Restoration of native plant communities: an examination of seed limitation and microsite limitation in the Garry oak ecosystem.

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Abstract

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Biology

The Garry oak ecosystem is one of the most highly degraded ecosystems in North America due to fragmentation, development, and conversion to incompatible uses, with less than three percent of the ecosystem dominated by native plants (Noss 1995; Crawford and Hall 1997). Despite recognition of the dire state of the ecosystem, the best path toward recovery has been unclear. The research in this dissertation addresses questions fundamental to the restoration of the Garry oak ecosystem. We ask (1) are the native plant species commonly used for restoration of this ecosystem more seed limited or more microsite limited (Chapter 1); (2) which common restoration treatments provide the best opportunity for recruitment when seed is added (Chapter 2); and (3) what is the

best way to determine the success of a restoration experiment that includes both seed addition and adaptive management techniques (Chapter 3)?

Introduction: The Garry oak ecosystem, which includes both prairies and oak savannahs, is considered one of the most threatened ecosystems in North America. Stretching from the southern tip of Vancouver Island, Canada, to northern California, U.S.A, it follows the troughs of the Puget Sound and Willamette Valley. Currently, less than three percent of its original extent is estimated to be dominated by the native plant community (Noss 1995; Crawford and Hall 1997). Restoration and maintenance of the Garry oak ecosystems is critical, as native ecosystems provide habitat for many sensitive, threatened, and endangered species. With little scientific data on the best approaches, restoration actions are currently supported primarily by anecdotal information, and this lack of data limits the pace and effectiveness of current efforts..

The research described in this dissertation focuses on addressing some of the basic questions about restoration for the Garry oak ecosystem. Chapter one examines whether or not native plant species commonly used in restoration are more seed limited or more microsite limited. Chapters two and three both focus on the results of a region-wide experiment that included both seed addition and a comparison of restoration treatments intended to reduce competition with non-native weedy competitors.

Chapter one examines the relative strength of microsite and seed limitation for a suite of ten focal species, each selected for their common use in restoration seed addition in the Garry oak ecosystem. I conducted a manipulative field experiment to examine the relative impact of seed and microsite limitation in a heavily invaded native prairie remnant located in western Washington. I created a gradient of microsites by using fire to establish treatment plots with four levels of manipulation: no burn (control), low, medium, and high levels of burn treatment. I then crossed those treatments with a seed addition gradient for ten native prairie plant species: no seed addition (control), low (50 seeds/species), medium (100 seeds/species), and high (200 seeds/species). All of the focal species were extremely seed limited, but both microsite limitation and seed limitation were significant in determining recruitment of native species in this prairie ecosystem.

Chapter two examines the result of a region-wide experiment focused on examining the effects of seed addition across several commonly used restoration treatments. The recruitment response of each species was site specific and largely attributable to variation in biotic and abiotic site stressors that varied along a north to south gradient of increasing abiotic stress. The native focal species were significantly seed limited at all sites, but where site stress was estimated to be highest, treatment effects had a greater influence on the recruitment of the focal species added, while at low stress sites, treatment effects were indistinguishable from the control treatments.

Chapter three asks whether different methods of data collection provide equivalent results from the same region-wide experiment. Both seedling count data and percent cover data were collected post-seed addition for all plots at ten sites in the spring of 2007. I compared the two methods of data collection and examine the benefits and detractors of each type of data. Seedling count data provided a better estimate of the success of seed addition, but when applied in concert with the percent cover data, several species-specific responses emerged.

Acknowledgements

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Chapter One

Home is where they have to let you in: seed *and* microsite limitation drive recruitment in a threatened native prairie ecosystem.

Abstract: Understanding the forces that limit plant species from recruiting into native plant communities has been an objective of theoretical ecologists and restoration practitioners alike. Much of this work has come down to focusing on seed limitation and microsite limitation, but the two options have often been treated dichotomously, making it difficult to allocate limited restoration funds appropriately. We conducted a manipulative field experiment to examine the relative impact of seed and microsite limitation in a heavily invaded native prairie remnant located in western Washington. We created a gradient of microsites by using fire to establish treatment plots with four levels of manipulation: no burn (control), low, medium, and high levels of burn treatment. We then crossed those treatments with a seed addition gradient for ten native prairie plant species: no seed addition (control), low (50 seeds/species), medium (100 seeds/species), and high (200 seeds/species). Both seed and microsite limitation were significant in determining recruitment of native species in this prairie ecosystem.

Key words: recruitment, seed limitation, microsite limitation, Garry Oak ecosystem, prairie, fire, *Balsamorhiza deltoidea, Castilleja hispida*, *Erigeron speciosus*, *Lomatium*

nudicaule, L. triternatum, L. utriculatum, Potentilla gracilis, Ranunculus occidentalis Solidago missouriensis, Festuca roemeri

Introduction

Understanding the factors that govern the ability of organisms to establish residence and thrive at a particular location has been a driving force in the development of ecological theory (Darwin 1859, Elton 1958, Hutchinson 1959, Sale 1977, Tilman 1994). In plant communities, two dominant hypotheses have emerged and are often treated as dichotomous choices in the literature: seed limitation and establishment limitation, sometimes also called micro-site limitation (Turnbull et al. 2000, Clark 2007, Poulsen 2007).

The seed limitation hypothesis posits that the opportunity for establishment and residence is akin to a race in which the first propagules that arrive at a site win the ability to establish and grow (Sale 1977, Chesson 1981, Warner and Chesson 1985). Species not present at a particular site are seed-limited, either because there are no seeds produced at the source (parent-plant) or due to the lack of seed dispersal to the site (Turnbull et al. 2000). In this model, increased propagule pressure (the number of propagules arriving in a defined area) is directly correlated with increased recruitment, regardless of competitive ability. The second model focuses on microsite limitation, a tradeoff between competition and colonization, and posits that the competitive ability of a species is primarily responsible for its ability to gain control of a site through the competitive acquisition of the site-specific resources available (Armstrong 1976, Hastings 1980, Tilman 1994). In this model, better competitors for finite resources associated with a microsite will be disproportionately represented when propagules arrive in equal quantities. Species that are not present or are underrepresented when the same number of propagules are available are considered microsite limited. Microsites for establishment and growth are defined as having the resources necessary for seedling recruitment; these typically include access to sunlight, nutrients, and moisture and the ability of seeds (propagules) to make contact with soil (Harper 1961), all of which may be modulated by the species already present at the site (Holmgren et al. 1997). Physical factors affecting the suitability of a microsite are complex and include temperature and soil pH, the capacity of the soil to hold moisture, and retain critical nutrients, such as nitrogen and carbon. Microsite quality also improves with the absence of plant pathogens. We term microsite limitation (also known as “establishment limitation”) as any restriction imposed by limited resources or the occurrence of any physical factors or conditions inappropriate for seed germination and establishment.

A meta-analysis of ecological studies conducted by Clark et al. (2007) concluded that seed-limitation and microsite-limitation are primarily portrayed as mutually exclusive in the literature, but within natural communities, both processes are often important (Eriksson and Erhlén 1992, Duncan et al. 2009). Because the application of these concepts directly affects how land managers and restoration biologists manage resources (e.g., when planning the reintroduction of native species), understanding their importance in natural communities has practical consequences. Seed of native plants is expensive and often difficult to procure, and thus availability of seed often places practical limits on habitat restoration. If plant species are primarily seed-limited, then simply adding more seed should be the most efficient way to increase the number of successful recruits. However, if the plant species are also microsite-limited, seed introduction efforts may be ineffective unless managers also increase microsite availability by removing established non-native competitors or through manipulation of abiotic variables such as changing the moisture or nutrient profile of the soil. Here we examine the relative importance of seed and microsite limitation, using a suite of native species in an attempt to restore a rare and rapidly vanishing native prairie plant community.

Methods

Experiments were conducted in native prairie communities within the Garry Oak ecosystem. The experimental site was located on Tenalquot Prairie, which is part of a larger fragmented native prairie system that stretches from the southern tip of Vancouver Island, British Columbia, Canada, along the western edge of the Cascade Mountain Range of Washington state, and south along western Oregon, just east of the Coastal Mountain Range and into parts of northern California. Due to changes in land use, including permanent conversion to croplands, industrial development, and increasing fragmentation, the Garry Oak ecosystem is one of the rarest and most threatened ecosystems in the world (Noss et al. 1995). In 1997, Crawford and Hall estimated that less than three percent of the ecosystem remained intact, with greater than ninety percent degraded or permanently converted to other uses.

The field experiments were initiated late in the summer of 2008 at Morgan Prairie, a 90-acre restoration site in Thurston County, Washington (46°54'4.18"N, 122°44'13.24"W) which is part of the larger Tenalquot Prairie. Historically a native prairie community, the site was grazed by horses until 1995, and is currently dominated by invasive Mediterranean grasses and weedy forbs (TNC species list, 2006). The soil type at the site is Spanaway gravelly sandy loam with grades of 0-3 percent (USDA, NRCS, SSURGO WA667).

To examine the relative effects of seed-limitation and microsite-limitation, we created a full-factorial experiment with four levels of burning treatment to control variation in microsite availability (increasing access to bare soil, reducing competition for light and moisture, increasing nitrogen availability in the soil) crossed with four levels of seed addition. We implemented four levels of burn treatment (CTL, LOW, MED, HIGH) in $5m^2$ plots and replicated the treatments four times for a total of sixteen plots (see Figure 1). Four levels of seed addition (CTL, LOW, MED, HIGH) were nested within each burn plot in randomized $1m^2$ plots, using ten plant species native to prairies in this ecosystem.

We also considered the possibility that small mammals, birds, or arthropods could affect the number of propagules available for recruitment in each plot after seed addition. To examine the potential for seed predation (propagule removal) we conducted a single un-replicated seed removal experiment. Replication and further consideration of this experiment was ultimately limited by the availability of native plant seed.

Microsite availability

Four burn treatments types were established prior to a prescribed burn. In the control plots, we prevented the ignition of standing fuel on the plot by wetting it immediately prior to the burn; in low burn plots, we removed 50% of the standing fuel, thereby reducing the temperature intensity of the burn and ameliorating its effects. In medium burn plots, we let the prescribed burn cross the plot without any plot manipulation, and in high burn plots, we added fuel to the plots through the addition of dried Douglas fir boughs (five boughs of equal size per high burn plot, evenly placed). To ascertain that burn treatments were effective in producing fire of different intensities, temperature at ground level was recorded by placing 16 brass discs evenly spaced across each plot (four in each subplot, 256 total for the site). Discs were painted with Tempilaq heat sensitive paints bracketing the expected range of fire temperatures. The control plots did not burn. Discs from low burn plots revealed an average temperature of 286˚ C (SE +/- 20˚ C), medium burn plots had average burn temperature of 342˚ C (SE +/- 19˚ C), and high burn plots had average burn temperature of 564˚ C (SE +/- 9˚ C). To control for the addition of nutrients released from the Douglas fir boughs added to the high burn treatment, 400g of Douglas-fir ash (equivalent to the amount of incinerated Douglas fir boughs placed in each plot) were spread across the control, low, and medium burn plots.

