Long-Term Prospects for Restoration of Coastal Sage Scrub: Invasive Species, Nitrogen Deposition, and Novel Ecosystems[1]

Edith B. Allen[2], Christopher McDonald[3], and Bridget E. Hilbig[4]

Abstract

Coastal sage scrub (CSS) is one of the most endangered ecosystem-types in California and is undergoing extensive restoration efforts. Major threats to CSS include agriculture and urban development, fragmentation, invasive species, frequent fire, and high levels of anthropogenic nitrogen (N) deposition that increases exotic species productivity, further increasing fuel for fire. In this review we compare a range of techniques that have been used with varying success to restore CSS, using examples from published and unpublished sources. Techniques that treat large scales and reduce the exotic seedbank are the most effective, such as herbicides or solarization, but each may also have drawbacks. Other methods include mulch, seeding or planting species with competitive functional traits, grazing, and fire. Regardless of method, invasive species recolonize to varying extents following restoration, and periodic treatment is needed. CSS in sites receiving more than the critical load of 11 kg ha^{-1} yr^{-1} of N deposition may become type-converted to exotic annual grassland in the absence of other disturbance such as fire. Such sites are not good candidates for restoration. Inability to control exotic species reinvasion and restore diversity of native forbs results in novel ecosystems with reduced conservation value and ecosystem services.

Keywords: Coastal sage scrub, invasive plant species, fire, functional traits, nitrogen deposition, critical load, restoration, smokewater, solarization

Introduction

Restoration of some ecosystem types has proved quite challenging for various reasons, including the degree of impact they have received or the extent of invasion by exotic plant species (Allen et al. 2000). Ecosystems that cannot be easily restored may have exceeded a threshold and moved into another stable state and will require major effort to return to original condition (Hobbs and Norton 1996). This might be the case where invasive species have formed a dense seedbank or soils have become eutrophied so that native plants adapted to low-nutrient soils cannot compete (Cione et al. 2002, Yoshida and Allen 2004, Rao and Allen 2010, Fenn et al. 2010). The effort required to restore these ecosystems to a predisturbance state may be higher than available resources allow, or in some cases impossible with any level of effort.

---

[1]A version of the paper was presented at the Chaparral Restoration Workshop, Arcadia, CA, June 17-20, 2013. We thank Sandra DeSimone and Kimberly Williams for reviewing the manuscript.
[2]Professor and Extension Specialist, Department of Botany and Plant Sciences, Center for Conservation Biology, University of California, Riverside, Riverside, CA 92521, edith.allen@ucr.edu
[3]Extension Advisor, UC Cooperative Extension - San Bernardino County, 777 East Rialto Avenue, San Bernardino, CA 92415-0730, cjmcdonald@ucanr.edu
[4]Graduate Student, Department of Botany and Plant Sciences, University of California, Riverside, Riverside, CA 92521, bridget.hilbig@email.ucr.edu

These have been defined as novel ecosystems, those that have no antecedents in any local vegetation types because they have a species composition that is completely or partially different from pre-disturbance communities (Hobbs et al. 2009). Another term, hybrid ecosystems, has been applied when the resultant vegetation is a mix of native and non-local species (Hobbs et al. 2009). When the goal of restoring a pre-disturbance ecosystem cannot be met, managers may have to settle for a hybrid ecosystem that retains important conservation values, such as habitat for rare species, and major ecosystem dynamics, such as an appropriate fire regime, but may include non-local species.

Coastal sage scrub of California is among the most endangered ecosystem types in the United States (Noss et al. 1995) because it is limited in extent and includes many federally listed, state listed and sensitive species. Conservation and protection measures for these species and their habitats have made CSS the object of major restoration research and management efforts (Allen et al. 2000, and studies reviewed below). CSS is also among the most challenging vegetation types to restore. It has been extensively converted to, and fragmented by, urban development and agriculture and subject to other impacts such as historic grazing, invasions by Mediterranean annuals, frequent fire, and high levels of anthropogenic nitrogen (N) deposition (Talluto and Suding 2008, Cox et al. 2014). Domestic grazing declined by the 1930's with increasing urbanization, and sites that were historically grazed were able to recover (Fleming et al. 2009, Cox et al. 2014), but exotic annual invasions continued to expand (Minnich 2008). Nitrogen deposition originates from automobile, industrial, and agricultural emissions, and began to increase in the 1950's. Current levels are above critical load (10 to 11 kg N ha^{-1} yr^{-1}) for 33% of CSS vegetation statewide (Fenn et al. 2010, Cox et al. 2014). By comparison, background N deposition in unpolluted regions is 2 kg N ha^{-1} yr^{-1}. CSS areas above critical load are highly invaded by Mediterranean annuals with a loss of native plant diversity. Some areas of CSS have been entirely converted to exotic annual grassland (Cox et al. 2014), including areas within Forest Service lands and conservation reserves that are being restored, or where restoration planning is under consideration (Western Riverside County Habitation Conservation Plan, n.d.).

The objectives of this review are to discuss techniques that have been used for restoration of invaded CSS, including some previously unpublished studies; to review projects and techniques that have been successful, and discuss factors that contributed to their success; and to help managers make decisions about techniques to use and sites to select to maximize the success of CSS restoration. In many cases exotic annuals cannot be permanently controlled, and managers will need to make decisions about how much effort to put into maintaining the site. In some cases, novel or hybrid ecosystems may be the product of restoration (Hobbs et al. 2009).

Restoration Techniques for CSS

The techniques used for CSS restoration depend on the degree and kind of disturbance. With the implementation of Habitat Conservation Plans in several southern California counties, abandoned agricultural areas, including citrus orchards, small grain fields and pastures, are being converted back into native habitat. These typically have little or no native seedbank, have been extensively invaded by Mediterranean annual grasses and forbs, and require the most intensive efforts to restore (Allen et al. 2005, Marushia and Allen 2011). Sites that have been burned frequently also have a depleted native seedbank (Cione et al. 2002), although their

soils have not been disturbed by tillage so soil nutrients and microorganisms are still largely intact (Dickens et al. 2013, Dickens and Allen 2014). In contrast, soils of a former citrus orchard had a legacy of fungal pathogens that selectively reduced growth of native forbs but not exotic grasses (Hilbig and Allen 2015). Sites that receive high levels of N deposition also have high concentrations of soil nitrogen, which promote exotic grass growth to the detriment of native species (Padgett et al. 1999, Yoshida and Allen 2001, 2004, Rao and Allen 2010). Increased grass biomass contributes to frequent and larger fires, further degrading native shrublands and promoting vegetation-type conversion. Each of these disturbance types can be addressed with multiple approaches to restoration.

