail presented in table 1. It is assumed that the diversity and ratios seen in this earlier accounting will remain approximately the same. An additional joint
survey is to be conducted by both entities before tree removal begins in 2015. These newer results will be tabulated more conclusively using a GPS/GIS format.

Table 1—Combined results from preliminary tree removal surveys conducted independently by Mendocino County Department of Transportation and by PG&E for the East Side Potter Valley Road Rehabilitation and Widening Project, current in December 2011

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Size ranges</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt; 6&quot;</td>
<td>6&quot; - 12&quot;</td>
</tr>
<tr>
<td>White oak</td>
<td>111</td>
<td>178</td>
</tr>
<tr>
<td>Oregon ash</td>
<td>8</td>
<td>54</td>
</tr>
<tr>
<td>Live oak</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Apple</td>
<td>22</td>
<td>4</td>
</tr>
<tr>
<td>Locust</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Willow</td>
<td>88</td>
<td>22</td>
</tr>
<tr>
<td>Walnut</td>
<td>1</td>
<td>13</td>
</tr>
<tr>
<td>Plum</td>
<td>28</td>
<td>6</td>
</tr>
<tr>
<td>Cottonwood</td>
<td>4</td>
<td>19</td>
</tr>
<tr>
<td>Sycamore</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td>Pear</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Cedar</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Catalpa</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Cypress</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pine</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Redwood</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Eucalyptus</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>Spruce</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Maple</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Mulberry</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td>279</td>
<td>331</td>
</tr>
</tbody>
</table>

**Jurisdictional sites**

During the agency permitting process, three construction sites along ESPV Road project were deemed jurisdictional. Two sites are related to culvert replacements that will occur during road construction. The first site will be at MP 5.23 where an existing road culvert will be replaced due to its age and increasing potential for failure. The unnamed creek involved was historically ephemeral, but now remains wetted much of the summer due to leakage from the Potter Valley Irrigation District (PVID) East Canal. This canal intercepts this unnamed creek channel upslope of the road culvert. The creek channel is boarded off from the canal during the irrigation season when the creek would normally be dry. The metal arch culvert carrying this unnamed drainage under ESPV is currently 1.1 m in width. This culvert may be replaced in kind, but more likely will be replaced with a 2.4 m x 1.5 m reinforced concrete box culvert. Design options are still being evaluated.

A second site considered jurisdictional is where a culvert replacement will occur about 536 m to the north of the first site (approx. MP 5.50). At this location, the East Canal of the PVID (pipe # D 19) passes under ESPV through a 0.9 m culvert. (Note: Pipe # D 19 is to be upgraded to 1.2 m culvert at the time of replacement.) This canal is man-made and typically flows between 1 cfs and 25 cfs (0.03 m³ to 0.7 m³ per second), depending on water delivery demands. During winter storm events, the canal may carry as much as 50 cfs to 70 cfs (1.4 m³ to 2.0 m³ per second) with excess...
water above that flow leaving the system through a series of overflow drains. The current overflow drain for this reach of the canal is located to the east of ESPV and will remain there following culvert replacement.

The third federal jurisdictional impact resulting from the proposed road construction activity is located approximately at M.P. 4.89 where there will be the filling of an estimated 0.07 ha of emergent wetlands as identified by the formal USACOE Wetland Delineation of 2002 and confirmed again in 2012. The filling of the wetland will occur as a result of the road widening. This wetland is located on the west side of ESPV, adjacent to a culvert passing under the road at that location. The wetland is not naturally occurring, but the result of a leaking irrigation pond. The crest of the pond’s leaking earthen berm is approximately 23 m west of the road. The wetland lies between the pond berm and the road and is predominately vegetated with cattails (*Typha latifolia*) and Himalayan blackberry (*Rubus armeniacus*). The cattails and other vegetation are removed periodically by the landowner or by PVID to assure movement of storm runoff flows.

**Discussion**

A collaborative effort between MCDOT, CDFG (now CDFW), USACOE, and NCRWQCB, continuing since 2007, has resulted in what is a complex but seemingly appropriate mitigation for biological impacts anticipated from the 6.4 km long ESPV road rehabilitation and widening project in Mendocino County. The resulting mitigation package is comprised of three elements, all encompassing some level of general public awareness about oaks and oak restoration. The element that is the primary focus of this paper has to do with the creation of a conservation easement, which creates and protect two habitats, oak woodland and wetland. The remaining two mitigation elements provided funding for environmental education and a public workshop on oaks, but those will not be covered here.

The existing vegetation in Potter Valley is somewhat of an artifact due to the abundant irrigation water available in that community. A number of factors result in an abundance of trees, especially valley oaks. The elevated earthen distribution canals of the irrigation district tend to leak water to a relatively shallow water table, the primary source for local domestic water supplies and deep-rooted trees. In many areas, the upper levels of the soil are left moist as a result of regular irrigation, both by flooding of pastures and the sprinkling of crops. This moist condition, along with protection offered by the fence lines, roadways, and riparian corridors, contributes to the proliferation of vegetation in the valley, and particularly, an abundance of valley oaks.

The current linear forest pattern of trees in fence lines adjacent to roadways is the primary reason for the high number of trees requiring removal. Fence lines are located along road margins as a means to differentiate private ownership from public right-of-way. Utility poles lines are frequently located in the same corridor for maximum transmission efficiency and minimal intrusion on lands in agricultural production. And now, as the existing road needs an upgrade, the trees must be removed to make way for progress.

While the trees and shrubs being removed along the length of the project are not considered species of special concern, this vegetation provides significant habitat value for foraging, nesting, and shelter for a variety of birds and other wildlife. Birds, both resident and migratory, are one of the most significantly impacted groups since over half of the trees being lost are valley oaks. These majestic trees provide an abundance of insects and acorns for a broad range of birds from warblers to
woodpeckers (Roberts 1979). As oaks age, they provide an increasing abundance of cavity habitat utilized for nesting and evening shelter by many species (Block and Morrison 1990). The valley oak habitat is a feature limited to the valley floor in Potter Valley. It is replaced by drier oak and mixed plant communities on the surrounding hillsides. Birds, such as orioles and chats which prefer the larger trees are, therefore, somewhat restricted to the valley oaks of the lower elevations.

Birds may be heavily impacted by the significant tree removal, but other groups may feel the loss, also. Loss of valley oaks will likely impact large numbers of small mammals as well since many species utilize the acorns and shelter provided by these trees.

Much of the existing linear forest will be lost along the 6.4 km ESPV Road project during construction, but it is likely that significant natural recruitment of new trees will occur in subsequent years. The present tree distribution is primarily an artifact which has arisen since the road and fences were originally built many decades ago. Most fence lines will need to be taken down to allow for construction. When rebuilt, these fences will typically be no more than 1.5 m further back from where they were originally; a substantial number of fences will actually be replaced on their original alignments once ditching and grading is complete. Revegetation will utilize natural recruitment just as had been the case with the previous trees and vegetation. It is unlikely that revegetation will occur in the vicinity of the relocated utility poles since there will be active vegetation management in place to meet new safety requirements (PG&E 2010). As a result, there is no way to quantify the long-term net loss of trees along the road project. New tree recruitment will be affected not only by newly established pole and line clearance standards, but also by the discretion of the individual landowners and their desire to allow seedlings to establish again, or not, in the new fence lines.

Despite some natural restoration of oaks along the project corridor, it was clear that additional mitigation for project-induced loss of trees would be needed. With agency collaboration, it was decided that off-site mitigation might be the most expedient and appropriate way to mitigate for both the removal of trees and the loss of jurisdictional wetlands. To accomplish this, landowners on the valley floor were contacted and asked if they might consider placing a conservation easement on a portion of their land where wetland and oak loss could be mitigated. Willing owners were found, and the process of placing protections on portions of their lands was initiated in 2012 with assistance from the local Mendocino Land Trust.

The location of the off-site mitigation offered distinct enhancements for Potter Valley oak and wetland habitats. The polygonal configuration of the conservation easement lands will replace the linear forest of the roadside, resulting in a more natural habitat. This blocky shape allows easier wildlife access to a larger number of arboreal destinations, especially for avian inhabitants. Mammals will also have a more natural forest setting, suitable for sustaining greater diversity and populations than the linear forest being replaced. The mitigation lands are also in a much quieter part of the valley where wildlife will not be constantly confronted with the noise and rumble from the traffic on ESPV Road.

The oak woodland and wetland easement sites are located immediately adjacent to other highly desirable habitats. To the south of the oak site on an adjacent parcel, there is a grove of towering, mature valley oaks, still in their prime of life and offering the type of high canopy habitat required by many of the seasonal migrant bird species. This older grove will provide age diversity while the young oaks on the easement site develop over future decades. Along its northwestern edge, the oak mitigation site is bounded by a perennial drainage, Adobe Creek, which provides...
approximately 300 meters of prime, mature riparian habitat (willows, Oregon ash, valley oak, bay laurel, and white alder). This mature habitat provides significant diversity to the site. The wetland easement site is located approximately 500 meters to the northwest of the oak easement site. It is also bounded by a perennial drainage, unnamed, which provides another approximately 200 meters of prime, mature riparian habitat along its western boundary. Once the adjacent agricultural uses cease, it is assumed that each of these riparian corridors will expand from their drainages, encroaching onto the easement lands. The extent of this expansion is unknown, but some increase in mixed species forest is expected, improving the overall habitat quality for both the oak and wetland easement areas. It has been demonstrated repeatedly that mixed species habitats tend to support far more diverse and stable wildlife populations; a greater variety of plant species helps prevent wildlife collapses due to a production failure by any one of the plant species (Block 1990, Roberts 1979, Yarrow 2009).

Conclusions

For the ESPV Road Project, much of the mitigation was triggered by the necessary removal of a large number of oak trees. Appropriately, much of the mitigation centers on restoration of oaks, their long-term protection, and enhanced public awareness regarding oaks. As of October 31, 2014, some portions of the biological mitigation package have been completed, other are pending. The status of those elements appears in table 2.

Environmental mitigation for road projects is increasing in complexity. The Clean Water Act (1972) and the Endangered Species Act (1973) are the basis for many direct mitigations resulting from impacts caused by large, disruptive projects such as road construction. The protections or mitigations emanating from these legislative
acts are very specific with the intent to maintain or improve the conditions of our natural environment and to protect the populations of sensitive creatures supported by that environment. The implementation of these acts requires that numerical goals be met, either in water quality parameters or in numbers of listed plants or animals.

Table 2—Status of the biological mitigation elements for the East Side Potter Valley Road Rehabilitation and Widening Project

<table>
<thead>
<tr>
<th>Mitigation Element</th>
<th>Component</th>
<th>Current Status</th>
<th>Completion Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redwood Valley Outdoor Education Program Total: $40,000</td>
<td>Habitat Restoration at 45-acre outdoor education site</td>
<td>-$20K paid to RCD for ongoing program of site rehabilitation and invasive plant control</td>
<td>RCD – July 2014</td>
</tr>
<tr>
<td></td>
<td>Environmental Education Supplement</td>
<td>-$20K supports education, primarily for bussing, remainder for supplies and staffing</td>
<td>RVOEPIUUUSD – June, 2014</td>
</tr>
<tr>
<td>Oak Woodland &amp; Wetland Conservation Easement Total: est. $75,000</td>
<td>Provide funding for procurement of easement and associated endowment</td>
<td>- Fund $30K for drafting and refining of easement between land trust and owners, then final review and approval by permitting agencies</td>
<td>Ongoing, but estimated complete by December 2014</td>
</tr>
<tr>
<td></td>
<td>Fund landowner legal review costs</td>
<td>- Covered under Agreement up to $5K</td>
<td>Ongoing, but estimated complete by December 2014</td>
</tr>
<tr>
<td></td>
<td>Fund RCD to build fence to separate wetland area from pasture</td>
<td>- Cost estimates running up to $15K, but may be less if CCC’s are available</td>
<td>Spring or summer, 2015</td>
</tr>
<tr>
<td></td>
<td>Finances an Environmental Enhancement Fund for the woodland and wetland sites</td>
<td>- Approximately $20K remains available to create fund for enhancements. - Working to determine what entity will hold the funds until needed</td>
<td></td>
</tr>
<tr>
<td>Potter Valley Oak Awareness Program Total: est. $40,000</td>
<td>Conduct a citizen workshop emphasizing protections and restoration of native oaks</td>
<td>- Speakers from University of California ANR and Mendocino County DOT, with program updates from RCD, NRCS</td>
<td>Conducted September 20, 2014 at Potter Valley Schools.</td>
</tr>
<tr>
<td></td>
<td>Agency support to landowners</td>
<td>- Programs pre-existing, so no need to create new. - P.V. High School Ag program to make tree hoops &amp; bird houses for local residents</td>
<td>Funding not determined. $3K for materials for Ag program is part of $23 pending MOU.</td>
</tr>
<tr>
<td></td>
<td>Institute an environmental education program at the Potter Valley Schools (PVCUUSD)</td>
<td>- RCD funded $15K to help choose curriculum, and to identify suitable grants. - Provide $20K to PVCUUSD for grant match, etc.</td>
<td>RCD funded July, 2014. $23K MOU to fund PVCUUSD awaiting completion of conservation easement.</td>
</tr>
</tbody>
</table>

Given its physical length, the ESPV Road Project has relatively few jurisdictional impacts. Most of these could likely have been mitigated with relative ease, probably on-site with protections, enhancements, or replacements. But parts of CEQA offer less-well defined mitigation goals for general habitat disturbances and loss of unprotected plant and wildlife species. There is no question that removing over 800 non-jurisdictional trees is a significant impact on many fronts. This tree loss, especially the larger oaks, amounts to a significant reduction in habitat for birds and small mammals. There are also other less quantifiable parameters such as aesthetics which must be considered, but can be challenging to mitigate.

The less-quantifiable CEQA impact mitigations are left somewhat to the discretion of the reviewing agency staff and the project lead agency. Public input can also play an important role in determining mitigation requirements. In the case of the ESPV Road project, the proponent, MCDOT, worked collaboratively with agency staff from the earliest project site reviews to identify mitigations that might encompass the full range of biological and water quality impacts, as well as addressing public concerns. The goal was to create a mitigation package acceptable to all three permitting agencies. Based on verbal acknowledgements and permitting efforts to date, this has been accomplished.
An important goal was also to keep the mitigation package cost-effective relative to the cost of the road project. Mitigation costs are as variable as locations and the road projects themselves. The original mitigation budget was based on an evaluation of property value at the impact sites. This number increased proportionally as it was determined that more trees would need to be removed. A goal of $160,000 was derived and is still on track in spite of some unexpected exceedances. At this time, predicting that the road project may escalate to approximately $15,000,000, a mitigation package running at approximately $160,000 is slightly more than one percent of the total project cost, near the bottom of the range documented by Washington State (2013) for a number of their recent road projects. The ESPV Road Project value does not yet reflect stormwater erosion protections that will be required during construction, and those may be significant. Some of Washington State’s mitigation numbers have exceeded 45 percent for total mitigation; the average for the projects they evaluated was approximately 13 percent.

The other hoped-for outcome of the agency and public collaboration process was to have mitigations approved and permits issued prior to the commencement of construction. This goal appears doable given that the earliest project work, pole relocation, is not scheduled until mid-spring 2015. As seen in table 2, some of the mitigation elements are in place and most appear likely early in 2015. The CDFW 1600 permit has already been issued and the remaining two permits are awaiting finalization of the conservation easement. It appears the remaining permits will also be issued in the near future.

The concept of acquiring a conservation easement geographically near the project site was the single mitigation element most desirable to the permitting agencies. The original mitigation element of funding to the RVOEP was acceptable in 2008, but as the scope of impacts increased over the years, it became clear that some habitat-based mitigation would be required. Going door to door to find landowners willing to enter into a conservation easement was a challenge, but persistence paid off. The pieces of land being protected are both exemplary examples of what they are meant to replace, so the agencies are satisfied with the results of the collaboration. The environmental education elements are also on track to bring enlightenment to numerous students, in the Ukiah Unified and Potter Valley Community Unified School Districts.

Mitigations are as varied as the projects. Can future road projects use this mitigation package as a template? Not likely due to the complexity involved. Most county road projects are not as large, at least not in physical length and associated impacts. But elements within the package, especially the conservation easement, should well be considered when circumstances permit. The process of acquiring the easement has been overly complex and time consuming. It would be desirable if sources of easements were more readily available to entities such as road departments, possibly a worthy challenge awaiting local land trusts and land banks.

Creating the multifaceted mitigation package for the ESPV project has been challenging and rewarding. Working cooperatively with the various resource agencies, it was first necessary to determine the extent of the impacts. That in itself was somewhat of a moving target since the actual construction details for the project were not finalized during the permitting phase. So to move forward, the mitigation goals were kept somewhat conceptual, not a tree-for-tree replacement as was typical in the past. This flexibility allowed creative options which were massaged until acceptable to all parties including management within the county road department. The unconventional nature of this mitigation created additional implementation effort since there were few clear precedents to follow. Nonetheless, a partnership developed with the common goal of making the sum greater than the parts. Not only has there
been a reasonable habitat replacement with protection in perpetuity, but there has been support given to two separate environmental education programs and outreach to the community in general. Might this be a model for encouraging more flexible mitigation options in the future?

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Status, Conservation, and Management of Oak Woodlands at Tejon Ranch, CA

Michael D. White

Abstract
Tejon Ranch, encompassing 109 000 ha, is the largest contiguous private property in California. In 2008, the Tejon Ranch Company and a coalition of five environmental organizations executed the Tejon Ranch Conservation and Land Use Agreement that placed 90 percent of the property into permanent conservation and created the Tejon Ranch Conservancy as its steward. Tejon Ranch supports extensive, diverse, and regionally significant oak woodlands. The Conservancy is characterizing the composition and structure of these woodlands to inform land management.

Deciduous oak woodlands at Tejon Ranch are well-stocked relative to deciduous oak woodlands previously surveyed by others in California, but like other California oak woodlands, Tejon Ranch also has a high proportion of low stocked areas. Annual grasses and forbs dominate valley and blue oak woodlands, while black oak woodlands have a higher shrub cover. Photo comparison of deciduous oak woodlands at Tejon Ranch indicates a decline in all three species between 1952 and 2009. The Conservancy proposes to assess ecological sites and vegetation states to inform management, increase oak recruitment with tree shelters, and assess grazing management to enhance understory biodiversity.

Key words: conservation, management, Tehachapi Mountains, Tejon Ranch

Introduction
Tejon Ranch (fig.1), at 109 000 ha, is the largest contiguous private property in California. The 2008 Tejon Ranch Conservation and Land Use Agreement (Agreement) between the Tejon Ranch Company, the property owner, and five environmental organizations (Audubon California, Endangered Habitats League, Natural Resources Defense Council, Planning and Conservation League, and Sierra Club) resulted in conservation of 97 000 ha of the Ranch, of which oak woodlands are a significant land cover type supporting numerous species of conservation interest. The Agreement created the Tejon Ranch Conservancy and charged it with developing and implementing a management plan for the conserved lands.

Over the past 200 years, human development and agriculture have eliminated extensive areas of oak woodlands. While 20 oak species still cover 4 million ha of the California landscape (Allen-Diaz and others 2007), they face a variety of threats. Perhaps the most well-studied threat is insufficient oak regeneration to maintain stable populations (Bolsinger 1988, Griffin 1976, Tyler and others 2008). Cattle grazing in oak rangelands is frequently cited as the cause of the regeneration problem (Allen-Diaz and others 2007).

Given the conservation significance of oak woodlands, understanding their ecology and identifying management approaches is a high priority of the Conservancy. This paper describes the conservation significance, structure and condition, and management priorities of oak woodlands at Tejon Ranch.

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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Methods

Study area

Straddling the Tehachapi Mountains of California, Tejon Ranch ranges in elevation from approximately 150 m to over 2070 m. Prominent ridges and associated valleys extend along the spine of the Tehachapis creating a complex landscape with highly variable elevations, aspects, and landforms. Tejon Ranch sits at the confluence of two floristic provinces (California Floristic Province and Great Basin Province) and four floristic regions (Great Central Valley, Sierra Nevada, Mojave Desert, and Southwestern California (Baldwin and others 2012).