Seed Addition

For the seed addition treatments, each 5m^2 burn treatment plot was divided into four quadrants and subdivided into 1m^2 subplots. Each quadrant was randomly assigned a seeding density treatment of no seed, low seed (50 seeds of each species), medium seed (100 seeds of each species), or high seed addition (200 seeds of each species) for a full factorial design. We used ten native prairie species; nine forbs and one grass, all perennial. The forbs included *Balsamorhiza deltoidea* (BADE), *Castilleja hispida* (CAHI), *Erigeron speciosus* (ERSP), *Lomatium nudicaule* (LONU)*, L. triternatum* (LOTR)*, L. utriculatum* (LOUT)*, Potentilla gracilis* (POGR)*, Ranunculus occidentalis* (RAOC)*,* and *Solidago missouriensis* (SOMI). The grass was *Festuca roemeri* (FERO). All species are commonly used in prairie restoration. Four of the species are known to occur at the study site (*Festuca roemeri*, *Lomatium utriculatum*, *Ranunculus occidentalis*, *Solidago missouriensis*), though only two mature plants of these species (both *Ranunculus occidentalis*) were observed in the study plots. Seed was collected in 2007 on the military installation Joint Base Lewis-McChord and processed at the Washington Department of Natural Resources seed cleaning facility. All seed was screened to remove foreign or malformed seeds and then processed on a gravity separation table with the exception of *Balsamorhiza deltoidea*, which was cleaned using a pneumatic separator. All seed was processed until 10/10 randomly selected seeds were found to contain an embryo when the seed coat was cut open. Seeds were broadcast after the onset of fall rains and surveys for recruitment were conducted in the spring of 2009.

Seed Removal Studies

To examine seed predator preference for large seeded species, we placed *Balsamorhiza deltoidea*, *Ranunculus occidentalis*, *Lomatium triternatum*, and *L. utriculatum* in sand-filled Tupperware containers approximately four inches deep. We used four different

kinds of seed offering trays; trays with no holes in the sides and with lids (CTL); trays with holes approximately three inches in diameter cut in the side and with lids to allow for the admittance of voles and mice, but exclude birds; trays with holes cut in the sides and without lids (in case rodents would not enter a covered box); and trays with no holes cut in the side and no lids (rodent exclosure). While it is possible that rodents could have entered from through the top of these trays with no holes and no lids, there was no evidence observed of such an entry during the seed removal study (i.e., no rodent paw prints in the sand in the bottom of the tray in conjunction with seed removal).
Once we determined which seeds were likely to be removed by late fall seed predators we proceeded with a second seed removal study to examine the likelihood of seed removal with the removal of vegetative cover.

In the late fall of 2010, four new 5m^2 plots were established and randomly designated as control (no burn), low, medium, or high burn treatments. The burn treatment was implemented using a blow torch and categorized based on the amount of bare ground after burning with the high burn treatment having > 40% bare ground, medium burn having > 20% bare ground, and the low burn having >10% bare ground. Fifty seeds of both *Balsamorhiza deltoidea* and *Ranunculus occidentalis* were placed in sand-filled Tupperware containers with rodent-sized holes (~3" in diameter) cut in the sides and replicated four times per burn treatment plot. Seeds for all seed predator studies were put out in the late afternoon and collected before dawn the next morning.

Data Analysis

Across all seed addition control plots (i.e., where no seeds were added), a single recruit of one of the ten focal species was found. For this reason we do not report effect size of the recruitment response, but give count data of the number of seedlings per species in each plot. All data were analyzed using linear mixed-effects models (LMERs) with a Poisson error distribution to characterize the effects of seed addition level and burn level on recruitment. Our analysis tested whether adding more seed or increasing microsite availability resulted in a greater number of recruits and if there was an interaction between seed addition and microsite availability. We examined the recruitment of all species as a group as well as the recruitment response of individual species. We used the dredge function in R to identify the pool of candidate models for all species together and for individual species. For all analyses, we identified the best subset of candidate models using Akaike's Information Criterion (AIC_c) and reported the top three models with their associated Δ_I values ($\Delta_I = AIC_i - AIC_{min}$). In all analyses, both likelihood ratio tests and model selection methodologies revealed the same best-fit model.

Results

The recruitment of all species combined, and all forbs combined, were both best described by the same candidate model (Table 1), which included Seed Addition Level, Burn Level, Species, and all two-way interaction terms. In both cases, this candidate model was far better than the next best candidate models (Table 1, $\Delta AICs > 40$, 2nd model weights = 0.00). For individual species (Table 2), the recruitment response varied, but all species showed strong seed limitation, meaning there was a significant increase in the number of seedlings for all of the focal species when seed was added as compared to the unseeded control plots. The seed addition level was the most important variable across all models. Burn level was the second most important variable and appeared in the best model for all but 3 species (*Erigeron speciosus*, *Potentilla gracilis*, and *Ranunculus occidentalis)* where burn level appeared in a close second best model for all species (Table 2, ΔAICs < 1.5 for 2nd models, model weights > 0.32). Interaction terms between seed addition and burn level were important in 4 of the 10 species (in the other 6 species, ΔAICs > 6 for models with interaction terms, model weights < 0.04; Table 2).

Discussion

All species demonstrated strong seed limitation and most species showed some level of microsite limitation. Considering the recruitment response of all species as a whole, when more seed was added to plots, the number of recruits increased in a non-linear fashion, and seed addition produced the strongest recruitment response at the medium burn levels (Figure 2). For seven out of ten species, the strongest recruitment response was in the un-manipulated (medium) burn plots at the high seed addition level (*Balsamorhiza deltoidea, Castilleja hispida, Lomatium nudicaule, L. triternatum, L. utriculatum, Potentilla gracilis,* and *Ranunculus occidentalis*). This suggests that even when microsites are opened by fire, the ability of these species to capitalize on the opening is limited by seed availability. However, there were not consistently greater numbers of recruits as microsite availability increased, suggesting that while these species are microsite limited, those microsites may be regulated by both positive and negative interactions with the established plant community. Removing more competitors for resources, such as in the high burn plots, did not solely release these species from competition, but instead created conditions under which seeds were left unprotected from biotic and abiotic pressures.

The three remaining species, *Festuca roemeri*, *Erigeron speciosus*, and *Solidago missouriensis*, demonstrated variable responses to the treatments. Recruitment for *Erigeron speciosus* and *Solidago missouriensis* was erratic across the site. Both species have small, wind-dispersed seeds and may be poor competitors for resources (Turnbull 1999; Skarpass 2011). Indeed, the strongest recruitment of *Solidago missouriensis* occurred in the high burn plots at the lowest level of seed addition (50 seeds/m^2) while *Erigeron speciosus* recruitment was strongest in the high burn plots at the medium seed addition level (Figure 2).

Density dependent seed predation, in combination with the competition/colonization trade-off, may explain the pattern of recruitment for the species that flourished in un-manipulated (medium) burn plots. The largest-seeded species in our study include *Balsamorhiza deltoidea*, *Lomatium spp.*, and *Ranunculus occidentalis*. *Balsamorhiza deltoidea* belongs to the Asteraceae, which includes sunflowers, and its seed is a staple in the diet of granivorous birds and rodents where it occurs in the prairies of western Washington (personal observation). *Lomatium spp.* are known to be subject to seed predation by an array of vertebrate and invertebrate seed predators in Washington (Thomson 1985).

Recruitment for *Balsamorhiza deltoidea* was low across the site, and as with other larger-seeded species, the greatest number of recruits occurred in the un-manipulated (medium) burn plot at the highest seed addition level. This pattern of recruitment could be explained if seed predators were deterred by the presence, or partial presence, of vegetative cover in plots, which could interfere with the animals' ability to locate and remove seeds. To test this, we conducted a seed-removal study using the large-seeded *Balsamorhiza deltoidea* and *Ranunculus occidentalis*. These species were chosen based on a preference study conducted at the same site demonstrating that none of the other large-seeded species were palatable to local seed predators present at the time of the study. The majority of seeds were removed from the high burn plot with removal of 90% and 85% of the *Balsamorhiza deltoidea* and *Ranunculus occidentalis*, respectively. The plot with the next highest rate of removal was the low burn plot, followed by the medium burn and the control plot. Motion activated cameras used at the site captured a single genus of rodent removing seeds; *Peromyscus*, probably a deer mouse (*P. maniculatus*). The inversion of the proportion of seed removed from the medium and low burn plots may be due to optimal foraging on the part of the mouse, as the randomized plots were placed in a single row and ordered HIGH, LOW, MED, CTL, based on a series of coin tosses. Regardless, the highest proportion of seed removed was in plots treated to remove the greatest proportion of the vegetative cover and the lowest seed removal was in the plot with standing vegetation suggesting that rodents were better at foraging for seeds where standing vegetation was low and the proportion of bare ground was high. Replication of this study was precluded by a dwindling seed supply, extreme low temperatures, and the lack of small mammals foraging during the cold winter months.

We were unable to assess the impacts or identities of other seed predators due to the seasonal absence of most avian and invertebrate predators. We posit that further examination of seed removal at a different season would reveal a wider variety of seed predators at Tenalquot prairie.

The interpretation of the results of these studies is hampered by the lack of replication between sites, which was curtailed by the lack of funding available to support this work at more than one site. To be able to generalize and predict recruitment success at other sites within the region, additional work must be conducted to confirm or contradict the results of this work.

Recommendations

Since all species used in this study were strongly seed limited and showed some level of microsite limitation, we recommend a combination of seed addition and site preparation when attempting habitat restoration in this prairie ecosystem. As we did not observe asymptotic recruitment response for any of our species, we conclude that more seeds result in more recruits at least up to 200 seeds per species per m^2. The optimal level of site preparation does not necessarily involve the removal of all standing vegetation. In fact, we recommend leaving at least some of the vegetative structure intact to deter seed removal by seed predators. Seed should be distributed evenly, if possible, to avoid density dependent seed removal by seed predators.

Figure 1.

