

# FIRE AND INVASIVE SPECIES IN MEDITERRANEAN-CLIMATE ECOSYSTEMS OF CALIFORNIA

Jon E. Keeley

U.S. Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon National Parks, Three Rivers, CA 93271 and Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles, CA 90095

## ABSTRACT

Within the Mediterranean-climate region of California and adjacent regions, invasive plants are largely concentrated in the lower-elevation valleys and foothills. Fire has historically been an important part of the ecology of many of these ecosystems; however, anthropogenic disruptions of natural fire regimes have contributed to the widespread invasion of certain communities. Throughout the Coast Ranges and foothills of the Sierra Nevada and Cascades, high fire frequency has contributed to the type-conversion of shrublands and closed woodlands to annual grasslands dominated by alien grasses and forbs of Mediterranean Basin origin. Returning these landscapes to their former closed-canopy state is the only likely means of reducing the presence of nonnatives. Valleys and other sites with deeper clay soils, which formerly were perennial grasslands, also have been type-converted to nonnative annual grasslands by intensive grazing and plowing. There is evidence that spring burning may be an appropriate management tactic for shifting the balance away from the annual alien grasses towards increased native cover, but only on sites with an existing perennial bunchgrass presence. This tactic, however, may not be an appropriate community restoration technique because it inhibits native annuals as well. Currently, the vast majority of grasslands in the state lack native bunchgrass, and on these sites different burning prescriptions may alter species composition; however, there is no convincing demonstration that fire alone is an effective technique for diminishing the dominance by nonnative annuals. Prescription burning is increasingly used to control invasion of particularly noxious weeds that are typically targeted because they alter the functioning of ecosystems, e.g., making rangelands unpalatable to livestock or wildlife. Such use of prescription burning may enhance resource benefits for some stakeholders, but generally burning of annual grasslands does not greatly alter the native to nonnative composition, unless accompanied by active native plant restoration.

Several aspects of current fire management practice may contribute to the increase in alien plants. Limited success in fire prevention is 1 key element because increasing population density has continued to add fire on the landscape, and this has contributed to continued type-conversion from native woody vegetation to nonnative herbaceous associations. Pre-fire fuel manipulations may likewise contribute to this trend; for example, use of prescription burning on sites that currently have higher than natural fire frequencies potentially favors aliens. Also, fuel breaks may act as invasive highways carrying alien species into uninfested wildland areas. Following fire, the reduced fuels in fuel breaks contribute to enhanced survivorship of alien seed banks, resulting in source populations poised for invasion of adjacent burned sites. Post-fire site "rehabilitation" is responsible for widespread introduction of alien species at a time when elevated soil nutrients may favor aliens over natives. Of most concern is the potential for these aliens to alter fuels in a way that increases fire frequency, which further increases expansion of aliens.

*keywords:* aliens, annuals, California Floristic Province, exotics, fire management, fuels, Native Americans, niche construction, restoration, type-conversion.

*Citation:* Keeley, J.E. 2001. Fire and invasive species in Mediterranean-climate ecosystems of California. Pages 81–94 in K.E.M. Galley and T.P. Wilson (eds.). Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.

## INTRODUCTION

The Mediterranean-climate region of North America is commonly delineated as the area to the west of the Great Basin, and the Mojave and Colorado deserts, running from southern Oregon to northern Baja California. Botanically this region is known as the California Floristic Province and comprises a vascular plant flora in excess of 4,400 species, nearly half of which are endemic (Raven and Axelrod 1978). Within this region approximately 25% of the plant species are nonnative (Rundel 2000), which is higher than the proportion for California as a whole (Hickman 1993). Nonnative plants are considered those species not present prior to the European colonization, which began in earnest during the late 18th century. In the literature they have been variously termed non-indigenous, exotics, aliens, adventives, invasives, naturalized, envi-

ronmental weeds, residents, and new-natives. They include many widespread firmly established species maintaining persistent populations as well as recent introductions of localized occurrence. Over the last 150 years the exponential increase in exotic plants has paralleled the increase in human population growth in California (Randall et al. 1998). Here I review the role that fire has played in the establishment and spread of these invasive plants within the California Floristic Province and consider the extent to which current fire management practices enhance or inhibit their spread.

## INVASIVE DISTRIBUTION

The California Floristic Province comprises a topographically heterogeneous region with a great diversity of vegetation types and high  $\beta$ -diversity (Richerson and Lum 1980, Cody 1986). Alien species are

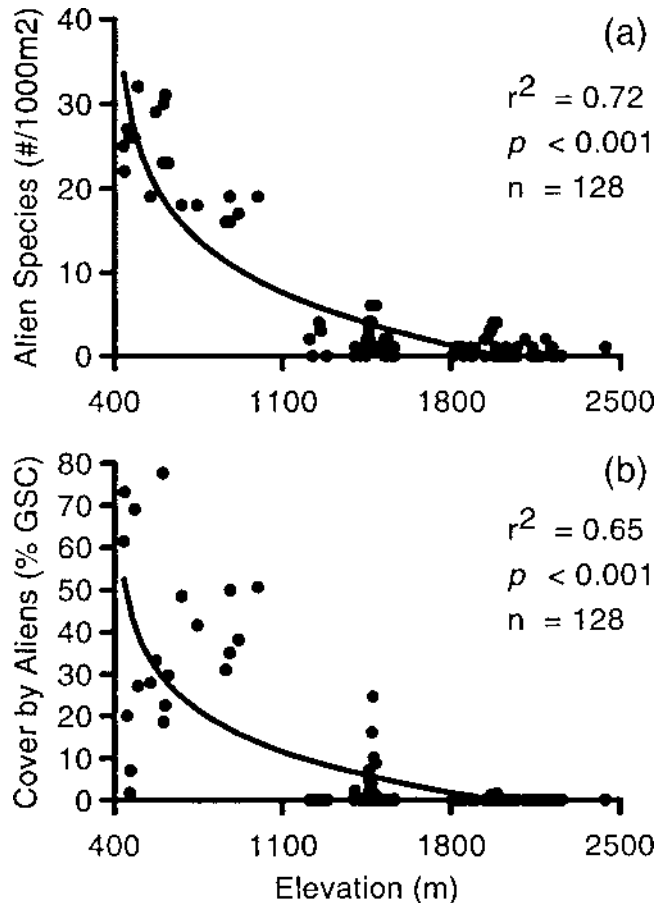


Fig. 1. Alien plant species richness (a) and cover (b) of alien vascular plants in Sequoia-Kings Canyon national parks in the southern Sierra Nevada Mountains, California (J.E. Keeley, D. Lubin, and C.J. Fotheringham, unpublished data from 1999 to 2000).

not randomly distributed across this region. Only 20% are distributed throughout the California Floristic Province and 33% are restricted to just a few of the 35 geographic subdivisions as defined in the Jepson Manual (Randall et al. 1998). Elevationally, exotics are clearly more dominant, both in numbers of species (Figure 1a) and dominance (Figure 1b) at lower elevations. This pattern has been noted (e.g., Mooney et al. 1986, Schwartz et al. 1996, Randall et al. 1998), but limited attention has been given to the factors influencing this relationship. Along this gradient (Figure 1), covariates with increasing elevation include greater dominance by woody vegetation and consequent decrease in light levels at the soil surface, reduced growing season, decrease in the potential propagule source, and decrease in the frequency and intensity of past and present human disturbance.

Past and present human activities may explain some of this elevational pattern (Figure 1). The majority of invasive species in California have their origins in the Mediterranean Basin, including southern Europe, North Africa, and Eurasia (Shmida 1981, Baker 1989, Fox 1990, Reichard 1997), where they potentially have been in association with anthropogenically altered landscapes through a significant portion of the

Holocene (Baker 1974, Pignatelli 1983, Stevenson 1985, Naveh and Kutiel 1986, Trabaud and Casal 1989, Le Floch et al. 1990, Atherden and Hall 1999, Magri and Sadori 1999). Valleys and foothills in the Old World have had the longest history of intensive land use and present the greatest opportunity for co-evolution with human-perturbed landscapes (e.g., evolutionary patterns in annual species of *Bromus* discussed by Sales 1994). In California, these valley and foothill habitats were also those most immediately and thoroughly exploited by Europeans, creating favorable sites for the establishment of exotics pre-adapted to such disturbed landscapes.

Anthropogenic landscapes commonly have undergone conversion from closed-canopy woody vegetation to open herbaceous associations. In the Mediterranean Basin such agro-pastoral environments are dominated by annual species, often with extraordinary levels of diversity. For example, undisturbed matorral in the eastern Mediterranean Basin typically have 40–50 species/0.1 ha, whereas degraded shrublands, created and maintained by burning and grazing, have diversity levels 2 to 3 times higher, largely from native annual grasses and forbs (Naveh and Whittaker 1979). A similar agro-pastoral history and biodiversity patterns are evident in the western part of the basin as well (Verdú et al. 2000). Thus, it is not surprising that undisturbed closed-canopy shrublands in California are relatively immune to serious plant invasion (Knops et al. 1995, Stromberg and Griffin 1996, Allen 1999; but compare D'Antonio and Mahall 1991). On the other hand, disturbed landscapes in California are readily invaded by Mediterranean annuals, which comprise nearly 60% of the California alien flora (Raven 1977). Even the woody invasive elements in California (e.g., *Cytisus*, *Genista*, and *Ulex*) are disturbance-dependent heliophytic taxa, in both California and their native region, the Mediterranean Basin (Bossard et al. 2000, Valderrábano and Torrano 2000).