Conservation analysis

To evaluate Tejon Ranch’s contribution to oak woodland conservation, I quantified the conserved area of oak woodlands on the Ranch and in the surrounding region, defined by the Level IV ecological subsections (USEPA 2011) that intersect Tejon
Ranch and support oak woodlands, an area totaling 3,891,000 ha. I estimated the total area of Blue Oak-Foothill Pine, Blue Oak Woodland, Coastal Oak Woodland, Montane Hardwood, Montane Hardwood-Conifer, and Valley Oak Woodland from the FVEG land cover data set (CalFire 2006) within protected area using the California Protected Areas Database (GreenInfo Network 2013) and National Conservation Easement Database (NCED 2013). I follow Allen-Diaz and others (2007) by collectively referring to all oak savanna, woodland, and forest communities as “oak woodlands.”

**Vegetation measurements**
Vegetation characteristics were measured within 105 plots, each 20 x 30 m, in woodlands dominated by blue oak (*Quercus douglasii*), valley oak (*Q. lobata*), and black oak (*Q. kelloggii*) (Hoagland and others 2011). In each plot all trees, including seedlings and saplings, were counted, and diameter at breast height (1.37 m above ground; DBH) of trees and saplings was measured. Stocking rates (oak densities expressed as basal area of trees per land area) were derived by estimating basal area of all trees in each plot, assuming a circular cross-section with diameters based on DBH measurements. Composition and cover of understory vegetation functional groups were measured at 1-m intervals along three 30 m point-intercept transects in each plot.Vegetation functional groups included tree, shrub, grass, and forb; non-vegetative categories were bare ground, rock, leaf litter, wood, or cow pie. Refer to Hoagland and others (2011) for detail on plot selection and vegetation measurements. Statistical comparisons of oak woodland types at Tejon Ranch were made with ANOVA or t-tests with plots as the sample unit. The characteristics of Tejon Ranch oak woodlands were compared to results from statewide sample of Forest Inventory Analysis (FIA) plots reported by Bolsinger (1988) and statewide summaries from Allen-Diaz and others (2007).

**Population growth rates**
To quantify the mortality and recruitment of blue, valley, and black oaks on Tejon Ranch, 1952 aerial photos of Kern and Los Angeles counties were compared with 2009 USDA National Agriculture Imagery Program (NAIP). From these photos, three blue oak, three black oak, and eight valley oak photo stands were surveyed in each year, and the locations of all oaks were marked. Trees present in the 1952 photo that were not present in the 2009 photo were interpreted as mortality, and trees present in the 2009 photo that were not present in the 1952 photo were interpreted as recruitment. These results were used to calculate annual population growth rates over the 57-year period spanned by the photos. Refer to Hoagland and others (2011) for details on this analysis.

**Results**

**Conservation analysis**
Within the 3,891,000 ha regional extent around Tejon Ranch (fig. 1), there are 228,000 ha of oak woodlands, and approximately 110,000 ha (48 percent) of these woodlands are within protected areas. The conserved lands at Tejon Ranch protect an additional 18,000 ha, increasing the protected area of oak woodlands in the region by 16 percent. Including the conserved lands at Tejon Ranch, over 70 percent of black
oak woodlands (Montane Hardwood + Montane Hardwood-Conifer), 42 percent of valley oak woodlands, and 27 percent of blue oak woodlands (Blue Oak Woodland + Blue Oak-Foothill Pine) in the region are within protected areas.

**Vegetation characteristics**

Tejon Ranch supports 11 oak taxa, including two recognized hybrids (table 1). The most extensive oak communities are blue oak, valley oak, black oak, canyon live oak (*Q. chrysolepis*), interior live oak (*Q. wislizeni* var. *wislizeni*), and Brewer oak (*Q. garryana* var. *breweri*) woodlands.

### Table 1—Oak taxa recorded at Tejon Ranch

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Quercus berberidifolia</em></td>
<td>Scrub oak</td>
</tr>
<tr>
<td><em>Quercus chrysolepis</em></td>
<td>Canyon live oak</td>
</tr>
<tr>
<td><em>Quercus douglasii</em></td>
<td>Blue oak</td>
</tr>
<tr>
<td><em>Quercus garryana var. breweri</em></td>
<td>Brewer oak</td>
</tr>
<tr>
<td><em>Quercus john-tuckeri</em></td>
<td>John Tucker oak</td>
</tr>
<tr>
<td><em>Quercus kelloggii</em></td>
<td>Black oak</td>
</tr>
<tr>
<td><em>Quercus lobata</em></td>
<td>Valley oak</td>
</tr>
<tr>
<td><em>Quercus wislizeni var. wislizeni</em></td>
<td>Interior live oak</td>
</tr>
<tr>
<td><em>Quercus wislizeni var. frutescens</em></td>
<td>Interior live oak (shrub form)</td>
</tr>
<tr>
<td><em>Quercus Xalvordiana</em></td>
<td>Alvord oak</td>
</tr>
<tr>
<td><em>Quercus Xmorehus</em></td>
<td>Oracle oak</td>
</tr>
</tbody>
</table>

Average stocking rates of blue (7.2 m²/ha) and valley (13 m²/ha) oaks at Tejon Ranch are within the ranges reported for California as a whole by Allen-Diaz and others (2007), while the average stocking rate of black oaks on Tejon (32 m²/ha) is higher than they reported statewide (11 to 22 m²/ha). Blue, valley, and black oak plots at Tejon Ranch more frequently support higher basal area of oaks than did a sample of statewide FIA plots (Bolsinger 1988, fig. 2). Twenty percent of valley oak plots and nearly 70 percent of black oak plots at Tejon Ranch had basal areas greater than 100 ft²/acre (units reported by Bolsinger 1988), while no valley oak plots and less than 30 percent of the black oak plots exceeded 100 ft²/acre of basal area in the statewide FIA data. However, nearly 50 percent of valley oak plots at Tejon Ranch support basal areas less than 25 ft²/acre, while there were no statewide FIA plots in this lowest category. Blue oaks at Tejon Ranch show a similar pattern to statewide FIA data, with about 75 percent of plots supporting less than 50 ft²/acre.

Considering just woodlands at Tejon Ranch, the composition of understory vegetation is similar in valley and blue oak woodlands, which differs significantly from black oak woodlands (Hoagland and others 2011). Mean relative cover of herbaceous functional groups (that is, the sum of annual grass and forb cover) exceed 75 percent in blue oak and valley oak woodlands, which is significantly higher (p <0.001) than the herbaceous cover of black oak woodland understories (mean cover <40 percent). Black oak woodlands have a significantly greater cover of understory shrubs than do blue or valley oak woodlands (25.6 percent vs. <2 percent, p <=0.001). Black oak woodlands support a significantly higher cover of tree species in the understory layer (p < 0.05) and downed wood (p <<0.001) than do blue or valley oak woodlands.
The DBH range of blue and valley oaks is comparable between Tejon Ranch and statewide data reported by Allen-Diaz and others (2007). The largest blue oak measured at Tejon Ranch has a DBH of 82 cm and the largest valley oak 240 cm (fig. 3), while Allen-Diaz and others (2007) reported blue oaks grew to 600 cm DBH statewide (largest >180 cm) and valley oaks to 120 cm (largest >240 cm). The largest black oaks at Tejon Ranch (>150 cm, fig. 3) exceed the largest individuals they reported statewide (up to 120 cm). The size structures of the three deciduous oak populations at Tejon Ranch are different (fig. 3), with valley and black oaks having a higher proportion of larger individuals in their populations than blue oaks. Over 13 percent of black oaks and nearly 27 percent of valley oaks at Tejon Ranch exceed 100 cm DBH. However, there are few very small individuals in any of the Tejon populations. Approximately 6 percent of the blue oaks measure less than 10 cm DBH, and no valley or black oaks measure less than 10 cm DBH.
At Tejon Ranch, valley oak saplings are more abundant than either black oak or blue oaks (Hoagland and others 2011). Within 55 plots containing valley oaks, 44 saplings were recorded within 11 plots. However, within 35 and 26 plots supporting black oaks and blue oaks, respectively, 17 black oak saplings were present in six plots, and 12 blue oak saplings were present in four plots. The densities of black oak and valley oak seedlings are similar, with 185 and 186 seedlings found in 26 and 27 valley oak and black oak plots, respectively. Only five blue oak seedlings were found in two plots.

Population growth rate

Population recruitment, mortality, and growth rates at Tejon Ranch are comparable among the three oak species (Hoagland and others 2001). While the valley oak recruitment rate is higher than either blue or black oaks, recruitment rates for all species are an order of magnitude less than mortality rates. Blue oaks have the highest mortality and lowest recruitment rates. Thus, population growth rates for all species are slightly less than 1.0, indicating declining populations. Blue oaks exhibit the lowest population growth rate of the three species, and Hoagland and others (2011) calculated that at an estimated annual population growth rate of 0.998, blue oaks could suffer a 9.3 percent population decline over the next 50 years.

Discussion

Conservation

The conserved lands at Tejon Ranch support over 18 000 ha of oak woodlands or 8 percent of the 228 000 ha of oak woodlands in the Tejon Ranch region (fig. 1). The Tejon Ranch Conservation and Land Use Agreement increased conservation of oak woodlands in the region by 16 percent to 128 000 ha. In particular, the conserved...
lands at Tejon Ranch contribute significantly to protection of blue oak and valley oak woodlands at the southern ends of their ranges. Oak woodlands conserved on Tejon Ranch are diverse, comprised of 11 taxa or one-third of the oak taxa in California.

**Structure and condition**

Landowners, policymakers, and the public are concerned about inadequate oak regeneration (Allen-Diaz and others 2007), although Tyler and others (2008) suggest there may not be an oak regeneration problem. Cattle grazing in oak rangelands is often identified as the source of poor oak recruitment; however, Davis and others (2011) showed that native grazers (for example, deer) and seed predators (for example, rodents) also control oak population growth. Sheep and cattle have grazed oak rangelands at Tejon Ranch since the 1840s. Over 50 percent of the oak rangelands at Tejon Ranch, primarily blue and valley oak woodlands, are in low-stocked conditions (<50 ft²/acre basal area). In contrast, less than 20 percent of higher elevation black oak woodlands, which are less important rangelands at Tejon Ranch, are in low-stocked conditions. However, relative to Bolsinger’s (1988) reported stocking rates of oak woodlands across California, much of the valley and black oak woodlands at Tejon Ranch are better stocked than other parts of California (fig. 2). One-third of valley oak woodlands at Tejon exceed 75 ft²/acre compared to only 16 percent of valley oak woodlands statewide, and while over 40 percent of black oak woodlands exceeded 75 ft²/acre statewide, nearly 70 percent of black oak woodlands at Tejon Ranch exceed 75 ft²/acre. Valley and black oak woodlands at Tejon Ranch support large individuals (fig. 3).

Seedlings of all species were observed in oak plots at Tejon Ranch, although blue oak seedlings were rare the year data were collected. Blue, valley, and black oak saplings comprised 7.7 percent, 21.2 percent, and 5.8 percent, respectively of the individuals of each species that were counted at Tejon Ranch. However the estimated growth rates of blue, valley, and black oak populations at Tejon Ranch are slightly less than 1.0, suggesting these species are declining over time (Hoagland and others 2011).

At Tejon Ranch, the understories of blue and valley oak woodlands are dominated by nonnative annual grasses and annual forbs with little shrub cover, while black oak woodlands have a significantly higher cover of shrub species (Hoagland and others 2011). The composition and structure of the oak woodlands at Tejon Ranch prior to European settlement are unknown. Bauer (1930) described Tehachapi Mountain foothill woodlands as having an open structure, but growing in dense stands in more favorable sites. He characterized the oak woodlands as having “layered societies,” possibly suggesting well-developed canopy, shrub, and herbaceous layers. However, Bauer (1930) also noted that human land uses had facilitated nonnative plant invasions and altered fire regimes that changed the structure and composition of woodlands.

**Management**

Conservation at the privately owned Tejon Ranch is via conservation easements (Tejon Ranch Conservancy 2013). Under these easements, the Tejon Ranch Company retains the right to graze livestock in conserved lands, but grazing is subject to management measures developed by the Conservancy to enhance conservation values. The Conservancy used the oak woodland ecology and condition
The information reported here and elsewhere to develop adaptive management strategies for conserved lands at Tejon Ranch.

The Conservancy’s current priority is to increase our understanding of oak woodland structure and function. As discussed by Allen-Diaz and others (2007), a residual dry-matter (RDM) model (George and others 1985) has been used for management of oak rangeland understory species composition and productivity, but there is little research to support extension of this model to biodiversity management. The Conservancy hypothesizes that human land use practices in this region over the past 170 years have reduced the native biodiversity of oak woodland understory communities. We are assessing whether the Ecological Sites framework (Bestelmeyer and Brown 2010) we are using to develop grasslands management strategies can be applied to oak woodlands. We propose to explore how woodland understories may respond to managed grazing regimes.

Oak populations appear to be in decline at Tejon Ranch; however, given the long life span of adult oaks and the current demography and population growth rates at Tejon Ranch, enhancing oak regeneration is not urgent. Davis and others (2011) found that excluding livestock and deer browsing and rodent seedling predation improved oak recruitment. As resources are available, we can enhance recruitment of oaks and other woodland tree species by using tree shelters to protect seedlings and saplings from grazers and browsers (McCreary and others 2011). Climate change research suggests that areas of Tejon Ranch will provide suitable climate envelopes for oaks into the next century (Hoagland and others 2011, Sork and others 2010) and that these stable climate refugia are logical areas for enhancing recruitment.

As with many other parts of California, Tejon Ranch supports a significant population of wild pigs (*Sus scropha*) that root and forage extensively in oak woodlands. The Conservancy hypothesizes that wild pigs alter oak woodland understory composition, elevate oak seedling mortality, and compete with other wildlife for acorns. The Conservancy has initiated research and planning for the management of wild pigs at Tejon Ranch to enhance the condition and native biodiversity of oak woodlands.

**Acknowledgments**

I would like to recognize the hard work and contributions of the 2011 Bren School Tejon Oaks Project team: Serra Hoagland, Anderson Shepard, and in particular Shannon Moy and Andrew Krieger who collected most of the field data reported here, and their faculty advisor Frank Davis. Jerre Ann Stallcup made valuable suggestions to improve this paper. This work was made possible by generous funding from an anonymous donor.

**References**


Conifer Encroachment in California Oak Woodlands

Matthew I. Cocking, J. Morgan Varner, and Eamon A. Engber

Abstract
California deciduous oak woodlands provide many ecological, cultural, and economic benefits, and often represent unique plant communities that harbor native rare and declining species. Oak woodlands have suffered substantial losses in area and ecological integrity in the post-settlement era due to land conversion and widespread fire exclusion. Remnant oak woodlands in many areas are undergoing further conversion to conifer forest as shade-tolerant, and often less fire-tolerant species invade and increase in abundance. This process, known as conifer encroachment, has been identified across the Pacific West; efforts to restore these ecosystems have increased in California over the past several decades. The process of conifer encroachment is known to occur in many ecosystems in California, but principally affects oak woodlands dominated or co-dominated by Oregon white oak (Quercus garryana) and California black oak (Quercus kelloggii). Encroachment proceeds through four phases including establishment, piercing, overtopping, and decadent; oak crown recession occurs by the third stage, after which oak mortality becomes abundant. The concomitant increased shading and needlecast from the conifers diminishes plant and animal biodiversity and ecosystem services, and alters fire regimes. We discuss encroached oak woodland structure and dynamics in northern California, identifying conifer species that have the capability and propensity under a fire-suppression management regime to invade and degrade remnant oak woodlands.

Key words: California black oak, ecosystem restoration, forest composition, forest structure, Garry oak, Oregon white oak, prescribed fire

Introduction
A century of fire suppression and management regimes has diminished the resilience of many of California’s ecosystems by disrupting natural disturbance processes. Deciduous oak woodlands, primarily those dominated by Oregon white oak (Quercus garryana) and California black oak (Quercus kelloggii), provide an example where removal of fire can result in the conversion from oaks to less fire-tolerant tree species, primarily native conifers. This process has been described variably as conifer invasion, forest densification, mesophication, succession, and conifer encroachment. The process of conifer encroachment has been observed and studied from California to British Columbia. Conifer species that typically encroach oak woodlands include Douglas-fir (Pseudotsuga menziesii), white fir (Abies concolor), incense-cedar (Calocedrus decurrens), and western juniper (Juniperus occidentalis). Frequent fire acts as a strong control on these coniferous species by killing regeneration, thereby

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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3 College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, 228C Cheatham Hall, 310 West Campus Drive Blacksburg, VA 24061.
4 Redwood National Park South Operations Center, National Park Service, 121200 Highway 101 S, Orick, CA 95555.
limiting recruitment to sapling and mature stages (Engber and Varner 2012a). When fire is excluded, proliferation and growth of conifers outpaces oaks resulting in eventual overtopping by conifers, and oak mortality (Barnhart and others 1996, Cocking and others 2012, Devine and Harrington 2006, Devine and Harrington 2013, Engber and others 2011, Sugihara and Reed 1987). In this paper, we present information on the process of conifer encroachment from observations and lab and field studies at various sites across northern California. We focus on the suite of conifer species predisposed to increase within oak woodlands, the effect this process can have on natural resources, and restoration methods currently being utilized to reverse encroachment in parts of northern California.

Effects of conifer encroachment on oak woodlands

Effects on stand structure and composition

Conifers pre-disposed to expand into oak woodlands are generally shade-tolerant, fast growing, and susceptible to fire as juveniles. Encroaching species and rate of encroachment vary by region depending on climate, substrate, and the local vegetation. In coastal sites, encroachment is often exclusively Douglas-fir (Barnhart and others 1996, Engber and others 2011, Sugihara and Reed 1987). In higher elevations and areas in the interior of northern California, Douglas-fir is joined or eclipsed by white fir and incense-cedar (Skinner and Taylor 2006, Skinner and others 2006). Encroachment by western juniper occurs in more arid environments (table 1). While a suite of other conifer species also regenerate in oak woodlands during fire-free intervals or following single fires (for example, ponderosa pine, gray pine, knobcone pine), these species have sparse crowns and tend to co-exist with deciduous oaks.
Table 1—The expected time to development of different stages of conifer encroachment after conifer establishment (values are based on data from published research and personal observations by the authors)

<table>
<thead>
<tr>
<th>Region</th>
<th>Encroaching species[^a]</th>
<th>Understory cessation (years)</th>
<th>Oak crown recession[^b] begins (years)</th>
<th>Oak mortality begins[^c] (years)</th>
<th>Oaks replaced[^d] (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Coast Ranges</td>
<td>PSME</td>
<td>5-10</td>
<td>20-30</td>
<td>30-40</td>
<td>60-100</td>
</tr>
<tr>
<td>Western Klamath</td>
<td>PSME</td>
<td>5-10</td>
<td>20-30</td>
<td>40-50</td>
<td>80-100</td>
</tr>
<tr>
<td>Central Klamath/Trinity</td>
<td>PSME, CADE, ABCO</td>
<td>10-20</td>
<td>30-40</td>
<td>60-80</td>
<td>100-150</td>
</tr>
<tr>
<td>Southern Cascades/northern Sierra</td>
<td>ABCO, PSME</td>
<td>10-20</td>
<td>30-40</td>
<td>60-80</td>
<td>100-150</td>
</tr>
<tr>
<td>Eastern Klamath/Shasta Basin[^e]</td>
<td>JUOC</td>
<td>20-30</td>
<td>not observed[^f]</td>
<td>≥20</td>
<td>not observed[^f]</td>
</tr>
<tr>
<td>Northern CA serpentine[^g]</td>
<td>CADE, PIJE, PSME</td>
<td>10-20</td>
<td>30-50</td>
<td>60-80</td>
<td>≥100</td>
</tr>
</tbody>
</table>

\[^a\]listed by commonality/importance. PSME = Pseudotsuga menziesii, CADE = Calocedrus decurrens, ABCO = Abies concolor, JUOC = Juniperus occidentalis, PIJE = Pinus jeffreyi.

\[^b\]Refers to the dieback of oak crowns during the piercing stage.

\[^c\]Oak mortality begins during the overtopping stage and peaks as stands reach the decadent stage.

\[^d\]Refers to timeline estimates for 90 percent or greater mortality of pre-encroachment oaks within a stand.

\[^e\]Earlier oak mortality in the Eastern Klamath and Shasta Basin is based on empirical observations at several Oregon white oak sites and might be accounted for by more severe competition for water in this arid region.

\[^f\]Complete replacement of oaks and dieback of oak crowns was not observed with western juniper encroachment; development of these stages may be limited by lower height potential and density of western juniper.

