

Invasive plants and fire management in California Mediterranean-climate ecosystems

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ABSTRACT: The most widespread alien invasion in California are the non-native dominated annual grasslands that originated by both decimation of native perennial grasslands and the type conversion of native shrublands. This latter process continues today at an accelerating pace due to increasing fire frequency resulting largely from human carelessness. These alien dominated grasslands are in a quasi-equilibrium that is relatively resistant to recolonization by native shrubs but vulnerable to invasion by new noxious alien weeds. Prescription burning is widely considered an appropriate means of controlling new alien invasions in these annual grasslands, however, successes appear to be short-lived. It is argued that because the grasslands owe their origin to widespread disturbance, application of fire and other disturbances will never create equilibrium conditions necessary to keep unwanted alien species out. Eliminating noxious aliens targeted for removal will require an understanding of the ecological processes that created these communities that are so vulnerable to invasion. Limited use of disturbance that is applied in a manner that impacts target species more than potential competitors, coupled with active restoration of the native flora is hypothesized to be the only means of eliminating noxious species on a sustainable basis.

1 INTRODUCTION

Alien species comprise 25% of the flora in Mediterranean-climate California (Rundel 2000). They are not randomly distributed but favor lower elevation grasslands and disturbed shrublands (Keeley et al. 2003). The greatest dominance of aliens is found in annual grasslands. The most common aliens include *Avena barbata*, *A. fatua*, *Bromus madritensis*, *B. hordeaceus*, *B. diandrus*, and forbs such as *Erodium cicutarium* and *Brassica nigra*, which are native to the Mediterranean Basin. This association represents a new type for the California region, as native annual grasslands were apparently unknown prior to these introductions. Physiognomically the closest approximation would have been annual forb-dominated herblands with species of *Amsinckia*, *Cryptantha*, *Plagiobothrys*, *Eschscholzia*, *Lupinus* and others (Wester 1981, Holstein 2001). This herbland occupied many of the drier sites in the Central Valley and likely graded into native perennial grasslands in the foothills of the coastal and interior ranges.

Historically the alien dominated annual grasslands had two origins. One was by displacement of native bunchgrass grasslands during the 19th century (Hamilton 1997). This is thought to have been driven by a combination of drought and over-grazing and today is not an important means of annual grassland expansion due to the limited area of remaining native grassland. A second origin was through type conversion of shrubland communities by repeated burning (Keeley 1990). This

may seem counterintuitive since California chaparral and sage scrub shrublands are widely recognized as fire adapted ecosystems. However, such ecosystems are not adapted to fire per se, but rather to a particular fire regime, one that includes a period of extended disturbance-free conditions for development following fire. High fire frequency stresses these systems beyond their level of tolerance, causing the displacement of many native shrub species with alien annual grasses and forbs (Zedler et al. 1983, Keeley 2001). Frequent burning has long been an important rangeland management technique for increasing grazing lands and this type conversion continues today through careless burning by our burgeoning population. It is a major means for alien plant invasion in California (D'Antonio et al. 1999).

2 ALIEN PLANT INVASION OF NATIVE SHRUBLAND LANDSCAPES

This process actually began long before aliens reached our shores. Native Americans routinely burned shrublands at a high frequency to favor native annual forbs and perennial grasses (Keeley 2002). Considering the very large Native American population in the California foothills, and the general unsuitability of shrublands for human habitation, it is very likely that much of the landscape at the time of European settlement was in a quasi-disequilibrium between herbs and shrubs. This landscape would have been primed for rapid alien invasion and undoubtedly this contributed to the rapid pace of invasion, which apparently occurred even before the widespread overgrazing that is thought to have been a major contributor to the formation of the annual grassland type (Heady 1977).

