Chapter 8
Fire and Invasive Plants on California Landscapes

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8.1 Introduction

Throughout the world, the functioning of natural ecosystems is being altered by invasions from nonnative plants and animals. Disturbances that alter ecosystem processes often initiate species invasions. Increasingly it is evident that fire-prone ecosystems can be highly vulnerable both to invasion during the immediate postfire period and to alterations of fire regime by altered fuel bed properties after invasion. Here we explore how temporal and spatial patterns of burning affect invasion and the prevalence of nonnative species, and how fundamental variation in fire regime characteristics pose challenges for articulating unifying principles of the relationship between fire and the invasion process at the landscape scale.

Many landscapes in the western United States are dominated by ecosystems where fire is a natural and necessary process for long-term sustainability of those systems. However, despite the obvious resilience of many ecological communities to periodic fire, it is misleading to think of species in these systems as being fire-adapted. Rather, they are adapted to a particular temporal and spatial pattern of burning. This is captured in the concept of a fire regime, which includes the fuel types consumed, frequency and timing of burning, intensity of the fire, and the spatial distribution of individual fire events (Keeley et al. 2009a). Fires are often referred to as disturbances but in many communities fire has been a historic, routine process, and the real "disturbances" to the system are perturbations to the fire regime that lie outside the historic realm. Such disturbances include increased fire frequency, as well as suppression and exclusion of fire, and these can create conditions conducive to species invasions.

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We address the complex relationship between fire and nonnative species invasions, by focusing on a complex landscape with diverse fire regimes and ecosystems that pose different challenges with respect to alien invasions. Our goal is to understand the features of the fire regime critical to thresholds that influence system susceptibility to invasion and how these thresholds vary between different ecosystems. In the context of future global changes in climate, human population growth, and landscape use, we will attempt to define the potential trajectories for these systems and how future fire regime characteristics may affect biological invasions.

8.2 The Setting: California

Fire is a prominent ecosystem process over much of the California landscape, including diverse plant communities of grasslands, shrublands and forests. These communities broadly sort out along a moisture gradient, although other factors, including substrate, land use history, and fire, can play important roles in determining their distribution. The Mediterranean climate of this region has characteristics that contribute to making it a fire-prone landscape. This includes a wet and cool winter with growing conditions sufficient to generate moderate primary productivity followed by a long, dry, and hot summer that converts much of this production into available fuel for wildfires. Many plant communities in California are resilient to fire, and species exhibit traits apparently selected for by fire. Thus, it is somewhat surprising that fire can be an important driver behind alien plant invasions in this landscape. Conversely, with the wide breadth of species introduced into California, it is not surprising that some would be fire responsive.

Fire regimes are markedly different across California both within and across vegetation types (Sugihara et al. 2006). Since settlement by Euro-Americans in the late eighteenth and nineteenth centuries, fire regimes have been greatly altered and fire regimes are outside the historical range of variability, although in very different ways in forests, shrublands, and grasslands.

Fire suppression has proven effective at excluding fire from conifer forests in mountainous regions of the state. As a result many of these forests have accumulated fuels in excess of what occurred historically. Higher elevation conifer-dominated forests have historically burned in high-frequency (scaled at approximately 10-year intervals) lightning-ignited fires that consumed predominantly surface understory fuels, or they have burned in a mixed pattern of low intensity surface and high intensity crown fires. Frequent fires contributed to landscape fuel mosaics conducive to small patchy burns.

Fuel loads in these forests include both surface fuels and increased density of saplings or ladder fuels. Fire suppression is only one of the factors contributing to these fuels. In ponderosa pine forests with herbaceous understory intense livestock grazing has reduced surface fuels, which have worked to exclude fires and allow

increased ladder fuels. Logging has contributed to both increased surface fuels as well as increased density of even-aged trees (Odion et al. 2004; Stephens and Collins 2004; van Wagtendonk and Fites-Kaufman 2006). This homogenization of stand structure has affected fire regimes. Efforts to restore high-frequency low-severity fire to these forested ecosystems (Keeley and Stephenson 2000) are greatly complicated by restrictions related to increased human settlement in mountain areas, the volume and homogeneity of the fuels, and nonnative plant species not present prior to Euro-American settlement.

By contrast, lower elevation shrublands retain most fuels in the canopy and historically had less frequent lightning ignitions resulting in longer intervals (closer to 100-year intervals) between high-intensity crown fires. Although fire sizes likely varied, these ecosystems would have burned periodically in massive landscape scale fires, probably much larger than fires in forested ecosystems (Moritz 2003; Keeley 2006a). Lower elevation ecosystems, particularly shrublands, have experienced increased fire frequency since the middle of the 20th century (Keeley et al. 1999), which is quite unlike the recent history in conifer forests (Fig. 8.1).

In contrast to both forests and shrublands in California, fire regimes in grasslands are poorly understood (Wills 2006). Since Euro-American settlement, grasslands have undergone profound changes in composition and today are dominated by nonnative annual grasses. These species are presumed to have displaced native bunchgrasses on some landscapes, native forbs on other landscapes, and shrublands on still other landscapes (Keeley 1990; Hamilton 1997). Prior to Euro-American settlement the distribution of native grasslands would have been most strongly influenced by edaphic factors and Native American settlement and burning patterns (Wells 1962; Huenneke and Mooney 1989; Keeley 2002). Due to the combination of fuel characteristics (ready ignition, rapid spread rates) and anthropogenic burning (e.g. Anderson 2005a), fires were likely frequent and of low intensity.

Although California's forests, woodlands, shrublands, and grasslands tend to occupy different elevational zones, the topographically diverse landscape often produces a fine-gain a mosaic of vegetation types. This mosaic is fine-scaled in the coastal ranges and xeric southern California mountains (Franklin and Woodcock 1997). Plant formations with very different physiognomy, fuel structure, fire regime types (crown fire, surface fire, mixed), and fire response of dominant woody species (resistance versus resilience) often occur in close proximity. Fire regimes in this landscape can also vary at fine spatial scales most likely as a function of fuel characteristics (Stephens et al. 2009). However, such patterns are often obliterated under extreme fire conditions as evident in some of the recent megafires that have consumed all fuels in their wake (Keeley et al. 2004, 2009b).

Nonnative plant species have been present in California for several centuries, primarily introduced during early Euro-American settlement (Klinger et al. 2006). The following sections will consider the interactions of fire, climate change, and invasive species on California's landscapes for each of three major terrestrial vegetation types: forest, shrublands and grasslands.