Conifer encroachment often occurs as an initial wave (establishment stage), preceding additional successional development. Tanoak (Notolithocarpus densiflorus), evergreen huckleberry (Vaccinium ovatum) and other common Douglas-fir understory species succeed Douglas-fir encroachment in coastal oak woodlands (Sugihara and Reed 1987). Encroaching conifers can reach high densities (Cocking and others 2012) especially in wetter climates (for example, Douglas-fir, Coast Ranges) as opposed to dry regions (for example, western juniper, eastern Klamath/Shasta Basin). During establishment, encroaching trees are subject to competition pressure with understory herbaceous and shrub species, especially in herbaceous-dominated Oregon white oak woodlands. As conifers ascend to the oak canopy (piercing stage), competition for sunlight between oaks and conifers becomes substantial, with Douglas-fir having the ability to grow through oak crowns without canopy gaps (Hunter and Barbour 2001). This stage is characterized by many conifers that have pierced pre-existing oak crowns, resulting in an abundance of interlocked crowns and competition for space within the same canopy stratum.
(Cocking and others 2012). As conifers emerge above the woodland canopy, increased shade causes dieback of shade-intolerant oaks (overtopped stage). This often results in structural failure of oaks and eventual oak mortality in late stages of encroachment (decadent stage, fig. 1).

Understory response and altered flammability

Un-encroached oak woodlands naturally produce fuelbeds conducive to fire spread with two primary components that are grown and replaced annually: cured herbaceous fuels and oak leaf litter. Understory grasses and forbs generate a porous, low bulk density fuelbed (Engber and others 2011) and senesced leaves of Oregon white and California black oak are highly flammable, rivalling litter from the most fire-adapted pines of the western United States (Engber and Varner 2012b, table 2).

Table 2—Comparison of flammability of deciduous oaks and three encroaching conifers

<table>
<thead>
<tr>
<th>species</th>
<th>functional group</th>
<th>flame ht (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Quercus kelloggii</em></td>
<td>deciduous oak</td>
<td>83.0&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Quercus garryana</em></td>
<td>deciduous oak</td>
<td>76.0&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Calocedrus decurrens</em></td>
<td>encroacher</td>
<td>47.1&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Pseudotsuga menziesii</em></td>
<td>encroacher</td>
<td>26.2&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Abies concolor</em></td>
<td>encroacher</td>
<td>21.8&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Sources of data: <sup>a</sup> Engber and Varner 2012; <sup>b</sup>Fonda and others 1998; <sup>c</sup>Varner and Banwell, unpublished data.
Flammable fuelbeds promote a frequent fire regime, allowing managers to utilize prescribed fire on about 5 year intervals (Underwood and others 2003); frequent fires serve as a bottleneck for conifer seedling establishment. Non-sprouting, seed reliant conifers are reduced in density, while oaks persist, via either survival as adults or re-sprouting if top-killed by fire. As the oak woodland fuelbed is shaded and replaced by conifer needles and timber litter, the fire feedback is reversed, understory flammability declines, and the bottleneck on conifer establishment is removed (Engber and others 2011). While encroachment results in reduced understory flammability under moderate fire weather (for example, prescribed fire windows), it may increase canopy (crown) fire risk during extreme fire weather events.

**Impacts to natural resources and ecosystem resilience**

California oak woodlands are important natural resources providing species diversity, water and nutrient cycling, rangeland production, and ecosystem resilience. As mast producers, oaks are essential for survival of many mammal and bird species (Standiford 2002). A critical consideration for the future of mast production at a landscape scale in northern California is the apparently bleak future for tanoak (*Notholithocarpus densiflorus*) due to mortality caused by sudden oak death (Rizzo and others 2002) and the resistance of Oregon white oak to the introduced pathogen responsible for this widespread mortality, *Phytophthora ramorum*. Oregon white oak and California black oak may be key to sustaining acorn-dependent wildlife in parts of northern California as tanoak declines. Oak woodlands are also essential to rangeland health; oaks provide shade for grazing animals during hot summer months and support better late season forage by sustaining higher soil moisture content and nutrients beneath their canopies than adjacent open grassland (Dahlgren and others 1997, Joffre and Rambal 1993) and stands encroached by Douglas-fir (Devine and Harrington 2007). Drought resilient native perennial grasses (Volaire and Norton 2006) and nearly all other understory herbaceous species decline early in the encroachment process, quickly reducing forage quality and quantity and disrupting natural carbon, nutrient, and water cycling processes. The effects of conifer encroachment on water yield may be the most important natural resource consideration relating to this specific issue in California and the Pacific Northwest. When viewed in the sole context of vegetation structure, conifer encroachment in northern California oak savannas, woodlands, and neighboring grasslands is akin to afforestation (Engber and others 2011, Sugihara and Reed 1987), which substantially and more permanently impacts water yield (Farley and others 2005). Furthermore, rainfall interception (a major factor affecting evapotranspiration and water balance; see Zhang and others 2001) is often substantially lower for deciduous as opposed to coniferous forests (Rutter and others 1967, 1975; Zinke 1967). Thus, increased groundwater infiltration and reduced evapotranspiration are a major benefit to the California’s water supply in un-encroached oak woodlands.

**Restoration effectiveness and feasibility**

**Treatments of encroaching conifers**

Restoration treatment intensity and methods vary depending on stage of encroachment. During establishment, conifer seedlings and saplings can be killed by prescribed fire in oak litter/grass fuels (fig. 2-top; Engber and Varner 2012a). Beyond
establishment (about 10 years on productive sites), some conifers become resilient to prescribed fire, and fuelbed changes reduce the likelihood that fire alone will achieve restoration objectives, necessitating mechanical or hand treatments (Cocking and others 2012, Engber and Varner 2012a, Sugihara and Reed 1987). As encroachment proceeds into the piercing and overtopping stages, mechanical treatments (for example, hand-felling or feller-buncher operations) become necessary to remove large, fire-resistant conifers prior to re-introduction of prescribed fire. Smaller cut material may be piled and burned or chipped for biomass utilization while larger material can be sold as saw logs to offset restoration costs while simultaneously achieving objectives. Research on growth release of Oregon white oaks following piercing and overtopping stages shows substantial growth response of oaks even for trees with severely reduced crowns and apparently low vigor (Devine and Harrington 2013). Once an oak stand reaches decadent stage, where oak mortality is widespread, restoration may not be feasible without planting a new cohort of oaks.

At Whiskeytown National Recreation Area, managers have utilized mechanical equipment (feller-bunchers) to remove commercial conifers up to 45.7 cm (18 inches) in diameter (fig. 2 – bottom left). Treatments have focused on full-release (crown thinning) around oaks and a substantial reduction in the proportion of Douglas-fir within stands. Where mature conifers have pierced oak crowns, branch and bole injuries may be sustained to the oaks during conifer removal. Conifer girdling (severing the vascular cambium in a strip around the tree bole) is an alternative treatment on individual trees that can mitigate damage concerns to oaks and provide snag habitat within post-treatment stands (fig. 2 – bottom right). Girdled trees decompose slowly and pose little threat to the structural integrity of oak crowns. Where ground-based equipment is employed for conifer removal, rehabilitation of bare ground should be prioritized to mitigate post-treatment erosion or invasion of non-native species (Devine and others 2007). At Whiskeytown NRA, up to 70 percent of the bare ground was mulched with pre-commercial stems and/or chips following treatments, and berms were pulled by hand. Seeding or transplanting native grass species can also help mitigate erosion and will hasten restoration of understory herbaceous cover. Follow-up treatments to reduce surface fuels may be necessary after erosion threats have abated.
Figure 12—Top - Fire-scorched Douglas-fir seedlings, 2013 Rx Burn, Redwood National Park. Bottom left - Mature California black oak/ponderosa pine stand following removal of encroaching Douglas-fir and tanoak at Whiskeytown National Recreation Area, 2014. Saplings were crushed by feller-buncher operations and used to mitigate post-treatment erosion. Bottom right – A girdled Douglas-fir tree that had grown through an Oregon white oak crown at a restoration site on private land in Humboldt County, NRCS, 2014.
Post-fire response of encroached oak stands

In the Bald Hills of Redwood National Park, oak mortality has been very low within units that have been prescribed burned five or more times at 3 to 5 year intervals, limited mostly to small oaks <15.2 cm (6 inches) DBH (Engber, personal observation). In wildfires, oak mortality is also rare due to re-sprouting (Cocking and others 2012). In high-severity fires oaks are able to reclaim sites by re-sprouting and new stems attain large size quickly where conifers are limited to re-establishment by seed from surviving trees. By contrast, low intensity fire has little effect on the later stages of encroachment (beyond piercing) since both conifers and oaks often survive, perpetuating conversion to conifer dominance (Cocking and others 2014). Data from the Klamath Mountains shows evidence that pierced and overtopped oaks undergoing crown recession may be more susceptible to fire in encroached stand conditions due to lower vigor as a result of competition (Cocking and others 2012).

Thresholds to potentially irreversible conversion

The stand dynamics of oak woodlands across an un-encroached to encroached gradient raises key questions about restoration feasibility, cost, and maintenance. As the amount of encroaching tree biomass increases within oak woodlands, the cost of treatment rises substantially, with few or limited available markets as outlets for restoration byproduct material. This increasing cost is not alleviated by prescribed fire (often a cheaper option) which is generally rendered ineffective in conifer encroached understories typical of pierced and overtopped stand conditions (Engber and others 2011). The relative cost of treatment can be thought of as required energy input to restore an oak dominant state (fig. 3).

Figure 13—A conceptual model with artwork adapted from Cocking and others (2012) showing the change in energy required to revert to oak dominance across encroached stages. Dashed arrows mark thresholds where stands pass out of maintenance or into conversion and are beyond the limits of restoration. Restoration energy input is the energy required to move stages back toward unencroached woodland. Stages further right in the diagram are more difficult to revert to previous states.

The relationship between encroachment stage and restoration cost is analogous to wildfire effects on encroached oak stands - increasing intensity of fire (in other words, higher energy input) is required to kill larger conifers and adjust overstory dominance back to re-sprouting oaks (Cocking and others 2014). This relationship is likely not linear, but asymptotal where the shifts to later stages of encroachment
represent crossing of thresholds, and reverting to a previous state requires large amounts of energy (or may not be possible).

**Conclusion**

Given the increasing costs of restoration at later stages of conifer encroachment, and subsequent losses of biodiversity and ecosystem services, the need to increase restoration efforts in California oak woodlands is urgent. The resource impacts associated with a decline of an unquantified total area of encroached oak woodlands are an additional consideration given the economic, ecological, and cultural importance of oak ecosystems in California. For restoration efforts to be successful managers will need access to information similar to that presented in this paper which provides an overview of the encroachment process, and, importantly, a framework to develop restoration or maintenance plans and identify limiting factors - depending on encroachment stage – for California oak woodlands.

**References**


Can the California Forest Practice Rules Adapt To Address Conifer Encroachment?1

Yana Valachovic2, Lenya Quinn-Davidson2, and Richard B. Standiford3

Abstract
The loss of oak woodlands to conifer encroachment is widely recognized as a major conservation concern. The increased occupancy of oak woodlands by Douglas-fir (Pseudotsuga menziesii) and other conifers has been reported throughout portions of California and the Pacific Northwest in multiple oak habitat types. In California, Oregon white oak (Quercus garryana) and California black oak (Quercus kelloggii) are particularly impacted by encroachment. Studies point to altered disturbance regimes, and the suppression of low-intensity fire in particular, as the primary cause of increased conifer establishment in these oak woodlands.

Much of the Oregon white oak and California black oak woodlands of California occur on privately owned land and as a result their management is subject to the standards of the California Forest Practice Rules. There are several issues in the current California Forest Practice Rules where there are disincentives to active management of the conifer encroachment issues. The California State Board of Forestry is considering development of an “oak woodlands restoration” approach to address these issues, but faces many challenges in the central design of the rules and the need to balance multiple species and management interests.

Key words: California black oak, California forest practice rules, encroachment, fire exclusion, forest policy, Oregon white oak

California forest policy history 1890s to 1970s
California has a long and rich history of developing policy to guide the management of its timberlands. Within this history there are several key policies that have influenced California black oak (Quercus kelloggii) and Oregon white oak (Quercus garryana) woodland management.

The Board of Forestry was established in California in 1885. The first State Forester was appointed in 1905. The board and state forester focused on development of a fire protection system and timber slash management, with some effort given toward pest outbreaks and the creation of work camps to address the large number of people out of work from the Great Depression (Arvola 1976). In 1927 the Division of Forestry was created within the new California Department of Natural Resources. As California’s timber industry was maturing, there were several efforts on the national front to develop a federal-state regulatory system that would be led by the U.S. Department of Agriculture, Forest Service. California interpreted this as a federal overstep, and the state legislature commissioned a committee, led by UC Berkeley Professor Emanuel Fritz, to provide a “forestry study” (Arvola 1976). The committee’s assessment led to a proposed set of forest policies that later became the

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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1945 California Forest Practices Act. This act established the creation of four Forest District Boards and each were given the authority to establish rules for their geographic areas. The four boards were largely populated with industry representatives and during their beginning there was little public interest in their actions (Arvola 1976). Following the 1964 flood, public concern about forest management gained momentum, which continues to the present.

In 1971, the California Forest Practices Act was found to be unconstitutional by an appellate court on the basis that the Board did not have sufficient public representation. Additionally, there was mounting public concern about the protection of water, fish, soil, wildlife and other resources in the first rules. In response, the state legislature commissioned UC Davis to write a study about the condition and policy of California’s forest lands. This 1972 study became the basis of the 1973 Z’berg Nejedly Forest Practices Act (Institute of Ecology 1972), which remains in effect today. Shortly after adoption of this new Act there were other changes to forest land taxation systems in California. In 1976, the Z’berg-Warren-Keene-Collier Forest Taxation Reform Act changed the method of taxing timber in California by replacing the ad valorem tax on standing timber with a yield tax on harvested timber. Concurrently, the 1976 Forest Taxation Reform created a property tax system that incentivized forest management through a reduced annual property tax for lands dedicated to the growing and harvesting of timber (and compatible uses).

Policy affecting forest regeneration and oak woodlands

In Fritz’s 1943 assessment, the committee noted that timber harvest rates were increasing faster than they could be reforested and that fragmentation was occurring (Arvola 1985). To address the reforestation and timberland issues, a related law was established in 1943 that limited the size of conifer trees that could be harvested to no less than 45.7 cm (18 inches) in diameter to ensure that there would be retained trees to provide a seed source on the harvested site (California Forestry Study Committee 1947). With only one state nursery, there was little else that could be done to augment reforestation efforts (California Forestry Study Committee 1947). The seed tree reforestation approach began to change following a 1959 storm that blew down a selectively logged redwood stand, leading to a ground swell of interest in clear-cutting during the 1960s (Arvola 1976). Aerial seeding was the chosen method to restock many of these harvested units (Able, personal communication). This policy changed with the adoption of the 1973 Forest Practices Act. With this act came the focus on ensuring regeneration success and the requirement of a post-harvest conifer restocking survey. At present a landowner has 5 years to achieve a fully stocked stand following timber harvest (in other words, 300 point count of seedlings on higher sites).

Taxation laws have also affected California’s forest conditions. Prior to 1977, each county in California assessed standing timber for ad valorem taxation, and landowners with timber were taxed for their trees. As a result, many landowners harvested their timber to reduce their annual property taxes. For many of the ranch landowners, this law encouraged them to harvest most of their large diameter conifers.

This history sets the stage for the today’s policy change strategies. Although it is widely recognized that landowners should not be forced to cut their timber to reduce property taxes, the pre-1977 property tax system may have helped reduce conifer encroachment in oak woodlands because it encouraged large diameter conifer harvest. These tax harvests included Douglas-fir (Pseudotsuga menziesii) that had
likely encroached into oak woodlands following fire suppression policies that began in the early 1900s. Furthermore, while the 1973 Forest Practices Act has led to better conservation of California’s forestlands, it has set up a preference for conifer management and for ensuring conifer regeneration success by requiring replanting where conifers are harvested. This emphasis on conifer regeneration is at odds with efforts aimed at restoring and conserving oak woodlands.

**Oregon white oak and California black oak ecology**

In California’s North Coast region, deciduous oaks are a component of both forestlands and woodlands (fig. 1). In some areas, stands are dominated by Oregon white oak or California black oak, forming intact woodlands that stretch across hillsides or along forest and prairie edges. In other areas, these species are scattered among conifers and other hardwoods. This range of habitats makes oaks an important component across many North Coast ecosystems, but it also complicates efforts aimed at managing and conserving oaks, which are often based on more simple characterizations of growth patterns and habitat types.

![Figure 1—Distribution map of Oregon white and California black oak.](image)

The presence of deciduous oaks in conifer-dominated forests is evidence of the complexity of soils types, topography, and plant communities for which the region is well known, and it is also an indicator of shifts in forest density and species composition over time. In forested settings in the North Coast, deciduous oaks have
been found to be older than many of their coniferous neighbors, and they are often in decline due to competition for sunlight and other resources (Barnhart and others 1996, Cocking and others 2012).

**Fire exclusion**

One of the primary concerns for sustaining deciduous oak woodlands in the North Coast is the absence of the disturbance regimes that historically shaped and maintained these ecosystems. Both black and white oak woodlands are fire adapted, depending on frequent, low- to moderate-intensity fires to prevent establishment of invading fire-sensitive vegetation and supply conditions suitable for regeneration (Agee 1993, Barnhart and others 1996, Stuart and Stephens 2006). Fire exclusion over the last century has resulted in both direct and indirect impacts to oak woodlands, affecting their recruitment and persistence, stand structures and fire regimes, and overall ability to persist on the landscape (Cocking and others 2012, Engber and others 2011, Sugihara and Reed 1987). Other land management activities, including changes in grazing regimes and management for timber resources, have also contributed to shifts in community composition toward conifer species and the decline of deciduous oak communities.

Though minimally studied, native conifer encroachment is widely recognized as one of the most widespread, direct outcomes of fire exclusion in North Coast oak woodlands (Barnhart and others 1996, Sugihara and Reed 1987, Thysell and Carey 2001). Conifer encroachment has been documented in a range of oak woodland types in northwestern California, and is commonly implicated in widespread decreases of woodland extent throughout the region. In their 1987 analysis of the Bald Hills of Redwood National Park, Sugihara and Reed (1987) documented a loss of almost 30 percent of white oak woodland area to encroachment by Douglas-fir since 1850. These landscape-scale losses of woodlands are pronounced throughout the region, and visible from many well-traveled highways in the North Coast region. In areas where oak stands are smaller, or where individual oak trees are growing in conifer-dominated forest, their decline may be less obvious, yet more accelerated and severe.

**Barriers in the California forest practices rules**

Much of the Oregon white oak and California black oak woodlands of California occur on privately owned land and as a result, their management is subject to California standards. There are several issues in the current rules where there are disincentives to active management of the conifer encroachment issues. First, the California Forest Practices Act, as written by the legislature, requires that a cover of commercial species be maintained or established after commercial timber harvest. PCR § 4561 defines a post-harvest stocking standard of 300 point count of trees on higher sites and 14 CCR 912.7, 932.7, 952.7 defines a countable tree. Subsection 14 CCR 912.7 (d) states that “the site occupancy of Group A species [these are conifer species] shall not be reduced relative to Group B [these are hardwoods and include both black and white oak]” (table 1). In essence these standards give preference to the conifers and encourage use of planting stock to meet the regeneration standards. Additionally, when thinning a stand, post-harvest conditions must meet these same stocking or proportionality standards (in other words, relative quantity of Group A to Group B species), and it may be necessary to thin across the species in the stand to meet the pre-harvest to post-harvest proportionality standards. The reason this proportionality rule exists is to prevent high-grading or removal of the highest quality
trees species with little regard to the future stand conditions. Furthermore, the removal of conifers for restoration purposes could be viewed as a “conversion” of timberland. While the site is likely to still be capable of growing commercial species, it is conceivable that 14 CCR 1100 (g) (B) would not be met, because stocking would not be ensured within five years following harvest. And finally, 14 CCR 913.11, 933.11, 953.11 sets standards for Maximum Sustained Production of High Quality Timber Products. When a Registered Professional Forester files a timber harvest plan, but does not have a long-term growth and yield plan such as a “Sustained Yield Plan” or “Non-industrial Timber Management Plan” to tie to, the forester will utilizes option (c) in this section. However for oak woodlands restoration, option c specifies that minimum stocking and basal areas standards must be met with Group A species only, thus providing an additional barrier to meeting stocking with the oak species.

