CASE STUDY

Multiple Treatment Combinations and Seed Addition Increase Abundance and Diversity of Native Plants in Pacific Northwest Prairies

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ABSTRACT

Invasive plants, especially non-native perennial grasses, are a critical threat to remnant prairies and oak savannas in the Pacific Northwest. Managers must control non-native plants without adversely impacting native species in fragmented prairie remnants. We describe results of a collaborative experiment replicated at 10 sites along a 500 km latitudinal gradient. Our objectives were to develop and test treatment combinations that reduce target non-native weeds with minimal nontarget impacts and increase native species diversity and abundance. By replicating experiments across the ecoregion, we tested strategies for widespread applicability. We compared four different combinations of seed addition and disturbance treatments comprising herbicide (sethoxydim and glyphosate), fire, and mowing. Each combination was created to target various factors likely to limit restoration in this system, including invasive species, litter accumulation, and limited dispersal of native species. After three years, the treatment combinations varied widely in their effectiveness. The most disturbance-intensive treatment combination (joint application of sethoxydim, burning, and postfire glyphosate) led to reduced abundance of non-native grasses and forbs without causing a decline in native species. Sethoxydim combined with fall mowing reduced non-native grasses, caused no change in non-native forbs, and increased total cover of native plants. In all cases, disturbance treatments reduced non-native cover to varying degrees but had no positive impact on native diversity except when seeds were added. Our results show that a combined treatment approach employing a variety of strategies codesigned by managers and ecologists is an efficient and effective way to improve degraded grasslands.

Keywords: grassland, herbicide, invasive species, prescribed burning, seed limitation

Invasion by non-native plant species and conversion of natural communities to human-dominated uses are the top threats to biodiversity and ecosystem function (Mack et al. 2000). North American grasslands are particularly affected; over 90% of grassland habitats have been lost, and most of the remainder is heavily invaded by non-native plants (Samson and Knopf 1994). Communities extensively invaded by non-natives but still retaining a desirable native biota present particularly difficult restoration challenges. Part of the dilemma is how to selectively remove non-natives without causing damage to natives. Native and non-native species often share many traits (for example, phenology, physiology, or degree of susceptibility to grazing or fire), and management actions that effectively control invasive species often impact many native species as well (Smith and Knapp 1999, Sheley and Krueger-Mangold 2003).

Practitioners have adopted several approaches to selectively remove non-natives from degraded grasslands (Sinclair et al. 2006). Selective herbicides and careful timing of broad-spectrum herbicides can target specific non-native weed groups while reducing impacts to nontarget or dormant native plants (e.g., Rice et al. 1997). Grazing or mowing can also successfully reduce certain invasive plants if they are more vulnerable than native species to herbivory or cutting (Wilson and Clark 2001). Fire was once common to many North American grasslands, and prescribed burning is thus a frequently used management tool (Grace et al. 2001). However, many non-native species have proven to either tolerate or benefit from fire in much the same way as native species (Grace et al. 2001). Many weed control treatments, particularly fire, also serve a vital role in the maintenance of historic disturbance regimes. In many grasslands, regular disturbance through fire, grazing, or mowing is required to prevent woody encroachment.

Although the science of grassland restoration has achieved significant gains, the ever-increasing rate of non-native plant invasions constantly creates new problems. One of the gaps between the science of restoration