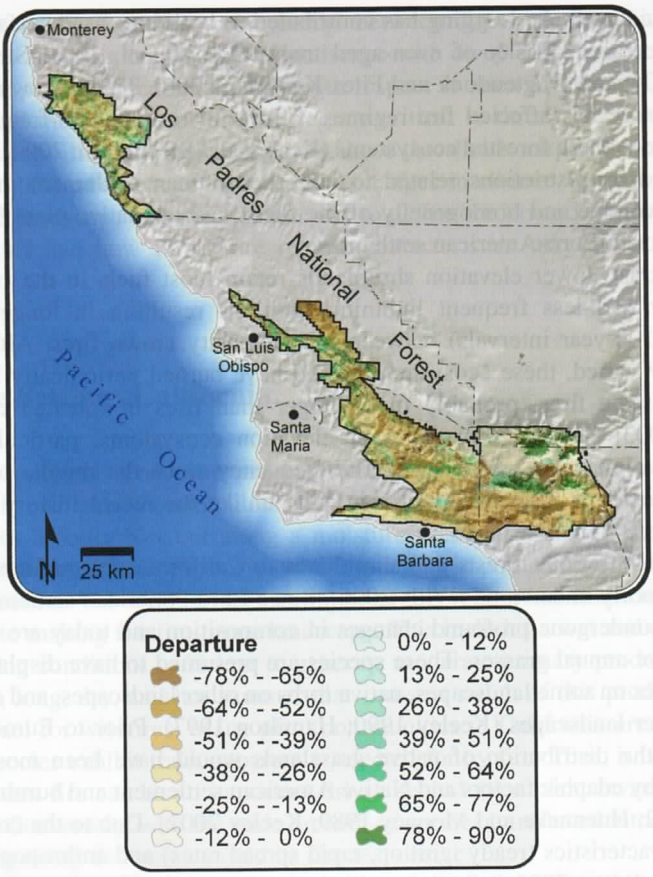

Fig. 8.1 Percentage departure of current mean fire return interval (1910–2006) from reference mean fire return interval (pre-Euro American settlement). Areas with negative departures (e.g., lowland chaparral and sage scrub) are experiencing more frequent fire today than in the presettlement period. Areas with positive departures (e.g., high elevation ponderosa pine) are experiencing less frequent fire today than in the presettlement period (Data courtesy of Dr. Hugh Safford, regional ecologist for U.S. Forest Service, Pacific Southwest Region)

8.3 Forests

Montane conifer forests in California generally have fewer alien plant species, a lower abundance of aliens, and a different collection of alien species than lower elevation foothill oak savanna or grassland (Keeley 2001; Keeley et al. 2003; Klinger et al. 2006). This follows a general pattern of decreased alien presence with increasing elevation in California (Mooney et al. 1986; Rejmanek and Randall 1994; Schwartz et al. 1996) and could involve numerous factors such as shorter growing seasons, forests with lower surface light levels, different disturbance regimes, fewer alien propagules, or fewer potential alien invaders adapted to conditions at higher elevations.

Present problems with invasive species are the result of repercussions from past management practices as well as unintended side effects of present management practices. The anomalously high woody fuel accumulation resulting from logging, livestock grazing, and fire suppression has put many forests on a trajectory away from low- or mixed-severity fire to larger, more intensive crown fires. California has experienced several of these anomalously high-intensity fires in the past decades. These have created crown gaps that appear to be outside the historical range of variability.

One such example occurred recently in southern California mountains in 2003 and eliminated most all of the conifer forests in Cuyamaca State Park (Franklin et al. 2006). Forest recovery has been slow, hindered by establishment of the early seral stage shrub layer as well as high cover of native and nonnative herbs around dry meadows (former homesteads and ranches) (Franklin et al. 2006). This is even though the dominant conifer, Coulter pine (*Pinus coulteri*), is partially cone serotinous (Borchert 1985), suggesting that it has potential for rapid reestablishment following fire. The slow recovery suggests that pine establishment, which is dependent on seed dispersal from burned cones or nearby adult trees, has been affected by the extent and severity of the fire. Also, cheatgrass (*Bromus tectorum*) was found in greater abundance in the second (wetter) postfire year than in the first (drier) (Franklin et al. 2006), and had increased further in abundance by the fourth growing season, even though it was a dry year (Franklin, submitted). However, we do not know if this nonnative grass will persist or spread as the forest regenerates and affect the future fire regime in this region.

To put this recent event into historical perspective, extensive stand replacing fires driven by easterly winds were reported in these mountains in fall 1899, in the Los Angeles Times (29 September, 1899) and the Julian Sentinel (4 October, 1899), where it was lamented "…above all we mourn the loss of our forests." It is not possible to glean details (size, severity, location) about a fire event from this kind of historical description, but it suggests that the recent crown-fire events in these forests may not have been entirely outside the historical range of variability.

Current fire management practices have the potential to influence alien plant invasions at nearly all stages, including both prefire treatments as well as postfire restoration responses (Keeley 2006b). Agencies are increasingly aware of this and are taking steps to minimize these impacts even during fire events, e.g., by checking firefighting equipment for alien propagules prior to entering wildland areas during fires.

Prefire fuel treatments pose one of the biggest risks for alien plant invasion largely because the treatments reduce surface fuels as well as open the forest canopy, both of which promote the growth of herbaceous species. Globally, forest management in western North America is unique in its focus on restoring historical conditions of forest structure and processes. The philosophy is that these forests persisted under such conditions prior to intensive contemporary land management, and thus returning forests to those conditions will bring us closer to ensuring sustainability (Millar 1997). One of the primary impacts of reintroducing historical fire frequencies is that it greatly reduces surface and ladder fuels to the point where forests retain their historical fire regime of low- or mixed-severity fires and are less

vulnerable to high-intensity crown fires. Alien species in western North America are recent introductions, however, and historical landscapes were allowed to recover after fire in an environment largely free from threat of invasion. Today the alien presence interferes with expected responses to fuel management. For example, following a series of prescription burns in ponderosa pine forests to reintroduce historical fire frequencies to the lower elevations of Kings Canyon National Park sites (Keeley and McGinnis 2007) were heavily invaded by cheatgrass (*Bromus tectorum*). When historical fire frequencies were applied through prescription burning, they were too frequent to allow canopy closure and enough litter accumulation to inhibit cheatgrass. They were also too frequent to generate sufficient fire intensity to destroy cheatgrass seedbanks. The conclusion from that experience is that future fire management may want to set its goals to some middle ground between short historical fire frequencies, which favor cheatgrass, and very long fire free periods, which lead to hazardous fuel loads.

Postfire management has also played a role in the spread of plant invaders. On USFS lands in the Sierra Nevada it has long been common silvicultural practice to utilize herbicides to eliminate the natural seral stage of ceanothus (*Ceanothus*) (Fig. 8.2a) and other shrubs in order to grow "better" ponderosa pine plantations by reducing competition between pine seedlings and shrubs. However, *Ceanothus* species are nitrogen-fixing (Delwiche et al. 1965; Conard et al. 1985) and important to ecosystem recovery following nitrogen volatilization by fires (Hellmers and Kelleher 1959; Binkley et al. 1982). The result of shrub removal is to increase the dominance of annual aliens, in particular various species of brome grass (*Bromus*) (Fig. 8.2b). Not only does this alter the native to nonnative understory composition, but it also affects habitat and seed sources for small mammals and greatly alters the fuel structure of young forests. The greater proportion of fine fuels increases the probability of fires spreading in these young stands. One example from the central Sierra Nevada is the Cleveland Fire in El Dorado County (Fig. 8.3). The extensive red brome (*Bromus madritensis*) and cheatgrass (*B. tectorum*) invasion after several

