

ARE INVASIVE SPECIES THE DRIVERS OR PASSENGERS OF CHANGE IN DEGRADED ECOSYSTEMS?

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Abstract. Few invaded ecosystems are free from habitat loss and disturbance, leading to uncertainty whether dominant invasive species are driving community change or are passengers along for the environmental ride. The “driver” model predicts that invaded communities are highly interactive, with subordinate native species being limited or excluded by competition from the exotic dominants. The “passenger” model predicts that invaded communities are primarily structured by noninteractive factors (environmental change, dispersal limitation) that are less constraining on the exotics, which thus dominate. We tested these alternative hypotheses in an invaded, fragmented, and fire-suppressed oak savanna. We examined the impact of two invasive dominant perennial grasses on community structure using a reduction (mowing of aboveground biomass) and removal (weeding of above- and belowground biomass) experiment conducted at different seasons and soil depths. We examined the relative importance of competition vs. dispersal limitation with experimental seed additions. Competition by the dominants limits the abundance and reproduction of many native and exotic species based on their increased performance with removals and mowing. The treatments resulted in increased light availability and bare soil; soil moisture and N were unaffected. Although competition was limiting for some, 36 of 79 species did not respond to the treatments or declined in the absence of grass cover. Seed additions revealed that some subordinates are dispersal limited; competition alone was insufficient to explain their rarity even though it does exacerbate dispersal inefficiencies by lowering reproduction. While the net effects of the dominants were negative, their presence restricted woody plants, facilitated seedling survival with moderate disturbance (i.e., treatments applied in the fall), or was not the primary limiting factor for the occurrence of some species. Finally, the species most functionally distinct from the dominants (forbs, woody plants) responded most significantly to the treatments. This suggests that relative abundance is determined more by trade-offs relating to environmental conditions (long-term fire suppression) than to traits relating to resource capture (which should most impact functionally similar species). This points toward the passenger model as the underlying cause of exotic dominance, although their combined effects (suppressive and facilitative) on community structure are substantial.

Key words: *British Columbia, Canada; dominance; facilitation; functional redundancy; oak savanna; plant competition; plant invasion; recruitment limitation; removal experiment; repeated-measures ANOVA.*

INTRODUCTION

Ecologists have long been interested in why some species dominate and how they impact the abundance of other species in communities (Preston 1948, McNaughton and Wolf 1970, Walker 1992, Fox 2002). There are two primary pathways to dominance: superior access to limiting resources by competition (highly interactive model) or limited susceptibility to noncompetitive processes that are highly restrictive to other species (weakly interactive model). In highly interactive communities, dominant species actively suppress or exclude subordinates by lowering resource availability to levels that only they can tolerate (Tilman

1988). Unless the intensity of competition is reduced (e.g., spatial heterogeneity, repeated disturbance), diversity levels in these communities will be constrained (MacArthur 1955, DeAngelis and Waterhouse 1987, Huston 1994). In weakly interactive communities, the dominant is largely unaffected by recruitment barriers or environmental stressors that are highly limiting to other species (Grime 2001, Seabloom et al. 2003a). Dominance occurs by default, therefore, and eliminating the barriers or stressors will lead to increased diversity.

Distinguishing between these models is difficult because the communities they produce are structurally similar (one or a few dominants, many subordinates), because they invariably interact (competition reduces reproduction, thus lowering dispersal; an inability to disperse prevents competition from occurring), and because, in both cases, the dominant species intercepts most of the available resources (Chapin et al. 1996,

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Smith and Knapp 2003). Resource interception occurs either by superior competitive ability or the sheer physical abundance of the dominant caused by noninteractive factors. As a result, dominant species can strongly influence resource availability in weakly interactive communities even though competition was not the initial cause of dominance (Keddy 2001). Understanding dominance, therefore, requires determining the connection between the mechanisms causing the abundance of the dominant and those limiting of occurrence of the other species, not just the impact of the dominant on limiting resources.

These issues are especially relevant for understanding the causes and consequences of plant invasion (Mack et al. 2000, Seabloom et al. 2003a, b). Numerous studies have established a correlation between high exotic abundance and the loss of native plant diversity, with an implied connection to competitive displacement. Although the connection between competition and community structure is almost axiomatic in plant ecology (Keddy 2001), the exact relationship between invasion success and competitive ability has rarely been confirmed experimentally (Davis 2003, Levine et al. 2003). Because the effects of habitat loss and disturbance also heavily impact many invaded systems, it is conceivable that exotic dominance may be less attributable to competition than has been supposed. Rather than driving the transformation of native plant communities, these exotics may be passengers of more fundamental environmental change that is most limiting to native flora (e.g., reduced dispersal due to fragmentation, altered disturbance regimes, climate change). If so, the eradication of invasive species will have a minimal impact if competition by these species is not the primary limiting factor for native species (Myers et al. 2000, Zavaleta et al. 2001). Determining the causes of exotic dominance, therefore, has theoretical relevance for understanding the structure and function of plant communities, and applied relevance for understanding why invasions occur and how they impact native systems.

We tested models of interactive vs. noninteractive dominance in a heavily invaded oak savanna in southwestern British Columbia, Canada (MacDougall and Turkington 2004, MacDougall et al. 2004). The savanna is dominated by two perennial grass invaders: *Poa pratensis* and *Dactylis glomerata* (hereafter called *Poa* and *Dactylis*). These species can be aggressive exploitation competitors (Grace et al. 2001, MacDougall and Turkington 2004), but they are also widely planted, leading to uncertainty whether dominance is caused by competition or by site history (e.g., Mack 2000). Using a factorial field experiment, we examined the impact of *Poa* and *Dactylis* on community structure with a reduction treatment (mowing of aboveground biomass), a removal treatment (weeding), and the experimental addition of seeds of both dominant and subordinate perennial grasses. By monitoring responses to the treatment by the entire community (79 species, Ap-

pendix A), we examined whether competition was most limiting for relative abundance. Because the impacts of disturbance on grass communities can be highly contingent on site conditions and the season of application (e.g., Howe 1994, Collins 2000, Harrison et al. 2003), we also varied the timing of the treatments (summer vs. fall application) and their location (deep soil vs. shallow soil).