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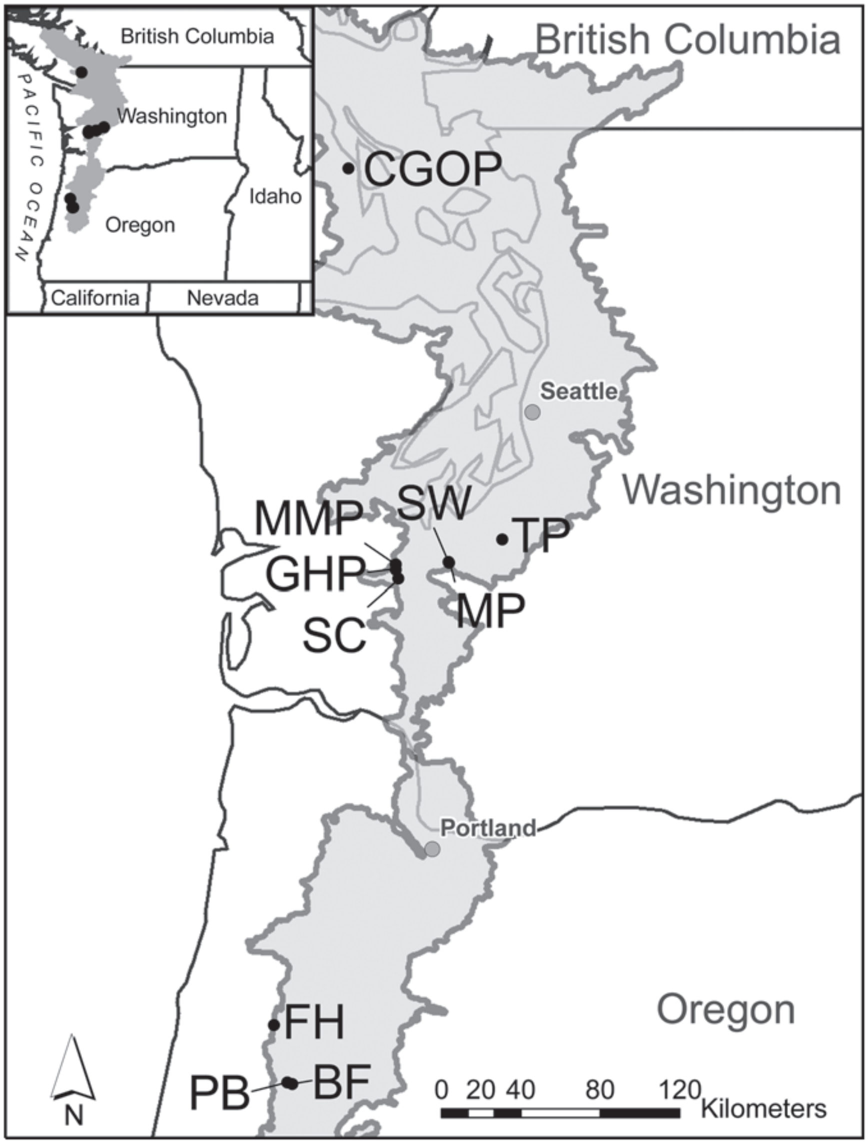

Figure 1. Map of study sites in the Willamette Valley/Puget Trough/Georgia Basin (WPG) ecoregion (shaded area): CGOP = Cowichan Garry Oak Preserve; SW = South Weir Prairie; MMP = Mima Mounds Preserve; GHP = Glacial Heritage Preserve; SC = Scatter Creek; TP = Triangle Prairie; MP = Morgan Property; FH = Fort Hoskins; PB = Pigeon Butte; BF = Bellfountain Road.

and on-the-ground application is that researchers often test single management techniques in order to preserve a robust experimental design (Cabin 2007, Simmons et al. 2007). In contrast, land managers almost always use various methods in combination, as no single approach is sufficient to accomplish the multiple objectives of most restoration projects. As a result, there is little guidance from well-controlled experiments on how multiple treatments applied in combination may be used to restore grasslands. In addition, most restoration experiments are narrow in geographical extent, making it difficult to generalize beyond the study site.

This project was developed as a collaboration between researchers and land managers to address this gap between scientists and practitioners (Stanley et al. 2008). We tested multifaceted restoration techniques for reducing invasive species abundance and increasing the diversity and abundance of native species in upland prairies and oak savannas. Our experiments were conducted at sites distributed latitudinally across the Willamette Valley/Puget Trough/Georgia Basin (WPG) ecoregion (Figure 1) (Noss et al. 1995, Dunn and Ewing 1997). While these habitats were historically maintained by frequent burning by Native Americans (Boyd 1986, Kruckeberg 1991), currently prairies in the WPG are highly threatened by fire suppression, habitat conversion, fragmentation, species invasion, and loss of diversity, and less than 2% remain (Floberg et al. 2004, Dunwiddie et al. 2006).

We selected ten natural areas and preserves for this project (Figure 1), protected and managed by various agencies and organizations (Table 1). Prairies in this ecoregion are low elevation and generally characterized by dry summers and wet, mild winters, with most vegetation growth occurring in spring and some regrowth in fall (Sinclair et al. 2006). Although there is considerable overlap in species composition among these prairies, they vary widely in terms of soils, climate, land use history, and degree of invasion (Floberg et al. 2004, Dunwiddie et al. 2006). Replicating our experiments across this range of variability ensures that our results are generalizable across the ecoregion.

The upland prairies and oak savannas in this study retained at least some native species, but also had a significant presence of non-native plants, particularly invasive grasses (Table 1). Common dominant non-native species at the sites included the grasses tall oatgrass (*Arrhenatherum elatius*), bentgrass (*Agrostis capillaris*), Kentucky bluegrass (*Poa pratensis*), sweet vernal grass (*Anthoxanthum odoratum*), velvetgrass (*Holcus lanatus*), orchard grass (*Dactylis glomerata*), and soft brome (*Bromus hordeaceus*), and the forbs hairy cat's-ear (*Hypochaeris radicata*) and ox-eye daisy (*Leucanthemum vulgare*). Common native species included the grasses Roemer's fescue (*Festuca roemeri*), oatgrass (*Danthonia* spp.), California brome (*Bromus carinatus*), and blue wild-rye (*Elymus glaucus*), the sedges and rushes split-awn sedge (*Carex tumulicola*) and long-stolon sedge (*C. inops*), and Pacific woodrush (*Luzula comosa*), and the forbs common yarrow (*Achillea millefolium*), small camas (*Camassia quamash*), bluebell bellflower (*Campanula rotundifolia*), wild strawberry (*Fragaria virginiana*), common lomatium (*Lomatium utriculatum*), common selfheal (*Prunella vulgaris*), and western buttercup (*Ranunculus occidentalis*).

