

# Experimental Approaches to Conservation Biology

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## 11 Tipping the Balance in the Restoration of Native Plants

### *Experimental Approaches to Changing the Exotic:Native Ratio in California Grassland*

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#### SUMMARY

As exotic species increasingly threaten native biodiversity, habitat managers have turned to a variety of tools designed to increase the efficiency of plant-restoration projects. These efforts include eliminating exotic competitors through mechanical removal, herbicide application, or fire, and increasing native species' competitiveness relative to that of exotic species through reduction of soil nitrogen availability, grazing, prescribed burning, or biological control. In this chapter, we evaluate the ability of experimental tests of these techniques to favor native species in California grassland ecosystems. We found no evidence that any of the strategies consistently favored native species relative to exotic species. Outcomes were highly case specific and likely varied with biotic and abiotic conditions in the experimental systems. Several studies suggest that these techniques are more successful in reducing specific invasive plant species in California grasslands rather than in increasing the success of native revegetation.

Limited availability of native propagules in the experimental systems likely limited the extent to which restoration techniques actually promoted native species. The most promising strategy for increasing native components in invaded ecosystems is likely to be the coordination of multiple strategies that address exotic-species abundance, native-seed or -seedling availability, and the postestablishment competitiveness of the native species. Such an application of an integrated "pest" management approach to the restoration of degraded habitats holds greater promise for the successful reestablishment of native biodiversity than simply targeting exotic species for removal.

## INTRODUCTION

Exotic species increasingly threaten native biodiversity in natural habitats worldwide. Habitat managers trying to restore native-species richness and abundance face the daunting challenge that exotic species frequently are superior competitors in sites where the natives and exotics co-occur. For example, invasive *Spartina* spp. (cordgrass) in western North American estuaries are capable of excluding such native salt-marsh species as *Spartina foliosa* (California cordgrass) and *Salicornia virginica* (pickleweed) (Daehler and Strong 1996). Reintroduction of native species into these invaded ecosystems is unlikely to succeed as long as the exotics are competitively superior.

Habitat managers and restoration ecologists must utilize a variety of tools to tip the competitive balance toward native species and away from exotic species while increasing the efficiency of plant-restoration projects. Current tools include eliminating exotic competitors through mechanical removal, herbicide application, or fire, and increasing native species' competitiveness relative to exotics' through reduction of soil nitrogen (N) availability, grazing, or prescribed burning or through the introduction of biological control agents. These tools are often applied repeatedly or in combination, but to provide a lasting increase in the native component of degraded ecosystems they frequently need to be used in conjunction with reintroduction of native-plant species either as seeds or seedlings. The application of these tools may also be constrained by practical considerations such as safety or toxicity concerns (e.g., fire or herbicide application) or limited habitat area (e.g., fire or grazing).

The need to enhance the success of native-plant restoration and to increase native species' competitiveness is particularly urgent in California grassland ecosystems. Grasslands are a major component of the state's natural vegetation, comprising nearly 10 million ha, or 25% of the state's surface area (Heady et al. 1991). The state's grasslands are used extensively for livestock production (Wagner 1989) and recreation and are habitat for many of California's state-listed threatened and endangered plants. During the last two centuries, invasion by European annual grasses and forbs into California grasslands, modifications of land use, and, possibly, changes in the region's climate have resulted in a dramatic, large-scale conversion from dominance by perennial bunchgrasses, forbs, or both to dominance by Eurasian annual species (Burcham 1970; Crampton 1974; Bartolome, Klukkert, and Barry 1986; Baker 1989; Hamilton 1997). Whereas perennial species such as *Nassella pulchra* (purple needlegrass), *Bromus carinatus* (California brome), *Elymus glaucus* (blue wildrye), *Danthonia californica* (California oatgrass),

*Poa secunda* (pine bluegrass), and *Festuca* spp. (fescue) were thought to dominate some of the region's grasslands prior to European settlement, introduced grasses such as *Bromus diandrus* (ripgut brome), *Bromus hordeaceus* (soft chess), *Avena* spp. (wild oat), and *Vulpia* spp. (annual fescue) are dominant today, even in stands where some native bunchgrasses have persisted.

Life-history and growth characteristics of exotic species offer substantial advantages over those of native perennial species in disturbed habitats that are frequently the targets of restoration efforts. Seedbank composition in California grasslands is highly skewed toward exotic annual species (Champness and Morris 1948; Major and Pyott 1966; Dyer, Fossum, and Menke 1996; Holl et al. 2000; Alexander 2001). Seed production by annual species substantially exceeds the number of seeds necessary to replace the population (Young and Evans 1989), whereas the establishment of perennial species has frequently been shown to be limited by seed availability (e.g., Peart 1989a; Kotanen 1996; Hamilton, Holzapfel, and Mahall 1999). Furthermore, annual seeds in growth chambers have been shown to germinate earlier and under a wider range of temperatures than native perennial seeds (Reynolds, Corbin, and D'Antonio 2001). The more abundant and earlier-germinating annual grass species can form dense stands and monopolize resources, thereby restricting the growth and survival of native seedlings (Bartolome and Gemmill 1981; Dyer, Fossum, and Menke 1996; Dyer and Rice 1997; Hamilton, Holzapfel, and Mahall 1999; Brown and Rice 2000). As a result, competitive interactions between native and exotic grasses in California have usually been shown to strongly favor the exotic species, especially in recently established native populations (Dyer, Fossum, and Menke 1996; Dyer and Rice 1997; Hamilton, Holzapfel, and Mahall 1999; Brown and Rice 2000).