At the time of Spanish and Mexican settlement it would appear that there was sufficient rangeland such that further expansion by shrubland burning was not actively practiced, at least there are few records of burning for rangeland expansion. However, soon after the American takeover and subsequent influx of settlers during and after the Gold Rush of 1849, rangelands were rapidly overstocked. By the 1880s rangeland was in short supply and settlers accelerated type conversion of chaparral and related shrublands to alien-dominated grasslands (Brown and Show 1944). These practices diminished the water-holding capacity of watersheds and were in part responsible for the formation of the first forest reserves that later became the U.S. Forest Service (Lockman 1981). With increasing government control this casual "rangeland improvement" practice was controlled by the state in formal programs of prescription burning and type conversion (Heady and Pitt 1979).

Today alien-dominated annual grasslands comprise about a third of all mediterranean-climate wildland landscape in California (Jones and Stokes 1987) and they continue to expand (Keeley 2001). Humans are the major cause of fires on these landscapes and as more and more people settle in the region, fire frequency increases (Keeley and Fotheringham 2003a). This pattern continues today as urban sprawl is expanding road infrastructure, bringing more and more people and fires in contact with shrubland ecosystems.

3 SHRUBLAND SUSCEPTIBILITY TO ALIEN PLANT INVASION

Susceptibility to invasion in native shrublands is greatest after fire or other disturbances and is best viewed as a race between rates of shrub recovery and alien colonization. The former is a function of life history and site factors and the latter a function of proximity of alien seed sources (D'Antonio et al. 2001). In addition to disturbance frequency and propagule source, there are three environmental variables that determine shrubland susceptibility to invasion: precipitation, solar insolation and soil nutrients. The first two determine site aridity and thus the dominant shrub life history type and the third affects annual plant success (Fig. 1).

Arid chaparral is typically dominated by non-sprouting obligate seeding species (Keeley 1986, Meentemeyer and Moody 2002). This life history is vulnerable to fires at less than 10 year intervals because of insufficient time for developing a dormant seedbank. Frequent fires decimate their

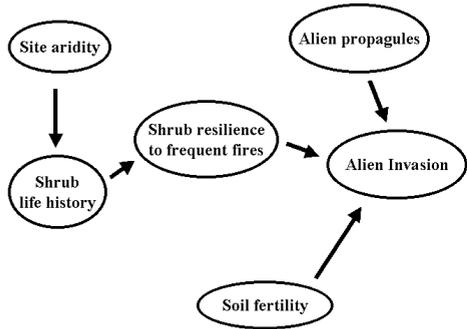


Figure 1. Conceptual model of relate site factors such as precipitation, solar insolation, soil fertility with disturbance and propagules source in the annual alien invasion process in California mediterranean shrubland landscapes.

populations and they are not rapidly replaced by indigenous species. This ecological vacuum is rapidly exploited by alien annuals. Once established these aliens persist because obligate seeding species are only weakly adapted to spatial dispersal (Keeley 1992). In contrast, mesic sites favor obgate resprouting shrub species that are more resilient to frequent disturbance. Fires once a decade will not generally displace these species because rapid resprout growth recaptures the site and replenishes vitality of roots and lignotubers. As a consequence of these differences in shrub life history, mesic and xeric sites differ markedly in the amount of disturbance required to effect changes in the herb/shrub ratio (Fig. 2), and on these landscapes herb colonization is largely by alien annuals.

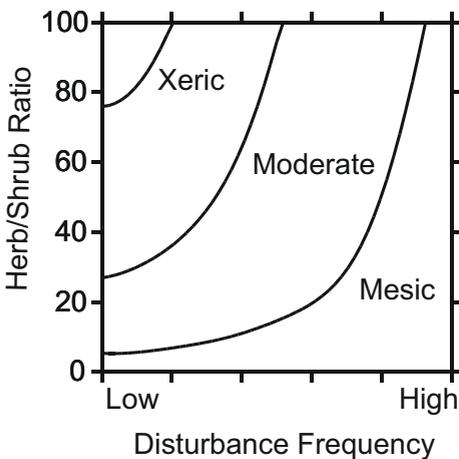


Figure 2. Interaction between disturbance frequency and aridity on the balance of herbs and shrubs.

