

Invasive Perennial Grasses in *Quercus garryana* Meadows of Southwestern British Columbia: Prospects for Restoration¹

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Abstract

Garry oak (*Quercus garryana*) meadows of the Pacific Northwest are heavily invaded but the dynamics surrounding this ecosystem transformation are poorly understood. Of particular uncertainty is the role of the invasive species in structuring the community, and the potential stability of this invasive-dominated system when disturbed. Clarifying such issues is central to restoration success for Garry oak meadows, one of Canada's most endangered terrestrial ecosystems. This paper examines the competitive inter-relationships among exotic and native flora, and how these inter-relationships are modified by a series of disturbance treatments (burning, mowing, and selective removal of invasives). Recruitment dynamics are also described. Pre-treatment surveys of vascular plant taxa identified 80 species within the study area located near Duncan, British Columbia, Canada. Thirty-nine of the species were non-native. Two of the invasives—Kentucky blue grass and orchard grass—were dominant, averaging a combined 80 percent of total cover in all plots. Disturbance treatments, regardless of type or intensity, caused significant decreases in total percent cover of the exotic dominant grasses, and significant increases in ground level light, total species richness, and total percent cover of native flora. A combination of disturbance and native seed additions revealed that native plant recruitment is limited by primarily by dispersal, though the dense invasive sward probably restricts recruitment success also. These results indicate that the invasive sward could be de-stabilized by disturbance treatments, though supplemental recruitment measures are also needed to restore native species dominance to these meadows.

Introduction

Plant invasions have transformed communities worldwide, changing fundamentally the composition, structure, and functioning of native floral assemblages (D'Antonio and Vitousek 1992, Mooney and Drake 1986). Of particular concern is the competitive displacement of native taxa by invading species. In the grasslands and oak savannas of western North America, displacement by exotic grasses approaches 100 percent in some areas (Harrison 1999, Heady 1977)

To restore invaded systems, we must understand how they function in their current state, and in particular, why the exotic invaders are so successful. Based on present-day dominance patterns in inundated plant communities, we tend to assume that the exotics are absolute competitive dominants. Compared to native flora, these species are better able to acquire limiting resources (e.g., light, soil moisture, soil nutrients, recruitment space) and over time displace native assemblages. And this

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may be the case. But there is an alternative competition model that may explain present-day dominance patterns: contingent dominance. Rather than relying on outright competitive superiority, contingent dominance might be driven by historical disturbance events. For example, the combination of intense domestic grazing, fire suppression, and intentional introductions of massive amounts of Eurasian pasture grass seed could easily create a dominant and stable exotic assemblage that need not rely on relative competitive superiority. Or, exotic flora may be competitively dominant, but only because they are better adapted to contemporary human disturbance regimes. In undisturbed habitats, native flora may be competitive equals.

Determining the competitive relationships among exotic and native flora enhances our understanding of how biotic interactions shape community structure. But such assessments also guide restoration activity. Whether or not exotic flora are “absolute” or “contingent” dominants will determine the appropriateness of particular restoration measures. If exotic species are absolute competitive dominants, it is unlikely that they can ever be removed from the community. Restoration must focus on continued suppression of exotics to offset their competitive dominance over the native species (e.g., Weiss 1999). Alternatively, if present-day exotic dominance is driven by historical factors, rather than absolute competitive superiority, then restoration effort could focus on shifting current conditions, such as disturbance regimes, to favor other assemblage dominants (i.e., native flora). Given these possibilities, untangling competitive inter-relationships within invaded communities may be a critical step in effective restoration.

This paper seeks to describe existing competitive interactions within the heavily invaded Garry oak (*Quercus garryana*) meadows of southwestern British Columbia, and how these interactions are modified by disturbance. Plant invasions in this region occurred within a few decades following European colonization in the mid- to late 1800s and thus the processes that drove exotic inundation are no longer evident. However, by experimentally de-stabilizing and re-assembling this assemblage with disturbance and species-addition treatments respectively, we can begin to untangle the current role of the exotics within the community, as well as the potential for native species to once again become dominant. To explore these issues, I ask three questions based on the initial results (2 years) of a longer-term study: 1) What is the current species composition and relative species abundance of exotic and native flora within Garry oak meadows? 2) How are these factors transformed by varying types and intensities of disturbance (burning, mowing, selective removals)? and 3) How does disturbance affect the recruitment dynamics of native and exotic flora?