The large competitive advantages that some exotic species enjoy over natives suggest that efforts to restore native-plant biodiversity in exotic-dominated grasslands in California must improve the competitiveness of native species relative to that of exotic species. In this chapter, we review the successes and failures of techniques either being proposed or employed over a large scale to improve conditions for native species during grassland restoration. These techniques include the reduction of N in N-enriched habitats through sawdust addition or repeated biomass removal, grazing, prescribed burning, herbicide application, and biological control. We focus on efforts to alter composition in sites that are currently grassland rather than on the *de novo* creation of grassland from recently plowed or otherwise heavily disturbed sites.

## REDUCTION OF PLANT-AVAILABLE NITROGEN

Ecosystem nitrogen enrichment is a common barrier to native-plant restoration. Past fertilization (Vitousek et al. 1997), atmospheric nitrogen deposition (Bobbink 1991; Jefferies and Maron 1997), fire (Wan, Hui, and Luo 2001), habitat disturbance (Hobbs and Mooney 1985), and invasion by nitrogen-fixing shrubs (Vitousek et al. 1987; Maron and Connors 1996) can all increase soil nitrogen availability. While general characteristics of non-native invading plant species have proven elusive (Mack et al. 2000), enhancement of N availability has been shown to favor fast-growing invasive species in a variety of habitats (e.g., Huenneke et al. 1990; Vinton and Burke 1995; Maron and Connors 1996). Restoration in N-enriched habitats must, therefore, deal with the question of how to promote slower-growing native species in competition with faster-growing exotic species.

Invasion of northern coastal prairie grasslands in California by a variety of N-fixing shrubs commonly known as brooms—for example, *Genista monspessulana* (French broom) and *Cytisus scoparius* (Scotch broom)—and *Ulex europaeus* (gorse) has been shown to have significant impacts on soil N availability and plant community composition (Randall, Rejmánek, and Hunter 1998; Haubensak 2001). Haubensak (2001) found that N availability was three times as high in a broom-invaded grassland than in an adjacent uninvaded grassland. The colonization of coastal prairie grasslands by the native shrub *Lupinus arboreus* (bush lupine) has had similar effects on N cycling and community composition as broom invasion (Maron and Jefferies 1999). Individual shrubs grow rapidly, producing a dense canopy that shades out native grassland species. In northern California coastal prairies, repeated cycles of lupine colonization and death lead to a doubling of total soil N, greatly increased N availability, and thus increased vegetative production (Maron and Jefferies 1999). Maron and Connors (1996) documented that these cycles cause a large-scale shift in grassland composition from native perennial to exotic annual species. Increased N levels even after broom removal or lupine dieback may continue to favor exotic species and hamper efforts to reintroduce native species.

Two promising methods to reduce plant-available N and increase the competitiveness of slower-growing natives in such N-enriched habitats are (1) the addition of a labile carbon source such as sucrose or sawdust (e.g., Morgan 1994; Alpert and Maron 2000; Paschke, McLendon, and Redente 2000) and (2) repeated mowing followed by biomass removal (Collins et al. 1998; Maron and Jefferies 2001). The addition of a carbon source is assumed

to increase microbial N immobilization and decrease plant-available N (Morgan 1994; Alpert and Maron 2000; Paschke, McLendon, and Redente 2000). Repeated mowing and biomass removal are assumed to remove N in plant biomass that would otherwise be remineralized as plant litter is produced and decomposes. Under lower N conditions, growth of all vegetation would be expected to decrease, but if faster-growing exotic species are disproportionately affected by lower soil N concentrations, slower-growing native species may benefit indirectly owing to reduced competition.

#### *Carbon Addition*

Carbon addition has successfully reduced the abundance of exotic species in California grassland (Alpert and Maron 2000), shrubland (Zink and Allen 1998), and sagebrush–bunchgrass (Young et al. 1998) communities, as well as in shortgrass steppe ecosystems in Colorado (Reever Morghan and Seastedt 1999; Paschke, McLendon, and Redente 2000). Alpert and Maron (2000) tilled 1.5 kg m<sup>-2</sup> of sawdust into bare N-rich patches left after the death of bush lupine individuals in a coastal prairie site. The patches were not experimentally seeded with natives, and recruitment into them depended on seed rain or the seedbank. Native biomass comprised only 8–12% of the total biomass in all treatments, reflecting the highly invaded nature of these ecosystems. Sawdust addition significantly reduced the aboveground biomass of exotic grasses, although the biomass of exotic forbs was unaffected. Sawdust addition also showed no significant benefit for native-species richness or biomass. Thus, while sawdust addition successfully reduced exotic grass abundance, there was no evidence that it increased the occurrence of native species.