METHODS

Study area

The experiments were conducted in two grass-dominated sites within the Cowichan Garry Oak reserve in the Cowichan Valley of southwestern British Columbia, Canada ($48^{\circ}48' N$, $123^{\circ}38' W$; see Plate 1). This savanna is part of an oak ecosystem complex that extends southward to California in the rainshadow of the Coast Mountain range (Fuchs 2001, MacDougall et al. 2004). The climate in British Columbia is submediterranean, with moderately infertile soils of postglacial origin. Annual rainfall averages 90–100 cm, most of which falls from October to March; winter temperatures rarely drop below $0^{\circ}C$. The savanna plant community is structured across a soil depth gradient; shallower soils (<15 cm) greatly restrict rooting depth and are more moisture limited in the summer months compared to deeper soils that can exceed 1 m in depth. The native plant community is species rich (454 taxa) compared to surrounding regions of British Columbia, and is also heavily invaded (144 naturalized exotic taxa). Exotic species dominate most remnant areas. Despite high invasion, there has been no concomitant loss of native flora (four extirpations since the 1840s) although many species are uncommon, rare, or provincially or nationally at-risk (Fuchs 2001). The primary impact of invasion, therefore, appears to be the reduction of abundance rather than the displacement of species, although this is speculative because the impacts of invasion covary with habitat loss >95% and long-term fire suppression (MacDougall et al. 2004). Invasion could be less relevant for species declines than their high abundances suggest, or invasion-mediated species loss is inevitable but has yet to occur.

The two sites vary greatly in soil depth, are ~300 m apart, and *Poa* and *Dactylis* dominate both. One site has average soil depths of 42.1 cm (range: 21–85 cm), the other 8.1 cm (range: 4.6–18.6 cm). Both sites were periodically grazed from the late 1800s to the early 1980s but never cultivated.

Reduction and removal of the dominant species

The experiment was a randomized complete block design with no within-block replication. In May 2000, 10 4×10 m blocks were placed in each site beyond the dripline of the surrounding oak canopy. Plots (1 m^2) within each block were randomly assigned to one of three treatments applied in July or early October



PLATE 1. Dense perennial grass understory in *Quercus garryana* savanna of southeastern Vancouver Island, British Columbia, Canada. Grasses are a mixture of exotic (*Poa pratensis*, *Dactylis glomerata*) and native (*Bromus carinatus*, *Elymus glaucus*) species. Photo taken at the Cowichan Garry Oak reserve, Nature Conservancy of Canada. Photo credit: A. MacDougall.

(prior to the rainy season): selective removal of *Poa* and *Dactylis*, mowing, and control (6 treatments \times 2 sites \times 10 blocks = 120 plots). The treatments were applied annually from 2000 to 2003. Mowing was done to ground level, and all cut material was raked and removed. Weeding removed all aboveground biomass of *Poa* and *Dactylis*. Roots and rhizomes were also removed although it was impossible to completely eliminate all of *Poa*'s rhizomes. As a result, this species remained in many weeded plots but at levels <2% cover each year. An explosion of *Cytisus scoparius* (exotic shrub) seedlings from the seed bank followed weeding in several deep-soil plots. These seedlings were removed each year because we were testing the impacts of the dominant exotic grasses on nonwoody species, although the potential impact of exotic grasses for suppressing woody plant invasion will be discussed. An additional 0.25-m buffer zone was weeded or mowed around all plots to reduce edge effects.

Prior to treatment application, all plots were assessed for (1) species richness (number of species/plot), (2) rare species richness (species in <2 plots/site [$n = 28$ species]), (3) relative species abundance (percent cover/plot), (4) species diversity (Simpson's 1/D), (5) reproductive output of the most common perennial grasses and forbs (flowering heads·species⁻¹·plot⁻¹; grasses: *Poa*, *Dactylis*, *Anthoxanthum odoratum* [exotic], and *Bromus carinatus*, *Elymus glaucus*, and *Carex inops* [native]; forbs: *Camassia quamash* and *Dodecatheon*

hendersonii [native]), (6) production of forbs, grasses, and litter/0.01-m² plot, and (7) light, soil moisture, bare soil, available soil nitrogen, and soil organic matter.

Relative species abundance and bare soil/plot were visually estimated using a 1-m² frame divided into 20 cells. Aboveground biomass was clipped in 10 \times 10 cm subplots at the end of May of each year and separated into grasses, forbs, and nonarboreal litter. Ground level light (percentage of full light) was measured with a LI-COR quantum sensor (LI-COR, Lincoln, Nebraska, USA). Soil moisture availability to 12 cm depth (volumetric water content) was measured with a Hydrosense TDR meter (Campbell Scientific, Logan, Utah, USA). Soil moisture levels were monitored at monthly intervals from March to August, and bimonthly for the rest of the year. Available soil N (mg/kg soil) was determined from 5 cm deep samples in half of the plots, extracted with 1 mol/L KCL, and analyzed for extractable NO₃ and NH₄. Percentage soil organic matter (OM) was determined by heating 20 g of soil at 400°C for 5 h and contrasting pre- and post-heating soil mass.

Most of the variables were remeasured in May of each year from 2001 to 2003. Soil NO₃, NH₄, and OM were measured twice: prior to the treatments and two years after the first application.

Seed additions

A seed addition experiment was conducted from October 2001 to July 2002 (37 weeks) between the first

and second years of treatment application. Seed of seven perennial C₃ grass species was collected in the summer of 2001, air dried, and planted just after the fall treatments were applied. Fifty seeds of each species were added to 15 × 15 cm subplots within all plots from two blocks at each site (24 plots/species). Besides *Poa* and *Dactylis*, the selected grass species had different relative abundances, phenologies, and soil depth preferences within savanna remnants of the Cowichan Valley (Appendix B). Germination tests in moistened and sand-filled petri plates showed germination >90% for each species. The number of established seedlings was counted at three intervals before the treatments were reapplied in late July 2002.

Statistical analyses

Separate repeated-measures analyses of variance (ANOVA) were used to analyze treatment responses over the four years of the experiment (e.g., changes in species richness/plot). The independent variables were site, block, year, treatment, season of application, and their various interactions (Appendix C). Significance levels were adjusted using Huynh-Feldt and Greenhouse-Geisser corrections to account for sphericity in the variance: covariance data matrices (Von Ende 2001). In all cases, these corrections were in agreement on significance. Post hoc contrasts were conducted with Tukey's multiple comparison test ($P < 0.05$). All ANOVAs were conducted on JMPIN (SAS 2001). Multi-dimensional scaling plots, derived from cluster analysis, were used to visually depict the functional group responses to the treatments (PRIMER-E, Plymouth Marine Laboratory, Plymouth, UK).

RESULTS

Pretreatment conditions

The pretreatment oak savanna plant community was characterized by a well-defined abundance hierarchy dominated by *Poa* and *Dactylis*, a thick litter layer, restricted light availability (<5% full light/plot), and little bare soil (<1% cover/plot). These conditions were maintained in the control plots throughout the experiment at both sites.