## FIRE AS A HISTORICAL FACTOR IN THE INVASION PROCESS

Some of the most widespread nonnative grasses and forbs began the invasion process from propagules left by Cortez and other explorers who first visited the California coastline during the 16th century (Hendry 1934). These species encountered an environment conducive to rapid spread because of the climatic similarity between coastal California and the Mediterranean Basin (Blumler 1984). Although the Mission Period began in 1769, it was not until a decade later that the livestock industry made the California missions economically independent (Burcham 1957). Livestock brought overland from Mexico likely contributed to the introduction of new invasives and certainly played an important role in promoting the establishment and spread of invasives. It is widely accepted that overstocking of native prairies, coupled with drought, caused the widespread replacement of perennial bunchgrasses with exotic annuals (Heady 1977, Heady

et al. 1992), a model most applicable to the Sacramento Valley and northern California. There are, however, many remnants of native bunchgrass prairie that have survived grazing; on some sites, plowing seems to have been the primary determinant as to whether or not these native grasses survived (Kellogg and Kellogg 1990, Stromberg and Griffin 1996).

Alternatively, invasion of native perennial grasslands may have been an inevitable feature of history because climatic changes since the end of Pleistocene have favored annuals (Raven and Axelrod 1978). The California flora is poor in native annual grasses, and all seem to be weak competitors against European annuals. Relative to this are the observations by Veblen (1975) of the remarkable similarity in alien weed floras between California and the highlands of Guatemala. He hypothesized that less severe drought in the latter region was an important factor preventing displacement of their native bunchgrass association. The continued persistence of bunchgrasses in the Palouse Prairie of the less arid eastern Washington, despite a long history of intensive grazing, would seem to support this hypothesis. Thus, the increasing aridity of the Holocene could stand as one of the more important factors driving the massive invasion of annual grasses and forbs in the California Floristic Province, and in particular the displacement of the native bunchgrass prairie.

Fire may have been an important factor in the early invasion process as the Native American populations along the coast apparently utilized fire to type-convert less productive shrublands to herbaceous associations (Knowles 1953, Bean and Lawton 1973, Lewis 1973, Timbrook et al. 1982). The exceptionally high density of Native Americans had the potential (and the motive) to type-convert a significant portion of the shrublands (J.E. Keeley, unpublished). Consequently, the European plant invaders likely arrived upon a disturbed shrubland landscape in which the competitive balance already had shifted towards the annual habit. This would have contributed to the extraordinary rapidity with which European weeds spread across the California landscape during the early 19th century (Frenkel 1970).

There is evidence that throughout the coastal ranges of central and southern California much of the exotic annual grassland association derives from fire-induced type conversion of shrublands (Cooper 1922, Wells 1962, Huenneke 1989, Keeley 1990, Hamilton 1997). European settlers continued this process initiated by Indians and, as the pressure for rangeland increased, Americans applied this practice on an even greater scale (Brown and Show 1944). This process of type-converting native shrubland to exotic weed fields (Figure 2) was formalized during the 1940s with the issuance by the California Division of Forestry of burning permits for rangeland improvement of chaparral (California Division of Forestry 1978, Heady and Pitt 1979).

Alien annuals also dominate many sites that originally were neither native grassland nor native shrubland, but rather native annual associations, e.g., the



Fig. 2. Vegetation mosaic in the coastal ranges of California (photo by J.E. Keeley).

interior Coast Ranges and the San Joaquin Valley (Hoover 1936, Wester 1981, Schiffman 2000).

Distinguishing between these alternative origins is critical to successful restoration of alien-dominated annual grasslands (Keeley 1993). Today, grasslands cover 3.4 million ha in California, the vast majority of which are dominated by nonnative annual grasses and forbs (Jones & Stokes Associates 1987). Many of the grasses—e.g., *Avena fatua*, *A. barbata*, *Bromus madritensis*, *B. diandrus*, *B. hordeaceus*—and forbs—e.g., *Erodium cicutarium* and *Brassica nigra*—are so widespread, there is little likelihood of eliminating them from the flora (Heady 1977). These exotic grassland associations are often considered to represent a new stable equilibrium association (Heady et al. 1992); however, they are also the sites of greatest vulnerability to newly introduced exotics (Bossard et al. 2000).

## FIRE MANAGEMENT AND THE INVASION PROCESS

The invasion process is affected by: (1) the extent to which fires and fire management practices encourage the further establishment and spread of alien species, and (2) the degree to which such practices inhibit or even reverse the process. In addressing these questions it needs to be acknowledged that the database comprises many case studies that are pseudo-replicated at best; thus, an unknown level of error is associated with these generalizations.

### Direct Fire Effects

The California Floristic Province is dominated by landscapes with very different anthropogenic influences on fire regimes. In the higher-elevation coniferous forests, fires have become less frequent, whereas in the valleys and foothills fire frequency has increased over the frequency naturally experienced by these ecosystems.

In the montane coniferous forests, fire suppression during most of the last century has been highly successful in bringing about the near total exclusion of



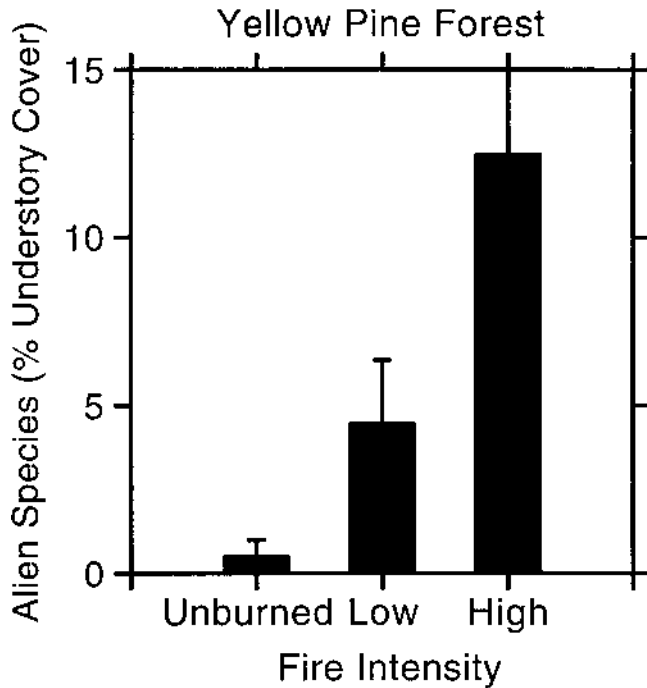


Fig. 3. Alien plant cover (as percentage of understory cover) for yellow pine forests in Sequoia and Kings Canyon national parks, in stands unburned for more than 30 years (Unburned), burned within the past several years in low intensity fires (Low), or high intensity fires (High). (From J.E. Keeley, D. Lubin, and C.J. Fotheringham, unpublished data from 1999 to 2000.)

fire from the bulk of the landscape (Skinner and Chang 1996, Stephenson 1999). Two factors account for this pattern: (1) understory fuel characteristics promote low-intensity surface fires, which make fires more tractable to suppression; and, (2) lightning, which is the primary source of ignition, generally occurs during conditions that favors suppression. Today an unnaturally large portion of the montane landscape has remained unburned for a century or more. This has likely inhibited alien plant invasion because closed-canopy forests are not generally favorable sites for invasive plants (Rejmánek 1989). Reintroduction of fire is likely to promote the establishment of alien species, particularly in gaps resulting from patches of high fire intensity (Figure 3). While gap formation is a natural and necessary feature of these forests, the long hiatus of burning due to fire suppression has put much of this landscape on a new trajectory leading toward high-intensity crown fires and massive landscape scale gaps (Keeley and Stephenson 2000). Changes in landscape patterns of burning may greatly affect the invasion process by altering the amount of perimeter area contributing to alien colonization (Turner et al. 1997).

In contrast to montane forests, foothill shrublands and woodlands in the coastal ranges of southern and central California have had an extraordinary increase in fire frequency during the 20th century (Keeley et al. 1999, Keeley and Fotheringham in press), directly paralleling the increase in population (Figure 4). This increased fire frequency has very likely favored invasion by nonnative plants.

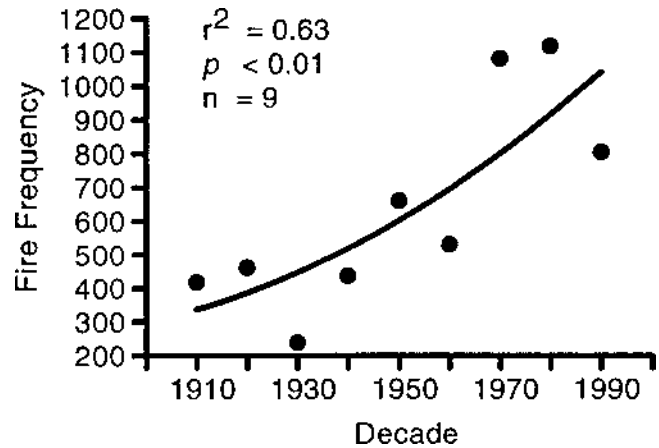


Fig. 4. Relative frequency of fires larger than 40 ha in southern California counties during most of the 20th century. (Data from the California Department of Forestry, Fire and Resource Assessment Program, Sacramento, CA.)