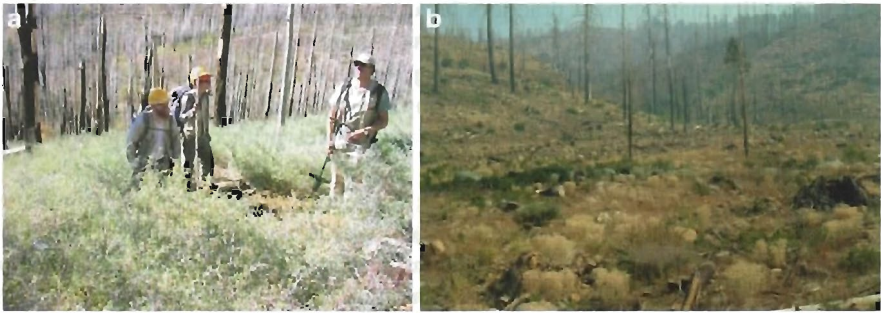

Fig. 8.2 The 2006 Star Fire in the northern Sierra Nevada burned across two national forests, which applied different postfire treatments: (**a**) The Tahoe National Forest did not use herbicides to eliminate early-seral stage shrubs such as Ceanothus, whereas (**b**) the Eldorado National Forest used repeated herbicide treatments to eliminate the shrub layer and replace it with herbaceous native and non-native species (Photos by (**a**) Tom McGinnis and (**b**) by Jon Keeley)

Fig. 8.3 The 1992 Cleveland Fire area was sprayed with herbicides and replanted with pine seedlings. Annual alien grass invasion fueled a repeat fire in 2001, the St. Pauli Fire, which destroyed a significant portion of the 8-year-old plantation (Photo by Tom McGinnis)

herbicide treatments to destroy shrubs, produced grass fuels sufficient to carry a fire at 8 years (St. Pauli Fire), which destroyed a substantial portion of the plantation.

8.4 Shrublands

Chaparral and California sage scrub are typically closed-canopy shrublands that are relatively resistant to invasion by nonnative species. The most common disturbance that sets them on a trajectory of invasion is a perturbation in the fire regime, in particular increases in fire frequency (Figs. 8.4 and 8.5). These ecosystems are highly resilient to fires at frequencies of more than 20 years but as the interval between fires decreases, more and more native species are lost due to insufficient time between fires for recovery (Zedler et al. 1983; Haidinger and Keeley 1993; Keeley et al. 2005). The lowest fire frequency threshold of tolenance varies with vegetation type and landscape position. Chaparral is generally not resilient to return intervals shorter than 20 years, whereas sage scrub in the interior cannot tolerate return intervals shorter than 10 years, although coastal versions of sage scrub can sometimes tolerate shorter return intervals. In general, these tolerances decrease with increasing site aridity; for example, pole-facing exposures are resilient to more frequent fires than those facing the equator. Other changes in fire regime that may have an impact on invasions include fire intensity (Fig. 8.6), fire season and fire size. Land management practices such as grazing and mechanical disturbance may also enhance invasion (Stylinski and Allen 1999).

Fig. 8.4 The entire chaparral scene shown here was burned in the 1970 Laguna Fire. The background has not re-burned since 1970 and this mature stand is largely free of alien species. The middle and front parts of the scene were burned in the 2001 Viejas Fire and the middle section is an early seral stage of chaparral dominated by short-lived natives and relatively few alien species. The foreground was burned a third time by the 2003 Cedar Fire and is dominated by aliens (Fig. 8.5). The high frequency of fires has also reduced the ability of natives to recover and placed the community on a trajectory that favors alien persistence (Photo by Richard Halsey)

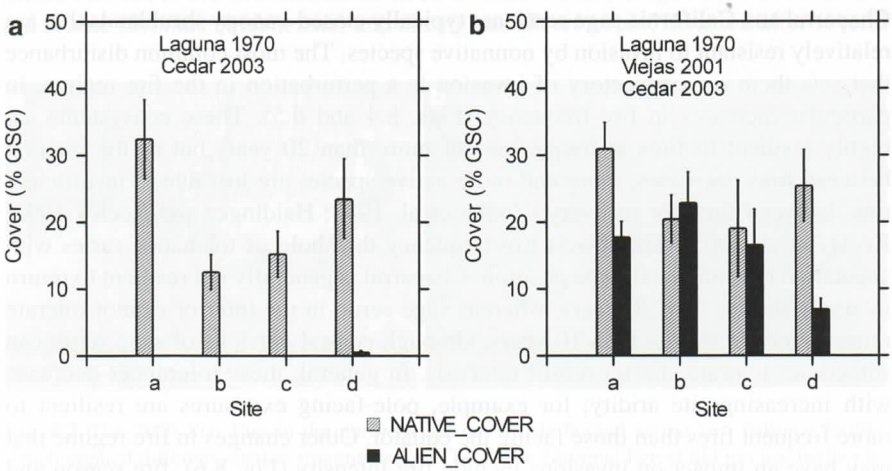

Fig. 8.5 Sites with 33 years between fires recover with little or no alien species whereas sites burned at shorter intervals have a substantial alien species load (Data from Tess Brennan and Jon Keeley)

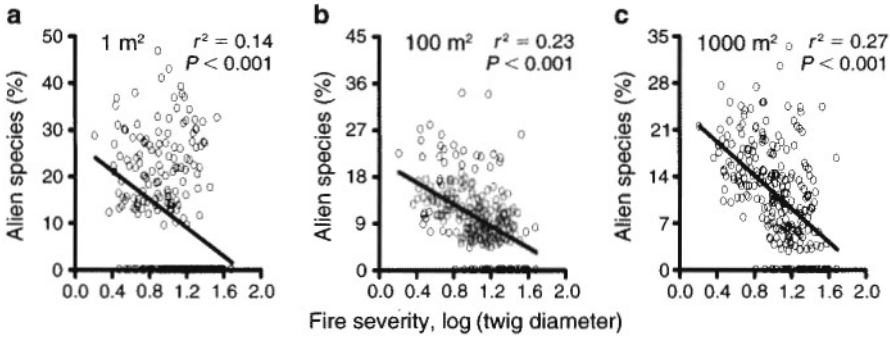

Fig. 8.6 In contrast to conifer forests where higher fire severity often increases alien invasion (e.g., Keeley et al. 2003), in chaparral increased fire severity, observed at three spatial scales, is associated with decreased alien invasion (Keeley et al. 2008)

Ozone pollution (Westman 1979) and nitrogen pollution (Allen et al. 1998) have been postulated to be involved in alien invasions of these shrublands, but probably only when coupled with some other disturbance that first opens the closed canopy shrubland and allows for annual grass and forb invasion (Keeley et al. 2005). Regional patterns of pollution, fire, and invasion are consistent with this model. Although there is a strong gradient of increasing pollution from the coast to the interior (Padgett et al. 1999), loss of native shrublands and invasion by alien grasses and forbs happens frequently in the unpolluted coastal plain and foothills (Keeley et al. 2005). Studies that have reported landscape patterns of invasion consistent with pollution have not adequately considered fire history. The frequency of fire is extremely high on interior polluted landscapes, and one of the commonly cited examples of pollution-driven type conversion from shrubland to grassland, Box Springs Mountain in Riverside County, has burned and reburned repeatedly in the last 50 years (Cal Fire 2007). Westman (1979) used landscape patterns of ozone pollution to demonstrate pollution-driven type conversion, but without any consideration of fire return intervals at his study sites. Recently Talluto and Suding (2008) found evidence for both fire and nitrogen as factors in alien invasion, and suggested that nitrogen was likely important on those parts of the landscape that were unburned. However, it is doubtful that very much of that landscape was unburned because their study used a fire history database that excluded fires less than 40 ha, and these smaller fires generally constitute more than 95% of all the fires in that region (Keeley, n.d.). Smaller fires on these landscapes likely play a crucial role in creating a patchwork mosaic of type conversion that increases alien propagule availability throughout the region.