Our efforts focused on reducing one of the main drivers of habitat degradation in these grasslands: non-native perennial grasses, whose rapid growth, structural dominance, and thatch accumulation limit establishment and growth of native species (Sinclair et al. 2006). Prescribed fire often benefits these fire-tolerant invaders as much as native species. Grass-specific herbicides, such as sethoxydim or fluazifop, provide an opportunity to target invasive perennial grasses, but most native grasses are also susceptible. However, Roemer's fescue, one of the most common matrix species in the region, is resistant to both sethoxydim (Dunwiddie and Delvin 2006) and fluazifop (Blakeley-Smith 2006).

Two widely supported observations guided our actions: 1) competition from non-native plants limits or prohibits native species from expanding or reestablishing in invaded habitats (D'Antonio and Kark 2002, Levine et al. 2003); and 2) seed availability in invaded prairies limits native species establishment and increase (Foster and Tilman 2003, Clark et al. 2007). Both processes may act together to control the success of restoration practices. Based on these observations, we framed three questions to guide this experiment:

1. Can combined treatments reduce the abundance of non-native grasses, and which combinations are most effective?
2. How do nontarget species (native and non-native forbs, native grasses, and annuals) respond to treatment combinations?
3. If dominant non-native grasses are reduced, does native plant diversity and abundance immediately respond, or is seed addition required?

Table 1. Overview of ten research sites in the Willamette Valley/Puget Trough/Georgia Basin ecoregion and initial pretreatment vegetation conditions in spring 2005. Native % cover was calculated as the percentage of total vegetative cover comprised of native species.

Site	State/ Province	Ownership	Species Richness: Non-native	Species Richness: Native	Native % Cover
Bellfountain Road	OR	Finley Wildlife Refuge, USFWS	34	34	40
Cowichan Garry Oak Preserve	BC	Nature Conservancy of Canada	19	31	40
Fort Hoskins Historical Park	OR	Benton County Natural Areas and Parks Dept.	24	13	36
Glacial Heritage Preserve	WA	Thurston County Parks	15	19	23
Mima Mounds Natural Areas Preserve	WA	WA Dept. of Natural Resources	17	24	32
Morgan Property	WA	The Nature Conservancy	12	22	28
Pigeon Butte	OR	Finley Wildlife Refuge, USFWS	32	28	43
Scatter Creek Wildlife Area	WA	WA Dept. of Fish and Wildlife	19	28	63
South Weir Prairie, Training Area 23	WA	Joint Base Lewis-McChord, Dept. of Defense	18	21	12
Triangle Prairie, Training Area 15	WA	Joint Base Lewis-McChord, Dept. of Defense	23	30	48

We tested combinations of treatments that simultaneously target a range of limiting factors, thereby making our results more directly applicable to management. Our treatment combinations included grass-specific herbicide (sethoxydim), broad-spectrum herbicide (glyphosate), fall burning, spring mowing, fall mowing, and seeding with native species.

Methods

Disturbance Treatments

Treatments were chosen that could be used effectively and efficiently at large scales. Timing of treatments was based on manager's recommendations for optimal effects. The grass-specific herbicide sethoxydim was applied in the spring to reduce abundance of non-native perennial grasses and timed to plant development rather than calendar date. Optimal spray time was slightly before the main target grass at each site was in the boot stage (when the seed head was still enclosed in the leaf sheath, typically mid-April–mid-May). Sethoxydim was applied in a 1.5% a.i. solution with a surfactant (crop oil) and marking dye.

Spring mowing occurred after vegetation sampling, when the target grass was flowering, to prevent seed set and reduce stored reserves of non-native perennial grasses. Fall mowing occurred just after the start of fall rain, when target grasses usually started a period of fall regrowth, to reduce thatch accumulation and set back new growth. Target mow height was 6–10 cm in spring and 2.5–6.5 cm in fall and biomass was left in place. While we considered removing the biomass,

Table 2. Manager-recommended disturbance treatment combinations. Sethoxydim (S) is an herbicide that targets all Poaceae; however, the native grass Roemer's fescue (*Festuca roemeri*) is resistant. Glyphosate (G) is a broad-spectrum herbicide and was applied two to three weeks after burning (B). Spring treatments occurred after data collection. In addition, native seed was added to half of each treatment unit, including controls, in fall of 2006.