There were pre-treatment site differences in richness, diversity, biomass production, flowering head production, and microenvironment. Total cover by *Poa* and *Dactylis* was $81.5 \pm 2.8\%$ /plot (mean ± 1 SE) in the deep-soil site and $49 \pm 2.6\%$ /plot in the shallow-soil site (Fig. 1). The deep-soil site had 59 species, mostly perennial grasses (in addition to *Poa* and *Dactylis*), annual exotic pasture species (*Vicia* spp., *Cerastium* spp.), and native forbs that are mostly nonobligate savanna species (*Sanicula crassicaulis*, *Osmorhiza berteroii*). The shallow-soil site had 69 species. There were few perennial grasses other than *Poa* and *Dactylis*, and many native obligate forbs occurred at low abundance (e.g., *Camassia*,

Dodecatheon, *Ranunculus occidentalis*). Total biomass production was significantly higher in the deep-soil plots (10.8 ± 0.27 g/0.01 m²) compared to the shallow-soil plots (7.8 ± 0.24 g/0.01 m²), and was composed mostly of grass and litter (Fig. 2). The production of flowering heads was mostly by perennial grasses at both sites (Fig. 3).

Pre-treatment site differences were associated with two environmental factors: soil moisture and ground-level light. Although soils at both sites were close to saturation during the rainy season, moisture levels were significantly lower in shallow-soil plots from April to September ($F = 9.96$, df = 1, 119, $P < 0.0001$). Light was significantly lower in the deep-soil plots year-round ($F = 2.93$, df = 1, 119, $P = 0.005$).

Soil nitrogen and soil organic matter did not show site differences. Deep-soil plots had higher but non-significant N availability (192.8 ± 94.4 mg·kg⁻¹·soil plot⁻¹) compared to shallow-soil plots (108.23 ± 35.6 mg·kg⁻¹·soil plot⁻¹, $t = 2.32$, $P = 0.135$). Percentage organic matter averaged $14.38 \pm 0.41\%$ in deep-soil plots and $15.35 \pm 0.52\%$ in shallow-soil plots. These values were not affected by any of the treatments during the experiment ($F = 0.0994$, df = 1, 55, $P = 0.754$).

Impact of removals

Removing the dominants caused significant increases in richness (mostly by exotic annual ruderals regenerating from the seed bank) and diversity after one year; these increases were maintained for the remainder of the experiment (Fig. 4, Appendix C). Forty-five of 79 species increased significantly in percent cover at one or both sites (Fig. 5). Many of the increasing species were in the shallow-soil plots where they were established prior to the experiment.

Total biomass production dropped significantly due to the reduction of perennial grasses and the near elimination of the litter layer (Fig. 2, Appendix D). There was a significant increase in forb production at both sites, but these increases did not match the lost production of grasses and litter (Fig. 2). There were gradual but significant increases in flowering by the subordinate forbs ($F = 5.41$, df = 1, 119, $P < 0.0001$; Fig. 3). There were no differences in treatment response between the summer and fall removals for richness, diversity, production, or percent cover for most species (e.g., Figs. 1–4).

The removals caused a gradual shift in dominance from perennial grasses to perennial forbs at both sites (Figs. 4 and 6). These changes were attributable to increased cover by several native forbs that were present in small numbers in many plots prior to the treatments (e.g., *Camassia* and *Sanicula*, Fig. 1).

After three years, 36 of 79 species showed no change (e.g., most legumes [Fig. 4] and many rare species [Appendix C]) or decreased significantly in cover (exotic ruderals of mesic pastures, nonobligate native forbs associated with mesic forest habitats) in response

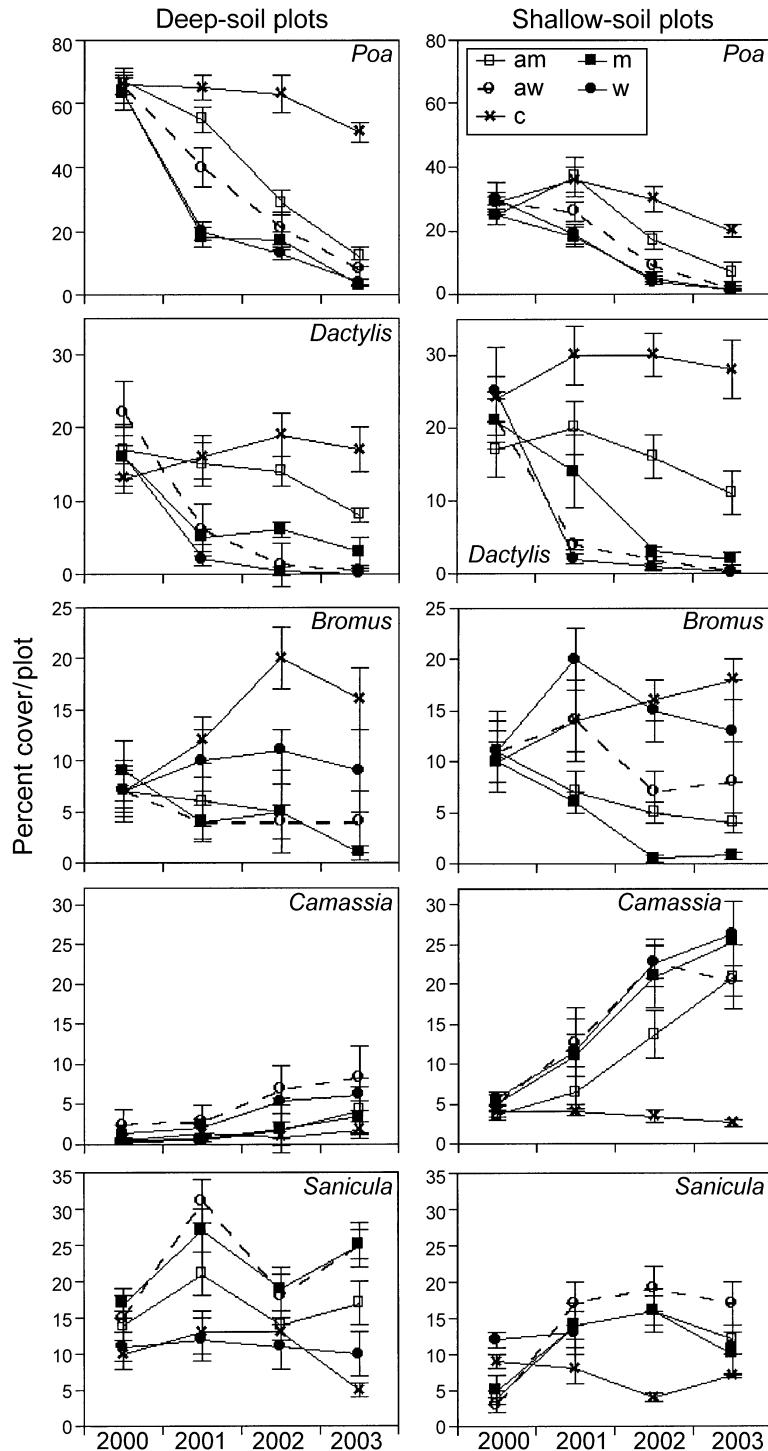


FIG. 1. Changes in percent cover/plot by the most abundant grass and forb species. *Poa*, *Dactylis* (both exotic), and *Bromus* (native) are perennial grasses. *Camassia* and *Sanicula* are native perennial forbs. Treatments are autumn mow (am), autumn weed (aw), control (c), summer mow (m), and summer weed (w). Error bars indicate ± 1 SE.

to the removals. There was virtually no recruitment by perennial forb and grass species for both native and exotic species in plots where they were not already established.