Two studies in our lab employed similar experimental approaches to assess the ability of sawdust addition to benefit native species in ecosystems invaded by two different types of N-fixing shrubs (Corbin and D'Antonio 2004a; Haubensak 2001). Following removal of shrubs and understory vegetation in a broom-invaded coastal scrub ecosystem and another lupine-invaded coastal prairie, seedlings of three species of native perennial grasses were transplanted into experimental plots, half of which were seeded with exotic annual grasses. In the postlupine site, we added a third treatment consisting of three species of exotic perennial grass competitors. Sawdust was added to half the plots (600 g m<sup>-2</sup> yr<sup>-1</sup>) for 2 years.

Native species did not benefit from the addition of sawdust following removal of French and Scotch broom in either growing season (Haubensak 2001). Instead, exotic annual grasses significantly reduced the growth and survival of all three native species, whether sawdust had been added or not.

Apparently, the effect of competition with annual species was so strong that it overwhelmed any potential effect of sawdust addition.

Sawdust addition showed greater promise in reducing the competitive advantage of exotic annual grasses in the lupine-invaded coastal prairie (Corbin and D'Antonio 2004a). In the first growing season, sawdust decreased the competitive suppression of seedlings of two native grass species by exotic annual grasses, but there was no benefit for native species competing with exotic perennial grasses. In the second year, sawdust addition did not affect the competitive interactions between natives and either exotic annual or exotic perennial grasses. In fact, the native perennial grasses that survived the first year of competition with annual grasses significantly reduced the aboveground productivity of annual grasses, even without sawdust addition. We concluded that sawdust addition provided no significant benefit to native plants in this system, where target individuals were planted as seedlings, and survival was high in all treatments. Competition between native species and exotic annual grasses was most asymmetric (in favor of the exotics) in the first growing season, after which native species were capable of significantly reducing the productivity of annual grasses (Corbin and D'Antonio 2004b). The possibility remains that sawdust addition may provide greater benefit to restoration projects in which seedling survival in the first year is less certain or in which native species are introduced as seeds.

#### *Mowing and Biomass Removal*

Maron and Jefferies (2001) examined the effectiveness of mowing and removing aboveground biomass in reducing soil N and favoring native species in a coastal prairie grassland that had experienced lupine invasion and dieback. The mowing and removal of plant biomass for five growing seasons reduced exotic grass biomass and doubled the number of forb species present as compared to unmanipulated control plots. However, mowing had no effect on the number of perennial grass species, most likely because of a lack of native propagules. The 5-year experiment removed approximately 9% of the total soil N as plant biomass but was not sufficient to induce N limitation of vegetation. In fact, unmowed plots experienced a significant reduction in soil N in the form of nitrate leaching losses in the fall and early winter, a reduction that was nearly equivalent to the biomass removal in mowed plots. The authors concluded that while mowing was effective in reducing exotic biomass and increasing the species richness of forbs (although many were exotic), mowing was unable to reduce soil N levels enough to favor the reestablishment of native grasses. The study also

suggested that reduction of soil N content in ecosystems that have become suitably enriched may require long-term treatment, owing to the slow turnover of soil organic N pools.

#### *Livestock Grazing*

Over the past decade there has been increased interest in the use of livestock grazing to reduce the biomass of introduced species and increase the diversity and abundance of native species in California grassland settings (e.g., Menke 1982; Edwards 1995, 1996; Reeves and Morris 2000). The California Cattlemen's Association, for example, suggested that carefully controlling the timing and intensity of livestock grazing can promote native diversity in California grasslands (Reeves and Morris 2000). Grazing may benefit native vegetation by disproportionately targeting exotic biomass, thereby reducing the exotics' competitive advantages; by reducing exotic seed production; or both. By contrast, some conservationists believe that livestock grazing has contributed to the degradation of many California grasslands and that its persistence is inimical to restoration of native-species richness (Fleischner 1994; Painter 1995).

D'Antonio et al. (2001) reviewed livestock-grazing studies from throughout California in an attempt to quantitatively evaluate the use of grazing as a tool to reduce exotic-species cover and promote native biological diversity (see Table 11.1 for a complete listing). Their initial goal was to conduct a meta-analysis of the size and direction of grazing's effects on native and exotic plants using all the available published and unpublished data sets from California. Meta-analysis is a statistical way of synthesizing results from different studies on a common topic (Gurevitch and Hedges 1993). They calculated an "effect size" in each study for each response variable (e.g., native forb cover) based on the ratio of the variable in the treated area (grazed) compared to the control (ungrazed). They assessed the effect of grazing on the measured response variables across studies using the mean of the pooled effect sizes. They found that most studies lacked adequate controls, lacked replication, or had no available measurement of among-plot variability and hence were not useable for meta-analysis. A summary of the six studies that fit the meta-analysis criteria demonstrated that livestock grazing was associated with an increase in the cover of native perennial grasses for those sites (Figure 11.1). Contrary to the claims of others (Thomsen et al. 1993; Kephart 2001), these studies showed a slight negative effect of livestock grazing on native-forb abundance and a positive effect of grazing on the abundance of exotic forbs. However, the results should be interpreted with caution because this small number of studies is inadequate for a true meta-analysis, and the