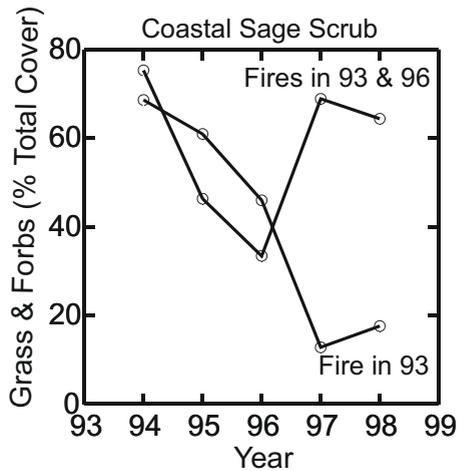


Figure 3. Postfire cover of herbaceous species after a single fire and after two fires 3 years apart (from Keeley 2002).

Soil nutrients also play an important role in determining rate of alien annual invasion. Under nutrient-limited conditions the ephemeral life cycle limits their ability to sequester sufficient nutrients

for growth. In mediterranean-climate ecosystems with severe soil nutrients, such as Western Australian heathlands or South African fynbos, the annual life history represents a minor portion of the flora, in contrast to relatively more nutrient-rich soils of the other three mediterranean-climate regions (Keeley and Fotheringham 2003b). Even within regions such as California there are marked differences in soil nutrients, e.g., nutrients in the chaparral of the San Pedro Martir Range of Baja California are comparable to the low nutrient status of fynbos and heathlands (Vizcaino and Ramirez 1997), and thus it is to be expected that annual aliens may be far less of an invasion threat on those sites.

At lower elevations evergreen chaparral is replaced by a more diminutive semi-deciduous shrubland known as sage scrub. Two very different forms, both floristically and ecologically, are the coastal and interior associations, and they have very different susceptibilities to alien plant invasion. In general sage scrub is more resilient to frequent fires than chaparral but there even this association can be displaced with fires more frequent than every 4-8 years (Fig. 3). As with chaparral there are markedly different susceptibilities dependent upon site aridity. This is most evident between coastal and interior sites. The former are dominated by vigorous obligate resprouting species that quickly regain their former stature within 5 years after fire. On interior sites many of the species are facultative sprouters and often sprouting is only marginally successful (Keeley 2004). The slow recovery of the dominant shrubs on these interior sites (Fig. 4) makes them susceptible to alien invasion and many of the most invaded landscapes are the interior valleys and foothills. In all of these vegetation types, alien persistence following fire is a function of the speed at which shrubs regain dominance (Fig. 5).

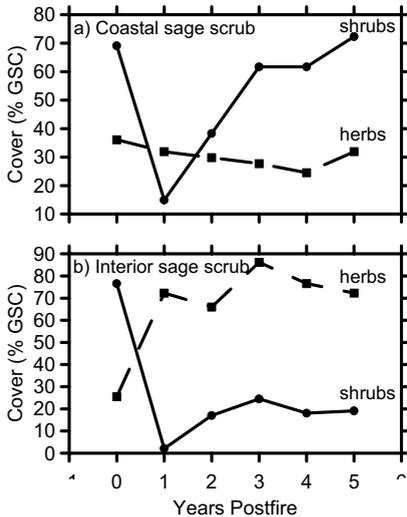


Figure 4. Postfire changes in herb and shrub cover for (a) coastal and (b) interior sage scrub (redrawn from O'Leary and Westman 1988).