The only previously unobserved species to establish were annual forbs (nine species). These included several native savanna obligates (e.g., *Lupinus polycarpus*, *Collinsia parviflora*). Most established after the third

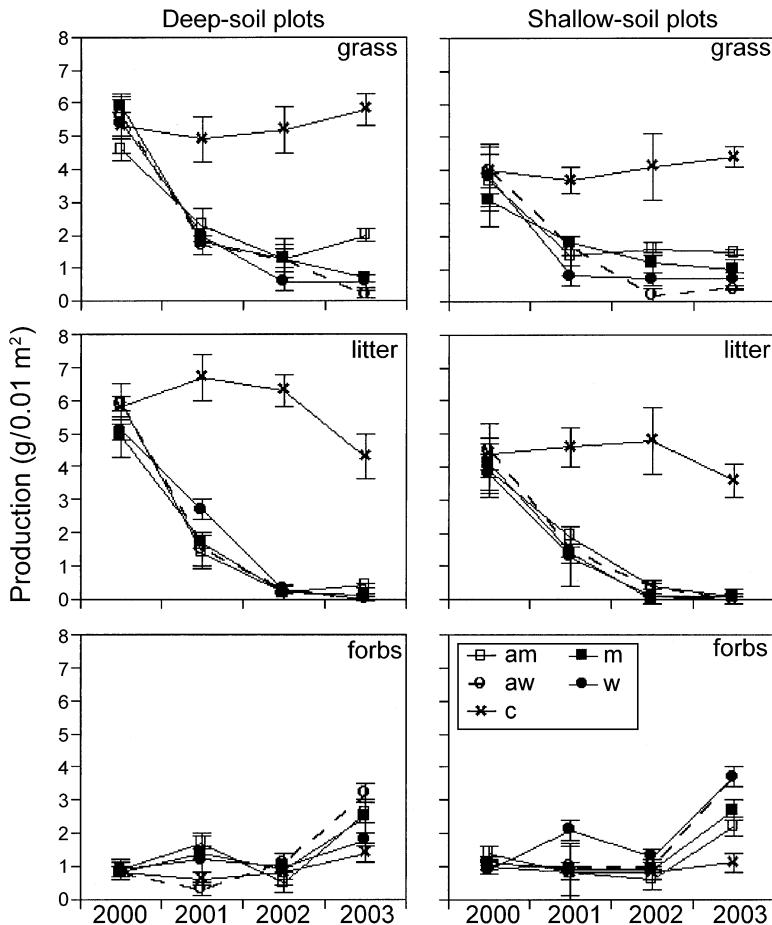


FIG. 2. Changes in grass, litter, and forb production over four years at the two sites. Treatment abbreviations are defined in Fig. 1. Error bars indicate ± 1 SE.

year of application, and most were only observed in one plot (of 120 plots). Some recruited from the seed bank (A. S. MacDougall, *unpublished data*) while others apparently dispersed from elsewhere in the reserve.

The removals caused significant increases in recruitment by woody plants, mostly *Cytisus* in deep-soil plots ($F = 12.88$, $df = 1, 119$, $P < 0.0001$). Although the removals reduced this species each year, its cover by 2003 (composed of hundreds of new seedlings) was still significantly greater than its pre-treatment cover in 2000 (Tukey's test). In the removal plots, there were also nonsignificant increases in recruitment by *Pseudotsuga menziesii*, *Acer macrophyllum*, and *Symporicarpus albus* (native woody plants), and *Craetagus* spp., (exotic shrub), at both sites.

Impact of mowing

Overall, there was no difference between the effects of the removal and mowing on community structure (Figs. 1–4, 6). By the third year, summer mowing reduced the cover of *Poa* and *Dactylis* to levels similar to the weeding treatment (Tukey's test, Fig. 1). Fall

mowing also significantly decreased *Poa* cover at both sites (Tukey's test) but did not significantly affect *Dactylis* (Tukey's test, Fig. 1). There were no observed differences between the response of functionally similar exotic and native species to mowing (e.g., all perennial grasses declined in cover, all annual forbs increased).

Impacts on resources

The impacts of weeding and mowing on light, soil $\text{NO}_3\text{-NH}_4$, soil moisture, soil organic matter, and bare soil were generally identical. Both treatments significantly increased light and bare soil. For light, there was no initial difference between the summer and fall mowing. In the second and third year, however, summer-mow plots had significantly more light at ground level. This change was associated with the difference in *Dactylis* cover that developed between the summer-mow and fall-mow plots at both sites (Fig. 1). There was no detectable treatment effect on any of the measured soil properties. Seasonal differences in soil moisture between the sites were maintained throughout the experiment but were unaffected by the treatments.

