Oak Woodland Vegetation Dynamics: A State and Transition Approach[1]

Melvin R. George[2] and Maximo F. Alonso[2]

Abstract

California's oak-woodlands are a complex, often multi-layered mosaic of grassland, shrubland, and woodland patches. While soil type and depth, topography, aspect, and geological substrate influence the distribution of these patches, disturbance and biological interactions are also important determinants of the patchy distribution of these plant communities. Fire intensity and frequency can change the structure of these patches, while grazing can affect the speed of the species replacement. Different re-establishment strategies of woody species interacting with prevailing weather following disturbance can also produce changes in the plant community composition at the patch level which are often smaller than a soil mapping unit or an ecological site. While our knowledge of vegetation dynamics in the oak-woodlands is not great, what we do know, or can reasonably hypothesize, is being organized into a format that is sensible and accessible to natural resource managers. State and transition models have been proposed as a format for organizing the complex body of knowledge and concepts describing vegetation dynamics in rangeland ecosystems. Natural and man-caused vegetation change can be incorporated into these models. In this review paper, we will describe oak-woodland vegetation dynamics using a state and transition format.

Keywords: Oak-woodlands, state and transition models, succession, vegetation dynamics.

Introduction

USDA Natural Resources Conservation Service is developing ecological site descriptions for the nation's rangelands (NRCS 1997). An ecological site 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. Soils with similar properties that produce and support a characteristic plant community are grouped into the same ecological site. Ecological site descriptions outline physiographic, climatic, hydrologic, soil, vegetation and wildlife characteristics of the site. Part of the ecological site description is a state and transition model that describes vegetation dynamics on the site. The purpose of this report is to describe the on-going development of state and transition models for the oak-woodlands. In this report. we will 1) review state and transition models, 2) review vegetation dynamics that will be embodied in transition descriptions, 3) briefly report on survey and analysis procedures used to determine vegetation states, and 4) present an example of an oak-woodland state and transition model.

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[2] [2] Specialist and Graduate Student respectively, University of California, Plant Sciences, One Shields Avenue, 1210 Plant and Environmental Sciences Bldg., Davis, CA 95616-8780. e-mail: mrgeorge@ucdavis.edu, malonso@ucdavis.edu.

State and Transition Models

Traditional theories of plant succession leading to a single stable end point (climax community) do not adequately describe non-equilibrium vegetation dynamics characterized by multiple successional pathways and multiple stable endpoints. Westoby and others (1989) proposed state and transition models as practical formats for describing multiple successional pathways, multiple steady states and discontinuous and irreversible transitions (Stringham and others 2003). The USDA NRCS adopted state and transition models for describing traditional succession dynamics, as well as non-equilibrium dynamics (USDA 1997).

A state and transition model includes 1) a catalog of possible alternative vegetation states associated with an ecological site and a catalog of transitions from one state to another. The level of detail may range from specific experimental results collected on the ecological site to general science-based or experience-based knowledge of ecological site response to natural or human-caused disturbances. Westoby (1989) defined a state as an alternative, persistent vegetation community that is not simply reversible in the linear successional framework. Stringham (2003) defined a state as a recognizable, resistant and resilient complex of the soil base and vegetation structure. Transitions are the pathways between states. Transitions are often triggered by natural or human-caused disturbances. Transitions may occur quickly, as with a fire or flood, or more slowly in response to repeated stress such as grazing or drought.

Oak-Woodland Vegetation Dynamics

Oak-woodland transitions are based on scientific literature and the experience of scientists and managers. While fire plays a major role in oak-woodland succession, life history traits of the oak-woodland vegetation contribute to the vegetation structure’s resistance to change and to the potential for multiple successional pathways.