On the surface it may seem counter-intuitive that fire would make fire-prone chaparral more susceptible to invasion, but plant species evolve not in association with fire per se, but with a particular fire regime. When the natural fire regime is altered, even highly fire-adapted plant communities may be vulnerable to alien competition. Plant life histories are often fine-tuned to a particular regime of fire frequency, intensity and seasonal distribution (Keeley 1986). For example, in chaparral many shrub species lack vegetative regeneration and recruit strictly from seedlings after fires at multi-decadal intervals, but are extirpated when fires occur more than once or twice per decade (Zedler 1995, Fabritius and Davis 2000, Keeley 2000). Even facultatively seeding species, such as the widespread chamise (*Adenostoma fasciculatum*), suffer in the face of frequent fires (Haidinger and Keeley 1993). Repeat fires close together in time deplete the chamise resprout population as well as the seedling population (Figure 5). Chaparral has a rich annual flora that spends most of its existence as a dormant soil seed bank until germination is triggered by fire (Keeley 2000). Some are specialized to the first post-fire year and others are more opportunistic, but most remain as dormant seed banks when the shrub canopy reestablishes. Despite being disturbance dependent, these native annual forbs are quickly replaced by nonnative annual grasses and forbs under high fire frequency.

In summary, herbaceous growth forms, annuals in particular, are resilient to higher fire frequencies than woody growth forms (Sampson 1944, Wells 1962) and nonnative annuals are more resilient to higher disturbance frequencies than native annuals. Intact shrublands are largely devoid of nonnative species (Knops et al. 1995, Stromberg and Griffin 1996, Allen 1999). Reasons for this include the fact that the closed canopy makes for very limited seedling recruitment opportunities (DeSimone and Zedler 1999, Keeley 2000). Indeed, this may generally be a factor reducing the invasibility of closed-canopy vegetation (Rejmánek 1989). Most chaparral species recruit during a very narrow window of time following fire. Invasion re-

FIRE AND INVASIVE SPECIES IN CALIFORNIA ECOSYSTEMS

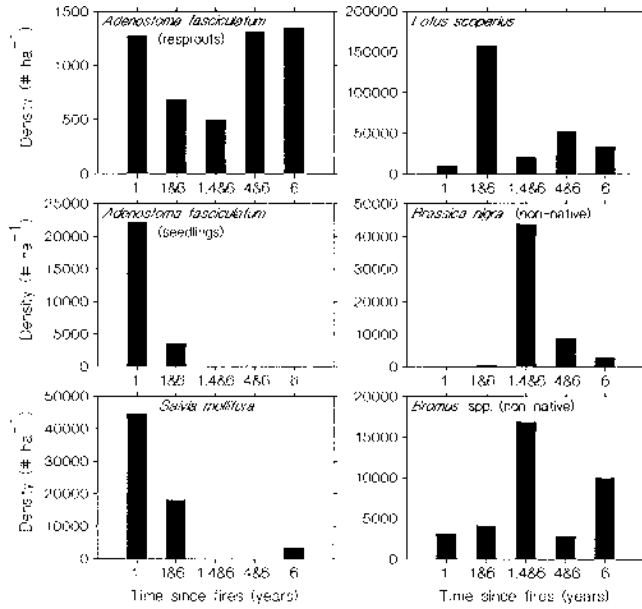


Fig. 5. Percentage ground surface covered by the dominant native shrub *Adenostoma fasciculatum*, the native subshrub *Salvia mellifera*, the native suffrutescent *Lotus scoparius*, the non-native grass *Bromus madritensis*, and the nonnative forb *Brasica nigra* in a control plot unburned for >30 years (Con), and adjacent sites burned 1 year; 1 and 6 years; 1, 4, and 6 years prior to study (from Haidinger and Keeley 1993).

quires a source of propagules precisely timed to the post-fire conditions. When exotic propagules are present at the time of fire their populations may expand (Zedler and Scheid 1988). As fire frequency increases, the canopy thins out and the sites available for non-natives increases (Figure 5). Thus, following fire, the extent of invasive plant success is closely linked to the rate of native shrub recovery (Figure 6). As fire frequency increases, exotics become more important in terms of species richness (Figure 7a) and dominance (Figure 7b). If fire is combined with grazing the pattern is exacerbated towards even greater alien invasion (Murphy and Leonard 1974).

Increased fire frequency coincident with urban expansion in most of the foothills and valleys of California (Keeley et al. 1999, Keeley and Fotheringham 2001) carries with it the propensity for type-conversion of shrublands to herbaceous communities dominated by nonnative annual grasses and forbs. Herbaceous communities due to anthropogenic burning (Cooper 1922, Wells 1962) have long dominated some landscapes that would naturally support woody vegetation. As discussed earlier, Indians may have played a role in type converting these woody associations to herbaceous vegetation. Mexican and American settlers continued intensive land use with fire and livestock grazing, but in recent decades grazing has been eliminated and anthropogenic fires reduced so that now woody vegetation is reestablishing (McBride 1974, Hobbs and Mooney 1986, Freudenberger et al. 1987). Along with the native shrubs we find European shrubs such as *Cytisus scoparius*, *Genista monspessulana*, and *Ulex europaea* colonizing these formerly disturbed

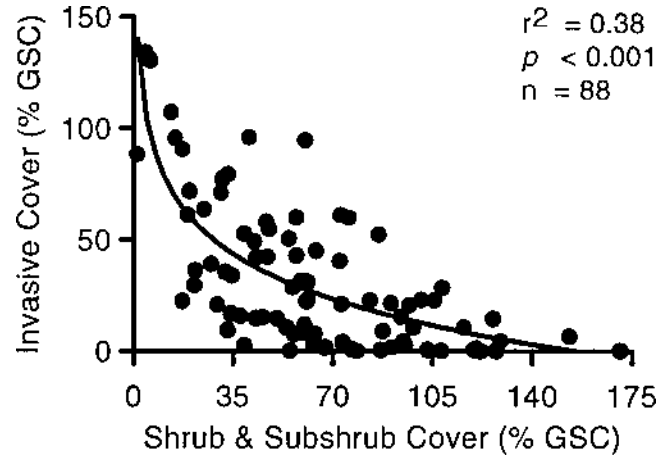


Fig. 6. Invasive plant species cover (percentage ground surface covered) relative to the shrub and subshrub cover 5 years after wildfire at 88 sites distributed across southern California (J.E. Keeley, M.B. Keeley, and C.J. Fotheringham, unpublished data from 1993 to 1998).

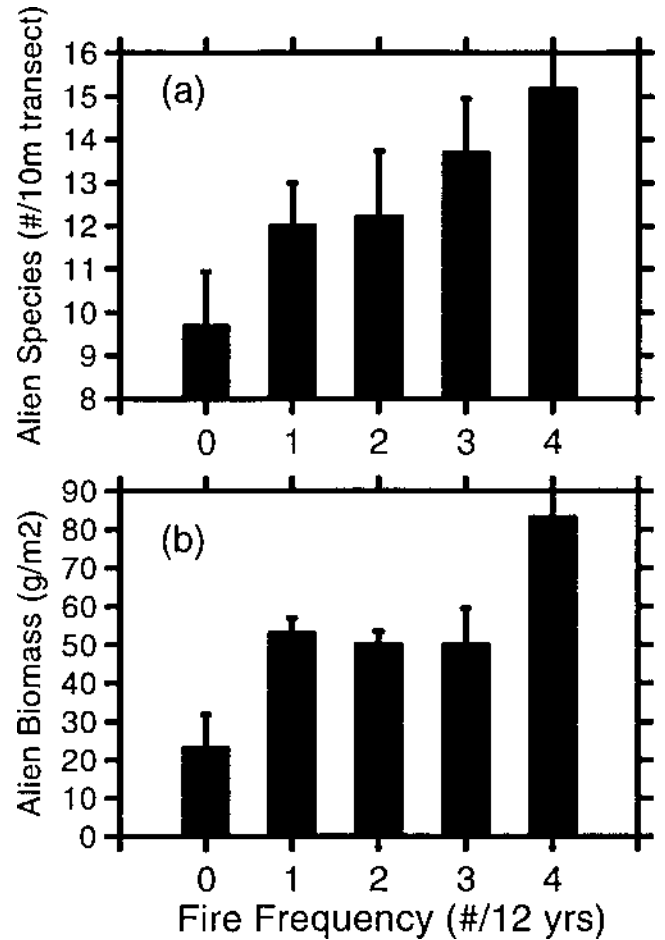


Fig. 7. Alien species richness (a) and dry biomass (b) in southern California coastal sage scrub burned 0, 1, 2, 3, or 4 times during 12 years (from Giessow and Zedler 1997).

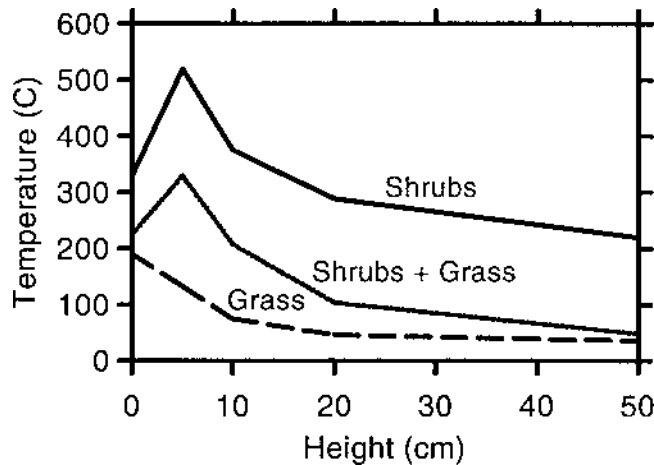


Fig. 8. Fire temperature (°C) reached under different combinations of shrubs (heavy fuels), shrubs + grasses (moderate fuels) or grasses (light fuels; redrawn from Smith and Sparling 1966).

sites (Bossard et al. 2000), in a manner similar to the recolonization of abandoned pastures and other degraded shrublands, in Spain and adjacent countries (Debussche et al. 1980, Fernández-Santos et al. 1999). Exotic shrub colonization of grasslands may decrease the incidence of fires (D'Antonio 2000) but invariably the enhanced fuel loads may exacerbate the fire hazard situation (Bossard et al. 2000, Valderrábano and Torrano 2000).