3.1 Air pollution impacts

Air pollution has long been proposed as a factor driving alien invasions on these landscapes. For example Westman (1979) proposed that ozone was an important factor driving the displacement of native shrubs with alien annuals. The evidence for this was the fact that ozone was more strongly correlated with alien annual presence than other factors he considered, however, he failed to include any measure of fire frequency. Since ozone levels in the Los Angeles Basin (where this study was conducted) follow aridity gradients with the highest levels in the interior valleys, it is certainly possible the important determinant in these correlations was the slower postfire recovery and thus greater susceptibility to invasion of interior sage scrub (Fig. 4).

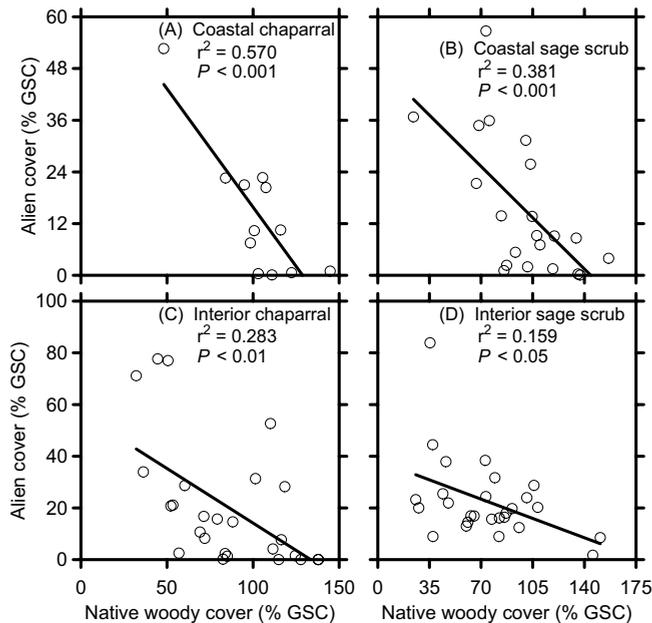


Figure 5. Relationship between shrub and subshrub cover and alien annual cover for coastal and interior populations of chaparral and sage scrub; % GSC = percentage of ground surface covered, number of sites were (A) n=14, (B) 22, (C) 26, and (D) 28 (data from J. Keeley unpublished data).

Nitrogen deposition has also been implicated in alien success (Allen et al. 2000) and this is likely to be more important on extremely nutrient deficient soils (Huenneke 1990). At present there is no clear cut evidence that nitrogen deposition alone can drive the invasion process on otherwise undisturbed communities. Possibly nitrogen deposition may affect the trajectory of alien invasion after disturbance, although in an extensive study of postfire regeneration in chaparral and sage scrub vegetation no correlation was found between postfire total soil nitrogen and invasive cover for the first 5 years after fire (Table 1). Other studies have also failed to find a relationship between total soil nitrogen and invasive success in these systems (Stylinski and Allen 1999).

3.2 Impact of landscape patterns

Landscape patterns are increasingly recognized as important drivers of the invasion process (With 2003). In general alien seed banks fare poorly under high intensity crown fires typical of shrubland fire regimes. As a consequence, following fires in mature shrublands, invasion will be highly dependent upon landscape patterns that place unburned sites or patches of low intensity burning in close proximity. For example, wildfire size and distribution have been shown to affect alien colonization (Turner et al. 1997). Natural landscape features may also play an important role in the invasion process. For example, in the foothills of central California the mosaic distribution of oak savanna and chaparral is a potentially critical factor in the invasion process in chaparral as these savannas are dominated by alien annuals, which are the same species that colonize chaparral after fire (Keeley et al. 2003). Even though fires may burn across both communities, the low intensity surface fires in savannas will ensure high alien seedbank survival that will provide a ready propagule source for invasion of adjacent burned chaparral.