CSS is one of the most invaded ecosystems in California, so restoration often begins with control of invasive species. Recovery by natural succession may occur (DeSimone 2011), but is infrequent in highly invaded or severely disturbed CSS (Stylinski and Allen 1999). Exotic annual species tend to displace native shrub seedlings and native annuals through competition and high propagule pressure. Propagule density of exotic species can be quite high even in CSS in relatively good condition. In invaded CSS with shrub cover, Cox and Allen (2008a) found 5000 seeds/m^2 of exotic grasses and forbs, 800 seeds/m^2 of native forbs, and only 4 seeds/m^2 of shrub species. Exotic seed density was even higher in former CSS that was converted to exotic grassland, with lower densities of native seed. The exceptions are constructed soils such as cut banks on roadsides or other urban construction sites where topsoil was removed. These soils are initially devoid of any seed, and planted seeds would be able to establish without competition from exotic species. However, in most degraded CSS lands, propagule pressure and the density of the exotic seedbank is a major obstacle to success following seeding. In general CSS shrub seedlings are poor competitors with exotic annuals, while established shrubs and perennial grasses fare better (Eliason and Allen 1997). Roots of exotic annuals tend to be shallow compared to mature CSS plants, but CSS seedlings have shallow roots that reduce their competitive ability (Wood et al. 2006, Eliason and Allen 1997). CSS plants at different life history stages compete with exotic annuals with varying success. Because of this, seedlings of CSS species need reduced competition by creating openings in the exotic annuals. Whether naturally occurring, caused by small mammal disturbances or by land managers, these openings are crucial to establishing native vegetation (DeSimone and Zedler 1999, Moyes et al. 2005). Any restoration of invaded lands would need to begin with controlling existing exotic species and controlling the exotic seed bank. Restoration researchers and practitioners have used a variety of techniques to restore degraded CSS, including fire, solarization, grazing, mowing, herbicides, and followed by seeding where the native seedbank is depleted. Effectiveness and limitations (Table 1) of these techniques are discussed

Fire

Fire is used as a restoration tool only when there are few or no native shrubs remaining, as managers are understandably reluctant to remove existing native vegetation. Fire is effective for controlling exotic annual grasses when it is timed in spring or early summer just before seed drop to reduce the contribution to next year's seed bank (Gillespie and Allen 2004, DiTomaso et al. 2006). This is an effective technique for control of grasses with very short-lived seedbanks (1-2 years) such as red brome (*Bromus rubens*; Salo 2004), but additional control is needed for longer-

lived grass seeds such as ripgut brome (*Bromus diandrus*) or longer-lived seeds of forbs such as storksbill or mustard (*Erodium* or *Brassica* spp.). Fire is often best used as part of an integrated pest management (IPM) plan (DiTomaso et al. 2006), particularly because post-fire fuel loads are often not sufficient to carry fires in successive years, unless precipitation is above average for multiple years. Thus, fire will need to be coupled with a second alternative treatment. Wildfires burn through CSS at intervals of 20-40 years (Cleland et al. 2016). When return intervals are sufficiently long, fire by itself is not detrimental to CSS stability, nor does infrequent fire by itself promote type conversion of CSS (Cox et al. 2014.).

Solarization

Solarization is the most effective method for controlling exotic seedbanks, but only on soils where vegetation has been removed for best contact with the plastic cover, such as on abandoned agricultural fields or urban construction sites (Moyes et al. 2005, Marushia and Allen 2011). In a comparison of winter solarization (using black plastic, also called tarping) mowing, grass-specific herbicide, and early season disking, solarization was the most effective technique in reducing the seedbank and promoting establishment of native plants (Marushia and Allen 2011). Summertime application of clear plastic is more effective because soils will heat to high temperatures providing greater weed seed mortality, but only in moist soil (Elmore et al. 1993). Since irrigation water is typically limiting, summer solarization is seldom an option. A comparison of winter and spring solarization (taking advantage of residual soil moisture and the warmer temperatures of spring) showed that spring was more effective in controlling the weed seedbank (Weathers 2013). However, all of these studies were conducted in small research plots. While solarization is common for agricultural seed bank control, few efforts have been made to extend it to large-scale restoration (Stapleton and Jett 2006). Solarization can be costly on a large scale, but the resulting depletion of most of the seed bank can also be highly rewarding (Stapleton 2000).

Grazing

While grazing studies are common in grasslands (e.g. Weiss 1999), no published studies address grazing as a technique for control of exotic grasses in CSS restoration. The removal of intensive grazing enabled CSS recovery on Santa Cruz Island (Yelenik and Levine 2010), but control of exotic grasses often requires limited, timed grazing. One previously unpublished study that addressed effects of controlled grazing for CSS restoration was conducted at the Lake Skinner Western Riverside County Multispecies Habitat Reserve in Lopez Canyon, an area grazed through the late 1980's (Allen unpublished). The site had sparse CSS shrubs (<20% cover), with an understory of red brome, ripgut brome, and filaree as the dominant exotic species, and some 70 native species (mainly annual forbs) per ha. Further background information for this study is in Allen et al. (2005). Twelve 1-ha plots were arranged in three replicate blocks with each of three treatments and a control per block: 1) Fusilade II ® (grass-specific herbicide)—February/March 1999 and 2000, using hand-held applicators at the lowest level of the manufacturer's recommended dose; 2) Dethatching plus herbicide—November 1998 using hand-held

Table 1—Effectiveness and limitations of restoration treatments to control invasive plants and seed with native species. Extent: small 100 m^2 - 1 ha, medium 1-100 ha, large >100 ha