Treatment Code	2005		2006		2007	
	Spring	Fall	Spring	Fall	Spring	Fall
SBG	Sethoxydim		Sethoxydim	Burn + glyphosate	Sethoxydim	
MBG	Mow			Burn + glyphosate		
MM	Mow	Mow	Mow	Mow	Mow	Mow
SM	Sethoxydim	Mow	Sethoxydim	Mow	Sethoxydim	Mow
Control	No disturbance treatment					

Table 3. Amount of native seed (g/m²) added to subplots at each site as part of a multifaceted restoration experiment in lowland prairie and oak savanna of the Willamette Valley/Puget Trough/Georgia Basin ecoregion. CGOP = Cowichan Garry Oak Preserve; SW = South Weir Prairie; MMP = Mima Mounds Preserve; GHP = Glacial Heritage Preserve; SC = Scatter Creek; TP = Triangle Prairie; MP = Morgan Property; FH = Fort Hoskins; BF = Bellfountain Road; PB = Pigeon Butte.

Species	Seeding Rate (g/m²)	Sites
Perennial Grasses		
California oatgrass (*Danthonia californica*)	0.392	MP, TP, SW
	0.436	MMP
	0.698	BF, PB, FH, CGOP
Poverty oatgrass (*D. spicata*)	0.544	GHP, SC
Roemer's fescue (*Festuca roemeri*)	0.234	All
Perennial Forbs		
Common yarrow (*Achillea millefolium*)	0.029	All
Oregon sunshine (*Eriophyllum lanatum*)	0.0.8	GHP, MMP, MP, SC, TP, SW
	0.065	BF, PB, FH, CGOP
Barestem biscuitroot (*Lomatium nudicaule*)	1.285	TP
Common lomatium (*Lomatium utriculatum*)	0.146	All except TP
Western buttercup (*Ranunculus occidentalis*)	0.168	GHP, MMP, MP, SC, TP, SW
	0.22	BF, PB, FH, CGOP
Annual Forb		
Shortspur seablush (*Plectritis congesta*)	0.04	All

haying is impractical and expensive, and several of our sites were too steep or remote for haying equipment. Burns occurred in early fall (September–October) at the end of the summer drought period when most species were dormant. The goal was to reduce biomass and thatch accumulation and prepare sites for reseeding. While some historical records indicate that Native American's burning might have occurred earlier in the summer (July–August), restoration burns in the ecoregion are typically done in fall due to permitting and safety issues.

After burning we applied glyphosate to reduce abundance of rapidly resprouting non-native species, particularly broadleaf weeds. This was developed based on managers' observations that many non-native species, including some of the most dominant invaders, resprout more quickly after fire than do most native species. Glyphosate was applied to burned plots approximately two weeks after the burn, in a 1.5% a.i. solution with surfactant (crop oil) and marking dye. Site managers assessed abundance of resprouting natives and non-natives before spraying and found that at most sites non-native species greened up quickly after the burn, but most natives had not yet resprouted. At two sites with high native abundance, Cowichan Preserve and Triangle Prairie, site managers decided to spot spray to avoid native plants. This flexibility in treatment application was a compromise between researchers' desire for uniform treatments across all sites and managers' need to avoid damaging high-quality prairie remnants.

Experimental Design and Data Collection

The five combinations of disturbance treatments (see Table 2) were developed in collaboration between managers and researchers. A fully factorial design was not possible, given the number of treatments and limitations on resources and space. Each of our ten sites contained a block of 20 experimental plots (each 5 × 5 m), with the five treatment combinations (four replicates each) randomly assigned to plots. At eight sites, plots were laid out in a grid, but other configurations were necessary at the other two sites. At Mima Mounds Preserve, plots were located on the tops of mounds, as vegetation communities on mounds were very different from intermound communities. Mounds average ca. 9 m in diameter and 2 m high. Plots at Cowichan Garry Oak Preserve were placed to avoid having oak trees within plots. Starting in 2005, all disturbance treatments were applied to the entire plot.

Plots were divided into 2 subplots (2.5 × 5 m), one of which was sown with native seed, creating a split-plot design. Seven species widespread throughout the ecoregion were sown at each site, with two congeneric substitutions based on the locally abundant species (Table 3). We chose these species to represent a range of growth forms and life histories typically found in these prairies. Native seed was either collected on site or from nearby sites, or purchased from local growers. Our seed mix was designed to have 40% grasses to 60% forbs (by seed number rather than seed weight), with a total seeding rate of approximately 1,200 seeds/m². Although we tried to standardize the quantities of seed sown at all sites, some variations occurred because seed availability was limited in certain areas (Table 3). Seed was broadcast onto seeded subplots in fall 2006 (late October–early November) followed by light raking to improve seed-soil contact. Unseeded subplots were also raked.