**Fire, Invasives, and Niche Construction**

Organisms often modify their environment in ways that may ultimately enhance their success, a process termed niche construction (Odling-Smee et al. 1996). Increasing flammability of stems and leaves is one means of niche construction whereby fire-dependent species are proposed to have characteristics selected for their propensity to ignite and carry fire (Mutch 1970, Bond and Midgley 1995, Keeley and Bond 1999, Kerr et al. 1999). Alien grasses that invade woody associations often have characteristics that alter the fire regime in ways that favor aliens over the indigenous vegetation (D'Antonio and Vitousek 1992). It is possible the fire-enhancing characteristics of California's alien grasses were selected as a means of furthering the success of these annuals since they originated in fire-prone habitats of the Mediterranean Basin (Baker 1974, Naveh 1975). Regardless of the selective basis, in their new setting these alien annuals succeed in part because of their propensity to shift the fire regime away from one that favors shrub reestablishment to one that favors further annual establishment.

The phenomenon of niche construction and alteration of disturbance regimes to favor invasive species is apparently quite wide spread (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998), although systems differ significantly in the mechanism of alien-altered fire regimes. In the well-studied Hawaiian ecosystems, fire-prone grasses invade mesic forests and increase both fire frequency and fire intensity, which

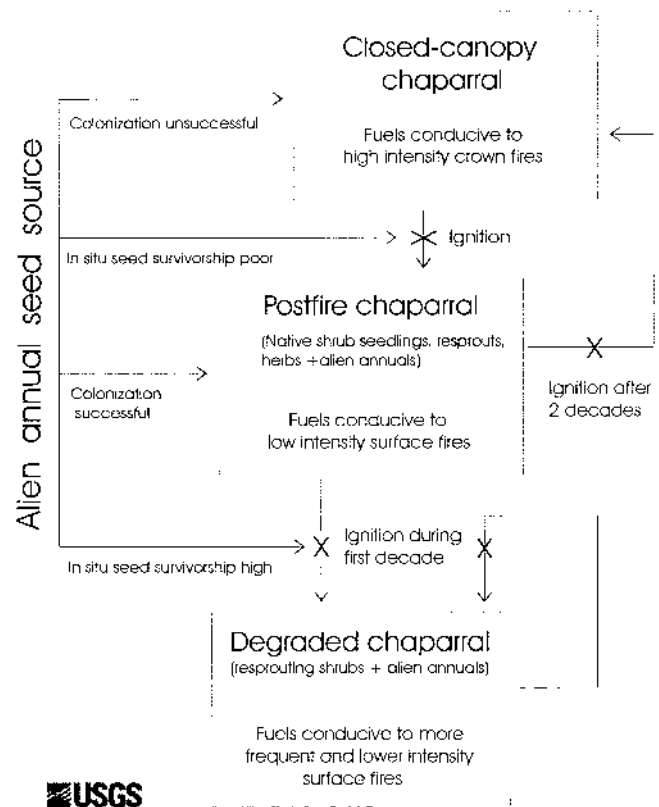


Fig. 9. Schematic diagram of how rate of fire ignitions in chaparral affects and alien invasion and how alien invasions affect fuel loads that increase the changes of fire frequencies favorable to further invasion.

directly favors their establishment over the native forest (D'Antonio 2000). A similar positive feedback is observed with the colonization of Mediterranean Basin woodlands by a native bunchgrass that favors repeat fires and maintains a fuel structure that inhibits survivorship of tree seedlings (Vilá et al. 2001). In contrast, in fire-prone shrublands, annual grass invasion shifts the fire regime towards one of lower-intensity fires (Figure 8), and this has profound impacts on alien persistence (Figure 9). Not only do alien annuals increase fire frequency, which in turn reduces shrub dominance, but as annual dominance increases, fire intensity declines, which enhances the survivorship of alien propagules. In general, it appears that the factors determining how invasive grasses affect natural ecosystems are tied to growth form of the invasive (i.e., annual vs. perennial bunchgrass) and fuel characteristics of the native ligneous vegetation.

*The Chaparral Model*

California chaparral is resilient to alien plant invasions (Knops et al. 1995, Stromberg and Griffin 1996, Allen 1999), even with close proximity to sources of alien propagules (Figure 9). Although aliens are favored by most disturbances, chaparral fires are typically of high intensity (Borchert and Odion 1995) and the large seeds of most alien species do not survive. Colonization of burned shrublands occurs when alien

seed sources are nearby—e.g., roadways, fuel breaks, adjacent grasslands, etc. (Haidinger and Keeley 1993, Rundel 2000)—however, persistence depends upon the timing of subsequent fires. If a source of ignition, coincident with suitable burning conditions, does not occur for 2 or more decades, the site will return to a closed canopy of largely native-dominated chaparral (Keeley 2000). This course will vary depending on site factors, such as substrate characteristics, annual precipitation, atmospheric nitrogen deposition, and other disturbances.

Alien annuals, however, have characteristics that contribute to increasing the frequency of fires. Normally, California shrublands do not possess sufficient litter or herbaceous plant matter to carry a surface fire and thus fires are carried through the crowns of closely spaced shrubs. Except under severe weather conditions, canopy fuels fail to carry fire until the shrubland canopy closes—in approximately 15–20 years (Keeley and Fotheringham in press). If alien grasses and forbs establish on recently burned sites, they potentially can alter the fire regime by increasing the probability that ignitions will successfully combust and spread before canopy closure eliminates them from the site. Being herbaceous, the leaves and stalks dry rapidly under even brief periods of low humidity. This, coupled with their high surface:volume ratio, makes them highly combustible (Rundel 1981). These annuals constitute a different functional type in shrublands, one that carries fire along the surface, allowing fires to be spread from shrub to shrub before the age at which the fires would normally spread from shrub canopy to canopy. In addition, these grasses often grow under the shrub canopy, thus acting as ladder fuels that bring the fire into the canopy of otherwise isolated shrubs. Being of European origin, these aliens have a phenological cycle that is quite unlike most California chaparral annuals in that they germinate during the fall and usually dry by mid-spring, well before many of the native annuals, thus increasing the length of the annual fire season.

Fires at intervals of every few years decimate woody plants by extirpating native obligate seeding shrub species, which require a decade or more to replenish soil seed banks (Keeley 2000). Also, fires at this frequency maintain the system at a lower fuel load and the lower fire intensity (Figure 8), enhances survivorship of alien seed banks (J.E. Keeley, personal observations; S. Davis, Pepperdine University, personal communication). In summary, aliens established in degraded shrublands increase the probability of repeat fires and ultimately increase the probability of propagules surviving repeat fires (Figure 9). Continued subsidies of the natural fire regime will lead to complete type conversion from shrubland to grassland (Minnich and Dezzani 1998).

Rangeland managers have long understood this process and have used artificial seeding of annual grasses as a means of producing fuels sufficient to carry repeat fires for the purpose of rangeland improvement of chaparral (Sampson 1944, Burcham 1957, Biswell 1989). Sometimes, however, the effect has

been inadvertent, and accelerated fire frequencies have resulted from management practices that had other intentions. For example, post-fire seeding of exotic grasses for the purpose of reducing soil erosion can cause an acceleration of the normal fire return interval with the consequent decimation of native shrubs (Zedler et al. 1983, Nadkarni and Odion 1986, Giessow and Zedler 1997, Minnich and Dezzani 1998).

Atmospheric deposition of nitrogen has been suggested as a causal factor driving the exotic annual invasion of shrublands in parts of southern California (Allen et al. 1999). While it is apparent that enhanced soil nutrients favor establishment of many invasive annuals, there is no evidence that this can happen in the absence of physical disturbance. Studies purporting to show direct effects of pollution on the native-to-invasive balance (e.g., Westman 1979) have not adequately documented past history of disturbance, including fire frequency and grazing history (Haidinger and Keeley 1993).

#### *Other Ecosystems*

Fire-enhanced niche construction has been implicated in the success of the exotic annual cheatgrass (*Bromus tectorum*) in the Great Basin (Whisenant 1990, Billings 1994, Knick and Rotenberry 1997) and alien perennial grasses in Hawaii (Hughes et al. 1991). Reversing the type-conversion induced by grasses in these systems is considered to be a significant conservation issue (D'Antonio 2000).

The Mediterranean Basin presents an interesting contrast. Increased fire frequency has long been used as a technique for converting woody plant communities to more open herbaceous associations suitable for grazing animals (Naveh 1975, Naveh and Kutiel 1986, Trabaud 1990, Pantis and Mardiris 1992). Although the change involves a similar alteration in functional types, the Mediterranean region differs in that the colonizing grasses and forbs are almost entirely natives (Noy-Meir et al. 1989, Dafni and Heller 1990, Peco et al. 1998, Vilá et al. 2001). During the latter part of the 20th century, abandonment of pastures has resulted in widespread shrub recolonization of grasslands, with subsequent loss of significant native annual biodiversity. This is perhaps a more significant conservation threat than the anthropogenic type-conversion of native shrublands that occurred long ago (Naveh 1998, Verdú et al. 2000).