Treatment	Effectiveness	Limitations	Extent	Citations
Fire	Spring burns are effective to control exotic annual seedbank. Typically applied in degraded CSS with few or no shrubs.	Managers are reluctant to burn healthy shrub stands, even with invaded understory. Many CSS shrubs are mainly reseeders with a sparse seedbank. Would need to reseed shrubs. Many CSS shrubs do not tolerate frequent fire (>1/decade).	Large scale	Gilllespie & Allen 2006, DiTomaso et al. 2006
Solarization	Highly effective in reducing or eliminating weed seed bank if applied on moist soil with high temperatures and bare soil.	Natural soil moisture is high only in winter rainy season, but temperatures are too cool. Laying down plastic after a spring rain, and allowing it to remain in place until hot summer temperatures, is possible. Used mainly in agriculture, few applications in actual restoration.	Small to medium	Elmore et al. 1993, Marushia and Allen 2011, Moyes et al. 2005, Stapleton 2000, Weathers 2013
Grazing	Controls exotic grass seedbank when properly timed before annual seed production. Shrubs will survive browsing. Useful in rugged or rocky terrain.	Grazers are not selective of exotic vs. native annuals, but native annuals have long-lived seedbank. Timing is difficult in dry years when exotic grasses go to seed early, grazers will not consume sharp seeds. Results vary with livestock species.	Large scale	Weiss 1999, Kimball and Schiffmann 2003, Allen unpubl. (see text)
Mowing	Effective in controlling weed seebank when properly timed before seed production.	Useful in degraded CSS with few or no shrubs on relatively level land.	Medium to large scale	Allen et al. 2005, Marushia and Allen 2011
Hand weeding, line trimmers	Effective for smaller sites needing complete weed control, e.g. to protect listed species or around visitor centers.	Labor intensive, must be applied periodically. Best when volunteers can be assembled.	Small to medium	Allen et al. 2005, Hasselquist et al. 2013, Marushia and Allen 2011
Mulch	Good control when applied before weed seed germinates and when native seed applied after mulching. Also immobilizes excess soil N, reducing competition from nitrophilous weedy species	Mulch adds organic matter to soils that are natually low. Arid land plants and soil microorganisms may not be adapted to elevated soil moisture. May need reapplication if weeds need continual control.	Small to medium	Zink and Allen 1999, Cione et al. 2002, Wolkevich et al. 2009
Herbicide	Effective when used properly, may be selective depending on target species. Often most cost efective weed control option.	Some agencies or managers are reluctant to use herbicides based on the "precautionary principle." Some potentially effective herbicides are not permitted on all potential lands or land uses (i.e. grazing).	Medium to large scale	Allen et al. 2005, Bell et al. 2015, Marushia and Allen 2011, Cione et al. 2002, Holl et al. 2014, Kimball et al. 2014,
Smoke stimulation	Many CSS species germinate without smoke treatment. Wildfires provide natural treatment, or seeds can be treated in the lab or nursery prior to seeding.	No known effective direct field application of smoke or smoke water treatment, other than actual fire.	Small to large	Dixon et al. 1995
Seeding	Essential when seedbank is depleted of native seeds	Seeds may not emerge in first year, or not at all due to drought, herbivory, or unknown causes	Small to large	Dickens and Allen 2014, Marushia and Allen 2011, Cox and Allen 2008
Nursery transplants	Used when a rapid vegetation stand is desired, or to avoid the seedling stage of species that are poor competitors with exotic species.	Expensive, time consuming, weed control surrounding young plants increases survival	Small to medium	Bowler 2000, Eliason and Allen 1997
Functional traits	Native plants with traits that make them more competitive (larger, higher growth rates) or have greater longevity than invasive annuals (shrubs vs. annuals) are better candidates for successful restoration.	A limited pool of native species is available to select from, so not all needed traits that are superior to invasive plants are available. Invasive species may have certain traits such as earlier germination that trump all other native traits.	Small to large	Cleland et al. 1993, Hilbig 2015, Kimball et al. 2014, Talluto et al. 2006

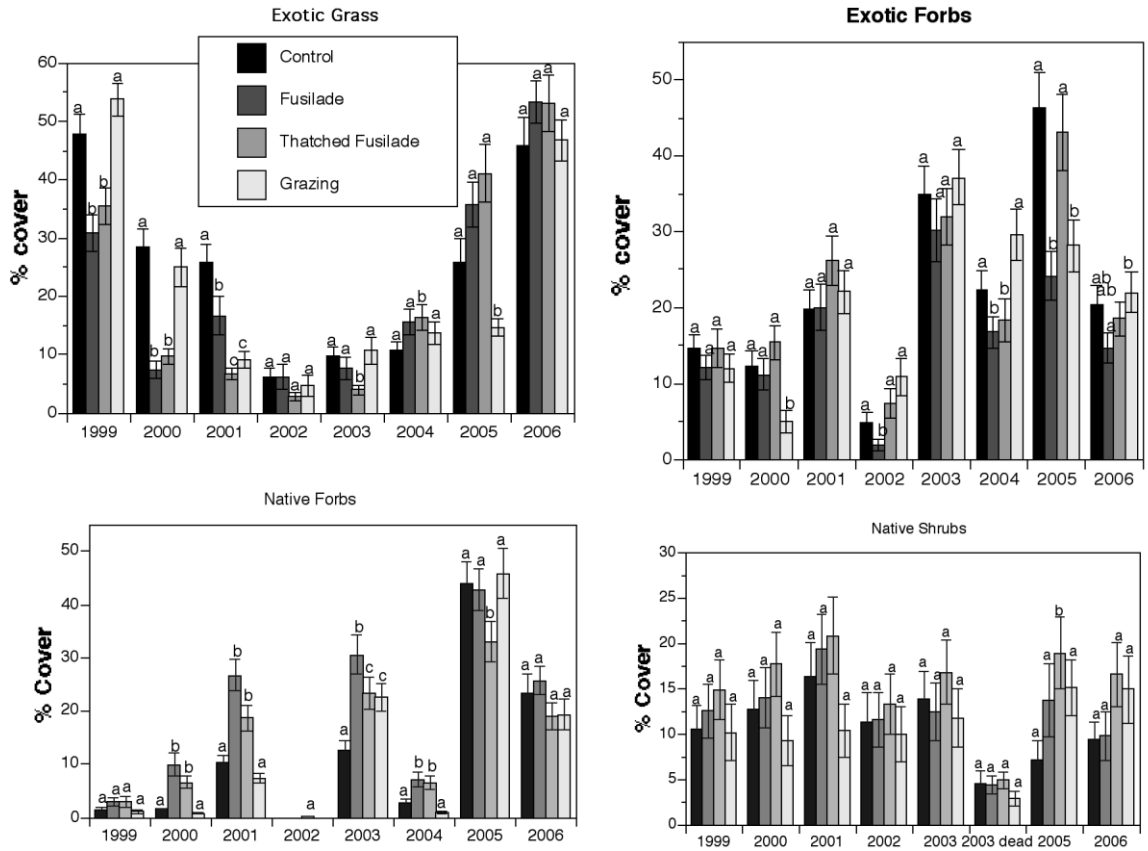

Figure 1—Responses of exotic grass, exotic forbs, native forbs, and native shrubs to three weed control treatments. Letters show significant differences within a year. Native forb responses to treatments were still significant through 2005. Dead shrub cover is shown for 2003, following the 2002 extreme drought year (Allen, unpublished).

weed trimmers, followed by Fusilade II ® in February/March 1999 and 2000; 3) Grazing—March/April in 1999, 2000, and 2001, using 200 sheep per hectare plot for 48 hours; and 4) control. Vegetation percent cover was sampled in 1 m x 0.5 m quadrats, 20 in each 1-ha plot, yearly in late April/early May. Data were analyzed using one-way ANOVA with blocking. Grass-specific herbicide alone and in combination with dethatching significantly reduced grass cover (mainly red brome and ripgut brome) in 1999-2001 compared to controls (fig. 1). During and after the extreme drought year of 2002 (5 cm, average is 26 cm), there was no longer a significant effect of herbicide on grasses. Grazing was not effective until the third year, 2001, when exotic grass in grazed plots was lower than in control plots. Exotic forbs (mainly filaree species) did not respond positively to grass reduction during 1999-2001, and their reduced cover in formerly-herbicide treated plots in 2004-2006 is difficult to explain. Alternatively, native forbs responded to reduced grass cover after herbicide control with increased cover in 2000-2004 and to reduced grass cover from grazing in 2003. The response of native forbs (some 60 species) to grass removal treatments after the 2002 drought is remarkable, suggesting the seedbank may have been affected by the treatments with a carryover to 2003, which had average rainfall. Shrubs were not significantly affected by any treatment. Drought in

2002 caused considerable mortality as measured by dead shrubs in 2003, but they recovered to pre-drought levels.