In each plot, data were collected from four 1 m² permanent sampling quadrats (two per subplot) in the spring (April–early June) before treatment (2005) and after two years of treatments (2007). Percent cover was visually estimated to the nearest 1% for all vascular plant species, as well as moss, litter, and bare soil. Total cover for a plot was at least 100% and often exceeded that if many layers of vegetation were present. We reduced the potential for observer bias by having the same lead data collector from year to year, combined with training and frequent calibration of observations with seasonal data collectors. Species nomenclature and supplementary information (provenance, duration, etc.) followed the USDA PLANTS database (USDA and NRCS 2008) and local floras (Hitchcock and Cronquist 1973, Kozloff 2005).

Data Analysis

We used linear mixed ANCOVA in SAS 9.13 (PROC MIXED) (SAS Institute, Carey NC) to test for treatment and seeding effects and their interactions. We analyzed the response of native and non-native species by richness, total vegetation cover of natives and non-natives, cover of functional groups (the summed cover of perennial forbs, perennial graminoids, and annuals), and the cover of litter, moss, and bare soil. Native graminoids included grasses, sedges, and rushes; non-native graminoids included only grasses as no non-native sedges or rushes were present at our sites. Site was treated as a random blocking factor (following Venables and Ripley 2002), as we are most interested in this paper in describing the general trends across all sites, rather than scrutinizing the variation between sites. Treatment and seeding were fixed interacting factors, and pretreatment data were used as the covariate. Seeding nested within treatment was used as the replicating unit (10 sites × 5 treatments × 4 replicates × 2 seeding treatments; $N = 400$). Data from the two sampling quadrats per subplot were averaged prior to analysis. Richness data were square-root transformed and cover data were log transformed to meet assumptions of normality and homogeneity of variance. Post hoc Tukey tests were used for testing for differences among treatment means. We used $p < 0.05$ as our criterion for significant results.

Results

Sites varied considerably in initial diversity, from 34 to 68 vascular plant species found in sampling quadrats at each site (Table 1). Native species accounted for 35–65% of total vascular plant diversity and 12–63% of total vegetative cover in 2005.

Non-native grasses were most successfully reduced where treatments included application of the grass-specific herbicide sethoxydim (SBG, SM) (Figure 2a). Repeated mowing (MM) had no effect on these grasses, but a significant reduction in non-native grasses did result when mowing was combined with burning and glyphosate application (MBG). Cover of perennial non-native forbs was significantly reduced with treatments that combined burning with glyphosate application (SBG, MBG; Figure 2c). Of the two treatments including sethoxydim, the combination with burning (SBG) had significantly higher cover of annuals than the combination with fall mowing (SM), although neither differed significantly from controls (Figure 2e). Collectively, these responses resulted in the greatest overall reductions in total non-native species cover in treatments that included burning and glyphosate, with or without sethoxydim (SBG, MBG). For statistical analyses, see Appendix 1 (available online at uwpress.wisc.edu/journals/journals/er_suppl.html).

In contrast to responses by non-native species, cover of native species generally exhibited little response to the disturbance treatments. The MBG treatment resulted in a small but significant reduction in native graminoids (Figure 2b). In contrast, treatments including sethoxydim (SBG, SM) did not reduce cover of native graminoids. Overall, the SM treatment resulted in a significant increase in total native cover (Figure 2h).

Seed addition caused a small but significant increase in total cover of natives; unseeded plots averaged 22.4%, while seeded plots averaged 24% $F_{1,45} = 4.88$, $p = 0.03$). The cover of native annuals was also greater in seeded plots (1.8%) than in unseeded (1.3%) ($F_{1,45} = 42.1$, $p < 0.0001$), but seed addition did not affect cover of native perennial graminoids or forbs (see Appendix 1). At the time of sampling in spring 2007, most seeded individuals were small seedlings except for shortspur seablush (*Plectritis congesta*), an annual species that was flowering at the time of sampling. While the statistical analyses showed a significant effect of disturbance treatments on the cover of native annuals (Appendix 1), this was driven by the significant interaction between seed addition and treatment (post hoc Tukey comparisons between treatments were nonsignificant). Owing