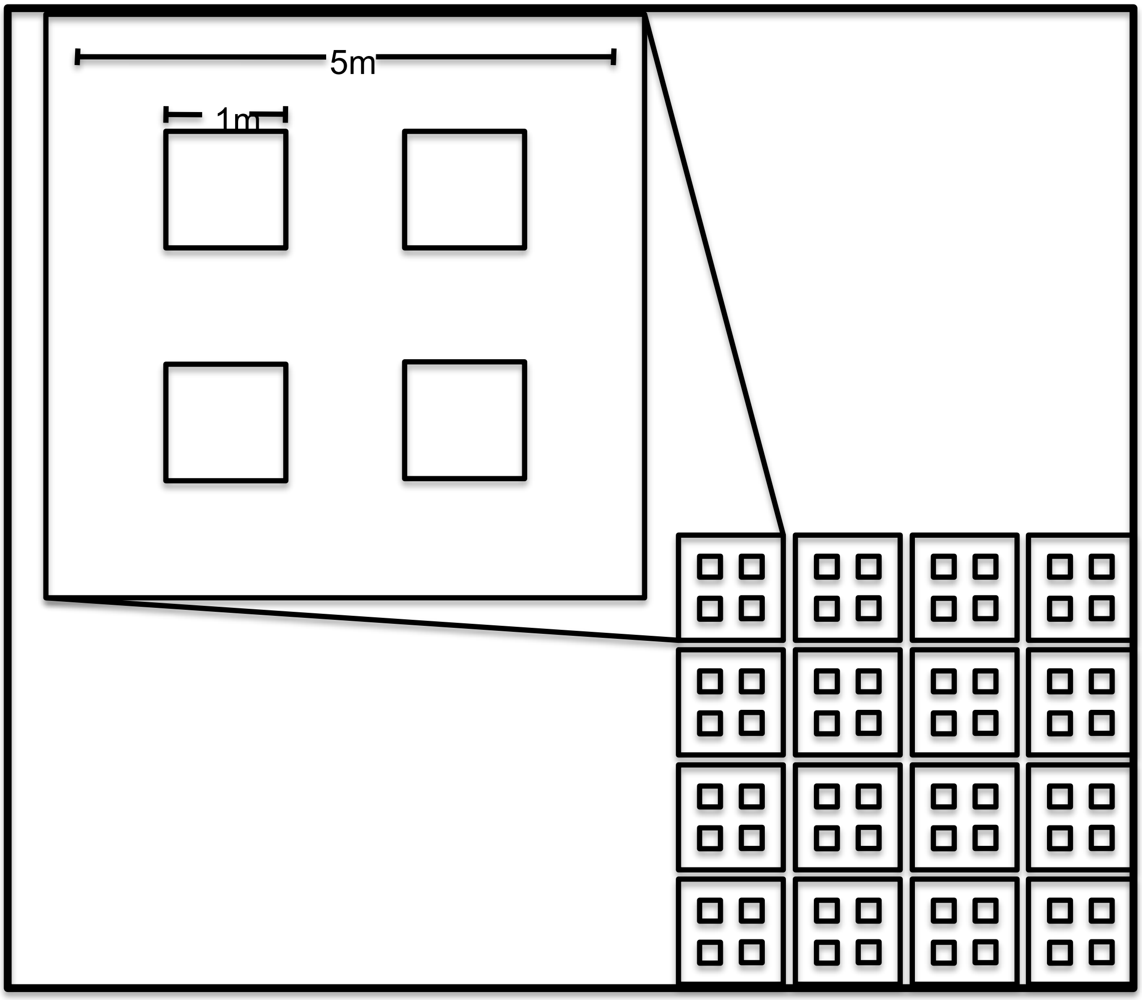

Figure 1. Layout of experimental design.

Table 1.

Recruitment	**Model Rank**		w_{ip}
ALL SPECIES COMBINED	**1**	**2**	
Seed Addition Level	*		1.00
Burn Level	*		1.00
Species	*		1.00
Seed Addition Level * Burn Level	*		1.00
Seed Addition Level * Species	*		1.00
Burn Level * Species	*		1.00
Seed Addition Level * Burn Level * Species			0.00
Δ_i	0.00		
W_i	1.00		
ALL FORBS COMBINED	**1**	**2**	
Seed Addition Level	*		1.00
Burn Level	*		1.00
Species	*		1.00
Seed Addition Level * Burn Level	*		1.00
Seed Addition Level * Species	*		1.00
Burn Level * Species	*		1.00
Δ_i	0.00		
W_i	1.00		
Balsamorhiza deltoidea	**1**	**2**	
Seed Addition Level	*	*	1.00
Burn Level	*		0.73
Seed Addition Level * Burn Level	*		0.66
Δ_i	0.00	1.77	
W_i	0.66	0.27	
Castilleja hispida	**1**	**2**	
Seed Addition Level	*	*	0.98
Burn Level	*		0.98
Seed Addition Level * Burn Level			0.00
Δ_i	0.00		
W_i	0.96		
Erigeron speciosus	**1**	**2**	
Seed Addition Level	*	*	1.00
Burn Level		*	0.32
Seed Addition Level * Burn Level			0.00

Δ_i	0.00	1.49	
W_i	0.68	0.32	
Festuca roemeri	**1**	**2**	
Seed Addition Level	*		1.00
Burn Level	*		1.00
Seed Addition Level * Burn Level	*		0.99
Δ_i	0		
W_i	0.99		
Lomatium nudicaule	**1**	**2**	
Seed Addition Level	*		1.00
Burn Level	*		1.00
Seed Addition Level * Burn Level	*		1.00
Δ_i	0.00		
W_i	1.00		
Lomatium triternatum	**1**	**2**	
Seed Addition Level	*	*	1.00
Burn Level	*	*	0.98
Seed Addition Level * Burn Level	*		0.50
Δ_i	0.00	0.02	
W_i	0.50	0.49	
Lomatium utriculatum	**1**	**2**	
Seed Addition Level	*	*	1.00
Burn Level	*		0.75
Burn Level * Seed Addition Level			0.01
Δ_i	0.00	2.19	
W_i	0.74	0.25	
Potentilla gracilis	**1**	**2**	
Seed Addition Level	*	*	1.00
Burn Level		*	0.35
Seed Addition Level * Burn Level			0.00
Δ_i	0.00	1.26	
W_i	0.65	0.35	
Ranunculus occidentalis	**1**	**2**	
Seed Addition Level	*	*	1.00
Burn Level		*	0.42
Seed Addition Level * Burn Level			0.00
Δ_i	0.00	0.64	

W_i	0.58	0.42	
Solidago missouriensis	**1**	**2**	
Seed Addition Level	*	*	1.00
Burn Level	*		0.87
Seed Addition Level * Burn Level			0.03
Δ_i	0.00	3.73	
W_i	0.84	0.13	

Table 1. The results of model selection and model averaging for linear mixed effects models (LMERs) of the probability of recruitment in response to seed addition and/or burn treatment. Table 1 shows the top models in all instances and gives Δ_I for each model. We include models where Δ_I is within four points of the top model. Variables included in each model are indicated with an asterisk (*). Akaike weights (w_i) are the likelihood that a given model is the best of models considered (Burnham and Anderson 2002). Relative variable importance (w_{ip}) is the sum of w_i across all candidate models in which the variable appears. w_i does not sum to 1.00 in for some of the combinations examined due to the exclusion of models deemed irrelevant (i.e., Δ_I > four points from top model)

Table 2.

BURN LEVEL	**HIGH**	**MED**	**LOW**	**CTL**
Balsamorhiza deltoidea	0.90 ± 0.09	0.55 ± 0.20	0.74 ± 0.25	0.25 ± 0.25
Ranunculus occidentalis	0.85 ± 0.12	0.45 ± 0.18	0.69 ± 0.23	0.25 ± 0.25

Table 2. Proportion of seeds removed from burn plots with SE.

Figure 2.

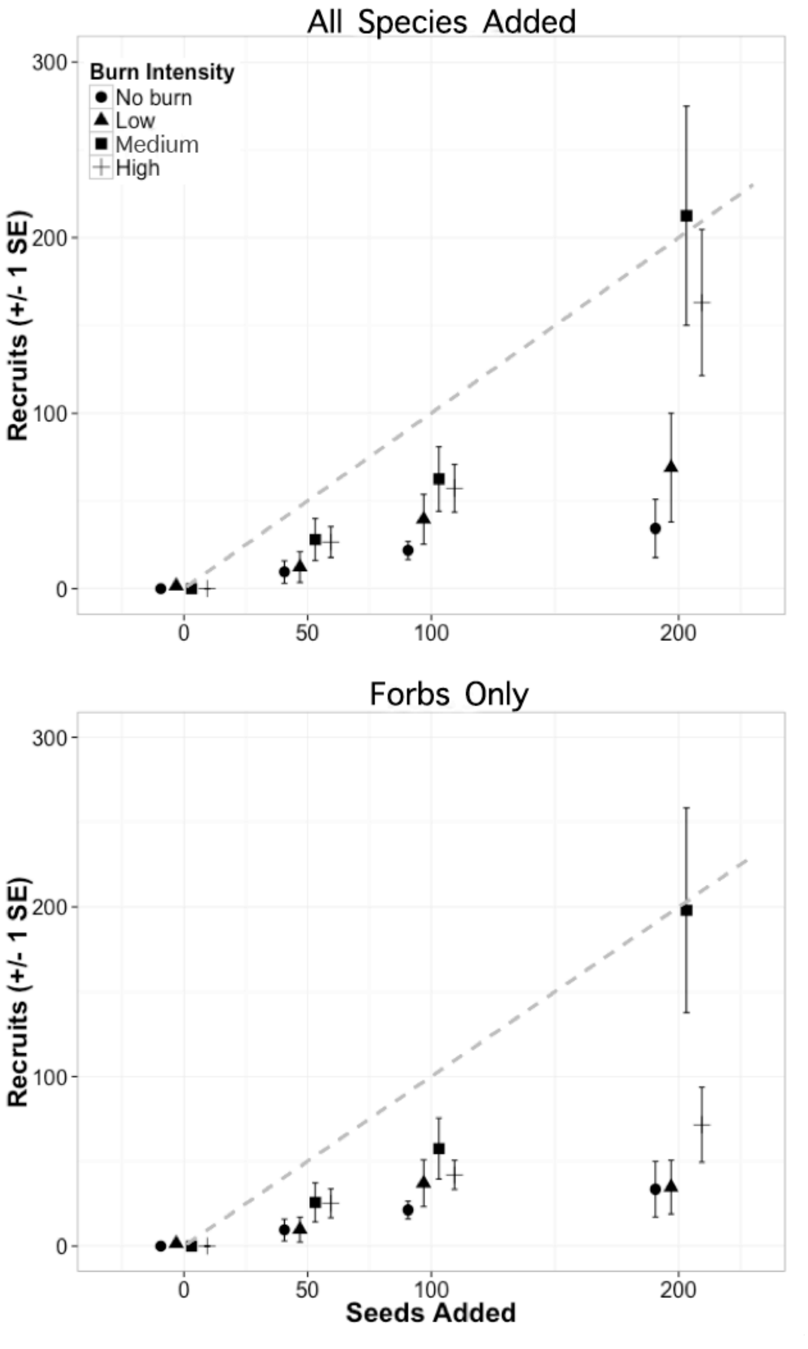

Figure 2. Mean +/- 1 SE for recruitment of all species (A) and all forbs (B) as a function of seed addition. Burn levels are indicated by symbols, dashed gray line indicates full recruitment (1:1 addition to recruitment ratio).

Figure 3.