While grazing was considered an effective strategy for restoration of Central California grasslands (Weiss 1999) that have higher precipitation and productivity, timing was difficult in the drier and variable climate of southern California. Exotic grass productivity is relatively low in most years, and there is only a 2-3 week window for grazing before brome grasses produce seeds. Sheep will not consume grasses with these sharp seeds, and graze native shrubs and forbs instead. Native forbs were also preferentially consumed by cattle in a Carrizo Plain grassland, and grazing was not considered to be an effective restoration treatment (Kimball and Schiffman 2003). In CSS grazing may be effective in a wet year with sufficient exotic grass production for a reasonably long window of time for grazing, but not in a dry year. Short duration timing of grazing is critical even in a wet year to assure that animals consume exotic grasses without excessive trampling of native plants.

Mowing, Weed Trimming, and Hand Weeding

Machine mowing to restore CSS is effective in relatively flat landscapes and that lend themselves to mowing such as abandoned agricultural fields that have no remnant shrubland, but it cannot be used in steep or rocky terrain. Annual mowing has allowed stands of CSS to spread into adjacent abandoned agriculture at the Johnson Ranch in Riverside County and into weedy parkland at Mt. Rubidoux Open Space Park in Riverside City (Cione et al. 2002, Marushia and Allen 2011, Allen, personal observations). Mowing at these sites ceased after shrubs were tall enough to interfere with the mower, at which time they were also tall enough to overtop exotic grasses (e.g., > 50 cm). Weed trimming (weed "whacking" with a line trimmer) is typically used for individual plants, in smaller areas such as research plots in small to medium sized infestations or in terrain inaccessible with a mower, and can be effective if applied annually or more times per season (DeSimone 2007, Marushia and Allen 2011). It has been used to control weeds in the interspaces between CSS shrubs in areas of several hectares, such as at the Western Riverside County Habitat Conservation Reserve, by using teams of workers. Hand weeding is done for small plots around high-visibility areas such as near park visitor centers, to protect sensitive species, or for research studies. Many exotic annual grasses have densities >500/m^2, so this is challenging work but very effective. After the first year the seed bank density begins to decrease, so subsequent years require only light maintenance. The Theodore Payne Foundation has several hectares of hand-weeded CSS maintained by staff and volunteers to provide a public exhibit of native vegetation (theodorepayne.org/visit-us/our-grounds/wildflower-hill/). Hand weeding provided the best exotic grass control to promote recovery of the endangered *Ambrosia pumila*, better than Fusilade II® although not practical on a large scale (Hasselquist et al. 2013). Persistent hand removal provides the best results for weed-free research plots as controls, and has been used in CSS restoration studies (Eliason and Allen 1997, Cox and Allen 2011, Dickens and Allen 2014).

Mulch

Application of a mulch barrier to prevent the establishment of annual plants can be highly effective at restoring CSS. Mulch (wood chips, bark or straw) reduces the ability of annual species to establish allowing for reduced competition when potted

perennials are installed (Zink and Allen 1998). Mulch is also used to immobilize excess soil N and improve soil moisture and subsequent seedling establishment and plant growth. In a study to restore CSS, bark mulch was more effective than straw, and both were better than no mulch for reducing soil mineral N to reduce competition from exotic grasses and restore seeded California sagebrush (Zink and Allen 1998). Bark mulch reduced soil N in another CSS restoration seeding study but was ineffective in promoting native shrub growth because it was applied after exotic grasses had germinated (Cione et al. 2002). In a mature, invaded stand of CSS, exotic grass litter addition increased both CSS shrub growth and exotic grass production by improving soil moisture (Wolkevich et al. 2009). Whether mulch is used to immobilize excess soil N or to reduce exotic seed germination by smothering, timing of mulch application before germination is critical. Small native seed may in some cases need to be broadcast after mulch application, but thick layers of mulch may reduce seed contact with soil. In this case, planting nursery stock may be the best option. Mulch application is not practical on a large scale, and is typically used in sensitive areas or near visitor centers. It is not a solution for mitigating landscape-scale N deposition, which will continue to elevate soil N after restoration. Furthermore, CSS soils have low organic matter (typically 1-2%), so adding mulch may artificially alter soil chemistry and moisture (Wolkevich et al. 2009). Additionally, mulch barriers eventually decay or disperse and need to be replenished if long-term control of invasive species is not attained by one application.

Herbicides

Herbicide treatments can be highly effective at reducing weed cover and if applied for several successive years can ultimately eliminate the seed bank of short-lived weed seeds. Few herbicide evaluations have been conducted in CSS on a large-scale or over a long-term, but results from small plots show weed populations can be significantly reduced by single or repeated applications (Allen et al. 2005, Cox and Allen 2008). In general, herbicide treatments will reduce exotics the most when treatments last longer than the longevity of dormant exotic seeds. Many exotic annual species in California have a sufficiently short-lived seed bank where repeated annual applications of herbicide can be effective at weed extirpation. For instance, red brome seed survives 24 months (Jurand et al. 2013, Salo 2004), ripgut brome lasts 2-3 years (Kleemann and Gill 2009), wild oat survives 3-5 years or longer (Conn and Werdin-Pfisterer 2010), short-podded mustard survives 4+ years (Chadoeuf et al. 1998) and tumbleweed 1-3 years (DiTomaso and Healy 2007),. While herbicides, mulching and solarization can provide significant weed control, herbicide treatments are the most cost-effective treatment when compared to mulching or solarization (Holl et al. 2014, Bell et al. 2015). Herbicide or other treatments are used for on-site control, but propagule pressure from surrounding untreated areas is a constant threat to restoration.

Herbicide success will depend on the active ingredient used and thus the herbicide mode of action, the rate at which it is applied, timing of application and efficacy of initial and follow up treatments. In general, the efficacy of using a broad combination of herbicides is well developed in agricultural systems; it is less commonly used in the restoration of wildlands. Future research on a variety of herbicide uses in wildlands could significantly improve CSS restoration and management. For example, in areas where exotic grasses dominate, broad spectrum and grass-specific herbicides as well as pre-emergent herbicides could control annual

exotics throughout the growing season. In addition, herbicide combinations could allow for management of exotics while planting nursery stock. Most published studies of CSS restoration strategies have relied on only two herbicides, glyphosate and/or fluazifop (Kimball et al. 2014, Marushia and Allen 2011, Cox and Allen 2008b, Cione et al. 2002) despite a variety of available products on the market.