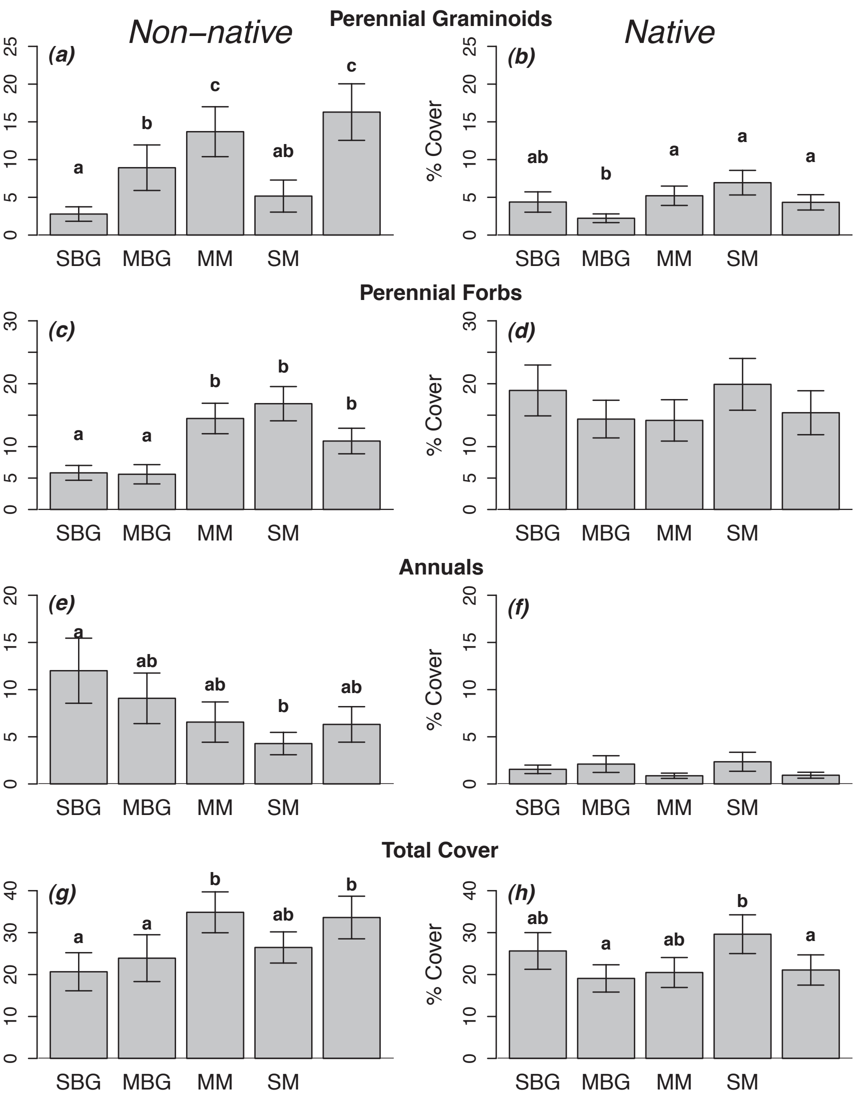

Figure 2. Effects of treatment combinations on mean (±2 SE) percent cover in 2007 of non-native and native vegetation, by functional group. Treatment combinations tested were SBG (sethoxydim + burning + glyphosate), MBG (mowing + burning + glyphosate), MM (spring + fall mow), and SM (sethoxydim + fall mow); see Table 2 for full description of treatment combinations. Different letters indicate significant statistical differences at $p < 0.05$ using Tukey post hoc comparisons based on ANCOVA models; graphs without letters indicate no significant differences.

to the response of the seeded annual shortspur seablush, treatments that included fire (SBG, MBG) led to an increase in native annuals only in the seeded subplots, averaging 2.2% for SBG, 2.7% for MBG, and 1.0% for seeded control plots ($F_{4,45} = 5.3$, $p = 0.001$).

Disturbance treatments had no effect on native or non-native species richness (Appendix 1). Seed addition increased total native richness across all treatments, with a mean plot richness of 12.9 species in seeded plots and 9.5 species in unseeded plots ($F_{1,45} = 141.6$, $p < 0.0001$), but the increase was not influenced by the different treatments.

While all disturbance treatments reduced the cover of litter, only treatments that included burning and glyphosate (SBG and MBG) resulted in a significant decrease in moss cover (Figure 3). Bare soil increased only in the SBG and MBG treatments (Figure 3). For statistical analyses, see Appendix 2 (available online at uwpress.wisc.edu/journals/journals/er_suppl.html).

Discussion

We set out to test the relative effectiveness of combined treatments in reducing non-natives and increasing natives in degraded habitats, using standard approaches (fire, mowing, herbicide, and seed addition), but in unique manager-recommended combinations. We suggest this approach has broad applicability, given that the challenges of our system (invasion, native rarity, long-term disturbance suppression) are common to many degraded grass-dominated systems (e.g., Bakker and Berendse 1999, Coulson et al. 2001, Lenz and Facelli 2005). We found that effectiveness of the tested treatment combinations varied significantly, with the most progress toward restoration goals achieved by the combination of sethoxydim, fire, glyphosate, and seeding. This disturbance-intensive treatment led to large reductions in perennial non-native grasses and forbs, litter, and moss, without causing declines in native species (Figures 2 and 3). Non-native perennial species (grasses and forbs combined) declined from 26.8% cover to 8% cover, a 70% reduction (Figure 2). While non-native annuals increased with this treatment, we predict the annual response to be short-lived (Dunwiddie 2002). This treatment combination also increased the success of a seeded native annual. Seeding was the only action that increased native diversity, suggesting that these systems are characterized by acute dispersal limitation.