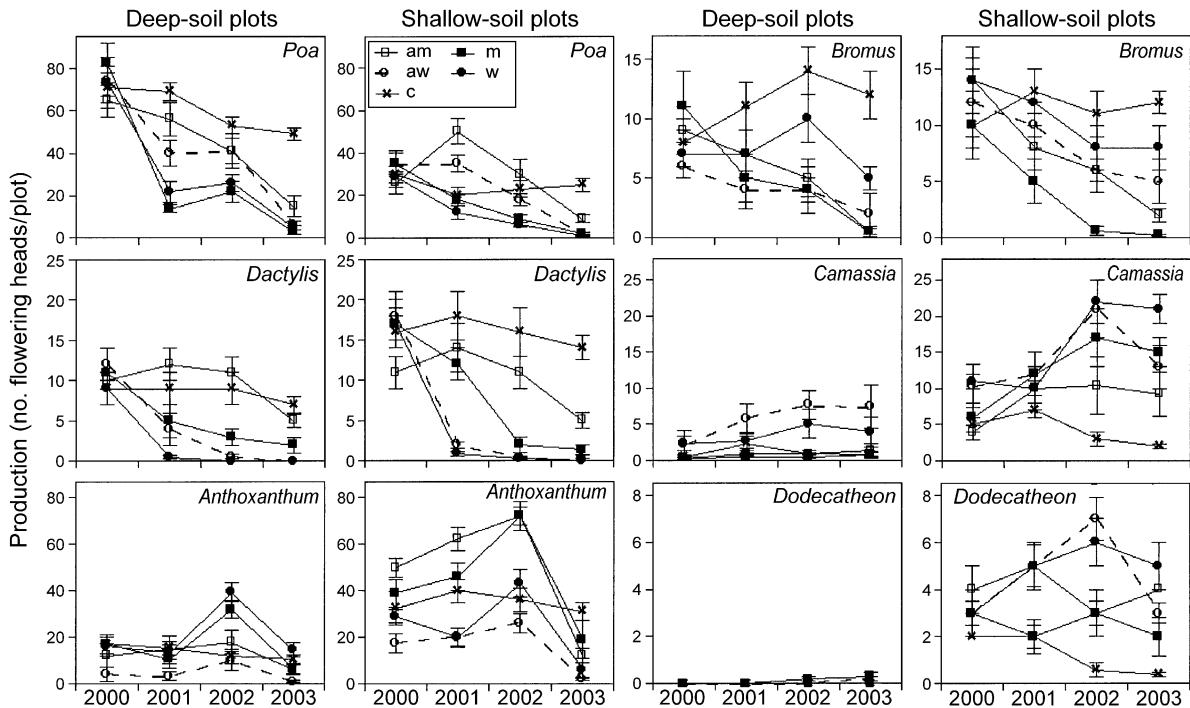


FIG. 3. Changes in flowering head production over four years at the two sites for the most abundant grass and forb species. Treatment abbreviations are defined in Fig. 1. Error bars indicate ± 1 SE.

Seed additions

At 12 weeks, five of seven species emerged in similar numbers in all treatments (Fig. 7). At 28 weeks in the control plots, seedling establishment was significantly higher for the native species compared to the exotics (Fig. 7, Appendix E, Tukey's test for all species-level comparisons). At 37 weeks in the control plots, the native species *Bromus* and *Elymus* had the highest number of established seedlings. This result was associated with the greater seed mass of these species compared to the others (Appendix B). Seedling mortality for *Poa* and *Dactylis* exceeded >95% despite their dominance in the overstory canopy.

Between 28 and 37 weeks, seedling survival among the seven species diverged significantly between the summer and fall treatments (Fig. 7). In the summer plots, all species except *Anthoxanthum* had >90% mortality (Tukey's test). In the fall plots, this trend was reversed—seedling survival was significantly higher for all species except *Anthoxanthum* (Tukey's test).

Survival differences between summer and fall plots were associated with the higher cover of exotic perennial grasses in the fall plots. Grass cover was higher in these plots because *Poa* and *Dactylis* were either unaffected (*Dactylis* in the fall mow plots) or were slower to respond (*Poa* in the fall removal plots) to these treatments. As a result of this higher cover, mid-summer light levels in 2002 were reduced significantly

for both mowing and removal compared to the summer plots ($F = 26.6$, $df = 1, 119$, $P < 0.0001$ for whole model; individual comparisons, Tukey's test, mean in summer plots, 64.4% full light ($SE = 5.9$); mean in fall plots, 33.5% ($SE = 4.1$).

DISCUSSION

Drivers or passengers of change?

We asked if the dominant grasses are driving community structure by competition or if noninteractive factors better explain relative abundance. While the net effects of these grasses on the growth, abundance, and reproduction of many species were negative, competition was insufficient to explain the rarity of some species. They appear to be restricted by noninteractive processes relating to dispersal limitation or were unable to respond due to demographic constraints associated with rarity (e.g., low seed set, slow growth). Further, the dominant grasses positively impacted the functioning of this savanna by suppressing woody plant invasion and facilitating juvenile survival following moderate disturbance. Finally, the species most functionally distinct from the dominants responded most significantly to the treatments. This suggests that relative abundance is determined more by trade-offs relating to environmental conditions (long-term fire suppression) than to traits associated with resource capture (which should most affect functionally similar species). This points to the pas-

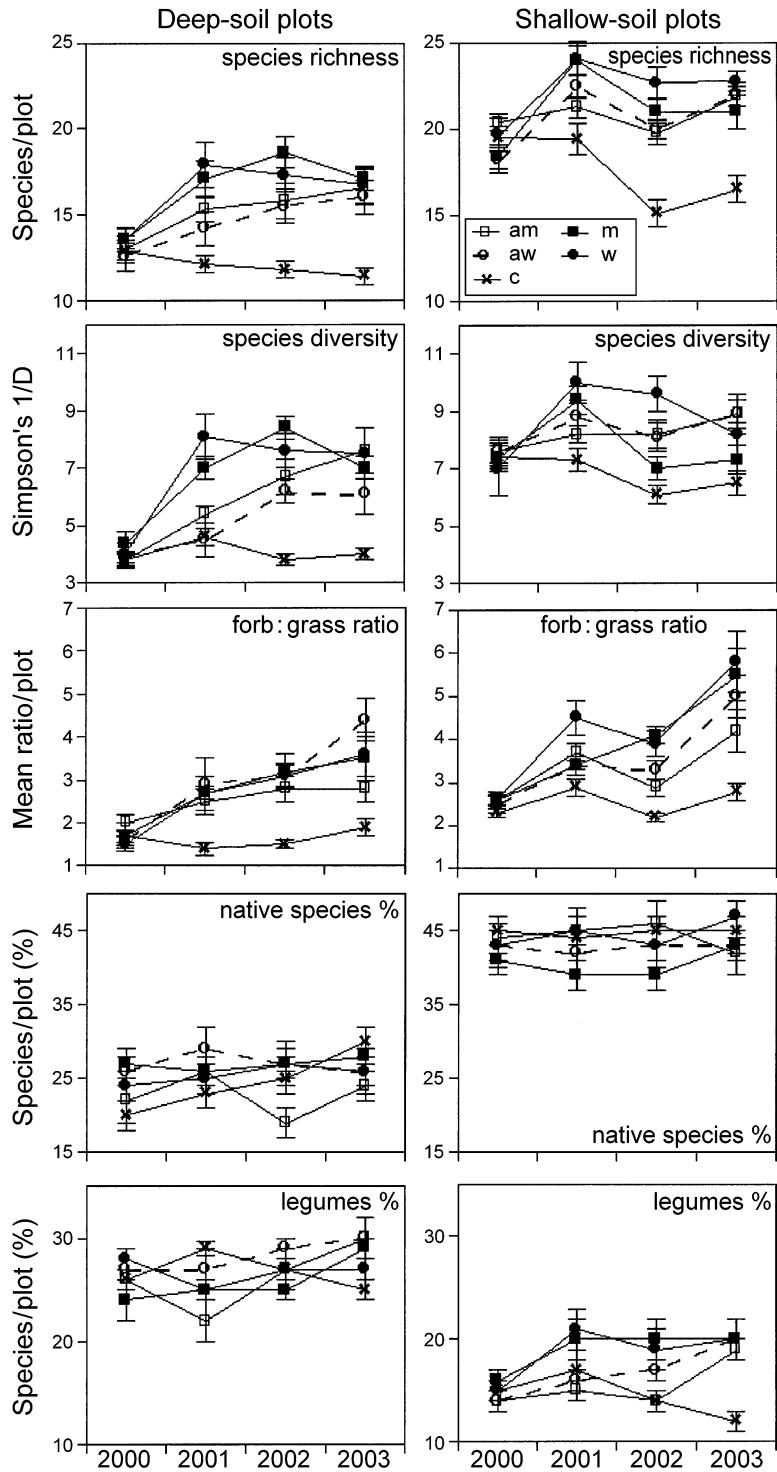


FIG. 4. Changes in species richness, species diversity (Simpson's 1/D), forb:grass ratio, and the percentage of native species and leguminous species per plot. Treatment abbreviations are defined in Fig. 1. Error bars indicate ± 1 SE.

ger model as the better explanation for exotic dominance, even though these species are highly competitive and strongly influence community structure including the abundance of many native species.