3.3 Fire management practices

Throughout the Western U.S. fire suppression policy has been highly effective at excluding fire from many conifer forest types, in particular ponderosa pine forests. This has created undesirable conditions such as increased probability of high intensity crown fires in forest types that historically burned in low intensity surface fires (Allen et al. 2000). This creates major problems for the sustainability of such forests because even though reproduction is highly dependent upon burned sites for successful seedling recruitment, survival of parent seed trees is required (Keeley and Stephenson 2000). Extensive crown fires that eliminate seed sources can result in a persistent type conversion to shrublands or even alien-dominated grasslands. As a consequence there is a widespread need for restoring low intensity pre-settlement fire regimes to these forest types (Allen et al. 2002). However, unlike pre-settlement conditions, these landscapes now have an extraordinary palette of alien species posed to take advantage of these natural disturbance regimes. Several studies indicate fire restoration may carry with it a cost in terms of increasing alien invasions (Crawford et al. 2001, Keeley et al. 2003).

One of major management activities directed at forests with unnaturally high fire hazard is the application of pre-fire fuel manipulations. Any fuel reduction treatment, for example fuel breaks, that is directed at removing woody plant cover has the potential for increasing alien plants (Fig. 6). Fuel breaks are particularly problematical because they are typically long roadway like manipulations, and like roads, which are known to act as conduits for alien dispersal (Gelbard and Belnap 2003), fuelbreaks too can act as corridors of alien propagules, conducting them deep into otherwise undisturbed wildlands. Fuelbreaks by themselves probably have limited direct impact on invasion of adjacent closed canopy chaparral shrublands. However, reduced fuel loads result in lower fire intensity on fuel breaks and thus greater alien seedbank survival during fire. Thus, in the early postfire years, when these developing shrublands are the most vulnerable, those sites adjacent to fuel breaks are subject to an unnaturally high rain of alien propagules.

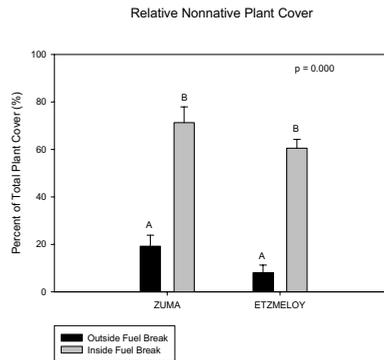


Figure 6. Proportion of total plant cover due to alien species on and off fuel breaks in southern California chaparral (data from K. Merriam and J. Keeley, unpublished data).

Postfire "rehabilitation" treatments are commonplace following fires throughout the Western U.S. Indeed, within days of a major wildfire, federal agencies provide a formal inventory of treatments perceived to be required in order to reduce the subsequent impacts on property and infrastructures such as roads and dams. Known as the BAER (Burned Area Emergency Rehabilitation) team, these investigators commonly prescribe seeding of alien grasses as a means of stabilizing slopes and reducing subsequent erosion (Robichaud et al. 2000). In recent years these projects have become increasingly sensitive to alien weed infestations. For example in the middle of the 20th century *Brassica nigra* (black mustard) was the preferred choice for these projects in burned chaparral. Due to the invasion of agricultural lands this practice was abandoned, however, the dormant fire-

stimulated seeds of this species persist and still produce abundant postfire populations on some sites (Went et al. 1952, Keeley 2001). For many years *Lolium multiflorum* (annual ryegrass) was the preferred species for seeding in chaparral because it was generally not persistent for more than a few years. However, this alien grass is capable of colonizing and persisting in mesic grasslands. Genetically altered cereal grains are increasingly used because of their weak persistence. However, weed contamination is a potential problem with any seeding treatment; e.g., one recent investigation calculated that a BAER seeding project had inadvertently broadcast seeded over 1 billion *Bromus tectorum* (cheatgrass; a major pest species in the Western U.S.) seeds on the 2000 Cerro Grande Fire in New Mexico (Craig Allen, personal communication, January 2004).

4 USE OF FIRE FOR CONTROL OF ALIEN INVASIONS

Fire is often proposed as a treatment for both restoring natural ecosystems as well as targeting noxious alien species, and a number of studies have demonstrated short term successes. However, there is reason to doubt that broadcast burning of California landscapes by itself will provide any lasting impact on alien persistence. In general alien species establish due to disturbance and thus the application of further disturbance is a bit like homeopathic medicine treating disease by application of the disease element. Neither has proven effective.