Non-Native Grasses

Several treatments reduced the abundance of non-native grasses. As expected, treatments that included the grass-specific herbicide sethoxydim, applied twice over two years, were most effective, reducing average non-native grass cover from over 16% to 5.2% (SM) or 2.8% (SBG) (Figure 2). Treatment MBG also reduced non-native grass cover (to 8.9%), but not as effectively as sethoxydim. Many of the non-native grasses are fire tolerant, but because they resprouted quickly after burning, they were reduced by the post-burn application of glyphosate in the MBG and SBG treatments. The repeated mowing treatment did not significantly reduce the cover of non-native grasses. While some studies have found mowing reduces non-native grasses at least temporarily (Wilson and Clark 2001, MacDougall and Turkington 2007), the problematic grasses at most of our sites, particularly tall oat grass with its substantial bulbous stem bases for underground storage, and bentgrass, which is sod forming and frequently used as a turf grass, appear to be very resistant to mowing.

Nontarget Species

Removal of dominant species can lead to different outcomes, depending on whether dominance arose through competitive superiority for limiting resources (Tilman 1988) or ability to tolerate conditions (e.g., herbivory, disturbance regime) that limit other species (Grime 2001, Seabloom et al. 2003b). MacDougall and Turkington (2005) found that many native species, including perennial grasses and rare species, did not respond positively to removal of dominant non-native grasses at the Cowichan Garry Oak Preserve, one of the sites included in our experiment. They concluded that although competitive release had a positive effect on the growth and reproduction of some native species, especially perennial forbs and annuals, overall competition was less important than environmental factors and seed limitation. Our results were similar in that reductions in non-native grasses did not lead to corresponding increases in cover of native graminoids, and that seed addition was required to increase native diversity.

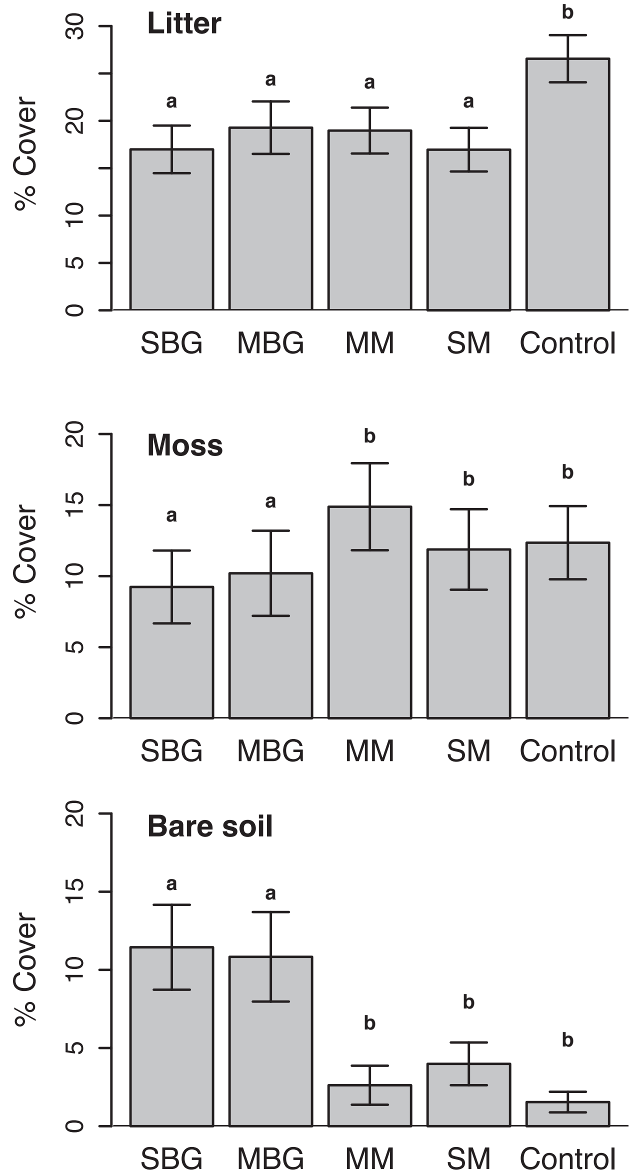

Figure 3. Effects of treatment combinations on mean percent cover (±2 SE) of litter, moss, and bare soil in 2007. Treatment combinations tested were SBG (sethoxydim + burning + glyphosate), MBG (mowing + burning + glyphosate), MM (spring + fall mow), and SM (sethoxydim + fall mow); see Table 2 for full description of treatment combinations. Different letters indicate significant statistical differences at $p < 0.05$ using Tukey post hoc comparisons based on ANCOVA models.

Disturbance treatments did not appear to have a detrimental impact on native species. Cover of native graminoids in treatments SBG and SM was not different from controls, indicating that any decline in sethoxydim-susceptible native grasses was offset by an increase in nonsusceptible species such as Roemer's fescue (Blakeley-Smith 2006), and native sedges and rushes. Native graminoids declined in treatment MBG, most likely because the dominant species at many sites, Roemer's fescue, tends to be set back by burning (Dunwiddie 2002). Mowing may have been a factor as well because postfire decline was not seen in treatment SBG.