Fire is a normal disturbance in California’s oak-woodlands. Cooper (1926) observed a coast live oak stand in Santa Clara County and concluded that an oak savanna requires disturbance and, in the absence of heavy grazing or frequent fires, live oaks and bird-dispersed shrubs will increase. Foothill pine and ceanothus shrubs have increased in an ungrazed (natural area) oak-woodland at the San Joaquin Experimental Range, which has not burned since 1929 (Woolfolk and Reppert 1963). In an extensive study of the relationship between vegetation type, substrate, and disturbance, Wells (1962) concluded the original vegetation of the San Luis Obispo area was broad-schlerophyll forest on all types of substratum. In his view, anthropogenically caused fires (starting with Native Americans and continuing with European settlers) and grazing eventually destroyed this forest, leading to the currently observed mosaic of grassland, shrubland, and forest (Hamilton 1997). According to Callaway and Davis (1993) California’s oak woodlands are in dynamic equilibrium with other plant associations, and depending on their location and disturbance regimes, they can be converted into grasslands as well as derived from coastal sage scrub and chaparral (Callaway and Davis 1993).

Life histories and life history traits of oak-woodland vegetation greatly influence the course of succession. Different rates of survival, tolerances to stresses and disturbance and abilities to compete lead to different community structures and rates of succession that result in the potential for multiple successional pathways, resulting in multiple stable states (Egler 1974; Drury and Nisbet 1973; Grime 1974, 1979; Connell and Slatyer 1977). The understory layer, dominated by annuals, produces a large, dense and diverse seed bank (Rice 1989a). Annually, some portion of the seedbank germinates and completes its life cycle in one growing season. Competition during germination, establishment and growth mediated by weather, microclimate and nutrients greatly influences the species composition of this layer and its competitive ability (Rice 1989b). The competitive ability of annuals for moisture and other resources contributed to the loss of the former native perennial understory and adjacent grassland. More recently, competition for soil moisture by annuals has been shown to be an important contributor to poor blue oak regeneration (Gordon and others 1989).

The tree layer is dominated by long-lived oaks (White 1966) that vary in their fire resistance and resprouting capacity (FEIS 2006). All produce acorns, often in pulses every several years. Germination and seedling survival to the sapling state are inhibited by the annual dominated understory (Gordon and others 1989, McCreary 2001). The shrub layer is characterized by two functional groups: 1) species that resprout from surviving sub-surface stems and roots following fire, and 2) species that are stimulated to germinate by fire or smoke. Resprouting species maintain live biomass below ground and recover rapidly following fire. Recovery is slower for non-resprouting species and depends on fire interval and the age of maturity. Species with fire-stimulated germination show a peak growth phase immediately following a fire and then a decrease in establishment and growth due to their low competitive ability (Pausas 1999).

Long-lived species provide the community with a great deal of inertia against vegetation change. Fire rejuvenates shrub stands. Without fire, the above ground portions of the shrub layer eventually become decadent and die. According to Hanes (1971), 60-year-old chamise and ceanothus stands are often decadent. Without fire for more than 70 years, ceanothus shrubs in the natural area at the San Joaquin Experimental Range are decadent and dying. The longevity of the below-ground portions of resprouting species is not known, but studies in Europe suggest that *Quercus ilex* root systems can be hundreds or thousands of years old (Pausas 1999). Consequently, establishment of long-lived species may not be related to current climatic conditions.

The oak-woodlands of California's coast range and Sierra Nevada foothills are often a mosaic of grassland, oak-woodland, and shrubland. California's central coast is dominated by a mosaic of grassland, oak-woodland, coastal sage scrub, and chaparral (Wells 1962, Griffin 1977, Heady 1977, Mooney 1977). In some locations, these mosaics have been correlated with geological substrate (Cole 1980) and soil characteristics (Harrison and others 1971). However, other researches have found each of these vegetation types on most soil depths, slopes, aspects and all geological substrates, suggesting that disturbance and/or biological factors are important determinants of the patchy distribution of these vegetation types on California's central coast (Wells 1962, Callaway and Davis 1991).