Table 1—Comparison of Group A versus Group B species for the Coast District

<table>
<thead>
<tr>
<th>Group A</th>
<th>Group B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coast redwood</td>
<td>Tanoak</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>Red alder</td>
</tr>
<tr>
<td>Grand fir</td>
<td>White alder</td>
</tr>
<tr>
<td>Western hemlock</td>
<td>California black oak</td>
</tr>
<tr>
<td>Western red cedar</td>
<td>Monterey pine</td>
</tr>
<tr>
<td>Bishop pine</td>
<td>Golden chinkapin</td>
</tr>
<tr>
<td>Sitka spruce</td>
<td>Pepperwood</td>
</tr>
<tr>
<td>Western white pine</td>
<td>Oregon white oak</td>
</tr>
<tr>
<td>Incense cedar</td>
<td>Pacific madrone</td>
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<tr>
<td>Port Orford cedar</td>
<td></td>
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<tr>
<td>California red fir</td>
<td></td>
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<tr>
<td>Jeffrey pine</td>
<td></td>
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<tr>
<td>Ponderosa pine</td>
<td></td>
</tr>
<tr>
<td>Sugar pine</td>
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</tbody>
</table>

Possible solutions

Techniques to achieve oak woodland management vary. Some landowners want to have the ability to commercially harvest the encroaching conifers, using any profits to help subsidize the oak restoration costs, while others may only have non-commercial management interests, often guided by state or federal cost-share assistance programs. For the non-commercial interests, California Environmental Quality Act (CEQA)-related permits are rarely required, and thus there is little room to offer legal compliance or protection for these landowners. However, for those forest landowners that are more commercially active, there are a few options. The California Board of Forestry can clarify the standards of 14 CCR 912.7 and state how to meet the intent of PCR § 4561. Furthermore, the legislature could change the approach to stocking from point counts to basal area evaluations, which are easier to conduct for oaks. The legislature could also develop an oak woodlands restoration exemption. At present, the California Board of Forestry is in consideration of an Oak Woodland Management Board Policy that may clarify for 14 CCR 912.7, “the director, after an initial inspection pursuant to PRC § 4604 [the standards for post-harvest inspection], shall approve use of Group B species, as exceptions to the pre-harvest basal area percentage stand, if in his judgment the intent of the Act will be met, and there will not be an immediate significant and long-term harm to the natural resources of the state.”

In conclusion, the California Forest Practices Act and the Forest Practices Rules are amendable. While the regeneration challenges of the early 20th century have
largely been met, there is now an urgent need to respond to the challenges of a century of fire suppression and the resulting conifer encroachment into these important California ecosystems.

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Lessons Learned in Historical Mapping of Conifer and Oak in the North Coast¹

Melissa V. Eitzel,² Maggi Kelly,² and Lenya N. Quinn-Davidson³

Abstract
Conifer encroachment into oak woodlands is becoming a pressing concern for oak conservation, particularly in California’s north coast. We use Object-Based Image Analysis (OBIA) with historical aerial imagery from 1948 and recent high-spatial-resolution images from 2009 to explore the potential for mapping encroachment using remote sensing. We find that pre-processing historical aerial imagery is time-consuming and that OBIA requires training and experience but has promise for mapping the phenomenon of interest. We also find that identifying conifer and oak in the imagery without ground-based information is not consistently possible. We recommend iterative mapping and field work, both for obtaining field samples to map encroachment and for mapping woody versus herbaceous cover as a way to screen for locations with potential oak recruitment.

Key words: conifer encroachment, high spatial resolution images, historical aerial images, National Agricultural Imagery Program, object-based image analysis, orthorectification, supervised classification

Background
Loss of oak woodlands is a widespread concern. Though some threats have been well studied, such as sudden oak death (Swiecki and Bernhardt, Phytophthora ramorum canker (sudden oak death) disease risk and progress in coast live oak, 2000-2012, these proceedings) and gold-spotted oak borer (Seybold and Coleman, The goldspotted oak borer: revisiting the status of an invasive pest six years after its discovery, these proceedings), quantifying encroachment from other woody species is just beginning. Encroachment and conversion of oak woodlands to closed-canopy forest is a frequent occurrence (Cocking and others 2012), and many species can encroach into woodlands (Cocking and others, Conifer encroachment in California oak woodlands, these proceedings). We focus in this study on Douglas-fir (Pseudotsuga menziesii) encroachment into Oregon white oak (Quercus garryana) and California black oak (Q. kelloggii) woodland in the north coast of California.

University of California Agricultural and Natural Resources supported a study of conifer encroachment in Humboldt and Mendocino Counties. This larger project included 1) a policy analysis and review of forest practice rules (Valachovic and others, Can the California Forest Practice Rules adapt to address conifer encroachment? these proceedings), 2) a field study of understory diversity, canopy species composition, and age and size structure at 10 sites (Schriver and Sherriff, Establishment patterns of Oregon white oak and California black oak woodlands in northwestern California, these proceedings), and 3) the work described here:

¹An abbreviated version of this paper was presented at the Seventh Symposium on Oak Woodlands: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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exploring the capabilities of historical aerial imagery for mapping encroachment over larger scales.

Given that the goal of the mapping component of the project was to understand the rate and extent of conifer encroachment, and that the time to replace oak with conifer can be 60 to 100 years (Cocking and others, Conifer encroachment in California oak woodlands, these proceedings), we need a source of geographical information that dates back far enough. Fortunately, historical aerial imagery does exist from the 1930s and 1940s and increasingly the discipline of historical ecology is developing rigorous methods for reconstructing historical landscapes (Grossinger 2012, Whipple and others 2011). Therefore we refined the goals of the mapping component of this study of encroachment to focus on exploring the use of historical aerial black-and-white imagery for quantifying the change from oak to conifer over the last 60 years. What is involved in obtaining, pre-processing, and classifying historical aerial imagery? Can we map encroachment? If so, what is the rate and extent of encroachment at our sites? If not, what can we map from the historical imagery, and what else would be needed in order to map encroachment?

For the larger study, we chose 10 sites throughout Humboldt and Mendocino Counties (fig. 1). They reflect a variety of latitudes as well as coast-to-inland locations for oak woodlands. They include both public and private lands. They were specifically chosen because they contained examples of the full spectrum of encroachment, from pure oak stands ranging up to highly encroached stands with Douglas-fir forming the majority of the canopy.

Figure 1—Study sites (named for their U.S. Geological Survey quad).

Our black-and-white historical images come from a 1947-1948 flight commissioned by the U.S. Department of Agriculture, Forest Service. They were scanned at 800 dots per inch by the California Geological Survey (CGS), which, after
pre-processing, results in a spatial resolution of less than a meter. The recent images come from the 2009 National Agricultural Imagery Program (NAIP) of the U.S. Department of Agriculture. These one-meter resolution images contain four bands: red, green, blue, and infra-red, and are already pre-processed (georegistered and orthorectified).

We have broken our study into four parts: 1) locating and pre-processing the historical imagery, 2) segmenting the imagery into objects to use Object-Based Image Analysis (OBIA) techniques on the high-resolution imagery, 3) determining what is visible in the imagery without ground-based data, and 4) using information from the field component of the study to attempt a supervised classification. We give details and lessons learned about each stage below, followed by comments on opportunities and recommendations.

**Part 1: Pre-processing historical imagery**

Several steps are involved in locating and pre-processing historical imagery. First, the images themselves (called 'frames') are found in a variety of university map and imagery libraries, museums, counties, and other sources. They may or may not be digitized. For our project, we obtained scans of frames covering all of Humboldt County from CGS. At the time of this project, we were only able to locate historical images for the Humboldt County sites, so analysts should be aware that finding imagery can be difficult. In order to identify frames for our study sites out of the hundreds of images which cover all of Humboldt County, we georegistered the flight map to county boundaries using a spline resampler (also called 'rubber sheeting') in ArcGIS 10.2 (ESRI 2013). We then overlaid the polygons for our sites and located frame numbers that were likely to contain our sites. We also obtained NAIP imagery based on a similar strategy. Using the NAIP and features which were unchanged over 60 years (for example, shapes of tree clusters, roads, or rocks), we confirmed which frames to use.

The next step in pre-processing the imagery involved georegistering (locating in space) and orthorectifying (correcting for topography and lens distortion) the historical images to the current NAIP image. We used Leica Photogrammetry Suite (LPS) to pre-process the imagery (Intergraph 2014). This involved locating metadata on the focal length of the camera and flight height associated with the images, which we were able to find at the University of California, Santa Barbara map library. We obtained a digital elevation model (DEM) from U.S. Geological Survey's national elevation dataset to use as a vertical reference for orthorectification and used the NAIP as a horizontal reference. We then located 50 to 150 ground control points (rocks, roads, and tree clusters which are identifiable in both NAIP and historical images) and used LPS to georegister and orthorectify the historical images, warping them into the correct locations. In some cases we then mosaiced the images together in ArcGIS to cover the analysis area. We orthorectified three to six images for each site, though we only use one or two per site for analysis. Note that finding control points was more difficult in heavily forested areas and for images with poor contrast. Even with adequate control points, there are still areas of misregistration. That said, using LPS to correct for topography is still more systematic and faster than the time-consuming and subjective method of using ArcGIS's georegistration tool with spline resampling as we did with the flight key.
Lesson 1:
Finding and pre-processing the imagery is time-consuming. Therefore mapping change over a large area would require a great deal of analyst time to pre-process the imagery.

Part 2: Segmenting imagery into objects
Object-based image analysis is an appropriate method for high-spatial-resolution imagery as opposed to traditional pixel-based methods of analysis. In pixel-based analysis, single pixels are classified independently. If the objects of interest are larger than the pixels in the image, this leads to problems (for example, the shaded side of a tree might be classified differently from its illuminated side). Instead, the image is segmented into objects (for example, an entire tree crown or stand of trees), which are then classified. One advantage of OBIA is that the classifier can use information about the object as well as its pixels. The texture within the object can be used for classification, as well as its context with respect to other objects (for example, nearness of objects of the same class), or the shape or size of the object.

We use eCognition Developer 8 (Trimble 2013) to segment the images. eCognition has several segmentation algorithms, but the most commonly used is multi-resolution segmentation, which creates objects by grouping similar pixels. This algorithm takes three parameters, scale (which controls the size of the objects created), and shape and compactness (which together control how much the pixel values influence the grouping and how compact the objects are). Choosing these parameters can be a trial-and-error process and is somewhat subjective. However, correctly segmenting the image is a prerequisite for later classification, as the objects constrain what can be classified. Procedures for selecting these parameters systematically are still being developed (Drăguț and others 2010) and were not appropriate for our images (these methods resulted in objects much larger than we needed). For our exploration of historical and NAIP imagery, we chose fairly small, compact objects and required them to be fairly homogenous.

Lesson 2:
Training and experience are necessary to choose adequate segmentation parameters. Even with training and experience, choosing segmentation parameters can be an art as well as a science.

Part 3: Looking for the process in the images
Before attempting to classify the image, we assessed whether we could identify oak versus conifer in the images without any ground information. This was a useful step because the field information collected as part of the project was not intended for classification of aerial images, and because classification of larger areas would be more feasible if field information were not necessary.

Unfortunately, it was impossible to consistently identify conifer and oak in the NAIP or historical images (fig. 2). The NAIP imagery tends to be captured in the middle of the day to minimize shadows and therefore the texture from the rougher, piercing crowns of the Douglas-fir is less apparent. The historical imagery shows a great deal of variation in sun angle, texture, and contrast from image to image and site to site. In some cases, we checked our guesses about species composition in the
NAIP image against the field crews' information and found we had guessed incorrectly.

Figure 2—Example of historical imagery (left) and NAIP imagery (right) from site BH where conifers and oaks can be distinguished. Other sites are not so clear.

Lesson 3:
It was only possible to differentiate between species by eye in very localized areas of some sites in some years.

Part 4: Supervised classification
Therefore, to classify the NAIP and historical images, we used the plots from the field component of the project (Schriver and Sherriff, Establishment patterns of Oregon white oak and California black oak woodlands in northwestern California, these proceedings). There were nine 1/10 ha plots at each site, stratified by level of encroachment: three plots had no conifer in the canopy in 2013, three had mixed dominance between oak and conifer, and three were dominated by conifer with only a few oaks in the canopy. None of these sites was pure conifer in 2013, nor were any plots chosen in the nearby prairie. Because the field crews were studying the age and size structure of the plots, we can be reasonably certain that because the age of nearly all Douglas-fir on the plots was less than 100 years in 2013, they were not visible in the canopy in 1948.

We used a supervised classification strategy where the field sites were samples of oak or conifer. We chose additional samples in pure conifer for 1948 and for prairie in both years. The resulting classifications are flawed but show promise (fig. 3).
Lesson 4:
Supervised classification, with samples in pure classes of oak, conifer, and prairie, has potential for mapping encroachment.

Opportunities and recommendations
At the general level it is possible to map woody versus herbaceous cover in these images without field-based samples (Eitzel Solera 2014). Mapping changes in woody cover alone may be useful for processes other than encroachment, for example oak recruitment. Anecdotally we found the potential for oak recruitment in valleys outside of forested areas. We recommend iterative mapping and field work, in which the map of woody cover change screens for locations to investigate in the field for potential oak recruitment. Iterative mapping and field work would also be necessary to obtain field samples for the supervised classification in order to map conifer encroachment. It may also be possible to classify encroached areas as oak, conifer, or mixed, and to observe the mixed class expanding.

One opportunity associated with mapping oak and conifer using field samples is the potential for validation of historical imagery. A trained forester could core the largest conifer on a plot and make a determination of whether it is old enough to have been in the canopy in the 1940s. The analyst could then use this point and others as
samples in a supervised classification of the historical image and later for validation of the classification, something that is rarely done for historical imagery.

Large-scale mapping of either woody cover or conifer encroachment will require both trained analysts and a large amount of time. One additional impediment to larger-scale mapping of these processes is unknown land use history. For five of our sites, the field crews found evidence of widespread harvest due to the tax on standing timber in the time between the historical photos and recent imagery. This invalidates the interpretation of the recent imagery as simply following standard forest dynamics from the condition depicted in the historical imagery.

Finally, a land-owner without access to the software or trained analysts could at least informally use historical imagery to locate areas which were woodland in the 1930s and 1940s to plan for conifer removal, if the forest practice rules are changed to allow it.

Acknowledgments

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References


Establishment Patterns of Oregon White Oak and California Black Oak Woodlands in Northwestern California

Madelinn Schriver and Rosemary Sherriff

Abstract
Mixed-Oregon white oak (*Quercus garryana*) and California black oak (*Q. kelloggii*) woodlands are unique ecosystems that support high biodiversity in the Pacific Northwest, yet little is known about their current and historical stand establishment patterns in northwestern California. With concerns of local extirpation due to Douglas-fir (*Pseudotsuga menziesii*) succession, research objectives were to characterize the variability of age structure, stand structure, and current tree regeneration in four mixed oak-conifer woodlands in northwestern California. Each site varied in stand type from open-oak woodland to transitional woodland-forest to closed mixed hardwood-conifer forest. While very low densities of white and black oak saplings (>30 cm tall and <5 cm DBH) characterized all stand types, regeneration of shade-tolerant tree species in closed-forest stands was common. Across all four sites most living white and black oak trees (≥ 5 cm DBH) established during the mid-to late 1800s with no establishment since 1937. Conversely, the majority of Douglas-fir trees have been continuously establishing since around 1950. Within sites, most oaks established over a relatively narrow period of time (40 years), suggesting a stand-level disturbance during the mid-to late 1800s that promoted regeneration. Less commonly (6 percent of plots), oaks established over a longer period of time (100 years) with plot-level age distributions indicating evidence of more localized stand-initiation events. The establishment of shade-tolerant tree species in some plots at each site, and the lack of oak tree establishment for the last 70 to 100 years, likely reflects the effects of altered disturbance regimes. Tree establishment patterns appear to be consistent with findings in Oregon and Washington, where studies suggest Oregon white oak ecosystems are transitioning into conifer-dominant stands due to land use changes, representing a loss of endemic biodiversity and structural heterogeneity on the landscape.

Key words: age structure, California black oak, conifer encroachment, Oregon white oak, stand dynamics

Introduction
Oregon white oak (*Quercus garryana*) and California black oak (*Q. kelloggii*) woodlands are unique ecosystems in the Pacific Northwest, interspersed primarily throughout a mixed Douglas-fir (*Pseudotsuga menziesii*)-hardwood landscape. They represent important refugia for one of the richest diversities of vertebrates, invertebrates, and native plant species in California (for example, Block and others 1990, Sugihara and Reed 1987). In the Pacific West studies suggest that Oregon white oak (Gedalof and others 2006, Gilligan and Muir 2011) and California black oak (Skinner and others 2009) ecosystems are at risk for local extirpation due to a lack of recent oak establishment and native conifer succession where open-oak woodlands transition between conifer-hardwood forests and more xeric ecosystems.

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
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such as oak savanna. For example, in relatively intact oak ecosystems in Oregon studies show most conifer establishment post-dates oak establishment (Gilligan and Muir 2011, Thilenius 1968). Limited information exists on northwestern California to assess if there are similar patterns of tree establishment, forest structure, and oak regeneration as found in Oregon and Washington. Thus, the primary objective of this study was to characterize the variability of age and stand structure in oak woodlands interspersed within conifer-dominated stands in northwestern California. The specific research questions were: (1) What tree age and stand structures characterize mixed-oak conifer woodlands in northwestern California? (2) Are there similar temporal patterns of oak and conifer establishment in mixed oak-conifer woodlands throughout northwestern California? And (3) what are the current tree regeneration patterns across stands throughout the study region?

**Methods**

**Study area**

The study area was located in the North Coast range of California, which hosts a mosaic of plant community types, ranging from conifer-dominated, mixed-evergreen forests to oak woodlands and savannas (Stein 1990). We focused on the mixed-white oak and black oak woodlands that transition between open oak stands and closed mixed-hardwood conifer forest stands. Additional tree species of this region include California bay laurel (*Umbellularia californica*), Pacific madrone (*Arbutus menziesii*), white fir (*Abies concolor*), big leaf maple (*Acer macrophyllum*), canyon live oak (*Quercus chrysolepis*), and tanoak (*Notholithocarpus densiflorus*). The climate is temperate Mediterranean with cool, moist winters, and warm, dry summers.