Methods

The study was conducted in the Cowichan Garry Oak Reserve near Duncan, British Columbia, Canada. The reserve is a 18 ha remnant of a highly fragmented oak meadow ecosystem extending along the coastal areas of southeastern Vancouver Island from Victoria to Courtney-Comox, and including many of the South Gulf Islands. Garry oak meadows in British Columbia contain approximately 350 vascular plant species, of which 139 are invasives (Fuchs 2000). Garry oak (*Quercus garryana*), the most visible native species (hence the moniker “Garry oak meadows”), occurs at varying densities from sporadic to closed canopy. The most abundant ground flora species include small camas (*Camassia quamash*), Henderson’s shooting-star (*Dodecatheon hendersonii*), long-stoloned sedge (*Carex*

inops), and Idaho fescue (*Festuca idahoensis*). The most abundant exotics include Kentucky blue grass (*Poa pratensis*), orchard grass (*Dactylis glomerata*), and sweet vernal grass (*Anthoxanthum pusillum*). The shrub Scotch broom (*Cytisus scoparius*) also dominates many sites (Fuchs 2000).

Two experiments were established in May 2000 at two locations within the Cowichan Reserve. The locations differed in soil depth (location A: soil >1 m deep; location B: soil depth 5-15 cm) to determine if treatment responses interacted with site factors. Oak meadow assemblages in British Columbia occur across a range of soil depths (from <1 cm to >1 m), which strongly determine relative native species abundances (Erickson 2002), and may also influence the type and intensity of invasion. In one experiment, focusing on the effects of disturbance treatments on species richness and abundance, 80 one m² plots were established in each of the two locations. Percent cover of all species was determined in May 2000 using a one m² frame divided into twenty “5 percent” cells. Four treatments were initiated in July 2000: control, burning, mowing, and selective removals of all exotic species. In October 2000, four additional treatments were implemented: control, autumn burning, autumn mowing, and autumn selective removals. The four July treatments were re-applied at this time also, for a total of eight treatments. Each of the eight treatments was replicated ten times per each location. Percent cover was re-assessed in May 2001. Beginning in July 2000, ground-level light levels (ratio of percent photosynthetically active radiation (PAR) above canopy vs. below-LiCor Quantum Sensor) and soil moisture (TDR 12 cm soil moisture probe) were measured every six weeks. Changes in total percent cover between May 2000 and May 2001 were compared for all identified species using t-tests for each treatment and for each location separately ($\alpha_{0.05/2}$). Percent PAR in April 1, 2001, a time when light availability is especially critical for seedling survival and vegetative growth of established individuals, was compared among treatments using a one-way ANOVA ($\alpha_{0.05/2}$). Soil moisture availability did not vary with treatment and is not discussed further.

In the second experiment, seedling recruitment was examined with and without burning, and with and without the experimental addition of native seed. Forty 0.6 m² plots were established in each of the two locations. Half of these plots were burned in July and October 2000. Seed from 13 native plant species was added to 20 of the 40 burned plots and 20 of the 40 unburned or control plots in October 2000 following the last burn. The number of established seedlings of all species, native and exotic, were tallied in late April and early May 2001.

Results

A total of 80 species were identified within the 160 plots at the two locations. Average species richness per plot was significantly higher ($t_{0.025,79} = 2.23$; $p < 0.001$) at the shallow soil location (mean = 28 species) than at the deep soil site (mean = 19 species). Disturbance history apparently does not differ between these two locations, based on interviews with the long-term owner (age: 102 years) and supported by examination of air photos dating back to 1950. The deeper soil location also had fewer native plant species occupying significantly less percent cover ($t_{0.025,79} = 4.31$; $p < 0.001$), suggesting that invasive plants have had a higher impact at this location. In addition, most the native plants in the deep soil site are considered habitat generalists rather than Garry oak meadows specialists in British Columbia (e.g., Sweet Cicely

(*Osmorhiza chilensis*). The reverse was true for most of the native flora found on the shallow soil site (e.g., spring-gold (*Lomatium utriculatum*), western buttercup (*Ranunculus occidentalis*), Menzie's larkspur (*Delphinium menziesii*), and prairie violet (*Viola praemorsa*)).

Significant treatment effects were detected for 21 of 29 species occurring at sufficient frequency to conduct a t-test. The remaining 51 species were rare, occurring typically in fewer than five of the 160 plots. However, treatment differences were not detected among any of the eight treatments except for the two controls (i.e., control vs. any of the disturbance treatments). This suggests that the most important effect of the disturbances initially was the removal of the exotic grass overstory and the exposure of bare soil, rather than any specific differences among the six disturbance types. The selective weeding plots did not differ in effect from the other disturbances and this is probably indicative of the low percent cover of native flora in many plots (typically <10 percent). It is unclear whether the lack of differences among treatments will remain consistent into the future or whether differences will develop in the subsequent years of this study. As a result of this lack of difference, the species response data for the disturbance plots were pooled.