Smoke-induced Seed Bank Stimulation

While the suppression of invasive plants and weeds is critical to establishment of CSS, there remains much to learn about the stimulation of seeds by smoke, both native and exotic species. Smoke can be used to break dormancy of seeds in Mediterranean-type ecosystems (Dixon et al. 1995, Keeley and Fotheringham 1998, Egerton-Warburton 1998), and is a natural process of seed bank stimulation in burned Mediterranean-type shrublands. Smoke treatments may be used to "flush out" weeds and/or native species that are dormant in the seed bank in areas where fire cannot be applied (Jefferson et al. 2014). A preliminary study of smokewater application to the soil surface showed marginal (most P values > 0.05) increases in native CSS species from the seedbank (Egerton-Warburton unpublished). Many CSS seeds will germinate in the absence of fire or smoke (Keeley 1987, DeSimone and Zedler 1999). However, germination of slender wild oats (*Avena barbata*) and possibly Mediterranean splitgrass (*Schismus* spp.) in southern California was significantly higher when stimulated by smokewater (Engel 2014). If the weed seed bank is depleted by long-term control, smoke could be applied to stimulate longer-lived and dormant CSS species. These potential methods require additional research.

Seeding, Planting, and Seedbanks

Many efforts to restore invaded CSS include seeding native species, with variable success depending on environmental and biotic conditions. Native species often survive in the seedbank, so seeding or planting may not be needed (Allen et al. 2005, Bell et al. 2015), but is required where the seedbank is depleted (Cione et al. 2002, Dickens and Allen 2014). Native seedbank loss occurs when soils are disturbed by agriculture or urban construction (Montalvo et al. 2002), but also with frequent fire followed by post-fire invasion and competition from high-density invaders (Cione et al. 2002). Seedbank density is also dependent on naturally occurring soil pathogens that decrease native seedbank density and subsequent seed germination, more so under high than low moisture conditions (Mordecai 2012). Plant community composition is an insufficient indicator of seedbank composition. In stands of mixed native and exotic plants, seed banks may be especially depleted of native seed (Engel 2014, Cox and Allen 2008a), while in other trials germination of native species from the seedbank was high after exotic species control (Cox and Allen 2008b, Cox and Allen 2011). Where the exotic seedbank was sparser, native plants established through natural colonization without weed control (DeSimone and Zedler 1999, DeSimone 2011). Preliminary tests of seedbank density, or germination responses to invasive plant control need to be done prior to restoration planning efforts.

Seeding is preferred to planting nursery-grown materials because of the reduced cost and labor. CSS seeds will establish readily in years of near average to above precipitation (Padgett et al. 2000). Nursery transplants require additional moisture to establish initially (Eliason and Allen 1997), that can be supplemented with irrigation or hand watering where available. Salvaged plants have also been used with success,

as in a Habitat Conservation Plan site in Orange County (Bowler 2000). The advantage of transplants is that they are past the initial drought-sensitive stages of seedlings. If they can survive transplant shock and establish, they will quickly overtop exotic grasses to develop a mature shrub stand. Nevertheless, exotic grass control improves success of nursery transplants (Eliason and Allen 1997, Bowler 2000).

Functional Traits

Recent studies have tested the concept of limiting similarity to restore native species in invaded vegetation. This theory predicts that coexisting species exhibit different resource-use traits to avoid competitive exclusion (Funk et al. 2008, Price and Pärtel 2013). In these studies, native species with traits similar to, or superior to, invaders were chosen for restoration. Common plant traits considered include plant height and biomass, growth rate, root depth, or some other morphological or physiological trait. Cleland et al. (2013) were able to establish native forb species common to CSS when early active forbs were used to match the phenology of exotic grasses. However, the native species chosen to represent functional groups in this study were not all locally native species, such as *Aristida adscensionis,* a non-local, warm season grass, so this was not technically a restoration. A similar approach was used by Talluto et al. (2006), who seeded a mix of native annual forbs and thereby reduced establishment of exotic annuals in a shrub understory and increased overall stand diversity. In another study, planting with shrub plus forb functional groups of native species within CSS communities resulted in greater competition for decreased available resources. This implies a successful approach would be to plant them sequentially, but exotic annuals would also need to be controlled (Kimball et al. 2014). Even when the best efforts are made to select native plants with superior traits, there are a limited number of species to choose from, and invasive species have many traits that make them successful. One trait is early germination, which gave the invasive annuals *Bromus diandrus* and *Erodium cicutarium* a competitive edge over any native species regardless of other traits such as size or growth rate (Hilbig 2015). Wainwright et al. (2012) took advantage of early germination phenology to control seedlings of exotic species and deplete the seedbank before native seeds germinated. Although there are some examples from other vegetation types (Price and Pärtel 2013), the promise of using competitive traits to fully restore CSS diversity based on limiting similarity has not been fulfilled, and at this time controlling exotic species will most often be necessary to assure restoration success.

Restoration Success and Reinvasion

The most successful seeding trials for CSS restoration have been done in soils with limited weed propagule pressure. A study in constructed soil where topsoil had been removed at the Diamond Valley Reservoir, Riverside County, and seeded using hydroseeding and drill seeding had high native shrub, grass and forb density regardless of seeding technique (Montalvo et al. 2002). Little weeding was required during the two-year experiment, and most seed colonized from adjacent areas. After the research was completed and weeding ceased, colonizing invaders were able to establish, and the site is now a shrubland with a sparse understory of native and exotic herbs (Allen, personal observations). Similarly, solarization of abandoned agriculture in former CSS greatly reduced the exotic seedbank and enabled seeded

native forbs and shrubs to establish at high density and cover (Marushia and Allen 2011). However, after the study was completed the site was recolonized by exotic grasses and forbs, likely both from the seedbank and adjacent surrounding weedy areas (Allen, personal observations). Grazing and herbicides were used in 1-ha plots at the Shipley Reserve (fig. 1 and Allen et al. 2005) and observed for 5 years. By the fifth year plots began to homogenize such that treatments were no longer significantly different from controls, suggesting that weed control must be done at least every 5 years to maintain increased native forb cover. There was no significant increase in shrub cover in these studies. Weed control in small, 5 m^2 plots at Mt. Rubidoux Park in Riverside enabled establishment of native shrubs (Cione et al. 2002). However, a wildfire burned the shrubs 10 years after establishment, exotic grasses quickly recolonized the plots, and post-fire native shrub establishment was < 1 shrub per 5 m^2 plot (Allen, personal observations, (fig. 2). One of the hallmarks of successful CSS establishment is that the site will regenerate naturally after a fire (Bowler 2000). Clearly this was not a long-term successful restoration. This was a