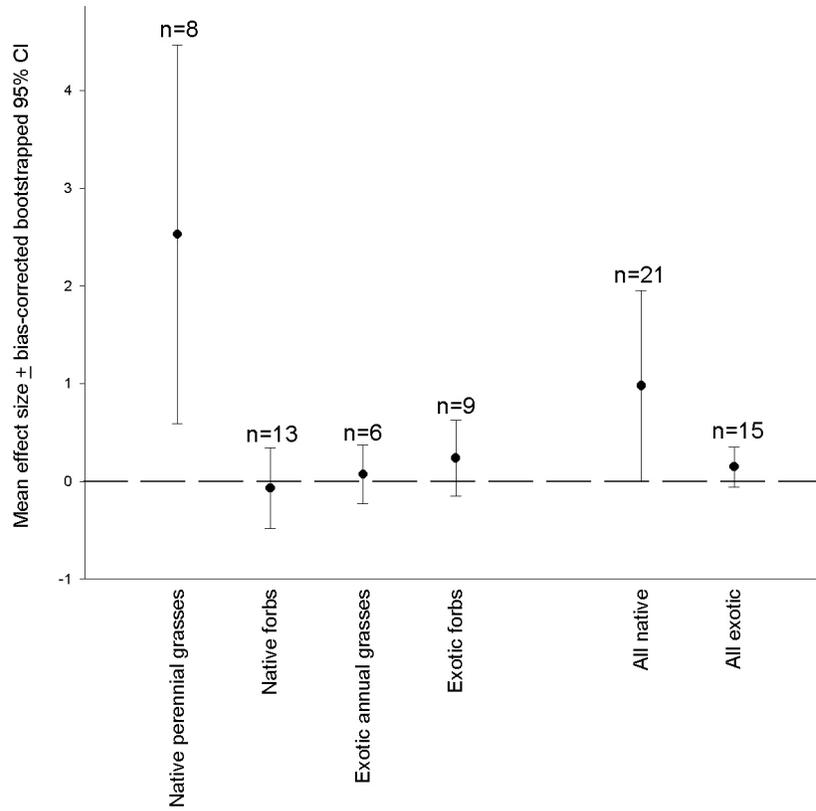


Figure 11.1. Effect of grazing on grassland plant life-form groups (based on studies reviewed by D'Antonio et al. [2001]). Values are the cumulative effect sizes (mean natural log of the response ratio  $[X_{\text{grazed}} / X_{\text{control}}]$  weighted by study variances  $\pm$  95% C.I.; n = number of effect sizes). Number of effect sizes may be greater than the number of published studies, owing to multiple comparisons within the same study.

addition of just a few studies could reverse the overall outcome. In addition, these studies represent a small subset of the California grassland and may not be representative of the state as a whole. Sadly, the often heated debates over the impact of livestock grazing and the role, if any, that grazing should play in grassland restoration are likely to continue until many additional careful quantitative studies are conducted across the full range of grassland habitats in the state.

Many grazing studies in California focus on the responses of particular native species, such as the native perennial bunchgrass *Nassella pulchra*, to

TABLE 11.1 *Studies of the impact of fire, grazing, or both on the species composition of California grasslands*

<i>Reference</i>	<i>Study Type</i>	<i>Grassland Type</i>
Ahmed 1983	Fire	Valley and foothill
Arguello 1994	Fire	Bald hills
Bartolome, Stroud, and Heady 1980; Jackson and Bartolome 2002	Grazing	Annual, valley, and foothill
Bartolome et al. in press	Fire and grazing	Valley and foothill
Bartolome and Gemmill 1981	Grazing	Various
Bett 2003	Fire	Valley and foothill
Cooper 1960	Grazing	Coastal prairie
Cox and Austin 1990	Fire	Vernal pool
Delmas 1999	Fire	Wildflower field
DiTomaso, Kyser, and Hastings 1999	Fire	Valley and foothill
Dyer and Rice 1997	Fire and grazing	Vernal pool
Dyer, Fossum, and Menke 1996; Fossum 1990	Fire	Vernal pool
Eller 1994	Grazing	Annual
Elliot and Wehausen 1974	Grazing	Coastal prairie
Foin and Hektner 1986	Grazing	Coastal prairie
Garcia-Crespo 1983	Fire	Valley and foothill
Graham 1956	Fire	Annual grassland–savannah
Hansen 1986	Fire	Alkali grassland–vernal pool
Harrison 1999	Grazing	Serpentine-forb
Hatch, Bartolome, and Hillyard 1991	Fire and grazing	Valley and foothill

the cessation of grazing or to particular grazing regimes. This species is, arguably, the most commonly used species in grassland restoration projects and the best studied of the native grasses. Yet a review of the relevant literature readily demonstrates the difficulties inherent to generalizing about the effects of livestock grazing. Huntsinger et al. (1996) and Dennis (1989) found substantial variation in the response of *N. pulchra* individuals to simulated grazing (clipping) among different populations. Genetic differences among the populations may explain the differential population response, although this variable was not explicitly examined. Likewise, enclosure