**Site selection and field sampling**

Four sites were sampled in 2013 in contiguous woodland community types dominated by white oak and black oak, with Douglas-fir as the primary co-dominant species that ranged between 500 m and 1500 m in elevation (table 1), and excluded stands with visible signs of past harvesting and other major land use disturbances (in other words, mining) (fig. 1). In each site, nine 0.1-ha circular plots were selected from randomly-generated locations and stratified by open-oak woodland (3 plots), transitional woodland-forest (3 plots) and closed mixed hardwood-conifer forest (3 plots) stand types based on visual assessment in the field. In each 0.1-ha plot, we tallied overstory (≥5 cm at 1.37 m above ground (DBH)) trees, each tree’s DBH, and recorded the physical environment (slope, aspect, slope position, elevation). The 10 closest white and black oak trees from plot center were mapped and cored at 30-cm height above the root-shoot interface to determine tree age (Stokes and Smiley 1996). Multi-stem trees were tallied, and when cored, the largest stem was selected to determine the tree age. Additionally, the 10 closest evergreen conifer/hardwood tree species from plot center were also mapped and cored. Up to five of the largest and closest living trees outside of the plot were also cored in order to best estimate the oldest establishment dates within the sampling area. Within each 0.1-ha plot, we also tallied seedlings (<30 cm tall) and saplings (<5 cm DBH and >30 cm tall) by species using six randomly-located nested 2-m² plots and one nested 0.025-ha plot, respectively.
Figure 1—Study area in Humboldt County, California. Bald Hills (BH), Lord-Ellis Summit (LE), Iaqua Buttes (IB), and Blake Mountain (BM). (map credit: M. Eitzel)

Table 1—Site information for contiguous mixed-oak woodlands in northwestern California. Site codes come from USGS quadrangle maps

<table>
<thead>
<tr>
<th>Site Name (Code)</th>
<th>Latitude (°N)</th>
<th>Longitude (°W)</th>
<th>Area (ha)</th>
<th>Elevation (m)</th>
<th>Aspect a</th>
<th>Slope (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bald Hills (BH)</td>
<td>41.18</td>
<td>123.89</td>
<td>152</td>
<td>500</td>
<td>NW</td>
<td>15</td>
</tr>
<tr>
<td>Lord-Ellis Summit (LE)</td>
<td>40.90</td>
<td>123.79</td>
<td>162</td>
<td>600</td>
<td>W</td>
<td>20</td>
</tr>
<tr>
<td>Iaqua Buttes (IB)</td>
<td>40.71</td>
<td>123.90</td>
<td>86</td>
<td>750</td>
<td>S</td>
<td>25</td>
</tr>
<tr>
<td>Blake Mountain (BM)</td>
<td>40.51</td>
<td>123.53</td>
<td>169</td>
<td>1200</td>
<td>SW</td>
<td>15</td>
</tr>
</tbody>
</table>

a Aspect: NW northwest, W west, S south, SW southwest.

Data analysis

Tree cores were mounted, sanded, and counted following standard dendrochronology techniques (Fritts 1979). When a tree core missed the pith a geometric model of annual tree growth was used to estimate the number of years to pith (Duncan 1989). Tree ages could be older than reported if seedlings or sprouts were browsed or lacked a single dominant stem dating to establishment (Hibbs and Yoder 1993), and due to the lack of correction for tree age at coring height. Thus, we summarized tree establishment dates into 20-year age bins. For oak trees annual growth was measured with a tree-ring scanning system (WinDendro software, Regent Instruments, version 2009b) in order to quantitatively crossdate annual ring widths using the COFECHA program (Holmes 1983).

At each site the proportion of tree establishment was examined for equal time periods prior to and during regional fire decline (a significant decline in fire frequency occurred around 1900 in nearby locations; Taylor and Skinner 1998). Fire is traditionally thought to have maintained oak woodlands in some locations; thus, altered fire regimes during the 20th century could have altered tree establishment dynamics. The youngest tree established in 2006, therefore this was our cutoff year for analysis. A chi-squared test was used to assess whether tree establishment was significantly different between tree types (in other words, oaks and evergreen conifer/hardwoods) prior to and during regional fire decline (1805-1904 and 1905-2006). All statistical analyses were conducted using R-studio.
Basal area (m² per hectare), stem density (trees per hectare), and sapling and seedling densities (per hectare) were calculated for each tree species in each stand type (in other words, open-oak woodland, transitional woodland-forest, closed mixed hardwood-conifer forest). Differences between basal area and stem density among stand types were examined using a one-way analysis of variance (ANOVA; \( \alpha = 0.05 \)). A pair-wise t-test using the Bonferroni correction was used when stand type showed a significant effect. The median proportion of dead versus live tree stems were calculated for each oak species to assess the average oak-tree mortality in each stand type (\( n = 12 \) plots per stand type across four sites; 3 plots per stand type at each of the sites).

**Results**

**Tree establishment patterns**

In total, 672 trees were sampled for age structure. The youngest tree (Douglas-fir; site IB) was 7 years old and the oldest tree (black oak; site: BM) was over 316 years old. However, the oldest tree and other trees that had rotten centers were excluded from future analysis for tree age structure (16 percent of all cored trees, mostly oaks). Across all four sites, the median tree age of oaks was 132 years (range: 75 to over 316 years). The median tree age of Douglas-fir was 45 years (range: 6 to 125 years). Only 2 percent of cored trees composed of evergreen hardwood species (bay laurel and canyon live oak) whose median age was 35 years (range: 28 to 72 years).

Across all sites, the majority (75 percent) of live white oak and black oak trees established before regional fire decline (pre-1905), whereas the majority (97 percent) of evergreen conifer/hardwood trees established during regional fire decline (fig. 2; \( \chi^2 = 310.777, \text{df} = 1, p\text{-value} \leq 0.001 \)). Across all sites, the majority of oak trees established between 1850 and 1937. At a stand-scale, each site shows the majority of establishment occurred during a relatively short (~40 years) period of time (fig. 2). None of the oaks sampled established after 1937 at any of the sites. Douglas-fir trees established from 1890 to 2006 with the majority occurring after 1950 across all sites (fig. 2).
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Figure 2—Proportion of tree establishment by tree species at each site (a) BH, b) LE, c) IB, and d) BM). Vertical-dashed line indicates the beginning of regional fire decline (1905). Species codes: QUKE, *Quercus kelloggii*; QUGA, *Q. garryana*; PSME, *Pseudotsuga menziesii*.

**Stand structure**

Across all sites, white oak, black oak, and Douglas-fir trees together accounted for 95 percent of the basal area on average. White oak had higher stem densities and basal areas than black oak across all stand types (fig. 3 a-d). Across sites, the median proportion of white oak and black oak tree mortality was 24 percent and 13 percent, respectively, and greater in closed vs. open stands (table 2). Predictively, Douglas-fir stem density and basal area was highest in closed-forest stands (fig. 3 e, f). Total basal area was greater in closed vs. open stands (fig. 3 h), but total stem density was not significantly different cross stand types (fig. 3 g). On average, open stands were composed of white oak (81 percent), black oak (12 percent), and Douglas-fir (7 percent); transitional stands were composed of white oak (38 percent), and black oak (14 percent), and Douglas-fir (45 percent); and closed stands were composed of white oak (17 percent), black oak (8 percent), Douglas-fir (72 percent), and evergreen-hardwood tree species (3 percent; tanoak, canyon live oak, and bay laurel).
Figure 3 a-h—Stem density and basal area of live trees in open-oak woodland (Open), transitional woodland-forest (Transitional), and closed mixed hardwood-conifer forest (Closed) stands in northwestern California \((n = 12\) plots per stand type). Stem density and basal area measurements include white oak (a, b), black oak (c, d), Douglas-fir (e, f), and all tree species (g, h), respectively. In each graph variables with different letters indicate significant differences (Paired t-test, \(p\)-value <0.05).
Table 2—Median proportion of dead Oregon white oak and California black oak trees in open-oak woodland, transitional woodland-forest, closed mixed hardwood-conifer forest, and across all stand types in northwestern California

<table>
<thead>
<tr>
<th>Stand Type</th>
<th>Oregon white oak</th>
<th>California black oak</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>0.14</td>
<td>0.10</td>
</tr>
<tr>
<td>Transitional</td>
<td>0.25</td>
<td>0.16</td>
</tr>
<tr>
<td>Closed</td>
<td>0.45</td>
<td>0.17</td>
</tr>
<tr>
<td>Across Stands</td>
<td>0.24</td>
<td>0.13</td>
</tr>
</tbody>
</table>

**Current tree regeneration patterns**

Density of oak seedlings varied the most between open and closed stands (fig. 4 a, c). White and black oak seedling densities were highest in open stands with white oak composing the vast majority (fig. 4 a, c). On average, seedlings in open stands were composed of white oak (84 percent), black oak (12 percent), and Douglas-fir (3 percent); seedlings in transitional stands were composed of white oak (49 percent), black oak (14 percent), Douglas-fir (26 percent), canyon live oak (5 percent), and bay laurel (5 percent); and seedlings in closed stands were composed of white oak (22 percent), black oak (18 percent), Douglas-fir (7 percent), canyon live oak (14 percent), bay laurel (11 percent), and tanoak (11 percent).

Sapling density did not vary between stand types (fig. 4 b, d, f, h). White and black oak sapling densities were low among all stand types (fig. 4 b, d). The proportion of evergreen conifer and hardwood species did vary between stand types. On average, saplings in open stands were composed of white oak (6 percent), black oak (2 percent), Douglas-fir (88 percent), and bay laurel (4 percent); saplings in transitional stands were composed of white oak (2 percent), Douglas-fir (54 percent), bay laurel (16 percent), and canyon live oak (28 percent); saplings in closed stands were composed of Douglas-fir (4 percent), bay laurel (2 percent), canyon live oak (83 percent), and tanoak (6 percent).
Figure 4 a-h—Density of live seedlings and saplings in open-oak woodland (Open), transitional woodland-forest (Transitional), and closed mixed hardwood-conifer forest (Closed) stand types in northwestern California (n = 12 plots per stand type). Seedling and sapling densities include white oak (a, b), black oak (c, d), Douglas-fir (e, f), and all species (g, h), respectively. In each graph variables with different letters indicate significant differences (Paired t-test, p-value <0.05).
Discussion

**Temporal patterns of oak and conifer establishment**

Across all sites, most live Oregon white oak and California black oak trees established during the mid-to late 1800s, while most Douglas-fir trees established after 1950. These findings are consistent with age distributions of conifer-encroached Oregon white oak ecosystems in Oregon and Washington (Gedalof and others 2006, Gilligan and Muir 2011, Thilenius 1968). Plot-level age distributions within sites indicted varying temporal periods of stand-initiation. Across all plots at individual sites, most oaks established over a relatively narrow period of time (40 years) suggesting a stand-level disturbance during the mid-to late 1800s that promoted regeneration. Less commonly (6 percent of plots; only located at site: IB), oaks established over a longer period of time (100 years) indicating evidence of more localized stand-initiation events. Stand-scale disturbances triggering establishment events may have been fire, livestock grazing, reduced anthropogenic burning (Gedalof and others 2006, Gilligan and Muir 2011), in addition to a favorable climate conditions for tree establishment (Duren and Muir 2012). However, there is a lack of information on the disturbance history at this time needed to evaluate the mechanisms for recruitment.

**Stand structure in mixed oak-conifer woodlands**

The higher proportion of oak-tree mortality in closed-forest stands suggests low-light conditions are highly unfavorable for oak trees. Where Douglas-fir trees overtop hardwood trees, research has shown reduced growth rates and eventual hardwood tree mortality due to shade intolerance (Hunter and Barbour 2001). While both oak species have higher proportions of mortality in closed-canopy conditions, the lower proportion of California black oak mortality in closed-canopy stands suggests a higher tolerance of low-light conditions than Oregon white oak. This may be due to California black oak’s ability to persist in conifer-dominant stands depending on environmental factors, such as soil type and topography (Taylor and Skinner 1998), which have yet to be investigated in these stands.

**Regeneration**

The lower density of oak seedlings in closed stands compared to open stands supports findings that Oregon white oak seedling survival is strongly associated with open-canopy conditions (Gedalof and others 2006, Thysell and Carey 2001). Low levels of Oregon white oak regeneration for the past half-century have also been noted in Oregon and Washington (Fuchs and others 2000, Gedalof and others 2006, Gilligan and Muir 2011). While the presence of Douglas-fir overstory likely reduces oak regeneration by limiting light resources, there is also a paucity of oak saplings in open stands. For example, the open-oak stands had the highest oak seedling densities but few saplings (99.99 percent reduction) on average, suggesting other limiting factors also contribute to the lack of oak regeneration.

In dry habitats with limited soil moisture, Oregon white oak seedling survival is reduced by herbaceous vegetation dominated by grasses (Devine and others 2007b, Fuchs and others 2000). Due to their fibrous root system, grasses can outcompete oak seedlings for soil water causing oak seedling desiccation and mortality. When grass
cover is controlled, oak seedlings grow more vigorously which allow them to grow above the height of animal browse (Devine and others 2007b).

**On-going research**

In the face of changing climate patterns and related drought stress (van Mantgem and others 2009), understanding these trends in context of biophysical interactions is important. Further investigations are necessary to evaluate if these findings are consistent across the North Coast region of California. Additional research will also explore if the trends in age, composition, and regeneration between stand types relate to environmental factors (soil type and topography). Recent conifer establishment into oak woodlands could be limited to mesic environments (for example, in and near drainages). Lastly, researchers will examine the interaction between stand structure and tree growth relationship to climate variability.

**Acknowledgments**

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**References**


Sudden Oak Death
Biomarkers Identify Coast Live Oaks That Are Resistant to the Invasive Pathogen *Phytophthora ramorum*<sup>1</sup>

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**Abstract**

California coast live oaks (*Quercus agrifolia*) trees have suffered large losses from sudden oak death, caused by the introduced oomycete *Phytophthora ramorum*. In this review paper, we discuss oak plant chemistry as a potential predictor of disease susceptibility. We have recorded an annual mortality rate of three percent in long-term monitoring plots in Marin County, resulting in greater than 40 percent loss since 2000. Despite this mortality rate, asymptomatic trees still persist in many heavily infected stands. We hypothesized that varying responses to *P. ramorum*, including apparent recovery from infections, reflected phenotypic differences in susceptibility. In a Marin County inoculation study, a logit model showed that external canker lengths measured 9 months following inoculation predicted both resistance and survival 7 years later. The distribution of canker length was consistent with quantitative resistance to *P. ramorum*. The role of plant chemistry in resistance was examined by quantifying soluble phenolics in phloem methanol extracts prepared from the surviving trees. A logistic regression model found that expression of resistance was associated with total phenolics and four phenolic compounds; ellagic acid, a partially characterized ellagic acid derivative, and two chromatographic peaks representing two uncharacterized phenolic compounds. *In vitro* tests showed that ellagic acid was fungistatic against *P. ramorum* and total phenolics were fungicidal at physiologically relevant concentrations. A subsequent inoculation study in Briones Regional Park, Contra Costa County, California, showed that some of the same compounds were correlated with resistance. The association of certain phenolics with resistance may facilitate the use of biomarkers in minimally invasive assays to predict the response of trees to *P. ramorum*, thereby increasing the options for managing threatened forests.

**Key words**: biomarkers, coast live oak, logistic regression, phenolic glycosides, *Phytophthora ramorum*

**Introduction**

Introduced pathogens characteristically encounter host plants with varying levels of resistance. Significant examples of such pathosystems affecting North American trees include chestnut blight [American chestnut (*Castanea dentata*) and *Cryphonectria parasitica*]; Dutch elm disease [American elm (*Ulmus Americana*) and *Ophiostoma ulmi* and related species]; butternut canker [butternut (*Juglans cinerea*) and *Sirococcus clavigignenti-juglandacearum*]; and beech bark disease [American beech (*Fagus grandifolia*) and *Neonectria faginata* and *N. ditissima*, which invade wounds caused by the scale insect *Cryptococcus fagisuga*]. Chestnut has been functionally eradicated from its original range in the eastern United States;

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<sup>1</sup> An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.

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American elms are now uncommon forest and urban trees; the uncommon butternut is becoming even less common and is considered endangered in certain areas; and beech is in decline across much of its habitat. This paucity of host resistance is likely due to the lack of coevolutionary history between the partners in each pathosystem.

Since the first observed tanoak mortality in Marin County in 1994, losses of tanoaks (*Notholithocarpus densiflorus*) and coast live oaks (*Quercus agrifolia*) to sudden oak death (SOD), caused by *Phytophthora ramorum*, have been estimated to be in the millions of trees. Despite concerns expressed early in the epidemic that coast live oak might become extinct in California, trees presently persist in heavily impacted stands that have been infested since the late 1990s (McPherson and others 2010). These survivors often exhibit evidence of previous infections, such as callus tissue at the margins of old cankers, but other trees show no evidence of infection (McPherson and others 2014, Swiecki and Bernhardt 2013). Lack of manifest infection suggests that those trees may be resistant, but until now it was not possible to establish if those individuals are truly resistant, and not just escapes, without resorting to invasive techniques based on artificial inoculation with the pathogen.

Efforts to stop the expansion of *P. ramorum* beyond its current geographic range in the coastal forests of California and southwestern Oregon have met with limited success (Goheen and others 2013). Within infested areas the options for affecting the course of the disease are quite limited. Removal of hosts that support sporulation, such as California bay laurel (*Umbellularia californica*) and tanoak, has been proposed and implemented in limited sites (Goheen and others 2013; Valachovic and others 2013), although the long-term efficacy of this approach has not been demonstrated and is only likely to slow an inevitable process, while altering the species composition and stand structure of those forests. In addition, such an approach does not account for other possible sources of inoculum. With a host range that encompasses most of the native woody species in these coastal forests, *P. ramorum* has a large array of potential hosts to support sporulation. It is also noteworthy that past efforts to control tree diseases by eliminating alternative hosts are not encouraging. Probably the best example is that of white pine blister rust (caused by *Cronartium ribicola*), which continues to expand its range despite a half century-long massive and costly project to remove the primary hosts, *Ribes* spp. (Maloy 1997).

Given the vast areas already infested and the large number of hosts that may support sporulation, the most practical, economical, and ecological approach to dealing with SOD in coast live oaks may be to let the pathogen cull the most susceptible individuals, thereby increasing the proportional representation of the survivors (Telford and others 2014). This approach is predicated on the existence of sufficient resistance within host populations. Here we present evidence for such resistance and consider the implications for managing forests and woodlands under the pressure of the SOD epidemic, based on the notion that “…genetic resistance is the cornerstone of plant protection against insect pests and diseases in conducive environments.” (Conrad and others 2014).

**Evidence for Resistance**

**Long-term studies**

Long-term observation plots are the best source of information about such disease parameters as infection and mortality rates, survival times, and environmental influences on likelihood of infection. In plots monitored since March 2000, we have recorded the persistence of coast live oaks in three categories: trees that survived
infections, with thick callus growth on the margins of cankers; trees that previously expressed bleeding cankers but subsequently were no longer symptomatic; and trees that never showed symptoms (McPherson and others 2010). In addition, the apparent rate of new infections has been falling since 2000, which suggests that there are trees in the populations that are less susceptible to infection (McPherson and others 2010).

**Mechanical Inoculation: long-infested stands**

Mechanical inoculation has been the most reliable means of assessing resistance and susceptibility of trees to pathogenic microorganisms (for example, Gordon and others 1998). Although the direct introduction of *P. ramorum* culture into subcortical tissue likely represents an excessive dose, the resulting disease expression is consistent with long-term observations in stands that have been naturally exposed to the pathogen. In 2002, we inoculated 40 asymptomatic mature coast live oaks in each of two Marin County sites. Some trees died in less than 18 months, others still survive, although clearly in decline (displaying beetle attacks and secondary fungal colonization), while some trees never bled (McPherson and others 2014). Removal of the outer bark showed distinct reaction zones associated with the inoculation sites, confirming that all inoculated trees were infected. Across the populations of inoculated trees, canker size varied widely between individuals. In another Marin County inoculation study (unpublished), inoculations in trees with multiple stems produced cankers that were almost exactly the same size in the stems sharing the same base, suggesting strong genetic control for resistance.

Other evidence that is suggestive of genetically-controlled variation in resistance was shown in branch inoculations of coast live oaks. Dodd and others (2005) found significant variation in lesion length among individuals, but little evidence for population-level variation in response to inoculations.

The observation that trees differ in their response to both mechanical and natural inoculation suggested that genetically-controlled host chemistry might explain this difference. Ockels and others (2007) showed that several phenolic compounds varied in concentration between coast live oaks that were classified as asymptomatic and naturally infected. The tissue attacked by *P. ramorum* is primarily phloem, the nutrient-rich substrate that also serves as the defensive zone against pathogens and insects once the outer bark is breached. In oaks, the principal defensive response is believed to be due to phenolics, aromatic compounds with alcohol substituents on the benzene ring. Many if not most plant phenolic compounds occur in vivo as glycosides, in which the aromatic moiety is esterified to various saccharides (Hopkinson 1969). In naturally infected trees, phenolic compounds varied quantitatively between samples taken adjacent to canker margins and those excised 60 cm away from the canker margins (Ockels and others 2007). Phloem concentrations of two phenolic compounds, gallic acid and tyrosol, differed by infection status of the host tree. *In vitro* bioassays of these two compounds showed dose-dependent inhibition of *P. ramorum*, as well as of *P. cinnamomi*, *P. citricola*, and *P. citrophthora*. However, the relationships between disease status and compound concentrations were not consistent. This inconsistency was attributed to uncertainty about disease stage, such as time since infection, possible changes associated with the presence of beetles and fungi, as well as possible between-tree variability in phenolic profiles (Ockels and others 2007).