Competitive impacts by the dominant grasses

These data provide considerable evidence for the impact of competition, based on the significant increases

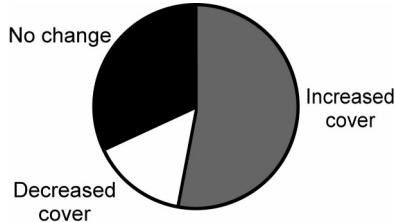


FIG. 5. Summary of percent cover changes for 79 species in response to the treatments. Increased, decreased, and no change were determined by *t* test ($\alpha = 0.05$, $df = 79$), comparison between 2000 cover (pretreatment) and 2003 cover (three years of treatment application) at one or both sites.

in richness, diversity, and the growth and reproduction of subordinate flora following the decrease of the dominants. These increases occurred in most plots, at both sites, and were most evident in the summer treatments where the reduction of perennial grasses was most severe. We detected no evidence for alternative noncompetitive explanations for these increases (e.g., temporary production increases caused by litter feedbacks; Berendse 1994). It seems clear, therefore, that asymmetric competitive interactions among the member species contribute to the structure and function of this community and are important for maintaining the high abundance of the dominants.

The key limiting resource in the absence of disturbance appears to be light availability, consistent with other productive grassland ecosystems (Turner and Knapp 1996, Knapp et al. 1998). This conclusion is based on the equivalent responses to the removal (above and belowground) and reduction (aboveground only) treatments by the subordinate species, and to the lack of measured change in available soil nitrogen or organic matter. *Poa* dominates these oak savannas by producing a dense layer of light-limiting litter and foliage, and by having the ability to regenerate under these conditions by tillering. *Dactylis* has a higher relative growth rate than other grass species (native and exotic) that favors its recruitment if and when small disturbances occur (e.g., vole mounding; MacDougall and Turkington 2004). Once established, adult *Dactylis* plants are long-lived and highly tolerant of competition because of their height (>150 cm) and their dense lateral foliage. Although some subordinates can recruit from seed under the light-limited grass canopy, success is generally low and many species remain rare.

High-impact invasive species (i.e., ecosystem “drivers”) are predicted to possess unique trait differences and to maintain their dominance under shifting environmental conditions (Vitousek 1990, Chapin et al. 1996). Although the exotic dominants of this savanna have a strong competitive impact, they are not distinct morphologically or functionally from their native counterparts. Under the current regime of no major disturbance, the dominants possess a combination of traits for accessing resources in these light-limited under-

ries. However, other native and exotic perennial grasses also appear to persist (albeit at lower abundances) with limited or no disturbance, coexisting by a range of recruitment and growth strategies relating to differences in seed mass, maturation rate, and tolerance of low light (MacDougall and Turkington 2004). All exotic and native perennial grass species, including the dominants, also demonstrated a high sensitivity to repeated disturbance. The percent cover and reproductive output of these grasses declined with repeated mowing, including the native species *Elymus glaucus* that was eliminated from all plots within two years. By implication, the ability of these functionally similar native and exotic species to coexist plus their shared sensitivity to repeated disturbance suggests that perennial grass dominance is not a contemporary phenomenon in this ecosystem (i.e., only the species composition has changed, not the functional dynamics). Historical records confirm this, as tall (>2 m) and dense thickets of grass were commonly reported in unburned areas prior to European settlement (MacDougall et al. 2004). *Poa* and *Dactylis* dominate, therefore, in situations where C_3 perennial grasses would normally be abundant.

The species that responded most strongly to the treatments were those most functionally distinct from the dominants: annual and perennial forbs. These species are highly light limited, with short growing seasons that free them from the impacts of fire that formerly occurred in this ecosystem during the summer and fall (MacDougall et al. 2004). This suggests that dominance is determined by a trade-off between the ability to tolerate low light vs. the ability to tolerate the repeated biomass loss, and is thus contingent on the disturbance regime of the ecosystem. If dominance were primarily driven by trait-based differences in competitive ability, we would predict that species most similar to the invasive dominants would demonstrate the greatest treatment responses (e.g., Christian and Wilson 1999). Most forbs in this ecosystem are winter or spring ephemerals, emerging once the rainy season begins in October and finishing their annual cycle by June. They compensate for their short growing season by avoiding the combined late-season regime of burning and seasonal drought that formerly characterized this ecosystem. With burning eliminated, their short phenologies become disadvantageous for energy capture in the light-limited understory of grass and litter. Present-day patterns of invasive dominance, therefore, appear to be determined more by fire suppression than by trait differences between the exotic and native species. Trait differences are relevant, allowing *Poa* and *Dactylis* to thrive in the light-limited understory, but their numerical abundance is contingent on the continued absence of perturbation.

Impacts of dispersal limitation on subordinate flora

In addition to the impacts of competition, there was evidence that dispersal limitation restricts the distribution of subordinate species. In plots where subor-