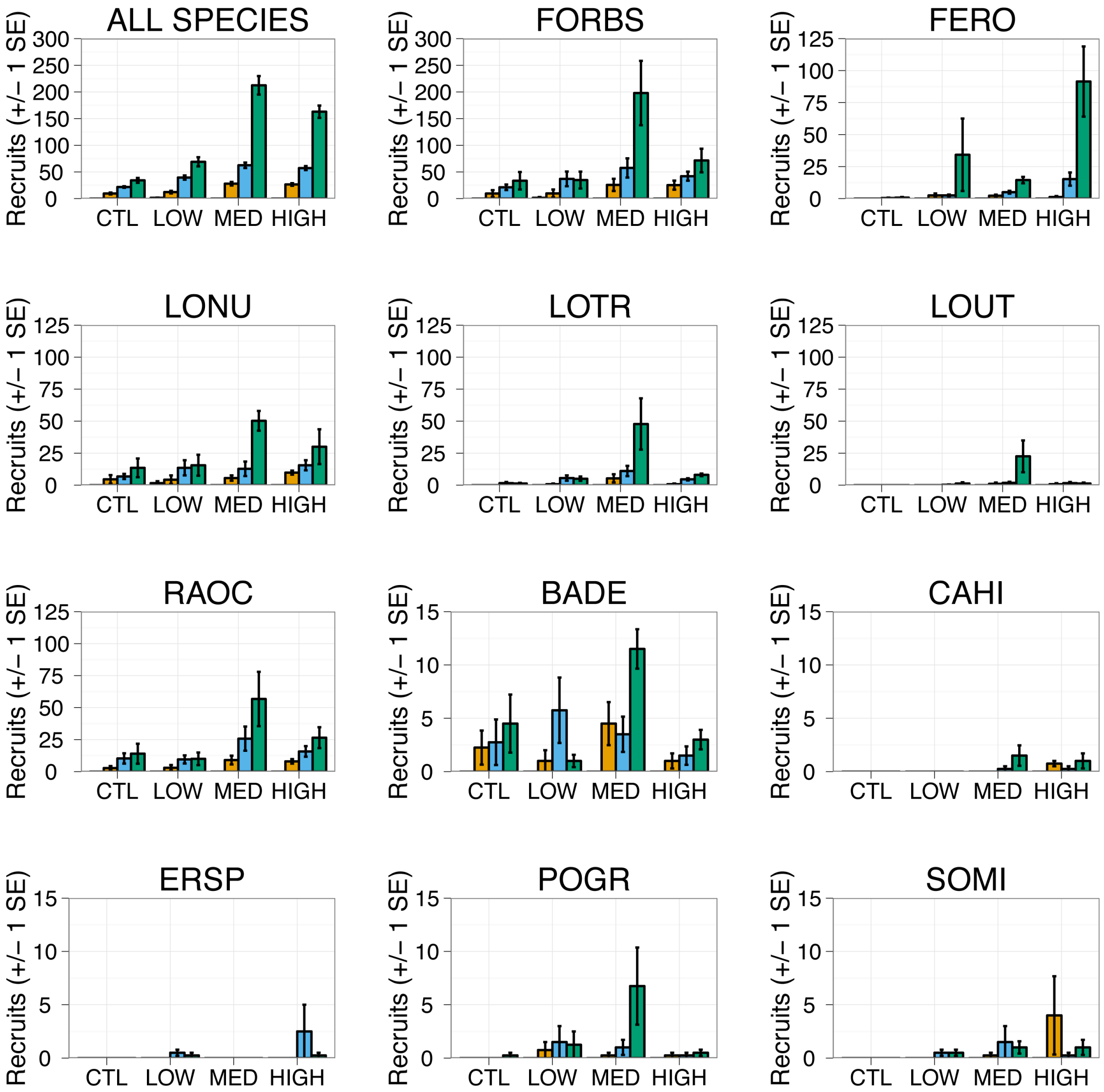

Figure 3. Germination response of all species combined and individually. Burn treatments are arranged along the x-axis (CTL, LOW, MED, HIGH), clustered bars represent seed treatments nested within each burn treatment (Control = no added seed = no fill; low = 50 seeds added per species = gold; 100 seeds per species added = blue; 200 seeds per species added = green). The number of recruits is shown on the y-axis. Note changes in scale on y-axis between charts.

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Chapter Two

Performance under pressure: seed addition has a greater impact where stress is high in remnants of a degraded prairie ecosystem.

Abstract: Restoration techniques commonly include seed addition and site preparation treatments in hopes of increasing the abundance of native plant species while reducing non-native competitors, but fail to take into account stressors at a restoration site that could dictate the success or failure of such an approach. Here we examine the significance of site stress along a 500km gradient as it pertains to the recruitment response for seed addition in the presence of four common restoration treatments and how the recruitment response shifts along the gradient. The native focal species were significantly seed limited at all sites, but where site stress was estimated to be high, treatment effects had a greater influence on the recruitment of the focal species added, while at low stress sites, treatment effects were indistinguishable from the control.

The ability of plants to recruit is affected by many forces, such as access to space and resources (microsite limitation), the ability to produce and disperse propagules into available sites for germination (seed limitation), and the interactions within and among species (conspecific and heterospecific interactions), which can be negative or positive (competitive or facilitative), weak or strong. Understanding the relative importance of these forces is especially important in an applied ecological context, particularly when restoration efforts focus on increasing the number and kind of native plant species at a site. Common approaches to the restoration of native ecosystems include using both manipulative actions to reduce competition between native plants with established non-native species and seed addition to bolster the recruitment of native species into the community. Understanding the role of competition and the effect it has on recruitment could provide insight into the amount and kind of effort needed to affect the ability of native species to recruit.

Theoretical ecology has long focused on disentangling the effect of competition on seedling recruitment from the effect of abiotic stress. In his 1979 book, Plant Strategies and Vegetation Processes, J.P. Grime posited that the intensity of environmental abiotic stress determines whether competition (negative interactions) or facilitation (positive interactions) is the dominant force in the organization of plant communities. Grime proposed that competition is the process that drives the availability of resources at low abiotic stress levels while facilitation does so at high abiotic stress levels (Figure 1; the stress gradient hypothesis). If competitive interactions are strong under low abiotic stress conditions but facilitative interactions predominate when abiotic stress is high, then removal of non-native competitors may not reduce competition and free up microsites for establishment in equal measures between high stress and low stress sites. Instead, efforts to reduce non-native plants may in actuality be removing facilitative partners that regulate some aspects of a site's abiotic stressors simply by being present, such as microclimate (i.e., microsite) parameters. Established plants regulate moisture, temperature, and light conditions in their immediate vicinity (Holmgren et al. 1997;

Claussen et al. 2010; Montgomery et al. 2010), which, if Grime's theory is correct, may mitigate environmental stressors that are inclement to seedling establishment. If this is true, restoration treatments focused on the removal of established non-native competitors in high-stress environments could unwittingly create harsher abiotic conditions in which propagules are unable to establish. Conversely, when a site's overall abiotic stress is low, the removal of non-native species may free up resources effectively creating available microsites for seedlings to establish (Figure 1b).

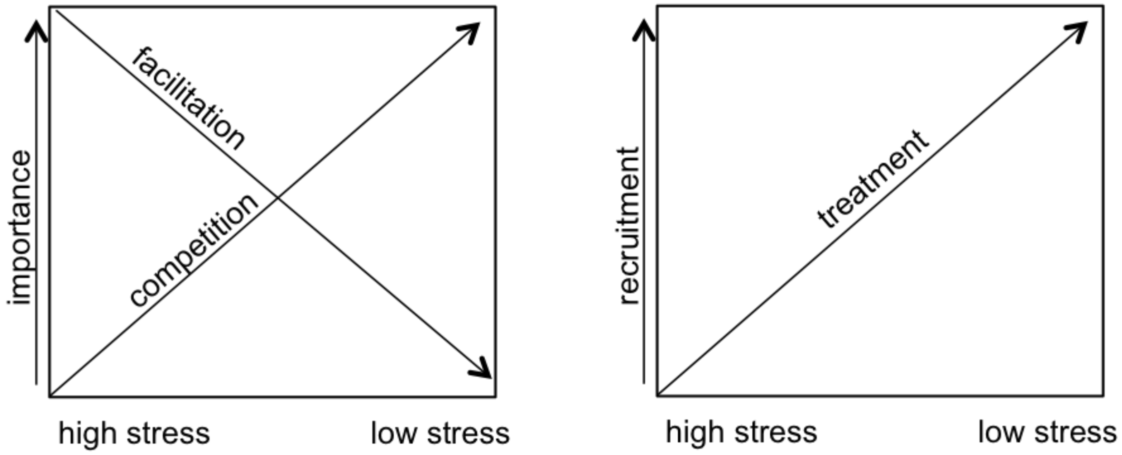

Figure 1. (a) If interactions are largely competitive in low-stress environments, but facilitative in high-stress environments, then removing non-natives could be expected to result in lower recruitment under high stress environments and higher recruitment under low stress environments. (b) If competition is more important in limiting seedling establishment at low stress levels, manipulative treatments focused on reducing competition should result in higher levels of recruitment when carried out in a low-stress environment.

Experimental work has increasingly focused on the role of facilitation where abiotic stress is high (Bertness and Callaway 1994; Callaway et al. 2002; Wright et al. 2014), lending increasing weight to the idea that positive plant interactions are important when exploring patterns of recruitment. Clarification of the interplay between interspecific interactions and the abiotic stress environment could go a long way toward demystifying scenarios in which manipulating competition levels leads to higher levels of recruitment of native species in some instances but not in others. Further, understanding the circumstances when seed addition results in higher levels of recruitment and when it does not can facilitate the optimal allocation of limited resources when conducting landscape level restoration work.

Here we present the results of a restoration-focused experiment conducted across a latitudinal stress gradient. To determine whether abiotic stress levels interact with non-native plant removal to affect native plant recruitment, we conducted an experiment that included both vegetative manipulation treatments and seed addition for six native species across a latitudinal stress gradient. We specifically asked (1) whether the focal species were microsite limited at our sites (constrained by competition for resources); (2) whether the focal species of our study were seed limited at our sites; and (3) how environmental stressors interact with the ability of the focal species to recruit and establish when these two variables were manipulated (i.e., is the effect size of seed addition greater under high or low stress sites and does the removal of non-native species improve or decrease recruitment the focal species).

We explored the relative strength of microsite limitation by examining the impact of non-native species removal on recruitment of the focal species (release from competition or loss of facilitation) in the absence of seed addition as compared to seed addition. If native plant species are microsite limited, but not seed limited, manipulating the level of competition should effectively free up available microsites where native species that are not seed limited could recruit (Seabloom et al. 2003). Where seed was added, the relative strength of seed limitation was estimated by examining the effect size of seed addition (the number of seedings in the seeded plots – the number of seedlings in the control plots). We further compared the strength of seed limitation between high- and low-stress sites, and manipulated and unmanipulated treatments. Finally, since species differ in their response to abiotic environments and competition, we expected to observe species-specific responses depending on their competitive abilities.