Oak-Woodland States

Methods

States describe alternative vegetation structures associated with an ecological site. To determine vegetation structures on oak-woodland ecological sites, vegetation was surveyed along 455 transects distributed on widespread soil series in Major Land Resource Areas (MLRA) 15 (294 transects) and 18 (161 transects) during the 2004 and 2005 growing seasons. These transects were 100 m in length and were used to determine understory productivity, canopy cover, and tree and shrub density.

To identify potential states, we examined species composition differences among the transects. For this purpose, we conducted non-metric multidimensional scaling (NMDS) with four ordination axes using R, version 2.2.1. A dissimilarity matrix using Manhattan distances was calculated from the species abundances in each transect. The distances in the ordination space represent community similarity (ter Braak 1995). The correspondence of the ordination diagram to the similarity distances is described by a stress value where 0 is a perfect fit (Kneitel and Chase 2004). The result for the four ordination axes was used to generate the cluster of vegetation types. The cluster analysis was conducted in JMP IN 5.1.

Results

Woody species were found in 267 of the 455 transects, and were grouped in 15 clusters. From a total of 54 woody species, only 14 were present in more than 10 transects: *Adenostoma fasciculatum, Aesculus californica, Arctostaphylos sp., Baccharis pilularis, Ceanothus cuneatus, Pinus sabiniana, Quercus agrifolia, Quercus douglasi, Quercus garryana, Quercus kellogii, Quercus lobata, Quercus wislizenii, Toxicodendron diversilobum, and Umbellularia californica*. The 15 clusters were classified into 11 oak classes (Allen-Diaz 1989): 1) Blue-Oak/Grass 2) Blue Oak-Interior Live Oak/Grass, 3)Blue Oak-Coast Live Oak/Grass, 4) Interior Live Oak-Blue Oak-Foothill Pine, 5) Coast Live Oak-Blue Oak/Grass, 6) Coast Live Oak/Sagebrush/Grass, 7)Coast Live Oak-California Bay/Toyon-Scrub Oak, 8) Valley Oak-Grass, 9) Valley Oak-Coast Live Oak/Grass, 10)Mixed Oak/Grass, and 11)Mixed Oak-Black Oak/Grass. These classes will be used to describe potential vegetation states in the oak woodlands.

Oak-Woodland States and Transitions: An Example

Models currently being developed describe the states and transitions of fire-adapted oak-woodland communities (Appendix A). Under normal fire regimes, we expect the tree layer (oaks and other species) to survive the fire more or less intact. It is the shrub and herbaceous layer that is most affected by the fire. In this situation, we expect a post fire succession in which some annuals rapidly germinate, establish and dominate much of the understory, setting seed and completing their life cycle as the dry season begins. Shrub replacement is a slower process. While resprouting shrubs may rapidly re-occupy the site, shrubs with seeds that are stimulated to germinate by fire, such as many species of ceanothus and manzanita, will require several years to re-dominate former patches or form new patches. In the state and transition models, this sequence is the normal or reference state for several oak-woodland ecological sites. Under catastrophic fire associated with long fire return intervals this normal sequence may be altered in several ways. One or more oak species may be lost or substantially reduced on the site. The seed bank may be reduced by the fire. In the extreme, this may result in loss of trees or shrubs or a slower recovery.

Following a fire, oak-woodland communities are characterized by standing live plants and by a seed bank/vegetative bud bank of species that survived the fire. This species composition is augmented by migration of propagules from adjacent undisturbed areas. The species represented in the seed/bud bank are characterized by different growth rates, different live histories and different longevities. Functionally, many of these species are annual herbaceous grasses and forbs that complete their life cycle in one year; some are shrubs that resprout while others have deposited seeds that are stimulated to germinate by heat. Most oak trees resprout following fire and all produce seeds (acorns).