#### *Indirect Fire Effects*

Some fire management activities may indirectly affect invasive species establishment and spread. For example, the U.S. Forest Service and local agencies have long conducted post-fire rehabilitation programs. These include, among other practices, the seeding of exotic species on recently burned sites for the primary purpose of reducing soil erosion (Beyers et al. 1998). Early during the last century, this involved seeding of some species that today are widespread noxious weeds (e.g., *Brassica nigra* or the very similar *Hirschfeldia incana*). Based on complaints from farmers and sci-



entific studies (e.g., Went et al. 1952), the noxious character of some of these species was recognized and their use discontinued. However, this early assistance in establishment has had profound influence in terms of their widespread establishment. Persistent seed banks of some of these fire-stimulated species (e.g., *Brassica nigra* and *Hirschfeldia incana*) are quite persistent and continue to reestablish after wildfires (J.E. Keeley, unpublished data). Today, local, state, and federal agencies still practice post-fire seeding, despite evidence that it is of limited value (Beyers et al. 1998, Keeley 1998). Two of the more important plant selections are exotic annual grasses Italian ryegrass (*Lolium multiflorum*) and Zorro fescue (*Vulpia myuros*). Although these species seem to be short-lived in chaparral (Beyers et al. 1998, Keeley 2000), they readily colonize other habitats (Bossard et al. 2000).

Pre-burn fuel manipulation is an important management tool for reducing fire hazard in shrublands, but potentially can influence the spread of alien plants. Fuel breaks are bands of 100–200 m wide where most woody fuels are removed. They are of questionable value in preventing the spread of fire under severe fire weather conditions, but they do provide firefighter access to fires ignited under moderate conditions (Keeley and Fotheringham in press). However, fuel breaks present an important alien invasion threat to shrublands and forests. Removal of the native shrubs and trees invariably results in the establishment of nonnative annual grasses and forbs (Giessow and Zedler 1997). Fuel breaks commonly cut a swath across otherwise undisturbed landscapes and thus act as invasive corridors, bringing seed sources into close association with otherwise pristine areas. Shrublands far removed from invasive seed sources normally recover from periodic fires and regain ground before invasives can take hold of the site. Part of this resiliency is due to the limited alien seed bank on most wildland sites. Fuel breaks not only maintain sizeable seed sources of invasion but, because of the reduced fuels within the fuel break, the seeds of most alien species survive fires, whereas their survival in the adjacent shrubland or forest would be doubtful due to higher temperatures during fire (Figure 8).

There are strategies to reduce these impacts and yet still provide effective fire protection. For example, associating fuel breaks with roadways would minimize the total landscape impact because roads share many of the same negative landscape features with fuel breaks.

## FIRE MANAGEMENT IN THE CONTROL OF INVASIVES

Prescription burning has been used in attempts to restore alien-dominated systems to their native composition and has also been used in the targeted control of particular noxious species. In the case of the former, the goal is to shift the balance of native to nonnative species. In the latter case, the primary goal is to eliminate a nonnative species; however, there is no neces-

sary expectation that the native to nonnative balance will be altered.

### Community Restoration

#### Grasslands

On sites where a native bunchgrass is present, removing disturbances, such as grazing, will result in some increase, although the native grasses never entirely displace the nonnative annuals (Bartolome and Gemmill 1981, Keeley 1990, Heady et al. 1992). Grasslands with populations of native bunchgrasses, such as *Nassella pulchra*, *N. cernua*, *Poa secunda*, *Koeleria macrantha*, *Danthonia californica*, or *Deschampsia caespitosa*, have been the target of restoration projects aimed at reducing the nonnative annual grasses and enhancing the populations of native grasses through the use of prescription burning. Both the annual life history and the perennial bunchgrass habit are highly resilient to natural wildfires, which is perhaps not too surprising in that worldwide grasslands have had a long association with natural fires (Sauer 1975). In California, natural fires occur during summer and fall when both annuals and herbaceous perennials are dormant. Under the fuel loads of typical grasslands, seeds of annuals and basal buds of perennials survive to regenerate the following spring.

One strategy for altering the balance between nonnative annuals and perennials is the introduction of fire early during the spring, prior to seed release (Menke 1992, Wills 2000). Fires at this time will destroy much of the current seed crop for both annuals and perennials, but the resprouting ability of the latter makes it more resilient to burning at this time—most herbaceous perennials are obligate post-fire resprouters (Keeley 1991). One concern with this late-spring burn strategy is that there may be negative impacts on native annuals. This is a significant concern because the native grasslands of central and southern California historically had a rich diversity of native annuals (Keeley 1990). Under repeated application of spring burns there should also be concern for the potential selection for greater seed dormancy in the alien annuals.

Season of burning does not affect the invasive-to-native composition in the central and northern coastal prairies, perhaps because the important invasives are perennial grasses. In these coastal prairies protection from grazing seems to be a more important factor in shifting the balance from exotics to natives (Elliot and Wehausen 1974, Hatch et al. 1999).

Today 99% of the grasslands in California are dominated by nonnative annuals and most grasslands completely lack any presence of native bunchgrass (Huenneke 1989). On these sites, burning alone will not restore native bunchgrasses (Parsons and Stohlgren 1989, Klinger and Messer 1999), due in part to the weak colonizing ability and poor seedling establishment by native grasses (Dyer et al. 1996). Repeated burning of alien-dominated grasslands has the potential for altering the species composition but usually



fails to generate large shifts in the native:nonnative species ratio.

Some grasslands such as those in the southern San Joaquin Valley probably never had a significant perennial bunchgrass component (Wester 1981, Hamilton 1997, Schiffman 2000). In these very arid ecosystems, late spring fires appear to be effective at increasing diversity and cover of native annuals, although alien grasses and forbs still dominate after such treatment (Meyer and Schiffman 1999).

### Shrublands

Fire is not recommended as a restoration tool in California shrublands. Chaparral in particular is relatively immune to alien invasions (Knops et al. 1995, Stromberg and Griffin 1996, Allen 1999), unless subjected to unnaturally high fire frequencies (Keeley 1995). As a consequence, little resource benefit is to be gained by the use of prescription burning in shrubland habitat. Degraded shrublands, with a sparse shrub canopy and dense populations of nonnative grasses and forbs in the spaces between shrubs are increasingly commonplace in the foothills surrounding metropolitan areas in the state. These are most commonly the result of repeated accidental burning that has eliminated obligate seeding shrubs, and prescription burning only exacerbates the situation. Here the primary fire management practice that is needed for plant community restoration is increased fire prevention and enhanced fire suppression (Keeley and Fotheringham in press).

### Forests

On the other hand, coniferous forests have a need for restoration fires after a century of near-total fire exclusion (Skinner and Chang 1996, Keifer 1998, Stephenson 1999, Keeley and Stephenson 2000). Fire restoration, however, is a double-edged sword as burning will promote alien species establishment (e.g., Figure 3). For example, fire management at Sequoia-Kings Canyon National Parks has halted the prescription burning program in the Cedar Grove section because it appears to have promoted a vigorous invasion of cheatgrass (Figure 10; T. Caprio, Sequoia-Kings Canyon National Parks, personal communication). Ultimately, fire managers in these parks and elsewhere will need to balance prescription fire with techniques for reducing alien invasion. Managing fires for lower intensity might reduce the potential for alien invasion (e.g., Figure 3), but this has the negative impact of inhibiting seedling recruitment of gap-dependent species, such as ponderosa pine (*Pinus ponderosa*) and giant sequoia (*Sequoiadendron giganteum*; Stephenson et al. 1991). A management technique that might inhibit alien invasion into high fire-intensity gaps would be elimination of exotic seed sources from roadsides and other disturbances adjacent to burn sites. Also, increasing size of burns may reduce invasion by increasing the distance from alien seed sources to the bulk of the burn (e.g., Turner et al. 1997).



Fig. 10. Cheatgrass invasion in Ponderosa pine forest of Kings Canyon National Park following prescription burning (National Park Service photo).

### Targeting Noxious Nonnatives

Particularly in grasslands there are a number of alien plants that have been targeted for removal by use of prescription burning. In general, using fire to target a single species commonly results in the replacement of 1 alien with another. Reasons why this tradeoff is acceptable include: (1) The targeted alien is a recent introduction and there is a reasonable expectation that extirpation is possible at an early stage of invasion. (2) The target species constitutes a different functional type that is considered more undesirable than the surrounding alien flora (DiTomaso 2000). For example, yellow starthistle (*Centaurea solstitialis*) is a widespread weed in western North America and when it infests a grassland it reduces the forage available for livestock and wildlife, as well as making the site less user-friendly (Thomsen et al. 1997). Other species have likewise been implicated in altering forage value, both as physical (e.g., gorse [*Ulex europaeus*], bull thistle [*Cirsium vulgare*]) and chemical repellants (e.g., leafy spurge [*Euphorbia esula*]; Bossard et al. 2000).