2A

2B

2C

Figure 2—Restoration at a site with high N deposition and frequent fire in Riverside (Cione et al. 2002). A.) CSS shrubs were established in 5 X 5 m plots in spring 1998 using grass-specific herbicide and hand cultivation (June 2005 photo). B.) Wildfire killed shrubs in October, 2008. C.) Shrub recovery was sparse in May 2010 (green vegetation in plots is exotic forbs), exotic grasses and forbs recolonized the site. (Photo credits: E.B. Allen).

site with high N deposition (20 kg N ha^{-1} yr^{-1}; Cione et al. 2002), and coupled with high exotic grass productivity and small plots that allow more rapid grass recolonization, the restoration had little prospect of long-term success without continual weed management. By contrast, a 2007 burn at a CSS restoration site at Siphon Reservoir in Orange County recovered its shrub component beginning only three years after the fire, and two other Orange County roadside sites that also recovered from fires in 2007 (Margot Griswold personal communication), as well as the Orange County site described by Bowler (2000). At this time the information on post-fire recovery of restored CSS is mainly anecdotal. Data on exotic seedbank density and exotic plant productivity and competition with native species are absent, so conclusions regarding mechanisms of post-fire recovery are difficult to make. One important difference is the lower N deposition in coastal Orange County, which has cleaner air than inland regions (see conclusions). A successful CSS reseeding effort occurred at the San Jacinto Wildlife area in 6.8 ha of abandoned farmland that had been cleanly cultivated to reduce the weed seedbank (fig. 3). Aerial photographs from the mid-1930s showed the site had been CSS, and was subsequently farmed. A mix of native forbs and shrubs (fig. 3) was drill-seeded in 2003, established successfully, and persist to the present. While no data were collected for this project, the photos (fig. 3) indicate that CSS can be restored with some degree of success However, the native forbs that were abundant in the early years declined, and exotic grasses, especially red brome, colonized the site. Three of the initial shrub species declined, and the site is dominated by *Eriogonum fasciculatum*,suggesting this species is best suited to the local conditions. There may be multiple reasons for success at this site compared to the other inland CSS sites reported above: no fires have occurred, the initial seedbank had sparse weed seed (based on field observations, Fig. 3B), the restored area is large so the dispersal of weed seed from adjacent sites was slower than into small plots, and the region has moderate N deposition of 11 kg N ha^{-1} yr^{-1}. This value is at the critical load for vegetation-type conversion (Cox et al. 2014), so long-term restoration success is not guaranteed.

Conclusions

Restoration research in California grasslands has shown that controlling invasive annual grasses promotes establishment of native species, but that within 3-5 years the treated and untreated sites homogenize, with equal proportions of native and exotic species (Larios et al. 2013, Holl et al. 2014). Resistance to restoration is similar in invaded CSS, where restored shrublands become dominated by understories of exotic grasses and forbs after 3-5 years (Allen et al. 2005, and post-publication observations of studies by Cione et al. 2002, Marushia and Allen 2011). The initial success of restoration is determined by the extent to which aboveground competition as well as the exotic seedbank can be controlled. Solarization has the potential to be most successful under appropriate conditions (bare, moist soil) because of the high seedbank mortality, but these conditions are typical only for abandoned agriculture. Solarization has been used experimentally in small plots, but seldom, if at all, on a large scale for actual restoration. Other large-scale techniques, such as fire or herbicides, are temporary because invasive species will eventually recolonize. Thus periodic treatment must be part of any long-term CSS restoration plan.

3A

3B

3C

Figure 3—Restoration of abandoned farmland at San Jacinto Wildlife Area. A.) After drill-seeding with native species, March 2003. B.) Establishment of native forbs and shrubs, sparse invasive species, March 2004. C.) Dominance of California buckwheat, invasive red brome, and sparse native forbs in 2013. Initial seed mix for this site was *Encelia farinosa* (brittlebush), *Artemisia californica* (California sagebrush), *Eriogonum fasciculatum polifolium* (California buckwheat), *Lotus scoparius* (common deerweed), *Amsinckia menziesii* (common fiddleneck), *Hemizonia fasciculata* (clustered tarweed), *Lasthenia californica* (California goldfields), *Layia platyglossa* (coastal tidytips), *Lepidium nitidum* (shining pepper-grass), *Lupinus succulentus* (arroyo lupine), and *Marah macrocarpus* (wild cucumber). (Photo credits: E. B. Allen).

Even after employing best techniques for seedbank control in large areas, long-term restoration success will depend on site factors. Nitrogen deposition is a major driver of exotic grass productivity, and CSS sites that had N deposition above 11 kg ha^{-1} yr^{-1}converted to exotic grassland even in the absence of recent fire (Cox et al. 2014). An additional factor driving conversion was the composition of surrounding vegetation, as CSS stands surrounded by exotic grass were more likely to convert to exotic grassland even in sites with lower N deposition. Such sites are poor candidates for successful restoration of CSS. Some 33% of CSS in California occurs above the critical load of N (Fenn et al. 2010), especially in inland regions where N deposition tends to be higher. Coastal regions have lower N deposition, and include a number of

successful efforts at restoration of CSS (Bowler 2006, DeSimone 2013). Restoration will be most successful in sites below critical load of N deposition. This information can be used to inform air quality legislation to improve environmental health of impacted ecosystems such as CSS (Pardo et al. 2011).

With some exceptions (DeSimone 2011), even the best-conserved CSS sites have been invaded, and restoration challenges range from stands with very low invasion to degraded sites dominated by exotic species. Given the high effort and often high cost of controlling exotic plants to restore native species (Bell et al. 2015, Kimball et al. 2015), managers must make decisions on which sites will be able to resist invasion in the long-term, and which will be quickly reinvaded. The latter include sites with high N deposition above critical load of 11 kg ha^{-1} yr^{-1}, continual disturbance impacts from humans or domestic grazers, frequent fire, or surrounding sources of invasive species in the landscape. If sites subject to high reinvasion need to be restored to meet conservation goals, such as to enhance populations of endangered species, then periodic efforts will be needed to control exotic species, and long-term planning is essential (Wilson et al. 2011). Even with the best restoration efforts, the outcome may best be classified as hybrid ecosystems that retain characteristics of the original ecosystem but include invasive species. However, this is an improvement over stands dominated by invasive species that are novel ecosystems with reduced ecosystem services and conservation value (Hobbs et al 2009).

References

Allen, E.B.; Cox, R.D.; Tennant, T.; Kee, S. N.; Deutschman, D.H. 2005. Landscape restoration in southern California forblands: Response of abandoned farmland to invasive annual grass control. Israel Journal of Plant Sciences 53:237-245.