One of the more widely studied applications of fire for treating alien invasions is for targeting noxious species. In general these studies are successful at short term elimination of the targeted species; however, in most all cases it is replaced by other alien species. This is often considered acceptable because either the target species is a recent introduction or there is reason to believe it offers an early opportunity for eradication, or the target species alters ecosystem processes in ways that are more undesirable than other alien species. For example, alien thistles (species of *Centaurea*, *Carduus*, *Cirsium*, and *Cynara*) represent new and undesirable functional types in annual grasslands. They affect ecosystem processes for example by reducing forage availability (Thomsen et al. 1997). One of the more widespread and noxious thistles in California annual grasslands is *Centaurea solstitialis* (yellow starthistle), and various burning treatments have shown some promise for greatly reducing this species (DiTomaso et al. 1999). However, longer term study shows that this species rapidly reestablishes once the burning is halted (Fig. 7).

A very different invasive plant problem is the colonization of annual grasslands by shrubs known as brooms (DiTomaso 1998). These species originate from fire prone habitats in the Mediterranean Basin, but like our own chaparral shrubs they are vulnerable to excessive frequency of burning. Thus, the application of repeat fires will kill shrubs and decimate the seed bank; however, residual seeds do persist as a source for continued colonization (Swezy and Odion 1998, Alexander and D'Antonio 2003).

The primary reason broadcast burning fails to effect long term changes in these invasive plant populations is because these treatments fail to recognize that in many cases it was disturbance of the native shrublands that created the annual grasslands to begin with and reestablishment of the endogenous woody vegetation is likely the only way to return stability to these systems. In general, fire is not likely to be a useful restoration technique unless accompanied by active replanting efforts. One misconception is that because perennials often out-compete alien annuals that seeding with perennials will displace the non-natives. This, however, fails to recognize that competitive characteristics of seedlings are often quite different from mature individuals. For example, established bunchgrasses would appear to be strong competitors against alien annuals, however, seeding with these perennials is doomed to failure because at the seedling stage they are weak competitors against the vigorous annuals. Seeding with native annuals, however, is a viable means of altering the competitive relationships between native and alien species (Seabloom et al. 2003). A viable strategy may be coupling of disturbances such as fire, that temporarily diminishes alien species, coupled with active restoration of natives is likely to be the only viable long term approach. In the event of limited resources for restoration, an over-riding philosophy should be one

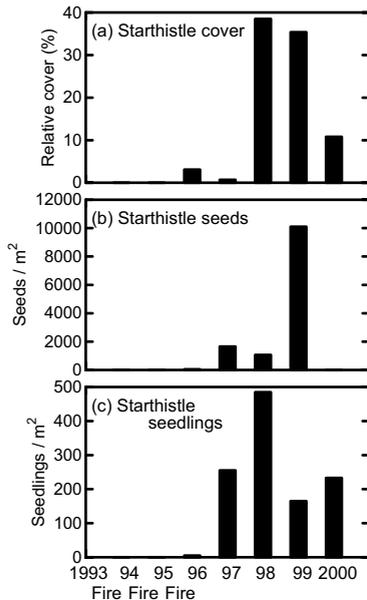


Figure 7. Yellow starthistle (*Centaurea solstitialis*) cover and seed and seedling production following three consecutive annual burns applied for the control of this noxious alien weed. Immediate results were very promising (DiTomaso et al. 1999) but follow-up studies indicate that burning destabilized these grasslands and allowed subsequent reinvasion (Kyser and DiTomaso 2002).

of restricting fire use and other disturbances to localized sites where it will maximize the impact on aliens and minimize the impact on natives. It is critical to work within the natural ecosystem processes by treatments that provide a sort of natural selection that favors natives over aliens.

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