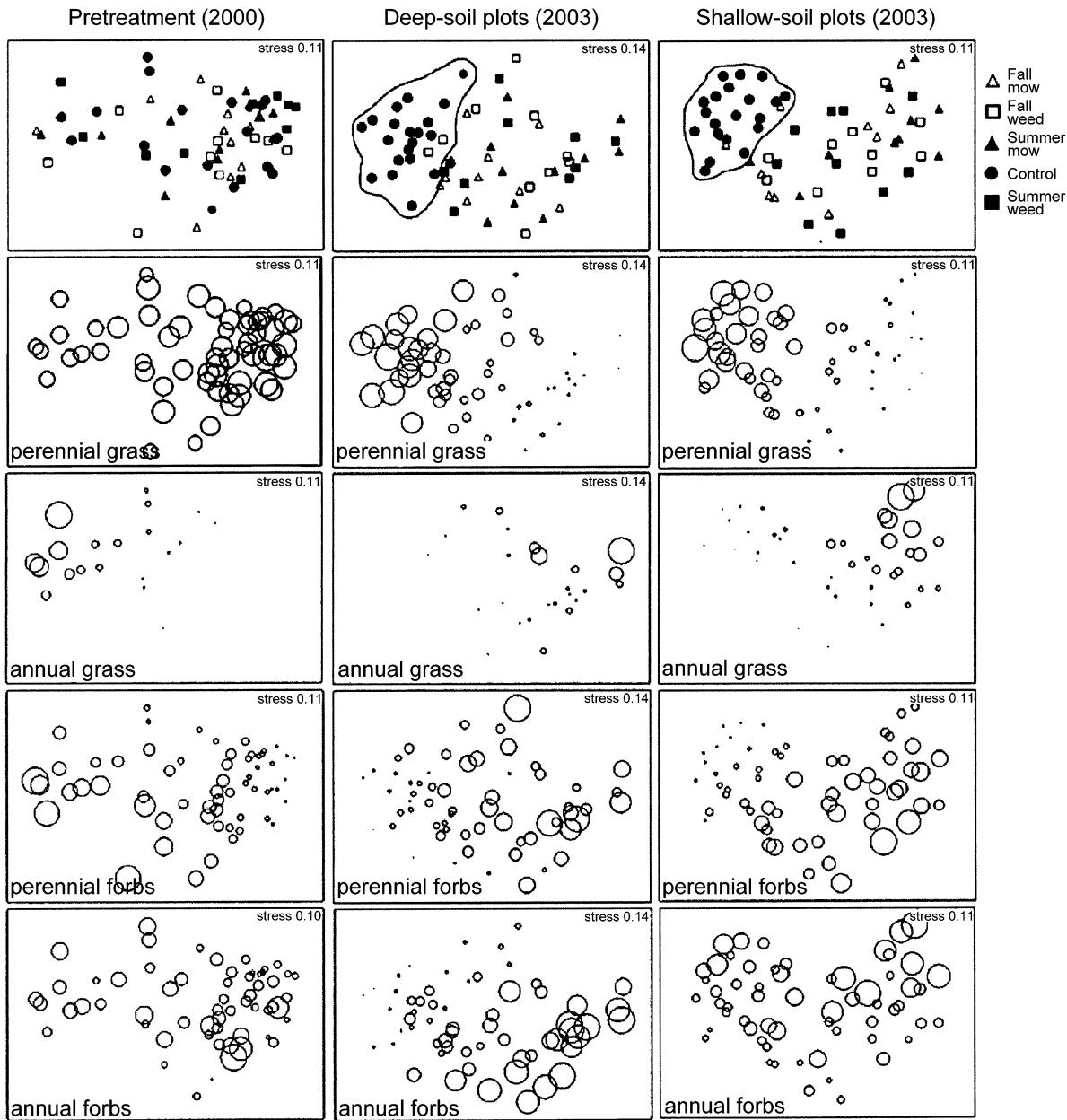


FIG. 6. Changes in community structure at the functional group level at the two sites, using nonmetric multidimensional scaling ordination (PRIMER-E, Plymouth Marine Laboratory). The pretreatment column was identical for both sites; only the deep-soil site is presented for brevity. The top row shows the distribution of similarity (Bray-Curtis) for the 60 plots/site prior to the experiment (no plot differences) and after three years (separation of control and treatment plots). Comparison of functional group pattern (rows 2–5) with the treatment plots (row 1) indicates that perennial grasses dominate all pretreatment plots but are largely restricted to control plots for both weeding and mowing treatments by 2003. In contrast, forbs and annual grasses are weighted toward the treatment plots by 2003.

dinate native taxa were not already established, there was little or no response to the reduction of the dominant grasses. The few species that colonized did so rarely, and most took several years to establish. Conversely, when seeds of locally rare species such as *Danthonia* and *Festuca* were experimentally added they established in large numbers prior to the onset of summer drought. Thus, although competition by the dom-

inant grasses exacerbates the dispersal problem (i.e., reduced reproduction, low establishment by most added grass species in the control plots), it is not sufficient to explain the limited occurrence of many species. Similar findings in heavily invaded systems have been reported elsewhere (Seabloom et al. 2003a, b).

An increasing number of studies have found evidence for dispersal limitation by plants (e.g., Zobel et

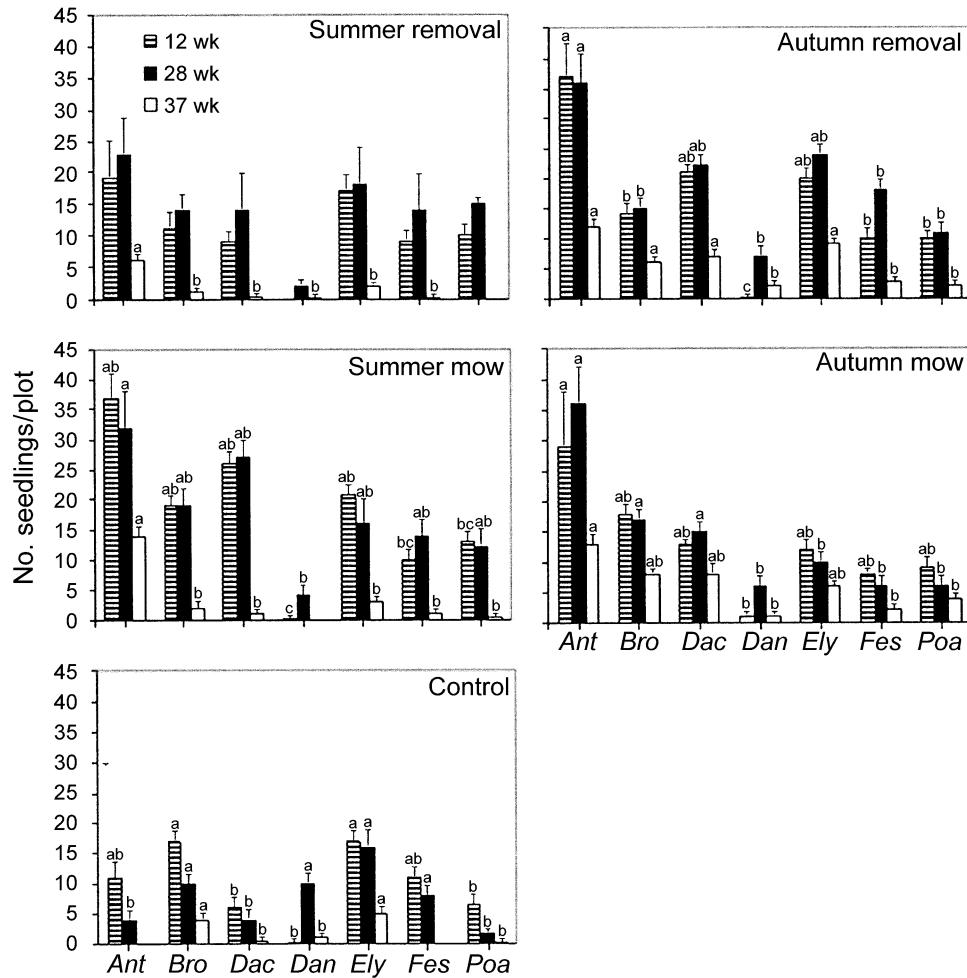


FIG. 7. Differences in seedling survival in the different treatment plots at 12, 28, and 37 weeks. Key to species abbreviations: *Ant*, *Anthoxanthum*; *Bro*, *Bromus*; *Dac*, *Dactylis*; *Dan*, *Danthonia*; *Ely*, *Elymus*; *Fes*, *Festuca*. Fifty seeds/species were added initially. Error bars show ± 1 SE. Letters indicate statistical differences within each of the three sampling periods, determined using Tukey's multiple comparison test ($P < 0.05$).