One of the primary limitations to the pollution model is a lack of a clear mechanistic basis for how grasses displace shrubs. Numerous experimental studies have failed to detect a competitive advantage of grasses over shrubs under elevated nitrogen (e.g., Allen et al. 1998; Padget and Allen 1999; Yoshida and Allen 2001). Recently it has been proposed that interactions between nitrogen pollution and mychorrizae may

inhibit shrub seedling recruitment and give invasive grasses a competitive edge (Siguenza et al. 2006). Such a model could not account for displacement of intact shrublands since recruitment is largely restricted to open sites after fire. The mechanism for how this would work remains to be determined since most all experiments have used soil nitrogen levels characteristic of the late summer dormant season whereas soil nitrogen levels during the winter growing season are often indistinguishable between polluted and unpolluted sites. In summary, we do not rule out the possibility that nitrogen pollution plays some role in nonnative plant invasion in coastal California, but there is no evidence this can occur without physical disturbance such as fire, mechanical disturbance, or livestock grazing first opening up the shrub canopy. Once this occurs, grasses promote further burning and these landscapes may develop into a more open mixed shrubland/grassland, depending on the availability of alien seed, potentially contributing to an acceleration of the invasion process (Fig. 8.7).

Fire is a necessary ecosystem process for the sustainability of California shrublands, but postfire conditions provide a window of opportunity for alien plants to invade. Generally, the shrub canopy regenerates rapidly and most aliens are excluded during the early seral stages. Most of these aliens are annual species. An exception appears to be occurring in chaparral and sage scrub along the southern and central coast

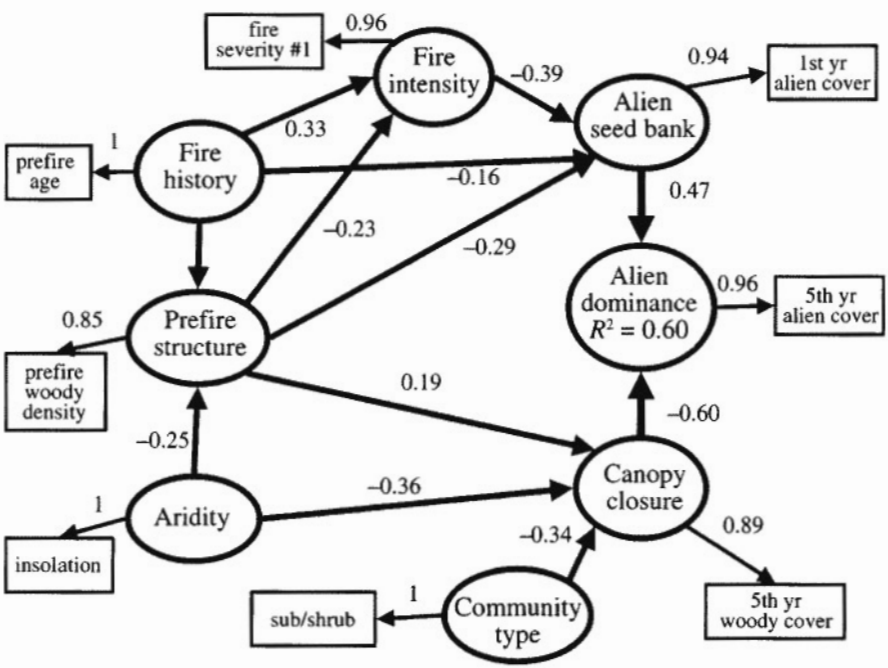

Fig. 8.7 Structural equation model for alien dominance 5 years after fire using a path analysis that separates latent (*ellipses*) and measured (*rectangles*) variables. Two latent variables in the original model, nitrogen deposition and landscape position, were not significant and were excluded. Path strength is indicated with standardized regression coefficients, and R^2 is given for the response variable of alien dominance (Keeley et al. 2005)

where an alien perennial grass, *Ehrharta calycina*, aggressively invades burned shrublands and appears to inhibit regeneration of native species (Roye 2004; D'Antonio personal observations).

When multiple fires occur within the time frame of one decade, shrub regeneration is compromised and often leads to permanent invasion. What is critical is the shortest interval between fires (Zedler et al. 1983; Haidinger and Keeley 1993; Jacobson et al. 2004). Thus, any increase in fire frequency, through either wildfires or prescription burning, should be viewed as a potential contributor to alien invasion.

Determining alien invasion is a multi-faceted problem and there are many factors that determine alien success (Fig. 8.7). One of the key factors is propagule availability (D'Antonio et al. 2001). After fire, alien propagule presence is determined by both temporal and spatial factors. Site history plays a major role and young seral stage stands are more likely to have aliens and alien seed banks than more mature stands.

Fuel structure also affects the invasion process. Heterogeneity of fuel distribution changes fire intensity (Odion and Davis 2000), and this can affect survival of alien propagules (e.g. D'Antonio et al. 1993). The invasion process can alter the dominant plant functional types, which in turn alters fire intensity. For example, invasive grasses, particularly annuals, reduce fire intensity and enhance seed survivorship in the soil (Keeley 2006b). In one case, evergreen shrublands were invaded after fire by a succulent (Zedler and Schied 1988) that altered fuel structure, potentially suppressing spread of future fires (D'Antonio 2000).

Fire management activities likewise may alter fire regimes in ways that favor alien species, both by providing suitable habitat and altering fire intensities. For example, trails or fuel breaks may promote alien invasions (Merriam et al. 2006). Although many fuel breaks have contributed to fire operations, doubtlessly many have not, and there is a need for careful evaluation of the benefits relative to the financial and resource costs of these activities.

Sites that have been highly disturbed from frequent short interval fires or other disturbances such as construction activities or livestock grazing in open shrubland/grassland associations will have a greater presence of alien species and hence seed prior to the fire than mature closed canopy systems (Stylinski and Allen 1999). Aliens tend to be annual grasses and forbs, and they alter the fire regime from an active crown fire to a mixture of surface and crown fires. This tends to increase fire frequency in younger shrubland stands. Soil temperatures during grass fires are lower than in shrub fires, favoring survival of alien propagules (Keeley 2006b).