The large reduction in dominant non-native grasses in treatments involving grass-specific herbicide (SBG and SM) could also create opportunities for other non-native species to increase, but postfire glyphosate application (as in SBG) reduced non-native perennial forbs by almost 50% (Figure 2). Because many non-native species resprouted more quickly after burning than most natives, this carefully timed application of a broad-spectrum herbicide was fairly selective in impacting the non-native species. Even so, one consequence of the SBG combination was a large increase in non-native annual weeds after burning compared with the SM treatment (Figure 2). Elsewhere in this ecoregion, similar postfire increases in both native and non-native annual species persisted for three to four years, followed by resumed dominance of perennials (Dunwiddie 2002). These responses suggest that native annuals may be largely missing from many of these systems and may need to be included in future native seeding applications to help fill the niche that was taken up by non-native annuals when non-native perennial grasses are controlled. The positive response of shortspur seablush, the only native annual seeded in this experiment, supports this hypothesis.

Native Seed Addition

Two main factors may limit plant establishment from seed: dispersal and microsite availability (Coulson et al. 2001, Münzbergová and Herben 2005). The implications for restoration are that seeding alone can overcome dispersal limitations, but that disturbance treatments may also be required if microsites are limited as well. In our study, we found strong evidence that seed limitation is an important factor in most Pacific Northwest prairies. By seeding just seven common native species, we increased native richness by an average of 36% and cover by 7% in one year. Similarly, many other researchers have found seed addition increases native diversity in restoration (Foster and Tilman 2003, Seabloom et al. 2003a, MacDougall and Turkington 2005). Dispersal limitation may result from both reduced seed production in heavily invaded sites as well as large distances between source plants. Also, the number of propagules from non-native species often vastly exceeds those from natives; one study in prairie habitats in western Washington found that nine common invasive weed species made up over 90% of the seed bank (Andreu 2005).

Our data do not provide a definitive answer regarding the role of microsite limitation in this system. If microsites were the key limiting factor, we would expect native cover and richness to increase with disturbance treatments alone, particularly in combinations including fire. Additionally, we would expect to find a significant seeding by treatment interaction, where seeded species added more to native cover and richness in certain treatments. Instead, we found that disturbance treatments have had no effect to date on native richness and only minimal impacts on native cover. Seeding in our study increased richness equally in controls and disturbance treatments, in contrast to restorations in British grasslands (e.g., Pywell et al. 2002) but in agreement with seedings in non-native-dominated grasslands in California (Seabloom et al. 2003a).

Our data also indicate that microsite limitation and competition may play a crucial role for establishment and persistence of annual species. We found disturbance treatments could strongly increase the influence of seeding on the cover of native annuals (Appendix 1), driven by the response of the seeded species, shortspur seablush (Stanley et al. 2008). This species had higher germination in the two burn treatments (K. Reagan, University of Washington, unpub. data), possibly because burning reduced the cover of litter and moss (Figure 3) and increased light transmission to the soil (A. Stanley, unpub. data). Although shortspur seablush established even in control plots, seedlings were smaller and produced fewer flowers than in treatment plots (A. Stanley, pers. obs.). We suspect that the disappearance of many native annuals from Pacific Northwest prairies (Dunwiddie et al. 2006) is due to fewer disturbances relative to historic patterns, primarily through fire suppression.

Our results show strong seed limitation of native diversity in prairies and oak savannas, a pattern common in similar habitats in other ecoregions (Seabloom et al. 2003a, Gross et al. 2005, Foster et al. 2007). Over time, release from competition through disturbance treatments may become more important to the continued growth and reproduction of seeded species.

Conclusions

The combination of abundant and widespread non-native plants, limited native seed production, and highly fragmented habitat patches in Pacific Northwest prairies presents a challenging environment for restoration. Our study tested 1) the ability of multiple disturbance treatments to reduce the abundance of invasive grasses; 2) the effects of treatment combinations on nontarget native and non-native species; and 3) the strength of seed limitation in prairies and oak savannas in the WPG ecoregion. Our treatment combinations, especially those that included sethoxydim, were effective at reducing invasive grass abundance. The combination of sethoxydim with fire also reduced accumulated thatch and increased the amount of bare soil, potentially improving conditions for seedling establishment and growth. These treatment combinations reduced non-native perennial grasses and forbs without causing negative impacts to native species. Seeding just seven commonly occurring native plants significantly increased native abundance and richness, indicating prairie and oak savanna remnants are strongly seed limited. Large-scale collaboration between scientists and managers can result in innovative treatment combinations backed by experimental rigor for rapid advances in restoration science and practice.

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