al. 2000, Foster and Tilman 2003), confirming theoretical predictions about the importance of immigration for structuring plant communities (e.g., Shmida and Ellner 1984). In this study, the causes of poor dispersal are unclear. Habitat fragmentation has been severe, but large populations of several native forb species (e.g., *Camassia*, *Dodecatheon*, *Ranunculus*) occur in the study area. Many disperse by gravity and thus may be naturally limited in their ability to occupy recruitment sites when they become available. Recent studies have suggested the importance of ungulates for the longer distance dispersal of herbaceous ground flora (e.g., Vellend et al. 2003). Black-tailed deer are common but their movement among savanna remnants is likely restricted due to suburban sprawl. Roosevelt elk, formerly common, are extirpated locally. Although it is tempting to blame the loss of habitat and dispersal agents for recruitment limitation, these changes prob-

ably exacerbate the naturally inefficient dispersal ability of many subordinates. Because native flora often demonstrate an inability to colonize suitable habitat in disturbed ecosystems (Singleton et al. 2001, Seabloom et al. 2003b), the causes of these limitations need to be determined.

Based on the slow rates of dispersal suggested by this study, it may take considerable time for new populations to establish even within a few hundred meters of existing populations. Disturbance would presumably hasten the process by increasing the probability of successful establishment by rare dispersal events. However, the rate by which the perennial grasses are reduced or eliminated by disturbance is much faster than the rate by which most native flora disperse. Recovery, therefore, will be slow or may be circumvented by species less limited by immigration in contemporary landscapes (i.e., exotics that are highly abundant in surrounding settled areas).

Positive effects of the dominant species

There was strong evidence that the dominant grasses have two positive impacts on community function: facilitating seedling survival following moderate disturbance, and slowing conversion to woodland by inhibiting recruitment by trees and shrubs. In the seed addition experiment, highest survival was in the fall treatments that eliminated the litter layer but maintained grass cover. This cover reduced light penetration to the soil surface in the summer, presumably reducing heat stress and other related factors. Complete removal of litter and living foliage resulted in high mortality, even for native species associated with habitats of shallow soil and high solar exposure (*Danthonia*, *Festuca*). Thus, the impact of the dominants in this system switches between suppressive or facilitative depending on the intensity of the disturbance in the previous year. Given the former frequency of fire in this system, combined with the intense summer moisture deficits that characterize mediterranean climates, dominant grass species may have always played an important role in facilitating plant recruitment. This role has now been assumed by invasive species.

Conversion to woodland (predominantly *Pseudotsuga*) or shrubland (predominantly *Cytisus* or *Symphoricarpos*) has occurred in oak savanna ecosystems throughout the Pacific Northwest (Tveten 1997), in part because of fire suppression. This conversion eliminates almost all savanna ground taxa, native and exotic. Our data reveal that dense swards of exotic grass can greatly slow woody plant invasion, as has been observed in grasslands elsewhere (Wilson 1998). In the control plots, newly emerging seedlings of shrubs and trees were occasionally observed but rarely survived. The highest levels of woody plant recruitment were in plots with little or no grass. Although the woody species were eliminated by the reapplication of the treatments, less frequent disturbance would hasten their recruitment.

The positive effects of the dominants support the view that invasives can sometimes preserve ecosystem function, and that their eradication may have unanticipated or negative results (Myers et al. 2000, Zavalata et al. 2001). In this case, there is a trade-off between the negative impacts of competition and the positive effect on juvenile survival and the suppression of woody plants. Although the negative impacts are currently substantial for many native species, the importance of the positive impacts increases with disturbance. Recruitment by all species appears to be more suppressed by the litter layer than the living foliage, a finding observed in other grasslands (Foster and Gross 1998, Jutila and Grace 2002). Disturbances in the fall such as mowing remove this layer but maintain a cover of living foliage, and seedling survival increases for all species measured.

CONCLUSION

It is critical to understand the causes and consequences of dominance by nonnative species because of

their potential to displace native flora and alter ecosystem function (Vitousek 1990, Levine et al. 2003). Although numerical dominance suggests competitive dominance, our work reveals that competitive ability alone cannot always explain the high abundance of exotic species or changes to the composition and diversity of invaded plant communities. Community structure, including dominance, was determined by an interacting array of factors relating to competition, dispersal limitation, environmental conditions, and disturbance. The exotic dominants were primarily "passengers" to long-term fire suppression, proliferating under conditions where perennial grasses are naturally abundant but easily displaced by repeated disturbance. Competition was highly relevant for community structure, restricting the growth and reproduction of many species, but was more a consequence of the effects of long-term fire suppression than a root cause of invasion initially. Further, some taxa appear to be more limited by noninteractive factors relating to dispersal or actually depend on the cover of exotic grasses for persistence. Such results are consistent with a growing body of work demonstrating that plant invasion cannot be explained solely by competitive ability but must be understood within a broader context of environmental change, evolutionary adjustment, and life history trade-offs (e.g., Callaway and Aschehoug 2000, Seabloom et al. 2003a, Corbin and D'Antonio 2004).

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APPENDIX A

A list of species and their responses to the removal and mowing treatments is available in ESA's Electronic Data Archive: *Ecological Archives* E086-002-A1.

APPENDIX B

A list of perennial grass species used in the seed addition experiment is available in ESA's Electronic Data Archive: *Ecological Archives* E086-002-A2.

APPENDIX C

A summary of repeated-measures split-plot ANOVA results for richness, diversity, rare species, and annual and perennial forbs is available in ESA's Electronic Data Archive: *Ecological Archives* E086-002-A3.

APPENDIX D

A summary of repeated-measures split-plot ANOVA results for biomass production is available in ESA's Electronic Data Archive: *Ecological Archives* E086-002-A4.

APPENDIX E

A summary of ANOVA results for the seed addition experiment is available in ESA's Electronic Data Archive: *Ecological Archives* E086-002-A5.