We would expect that this phenomenon is not unique to chaparral and sage scrub but also applies to other ecosystems, particularly those closed-canopy systems that typically burn in crown fires. The level of disturbance is likely to depend on the system. As a general rule, in crown-fire ecosystems the historical fire return interval was much greater than the time to canopy closure, and this seems to hold for shrubland as well as crown-fire forested systems (Baker 2006).

Disturbances that lead to alien invasion are those that reduce the ratio, current fire-return interval : time-to-canopy closure, and when this ratio drops to less than 1, alien invasion is very likely.

Spatial patterns at many scales may affect the invasion process. One of the critical factors is the regeneration mode of the dominant shrub species. Typically mesic north facing slopes in California shrublands are dominated by vigorous resprouting species. Recovery from fire is not dependent on seedling recruitment; basal resprouts recover very rapidly. In contrast, drier sites are often dominated by non-sprouting obligate seeding species that require up to two decades of regrowth to replenish the soil seed bank. On these sites a fire interval of less than a decade hinders shrub recruitment and creates an ecological vacuum that is readily filled by alien species. However, on more mesic slopes much more frequent fires may be required to effect such a change.

The extent to which the conversion of native shrublands to alien dominated grasslands has already occurred on the California landscape is unknown, although early observations suggested that it was substantial and that Native Americans had played a significant role in the process (Cooper 1922). Nonnative-dominated annual grasslands cover a substantial portion of the wildland landscape in the state and are derived from shrublands, native grasslands or forblands. Wells (1962) examined substrate preferences for a portion of San Luis Obispo County in the central coast region and concluded that a significant portion of annual grasslands were formerly shrublands that had been displaced by frequent fires, perhaps long before Euro-Americans arrived. He suggested that substrate was an important determinant of native shrubland and native grassland distribution but not for alien-dominated grasslands, whose distribution was largely influenced by disturbance. Although fire frequency plays a major role in driving alien invasions in shrubland landscapes, other perturbations in the fire regime likewise play a role. For example, fire intensity, often measured as fire severity, is generally high in most shrubland fires. These systems are very resilient to high fire intensity and variations in intensity have little impact on native plant recovery (Keeley et al. 2008). However, as fire intensity decreases, alien invasion increases due to a variety of correlated factors. Lower fire intensity occurs in more open stands with a mixture of grasses and shrubs; thus, they are likely to have more alien propagules in the soil at the time of fire. These stands also generally have burned in the recent past and thus reburning presents an obstacle for the regeneration of the native species. Lastly, lower intensity likely enhances survivorship of alien propagules.

Fire season may have a profound role in affecting alien invasions. For example, reduced native recovery has been reported for out-of-season prescribed burns (Keeley 2006b) and this vacuum is always filled with alien species. The mechanism by which out-of-season burning decreases native plant recovery is unknown, but it is commonly attributed to prescribed burns during winter or spring that cause heating of seed banks with moist heat, which is often lethal (Parker 1987). Perhaps more important though is that winter burning greatly decreases the length of the first growing season. For most seedlings having the growing season reduced from a typical 6 months (following summer or fall burns) to perhaps as little as 1 month (following a winter burn) could limit survival during the ensuing dry summer.

We expect fire size to play a role because it increases the chances of reburning sites that were recently burned. In the 2007 wildfire season, more than 30,000 ha

that burned in southern California overlapped fires from 2002 and 2003 (Keeley et al. 2009b). Such a short return interval increases the likelihood that alien species were present, reduces fire intensity in reburned areas, and decreases native shrub survival. It is unclear if this in turn increases continuity of alien dominated sites. Fires on these landscapes burn through a mosaic of native shrublands and alien-dominated grasslands and as fire size increases the mixtures become more diverse. It is to be expected that as the boundary between burned shrublands and alien-dominated grasslands increases the latter would provide a source of alien propagules and increase the chance that adjacent shrublands would act as a sink for these aliens.

8.5 Grasslands

Although fire has long been considered to be a dominant structuring force in grasslands around the world, its history and role in California's Mediterranean grasslands are murky. Early Euro-American visitors to California reported that the indigenous peoples were burning frequently, presumably to keep landscapes free of woody species and thus creating open forblands or grasslands (Keeley 2002; Anderson 2005a, b; Minnich 2008). Reports of indigenous burning exist from coastal, Central Valley and Sierra Nevada foothill grassland-type habitat suggesting that grassland fires were an important landscape feature across the state (Anderson 2005a, 2007). Indeed, records of individual tribes suggest that at least 35 tribes used fire to manage grassland (here defined broadly to include forblands) for particular plants or for hunting (Reynolds 1959; Anderson 2007). Historical journal observations and ethnographic records present a reasonable basis for inferring that fire played a significant role in the expansion of pre-Euro-American grasslands, and this is supported by pollen records (Anderson 2005b) and phytoliths (Hopkinson 2003).

After Euro-American colonization, it is likely that the role of fire changed. The initially "open" (grassland or forbland) habitats created by indigenous burning likely were maintained by intensive livestock grazing during the mission era (Minnich 2008). During the last 100 years, fire was apparently used to convert shrublands to annual grasslands as the expansion of agriculture in the late 1800s reduced available open lands for grazing (Tyler et al. 2007). As these newly formed and existing grasslands were utilized for livestock and crop production, burning appears to have become an uncommon activity although records about this are poor. Indeed, Greenlee and Langenheim (1990) estimate that prior to widespread livestock grazing, fire frequencies in the central coast near to human settlements were potentially every 1–5 years. After the cessation of indigenous burning and with the advent of widespread crop agriculture and livestock grazing they estimate that fire frequencies dropped to every 20–30 years. Although these numbers are largely speculative, it is conceivable that there have been dramatic changes in fire occurrence in grass-like habitats over the past two centuries.

The invasion of European annual grasses into California's grasslands that apparently occurred beginning in the late 1700s is thought to be due to a combination of intensive year round livestock grazing and conversion to crop agriculture followed by land abandonment (Jackson 1985). The frequent use of fire by indigenous peoples to manipulate composition likely aided the establishment of opportunistic annual grasses that arrived with Euro-American settlers (Keeley 2002). It has been hypothesized that frequent burning of shrublands to create grasslands resulted in landscapes susceptible to rapid establishment of alien grasses and forbs without any grazing or crop agriculture (Keeley 2002). Although the hypothesis that frequent indigenous burning contributed to the vulnerability of California grassland to the initial invasions cannot be tested, it also cannot be discounted since it is now known that many nonnative annual species can tolerate or increase with grassland fires. Thus, it is reasonable to assume that the common occurrence of "grassland" fires in the 1700s and early to mid 1800s contributed to the rapid spread of some nonnative grassland species.

In contrast to the other ecosystems discussed in this chapter, California grasslands are already very heavily invaded by nonnative species and it is not clear that fire will make them more susceptible to further invasion. Since European annual grasses dominate sites that have not burned for decades, it is also clear that they do not rely on fire in any way to maintain their dominance. Hypotheses regarding the persistent dominance of annual grasses are reviewed elsewhere (e.g. Corbin et al. 2007). Also in contrast to forests and shrublands, managers of grassland are trying to use fire to manipulate composition away from nonnative species or to "tip the balance" in favor of native species (Corbin et al. 2004). Given the highly diverse nonnative flora in California grasslands, and that on many landscapes annual grasslands occupy former shrubland sites, a goal of eliminating nonnative species and reestablishing native grasslands is unrealistic. Nevertheless, fire is a useful tool for manipulating composition in some areas and under some circumstances.