In 2009 we documented the progress of the disease for each tree in the Marin County inoculation study. Phloem samples were collected from inoculated trees in one of the two sites; the trees were categorized as **Symptomatic** (S; bleeding, with or
without beetle attacks), **In Remission** (IR; formerly recorded as bleeding, but subsequently asymptomatic by 2009), and **Putatively Resistant** (PR; never bled). IR and PR trees can be considered functionally resistant to the pathogen, and comparisons between phloem phenolics extracted from S and (IR + PR) trees showed consistent differences in ellagic acid, a partially characterized tyrosol derivative, and an unidentified compound (Nagle and others 2011).

We reanalyzed the data of Nagle and others (2011) using a logit model, based on 79 observations for survival and 64 observations for resistance from the 79 original randomly selected trees from two sites in 2002, to explore the relationship between external canker length measured early in the infection process (9 months after inoculation) and two measures of response to inoculation after 7 years: resistance and survival (McPherson and others 2014). We defined a tree as resistant if it never bled or ceased bleeding and was never attacked by beetles. Approximately 30 percent of the inoculated trees never developed the external bleeding cankers that are the most obvious symptom of *P. ramorum* infection, yet removal of bark at the inoculation sites showed reaction zones confirming that the inoculations had been initially successful. Canker length measured 9 months after inoculation predicted both resistance and survival after 7 years. For both, resistance and survival logistic regressions, the canker length was significant (P <0.0001) (fig. 1).

Phloem concentrations of phenolic compounds predicted resistance, specifically ellagic acid, a partially characterized ellagic acid derivative, two putative uncharacterized compounds (represented by chromatographic peaks), and total phenolics (the phloem extract) (McPherson and others 2014). A logit model found that increasing concentrations of ellagic acid and two other compounds were associated with increased probability of resistance, and one compound was associated with reduced resistance (fig. 2). The model could be used to identify a threshold level corresponding to 80 percent probability of resistance. *In vitro* assays against *P. ramorum* confirmed that both ellagic acid and total phenolics were fungistatic at physiologically relevant concentrations and total phenolics were fungicidal at the highest concentration tested, which was within the range found in the phloem. These studies offer the prospect that the resistance status of a coast live oak can be predicted by analyzing biomarkers of resistance in small samples of phloem from trees prior to exposure to the pathogen. The logit model also helps to illustrate that biomarkers need not be positively associated with resistance to be valuable indicators of the host response.
Figure 1—Probability that an infected coast live oak will (a) express resistance (either Putatively Resistant or In Remission) or (b) survive 7 years after inoculation. Observed proportions denote mean canker lengths binned into discrete intervals for illustration purposes. Dashed vertical lines in (a) show threshold canker lengths for 80 and 60 percent probabilities of resistance and in (b) show threshold canker lengths for 90 and 80 percent probabilities of survival (McPherson and others 2014).
Mechanical inoculations: lightly or uninested stands

We recognized that infection might change the phloem phenolics composition, particularly if defensive compounds are mobilized in response to the pathogen, bark and ambrosia beetles, or fungi that follow infection. In addition, the coast live oaks in Marin County already had been exposed to *P. ramorum* for an unknown time period when we inoculated them, likely 5 or more years, and thus the most susceptible trees probably had already been infected and a significant fraction killed. A better assessment of the validity of the relationship of phloem phenolic composition to resistance would be found in uninested stands, where *P. ramorum* was still absent or in the earliest stages of invasion. The presence of *P. ramorum* was first confirmed in the East Bay in 2001 near Castro Valley and in Wildcat Canyon Regional Park. We chose to work in Briones Regional Park, which lies about 8 km east of the East Bay Hills. In 2010 the disease was only recorded in a small number of oak-bay stands at lower elevations. We reasoned that if the extensive coast live oak stands at higher elevations had yet to be exposed to *P. ramorum*, trees in these sites would provide a truer representation of the population-level response to this pathogen because the more susceptible coast live oaks would still be present and in addition, any possible induced defensive response to the pathogen would be unlikely.

At two sites 2 km apart, we randomly selected 600 asymptomatic mature coast live oaks and collected phloem from each tree, then inoculated 154 randomly selected trees at two locations with *P. ramorum* (courtesy of Dr. David Rizzo; initially isolated from California bay laurel), and left the other 450 trees for long-term monitoring. After 1 year we collected a second set of phloem samples from all the trees. Phloem from a group of 14 mature asymptomatic coast live oaks in a different part of the park was sampled at 3-month intervals over a 1-year period to determine if phenolic composition changed seasonally (Conrad and others, unpublished data). The uninoculated trees will be revisited annually as the expected expansion of *P. ramorum* into these stands proceeds. In 2014 about 5 percent of this initially
asymptomatic cohort showed symptoms of *P. ramorum* infection (Conrad and others, unpublished data).

The inoculated trees were rated after 22 months as: **Susceptible** – brown leaves, or stem failure resulting from *P. ramorum* infection – dead and thus having no effective resistance; **Symptomatic** – long-term bleeding and/or beetle attacks and fungal fruiting observed – susceptible but with some ability to prolong survival; and **In Remission** – showing bleeding soon after inoculation, but no longer bleeding and without beetle attacks – the most likely to survive for the long-term. Consistently with our previous studies, trees classified as In Remission were considered resistant. The mean length of the two external cankers on each tree was determined 10 months after inoculation. Trees that were classified as In Remission or Susceptible, that is, those at the extremes of the symptom expression distribution, had significantly different canker lengths (independent t-test, P <0.001) (Conrad and others 2014). For purposes of phenolics characterization, we limited the analyses to these two groups of trees.

The consistent relationship we found between phenolic composition and the In Remission phenotype requires high performance liquid chromatography (HPLC) chromatography to separate peaks for subsequent analysis (McPherson and others 2014). On the other hand, Fourier transform infra-red spectroscopy (FT-IR) is an analytical method for characterizing complex organic mixtures that can provide “chemical fingerprints”. These are based on spectra that are unique to specific mixtures or individual compounds, and do not necessitate specific knowledge of the underlying chemical composition. Methanol extracts of phloem samples were analyzed using an Excalibur 3500GX FT-IR benchtop unit (Digilab, Randolph, MA). After signal processing and statistical analysis using soft independent modeling of class analogy (SIMCA) (Subramanian and others 2007), 100 percent of the FT-IR spectra from each category, Susceptible and In Remission (with outliers removed), were classified correctly (Conrad and others 2014). The FT-IR analysis also could predict the concentrations of both ellagic acid and an unidentified phenolic compound, as determined independently by HPLC analysis, that differ quantitatively between resistant and susceptible coast live oaks (Conrad and others 2014).

**Discussion**

As *P. ramorum* becomes established in a coast live oak stand, the early phase of the epidemic is characterized by the appearance of numerous dying trees where not long before the forest had appeared healthy: hence the term sudden oak death (Svihra 1999). We have recognized for some time that the sudden appearance of oak mortality is a function of our perception; although some infected trees die rapidly, more often the disease process is one of slow decline. The distribution of canker lengths following inoculation with the pathogen is consistent with quantitative, multi-gene, potentially durable resistance (Geiger and Heun 1989). We can now recognize that coast live oaks within a stand express a range of potential responses to *P. ramorum*. Realizing that a significant core of potentially resistant trees will remain after the primary impact of the epidemic has passed, new less destructive, and likely more successful management options become available.

Based on our spatially distributed, extensive longitudinal surveys, it appears that coast live oaks less than 10 to 15 cm diameter at breast height (1.37 m) only rarely become infected with *P. ramorum* (McPherson and other 2005, 2010). This phenomenon of age- or size-dependent susceptibility is presently not understood. If resistance is durable and heritable, the preservation of mature resistant trees may
maintain seed sources for future stands, even if this results in smaller mean tree size. To date there has been no practical way to assess the response of an individual coast live oak to natural infection by *P. ramorum*, other than by mechanical inoculation. Clearly, this is not useful other than as an experimental technique. The ability we have developed to predict the response of a specific tree to the pathogen provides a tool that may allow land managers to design proactive approaches to dealing with this epidemic. For example, one might wish to protect stands with large components of resistant trees from fires or development and to propagate resistant germplasm.

We have shown that even in mixed evergreen forests in which *P. ramorum* has been present for as long as 15 years, new infections continue to occur, although at lower rates than early in the epidemic (McPherson and others 2010). The survivors appear to have phloem chemistry that is correlated with resistance/susceptibility to the pathogen. Some of the compounds occurring in higher concentrations in resistant trees exhibit *in vitro* activities that are consistent with roles as anti-pathogen agents. Other compounds may not be physiologically active in defense against the pathogen, but are correlated with the tree’s response to the pathogen and may serve as readily identifiable biomarkers of resistance. Unidentified compounds associated with resistant phenotypes (Conrad and others 2014, McPherson and others 2014) remain to be tested *in vitro*. The HPLC method requires skilled technical operators and laboratory space equipped with expensive instrumentation. On the other hand, while the FT-IR method also involves specialized instruments and skilled technicians, it requires much less lab preparation per sample and may be amenable to portable field operation. We are currently working to refine the methodology and to assess its reliability for detecting resistance in naturally exposed coast live oaks (McPherson and others, unpublished). If this method is shown to be consistently accurate, other forest tree species affected by introduced and co-evolved pathogens may be amenable to similar screening for resistance.

**Acknowledgments**

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Development of a Management Plan for Coast Live Oak Forests Affected by Sudden Oak Death in East Bay Regional Parks

Brice A. McPherson, Joshua O'Neill, Gregory Biging, Maggi Kelly, and David L. Wood

Abstract
The East Bay Regional Park District maintains the largest urban park system in the United States, comprising over 45,000 ha, and more than 1900 km of trails, with extensive forests bordering residential areas. Sudden oak death (SOD), caused by the introduced oomycete Phytophthora ramorum, was first detected in a district park in 2001. Both increased fire risk and structural failure of large trees located near sites with heavy public usage are concerns for managers. Management requires reliable data about the location and severity of the disease. To produce disease incidence and risk maps, between 2008 and 2013 we placed 537 georeferenced 10-m radius fixed plots in oak-bay stands in five parks in the East Bay Hills in the San Francisco Bay Area. We recorded data for all woody vegetation and the disease status of coast live oaks. Between 6 and 17 percent of coast live oaks were symptomatic and 2 to 8 percent were dead with symptoms of SOD. Infection rates of 2.1 and 3 percent/year were estimated for Tilden Park and Huckleberry Preserve, respectively. Logistic regression analysis for Anthony Chabot Park identified two predictors of SOD incidence: topographic moisture indices and increasing coast live oak diameter at breast height (1.37 m; DBH). Model results for the other parks confirm that DBH is a significant predictor of SOD infection. Modeled results for the other four parks found consistently significant associations between symptomatic coast live oak and remote sensing derived tasseled cap greenness vegetation index values, and distance to stream channels.

Key words: coast live oak, East Bay Regional Parks, logistic regression analysis, management, mapping, sudden oak death

Introduction
The sudden oak death (SOD, caused by the introduced oomycete Phytophthora ramorum) epidemic has potential to significantly alter species composition, stand structure, ecosystem services, fire risk, and wildlife populations in susceptible forests. Coast live oak (Quercus agrifolia) is the dominant oak species in many hardwood forests in the Coast Ranges of California.

The East Bay Regional Park District (EBRPD) maintains the largest urban park

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system in the United States, comprising over 45,000 ha, more than 1900 km of trails, and numerous picnic grounds and campsites. The urban-wildland interface, much of which is composed of coast live oak-California bay laurel (*Umbellularia californica*) forests, lies adjacent to the cities of Richmond, El Cerrito, Berkeley, Oakland, and San Leandro. Sudden oak death was first detected in Wildcat Canyon Regional Park in 2001. The pathogen was already established in Marin County when the first mortality was observed in 1994 and the effects on impacted forests have been well documented (McPherson and others 2005, Rizzo and Garbelotto 2003). Due to the more recent establishment in the East Bay (Alameda and Contra Costa Counties), the disease has inflicted considerably less damage to date. A principal management concern is the effect of the death of large numbers of coast live oaks on fire risk and structural failure of large trees located near sites with heavy public usage. Reliable data for location and severity of the disease in coast live oaks is necessary to produce disease incidence and risk maps, which help to inform and prioritize management decisions.

In 2008, we found large numbers of coast live oaks showing the full range of SOD symptoms in a stand adjacent to a picnic site in Tilden Park. Symptomatic bay laurel foliar samples in the stand were confirmed positive for *P. ramorum* by the California Department of Food and Agriculture. Following discussions with EBRPD’s IPM specialist, the late Nancy Brownfield, we proposed to define the extent and intensity of the disease in Tilden Park. The goal of this study was to apply what we had learned from long-term disease progression plots in Marin County to the East Bay forests, in which the pathogen was a more recent arrival, to help the park district develop approaches to managing their lands while there might still be time to be proactive.

This study was designed to determine where SOD was established and the extent of the damage, to project change at the stand level, and to evaluate the influence of environmental variables that might affect disease propagation. To accomplish these goals, we created detailed georeferenced maps of disease incidence and intensity. Sudden oak death in coast live oaks progresses in identifiable stages (early stage – bleeding only; late stage – bleeding plus beetles, with or without the secondary fungus *Annulohypoxylon thouarsianum*; dead) (McPherson and others 2005, 2010). A major concern is the risk posed by structurally weakened coast live oaks. Once infected by *P. ramorum*, a large majority of coast live oaks are attacked by up to six species of ambrosia and bark beetles (McPherson and others 2008), with subsequent fungal introductions into the sapwood (McPherson and others 2013), leading to considerably increased likelihood of structural failure. Our work in Marin County showed that beetle attacks reduced median survival times of infected trees from about 8 years without beetle attacks to about 3 years after attacks (McPherson and others 2010). By introducing a temporal component, we could then apply a stage-structured approach to mapping and have greater ability to predict which locations are likely to show increased disease impact. Additional spatial information is beneficial to park managers because tree failure often occurs while foliage is still green, which untrained personnel may not recognize as posing a hazard. Larger coast live oaks tend to have higher infection rates than smaller trees, (McPherson and others 2005, 2010) and therefore pose a greater risk to park users. Such trees are frequently found in picnic areas, campgrounds, along roads, and adjacent to playing fields.

Monitoring plots were placed in Tilden, Wildcat Canyon, Redwood, and Anthony Chabot Regional Parks and Huckleberry Regional Botanic Preserve. These parklands generally lie to the east of the westernmost ridge in the East Bay Hills from Richmond to near Castro Valley, a distance of approximately 34 km (fig. 1). Except
for a discontinuity between Tilden Park and Huckleberry Preserve, the coast live oak-bay laurel forest cover under EBRPD’s jurisdiction is largely continuous. Park District vegetation type maps based on aerial photography and ground assessments were used to classify the dominant plant communities, which include eucalyptus stands, redwood forests, chaparral, and oak-bay forests.

Figure 1—Monitoring plots were placed in the coast live oak-bay laurel vegetation type in five parks of the East Bay Regional Park District. These parks lie at the urban-wildland interface along their western boundaries.

Methods
Two sampling and plot distribution methods were used in the study. In Tilden Park and Huckleberry Preserve, where vegetation type and cover are highly variable, we employed the point-centered-population density estimation (PDE) method (Engemann and others 1994, Kelly and others 2008). This method allows for efficient sampling of isolated stands within a larger fragmented landscape. Sampling nodes
were placed at 40-m intervals along transects established through oak-bay stands with a minimum length of 150 m from 2008 to 2010. The minimum length assured at least three sample nodes per transect. In each node, a center tree was selected and data were taken for the nearest mature coast live oak in each cardinal direction, for a maximum of four trees per sampling node. Only trees within 15 m of the center were included in a node to avoid overlap with other nodes. A 10-factor foresters’ prism was used to estimate basal area by tree species.

The other three parks are not only larger, but the forest cover is considerably more extensive. We randomly placed plots in Redwood, Anthony Chabot, and Wildcat Canyon Parks based on the area of oak-bay habitat within each park. Numbers of plots per park were determined with well-known sample size formulas for estimating a population proportion (in this case the proportion of diseased trees) assuming we want our sample estimate to be within ten percent of the true, but unknown, population proportion with an alpha level of 0.05. To make these calculations we used the estimated proportion \( \hat{p} \) and the variance of \( \hat{p} \) from Tilden Park, which could be reasonably assumed to represent the level of disease in the other parks for the purposes of calculating sample sizes needed in the other parks. Plots were randomly assigned to the habitat type with GPS coordinates in 2011 and were restricted to sites with < 30 percent slope to improve access. In each 10-m radius fixed plot, a center, north, and south tree was tagged for permanent reference. Every woody stem \( \geq 1.5 \) cm diameter at breast height (1.37 m; DBH) was recorded. Additional SOD symptom data were collected for coast live oaks (McPherson and others 2005, 2010). Each stem of a multiple stem coast live oak was counted as a tree because on such trees \( P. \) ramorum infections appear to be distributed independently (McPherson and others 2005, Swiecki and Bernhardt 2013). Regeneration data were collected for all woody seedlings and saplings by placing two 2 x 10-m belt transects aligned approximately north and south in each plot. These data (McPherson and others, unpublished) are not discussed here. In 2013 we revisited the Tilden Park and Huckleberry Preserve transects and converted each node to a 10-m radius plot to update the data and to standardize the data for analysis.

A logistic regression modeling approach was used to measure the association between coast live oak symptom status treated as a binary variable (symptomatic/asymptomatic) and a number of plot and landscape level environmental variables. We chose to conduct an analysis of Anthony Chabot Park as the model park. The probability that a coast live oak will become symptomatic was estimated for three distinct risk levels within the park (O’Neill 2014). Briefly, a combination of ground sampled plot-level variables and landscape level environmental variables based on GIS (Geographic Information Systems) software and remotely sensed image analysis were chosen as inputs to the model. Plot level variables included DBH and basal area for coast live oaks and two proven foliar hosts, bay laurel and madrone (Arbutus menziesii), and one associated host, beaked hazel (Corylus cornuta) (USDA APHIS 2012). Landscape level variables produced from GIS data included percent slope, aspect, a topographic wetness index - slope area ratio, total summer solar radiation, and distance to roads and trails, forests edges, and streams. Two vegetation indices, NDVI (Normalized Difference Vegetation Index) and tasseled cap brightness, greenness, and wetness, were derived from National Agriculture Imagery Program (NAIP) 4-band color infrared (CIR) tiles (NAIP 2014).
Results
Summed across the five parks, data were recorded for 8,179 coast live oak stems ≥1.5 cm. The coast live oak-bay laurel vegetation type accounts for 35 percent of the total area in the five parks (table 1). The total numbers of trees per park in the oak-bay vegetation type were calculated by assuming that vegetation in each plot (area = 315 m²) was representative of the surrounding forest. We estimate that these five parks hold 6.62 x 10⁵ coast live oaks.

Table 1—Coast live oak summary data for the five East Bay parks

<table>
<thead>
<tr>
<th>Park</th>
<th>Total park area, ha</th>
<th>Area in oak-bay, ha</th>
<th>Percent in oak-bay</th>
<th>N of plot trees by park</th>
<th>Total N of trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tilden, 2013</td>
<td>838</td>
<td>176</td>
<td>21</td>
<td>1850</td>
<td>7.89 x 10⁴</td>
</tr>
<tr>
<td>Huckleberry, 2013</td>
<td>94</td>
<td>62</td>
<td>66</td>
<td>391</td>
<td>2.48 x 10⁴</td>
</tr>
<tr>
<td>Redwood, 2011</td>
<td>726</td>
<td>306</td>
<td>42</td>
<td>1702</td>
<td>1.55 x 10⁵</td>
</tr>
<tr>
<td>Anthony Chabot, 2011</td>
<td>1238</td>
<td>490</td>
<td>40</td>
<td>2101</td>
<td>2.48 x 10⁵</td>
</tr>
<tr>
<td>Wildcat Canyon, 2011</td>
<td>988</td>
<td>310</td>
<td>31</td>
<td>2135</td>
<td>1.55 x 10⁵</td>
</tr>
<tr>
<td>Sum</td>
<td>3884</td>
<td>1344</td>
<td>35</td>
<td>8179</td>
<td>6.62 x 10⁵</td>
</tr>
</tbody>
</table>

*Average percent of all parks in the oak-bay vegetation type.