For species showing significant responses to disturbance (table 1), 16 are considered "increasers," demonstrating a significant increase in percent cover following the treatments in both locations. Nine of the 16 "increaser" species were native, and included both annual ruderal species and late-successional geophyte species (e.g., *Camassia quamash*, *Dodecatheon hendersonii*). Two of the native annual ruderals, two-colored Lupine (*Lupinus bicolor*) and small-flowered lotus (*Lotus micranthus*), were not observed during the May 2000 census. Among the seven exotic "increaser" species, five were uncommon (≤ 2 percent mean cover) during the May 2000 surveys compared to the two dominant exotic species (Kentucky blue grass and orchard grass).

Four additional species had significant increases in one of the two locations only. Of note was sweet vernal grass, an exotic perennial grass that doubled in percent cover in response to the disturbances at the shallow soil location (10 percent to 22 percent). This species is considered a problematic invasive in other Garry oak meadow sites on southeastern Vancouver Island.

Only two of 29 species showed significant decreases in percent cover—Kentucky blue grass and orchard grass—though this was not consistent at both locations. At the deep soil location, Kentucky blue grass declined from 65 percent to 45 percent following the disturbances; it was the dominant species prior to perturbation. At the shallow soil site, where this species is less abundant (average cover = 26 percent), treatment responses were not significant. Orchard grass, the second most dominant species within the study area, decreased by 4-6 percent at both sites.

Six species showed no significant change after the disturbances, suggesting that they were slow to respond or were impervious to the perturbations. Two of these were native graminoids—California brome (*Bromus carinatus*) and blue wildrye (*Elymus glaucus*).

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Table 1—Species responses ($n = 29$) between May 2000 and May 2001 within 120 one m^2 plots from the deep-soil (Location A) and shallow-soil (Location B) sites. Values are percent cover per plot averaged for the 60 treatment plots per location (i.e., control comparisons not included). All treatment responses (“increasers,” “decreasers”) were significant using a t -test ($\alpha_{0.05/2}$). “Inconsistent change” species had different responses between the two sites.

Response	Life form	Location A change	Location B change
Increaser species			
<i>Camassia quamash</i>	perennial forb	1.6 pct to 2.8 pct	5 pct to 10 pct
<i>Dodecatheon hendersonii</i>	perennial forb	does not occur	3.1 pct to 8.3 pct
<i>Cardamine oligospora</i>	annual forb	0 to 3.7 pct	0 to 1.5 pct
<i>Cerastium arvense</i>	perennial forb	does not occur	3.6 pct to 7.6 pct
<i>Cytisus scoparius</i>	perennial shrub	3.5 pct to 12.8 pct	0.7 pct to 3 pct
<i>Lathyrus sphaerica</i> ¹	annual forb	1.4 pct to 1.6 pct	4.7 pct to 8.1 pct
<i>Lomatium utriculatum</i>	perennial forb	does not occur	3.3 pct to 7.4 pct
<i>Myosotis discolor</i> ¹	annual forb	0.8 pct to 8.2 pct	0.1 pct to 1.1 pct
<i>Ranunculus occidentalis</i>	perennial forb	does not occur	2 pct to 6.9 pct
<i>Sanicula crassicaulis</i>	perennial forb	11.9 pct to 19.3 pct	5 pct to 12.8 pct
<i>Trifolium dubium</i> ¹	annual forb	0.1 pct to 3.1 pct	0.1 pct to 2.7 pct
<i>Valerianella locusta</i> ¹	annual forb	0.5 pct to 4.5 pct	1.3 pct to 8.4 pct
<i>Veronica arvensis</i> ¹	annual forb	0.04 pct to 0.25 pct	0.3 pct to 1 pct
<i>Vicia hirsuta</i> ¹	annual forb	2.1 pct to 4.4 pct	0.8 pct to 2.6 pct
<i>Vicia sativa</i> ¹	perennial forb	7.8 pct to 22.1 pct	7.7 pct to 11 pct
<i>Viola praemorsa</i>	perennial forb	does not occur	0.8 pct to 2.4 pct
Decreaser species			
<i>Dactylis glomerata</i> ¹	perennial graminoid	16.1 pct to 10.3 pct	22 pct to 17.6 pct
No change species			
<i>Bromus carinatus</i>	perennial graminoid	7.2 pct to 7.8 pct	10.46 pct to 11.01
<i>Bromus mollis</i> ¹	annual graminoid	0.9 pct to 0.4 pct	1.2 pct to 1.5 pct
<i>Elymus glaucus</i>	perennial graminoid	0.6 pct to 0.1 pct	0 to 1.13 pct
<i>Geranium molle</i> ¹	annual forb	0.4 pct to 0.8 pct	1.2 pct to 2.7 pct
<i>Rumex acetosella</i>	perennial forb	does not occur	0.3 pct to 0.6 pct
<i>Claytonia perfoliata</i>	annual forb	0.4 pct to 0.6 pct	1 pct to 0.8 pct
Inconsistent change			
<i>Anthoxanthum odoratum</i> ¹	perennial graminoid	5.2 pct to 5.8 pct ²	11.5 pct to 20.6 pct
<i>Poa pratensis</i> ¹	perennial graminoid	65.4 pct to 43.3 pct	27 pct to 27 pct ²
<i>Bromus sterilis</i> ¹	annual graminoid	2.7 pct to 4.3 pct	6.4 pct to 4.6 pct
<i>Carex inops</i>	perennial graminoid	5.9 pct to 10.2 pct	2.4 pct to 2.3 pct ²
<i>Galium aparine</i>	annual forb	2.5 pct to 2.3 pct ²	9.8 pct to 22.58 pct