In a meta-analysis of the outcome of fire management treatments across California grasslands, Bainbridge and D'Antonio (in prep.; reanalysis of Corbin et al. 2004) found that fire can depress the abundance of European annual grasses, but only for the immediate season after fire. Whether a single fire tips composition towards natives is site-dependent and generalities are difficult to find. Generally, single fire events slightly depress alien annual grasses but may increase exotic forbs, depending on the site and species pool. For example, in annual grass-dominated sites in the Carrizo plains, experimental burning in spring promoted the exotic forb *Erodium cicutarium* and the native forb *Phacelia ciliata* (Meyer and Schiffman 1999) but the dominant invasive annual grasses were unaffected by fire. Likewise, Reiner et al. (2006) and Reiner (2007) report an increase in both native and nonnative forbs with fire. They used repeated fires (up to 13) to reduce nonnative grass dominance on their sites in the California Central Valley.

Efforts to reduce specific invasive species with fire may be more successful than general efforts to shift composition, but only if fire is repeated often. For example, DiTomaso et al. (1999) used repeated fire to reduce the abundance of yellow star thistle (*Centaurea solstitialis*), a noxious weed in California grasslands. Because

the seeds of this species live for many years (Callihan et al. 1993), at least three fires are necessary to obtain reductions in star thistle. However, these treatments were never sustainable, as within a few years of ending burning, starthistle populations rebounded (Kyser and DiTomaso 2002). Clearly, prescribed burning provides only temporary reduction and does not affect sustainable control of this alien, and may even exacerbate the alien situation (Fig. 8.8). Likewise, DiTomaso et al. (2001) and Betts (2003) used multiple fires to reduce the abundance of the invasive grasses medusahead (*Taeniatherum caput-medusae*) and barbed goat grass (*Aegilops triuncialis*), but what happens once fire is removed is unknown.

Several studies point to the important role of preburn composition in determining the relative effects of fire on native vs. nonnative species. Native species tend to

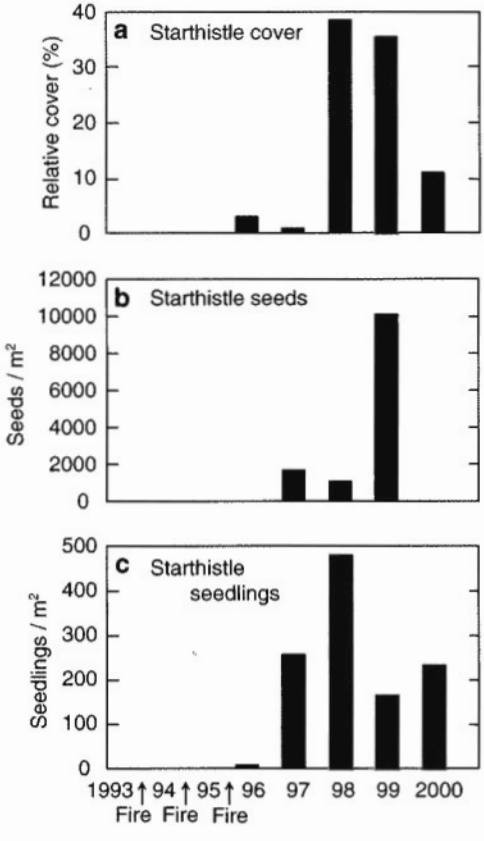

Fig. 8.8 Yellow starthistle (*Centaurea solstitialis*) cover and seed and seedling production following three consecutive annual burns applied to extremely dense populations of this noxious alien weed. Immediate postfire results were very promising (DiTomaso et al. 1999), but follow-up studies indicate that burning destabilized these grasslands and allowed subsequent reinvasion once burning was stopped (Kyser and DiTomaso 2002)

increase in sites where they were already reasonably abundant (Harrison et al. 2003), but decrease in sites where they are rare to begin with. DiTomaso and Johnson (2006) reported that the invasive black mustard (*Brassica nigra*) increased to almost complete dominance after management fires in a Sierra Nevada foothill grassland site. The species was present as a dormant seed bank prior to fire and can respond rapidly after fire. As a consequence, this species can present surprises when fire is used to target other species. For example, Moyes et al. (2005) used prescription burning with the goal of targeting ripgut brome (*Bromus diandrus*). The treatment was successful in nearly eliminating this grass, but the space was readily occupied by fire-stimulated germination of the mustard seed bank (Fig. 8.9).

It is widely believed that cattle grazing or targeted grazing by goats can reduce fuel accumulations, and create discontinuities in fuel. Conceptually then, grazers should be a useful tool for reducing the spread of fire over landscapes. However, every year fires ignite in grassy vegetation and grazed grasslands are observed to burn. To evaluate how grazing influences the probability of successful ignition or fire spread would require a landscape analysis of where fires start, the patterns they follow as they spread, and a knowledge of the grazing regime at the local scale across the region. Fire-spread modeling does support the notion that fuel discontinuities can reduce fire spread rates and fireline intensities (Finney 2001), but strongly wind-driven fires have been shown to burn across a range of vegetation types, fuel ages, and fuel structures (Moritz 2003). These fires may be indifferent to past grazing in grasslands, as was observed in October 2007 when a Santa Ana-wind-driven fire burned through heavily grazed pastureland (Fig. 8.10) that fire behavior models would predict should not carry fire. Indeed, a study of fire spread

Fig. 8.9 Postfire shift in cover from the non-native annual grass *Bromus diandrus* (lower left foreground), which was targeted in a prescribed burn, to mustard (upper right foreground) in the Santa Monica Mountains National Recreation Area of Ventura County, California (Photo by Andrew Moyes)

Fig. 8.10 Heavily grazed grasslands in Pamo Valley, San Diego County, burned in the 2007 Witch Fire (Photo by Richard Halsey)

rates in 121 grass-fueled fires suggested that wind speed is more important than grass type or fuel structure (e.g. standing versus cut, dense versus thinned) in driving fire spread rates (Cheney et al. 1993). Nevertheless, fire intensity and spread rates are demonstrably lower in grazed grassland under some conditions (Diamond et al. 2009) and grazing, if it leaves little residual dry matter, can reduce standing fuel and fireline intensity (Davison 1996; Diamond et al. 2009). Thus, grazing is being used to create a landscape scale fuel mosaic that under the right conditions (not extreme) could reduce fire spread rates and intensity in grass-dominated vegetation (McAdoo et al. 2007). Many of the large fires in California, however, burn under extreme weather conditions (Mensing et al. 1999; Moritz 2003), and under these conditions, grazing is unlikely to be important in modifying fire behavior (e.g. Launchbaugh et al. 2008).