Coast live oak mean DBH (standard error) varied from 25.09 (0.31) cm in Anthony Chabot Park to 33.56 (0.82) cm in Huckleberry Preserve (table 2). Stem densities per plot were lower in Huckleberry Preserve and Tilden Park, but varied little among the other parks.

Table 2—Coast live oak plot data for five East Bay parks

<table>
<thead>
<tr>
<th>Park</th>
<th>N of plots</th>
<th>Stems/plot</th>
<th>Mean DBH (se)</th>
<th>Mean basal area, m²/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tilden, 2013</td>
<td>131</td>
<td>14.1</td>
<td>26.56 (.39)</td>
<td>2.45 (.07)</td>
</tr>
<tr>
<td>Huckleberry, 2013</td>
<td>31</td>
<td>12.6</td>
<td>33.56 (.82)</td>
<td>3.47 (.16)</td>
</tr>
<tr>
<td>Redwood, 2011</td>
<td>107</td>
<td>15.9</td>
<td>28.99 (.29)</td>
<td>2.45 (.05)</td>
</tr>
<tr>
<td>Anthony Chabot, 2011</td>
<td>132</td>
<td>15.9</td>
<td>25.09 (.31)</td>
<td>2.1 (.05)</td>
</tr>
<tr>
<td>Wildcat Canyon, 2011</td>
<td>136</td>
<td>15.7</td>
<td>30.21 (.41)</td>
<td>3.12 (.08)</td>
</tr>
</tbody>
</table>

Percent living symptomatic coast live oaks (trees with only bleeding and those with bleeding and beetle tunneling activity, with or without A. thouarsianum fruiting bodies) ranged from 6 percent for Chabot Park in 2011 to 17 percent for Huckleberry Preserve in 2013 (table 3). Mortality attributed to P. ramorum ranged from 2 percent for Tilden Park (2013) to 8 percent for Redwood Park (2011). Total numbers of symptomatic and dead coast live oaks per park were calculated from the estimated percentages of trees in these categories in the 2011 and 2013 field evaluations. For the five parks, we calculated totals of 6.5 x 10⁴ symptomatic and 2.7 x 10³ dead coast live oaks (table 3).
### Table 3—Percentages of symptomatic and dead coast live oaks for five parks

<table>
<thead>
<tr>
<th>Park</th>
<th>Percent infected</th>
<th>Percent dead</th>
<th>Total infected</th>
<th>Total dead</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tilden, 2013</td>
<td>9</td>
<td>2</td>
<td>7.1 x 10^3</td>
<td>1.58 x 10^3</td>
</tr>
<tr>
<td>Huckleberry, 2013</td>
<td>17</td>
<td>3</td>
<td>2.22 x 10^3</td>
<td>7.44 x 10^2</td>
</tr>
<tr>
<td>Redwood, 2011</td>
<td>11</td>
<td>8</td>
<td>1.71 x 10^4</td>
<td>1.24 x 10^4</td>
</tr>
<tr>
<td>Anthony Chabot, 2011</td>
<td>6</td>
<td>3</td>
<td>1.49 x 10^4</td>
<td>7.44 x 10^3</td>
</tr>
<tr>
<td>Wildcat Canyon, 2011</td>
<td>14</td>
<td>4</td>
<td>2.17 x 10^4</td>
<td>6.2 x 10^3</td>
</tr>
</tbody>
</table>

Reanalysis of the plots in Tilden Park and Huckleberry Preserve in 2013 provided estimated infection rates of 2.1 percent per year and 3 percent per year, respectively. Based on these rates, new coast live oak infections of 1400 and 594 per year are expected in Tilden Park and Huckleberry Preserve, respectively (table 4). Assuming an arbitrary but probably low infection rate of 2 percent per year, 9,900 new infections per year would be expected in coast live oaks across the five parks.

### Table 4—Projected annual new *P. ramorum* infections by park

<table>
<thead>
<tr>
<th>Park</th>
<th>Infection rate</th>
<th>Estimated starting population</th>
<th>Annual new infections</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tilden</td>
<td>2.1</td>
<td>7.02 x 10^4</td>
<td>1.4 x 10^3</td>
</tr>
<tr>
<td>Huckleberry</td>
<td>3.0</td>
<td>1.98 x 10^4</td>
<td>5.94 x 10^2</td>
</tr>
<tr>
<td>Redwood</td>
<td>2.0</td>
<td>1.26 x 10^5</td>
<td>2.52 x 10^3</td>
</tr>
<tr>
<td>Anthony Chabot</td>
<td>2.0</td>
<td>2.26 x 10^5</td>
<td>4.52 x 10^3</td>
</tr>
<tr>
<td>Wildcat Canyon</td>
<td>2.0</td>
<td>1.27 x 10^5</td>
<td>2.54 x 10^3</td>
</tr>
</tbody>
</table>

*aRates for Tilden and Huckleberry were derived from re-evaluation of plots. For the other three parks, a conservative estimate below that for Tilden Park was assumed.*

*bCalculated by removing estimates for infected and dead coast live oaks from the starting populations (2011 or 2013, depending on park).*

Disease incidence maps were produced to guide management decisions by documenting areas within each park with infected and dead coast live oaks. Within individual parks, disease levels can differ considerably. In southern Tilden Park, 25.7 percent of the coast live oaks were symptomatic in 2013, as opposed to 7.6 percent in the northern section. In Wildcat Canyon Park, contiguous with northern Tilden Park, 18.3 percent of coast live oaks were symptomatic in 2011. Because SOD infections in coast live oaks occur in characterizable stages, maps can identify areas where the disease has recently become established as well as areas with larger numbers of coast live oaks with late stage disease that pose elevated risks to the public from structural failure. Within individual parks, disease levels differ considerably. Stage-structured maps, based on disease stages, include a temporal component and can be used to identify areas that are expected to show increases in late stage diseased trees.

Two logistic regression models that were constructed using coast live oak-specific data and environmental variables for Anthony Chabot Park differed slightly in selection of statistically significant predictors of risk factors. Model I identified two significant predictor variables, coast live oak DBH and CTI, a topographic moisture index. In Model II, significant predictors were coast live oak DBH, SAR (slope area ratio, a different derived moisture index), and tasseled cap greenness (O’Neill 2014). The derived index CTI assigns low values to steep slopes and small catchments and high values to large watersheds and valley bottoms with gentle slopes. Slope area ratio also weighs the contribution of water flow from adjacent areas as a function of
slope. Both the moisture indices identified drier ridges and upslope areas as having elevated SOD risk, which is consistent with the habitats in which coast live oaks are found. Holding DBH constant in the model, increasing CTI decreased the likelihood that a coast live oak will exhibit SOD symptoms. This relationship suggests that soil moisture influences infection of coast live oaks.

Both models predicted that an increase of 10 cm DBH increases the probability that a coast live oak will be symptomatic by approximately 20 percent. For example, a coast live oak with 50 cm DBH in a site with greenness and moisture indices in the average range was predicted to have 15 percent probability and a coast live oak with 80 cm DBH was predicted to have 25 percent probability of becoming symptomatic. Where risk was increased, as determined by SAR and greenness values, an 80 cm coast live oak was predicted to have 70 percent probability of infection.

Contrary to expectations, neither model found that a variable composed of the summed basal areas of the known foliar hosts bay laurel and Pacific madrone, plus California hazel (*C. cornuta*) was a significant predictor of disease incidence.

Preliminary results of analyses of the other four parks led to some differences in the variables that were identified as significant predictors of infection. In contrast to the model results for Anthony Chabot Park, foliar host basal area was significant for three of the other four parks. The tasseled-cap greenness vegetation index, which was consistently significant, establishes a connection between symptomatic coast live oak and areas with decreased levels of green biomass. Closeness to streams was a significant predictor that a coast live oak will be symptomatic, holding other variables constant. These findings also support the conclusion that disease dispersal and hydrologic dynamics are somehow related.

**Conclusions**

The network of permanent georeferenced plots in the five principal parks in the East Bay Hills provides the opportunity to follow the course of the *P. ramorum* epidemic in forests where the host of greatest management interest, coast live oak, is a dominant species. Management of parklands for multiple uses, including recreation, maintenance of healthy wildlife populations, and watershed protection is a complex challenge. Accurate information is always prerequisite for informed planning. The collection of data by disease stage makes it possible to follow the progression of the disease through time and to detect new areas of increasing disease. For example, SOD incidence in oak-bay stands above the Tilden Nature Area in the northern part of the park increased from 3.1 percent to 4.9 percent over 4 years to 2013. Across the northern section of Tilden Park overall, symptomatic coast live oaks increased from 4.7 percent in 2009 to 7.6 percent.

Projections of coast live oak infection presented in table 4 include all size classes, including the smallest trees, which are known to have very low infection levels. In addition, the possible role of resistance was not considered in these estimates. At present, the extent and durability of resistance to *P. ramorum* are not known, but may affect the long-term impacts of the disease in forests (McPherson and others 2014). Studies to evaluate the extent of resistance in coast live oaks in these parks are planned for 2015 (McPherson and others, Biomarkers identify coast live oaks that are resistant to the invasive pathogen *Phytophthora ramorum*, these proceedings).

The logistic regression model quantifies the relationship between coast live oak stem diameter and probability of *P. ramorum* infection, consistent with findings in other studies (McPherson and others 2005, 2010). The association of bay laurel with elevated risk of infection of coast live oaks has been reported by Kelly and
Meentemeyer (2002), Swiecki and Bernhardt (2002), and McPherson and others (2010). Further, the role of this tree as a source of inoculum is well established (Davidson and others 2002). The lack of a relationship between basal area of bay laurel and two other foliar hosts and coast live oak infection in Anthony Chabot Park may reflect the specific properties of the stands in this particular park. A similar lack of positive association between foliar host basal area and symptomatic coast live oaks was also found in the Redwood Park model, but in models for Wildcat Canyon and Tilden Parks and Huckleberry Preserve the associations was significant. It is worth noting that the presence or lack of a relationship in a model must be understood in light of the recognition that models are abstractions and are only meaningful when interpreted in the context of the system under analysis.

The presence of *P. ramorum* in these parklands is now a fact that land managers will need to address. In areas with little or no detected disease, the pathogen will certainly continue to infect and kill coast live oaks in the near future. Faced with the need for adaptive management of these resources, the mapping project provides the foundation for development of models to identify the factors with the greatest probability of affecting the trajectory of the disease. The production of disease incidence and severity maps is thus fundamental to all that follows.

**Acknowledgments**

Funding for this study was provided by the East Bay Regional Park District. We particularly wish to acknowledge the late Nancy Brownfield, integrated pest management specialist for the District, who recognized that understanding the epidemic was necessary for developing rational strategies for managing this unique resource. Matt Graul of the District helped the transition following her passing. A number of students labored on this project, in the forests and in front of computers, many supported through the Calteach program, University of California Biological Scholars program, and the Environmental Leadership Pathway program.

**References**


McPherson, Brice A.; Mori, Sylvia R.; Wood, David L.; Storer, Andrew J.; Svihra, Pavel;


Phytophthora ramorum Canker (Sudden Oak Death) Disease Risk and Progress in Coast Live Oak, 2000-2012

Tedmund J. Swiecki and Elizabeth Bernhardt

Abstract
From 2000 through 2012, we collected annual observations on disease symptoms and stand conditions in 128 coast live oak plots in forests affected by sudden oak death (SOD), caused by the introduced pathogen Phytophthora ramorum. Elevated rainfall in one or both of the previous wet seasons was associated with pulses of new infections. However, persistent differences in infection rates between nearby locations and among plots within locations show that tree and site specific factors influence disease risk on the local scale. Because California bay is the primary source of P. ramorum spores in these affected forests, variables describing the proximity and density of California bay in the local oak neighborhood are the strongest predictors of disease risk. Tree growth rate and bark characteristics are also predictors of disease risk. Faster-growing, more dominant trees had elevated SOD risk whereas trees declining from other diseases had reduced SOD risk. Coast live oaks with SOD followed one of several disease progress trajectories, ranging from rapid decline to disease remission. Extensive initial trunk girdling by cankers was associated with rapid decline. More than half of the trees that developed symptoms between 2001 and 2010 had inactive or undetectable cankers by 2012.

Key words: California bay, disease remission, Quercus agrifolia, resistance, risk model, susceptibility, symptoms, Umbellularia californica

Introduction
In 2000, the exotic plant pathogen Phytophthora ramorum was identified as the cause of sudden oak death (SOD), a lethal trunk canker disease. In California, coast live oak (Quercus agrifolia), California black oak (Q. kelloggii), canyon live oak (Q. chrysolepis) and tanoak (Notholithocarpus densiflorus) are among the species that have been most severely affected to date (Garbelotto and others 2001, Rizzo and others 2002, Swiecki and others 2013). Mycelium of P. ramorum colonizes and kills phloem tissues in the bark and can spread to the cambium and outer xylem in these susceptible species. Infections cause bleeding bark cankers that can expand over time and eventually girdle susceptible trees. The sapwood-decaying fungus Annulohypoxylon thouarsianum, ambrosia beetles (Monarthrum spp.), and oak bark beetles (Pseudopityophthorus spp.) commonly attack P. ramorum-infected trees and contribute to tree decline (Garbelotto and others 2001).

We initiated a long-term, permanent-plot study in September 2000 in areas where SOD had already become established to evaluate disease risk factors and monitor disease outcomes over time. Original plot setup and all plot data collection between 2000 and 2012 were performed by the authors. This has allowed for a high degree of uniformity in assessment methodology and has increased our ability to detect and track trends in disease progress. Based on our field observations, we initiated data
collection on additional variables not considered in the original study design. These variables have been used to improve risk models to predict disease development. In this paper we discuss risk models and disease outcomes in coast live oaks.

Methods

Plot selection

During September 2000, we established circular 8 m radius (0.02 ha) plots at nine coast live oak study locations in Marin County and one in Napa County. Plots were established in areas where *P. ramorum* was prevalent. Each plot was centered around a case or control tree. Case trees had only early symptoms of *P. ramorum* canker (bleeding cankers), with the exception of nine cases that had minor amounts of beetle boring or a few small *Annulohypoxylon thouarsianum* stromata, typically on a single scaffold or on a localized portion of the bole. Control trees were lacking any *P. ramorum* canker symptoms. We established 128 coast live oak plots (53 cases, 75 controls). The locations of study sites and methods used to select plots have been previously described in detail (Swiecki and Bernhardt 2002).

Disease ratings

The authors evaluated trees in plots each year from 2000 through 2012 in September or October. Trees that had at least one stem 3 cm in diameter at 1.37 cm height (DBH) were included in the tree size class.

For coast live oak trees in each plot, we noted whether *P. ramorum* canker symptoms were present on the main stems and the stage of disease development. Trees were classified as having early symptoms if only bleeding cankers were present. Late disease symptoms were defined as including cankers and *A. thouarsianum* stromata and/or beetle boring. Trees killed as a result of extensive *P. ramorum* cankers were classified in the dead *P. ramorum* symptom class. Symptomatic trees that later stopped bleeding and showed no other evidence of disease progress for at least 2 consecutive years were classified as inactive infections (early or late depending on other symptoms). Trees in which inactive cankers became undetectable were rated as asymptomatic. Severe decline (tree death likely within 10 years) and death due to agents other than *P. ramorum* (primarily canker rot fungi) were also evaluated for each oak tree.

Disease ratings were based primarily on visual assessments. When necessary, we chipped away outer bark to expose and sample cankers, but this was minimized to avoid possible effects on future observations. To culture the pathogen from sampled cankers, we placed bark tissue pieces from canker margins into PARP semi-selective media (Erwin and Ribeiro 1996) to isolate the pathogen. In a few instances, we resampled cankers that had yielded negative results in previous years.

Trunk girdling by *P. ramorum* cankers, *A. thouarsianum*, and beetles were scored by estimating the percent bole circumference girdled as if all affected areas were projected onto the same cross section. A pretransformed 0 to 6 scale was used for these and most other visual estimates of percentages: 0 = not observed, 1 = trace to 2.5 percent, 2 = 2.5 to 19 percent, 3 = 20 to 49 percent, 4 = 50 to 79 percent, 5 = 80 to 97.4 percent, 6 = >97.5 percent. We noted whether cankers had oozed during the previous year. Canopy dieback and the abundance of unweathered bark fissures in the lower bole were also rated using 0 to 6 scale.
The influence of California bay (*Umbellularia californica*) on disease risk was assessed by recording the number of bay stems (3 cm DBH or greater) in each plot and bay canopy cover in the plot (0-6 scale). For each oak in the plot, we also measured the minimum bay foliage-oak trunk clearance, and bay canopy cover within 2.5 m and 5 m of the oak trunk using a 0-4 scale (0 = no bay canopy, 1 = 1 to 25 percent cover, 2 = 26 to 50 percent cover, 3 = 51 to 75 percent cover, 4 = more than 75 percent cover). Presence of bay within 5 to 10 m and 10 to 20 m from each oak trunk was also recorded.

**Results**

Figure 1 shows the overall disease status of study trees from 2000 through 2012. Slight declines in SOD incidence after 2003 and 2007 are due to complete symptom remission in some trees. In periods when disease levels were static, the percentage of trees with early symptoms declined as trees advanced to late or dead stages (fig. 1 bottom).

Overall mortality from SOD increased in a linear fashion between 2000 and 2012, as has mortality due to other factors. Total SOD mortality was slightly below mortality due to other factors in 2000, but has exceeded non-SOD background mortality from 2002 onward. Live trees with SOD symptoms were at least two to three times more numerous than trees declining due to other factors over the entire study period.
Between 2001 and 2012, 107 trees developed initial SOD symptoms. This represents 21 percent of the noninfected trees present in 2001. The number of newly symptomatic trees varied widely from year to year, with a large pulse of new infections starting in 2005 and smaller pulses in 2003 and 2012 (fig. 2). No newly diseased trees were observed in 2009 and only one was seen in 2008.

Figure 1—Disease status of 655 coast live oak trees from 2000 through 2012. Top graph shows percentages of trees with SOD symptoms (all Pr) as well as asymptomatic trees and trees declining or dead due to causes other than SOD. Bottom graph shows percentages of trees in various P. ramorum canker stages (early, late, or dead).
The number of newly symptomatic (fig. 2) trees seen in a given year was correlated with weather conditions favorable for disease cycling and infection. Both current year and previous year rainfall totals were significant predictors of the number of coast live oaks with new SOD symptoms in Poisson models. The best model overall for predicting new infections over the observation period included both previous and current year seasonal rainfall (model P < 0.0001).

**Disease trajectories**

Through repeated observations of trees with *P. ramorum* canker symptoms, we found that most symptomatic trees followed one of the following disease progress patterns.

**Rapid decline**

Trees developed extensive *P. ramorum* bole cankers that were heavily colonized by secondary organisms (beetles and *A. thouarsianum*) usually within a year of canker development. Trees died within 2 years of initial symptoms without significant canopy thinning, typically with rapid drying and browning of the entire canopy.

Rapid decline developed most commonly in trees that had extensive cankers at initial symptom onset. For trees that developed initial symptoms between 2000 and 2010, the average initial *P. ramorum* canker girdling rating was significantly higher (Tukey-Kramer HSD p < 0.05) in trees that died within two years (mean 5.1, n=15) than for those that died 3 to 11 years after initial symptom development (mean 2.3, n = 10) or were still alive in 2012 (mean 1.9, n = 43).

**Slow decline**

Canker development was moderate to extensive, sometimes increasing gradually over several years. Invasion by secondary organisms often occurred within 2 years of canker appearance but was sometimes delayed. After a few years, cankers commonly developed callused margins. The canopy showed slow progressive thinning and decline as bole girdling approached or exceeded 50 percent. Most oaks with this...
trajectory survived for 4 to 6 years but many survived for 10 years or more. Tree with extensive cankers were often killed by bole failure before canopy death occurred.