¹ Invasive species

² Changes not significant

Within each of the two site locations, light levels differed significantly only between control and non-control treatments; they did not differ among the disturbance conditions (*fig. 1*). The biggest contrasts in ground-level light intensity occurred between the two locations. In the deep-soil plots (Location A), the percentage of full light ranged mostly between 1-2 percent in the control plots while in the shallow soil plots (Location B), light levels were between 3-6 percent. Among the six disturbance treatments, light-level increases were also much higher in the shallow soil plots.

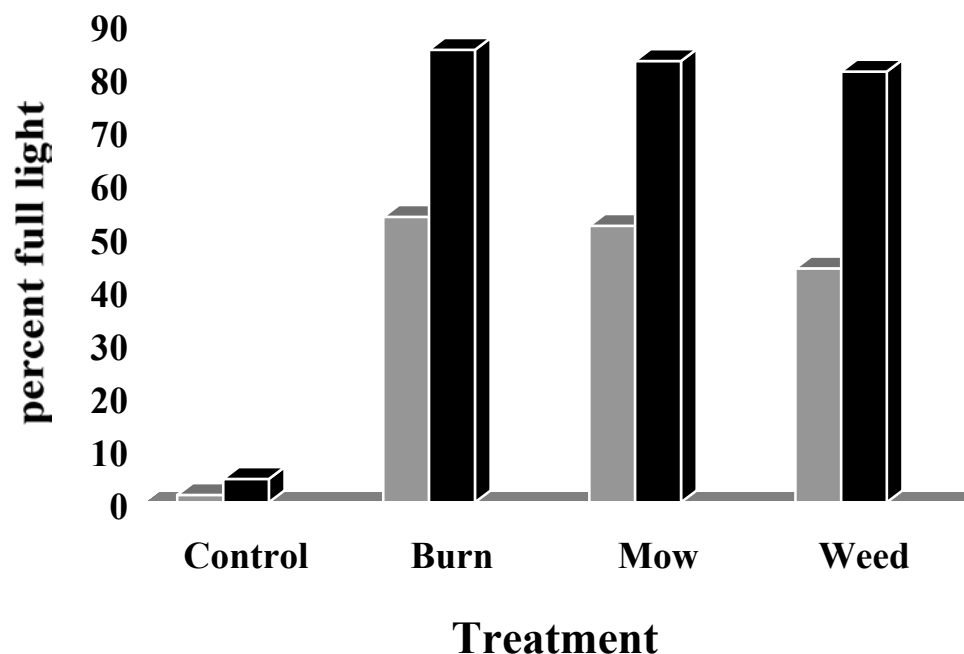


Figure 1—Percentage of full light among the disturbance treatments for April 2001; disturbances were last implemented in October 2000. Gray columns = deep-soil site (Location A); black columns = shallow-soil site (Location B). Derived from 160 one-m² plots. The burn, mow, and weed columns are the combination of summer and fall treatment response data, which did not differ significantly.