Methods

The experiment was conducted at ten sites across a 500km latitudinal stress gradient in remnant fragments of the Garry Oak Ecosystem, an increasingly rare and threatened ecosystem at the western edge of North America (Noss 1995, Crawford and Hall 1997). The northernmost site was in the Cowichan Valley, located on the south end of Vancouver Island, British Columbia, Canada; the six-midrange sites were centered on Olympia, Washington; and the three southernmost sites were clustered near Corvallis, Oregon. In 2005, four vegetative manipulation treatments (focused on removing non-native dominant species) and a control (no vegetative manipulation) were established at each site in $5m^2$ plots. The treatments were implemented over a two-year period starting in the spring of 2005, with actions taken in the spring and the fall of each year (Table 1.). Each site contained four replicates for a total of twenty $5m^2$ plots per site. Plots were arranged in a block design and treatments were randomly assigned to plots at each site (Figure 2.). Treatments included a combination of burning and herbicide application, mowing, or a combination of mowing and herbicide application. Poast (sethoxydim) is an herbicide used to target grasses, while glyphosate is a nonselective herbicide that kills broadleaf annuals and grasses.

Table 1.

	2005		**2006**	
Treatment	**Spring**	**Fall**	**Spring**	**Fall**
Control	No vegetative manipulation			
Mow Burn Glyphosate	Mow high			Burn/Glyphosate
Mowing Only	Mow high	Mow low	Mow high	Mow low
Poast Mow Poast Mow	Poast	Mow low	Poast	Mow low
Poast Poast Burn	Poast		Poast	Burn

Table 1. Manipulative treatments implemented in 5m^2 plots prior to seed addition in the fall of 2006.

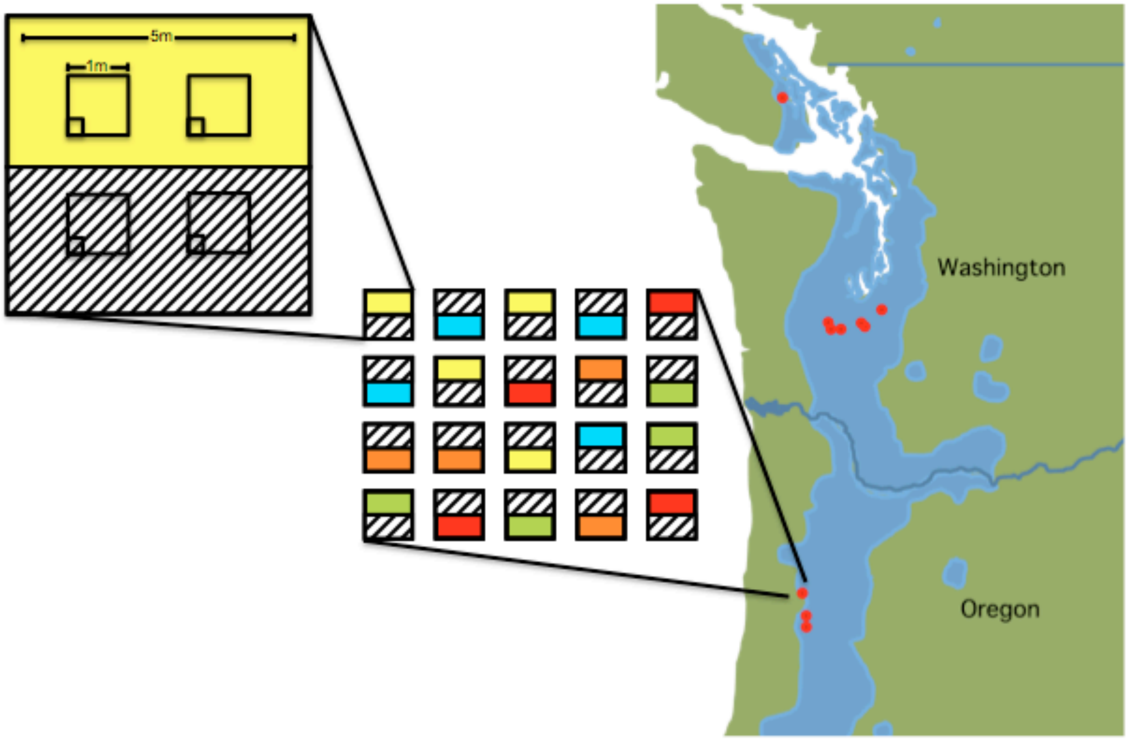

Figure 2. The location and arrangement of experimental sites. The sites were located on Vancouver Island, British Columbia, Canada, and in Washington and Oregon State, USA. Each site included four replicates of four treatments and a control (represented by different colors) for a total of twenty 5m^2 plots per site. One half of each 5m^2 plot was seeded and each 5m^2 plot had four 1m^2 subplots inset to avoid edge effects during sampling. A complete census of the focal species was conducted in the lower left corner of each 1m^2 subplot.

In 2006, a mixture including the seed of six native species was added to one half of each $5m^2$ plot. These six native focal species included: *Achillea millefolium*, *Eriophyllum lanatum*, *Danthonia californica* or *spicata*, *Plectritis congesta*, *Lomatium nudicaule* or *utriculatum*, and *Ranunculus occidentalis*. The species of *Danthonia* and *Lomatium* added to the plots varied depending on which plant was documented as naturally occurring at the site. The recruitment response for *Danthonia* and *Lomatium* was examined at the genus level. Seedling surveys were conducted in the spring of 2007 before peak flowering to facilitate the capacity to see each plant in the sampling locations. Each $5m^2$ plot was divided into quadrants and $1m^2$ survey plots were established at the center of each quadrant to control for edge effects. All seedlings of the focal species were counted within the lower left sixteenth of each $1m^2$ plot (see Figure 1) for a total of eighty seedling plots surveyed per site. Because there were four survey plots inset within each $5m^2$ plot, survey results were averaged within each seeded and unseeded half, respectively, of each $5m^2$ plot to avoid pseudo-replication.

The seeded focal species were all historically present at the experimental sites, but occurred in low numbers across each site. Because there was the potential for naturally occurring populations to disperse seed into the experimental plots, the effect size of seeding (number of seedlings in seeded plots – number of seedlings in unseeded control plots) was used as the metric for recruitment response. Those plots with a negative effect size (greater number of seedlings in the unseeded (control) half of the plot than in the seeded half of the plot) were converted to zero, since, biologically, it is does not make sense to consider a negative number of a focal plant. The recruitment response of all focal species was first examined together as a group to determine if any generalizations could be drawn for all species across all sites. The recruitment response was then analyzed individually for each species across all sites and then for each species at each site to explore any species- or site-specific response. When all sites were pooled together for analytical purposes, the candidate models included "site" as a random effect in order to account for the site-specific features of the experimental design, such as random distribution of manipulative treatment plots at each site, random allocation of seed addition subplots within the treatment plots, and the varying levels of individual stressors that were measured to describe the stress gradient (See Richardson et al. 2012).

Abiotic stress was quantified with a Site Stress Index value (SSI) by combining latitude with a set of eight environmental variables from each site and conducting a principal component analysis (PCA). We collected soil cores to determine the percent soil moisture, total extractable nitrogen (N) and carbon (C), concentration of nitrate and ammonium, and microbial biomass. We also included percent surface cover by organic litter and the percent bare soil in each plot. The eight environmental measures were taken at peak flowering times at each site, which ranged from late April at the southern sites to mid-May at the northern sites. Figure 3 illustrates the latitudinal range of sites plotted against their PCA eigenvector values. Figure 6 provides r^2 values for the variables used to quantify stress and produce the Site Stress Index scores. With the exception of percent bare soil, the higher values of these environmental measures correlated with low stress levels and positive SSI scores; negative SSI scores indicated a high stress environment.

(See Richardson et al. 2012 for additional information on the formulation of the PCA eigenvector values.)

Data were analyzed with R 2.15.1 using a generalized linear mixed effects model package that accommodates common error distributions associated with count data (package: glmmADMB. See Fournier et al. 2012 for more details). Error distributions for each subset of data were identified based on lowest AIC_c scores for each respective best-fit model. Model selection was conducted with the dredge function. Best-fit candidate models within Δ25 AIC_c points were ranked and the top three candidate models for each subset of the data are included in Table 2. Post-hoc Tukey tests were conducted for each species at the site level using the glht (generalized linear hypothesis testing) function in the multcomp package for R. Levels of significance (p-values) provided for treatment effects for each species at each site are the results of generalized linear models run with the R package glmmADMB.

Figure 3.

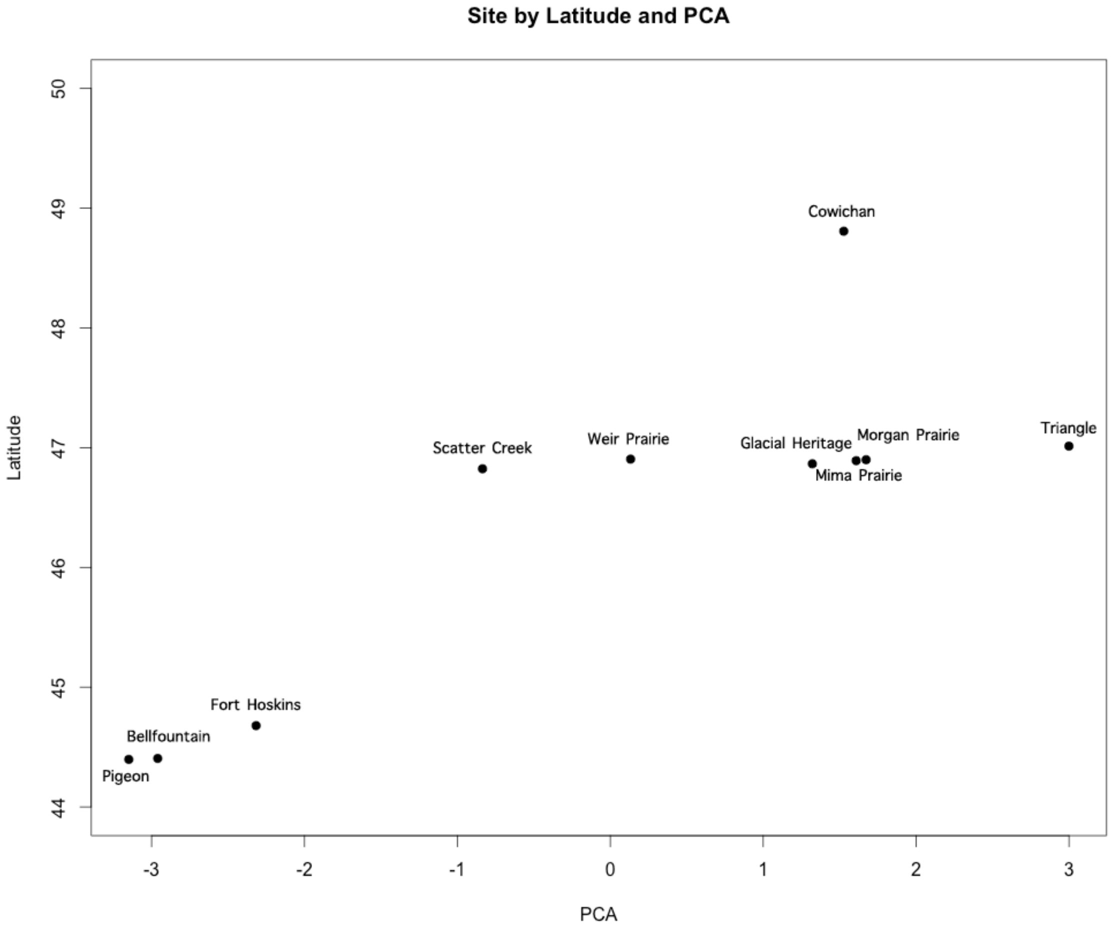

Figure 3. Lower PCA eigenvector values align with sites with higher levels of abiotic stress. Generally, lower latitudes correlate with higher stress scores on the Site Stress Index (SSI), and higher latitudes with lower stress scores, with the exception of Cowichan. See Figure 6 for relative correlations between the environmental values measured and PCA scores estimating site stress.