TABLE 11.1 (continued)

Reference	Study Type	Grassland Type
Hatch et al. 1999	Fire and grazing	Coastal prairie
Heady 1956	Grazing	Valley and foothill
Hektner and Foin 1977	Grazing	Coastal prairie
Keeley, Lubin, and Fotheringham 2003	Grazing	Oak woodland
Kephart 2001	Fire and grazing	Valley and foothill
Kneitel 1997	Fire	Valley and foothill
Langstroth 1991	Fire and grazing	Vernal pool
Larson and Duncan 1982	Fire	Annual
Marty 2001, 2002	Fire and grazing	Vernal pool
Merenlender et al. 2001	Grazing	Valley and foothill
Meyer and Schiffman 1999	Fire	Annual
Micallef 1998	Grazing	Annual, valley, and foothill
Parsons and Stollgren 1989	Fire	Annual
Pollack and Kan 1998	Fire	Vernal pool
Porter and Redak 1996	Fire	Valley and foothill
Reeves and Morris 2000	Grazing	Various
Saenz and Sawyer 1986	Grazing	Bald hills, woodland
Stromberg and Griffin 1996	Grazing	Valley and foothill
Thomsen et al. 1993	Grazing	Annual
TNC 2000	Fire and grazing	Wildflower field
White 1967	Grazing	Valley and foothill
York 1997	Fire	Annual
Zavon 1977	Fire and grazing	Annual

studies from several parts of central and northern California have demonstrated increases (Hatch et al. 1991), decreases (Hatch et al. 1999), and no change (White 1967; Stromberg and Griffin 1996) in the abundance of *N. pulchra* in response to protection from grazing. Some studies have observed fluctuations of *Nassella* abundance at the same site, but because of a lack of appropriate controls, the changes could not clearly be attributed to cessation of grazing (Bartolome and Gemmill 1981; Merenlender et al. 2001).

Several investigators have attempted to use livestock grazing to control particular exotic species, such as *Centaurea solstitialis* (yellow starthistle),

in California grasslands. For example, Thomsen et al. (1993) found that the timing of grazing was critical to the outcome of their experimental grazing treatments: late-spring and early-summer grazing greatly reduced yellow starthistle abundance relative to controls, although grazing did not eliminate the starthistle populations. At the same time, though native-plant-species richness was not recorded, the investigators observed an increase in populations of three disturbance-responsive native forbs with this late-spring grazing. Such targeted grazing may be useful in grassland restoration projects if the goal is simply to reduce a noxious weed.

Careful timing of grazing to coincide with the period of exotic seed production has the potential to benefit native species by reducing exotic germination and productivity in subsequent growing seasons. However, few studies have quantified the effect of grazing on the seed production of exotic species. Stromberg and Kephart (1996) argued that mowing or grazing for 2–3 years following native-plant restoration is likely to reduce exotic annual biomass and exotic seed production. Maron and Jefferies (2001) found that mowing reduced annual propagules and induced seed limitation of one of the most abundant exotic grass species, *Bromus diandrus*. We do not know, however, whether livestock grazing is capable of producing the same effect.

Overall, the existing data are insufficient to conclusively discern a relationship between livestock grazing and California's native grassland plants, or to evaluate the potential of grazing to enhance native-species richness and cover. Grazing has been shown to benefit native species in some individual studies, but its effects do not appear to be generalizable among studies or among years. Studies such as those of Stromberg and Griffin (1996) and Safford and Harrison (2001) suggest that grazing does not have as strong an effect on native species as has previously been suspected, but more research is needed to explore the generality of such conclusions. Many managers are now using controlled burning in combination with grazing to reduce exotic species and promote natives, and grazing may have a more predictable impact in combination with other techniques such as fire. Specific grazing regimes, with modest levels of grazing carefully timed to coincide with critical periods of exotic vegetation growth and seed production, have the greatest potential to be useful in a restoration context. Further research that employs both extensive quantitative surveying of properties with different grazing histories over a range of carefully recorded environmental conditions plus properly designed experiments is necessary to clarify the utility of grazing in increasing native competitiveness.

### *Prescribed Fire*

Land managers are increasingly turning to prescribed fire in an attempt to reduce the dominance of exotic plant species such as N-fixing shrubs (e.g., brooms and gorse), herbaceous forbs (e.g., yellow starthistle and *Taeniatherum caput-medusae* [medusahead]), and exotic grasses (Pollack and Kan 1998; DiTomaso, Kyser, and Hastings 1999; Bossard, Randall, and Hoshovsky 2000; Alexander 2001). Fire has the potential to instantaneously reduce exotic vegetation biomass, including standing biomass and residual litter, and can be applied to a relatively large landscape. Fire can also influence the seed crop and germination of native and nonnative species in subsequent growing seasons. Although fire can directly kill seeds on adult plants or fire-intolerant seeds in the soil, transient increases in light availability, soil surface temperatures, and soil nitrogen availability frequently associated with fire can also increase seed germination and seedling survival of fire-tolerant species. Frequent fires, however, may reduce available soil N and grassland productivity because they cause repeated volatilization of N and increased root death (Seastedt, Briggs, and Gibson 1991).