Seedling recruitment patterns were influenced significantly by both disturbance (fire) and the experimental introduction of native seed (*fig. 2*). Under control conditions (unburned, no native seed additions) where exotic grass swards are dense, only 12 of 1,479 ($n = 20$ plots) of the recruiting individuals were native species. Burning alone increased the number of recruiting individuals, but it was mostly by exotic species that dispersed into the plot or were in the seed bank. Only 83 native species individuals (of 4,278 total individuals) established. Seedling establishment by experimentally introduced native seed was surprisingly high in both burned and unburned plots, suggesting that germination is not fully inhibited by the exotic sward.

Nonetheless, recruitment was highest for all species, native and invasive, in burned plots. Survival of these established native seedlings will be monitored in subsequent years of this study.

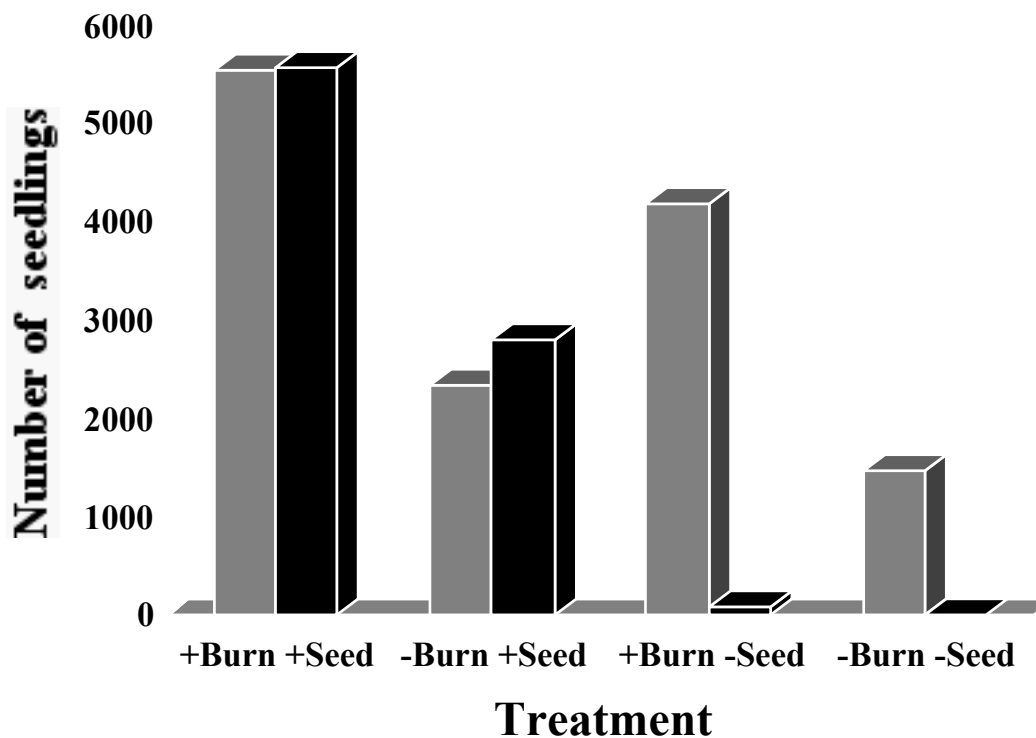


Figure 2—Total number of established seedlings (gray = exotic species; black = native species) within forty 0.60 m² plots. Treatments are 1) burned and native seed added (+Burn +Seed), 2) unburned and native seed added (–Burn +Seed), 3) burned and no native seed added (+Burn –Seed), and 4) unburned and no native seed added (i.e., control).

Discussion

Current abundance patterns within the Cowichan Reserve, one of the best remaining Garry oak meadows in Canada, are dominated by invasive flora, mostly the perennial grasses Kentucky blue grass and orchard grass. In the absence of disturbance, these two species form a dense sward of live material and litter that cover over 80 percent of the ground area in all study plots combined, and reduce ground light levels below five percent full light on average. All other species within the study area, invasive or native, are rare by comparison; few exceed 5 percent ground cover. Of the remaining invasives, most are small annual forbs (<15 cm height) or a mixture of annual and perennial grasses restricted mostly to drier

shallow-soil sites (e.g., sweet vernal grass, annual *Bromus* spp., annual *Vulpia* spp., annual *Aira* spp.).