8.5.1 Fire and the Grassland/Shrubland Matrix

At the time of Euro-American settlement, it is possible that vegetation heterogeneity was less than today due to the widespread use of fire to keep vegetation "open." It has been documented today that fire contributes to the current landscape mosaic of grassland, shrubland, and woodland (e.g., Callaway and Davis 1993). On grassland sites prone to shrub colonization, a reduction in fire frequency gradually leads to conversion of grassland to shrubland (Keeley 2002) with accompanying increases in standing fuel and the potential therefore for higher-intensity fires. The trend of increased presence of woody vegetation on landscapes previously supporting extensive grassland is particularly apparent in the San Francisco Bay area. Contrary to conventional wisdom, this trend is not related to disruption of the natural fire regime by fire suppression, but rather due to a reduction in anthropogenic ignitions and

cessation of intensive livestock grazing (Keeley 2005). Thus, this so-called shrubland invasion is perhaps better viewed as a recolonization following the cessation of anthropogenic disturbance, at least for the dominant native shrub, coyote bush (*Baccharis pilularis*). However, non-native invasive shrubs such as scotch, french, and spanish brooms (*Cytissus scoparius, Genista monspessulana* and *Spartium junceum* respectively) and gorse (*Ulex europaeus*) are spreading widely into grasslands in the northern and central coast regions. Germination of the brooms is stimulated by fire, and recurrent short return interval fires can be used to reduce the broom seedbank and reduce standing adult plants (Alexander and D'Antonio 2003a, b). Nevertheless, using fire to control these nonnative invaders presents a challenge in increasingly urban or suburbanized landscapes and with rising societal concern about the efficacy, safety, and environmental impacts of controlled burning.

Over the past decade, the potential role of atmospheric nitrogen (N) deposition in influencing California vegetation has been recognized (Weiss 2006) and detailed mapping of nitrogen plumes suggests that a substantial fraction of coastal habitats and portions of the California deserts could be affected by N deposition. Nitrogen deposition promotes invasive annual grasses in open scrub vegetation of the Mojave Desert (Brooks 2003), and in nutrient-stressed serpentine grasslands near the coast (Weiss 1999). These alien grasses in turn either increase, or have the potential to increase, fire frequency (Beatley 1966; D'Antonio and Vitousek 1992). Although this grass/fire cycle can happen independent of N deposition (D'Antonio and Vitousek 1992; Keeley 2006b), N deposition could accelerate the onset of such a cycle in some habitats.

8.6 Future Directions for Fire and Invasive Species Interactions in California

Alien species presence on California landscapes will likely increase under future conditions. Two issues that need to be given serious consideration are the continuation of certain fire management practices and changes in fire regimes induced by global changes in human demography and climate. The most critical stressors are likely to vary with vegetation type.

8.6.1 Forests

In understanding future impacts on forests, we distinguish between two fire regime types in forests of western North America: those driven by herbaceous understory fuels (e.g., ponderosa pine forest) and those with dead litter as the fuel source (e.g., mixed conifer forest). Each is likely to respond differently to climate change and they may not be equally susceptible to invasion by alien species under altered fire regimes. A major paleoecological reconstruction of the American Southwest

based on tree ring analysis showed that major fire years coincided with extreme drought. However, antecedent (1–3 years prior) wet conditions affecting grass (fine fuel) production were significantly correlated with fire extent only in ponderosa pine forest. The lack of any significant lag effect of antecedent moisture on fire activity in mixed-conifer forest was explained in terms of the greater persistence of snow pack in spring and lack of importance of fine fuels in fire dynamics (Swetnam and Betancourt 1998). Ponderosa pine forests may be more susceptible than other forest types to altered fire regimes under global warming, and to invasion by non-native herbaceous species that could, in turn, affect the fire regime.

In conifer forests throughout the mountainous western USA, the interactions of fire, a warming climate, and invasive herbaceous vegetation are of great concern (Dale et al. 2001; Brooks et al. 2004; Keeley 2006a; Millar et al. 2007). Fewer but larger higher-severity fires resulting from warmer windier conditions predicted under climate-warming scenarios could homogenize the forest landscape mosaic into large even-aged patches. On the other hand, reduced fuels due to higher decomposition rates and reduced tree seedling establishment, or to the establishment of annual grasses, could lead to lower fire intensity and higher frequency under global warming. How might changes in the patch mosaic size, in conjunction with spatially varying pressure from invasive plant species, affect forest succession on these landscapes? Will it lead to increasing "type conversion"? How big a role will exotic invasive species play in forested areas? Will nonnative grass cover increase in forested areas leading to feedbacks in the fire cycle, promoting high–frequency low-severity fire?

Predicted changes in fire regime, driven by climate warming, are likely to reduce the extent of old-growth fire-affected forests. Kaufmann et al. (2007) describe a conceptual model of late successional or old-growth forest structure in fire-prone forest types. An important factor is the scale of patchiness. Increase in very large fires will erase fine-scale mosaics of differently aged stands, especially if they are severe.

Increased spring and summer temperatures, projected by virtually all climate models for future decades owing to anthropogenic climate change, could reinforce the trend toward longer fire seasons and large wildfires. A study of northern California also projected similar trends of more fires and larger burned areas in some regions of the state under the warmer windier conditions that are projected by climate models (Fried et al. 2004). However, ecological feedbacks are likely to complicate these projections, and will be discussed in the following sections. More frequent larger fires in recent decades in mid- to high-elevation western forests coincide with warmer temperatures and earlier spring snowmelt (Westerling et al. 2003, 2006), although the number of fires *per se* and snowpack are not generally correlated in the west (Medler et al. 2002).

Extensive areas of the California Floristic Province comprise broadleafed evergreen forest (Douglas-fir–tanoak–madrone, ponderosa pine–black oak, and canyon live oak–Coulter pine)—about 20% of the land area of California or about equal to the conifer forest area (Lenihan et al. 2003). The mixed evergreen forest formation is predicted to expand northward and upslope at the expense of subalpine conifer forest types under global warming scenarios. Lenihan et al. (2003) also suggested

that anthropogenic climate change in the coming century might be less likely to affect fire weather (summer drought will persist) and more likely to affect California's fire regimes by changing the amount and character of fuels. This might increase inter-annual variability in the area burned—i.e., with more extreme events. Therefore, fire-prone forests, extensive and perhaps severe forest fires, and invasive species are all likely to expand in California forests under global warming.

In addition to nonnative grass invasions, there is also growing concern about the outbreaks of insects (such as pine beetles) and emerging infectious diseases on the landscape. For example, historic fire suppression in mixed-evergreen forest of northern coastal California has led to land cover change, the expansion of broadleaf woodland at the expense of chaparral, reduction in spatial heterogeneity of plant communities, and subsequent increased susceptibility of oak woodlands to lethal infection of *Phytophthora ramorum*, an introduced plant pathogen causing Sudden Oak Death (Moritz and Odion 2005). Somewhat more subtle changes in forest structure due to fire suppression are considered to be factors contributing to the effect of white pine blister rust (*Cronartium ribicola*) on *Pinus lambertiana* in the Sierra Nevada (van Mantgem et al. 2004). Despite disturbing trends in losses of this tree, models suggest managers still have time to alter the outcome of this invasion and prevent complete demise of this key forest species.