Allen, E.B.; Eliason, S.A.; Marquez, V.J.; Schultz G.P.; Storms, N.K.; Stylinski, C.D.; Zink, T.A. ; Allen, M. F. 2000. What are the limits to restoration of coastal sage scrub in southern California? In Keeley, J.E.; Keeley, M.B.; Fotheringham, C.J., eds. 2nd Interface between Ecology and Land Development in California. USGS Open-File Report 00-62, Sacramento, California; 253-262.

Bell, C.E.; Allen, E.B.; Weathers, K.A.; McGiffen, M. 2015. Simple approaches to improve restoration of coastal sage scrub habitat in Southern California. Natural Areas Journal 36(1): 20-28.

Bowler, P.A. 2000. Ecological restoration of coastal sage scrub and its potential role in habitat conservation plans. Environmental Management 26: S85-S96.

Chadoeuf, R.; Darmency, H.; Maillet, J.; Renard, M. 1998. Survival of buried seeds of interspecific hybrids between oilseed rape, hoary mustard and wild radish. Field Crop Research 58: 197-204.

Cione, N.C.; Padgett, P.E.; Allen, E.B. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire and nitrogen deposition in southern California. Restoration Ecology 10: 376-384.

Cleland, E.E.; Larios, L.; Suding, K.N. 2013. Strengthening invasion filters to reassemble native plant communities: soil resources and phenological overlap. Restoration Ecology 21: 390-398.

Cleland, E.E.; Funk, J.; Allen, E.B. 2016. Coastal sage scrub. In: Zavaleta, E.S.; Mooney, H., eds. Ecosystems of California. University of California Press, Berkeley. 429-448.

Cox, R.D.; Preston, K.L.; Johnson, R.F.; Minnich, R.A.; Allen, E.B. 2014. Influence of landscape-scale variables on vegetation conversion in southern California, USA. Global Ecology and Conservation 2: 190-203.

Cox, R.D.; Allen, E.B. 2008a. Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. Plant Ecology 198: 37-46.

Cox, R.D.; Allen, E.B. 2008b. Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. Journal of Applied Ecology 45: 495-504.

Cox, R.D.; Allen, E.B. 2011. The roles of exotic grasses and forbs when restoring native species to highly invaded southern California annual grassland. Plant Ecology 212: 1699-1707.

DeSimone, S.A. 2007. Non-chemical restoration of coastal sage scrub in artichoke-infested grasslands (California). Ecological Restoration 24: 278-279.

DeSimone, S.A. 2011. Balancing active and passive restoration in a nonchemical, research-based approach to coastal sage scrub restoration in southern California. Ecological Restoration 29: 1–2.

DeSimone, S.A. 2013. Restoration and science: a practitioner/scientist's view from rare habitat restoration at a southern California preserve. Restoration Ecology 21: 149-152.

DeSimone, S.A.; Zedler, P.H. 1999. Shrub seedling recruitment in unburned Californian coastal sage scrub and adjacent grassland. Ecology 80: 2018-2032.

Dickens, S.J.M; Allen, E.B. 2014. Soil nitrogen cycling is resilient to invasive, exotic annuals following restoration of coastal sage scrub. Journal of Arid Environments 110: 12-18.

Dickens, S.J.M., Allen, E.B.; Santiago, L.S.; Crowley, D. 2013. Exotic annuals alter the variation in coastal sage scrub soil chemical and biological characteristics. Soil Biology and Biochemistry 58: 70-81.

DiTomaso, J.M.; Healy, E.A. 2007. Weeds of California and Other Western States. ANR Publications.

DiTomaso, J.M.; Brooks, M.L.; Allen, E. B.; Minnich, R.; Rice, P.M.; Kyser, G.B. 2006. Control of invasive weeds with prescribed burning. Weed Technology 20: 535-548.

Dixon, K.W.; Roche, S.; Pate, J.S. 1995. The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. Oecologia 101: 185-192

Egerton-Warburton, L.M. 1998. A smoke-induced alteration of the sub-testa cuticle in seeds of the post-fire recruiter, *Emmenanthe penduliflora* Benth. (Hydrophyllaceae). Journal of Experimental Botany 49: 1317-1327.

Eliason, S.A.; Allen, E.B. 1997. Competition as a mechanism for exotic grass persistence following conversion from native shrubland. Restoration Ecology 5: 245-255.

Elmore, C.L.; Roncoroni, J.A.; Giraud, D.D. 1993. Perennial weeds respond to control by soil solarization. California Agriculture 47: 19-22.

Engel, M.D. 2014. The feasibility of chaparral restoration on type-converted slopes. M.S. thesis. California State University San Bernardino. 174 p.

Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K. R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W. 2003. Ecological effects of nitrogen deposition in the western United States. Bioscience 53: 404-420.

Fenn, M.E.; Allen, E.B.; Weiss, S.B.; Jovan, S.; Geiser, L.; Tonnesen, G.S.; Johnson, R.F.; Rao, L.E.; Gimeno, B.S.; Yuan, F.; Meixner, T.; Bytnerowicz, A. 2010. Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. Journal of Environmental Management 91: 2404-2423.

Fleming, G.M.; Diffendorfer, J.E.; Zedler, P.H. 2009. The relative importance of disturbance and exotic-plant abundance in California coastal sage scrub. Ecological Applications 19: 2210-2227.

Funk, J.L.; Cleland, E.E.; Suding, K.N.; Zavaleta, E.S. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution 23: 695-703.

Gillespie, I.G.; Allen, E.B. 2004. Fire and competition in a southern California grassland: impacts on the rare forb *Erodium macrophyllum.* Journal of Applied Ecology 41: 643-652.

Hasselquist, E.M.; Hasselquist, N.J.; Rogers, D. L. 2013. Management of non-native annual plants to support recovery of an endangered perennial forb, *Ambrosia pumila*. Restoration Ecology 21: 224-231.Fusilade-hand pulling best

Hilbig, B.E. 2015. Ecological Assembly rules and soil legacy effects in the restoration of an invaded plant community. Ph.D. Dissertation, University of California, Riverside. 129 p.

Hilbig, B.E.; Allen, E.B. 2015. Plant-soil feedbacks and competitive interactions between invasive *Bromus diandrus* and native forb species. Plant and Soil 392: 191-203.

Hobbs, R.J.; Norton, D.A. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4: 93-110.

Hobbs, R.J.; Higgs, E.; Harris, J.A. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution 24: 599-605.

Holl, K.D.; Howard, E.A.; Brown, T.M.; Chan, R.G.; de Silva, T.S.; Mann, E.T.; Russell, J.A.; Spangler, W.H. 2014. Efficacy of exotic control strategies for restoring coastal prairie grasses. Invasive Plant Science and Management 7: 590-598.

Jefferson, L.; [et al.] 2014. Ecology of Plant Derived Smoke: Its Use in Seed Germination. Oxford University Press. 307 p.