Results

The highest ranked candidate model for all focal species pooled across all sites included SSI (Site Stress Index scores), Treatment, and the interaction between SSI and Treatment. There is no reliable post-hoc testing for a model with both an interaction term and random effects. The second highest ranked candidate model included only the SSI and Treatment ($\Delta_i = 0.11$, $w_i = 0.49$). A post-hoc Tukey test conducted on the second model indicates that the Poast Poast Burn and Mow Burn Glyphosate treatments both result in significantly greater recruitment than the control treatment ($p < 0.001$ for both), but no other treatment emerged as significant. See Figure 4.

Individual species responses are discussed below.

Achillea millefolium

Overall, the germination response of *A. millefolium* was higher at sites where stress was estimated to be high and lower at sites where stress was estimated to be less. This was generally true for both control plots and non-native removal treatments. The highest ranked candidate model for *A. millefolium* across all sites included the SSI and Treatment, indicating that both are important to the recruitment response of the species. The next highest ranked candidate model ($\Delta_i = 3.09$, $w_i = 0.17$) additionally included the interaction term between the SSI and Treatment. When pooled across all sites, post-hoc testing revealed two treatments resulting in a significantly greater number of seedlings than in the unmanipulated control plots for *A. millefolium.* The Poast Poast Burn treatment yielded the most significant difference ($p = 0.007$) while the Mow Burn Glyphosate treatment did increase the number of seedlings, but to a lesser degree of significance ($p = 0.020$). Individual analysis of the recruitment response of *A. millefolium* at each site revealed that the Poast Poast Burn treatment was significantly different than the control at Weir ($p = 0.0152$), but not at any other site.

Danthonia spp.

The germination response of *Danthonia spp.* was lower at sites with high level of estimated stress and higher at site where stress was estimated to be low. This was generally true for both treatment and control plots. While the most parsimonious model across all sites included SSI and Treatment, post-hoc testing revealed that no one treatment was better than the control. This supports the second most parsimonious model ($\Delta_i = 1.01$, $w_i = 0.35$), which included only the SSI, suggesting that the abiotic stress level is the most important variable affecting the recruitment of *Danthonia* at a site. Site by site examination of the effects of treatment on the recruitment of *Danthonia* revealed only marginally significant increase in germination for the Poast Poast Burn treatment ($p = 0.077$) at Weir.

Eriophyllum lanatum

The germination response of *E. lanatum* was higher at sites where stress was estimated to be high and lower at sites where stress was estimated to be less. This was generally true for both treatment and control plots. The highest ranked candidate model for *E. lanatum* across all sites included the SSI and Treatment, indicating that both are important for recruitment of the species. The next highest ranked model ($\Delta_i = 5.89$, $w_i = 0.05$) includes the SSI, Treatment, and the interaction term between the two. Post-hoc testing for *E. lanatum* across all sites indicated the Mow Burn Glyphosate treatment resulted in a significantly greater number of seedlings than the control ($p = 0.008$) and the Poast Poast Burn treatment was marginally significant ($p = 0.055$). When each site was examined individually, the Mow Burn Glyphosate treatment resulted in a significantly greater number of seedlings at Bellfountain ($p = 0.006$) and Weir Prairie ($p = 0.048$) but at Triangle, the site with the lowest estimated stress level, resulted in significantly fewer seedlings than in the control plots ($p = 0.033$). Poast Poast burn resulted in significantly higher germination at Fort Hoskins ($p = 0.043$) and Weir Prairie ($p = 0.015$).

Lomatium spp.

The germination response of *Lomatium spp.* in the unmanipulated control plots tended to be higher at sites where stress was estimated to be higher and lower at sites where stress was estimated to be lower. This general trend reversed for the treatment plots, where germination response tended to be lower at sites where stress was estimated to be higher and higher at sites where stress was estimated to be lower. The highest ranked candidate model for *Lomatium spp.* across all sites included only Treatment as the best explanatory variable for recruitment response. The second highest ranked candidate model ($\Delta_i = 2.08$ $w_i = 0.21$) also included the SSI. Post-hoc testing pooled across all sites indicated that the Poast Poast Burn treatment resulted in a marginally significant increase in germination when compared with the control (p = 0.075). When sites were examined individually, the Poast Poast Burn treatment resulted in significantly lower levels of germination at Bellfountain Prairie (p = 0.013) and marginally significantly lower levels at Cowichan (p = 0.080), but significantly higher germination than the control at Glacial Heritage (p = 0.014), Mima Prairie (p = 0.011), Morgan Prairie (p = 0.032), Scatter Creek (0.002) and Triangle (p = 0.046); and higher germination that was marginally significant at Fort Hoskins (p = 0.079), Pigeon Butte (p = 0.069). The Mow Burn Glyphosate plots had significantly lower germination than the unmanipulated control at Cowichan (p = 0.021), but significantly higher germination at Mima Prairie (p = 0.017), Pigeon Butte (p = 0.037), Scatter Creek (p = 0.046), Triangle (p = 0.004), and Weir Prairie (p = 0.028); and marginally significant higher germination at Glacial Heritage (p = 0.082). The Poast Mow Poast Mow treatment resulted in significantly higher germination at Pigeon Butte (p = 0.020) and Triangle (p = 0.023); and marginally significant germination at Morgan Prairie (p = 0.080). The mowing only treatment resulted in significantly higher germination at Triangle (p = 0.007), but significantly lower germination at Weir (p = 0.058).

Plectritis congesta

The germination response of *P. congesta* tended to be higher at sites where stress was estimated to be high and lower at sites where stress was estimated to be less. This was true for three of the treatments and the control plots, but the reverse was true for the Poast Poast Burn treatment; in the Poast Poast Burn plots, germination tended to be lower at sites with a higher stress index score and higher at the sites estimated to have a lower complement of stressors. The highest ranked candidate model for *P. congesta* included only Treatment as the best explanatory variable for recruitment response. The second highest ranked model was the null model ($\Delta_i = 1.63$, $w_i = 0.24$) and the third included the SSI and Treatment ($\Delta_i = 1.85$, $w_i = 0.23$). Post hoc testing pooled across all sites indicated that the Poast Poast Burn treatment was significantly different from the control ($p = 0.024$) and the Mow Burn Glyphosate treatment was marginally significant ($p = 0.073$). The germination response of *P. congesta* examined by each site individually indicated that Mow Burn Glyphosate resulted in significantly greater germination than the control at Bellfountain Prairie, but no other site showed significantly higher germination for any one treatment over the control.

Ranunculus occidentalis

The germination response of *R. occidentalis* tended to be higher at sites where abiotic stress was estimated to be higher and lower where abiotic stress was estimated to be less. This was true for all of the treatments and the control. The highest ranked candidate model for *R. occidentalis* included only the SSI as the best explanatory variable. The next highest ranked model ($\Delta_i = 6.00$ $w_i = 0.05$) included the SSI and treatment. Post hoc testing pooled across all sites did not indicate that any one treatment significantly increased germination over any other treatment. When sites were examined individually, though, the Poast Poast Burn treatment resulted in significantly more seedlings than in the control plots at Mima Prairie ($p = 0.010$) and at Pigeon Butte ($p = 0.009$). The Mow Burn Glyphosate treatment also resulted in significantly more recruits at Pigeon Butte (p

= 0.001). At Triangle the treatment that combined Poast with mowing resulted in significantly greater recruitment than in the control plots ($p = 0.020$).

Discussion

None of the focal species exhibited only microsite limitation, as evidenced by the lack of recruitment response to the removal of non-native competitors when seed was not added. Conversely, all of the focal species exhibited strong seed limitation at all sites ($p < 0.001$). When seed was added in high stress environments, a greater number of seedlings resulted, regardless of treatment, suggesting that the focal species, on the whole, are more seed limited than microsite limited at the high stress sites. Additionally, where stress is greater, the variance among treatment is greatest, and as stress decreases, treatment variance (and thus choice of treatment) matters less. At low stress sites, where competition was hypothesized to have the greatest effect, removal of non-native species significantly increased germination, when compared to the control, while at high stress sites, where the number of seedlings was higher, no manipulative treatment was significantly better than the control. This suggests an interaction between site stress and the level of competition for microsites between high- and low-stress sites.

Our analytical model selection supports these results. When examined across all species and all sites, Grime's stress gradient hypothesis appeared to be supported by the appearance of the interaction term between Site Stress and Treatment in the highest ranked candidate model. Removing non-native species had opposite effects contingent upon location along the environmental stress gradient.

On the whole, both Site Stress and Treatment are important variables in predicting germination success of most focal species, but these factors interacted differently depending on native species' identity. For example *A. millefolium* and *E. lanatum* both exhibited high levels of variance in their response to treatment at sites high stress, including high numbers of seedlings in the control plots, which suggests that the presence of non-native plants may facilitate germination. Variance in the germination response declined for *A. millefolium* and *E. lanatum* as site stress decreased, but *Danthonia spp.* exhibited the opposite response. Model selection for all three of these species that Site Stress and Treatment was important to all of them (with the interaction term appearing in the second best models for all three), but when those results were examined, the variables were important in opposite ways.

Two restoration treatments were generally more effective than the others when examined for all species pooled across all sites. Both the Poast Poast Burn treatment and the Mow Burn Glyphosate treatments resulted in a significantly greater number of recruits from the control ($p < 0.001$ for both, Figure 4). However, in some cases, the effect of treatment was influenced by stress level, reflecting Grime's hypothetical trade-off.
While this generalization is statistically supported, it should be noted that at the highest stress sites, Poast Poast Burn had fewer seedlings than the control. This highlights a trend for all but *Danthonia*; at sites where stress was estimated to be highest, treatment effects

were much more variable, and in most cases the effect size of germination was indistinguishable from the control (Figure 4). As site stress decreased (SSI values becoming positive), treatment effects became more significant, though the identity of the treatment became less important. This indicates that competition for finite resources does affect the number and kind of sites available for seeds to exploit and that when competitors are removed, seeds do germinate, though not in great numbers.

Plotting the SSI scores (the PCA eigenvector values) and the percentage of bare ground in sampling plots at each site revealed that there is a significant correlation between the high abiotic stress and the percentage of bare soil in the survey plots ($R^2 = 0.46$; $p < 0.05$) (Figure 6.). The generally higher variance in germination levels at high stress sites, regardless of treatment, suggests that the focal species, considered as a whole, are able to germinate in greater numbers where competition is naturally low, but where stress is high. The high numbers of seedlings in the control plots suggests that while the interaction between Site Stress and Treatment may not be the strongest predictive variable, facilitation may play a role in germination success at high stress sites for most of the focal species.