Efforts to generalize as to the impacts of fire on native-plant abundance and species diversity have proven difficult, in part because of the differential responses of various life-form groups to fire. Whereas some studies have shown dramatic increases in native-forb abundance in the first year following fire (Pollack and Kan 1998; Meyer and Schiffman 1999; DiTomaso, Kyser, and Hastings 1999), other studies have demonstrated minimal or negative effects of fire on native perennial grasses (Dyer, Fossum, and Menke 1996; Hatch et al. 1999). The effects of fire on the grassland vegetation also vary with time because the reductions in annual productivity that are frequently observed following fire tend to be temporary (Keeley 1981).

D'Antonio et al. (2001) reviewed the role of fire in structuring California grassland vegetation and the abundances of four life-form groups: native perennial grasses, native forbs, exotic annual grasses, and exotic forbs (see Table 11.1 for a complete listing). They conducted a meta-analysis on nineteen studies of prescribed or natural fires in California grassland. The investigators did not augment native propagules or seed availability, so the effect of seed limitation on the grassland response was not a controlled factor. They found that fire tended to shift grassland composition toward native forb species in the first year, but native perennial grasses were generally negatively affected by fire. The abundance of exotic species was, for the most part, unaffected by fire in the first growing season, apparently because the composition of exotic vegetation shifted from annual grasses, which

decreased, to annual forbs, which increased, after fire. In subsequent seasons following a single burn, total plant biomass increased to an average of 13% more in burned areas than in unburned areas. Where native perennial grasses were studied, *Nassella pulchra* abundance generally rebounded during the second postfire year, whereas *Danthonia californica* was slower to recover. Although germination of native grasses increased following fire, there was no detectable increase in native-grass abundance in subsequent years. Similarly, Dyer, Fossum, and Menke (1996) found that the establishment of native perennial grass seedlings was about the same in burned and unburned areas, whereas seedling mortality in burned areas was high. By the third year, the cover of native species relative to that of exotic species was not significantly different in burned areas and unburned areas, probably because of the rapid recovery of exotic annual grasses.

The observation that repeated burning reduces soil N availability suggests that prescribed burning could be used to tip the balance of competition in favor of native species if nitrogen is an important resource for both native and nonnative grassland species. For example, Seastedt, Briggs, and Gibson (1991) found that productivity of frequently burned tallgrass prairie grasslands was limited by N availability. The influence of fire frequency on soil N levels and N limitation of productivity in California grasslands is not known, though 2 or 3 consecutive years of burning have been shown to either decrease (Parsons and Stohlgren 1989; Delmas 1999) or have no significant effect on (Hansen 1986; DiTomaso, Kyser, and Hastings 1999) aboveground productivity beyond the effect of a single burn. D'Antonio et al. (2001) concluded that annual burning (after two or three burns) in ungrazed grassland resulted in higher native-forb and exotic-forb abundance than a single burn, but exotic annual grasses apparently did not respond further to the additional fires. Unfortunately, data were insufficient to conduct a meta-analysis on the effects of repeated burning on native perennial grasses. A single study of the effects of repeated fire reported a dramatic increase in native perennial grasses, particularly *Nassella pulchra* (DiTomaso, Kyser, and Hastings 1999), but more work is needed at other sites to evaluate the generality of this finding. Further investigation of the importance of fire frequency to soil N levels, N limitation, grassland productivity, and native species' competitiveness in California grasslands would help to determine whether repeated burning provides benefits to native biodiversity.

The meta-analysis by D'Antonio et al. (2001) determined that a combination of a single burn and cattle grazing likely did not improve the magnitude of the benefits of a single burn for native forbs, but grazing did sustain the benefits of a single fire for native forbs into the third postfire growing

season. Likewise, grazing sustained the decrease in exotic annual grasses observed in the first year after a single fire into the third year. Grazing also lessened the negative impact of fire on native perennial grasses in the first growing season. Exotic forb suppression was successful only when a site was burned annually for several consecutive years and also grazed. However, this suppression did not appear to benefit native forbs: there was no increase in the abundance of native forbs by the third year in repeatedly burned and grazed sites. So, as with other techniques described in this chapter, combining fire and grazing reduced exotic species but did not increase the diversity and abundance of native forbs.

The time of year in which controlled burns are performed may have a significant effect on the impact on grassland species composition. D'Antonio et al. (2001) found that the month in which grasslands were burned significantly influenced native perennial grasses, with growing-season burns (e.g., November–June) having significantly more detrimental impacts on native cover than summer or fall burns. Burn season did not have a strong effect on native forbs or exotic annual grasses. Burns can also be specifically timed to limit invasive species' seed dispersal. Fires targeting medusahead and yellow starthistle before mature plants dispersed their seeds effectively suppressed these species and their soil seedbanks (Pollack and Kan 1998; DiTomaso, Kyser, and Hastings 1999).