The efficacy of burning to control noxious species has not been well studied. Repeated prescription burn-

ing during summer has shown promise for reducing the level of infestation of yellow starthistle, although native bunchgrasses were unaffected and alien annual grasses increased (DiTomaso et al. 1999). This burning regime did increase diversity and cover of native forbs, although it was thought this was due more to the reduction in surface litter from burning than due to removal of yellow starthistle. Nonetheless, aliens still dominated the sites, a pattern seen in other studies (Meyer and Schiffman 1999).

Fennel (*Foeniculum vulgare*) is another species that has been targeted for removal, apparently because it is capable of dominating sites to the exclusion of other species, both native and nonnative. Prescription burning has shown promise for reducing this species, but replacement is generally with other alien species (Colvin and Gliessman 1999).

Another reason for targeting a particular alien is when there is evidence they may upset ecosystem processes (e.g., Robles and Chapin 1995). For example, in coniferous forests, bull thistle threatens ponderosa pine seedling recruitment (Randall and Rejmánek 1993). It is doubtful that prescription burning would be effective at inhibiting this exotic without decimating the ponderosa pine seedlings at the same time.

Nonnative legume shrubs known as brooms (*Cytisus scoparius* and *Genista monspesulanus*) are often targeted for removal, in part because they type-convert grasslands to shrublands and are associated with low native biodiversity. These shrubs seldom invade intact shrublands, but they readily colonize open woodlands and grasslands. As discussed earlier, many of these sites originally were closed-canopy shrublands or woodlands that have been opened up through repeated burning, grazing and logging, and when those disturbances are reduced, these sites become vulnerable to recolonization by nonnative shrubs such as brooms. Techniques for removing these invasives include repeated burning before seedlings that were recruited after the last fire have had time to mature (Swezy and Odion 1998). This technique is capable of significantly reducing cover and seed banks of brooms, but invariably this technique replaces brooms with exotic annuals (C. D'Antonio, University of California-Berkeley, personal communication).

#### Prospects for Managing Aliens with Fire

Long-term goals of many resource managers in Mediterranean-climate California center on the restoration of perturbed ecosystems currently dominated by nonnative species. In the case of annual grasslands, particularly on slopes with shallow soils, this is often the result of type-conversion from the natural shrubland or woodland vegetation that once occupied the site. Restoration requires serious thought to type-converting these grasslands back to their original ligneous vegetation. The primary management strategy should be one that begins with reducing the incidence of anthropogenic fire. Failure to do so will doom such sites to perpetual domination by nonnative species. In some instances merely removing disturbance factors, such as

fire and grazing, is sufficient to return grasslands to their original woody associations (McBride 1974, Saford 1995).

On more level terrain with finer-textured soils, annual grasslands have likely replaced native grasslands (Robinson 1971, Keeley 1993, Stromberg and Griffin 1996). There is reason to be optimistic that prescription burning during the spring may shift the balance between native and nonnative species. In general, using fire to target nonnative species nearly always carries with it the potential for inhibiting some native component of the flora. In addition, judging from the tenacity of species of *Avena* and *Bromus*, which have dominated California grasslands for nearly 200 years, it seems doubtful aliens will ever be eliminated from some sites, expressed in the term "new natives" (Heady 1977).

#### ACKNOWLEDGMENTS

I thank Matt Brooks and Stan Coloff for organizing this symposium and subsequent proceedings. Thanks also to Carla D'Antonio, John Gerlach, and Phil van Mantgem for comments on an earlier version of this paper.

#### LITERATURE CITED

- Allen, E.B. 1999. Restoring habitats to prevent exotics. Proceedings of the California Exotic Pest Plant Council Symposium 4:41-44.
- Allen, E.B., P.E. Padgett, A. Bytnerowicz, and R. Minnich. 1999. Nitrogen deposition effects on coastal sage vegetation of southern California. Pages 131-140 in A. Bytnerowicz, M.J. Arbaugh, and S.L. Schilling (technical coordinators). Proceedings of the international symposium on air pollution and climate effects on forest ecosystems. General Technical Report PSW-GTR-166, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.
- Atherden, M.A., and J.A. Hall. 1999. Human impact on vegetation in the White Mountains of Crete since AD 500. Holocene 9:183-193.
- Baker, H.G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics 5:1-24.
- Baker, H.G. 1989. Sources of the naturalized grasses and herbs in California grasslands. Pages 29-38 in L.F. Huenneke and H.A. Mooney (eds.). Grassland structure and function: California annual grassland. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Bartolome, J.W., and B. Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. Madroño 28:172-184.
- Bean, L.J., and H.W. Lawton. 1973. Some explanations for the rise of cultural complexity in native California with comments on proto-agriculture and agriculture. Pages v-xlvii in H.T. Lewis (ed.). Patterns of Indian burning in California: ecology and ethnohistory. Ballena Press, Ramona, CA.
- Beyers, J.L., C.D. Wakeman, P.M. Wohlgemuth, and S.G. Conard. 1998. Effects of postfire grass seeding on native vegetation in southern California chaparral. Proceedings of the Annual Forest Vegetation Management Conference 19:52-64.
- Billings, W.D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. Pages 22-30 in S.B. Monsen and S.G. Kitchen (eds.). Proceedings—ecology and management of annual rangelands. Gen-



## FIRE AND INVASIVE SPECIES IN CALIFORNIA ECOSYSTEMS

91

- eral Technical Report INT-GTR-313, U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.
- Biswell, H.H. 1989. Prescribed burning in California wildlands vegetation management. University of California Press, Los Angeles.
- Blumler, M.A. 1984. Climate and the annual habit. M.A. thesis, University of California, Berkeley.
- Bond, W.J., and J.J. Midgley. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* 73:79–85.
- Borchert, M.I., and D.C. Odion. 1995. Fire intensity and vegetation recovery in chaparral: a review. Pages 91–100 in J.E. Keeley and T. Scott (eds.). *Brushfires in California wildlands: ecology and resource management*. International Association of Wildland Fire, Fairfield, WA.
- Bossard, C.C., J.M. Randall, and M.C. Hoshovsky (eds.). 2000. *Invasive plants of California's wildlands*. University of California Press, Berkeley.
- Brown, W.S., and S.B. Show. 1944. California rural land use and management. A history of the use and occupancy of rural lands in California. U.S. Department of Agriculture, Forest Service, California Region, Berkeley.
- Burcham, L.T. 1957. California range land: an historic–ecological study of the range resources of California. State of California, Department of Natural Resources, Division of Forestry, Sacramento.
- California Division of Forestry. 1978. *Brushland range improvement*. State of California, Resources Agency, California Division of Forestry, Sacramento.
- Cody, M.L. 1986. Diversity, rarity and conservation in Mediterranean-climate regions. Pages 122–152 in M.E. Soulé (ed.). *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, MA.
- Colvin, W.I., III, and S.R. Gliessman. 1999. Fennel (*Foeniculum vulgare*) management and native species enhancement on Santa Cruz Island, California. *Proceedings of the California Islands Symposium* 5:184–189.
- Cooper, W.S. 1922. The broad-sclerophyll vegetation of California. An ecological study of the chaparral and its related communities. Publication No. 319, Carnegie Institution of Washington, Washington, D.C.
- D'Antonio, C.M. 2000. Fire, plant invasions, and global changes. Pages 65–93 in H.A. Mooney and R.J. Hobbs (eds.). *Invasive species in a changing world*. Island Press, Covelo, CA.
- D'Antonio, C.M., and B.E. Mahall. 1991. Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany* 78:885–894.
- D'Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Dafni, A., and D. Heller. 1990. Invasions of adventive plants in Israel. Pages 135–160 in F. di Castri, A.J. Hansen, and M. Debussche (eds.). *Biological invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Debussche, M., J. Escarré, and J. Lepart. 1980. Changes in Mediterranean shrub communities with *Cytisus purgans* and *Genista scorpius*. *Vegetatio* 43:73–82.
- DeSimone, S.A., and P.H. Zedler. 1999. Shrub seedling recruitment in unburned Californian coastal sage scrub and adjacent grassland. *Ecology* 80:2018–2032.
- DiTomaso, J.M. 2000. Invasive weeds in rangelands: species, impacts and management. *Weed Science* 48:255–265.
- DiTomaso, J.M., G.B. Kyser, and M.S. Hastings. 1999. Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. *Weed Science* 47:233–242.
- Dyer, A.R., H.C. Fossum, and J.W. Menke. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. *Madroño* 43:316–333.
- Elliot, H.W., and J.D. Wehausen. 1974. Vegetational succession on coastal rangeland of Point Reyes Peninsula. *Madroño* 22: 231–238.
- Fabritius, S., and S. Davis. 2000. Increased fire frequency promotes vegetation-type conversion in southern California chaparral: a 15-year study. Abstract in *Mediterranean-type ecosystems: past, present and future*. MEDECOS 2000, Stellenbosch University, Stellenbosch, South Africa.
- Fernández-Santos, B., J.M. Gomez-Gutierrez, and G. Moreno-Marcos. 1999. Effects of disturbance caused by traditional Spanish rural land use on the regeneration of *Cytisus multiflorus*. *Applied Vegetation Science* 2:239–250.
- Fox, M.D. 1990. Mediterranean weeds: exchanges of invasive plants between the five Mediterranean regions of the world. Pages 179–200 in F. di Castri, A.J. Hansen, and M. Debussche (eds.). *Biological invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Frenkel, R.E. 1970. Ruderal vegetation along some California roadsides. *University of California Publications in Geography* 2:1–163.
- Freudenberger, D.O., B.E. Fish, and J.E. Keeley. 1987. Distribution and stability of grasslands in the Los Angeles Basin. *Bulletin of the Southern California Academy of Sciences* 86:13–26.
- Giessow, J., and P. Zedler. 1997. The effects of fire frequency and firebreaks on the abundance and species richness of exotic plant species in coastal sage scrub. *Proceedings of the California Exotic Pest Plant Council Symposium* 2:86–94.
- Haidinger, T.L., and J.E. Keeley. 1993. Role of high fire frequency in destruction of mixed chaparral. *Madroño* 40:141–147.
- Hamilton, J.G. 1997. Changing perceptions of pre-European grasslands in California. *Madroño* 44:311–333.
- Hatch, D.A., J.W. Bartolome, J.S. Fehmi, and D.S. Hillyard. 1999. Effects of burning and grazing on a coastal California grassland. *Restoration Ecology* 7:376–381.
- Heady, H.F. 1977. Valley grasslands. Pages 491–514 in M.G. Barbour and J. Major (eds.). *Terrestrial vegetation of California*. John Wiley & Sons, New York, NY.
- Heady, H.F., J.W. Bartolome, M.D. Pitt, G.D. Savelle, and M.C. Stroud. 1992. California prairie. Pages 313–335 in R.T. Coupland (ed.). *Ecosystems of the world: natural grasslands: introduction and Western Hemisphere*. Volume 8A. Elsevier, New York, NY.
- Heady, H.F., and M.D. Pitt. 1979. Reactions of northern California grass-woodland to vegetational type conversions. *Hilgardia* 47:1–73.
- Hendry, G.W. 1934. The source literature of early plant introduction into Spanish America. *Agricultural History* 8:64–71.
- Hickman, J.C. (ed.). 1993. *The Jepson manual. Higher plants of California*. University of California Press, Berkeley.
- Hobbs, R.J., and H.A. Mooney. 1986. Community changes following shrub invasion of grassland. *Oecologia* 70:508–513.
- Hoover, R.F. 1936. Character and distribution of the primitive vegetation of the San Joaquin Valley. M.A. Thesis, University of California, Berkeley.
- Huenneke, L.F. 1989. Distribution and regional patterns of Californian grasslands. Pages 1–12 in L.F. Huenneke and H.A. Mooney (eds.). *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Hughes, F., P.M. Vitousek, and T. Tunison. 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawaii. *Ecology* 72:743–746.
- Jones & Stokes Associates. 1987. *Sliding toward extinction: the state of California's natural heritage*. Jones & Stokes Associates, Sacramento, CA.