Following fire, complex species interactions on variable soil and geologic substrates may result in the mosaic of vegetation types. Callaway and D'Antonio (1991) found that seedlings of coast live oak were spatially associated with shrub communities, and that survival of seedlings was improved by shrub cover. They suggested that a sequence of nurse plant facilitation and oak-shrub competition may affect patterns and boundaries of these communities. Chaparral species have been reported to out-compete coast sage scrub species for light and to replace them successionally (McPherson and Muller 1967, Hanes 1971, Gray 1983). Coastal sage scrub and chaparral shrubs suppress grass species (Muller and del Moral 1966, Bartholomew 1970, Halligan 1976), and some of the same grass species suppress growth of oak seedlings (Gordon and others 1989). These types of biological interactions, acting in concert with natural disturbance, and variation in topography and substrate, may produce complex transitional changes among community mosaics along the central coast of California.

While fire has an immediate and sometimes catastrophic effect on oak-woodland communities, grazing effects are slow and relentless. In a few studies that compare post fire recovery with and without livestock or deer grazing/browsing, recovery is slower when grazers/browsers are present (McBride and Heady 1968, Johnson and Fitzhugh 1990, Callaway and Davis 1993).

Besides changing fire intervals, managers can alter the course of succession through the practices that they apply. Type conversions in which woody plants were permanently removed using mechanical and chemical controls are the extreme case in which woodlands have been converted to grasslands. Firewood cutting can also convert woodland to a savanna or grassland. Frequent fire (short return intervals) and goat grazing can effectively remove shrubs from the shrub layer, producing an oak-savanna. Sometimes these changes are irreversible, resulting in new pathways of change and new stable states.

Research Needs

There is a great deal about oak-woodland vegetation dynamics that is not known. Life histories and life history traits are poorly known. Competition is a major driver of changes in vegetation structure but has not been adequately studied. How will these plant communities respond to long-term fire suppression, climate change, and biological invasions? What are the transitions that lead to conversions between grasslands, shrublands, savannas, and woodlands. What are the rates of these transitions. At what thresholds are these transitions no longer reversible? There are many questions.

Studies of vegetation change involve indirect and direct methods. Indirect methods involve inference of successional patterns based on data or observations taken at a single time during a successional sequence. For communities with long-lived species, this is often the method of choice.

Direct methods of study are based on observation of succession on permanent plots or through the use of historical documents that give details of former vegetation. Direct observation and study of succession in plant communities that include long-lived species is an intergenerational endeavor. Thus there is a need to initiate and maintain long-term studies of vegetation change in California's oak-woodlands and associated communities. The Vegetation Type Mapping (VTM) plots initiated by Weislander in the 1920s and recently cataloged by Kelly and others (2005) represent a unique opportunity to estimate vegetation change over the last century.

The results of this project will be incorporated into ecological site descriptions and, following peer review, will become part of the Ecological Site Information System (http://esis.sc.egov.usda.gov) maintained by USDA Natural Resources Conservation Service.