In addition to trying to manipulate the abundance of native and exotic grasses and forbs using fire, many managers use fire to control woody invaders in California grasslands. Alexander (2001) surveyed species composition and broom seedbank density and aboveground cover in numerous managed grassland sites in northern California to determine whether controlled burning was capable of controlling invasive shrubs (primarily *Genista monspessulana* and *Cytisus scoparius*) and opening suitable habitat for native species. She found that although fire reduced aboveground biomass of adult broom plants, it stimulated germination of broom seeds from the soil seedbank, which resulted in very dense broom stands in the first few years. The germination occurring after the first fire significantly reduced the number of live broom seeds in the soil seedbank, but because of the resulting increase in number of new broom plants, the seedbank has a great potential to become large again if the new crop of seedlings is not controlled. Hence, later fires must occur before the new crop of broom seedlings becomes reproductive (within 3–4 years). Alexander (2001) also found that the postbroom grasslands created by controlled burning were dominated largely by non-indigenous grasses and forbs. The only places where the postbroom grassland had substantial native cover were a few sites where broom

had been pulled repeatedly by hand and no burning had been conducted. In these few sites, native perennial grasses and forbs codominated with exotic annual grasses. Overall, Alexander's study suggests that repeated fire effectively reduces the broom seedbank and the cover of adult plants. However, the study points out that the reduction of broom dominance through prescribed burning alone is unlikely to increase native-species richness and cover in landscapes in which exotic forbs and grasses are so abundant.

#### *Herbicide Application*

Herbicide application has been suggested as a way to reduce established exotic vegetation in heavily invaded ecosystems and to control the flush of exotic annual species from the soil seedbank prior to planting of native species (e.g., Wilson and Gerry 1995; Stromberg and Kephart 1996; Rice and Toney 1998). Herbicides such as glyphosate, picloram, and clopyralid have been shown to substantially reduce exotic biomass and increase native-seedling establishment in a variety of grassland systems (e.g., Wilson and Gerry 1995; Rice et al. 1997; Rice and Toney 1998). Stromberg and Kephart (1996) recommended repeated herbicide application to reduce the exotic annual seedbanks prior to native-plant establishment in coastal California old fields. Our own experience in a northern coastal prairie grassland dominated by a mixture of exotic annual and perennial grasses and biennial forbs supports the utility of herbicide application in favoring native-grass establishment (Corbin and D'Antonio 2004a). Though we are not aware of controlled experiments comparing the efficacy of herbicides in restoration of California grasslands, herbicide application is likely an effective tool to facilitate site preparation and reduce exotic reestablishment (Anderson and Anderson 1996; Stromberg and Kephart 1996).

#### *Biological Control*

The introduction of biological control agents holds great promise in reducing the competitiveness of invasive plants in cases where insects, pathogens, or vertebrates specifically target undesirable species (Hoddle, this volume). However, in spite of the advantages of biological control—which include relatively low costs and long-term, self-sustaining management of invasive species—cases of successful control of nonnative grassland species in California are rare. DeLoach (1991) found that of twenty-three native and exotic weed species in western rangelands (including the northwestern United States and western Canada) where biological control had been attempted, only seven were successfully controlled. In California several insects have been introduced to control seed production of the pernicious yellow star-

thistle, and although the insects have been established successfully in many areas, starthistle remains a widespread, abundant weed (Turner, Johnson, and McCaffrey 1995; Villegas 1998; Roché et al. 2001). The introduction of three biological control agents in coastal Oregon grasslands to control *Senecio jacobaea* (tansy ragwort) has been far more successful, reducing the exotic to 1% of its former abundance (McEvoy, Cox, and Coomes 1991; McEvoy and Coomes 1999). One of the few investigations of biological control of exotic grasses (Carsten et al. 2000) found evidence that augmentation of a natural crown rust of *Avena* spp. (wild oat) on San Clemente Island reduced seed production of these annual grasses. In the cases of both yellow starthistle and wild oats, the biological control agents have been more effective at reducing seed production than at reducing exotic population sizes, but the agents could reduce exotic competitiveness in combination with other control techniques (DiTomaso 2000).

#### DISCUSSION

A review of attempts to increase the efficiency of California grassland restoration did not yield a strategy that consistently favored native species over exotic species. Although some individual techniques showed promise for increasing native-plant growth or seedling survival, no technique consistently increased native-grass or native-forb diversity or biomass. Rather, the outcomes were highly case specific and likely varied with such factors as initial vegetation composition, nutrient availability, past land-use history, and climatic conditions. Further exploration of the restoration tools under a wider range of habitat conditions is required before habitat managers can predictably apply them to revegetate degraded ecosystems.