- Keeley, J.E. 1986. Resilience of Mediterranean shrub communities to fire. Pages 95–112 in B. Dell, A.J.M. Hopkins, and B.B. Lamont (eds.). Resilience in Mediterranean-type ecosystems. Dr. W. Junk, Dordrecht, Netherlands.
- Keeley, J.E. 1990. The California valley grassland. Pages 2–23 in A.A. Schoenherr (ed.). Endangered plant communities of southern California. Special Publication No. 3, Southern California Botanists, Fullerton.
- Keeley, J.E. 1991. Seed germination and life history syndromes in the California chaparral. *Botanical Review* 57:81–116.
- Keeley, J.E. 1993. Assessing suitable sites for grassland restoration. Pages 277–281 in J.E. Keeley (ed.). Interface between ecology and land development in California. Southern California Academy of Sciences, Los Angeles.
- Keeley, J.E. 1995. Future of California floristics and systematics: wildfire threats to the California flora. *Madroño* 42:175–179.
- Keeley, J.E. 1998. Postfire ecosystem recovery and management: the October 1993 large fire episode in California. Pages 69–90 in J.M. Moreno (ed.). Large forest fires. Backhuys Publishers, Leiden, Netherlands.
- Keeley, J.E. 2000. Chaparral. Pages 203–253 in M.G. Barbour and W.D. Billings (eds.). North American terrestrial vegetation. Cambridge University Press, Cambridge, United Kingdom.
- Keeley, J.E., and W.J. Bond. 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. *American Naturalist* 154:383–391.
- Keeley, J.E., and C.J. Fotheringham. 2001. The historic fire regime in southern California shrublands. *Conservation Biology* 15:1536–1548.
- Keeley, J.E., and C.J. Fotheringham. In press. Impact of past, present, and future fire regimes on North American shrublands. In T.T. Veblen, W.L. Baker, G. Montenegro, and T.W. Swetnam (eds.). Fire regimes and climatic changes in temperate ecosystems of the western Americas. Springer-Verlag, New York, NY.
- Keeley, J.E., C.J. Fotheringham, and M. Morais. 1999. Reexamining fire suppression impacts on brushland fire regimes. *Science* 284:1829–1832.
- Keeley, J.E., and N.L. Stephenson. 2000. Restoring natural fire regimes to the Sierra Nevada in an era of global change. Pages 255–265 in D.N. Cole, S.F. McCool, W.T. Borrie, and J. O'Loughlin (eds.). Wilderness science in a time of change conference. Volume 5: wilderness ecosystems, threats, and management. Proceedings RMRS-P-15-Vol-5, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Keifer, M. 1998. Fuel load and tree density changes following prescribed fire in the giant sequoia–mixed conifer forest: the first 14 years of fire effects monitoring. Proceedings of the Tall Timbers Fire Ecology Conference 20:306–309.
- Kellogg, E.M., and J.L. Kellogg. 1990. A study of the distribution and pattern of perennial grassland on the Camp Pendleton Marine Corps Base. Contract No. M00681-88-P-3161, U.S. Marine Corps, Camp Pendleton, CA.
- Kerr, B., D.W. Schwilk, A. Bergman, and M.W. Feldman. 1999. Rekindling an old flame: a haploid model for the evolution and impact of flammability in resprouting plants. *Evolutionary Ecology Research* 1:807–833.
- Klinger, R.C., and I. Messer. 1999. Composition and structure of a grassland community following prescribed burns on Santa Cruz Island. Proceedings of the California Islands Symposium 5:190–200.
- Knick, S.T., and J.T. Rotenberry. 1997. Landscape characteristics of disturbed shrubsteppe habitats in southwestern Idaho (U.S.A.). *Landscape Ecology* 12:287–297.
- Knowles, C. 1953. Vegetation burning by California Indians as shown by early records. Forestry Library, Pamphlet 16, Fire Volume 28. University of California, Berkeley.
- Knops, J.M.H., J.R. Griffin, and A.C. Royalty. 1995. Introduced and native plants of the Hastings Reservation, central coastal California: a comparison. *Biological Conservation* 71:115–123.
- Le Floch, E., H.N.L. Houérou, and J. Mathez. 1990. History and patterns of plant invasion in northern Africa. Pages 105–133 in F. di Castri, A.J. Hansen, and M. Debussche (eds.). Biological invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Lewis, H.T. 1973. Patterns of Indian burning in California: ecology and ethnohistory. Ballena Press, Ramona, CA.
- Mack, M.C., and C.M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution* 13:195–198.
- Magri, D., and L. Sadori. 1999. Late Pleistocene and Holocene pollen stratigraphy at Lago di Vico, central Italy. *Vegetation History and Archaeobotany* 8:247–260.
- McBride, J.R. 1974. Plant succession in the Berkeley Hills, California. *Madroño* 22:317–380.
- Menke, J.W. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* 20(2):22–25.
- Meyer, M.D., and P.M. Schiffman. 1999. Fire season and mulch reduction in a California grassland: a comparison of restoration strategies. *Madroño* 46:25–37.
- Minnich, R.A., and R.J. Dezzani. 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *Western Birds* 29:366–391.
- Mooney, H.A., S.P. Hamburg, and J.A. Drake. 1986. The invasions of plants and animals into California. Pages 250–272 in H.A. Mooney and J.A. Drake (eds.). Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, NY.
- Murphy, A.H., and O.A. Leonard. 1974. Chaparral shrub control influenced by grazing, herbicides and fire. *California Agriculture* 29(1):10–13.
- Mutch, R.W. 1970. Wildland fires and ecosystems: a hypothesis. *Ecology* 51:1046–1051.
- Nadkarni, N.M., and D.C. Odion. 1986. Effects of seeding exotic *Lolium multiflorum* on native seedling regeneration following fire in a chaparral community. Pages 115–121 in J.J. DeVries (ed.). Proceedings of the chaparral ecosystems research conference. Report No. 62, University of California, Water Resources Center, Davis.
- Naveh, Z. 1975. The evolutionary significance of fire in the Mediterranean region. *Vegetatio* 29:199–208.
- Naveh, Z. 1998. From biodiversity to ecodiversity—holistic conservation of the biological and cultural diversity of Mediterranean landscapes. Pages 23–53 in P.W. Rundel, G. Montenegro, and F.M. Jaksic (eds.). Landscape disturbance and biodiversity in Mediterranean-type ecosystems. Springer, New York, NY.
- Naveh, Z., and P. Kutiel. 1986. Changes in the Mediterranean vegetation of Israel in response to human habitation and land use. Pages 257–299 in G.M. Woodwell (ed.). The Earth in transition—patterns and processes of biotic impoverishment. Cambridge University Press, New York, NY.
- Naveh, Z., and R.H. Whittaker. 1979. Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. *Vegetatio* 41:171–190.
- Noy-Meir, I., M. Gutman, and Y. Kaplan. 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77:290–310.
- Odling-Smee, F.J., K.N. Laland, and M.W. Feldman. 1996. Niche construction. *American Naturalist* 147:641–648.
- Pantis, J.D., and T.A. Mardiris. 1992. The effects of grazing and fire on degradation processes of Mediterranean ecosystems. *Israel Journal of Botany* 41:233–242.
- Parsons, D.J., and T.J. Stohlgren. 1989. Effects of varying fire regimes on annual grasslands in the southern Sierra Nevada of California. *Madroño* 36:154–168.
- Peco, B., T. Espigares, and C. Levassor. 1998. Trends and fluctua-