8.6.2 Shrublands

During the Zaca Fire of 2007, over 800 km of fire breaks were bulldozed through relatively pristine old-growth chaparral. Although restoration is planned, these areas have the potential for greatly exacerbating the alien species problem in this region. Particularly troubling is that they surround and dissect a wilderness area that previously was relatively isolated from aliens. The strategy behind this extensive use of clear-cutting chaparral is akin to what political commentator Ron Suskind (2006) describes as the 1% doctrine. Namely, in some circles if there is a 1% chance that an action will pay off, it is considered a legitimate course of action. In other words, there is a hierarchy of values that preempt any sort of cost–benefit analysis. Although fire management has never had such an extreme policy, if a treatment had any potential benefit in reducing fire hazards it was considered a legitimate strategy. However, agencies are increasingly faced with having to balance numerous issues other than just fire hazard reduction, and often conservation of natural resources comes in conflict. Balancing these issues will necessitate a more thorough cost-benefit analysis to fire management decisions so that the impacts on resources such as alien plant invasion are considered in the equation. One might expect that a cost-benefit analysis that considered potential alien invasions might have resulted in a more judicious use of fire breaks in the Zaca Fire. Of course, these decisions cannot be made during major fire events, but rather must be thoroughly considered and incorporated into a fire management plan with specific analyses that consider all resource costs in association with perceived benefits of reduced fire hazard.

Application of a cost benefit analysis to fire management will be easier in some ecosystems than in others. Besides the economics, the issues to be balanced are fire hazard and resources. Forested ecosystems with a history of frequent surface fire regimes are assembled from both overstory and understory species well adapted to frequent fires. A frequent fire regime is also compatible with reducing fire hazard, and thus balancing the resource costs and fire hazard–reduction benefits of prescribed burning is relatively easy compared to many other ecosystems such as chaparral.

Crown-fire ecosystems like chaparral are a different story. The historical fire frequency was significantly longer than forested ecosystems and the vegetation comprises many species that are rather vulnerable to frequent fire. Fire management strategies designed to incorporate frequent prescription burning as a cure for fire hazard are often at odds with resource conservation. Because humans share much of this landscape it is inevitable that in some cases fire hazard reduction will preempt resource issues. When fuel treatments such as frequent prescribed burning or mechanical crushing (Fig. 8.11) are applied to this landscape they have the potential for doing resource damage. Thus, a cost-benefit analysis might result in a more judicious use of such treatments.

Of course, with no end in sight for population growth, the fire management and alien plant problems are destined to become worse unless some changes occur in development patterns. Smart growth that promotes infilling within the development footprint, rather than continuing urban sprawl, has some potential for slowing this problem.

Fig. 8.11 Fuel treatment of chaparral through crushing. Such sites will invariably become dominated by alien species and native communities are not likely to regain this site for an extremely long time. These treatments are designed solely for fire hazard reduction and can be viewed as sacrificing natural resources (Photo by Wendy Boes)

8.6.3 Grasslands

The future frequency and impact of fire in California grasslands will depend on climate, nitrogen deposition, and grazing, all of which influence the density and nature of the fuel bed. Development and human presence within the landscape will also influence the nature of fuels, frequency of ignitions, control efforts, and subsequent burning patterns. The regional species pool will also determine which species are present to respond to fire events.

Models of future climate vary in terms of the direction and amount of rainfall change projected for California grasslands. Substantial increases in California precipitation were predicted by early general circulation models (Hadley Centre HadCM2) and CCM1 (Dukes and Shaw 2007). Increased precipitation within the growing season, however, may have little effect on productivity in California grassland settings (Pitt and Heady 1978; Reever-Morghan et al. 2007; Dukes and Shaw 2007). Thus, it may have little effect on fire frequency or intensity. The recent Hadley Centre model version 3 (HadCM3) and the Geophysical Fluids Dynamic Laboratory model (GFDL) predict decreases in total annual precipitation in California (Pope et al. 2000; Cayan et al. 2006). Reduced growing season precipitation events could lead to a decline in grassland productivity. A reduction in fuel density and biomass could reduce fire intensities when fires burn through grassy vegetation.

Recent Global Change Models that predict a decrease in growing season precipitation for California grasslands also predict that precipitation will be packaged into fewer more extreme events. To date there have been no field experiments that recreate these climate conditions. We suggest here that such repackaging could favor native perennial species because individual events will saturate the soil beyond the ability of introduced annual grasses to transpire water. Native perennial species, by contrast, with their deeper roots and longer period of activity, could access this water over a wider range of depths and time periods. Native perennial shrubs such as coyote brush (*Baccharis pilularis*) readily colonize grassland under wet conditions (Williams et al. 1987). Conversion to coyote brush shrublands should decrease fire frequency due to the change from fine summer–dry fuel to evergreen shrub fuel (though not everywhere, c.f. Keeley 2005). Fire intensity might increase, however, due to the greater biomass accumulation in such a shrubland and the tendency for shrublands to burn as crown fires. If the beneficiaries of altered precipitation events are native perennial grasses, it is more difficult to predict their impact on fire regimes. In tropical savannas, some recent studies have shown that introduced grasses can increase fuel loads by up to seven-fold greatly increasing fire intensities (D'Antonio 2000; Rossiter et al. 2003), but these systems contain both native and nonnative grasses that are substantially larger than typical grasses in California. No studies have yet compared fire frequency and intensity between native perennial bunchgrass-dominated vs. alien annual grass-dominated California grassland.

8.7 Conclusions

The California Floristic Province spans a large latitudinal range in a topographically diverse area of western North America. The entire region experiences a Mediterranean climate with warm dry summers, but the fire regimes in the grasslands, shrublands, woodlands and forests of California are as diverse as the terrain. In the historical period the landscape mosaic was affected by half a millennium of grazing, anthropogenic burning, logging, fire suppression, urban expansion, and the deliberate or accidental introduction of invasive plants and other alien species. The future of the regional ecosystems facing combined impacts of climate change, land use change, nitrogen deposition, altered fire regimes, and species invasions must be considered in light of the history of the landscape.

Montane forests were subjected historically to logging, grazing, and fire suppression, leading to fire exclusion. Restoration of fire in these landscapes must be implemented cautiously in light of the threat of invasive herbaceous plant species. This is particularly urgent because although forested areas at higher elevations have historically been less threatened by alien plants than lower elevation shrublands and grasslands, this threat is likely to increase, as is the likelihood of large or severe fire, in association with anthropogenic climate warming. Native shrublands have been altered in the distant and recent past by frequent human-ignited fire. The greatest future threat to this ecosystem again lies in the combined impacts of increased fire frequency due to human population pressure and climate change, and the subsequent spread of invasive plant species. Exotic species probably became well established in native herbaceous plant formations several centuries ago as a result of the deliberate use of fire by people. In some cases, a specific prescription of repeated fire treatments has been used successfully to control non–native species, but in other cases prescribed fire has actually promoted them. Anthropogenic global warming may reduce fire frequency or intensity in native grasslands, but the altered precipitation regime that is predicted to occur may actually favor native plant species. A systematic approach is required to understand the complex and potentially synergistic impacts of fire, invasive species, climate change, and land use change on the landscape mosaic.

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