Abiotic stressors played an important role in the recruitment response for four of the six focal species (Table 2). *A. millefolium*, *E. lanatum*, and *R. occidentalis* all tended to exhibit higher levels of germination success at sites where stress was estimated to be high, regardless of treatment, while *Danthonia spp*. showed the opposite trend.

There were more seedlings of *A. millefolium*, *E. lanatum*, and *R. occidentalis* recorded in the unmanipulated control plots at high stress sites than at low stress sites, supporting the stress gradient hypothesis by demonstrating that facilitation plays a role in germination success for these species.

Treatment alone was the strongest explanatory variable for germination of *Lomatium spp.* and *P. congesta*. For these two species, treatment effects were significant or nearly significant at all but one site and at several sites two or more treatments had strong positive effects on germination. For *P. congesta*, all but one of the significant treatment effects were positive. For *Lomatium spp.,* treatments had strong positive effects on germination at eight sites and strong detrimental effects at three sites. The number of *Lomatium* seedlings in the treatment plots increased significantly as site stress decreased, suggesting that *Lomatium spp.* are not strong competitors for germination sites and that they benefit from changes to the plant community at low stress sites. The high number of seedlings recorded in the unmanipulated control plots at high stress sites suggests that *Lomatium spp.* benefit from facilitation within the plant community where stress is high.

Germination patterns for *Danthonia spp.* were unlike the rest of the focal species. At the high stress sites, germination was nearly undetectable, but as site stress decreased, germination increased. This is a difficult genus about which to make generalizations. *Danthonia spp.* are notoriously sporadic germinators, producing both cleistogamic (self-fertilized) and chasmogamic (out-crossed) seed (Hitchcock et al. 1977). Bruns (2005) found differences in germination rates between the cleistogenes and chasmogenes of *D.*

californica with chasmogamous seed germinating more rapidly and at a higher rate than cleistogenes. Laude (1949) reports germination rates varying between 3-80% across the genus and describes differences in seed dormancy (which can be single or double), depending on the year and the population from which seed was collected. The differences in germination rates, the potential differences in viability, and the capacity for double dormancy may explain the extremely low germination at the low stress sites.

The relatively greater number of seedlings detected at the low stress sites may be attributable to morphological characteristics of *Danthonia* seed itself. Moslovat (2002) reports that *D. californica* has hygroscopic awns, allowing the seeds to "move along the surface of the soil until they lodge in a microsite and become buried". While no single life history trait alone explains the higher germination at low stress sites and the near complete absence of seedlings at the high stress sites, it is possible that local environmental cues at the very southern sites induced dormancy instead of germination and that morphological characteristics of the seed at low stress sites made them better competitors for the available microsites.

Conclusion

When approaching the restoration of prairies in the Garry oak ecosystem, understanding site stressors can inform the decision making process when it comes to the allocation of restoration resources. On the whole, adding seed in high stress environments resulted in a greater number of seedlings than in the lower stress environments, regardless of treatment. Thus, if choosing to allocate funds between pre-seeding site preparation and the acquisition of greater quantities of native seed, our work suggests the latter is the more reasonable option where site stress is high.

The converse is also true: low stress environments resulted, on the whole, in lower germination and two site preparation treatments emerged as significantly better at increasing recruitment of the focal species in low stress environments than the rest: Poast Poast Burn and Mow Burn Glyphosate. The Poast Poast Burn treatment (Table 1) involves spring herbicide application of Poast over a two year period followed by a fall burn in the second year prior to seed addition, which we timed to coincide with the first fall rains. The Mow Burn Glypohosate treatment is comprised of a spring mowing treatment, with the mower blades set high to avoid cutting the flowering heads of native plants while targeting early germinating non-native species, such as invasive Mediterranean grasses. This is followed by a burn in the fall of a following year and the application of glyphosate with the first greening after the burn and prior to seed addition. While seed addition is important for all of these focal species, if the objective is to increase the number of *Danthonia spp.* at a site, close attention should be paid to the condition of the seed; a treatment to break one or more kinds of seed dormancy may be necessary to ensure germination depending on how the seed was collected and handled (see Laude 1949 for more details).

Figure 4.

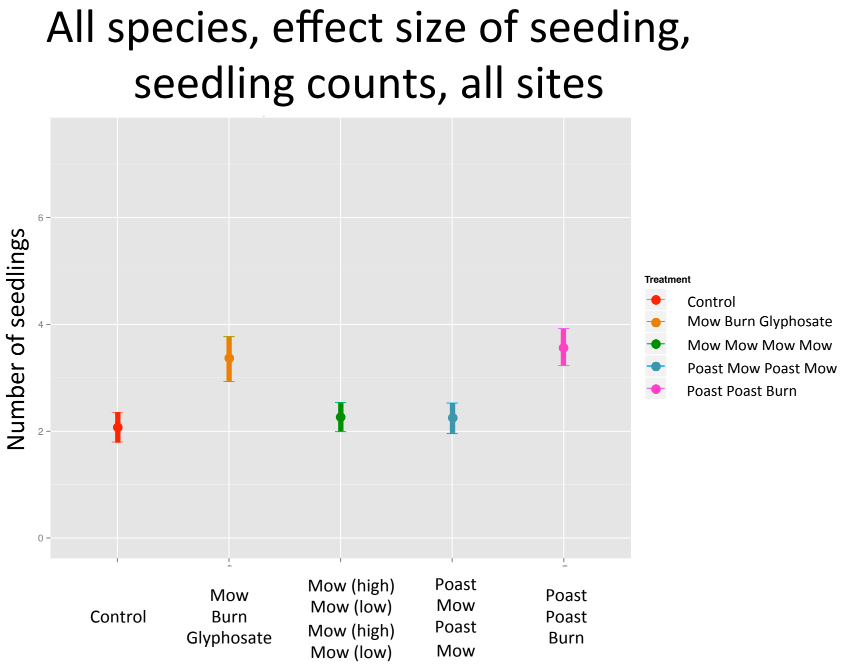

Figure 4. Effect size of germination for all species for all treatments as pooled across all sites. Two treatments emerge as significantly better than the control: Mow Burn Glyphosate and Poast Poast Burn, both with a p-value of < 0.001.

Table 2.

Recruitment	**Model Rank**			w_{ip}
ALL SPECIES COMBINED	**1**	**2**	**3**	
PCA1	*	*	*	1.00
Treatment	*	*		1.00
PCA1 * Treatment	*			0.51
Δ_i	-	0.11	22.94	
W_i	0.51	0.49	0.00	
Achillea millefolium	**1**	**2**	**3**	
PCA1	*	*	*	1.00
Treatment	*	*		1.00
PCA1 * Treatment		*		0.17
Δ_i	-	3.09	10.87	
W_i	0.83	0.17	0.00	
Danthonia spp	**1**	**2**	**3**	
PCA1	*	*	*	1.00
Treatment	*		*	0.65
PCA1 * Treatment			*	0.07
Δ_i	-	1.01	4.17	
W_i	0.58	0.35	0.07	
Eriophyllum lanatum	**1**	**2**	**3**	
PCA1	*	*	*	1.00
Treatment	*	*		0.98
PCA1 * Treatment		*		0.05
Δ_i	-	5.89	7.75	
W_i	0.93	0.05	0.02	
Lomatium spp	**1**	**2**	**3**	
PCA1		*	*	0.41
Treatment	*	*	*	1.00

PCA1 * Treatment			*	0.20
Δ_i	-	2.08	2.11	
W_i	0.59	0.21	0.20	
Plectritus congesta	**1**	**2**	**3**	
PCA1			*	0.31
Treatment	*	(null)	*	0.67
PCA1 * Treatment				0.05
Δ_i	-	1.63	1.72	
W_i	0.54	0.24	0.23	
Ranunculus occidentalis	**1**	**2**	**3**	
PCA1	*	*	*	1.00
Treatment		*	*	0.05
PCA1 * Treatment			*	0.02
Δ_i	-	6.00	7.53	
W_i	0.93	0.05	0.02	

Table 2. The results of model selection and model averaging for generalized linear mixed effects models (glmms) of the probability of recruitment in site stress (PCA1), treatment or the interaction between site stress and treatment. Table 2 shows the top models in all instances and gives Δ_i for each model. We include the top three models where Δ_i is within twenty-five points of the top model. Variables included in each model are indicated with an asterisk (*). Akaike weights (w_i) are the likelihood that a given model is the best of models considered (Burnham and Anderson 2002). Relative variable importance (w_{ip}) is the sum of w_i across all candidate models in which the variable appears. w_i does not sum to 1.00 in for some of the combinations examined due to the exclusion of models deemed irrelevant (i.e., Δ_I > twenty-five points from top model)

Figure 5.

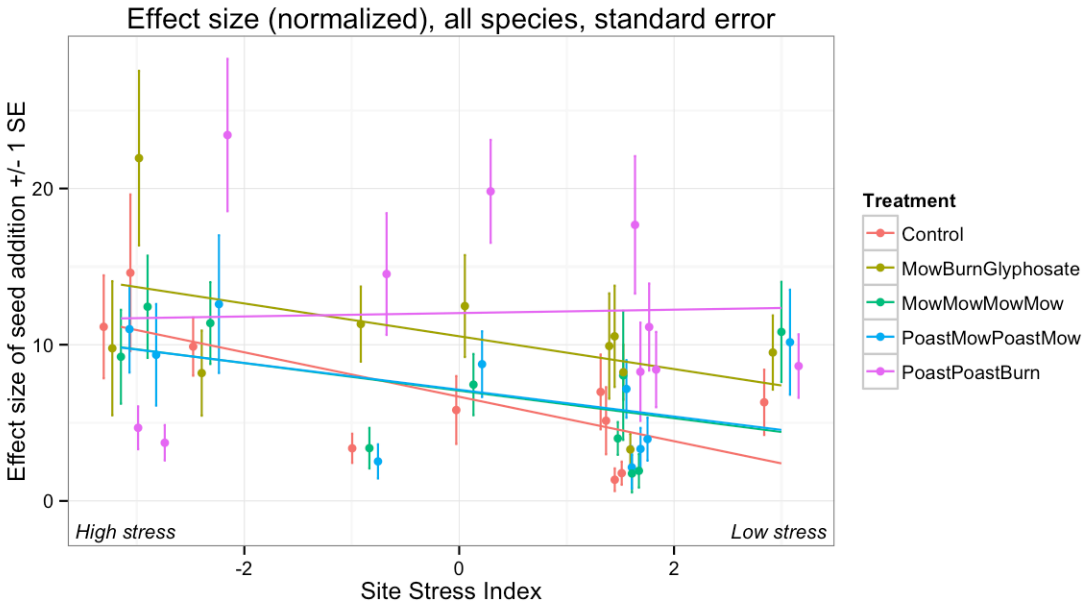

Figure 5. Effect size of germination response normalized for each species (scale 0-100) and pooled across all sites. Sites estimated to have higher stressors had lower PCA values (appearing on the left of the chart) while sites estimated to have lower stress levels at positive PCA values (appearing on the right of the chart). Two treatments were significant when examined for all species across all sites. Poast Poast Burn (pink) and Mow Burn Glyphosate (green) both significantly increased germination over the control ($p < 0.001$ for both).