Some techniques showed promise in reducing the exotic components of degraded ecosystems even though they were unable to increase the native component. Reduction of plant-available N (Alpert and Maron 2000; Maron and Jefferies 2001), mowing or grazing (Thomsen et al. 1993; Stromberg and Kephart 1996), prescribed fire (Pollack and Kan 1998; DiTomaso et al. 1999; Alexander 2001), and herbicide application (Stromberg and Kephart 1996) were able to reduce specific invasive plant species in California grasslands. While these techniques would be of even greater use in a restoration context if they were capable of consistently increasing the competitiveness or abundance of native species, the control of exotic species is frequently a primary goal of habitat management (Ehrenfeld 2000).

The absence of native plant species, either as individuals or as seeds from nearby populations, frequently limits the success of efforts to restore de-

graded habitats. Many natural areas that are chosen for restoration are chosen precisely because their native component has been lost. For example, invasion by exotic species can be a major factor in the elimination of native-plant populations in natural habitats (Baker 1989; Bossard, Randall, and Hoshovsky 2000). Agricultural activities, especially plowing and other intense farming activities, are also capable of directly removing native individuals and likely exhausting the seedbank of the former dominants (Milberg 1992). The effects of agricultural activities on native-grass abundances have been shown to persist for decades after cessation of the agricultural activity (Stromberg and Griffin 1996). In cases where exotic species invasion or past land-use history have degraded native abundance, native species are unable to take advantage of even the most diligent efforts to remove exotic species or modify the competitive environment.

Habitat restoration strategies must, therefore, take into account not only the vulnerability of native individuals to competition with exotic species but also the limited source of native propagules in degraded ecosystems. There is strong evidence that the colonization of appropriate habitats by native-plant populations is often limited by seed availability. The soil seedbanks of native grasses and some forb species have been shown to be negligible in both disturbed (Kotanen 1996) and undisturbed (Peart 1989a) habitats in California. Seed rain of native grasses and forbs is generally substantially lower than that of exotic species when all groups are growing in the same environment (Hobbs and Mooney 1985; Peart 1989a; Kotanen 1996). Native species also have limited ability to repopulate degraded sites from nearby remnant populations (if such populations even exist), owing to low seed production (Hobbs and Mooney 1985; Peart 1989a; Kotanen 1996) and limited seed dispersal relative to exotic species (Hobbs and Mooney 1985; Peart 1989a–c; Kotanen 1996, 1997). We believe that restoration projects that augment the pool of native propagules via seed addition or seedling out-planting are much more likely to succeed than projects that rely on natural seed dispersal and recolonization. Some efforts to increase the competitiveness of native species, including sawdust addition (Alpert and Maron 2000), mowing and biomass removal (Maron and Jefferies 2001), grazing (Hatch et al. 1999) and prescribed burning (e.g., Alexander 2001 and others), may have had more success if more native propagules had been available to take advantage of the modified competitive environment.

Seedling establishment and persistence exert a major influence on plant population dynamics (Harper 1977), particularly in a restoration context in which native-plant species must revegetate habitats from which they have been extirpated. A variety of studies in California grasslands have demon-

strated that exotic grasses restrict the establishment of native perennial grass (e.g., Peart 1989a; Dyer and Rice 1997; Hamilton et al. 1999; Brown and Rice 2000). However, there are indications that mature native perennial grasses are capable of competing with exotic species and reducing future species invasion (Peart 1989b; Corbin and D'Antonio 2004b; but see Hamilton, Holzapfel, and Mahall 1999, in *N. pulchra*-dominated grassland). We have found that mixed communities of native perennial bunchgrasses are able to reduce the aboveground productivity of exotic annual grasses and resist invasion by exotic forb species within 2 years after native-seedling establishment (Corbin and D'Antonio 2004b). These results indicate that the period of seedling establishment in the first year after seed or seedling planting is a critical phase for native-grass restoration. Habitat managers should, therefore, concentrate on increasing native competitiveness during this window of establishment, after which mature native individuals may be better able to compete with exotic species.

We believe that a strategy that uses multiple tools to both reduce the competitiveness of exotic plant species and increase the establishment of native species holds promise for more successful restoration of native biomass. The coordination of multiple approaches to deal with undesirable species, a hallmark of integrated pest management (IPM) theory (Buhler, Liebman, and Obrycki 2000; Hoddle, this volume), has been well-developed in agricultural systems and to a lesser extent in rangeland management (reviewed in DiTomaso 2000). The most common application of IPM in the control of exotic species in natural systems is the introduction of biological control agents, but IPM can also include such strategies as prescribed burning and mechanical removal. Stromberg and Kephart (1996) argued that the establishment of native grasses in abandoned agricultural fields in central California is facilitated by a three-step program that includes site preparation by either plowing or applying herbicides to exotic grasses, seeding or planting seedlings of the desired native species, and instituting postestablishment management practices designed to increase the competitiveness of the native species. Such a program, though likely more expensive and labor intensive than other restoration techniques, should be considered if it is more likely to accomplish the goal of increasing population sizes of native-plant species and creating communities with greater resistance to further invasion.

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