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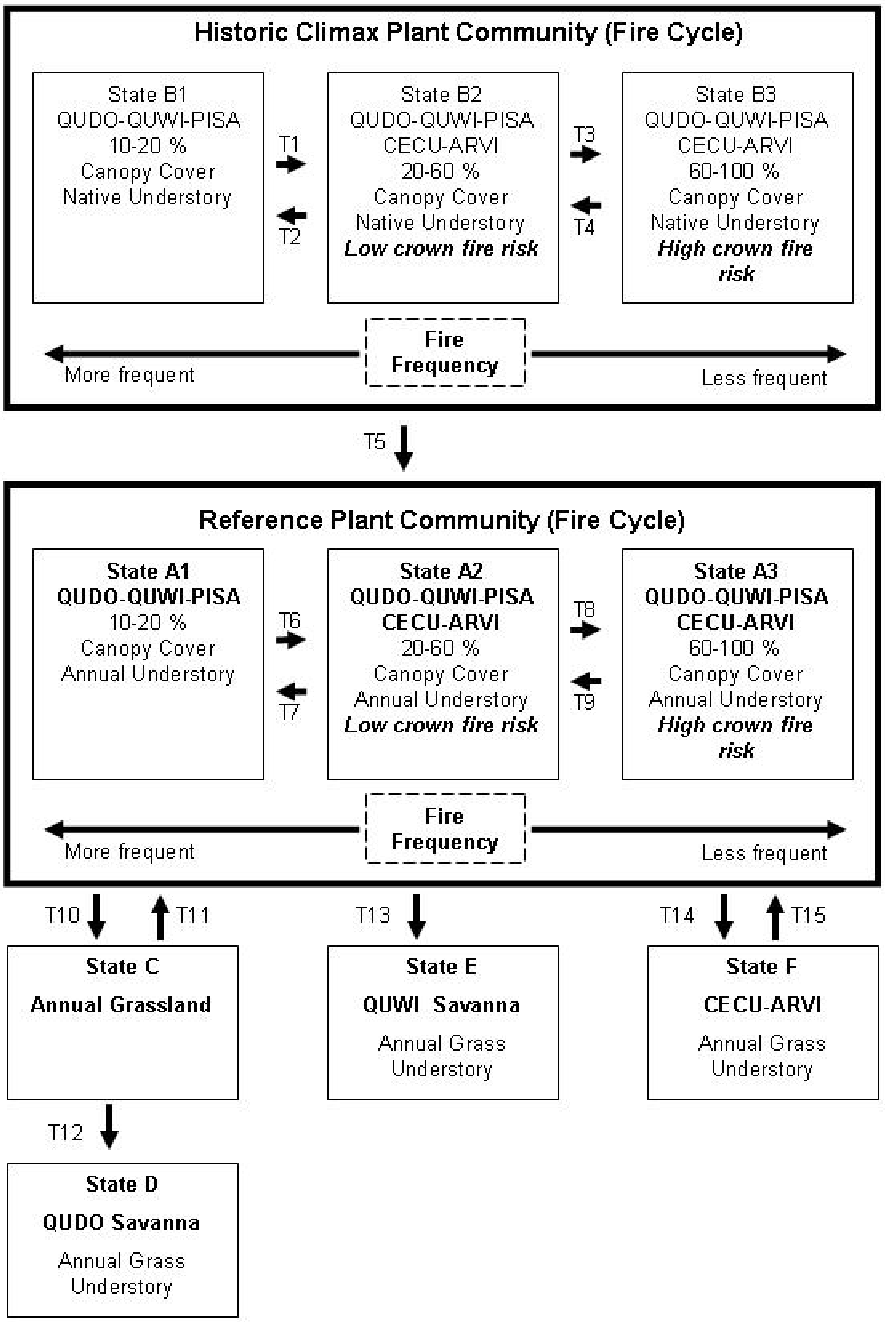
Appendix A.

State and Transition Model for the woody layers of a granitic soil



State Descriptions

State A1: Savanna community (10 – 20 percent canopy cover) consisting of a blue oak, interior live oak, and foothill pine tree layer and few or no shrubs. Blue oaks are fire resistant and evolved under low-severity grassland fires. Interior live oak is sensitive to fire but resprouts vigorously following most fires. Foothill pine is sensitive to moderate or intense fires but is increasing due to fire suppression. Ceanothus and manzanita seeds germinate following fires. Understory is generally dominated by annual grasses and forbs of Eurasian origin. Allen Class: Blue Oak-Interior Live Oak/grass.

State A2: Savanna community (20 – 60 percent canopy cover). Allen Class: Blue Oak-Foothill Pine/Whiteleaf Manzanita/Grass or Blue Oak-Foothill Pine/Wedgeleaf Ceanothus/Grass.

State A3: Woodland community (canopy cover >60 percent). Allen Class: Blue Oak-Foothill Pine/Whiteleaf Manzanita/Grass or Blue Oak-Foothill Pine/Wedgeleaf Ceanothus/Grass.

States B1, B2, and B3: Historic climax plant community assumed to consist of tree and shrub layers similar to those in State A. Perennial-dominated understory species composition is not known. States B1, B2 and B3 assume that native annual and perennial grasses and forbs were common in the understory of the tree and shrub layer of these oak-woodland ecosystems.