## FIRE AND INVASIVE SPECIES IN CALIFORNIA ECOSYSTEMS

93

- tuations in species abundance and richness in Mediterranean annual pastures. *Applied Vegetation Science* 1:21–28.
- Pignatti, S. 1983. Human impact on the vegetation of the Mediterranean basin. Pages 151–161 in W. Holzner, M.J.A. Werger, and I. Kusima (eds.). *Man's impact on vegetation*. Dr. W. Junk, The Hague, Netherlands.
- Randall, J.M., and M. Rejmánek. 1993. Interference of bull thistle (*Cirsium vulgare*) with growth of ponderosa pine (*Pinus ponderosa*) seedlings in a forest plantation. *Canadian Journal of Forest Research* 23:1507–1513.
- Randall, J.M., M. Rejmánek, and J.C. Hunter. 1998. Characteristics of the exotic flora of California. *Fremontia* 26(4):3–12.
- Raven, P.H. 1977. The California flora. Pages 109–138 in M.G. Barbour and J. Major (eds.). *Terrestrial vegetation of California*. John Wiley & Sons, New York, NY.
- Raven, P.H., and D.I. Axelrod. 1978. Origin and relationships of the California flora. University of California Publications in Botany 72:1–134.
- Reichard, S.H. 1997. What traits distinguish invasive plants from non-invasive plants? Proceedings of the California Exotic Pest Plant Council Symposium 2:31–38.
- Rejmánek, M. 1989. Invasibility of plant communities. Pages 369–388 in J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, and M. Rejmánek (eds.). *Biological invasions: a global perspective*. John Wiley & Sons, New York, NY.
- Richerson, P.J., and K.-L. Lum. 1980. Patterns of plant species diversity in California: relation to weather and topography. *American Naturalist* 116:504–536.
- Robles, M., and F.S. Chapin, III. 1995. Comparison of the influence of two exotic communities on ecosystem processes in the Berkeley Hills. *Madroño* 42:349–357.
- Robinson, R.H. 1971. An analysis of ecological factors limiting the distribution of a group of *Stipa pulchra* associations. *Korean Journal of Botany* 14:61–80.
- Rundel, P.W. 1981. Structural and chemical components of flammability. Pages 183–207 in H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners (eds.). *Fire regimes and ecosystem properties*. General Technical Report WO-26, U.S. Department of Agriculture, Forest Service, Washington, D.C.
- Rundel, P.W. 2000. Alien species in the flora and vegetation of the Santa Monica Mountains, California: patterns, processes, and management implications. Pages 145–152 in J.E. Keeley, M. Baer-Keeley, and C.J. Fotheringham (eds.). *2nd interface between ecology and land development in California*. Open-File Report 00-62, U.S. Geological Survey, Sacramento, CA.
- Safford, H.D. 1995. Woody vegetation and succession in the Garin Woods, Hayward Hills, Alameda County, California. *Madroño* 42:470–489.
- Sales, F. 1994. Evolutionary tendencies in some annual species of *Bromus* (*Bromus* L. sect. *Genea* Dum. (Poaceae)). *Botanical Journal of the Linnean Society* 115:197–210.
- Sampson, A.W. 1944. Plant succession and burned chaparral lands in northern California. Bulletin 685, Agricultural Experiment Station, University of California, Berkeley.
- Sauer, C.O. 1975. Man's dominance by use of fire. Pages 1–13 in R.H. Kesel (ed.). *Grasslands ecology: a symposium*. Geoscience and man. Volume 10. Louisiana State University, Baton Rouge.
- Schiffman, P.M. 2000. Mammal burrowing, erratic rainfall and the annual lifestyle in the California prairie: is it time for a paradigm shift? Pages 153–160 in J.E. Keeley, M.B. Keeley, and C.J. Fotheringham (eds.). *2nd interface between ecology and land development in California*. Open-File Report 00-62, U.S. Geological Survey, Sacramento, CA.
- Schwartz, M.W., D.J. Porter, J.M. Randall, and K.E. Lyons. 1996. Impact of nonindigenous plants. Pages 1203–1218 in *Sierra Nevada Ecosystem Project: final report to Congress*. Volume II: assessments and scientific basis for management options. Centers for Water and Wildland Resources, University of California, Davis.
- Shmida, A. 1981. Mediterranean vegetation in California and Israel: similarities and differences. *Israel Journal of Botany* 30:105–123.
- Skinner, C.N., and C.-R. Chang. 1996. Fire regimes, past and present. Pages 1041–1069 in SNEP Team (eds.). *Sierra Nevada Ecosystem Project: final report to Congress*. Status of the Sierra Nevada. Centers for Water and Wildland Resources, University of California, Davis.
- Smith, D.W., and J.H. Sparling. 1966. The temperature of surface fires in jack pine barren. I. The variation in temperature with time. *Canadian Journal of Botany* 44:1285–1292.
- Stephenson, N.L. 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. *Ecological Applications* 9:1253–1265.
- Stephenson, N.L., D.J. Parsons, and T.W. Swetnam. 1991. Restoring natural fire to the sequoia-mixed conifer forest: should intense fire play a role? Proceedings of the Tall Timbers Fire Ecology Conference 17:321–338.
- Stevenson, A.C. 1985. Studies in the vegetational history of S.W. Spain. II. Palynological investigations at Laguna de las Madres, S.W. Spain. *Journal of Biogeography* 12:293–314.
- Stromberg, M.R., and J.R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. *Ecological Applications* 6:1189–1211.
- Swezy, M., and D.C. Odion. 1998. Fire on the mountain: a land manager's manifesto for broom control. Proceedings of the California Exotic Pest Plant Council Symposium 3:76–81.
- Thomsen, C.D., M.P. Vayssieres, and W.A. Williams. 1997. Moving and subclover plantings suppress yellow starthistle. *California Agriculture* 51(6):15–20.
- Timbrook, J., J.R. Johnson, and D.D. Earle. 1982. Vegetation burning by the Chumash. *Journal of California and Great Basin Anthropology* 4:163–186.
- Trabaud, L. 1990. Fire as an agent of plant invasion? A case study in the French Mediterranean vegetation. Pages 417–437 in F. di Castri, A.J. Hansen, and M. Debussche (eds.). *Biological invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Trabaud, L., and M. Casal. 1989. Fire and pastoralism in southern Europe. Pages 120–132 in W.J. Clawson (ed.). *Landscape ecology: study of Mediterranean grazed ecosystems*. U.S. Man and the Biosphere Program, Program International L'Homme et la Biosphère, Paris, France.
- Turner, M.G., W.H. Romme, R.H. Gardner, and W.W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67:411–433.
- Valderrábano, J., and L. Torrano. 2000. The potential for using goats to control *Genista scorpius* shrubs in European black pine stands. *Forest Ecology and Management* 126:377–383.
- Veblen, T.T. 1975. Alien weeds in the tropical highlands of western Guatemala. *Journal of Biogeography* 2:19–26.
- Verdú, J.R., M.B. Crespo, and E. Galante. 2000. Conservation strategy of a nature reserve in Mediterranean ecosystems: the effects of protection from grazing on biodiversity. *Biodiversity and Conservation* 9:1707–1721.
- Vilá, M., F. Lloret, E. Ogheri, and J. Terradas. 2001. Positive fire-grass feedback in Mediterranean Basin woodlands. *Forest Ecology and Management* 147:3–14.
- Wells, P.V. 1962. Vegetation in relation to geological substratum and fire in the San Luis Obispo quadrangle, California. *Ecological Monographs* 32:79–103.
- Went, F.W., G. Juhren, and M.C. Juhren. 1952. Fire and biotic factors affecting germination. *Ecology* 33:351–364.
- Wester, L.L. 1981. Composition of native grasslands in the San Joaquin Valley, California. *Madroño* 28:231–241.
- Westman, W.E. 1979. Oxidant effects on Californian coastal sage scrub. *Science* 205:1001–1003.
- Whisenant, S. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. Page

- es 4–10 in E.D. McArthur, E.M. Romney, S.D. Smith, and P.T. Tueller (compilers). Proceedings—symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management. General Technical Report INT-276, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Wills, R. 2000. Effective fire planning for California native grasslands. Pages 75–78 in J.E. Keeley, M. Baer-Keeley, and C.J. Fotheringham (eds.). 2nd interface between ecology and land development in California. Open-File Report 00-62, U.S. Geological Survey, Sacramento, CA.
- Zedler, P.H. 1995. Fire frequency in southern California shrublands: biological effects and management options. Pages 101–112 in J.E. Keeley and T. Scott (eds.). Wildfires in California brushlands: ecology and resource management. International Association of Wildland Fire, Fairfield, WA.
- Zedler, P.H., C.R. Gautier, and G.S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64:809–818.
- Zedler, P.H., and G.A. Scheid. 1988. Invasion of *Carpobrotus edulis* and *Salix lasiolepis* after fire in a coastal chaparral site in Santa Barbara County, California. *Madroño* 35:196–201.