Patches of native ground flora are common in the reserve but occur typically in areas with shallow soil. Most abundant are spring-flowering geophyte species (small camas, great camas, Henderson's shooting star, spring-gold, and western buttercup) and various graminoids (California brome grass, blue wildrye, long-stoloned sedge, and Alaskan onion-grass (*Melica subulata*)). The grasses *Danthonia californica* and *Festuca idahoensis* are both very rare on the reserve, but do occur in abundance in nearby (<3 km) upper-slope and ridge-top remnant patches where solar exposure is high and soils are especially thin (<5 cm). Within the reserve, the apparent restriction of native species to drier micro-sites suggests that such assemblages are more resistant to invasion at these locations (i.e., competitively dominant), or that they are better able to tolerate summer moisture restrictions compared to Kentucky blue grass and orchard grass (i.e., competitive refuge). While the number of exotic species is higher on shallow soil sites compared to deep soil sites, these species rarely occur in abundance.

Disturbance treatments, regardless of type (burning, mowing, selective removals) or intensity (one or twice per year), all produced a similar response: a significant drop in percent cover of the dominant invasive grasses (except for Kentucky blue grass at Location B), and significant increases in ground level light, total species richness per plot, and total percent cover of established native flora. These responses suggest a suppressive effect of the exotic dominant grasses on other species. If we assume that the two grasses are able to continually regenerate within the dense sward, probably by vegetative spread rather than seed recruitment, then this assemblage would presumably be highly stable over time unless disturbed. Given that the Cowichan Garry Oak Reserve has not been actively grazed since the 1940s, this has probably been the case. Such suppressive dominance by a small number of grass species has been observed repeatedly in other ecosystems, including the tall grass and mixed-grass prairies of central North America (Collins 1987, Turner and others 1993). In these other systems, the dominance and stability of the grasses is perpetuated by their control of the surrounding micro-environment. Not only is ground-level light attenuated, but soil nutrient dynamics (e.g., increased carbon-nitrogen ratios) and soil moisture availability are also transformed compared to pre-invasion conditions. The restoration of these systems depends on breaking the control of dominant species with a range of disturbance treatments (e.g., grazing, burning, mowing), a finding that will likely apply to the Garry oak meadows.

The results of the recruitment treatments confirmed the suppressive effects of the dominant grasses: seedling establishment was highest when plots were disturbed. However, the data suggest that dispersal limitation may be even more restricting for native flora. Without the experimental introduction of native seed, native plant recruitment was close to nil, even within burned plots. Conversely, when seed was added to unburned plots dominated by the dense exotic sward, germination and initial establishment levels were high. While the survival of these germinants over time has yet to be determined, and may be extremely low, it suggests that dispersal inability is severely restricting native species' population spread within this exotic-dominated remnant. Given that the Cowichan Garry Oak Reserve contains large populations of native forbs which probably produce hundreds of thousands of seeds per year, this dispersal inability leads to questions regarding the long-term persistence of native flora. Or, at best, it suggests that species may only be replacing themselves in sites

where they remain abundant, and they would be unable to re-colonize areas where native species have been eliminated. If this is the case, it highlights the need to protect remaining sites containing native plants, and to actively restore degraded remnants via seed and seedling introductions combined with exotic species control.

Conclusion

Results from this study, derived from the initial two years of a longer-term project, demonstrate the suppressive effect of dominant grasses within the Cowichan Garry Oak Reserve on Vancouver Island. It suggests that conservation management effects must focus on both disturbance treatments and recruitment supplementation to restore degraded oak meadow remnants. What remains unclear, however, is the longer-term prospects for re-establishing native ground assemblages that are not only dominant in species richness and percent cover, but are also resistant to re-invasion by exotics. If the exotic grasses are “absolute” competitive dominants, we will expect them to recover eventually from any and all disturbance applications and once again dominate. If this is true, then restorative efforts must focus on the continual suppression of Kentucky blue grass and orchard grass to reduce their suppressive impact on native flora. If the exotics are not absolute dominants, however, but instead have relied on a combination of European management practices and an absence of recent grazing to dominate (i.e., “contingent” dominance), then the re-establishment of a dominant and stable native assemblage could occur. Based on the initial results of this study, this later competitive model may be in effect. The percent cover of exotic dominants has dropped after only one year of treatments, and many native geophytes have doubled in percent cover. Given that many of these natives, especially small and great camas, can form dense and light-suppressing vegetation layers in a similar fashion as the invasive perennial grasses, it may be possible for native-dominated assemblages to resist re-invasion. Future efforts of this study will attempt to determine if such a development can occur.

Acknowledgments

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