**Partial to complete symptom remission**

Relatively small cankers ceased bleeding or expanding after 1 to 2 years. Cankers dried out and became inactive. Larger cankers developed callus around the margins that eventually closed the cankered area. Small cankers disappeared without obvious callus development. Secondary invasion by beetles and *A. thouarsianum* did not develop on smaller cankers and was limited and became inactive within a few years in larger cankers.

Among the 97 trees that showed initial SOD symptoms between 2001 and 2010, about a third were dead by 2012 (fig. 3). Most of these died within 2 years, while the remainder declined more slowly. However, more than half of all trees that developed symptoms over this period either had inactive cankers or had become asymptomatic by 2012. The cohort of trees that had early SOD symptoms at the start of this study in 2000 (*n* = 93), showed similar disease trajectories (fig. 3). Fewer trees from this latter cohort died within 2 years, possibly because many of the rapidly-declining trees were already dead or had late symptoms by 2000.

*Phytophthora ramorum* was isolated on selective media from cankers on 73 trees between 2002 and 2011. Among these confirmed SOD-positive trees, 25 percent died and 42 percent either developed inactive cankers or were no longer symptomatic by 2012. Trees with sampled or non-sampled cankers showed similar rates of symptom remission or further symptom development, indicating that sampling did not affect disease progress.

Many trees showing symptom remission were re-infected in subsequent years. In 2004, 40 trees that had previously (2000-2003) exhibited early symptoms with bleeding cankers had inactive infections or were asymptomatic. Of these, 15 (37.5 percent) developed new bleeding in 2005 or 2006. The bleeding in most of these trees came from cankers that were offset both radially and vertically from previous cankers, suggesting that most of the new bleeding arose from new cankers rather than reactivated existing cankers.
Factors related to disease risk

Although year to year increases in new infections were clearly associated with above-average rainfall, disease levels between locations varied greatly in a fashion that could not be explained by climate differences. In 2000, SOD incidence in coast live oak at the 10 study locations ranged from 6.2 to 52 percent; in 2012, the range was 8.9 to 56 percent. Significant differences in SOD incidence (likelihood ratio test P <0.0001) have persisted between locations over the study period even between many locations are only one to a few kilometers apart and do not differ substantially with respect to rainfall or temperature regimes. Between 2000 and 2012, the increase in disease incidence between locations ranged from 0 to 14.8 percent, again with no clear relationship to either geographic location or initial (2000) disease incidence.

We used several modeling techniques to identify variables that were related to disease development. Variables that describe both the proximity and amount of California bay located near oaks within the plots were consistently strong predictors of SOD occurrence. However, additional explanatory variables greatly improved prediction of SOD in coast live oak. High stem water potential (low water stress) and greater bark thickness were significant positive predictors of SOD symptoms. These variables were only recorded for case and control trees because measuring these variables requires extra time and effort. Among more easily observed variables that were recorded for all trees, higher density of unweathered bark fissures, greater stem diameter (strongly correlated with bark thickness), and high canopy exposure (dominant canopy position) were significant predictors of SOD symptom development.

To develop a multivariate logistic regression model, we used a binary variable indicating that SOD symptoms were present in any year between 2000 and 2012 as the outcome. Models were compared using AICc and the area under the ROC curve. The best model to date is shown in table 1. The overall misclassification rate of the
model is 23 percent and the area under the ROC curve was 0.826. The model includes two terms describing the local bay neighborhood, indicating that bay close to the trunk (2 m or less) and high bay cover within 5 m of the trunk increase SOD risk. The other two terms indicate that trees that are more dominant (higher sky exposure, often larger) and faster growing (more unweathered bark fissures) have a higher risk of SOD. Expanding bark fissures are also common sites of infection, based on field observations of recent cankers.

Table 1—Logistic regression model for SOD symptoms for any year 2000 – 2012 based on all plot trees (n=521, overall model P <0.0001)

<table>
<thead>
<tr>
<th>Source</th>
<th>Likelihood ratio $\chi^2$</th>
<th>$P$ level</th>
<th>Odds ratio per regressor unit</th>
<th>Odds ratio per regressor range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bay cover within 5 m (0-4 scale)</td>
<td>23.36</td>
<td>&lt;0.0001</td>
<td>1.94</td>
<td>14.24</td>
</tr>
<tr>
<td>Minimum bay clearance 2 m or less</td>
<td>10.90</td>
<td>0.0010</td>
<td>2.67</td>
<td>2.67</td>
</tr>
<tr>
<td>Unweathered bark fissure rating 1 (2005)</td>
<td>29.98</td>
<td>&lt;0.0001</td>
<td>1.53</td>
<td>13.00</td>
</tr>
<tr>
<td>Sky exposed canopya (2002)</td>
<td>39.18</td>
<td>&lt;0.0001</td>
<td>1.53</td>
<td>12.79</td>
</tr>
</tbody>
</table>

*aRated using 0-6 pretransformed percentage scale

Compared with relatively healthy trees, trees declining due to other diseases only rarely developed *P. ramorum* cankers. Among 165 trees rated as in decline or that died from other causes by 2012, only 13 percent developed any SOD symptoms between 2000 and 2012. In contrast, 48 percent of 489 otherwise healthy trees developed SOD symptoms at some point over this period (difference in proportions P <0.001).

**Discussion**

Sudden oak death has become the primary cause of coast live oak mortality in the study plots (fig. 1). This disease is especially destructive because it preferentially affects tree that are dominant, healthy, and relatively fast growing (table 1; Swiecki and Bernhardt 2002, 2006). Over the course of this study, no predisposing host stressors have been identified or suggested from extensive field observations. Opportunistic secondary invaders, including various wood-boring beetles and decay fungi such as *A. thouarsianum* and *Phellinus gilvus*, are involved in SOD, but attack trees only after *P. ramorum* cankers have caused extensive phloem death.

The effects of SOD would be much greater if the disease epidemic were not constrained by a number of factors. Precipitation is clearly one of the strongest constraints within the study areas (fig. 2). Substantial numbers of new infections develop only in years with high rainfall and successive years of heavy precipitation are especially favorable for disease. These conditions favor the build up of inoculum on infected California bay foliage which moves to oaks mainly via splashed and windblown rain droplets (Davidson and others 2005).

The importance of nearby California bay as an inoculum source is apparent from disease models (table 1; Swiecki and Bernhardt 2002, 2008). California bay cover and density are also good predictors of SOD in disease risk models focused on the landscape scale (Kelly and Meentemeyer 2002, Meentemeyer and others 2004). For individual trees, the proximity of California bay foliage increases the likelihood that
the amount of inoculum splashed onto oak trunks is sufficient to initiate infections. More abundant California bay cover in the oak neighborhood increases the amount of inoculum that will impact an oak and also increases the size of the local reservoir for inoculum carryover during dry seasons (Davidson and others 2011). Because disease risk is highest when California bay is close to the oak, removal of bay within a few meters of susceptible oaks can greatly reduce disease risk (Swiecki and Bernhardt 2013).

Sudden oak death risk and disease progress are also strongly affected by tree characteristics (table 1; Swiecki and Bernhardt 2002, 2006). In particular, actively expanding bark fissures may be susceptible to infection due to their minimal layer of dead rhytiderm, allowing for easier infection by zoospores and sporangia. Wet conditions favor *P. ramorum* inoculum production, but also promote tree radial growth. Healthy, dominant oaks with relatively low water stress develop expanding bark fissures as the result of strong radial growth. Trees with more bark fissures also develop greater numbers of infections, which can consolidate to form larger and more severe cankers.

Based on repeated observations of hundreds of trees over a 13 year period, we now know that *P. ramorum* infections in coast live oak do not follow a single trajectory of rapid decline and mortality. That pattern, seen in less that 20 percent of symptomatic trees (fig. 3) is only one of several alternative outcomes. Slow decline over many years is about as common as rapid decline. More significantly, canker inactivation and disease remission were seen in more than half of the trees in cohorts that developed first symptoms in 2001 to 2010 or had early SOD symptoms in 2000 (fig. 3). These different patterns of disease progress were not apparent when SOD was originally described in California (Garbelotto and others 2001, Rizzo and others 2002). Understanding of these potential disease outcomes is essential for the informed management of SOD-affected forests over time (Swiecki and Bernhardt 2013).

The relatively high incidence of canker inactivation and disease remission suggests that many coast live oaks have some level of general or horizontal resistance. Such resistance may be overcome by high inoculum levels or particularly favorable environmental conditions (Erwin and Ribeiro 1996), which is consistent with the reinfection we observed in trees that had limited initial cankers. Phenolics have been identified as possible biomarkers of disease resistance in coast live oaks (McPherson and others, Biomarkers identify coast live oaks that are resistant to the invasive pathogen *Phytophthora ramorum*, these proceedings). The development of phenolics or other host defense compounds related to resistance, though ultimately under genetic control, may be strongly influenced by host stress and growing conditions, and could account for differences in susceptibility between declining and vigorous oaks.

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References


Managing Redwood Ecosystems Using Sudden Oak Death as a Silvicultural Tool

Frederick D. Euphrat

Abstract
In response to the wave of sudden oak death (SOD), caused by Phytophthora ramorum, sweeping the redwood forest ecosystems of California's North Coast, the role of foresters and other ecosystem managers is being tested. On Bear Flat Tree Farm, near Healdsburg, California, Forest, Soil & Water, Inc. (FSW) has conducted a multi-year, multi-treatment approach to take advantage of SOD. Because the seral stage of tanoak is a component of hardwood dominance intermediary between brush and conifers, FSW has used the oncoming wave of SOD to accelerate the ecosystem towards redwood (Sequoia sempervirens).

The combination of pathogen and cultural treatments of harvest, planting, pruning and thinning has quickly created a redwood-dominated, vigorously growing stand. The key to this rapid change was planting redwoods near tanoaks prior to mortality and timely thinning. These actions have nearly doubled diameter growth of redwood saplings in a statistically significant test. In addition, the timely management of large woody debris from dead tanoaks creates greater stocking in the forest and addresses damaged crop trees.

Key words: forest, redwood, release, SOD, tanoak, thinning

Introduction
In response to the wave of sudden oak death (SOD), caused by Phytophthora ramorum, sweeping the redwood forest ecosystems of California's North Coast, the role of foresters and other ecosystem managers is being tested. The disease strikes tanoak (Notholithocarpus densiflora) with unchecked vigor, rapidly altering the species mix, density and lower canopy insolation. Most tanoak are infected to the point of mortality; bay laurel (Umbellularia californica) are also infected, but not killed, acting as active host trees for the pathogen. Through the bay laurel, the fungus maintains purchase in the ecosystem (Cobb and others 2013).

Treatment of SOD at the one tree level (for example, potassium phosphite) has been used (Garbelotto and others 2007), but is neither practicable nor desirable at the landscape level. Suggestions for management range from no response to multi-square-kilometer exclusion zones (Cobb and others 2013). Ironically, foresters have been trying to limit tanoak for years; managing the consequences of SOD is a unique opportunity at the ecosystem level.

On Bear Flat Tree Farm, near Healdsburg, California, Forest, Soil & Water, Inc. (FSW) has conducted a multi-year, multi-treatment approach to take advantage of SOD. Because the seral stage of tanoak is a component of hardwood dominance intermediary between brush and conifers, FSW has used the oncoming wave of SOD to accelerate the ecosystem towards redwood. The location of this research is on a Non-Industrial Timber Management Plan (NTMP 1-06NTMP-03 SON) as approved by the California Department of Forestry.

The combination of pathogen and cultural treatments of harvest, planting, pruning and thinning has quickly created a redwood-dominated, vigorously growing stand.

1 An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.
2 Adjunct Professor, Santa Rosa Jr. College, Santa Rosa, CA 95401.
The key to this rapid change was planting redwoods near tanoaks prior to mortality. Following mortality, the tanoak sites were quickly replaced by young redwoods (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*) and sub-canopy species, such as whiteleaf manzanita (*Arctostaphylos manzanita*), western raspberry (*Rubus leucodermis*), poison oak (*Toxicodendron diversilobum*), coyote brush (*Baccharis pilularis*) and resprouting tanoaks. This growth was encouraged by increased moisture availability, direct sunlight and canopy space, and reinforced by precommercial silvicultural practices.

The tanoak loss, which is spotty and continuing, has quickly been replaced by the young redwoods. This growth was encouraged by increased moisture availability, direct sunlight and canopy space, and reinforced by cultural practices.

Addressing SOD as an active component of forest management is an opportunity to accelerate ecological succession to a redwood-dominated ecosystem. This research presents quantitative outcomes of the Bear Flat Tree Farm case study.

**Study location**

This research occurred at Bear Flat Tree Farm, a private forest landholding 8 km (5 miles) due east of Healdsburg, California. The site is a redwood-Douglas-fir ecosystem managed for timber production. Redwood is promoted in this forest, because of its unique qualities both as an ecosystem component and market value. The study site has been logged four times, in approximately 1900 and 1930, then again in 1960 and 2007. The most recent harvest was a single-tree selection, removing about 1/3 of the basal area to a residual of 22.96 to 34.44 m² per hectare (100 to 150 ft² per acre), and stocking of about 210 m³/ha (15,000 board ft/acre.

The location of the study area, indicated as the NTMP, is shown on fig. 1.
Rainfall averages 114.3 cm (45 inches) per year (Rantz 1969). Climate is temperate, with snow only rarely. Ocean fog and radiation fog are both common on the site. The moderate temperatures are due to the proximity of the ocean, about 24.1 km (15 miles) to the west, and the topographic conditions of the Russian River watershed, of which this site is a part (Euphrat and others 2006).

Elevation of the sample plots was 274.3 to 304.8 m (900 to 1000 ft) above sea level. The soils are Hugo gravelly loam (HnG) developed on a greywacke parent material (Miller 1972). The aspect of the sites was northerly, approaching a ridgetop. The study area was selected for its distinct uniformity of ecosystem, harvest history, treatment differences, and homogeneity of soils and topographic position.

**Treatment**

The saplings studied were planted in 2008 and 2009, so are presently 5 and 6 years in the ground. Seedlings were a combination of bare root and plug stock, 1 and 2 years old at planting. Those seedlings are in both control and treated areas.

Following planting, a precommercial thinning was implemented in 2012 to release the redwoods and to reduce tanoak slash. This practice is tree specific, and reduces competition around redwood saplings. With SOD in the stand and redwoods planted near the at-risk trees, a great deal of clearing is already occurring. Stand management
tunes those clearings and releases redwood from the physical effects of the falling tanoak.

The control area was not thinned, though it had mortality from SOD.

**Hypothesis**

Stand improvement following SOD increases the growth of pre-planted redwood seedlings significantly. This is being tested for management of the redwood stand as a commercial forest.

**Study design**

Two areas of regenerating redwood-Douglas-fir forest received similar historical treatments of timber harvest, thinning and tree planting. Both areas were similarly infested with SOD, affecting tanoak and bay laurel species. Tanoak trees died and fell on both sites, creating breaks in the canopy. This study focused on the redwoods near those dead tanoak trees (snags) and stumps.

Thirty-one 3 m (10 ft) diameter plots were centered on SOD-killed tanoak snags and stumps. Within those circles, 0.00024 ha (1/139 of an acre), all redwood saplings were measured for diameter (with a ruler) at 15.24 cm (6 inches) from the ground, height (taped or estimated), and distance from the stump (taped). Ten plots were in the control area, and the remainder in the treated area.

Data were collected by the students of Santa Rosa Jr. College NRM70 class, as a field exercise, as well as by the principal investigator. All data were collected within one month.

**Data summary**

Of the 77 saplings inventoried, 19 were in the control area, or 25 percent. This is notable, because the control represented 33 percent of the area observed (table 1). This is reflected in the saplings per acre values; treated saplings averaged 360 trees per acre, and control less than 240. For comparison, normal reforestation plantings range from 10 x10 foot spacing to 15 x 15 foot, values of 436 to 154 seedlings per acre (Arvola 1978).

There was little difference in distance to stump on both treated and control. Diameter and height, however, showed important trends, increasing on treated sites. Range of heights was highly variable, up to 4.57 m (15 ft). Diameters, however, were significantly different. Diameter averages were 2.46 and 1.37 cm (0.97 and 0.54 inches) for the treated and control sites, with standard deviations, respectively of 0.271 and 0.356. A t-test with these values is shown in fig. 2.
Table 1—Data summary

<table>
<thead>
<tr>
<th></th>
<th>Treated</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redwood saplings (n)</td>
<td>58</td>
<td>19</td>
</tr>
<tr>
<td>Redwood saplings/acre (TPA)</td>
<td>360</td>
<td>236</td>
</tr>
<tr>
<td>Mean diameter (inch)</td>
<td>0.97</td>
<td>0.54</td>
</tr>
<tr>
<td>Mean height (ft)</td>
<td>4.6</td>
<td>3.7</td>
</tr>
<tr>
<td>Mean distance to tanoak (ft)</td>
<td>6.8</td>
<td>6.4</td>
</tr>
</tbody>
</table>

Figure 2—t-test of diameter (0 = Control, 1 = Treated) (inches). P = 0.093.

Hypothesis testing and results

Statistical testing found a very significant relationship between treatment and diameter of saplings with the Kolmogorov-Smirnov test (p = 0.098) and a significant relationship with the t-test (p = 0.093), not disproving the original hypothesis. Because diameter reflects actual growth and vigor of trees, and because the difference between control and treated was close to twofold, this result is notable. As stated above, saplings are presently 5 and 6 years in the ground. The increased diameter at this early age reflects root growth and, with it, the ability to compete for canopy co-dominance. Height and distance to dead tanoak were not significant.

One factor which was not tested under the hypothesis, however, was an unusual finding. Two of the 10 plots (20 percent) in the control area had sapling damage from fallen tanoaks, as in fig 3. The fallen tanoaks bend the saplings down, creating uneconomic, suppressed and deformed trees. This damage is reflected in the lower trees per acre value (these trees were not counted). While this situation has not been tested statistically, any damaged redwood in this management regime represents a lost opportunity relative to forest production goals.
Conclusions and recommendations

Sudden oak death infestation on Bear Flat Tree Farm in Healdsburg, California is both promoting and interfering with the regrowth of coast redwoods. The mortality of tanoaks creates gaps in the canopy, allowing redwood and a suite of other species to grow rapidly. When redwoods are planted prior to the individual tanoak trees’ death and in-situ decay, they are able to capture the site when it is subsequently thinned.

If the site is not thinned, there are two effects of the SOD passage. First, it promotes all species, capturing the increased water and sun. That suite of species, including resprouting tanoak, suppresses the newly established redwoods. This relationship has been explored in this study, showing that redwoods in thinned areas will have grown nearly twice as much just 2 years after the thinning, from an average of 1.37 cm (0.54 inches) diameter at 15.24 cm (6 inches) height (control) to 2.46 cm (0.97 inches) (treated).

The other effect of SOD is large woody debris damaging crop trees. The debris bends and stunts redwood saplings, affecting 20 percent of the control plots and reducing the trees per acre of redwood from 360 to 236. While the reduction in sapling frequency was not demonstrated to be significant in this study, the effect was nonetheless notable and of concern. To a forest manager, no crop tree is expendable.

The conclusion of this study is simple: SOD-affected tanoak stands must be managed for regrowth. The opportunity presented to the forest manager is important; tanoak has challenged site from redwood occupancy for many years. With SOD in the landscape, redwoods may now recapture sites without herbicides while maintaining a mixed species stand. The tools for guiding the mortality created by
SOD are planting and thinning. Actively managing the SOD may take several minor treatments in a stand because of the slow passage of the pathogen, but the results of lower redwood mortality and a much more vigorous stand are ideal.

Further research indicated by this study is evaluating the cost-effectiveness of thinning and planting in the SOD-affected forest. Forest managers would like to capture all space with crop trees, but that is never possible. How many entries are cost-effective for landowners of various classes to use? How much assistance is needed from the state or federal government to respond to spur landowners to conduct SOD response practices in the Redwood Region? Are existing cost-share programs adequate?

While questions linger over cost, there should be no hesitation for landowners to begin implementing a program as soon as SOD arrives. Identifying areas of infestation, finding suitable planting stock, and beginning a program of planting near susceptible trees is a start. Subsequent thinning will change the look, economics and ecology of the redwood forest.

Acknowledgments

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References