Jurand, B.S.; Abella, S.R.; Suazo, A.A. 2013. Soil seed bank longevity of the exotic annual grass *Bromus rubens* in the Mojave Desert, U.S.A. Journal of Arid Environments. 94: 68-75.

Keeley, J.E. 1987. Role of fire in seed-germination of woody taxa in California chaparral. Ecology 68: 434-443.

Keeley, J.E.; Fotheringham, C.J. 1998. Smoke-induced seed germination in California chaparral. Ecology 79: 2320-2336.

Kimball, S.; Schiffman, P.M. 2003. Differing effects of cattle grazing on native and alien plants. Conservation Biology 17: 1681-1693.

Kimball, S.; Lulow, M.E.; Mooney, K.A.; Sorenson, Q.M. 2014. Establishment and management of native functional groups in restoration. Restoration Ecology 22: 81-88.

Kimball, S.; Lulow, M. E.; Sorenson, Q.M.; Balazs, K.; Fang, Y.C.; Davis, S.J.; O'Connell, M.; Huxman, T.E. 2015. Cost-effective ecological restoration. Restoration Ecology 23(6): 800-810.

Kleemann, S.G.L.; Gill; G.S. 2009. Population ecology and management of rigid brome (*Bromus rigidus*) in Australian cropping systems. Weed Science 57: 202-207.

Larios, L.; Aicher, R. J.; K.N. Suding. 2013. Effect of propagule pressure on recovery of a California grassland after an extreme disturbance. Journal of Vegetation Science 24: 1043-1052.

Marushia, R.G.; Allen, E.B. 2011. Control of exotic annuals to restore native forbs in abandoned agricultural lands. Restoration Ecology 19: 45-54.

Minnich, R.A. 2008. California's Fading Wildflowers. University of California Press, Berkeley.

Montalvo, A.M.; McMillan, P.A.; Allen, E.B. 2002. The relative importance of seeding method, soil ripping and soil variables on seeding success. Restoration Ecology 10: 52-67.

Mordecai, E.A. 2012. Soil moisture and fungi affect seed survival in California grassland annual plants. Plos One 7.

Moyes, A.B.; Witter, M.S.; Gamon, J.A. 2005. Restoration of native perennials in a California annual grassland after prescribed spring burning and solarization. Restoration Ecology 13: 659-666.

Noss, R.F.; Laroei, E.T.; Scott, J.M. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Biological Report 28. US National Biological Service, Washington, DC. Available at: http://biology.usgs.gov/pubs/ecosys.htm, (Accessed May 2012).

Padgett, P.E.; Allen, E.B. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. Plant Ecology 144: 93-101.

Padgett, P.E.; Kee, S.N.; Allen, E.B. 2000. The effects of irrigation on revegetation of semiarid coastal sage scrub in southern California. Environmental Management 26: 427-435.

Pardo, L.H.; Fenn, M.E.; Goodale, C.L.; Geiser, L.H.; Driscoll, C.T.; Allen, E.B.; Baron, J.; Bobbink, R.; Bowman. W.D.; Clark. C.; Emmett, B.; Gilliam, F.S.; Greaver, T.; Hall, S.J.; Lilleskov, E.A.; Liu, L.; Lynch, J.; Nadelhoffer, K.; Perakis, S.; Robin-Abbott, M.J.; Stoddard, J.; Weathers, K.; Dennis, R.L. 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecological Applications 21: 3049-82.

Price, J.N.; Pärtel, M. 2013. Can limiting similarity increase invasion resistance? A meta-analysis of experimental studies. Oikos 122: 649-656.

Rao, L.E.; Allen, E.B. 2010. Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts. Oecologia 62: 1035-1046.

Salo, L.F. 2004. Population dynamics of red brome (*Bromus madritensis* subsp. *rubens*): times for concern, opportunities for management. Journal of Arid Environments 57: 291-296.

Stapleton, J.J.; Jett, S. 2006. A large-scale demonstration of solar inactivation of invasive weed propagules for revegetation of California native wildflower communities. California Conference on Biological Control V, Riverside, CA; 182-183

Stapleton, J.J. 2000. Soil solarization in various agricultural production systems. Crop Protection 19: 837-841.

Stylinski, C.D.; Allen, E.B. 1999. Lack of native species recovery following severe exotic disturbance in southern California shrublands. Journal of Applied Ecology 36: 544-554.

Talluto, M.V.; Suding, K.N. 2008. Historical change in coastal sage scrub in southern California in relation to fire frequency and air pollution. Landscape Ecology 23: 803-815.

Talluto, M.V.; Suding, K.N.; Bowler, P.A. 2006. Factors affecting understory establishment in coastal sage scrub restoration. Madroño 53: 55-59.

Wainwright, C.E.; Wolkovich, E.M.; Cleland, E.E. 2012. Seasonal priority effects: implications for invasion and restoration in a semi-arid system. Journal of Applied Ecology 49: 234-241.

Weathers, K.A. 2013. The role of invasive *Erodium* Species in restoration of coastal sage scrub communities and techniques for control. Ph.D. Dissertation, University of California, Riverside.

Weiss, S.B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. Conservation Biology 13: 1476-1486.

Western Riverside County Multiple Species Habitat Conservation Plan (n.d.) http://rctlma.org/Portals/0/mshcp/index.html (accessed 5-2015).

Wilson, K.A.; Lulow, M.; Burger, J.; Fang, Y.C.; Andersen, C.; Olson, D.; O'Connell, M.; McBride, M.F. 2011. Optimal restoration: accounting for space, time and uncertainty. Journal of Applied Ecology 48: 715-725.

Wolkovich, E.M.; Bolger, D.T.; Cottingham, K.L. 2009. Invasive grass litter facilitates native shrubs through abiotic effects. Journal of Vegetation Science 20: 1121-1132.

Wood, Y.A.; Meixner, T.; Shouse, P.J.; Allen, E.B. 2006. Altered ecohydrologic response drives native shrub loss under conditions of elevated N-deposition. Journal of Environmental Quality 35: 76-92.

Yelenik, S.G.; Levine, J.M. 2010. Processes limiting native shrub recovery in exotic grasslands after non-native herbivore removal. Restoration Ecology 18: 418-425.

Yoshida, L.C.; Allen, E.B. 2001. Response to ammonium and nitrate by a mycorrhizal annual invasive grass and a native shrub in southern California. American Journal of Botany 88: 1430-1436.

Yoshida, L.C.; Allen, E.B. 2004. ^{15}N uptake by mycorrhizal *Artemisia californica* and the invasive *Bromus madritensis* of a N-eutrophied shrubland. Biology and Fertility of Soil 39: 243-248.

Zink, T.A.; Allen, M.F. 1998. The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. Restoration Ecology 6: 52.