State C: Annual grass- and forb-dominated grassland. Soil quality, especially fertility, declines following tree removal.

State D: Blue oak savanna. Artificially regenerated oak woodland with an annual grass understory. Allen Class: Blue Oak/Grass or Blue Oak-Understory Blue Oak/Grass.

State E: Live oak savanna. Live Oak dominated savanna. Allen Class: Live Oak/Grass

State F: Ceanothus and/or manzanita chaparral.

Transition Descriptions

T1-State B1 to State B2: Under natural fire frequencies shrub and tree canopy cover increases toward State B2 following fire.

T2-State B2 to State B1: Natural fire frequencies estimated to be 25 years; maintains an oak savanna with a few shrubs and an herbaceous understory. More frequent burning can result in a savanna free of shrubs and understory trees. Application of mechanical and/or chemical brush control practices can result in a similar transition.

T3-State B2 to State B3: Prolonged periods without fire result in increased shrub and tree canopy cover to the point where the savanna is classified as woodland. Increasing ladder fuels increase the chances of a high intensity crown fire.

T4-State B3 to State B1 or B2: Burning woodlands with dense shrub layers results in removal of most shrub and understory tree canopy. In extreme cases, this transition could return from State B3 to State B1. Implementation of mechanical or chemical brush control practices can result in a similar transition.

T5-State B to State A: Invasion by exotic annual species, yearlong continuous grazing, drought, fire suppression and cultivation reduced or destroyed the native perennial grass and forb component of the historic climax plant community. Apparently an irreversible transition in a time frame relevant to management. Restoration of native perennial herbaceous vegetation is a recurring management objective that has been largely unsuccessful. Researchers, managers and citizens groups have been unsuccessful at reversing the loss of native perennial grasses. Competition from invasive annuals and long dry summers apparently are insurmountable. Annual grasses and forbs are more competitive for soil moisture than native perennials reducing oak seedling survival (Gordon and others 1989)

T6-State A1 to A2: Same as T1

T7-State A2 to A1: Same as T2

T8-State A2 to A3: Same as T3

T9-State A3 to A1 or A2: Same as T4

T10-State A to State C (Type conversion from woodland to grassland): Use of mechanical and chemical tree and shrub control and prescribed burning remove all trees and shrubs resulting in a conversion from woodland to annual grassland. In some cases, this transition may be irreversible without artificial regeneration of native woody species, especially if frequent fires and grazing suppress seedlings of woody species. Seeding and fertilization often accompanied tree and shrub control. At low-canopy covers, fire or natural mortality could remove woody species and conditions for resprouting or acorn germination and seedling establishment may be unfavorable.

T11-State C to State A: Recovery from grassland conversions may take decades or may be irreversible depending on the intensity and type of brush control practices. Repeated fires and grazing help to maintain the grassland. Blue oaks and other woody plants may colonize adjacent open grasslands but seedlings are seldom found more than 30 m from existing tree canopy.

T12-State C to State D: Planting, weed control, and protection of blue oak seedlings from animal damage can successfully restore blue oaks (McCreary 2001).

T13-State A to State E: Intense fire, wood cutting or vegetation management kills blue oaks and they do not resprout due to old age (Burns and Honkala 1990) or site conditions (DeLasaux and Pillsbury 1987; Haggerty 1991). Interior live oaks are top killed but resprout vigorously. With fire protection shrubs gradually increase producing a State similar to a but without blue oak.

T14-State A to F: Intense fire kills all trees and they do not regenerate (Haggerty 1991). Manzanita and/or Ceanothus reestablish from seed producing patches of shrubs mixed with open grassland.

T15-State F to A: On deeper soils with better moisture holding capacity interior live oak and/or blue oak regenerate from acorns that germinate under canopy of shrubs (Callaway and D'Antonio 1991; Muick 1997). This is a slow successional process.

Continue