Figure 6.

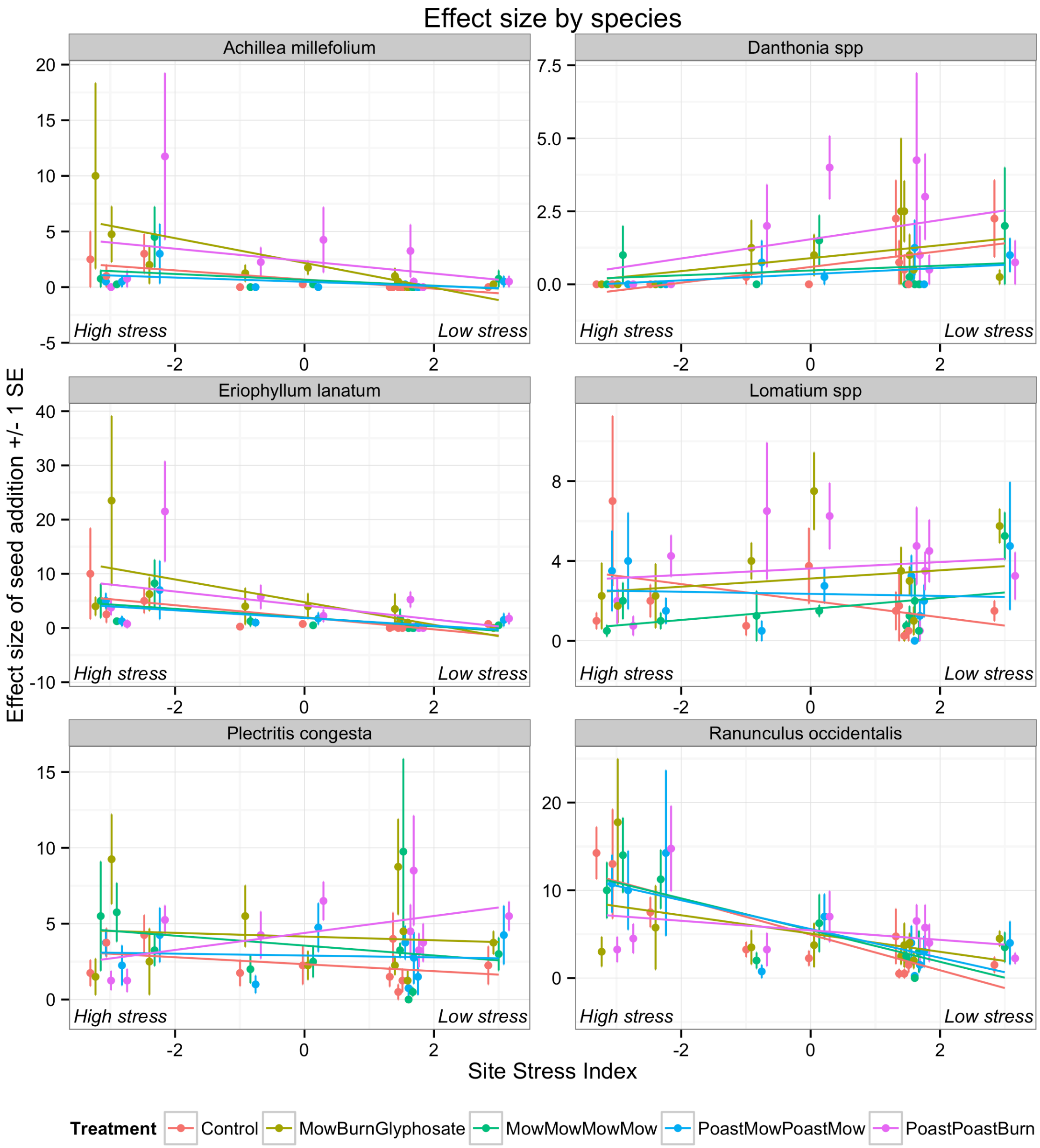

Figure 6. Effect size of germination response by species across all treatments at all sites. Note the change in the y-axis numbers between plots.

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Chapter Three

Does the metric matter? A comparison of measures of recruitment success across a 500km ecological experiment.

Quantitative vegetative sampling methods used to assess the relative importance of different plant species emerged in early publications as a way to quantify the composition (and thus the quality) of pastures (Fream 1888; Armstrong 1907; Levy and Madden 1933). Records of early sampling techniques all focused on one or more of the following four concepts: the number of individuals present, the frequency of occurrence, the area occupied, and the weight of the plant matter (Smartt 1974). The application of increasingly complex statistical methods progressed from relatively simple techniques used to analyze plant distribution in the 1930s to more involved methods such as pattern analysis in the 1950s and, with the advent of computer technology, multivariate analysis has become commonplace (Smartt 1974). Quantitative vegetative sampling techniques have progressed beyond the simple description of pasture composition and distribution of plant species and are now frequently relied upon as indicators of the success or failure of efforts to restore native ecosystems.

Seed addition is an increasingly common approach to the restoration of degraded native ecosystems, as fragmentation of the landscape, local extinctions, and dispersal limitation all restrict the ability of native plants to recruit into previously occupied portions of their known range (Fahrig 2003; Foster and Tilman 2003; Seabloom et al. 2003; Clark et al. 2007), but what is the optimal way to measure the success of seed addition in a restoration context? We are interested in the demographic effect of seed addition under different treatment conditions, but while direct assessment (seedling surveys) leave little doubt as to the presence or absence of the focal species after seed addition, they are onerous and time consuming. Collection of visually estimated percent cover data is a commonly employed sampling technique that can also detect demographic differences, but evaluations of whether or not it can be used as a surrogate for individual count data are rare. While this approach is far more efficient than conducting surveys of individual seedlings, it has been shown to be strongly affected by observer bias (Kennedy and Addison 1987; Klimeš 2003; Damgaard 2014), and to be inconsistent over time, due in large part to the constantly changing life history stages of the plants present.

During a region wide collaboration focused on honing restoration strategies for the invaded prairies of the Garry oak ecosystem, we collected both seedling count data and percent cover data for the same plots from ten field sites across a 500 km ecological experiment. The experiment also examined the recruitment response to abiotic stress, as the plots were aligned along a south-north stress gradient, allowing us to ask whether treatment, site stress, or the interaction between the two had a greater affect on recruitment of the focal species. Here we conduct a direct comparison of count and cover data, using the same statistical analyses to ask (a) whether or not percent cover data serves as a reasonable surrogate for count data and, (b) under what conditions does the count data and the percent cover data differ? We might expect these differences to emerge where a growth response is more likely than a demographic response (more extreme treatments, nutrient addition through burning, etc.) and they may interact with abiotic stress.

Methods

The experiment was conducted in remnant fragments of the Garry oak ecosystem, an increasingly rare and threatened ecosystem at the western edge of North America (Noss et al 1995; Crawford and Hall 1997). The northernmost site was in the Cowichan Valley, located on the south end of Vancouver Island, British Columbia, Canada; the six-midrange sites were centered on Olympia, Washington; and the three southernmost sites were clustered near Corvallis, Oregon. In 2005, four vegetative manipulation treatments and a control (no vegetative manipulation) were established at each site in 5m^2 plots. The treatments were focused on the reduction of non-native plant species and consisted of combinations of mowing, burning, and herbicide application (Table 1.). Each site contained four replicates for a total of twenty 5m^2 plots per site. Plots were arranged in a block design and treatments were randomly assigned to plots at each site (Figure 1).

In 2006, a mixture of seed of six native species was added to one half of each 5m^2 plot. These six native focal species included: *Achillea millefolium*, *Eriophyllum lanatum*, *Danthonia californica* or *spicata*, *Plectritis congesta*, *Lomatium nudicaule* or *utriculatum*, and *Ranunculus occidentalis*. The species of *Danthonia* and *Lomatium* added to the plots varied depending on which plant was documented as naturally occurring at the site. The recruitment response for *Danthonia* and *Lomatium* was examined at the genus level. Seedling surveys were conducted in the spring of 2007 before peak flowering to facilitate the capacity to see each plant in the sampling locations. Each 5m^2 plot was divided into quadrants and 1m^2 survey plots were established at the center of each quadrant to control for edge effects (Figure 1).

Count data and percent cover were collected from the same plots, but the area of measurement for the count data was much smaller (subsampled) than the area for which percent cover was estimated. For the count data, all seedlings of the focal species observed within the lower left sixteenth of each 1m^2 subplot were recorded. The percent cover surveys were conducted across the entirety of each 1m^2 subplot. There were a total of eighty survey subplots per site. Because there were four subplots inset within each 5m^2 plot, survey results were averaged within each seeded and unseeded half, respectively, of each 5m^2 plot to avoid pseudo-replication.

Those collecting the percent cover included precautions to ensure consistency between estimates. These precautions included daily calibrations at the beginning of each site survey, and working in collaborative survey teams to collect data, thereby providing support to each other if there was any question as to an appropriate estimate of cover. Incorporating calibration as a team practice allowed surveyors to collect the highest quality percent cover estimates possible.

The seeded focal species were all historically present at the experimental sites, but occurred in low numbers. Because there was the potential for naturally occurring populations to disperse seed into the experimental plots, the effect size of seeding was used as the metric for recruitment response. The effect size for the seedling count data and the percent cover data were generated in same way for purposes of comparison. For the seedling count data, the number of seedlings in the unseeded half of each plot (control) was subtracted from the number of seedlings in the seeded half of the plot (seed addition treatment). For the percent cover data, the percent cover of the focal species in the unseeded half of each plot was subtracted from the percent cover in the seeded half of the plot. All of the data used were collected in the spring of 2007 after seed addition in the fall of 2006. (See Figure 1.). For both methods of estimating effect size, those plots with a negative effect size (greater number of seedlings in the unseeded (control) half of the plot than in the seeded half of the plot) were converted to zero, since, biologically, it is does not make sense to consider a negative number of a focal plant.

The recruitment response of all focal species was first examined together as a group to determine if any generalizations could be drawn for all species across all sites. The recruitment response was then analyzed individually for each species across all sites. When all sites were pooled together for analytical purposes, the candidate models included "site" as a random effect in order to account for the site-specific features of the experimental design, such as random distribution of manipulative treatment plots at each site, random allocation of seed addition subplots within the treatment plots, and the varying levels of individual stressors that were measured to describe the stress gradient (See Richardson et al. 2012).

Abiotic stress was quantified with a Site Stress Index value (SSI) by combining latitude with a set of eight environmental variables from each site and conducting a principal component analysis (PCA). The environmental variables were percent soil moisture, total extractable nitrogen (N) and carbon (C) from the soil, concentration of soil nitrate and ammonium, soil microbial biomass, surface cover by organic litter, and surface cover by bare soil. The eight environmental measures were taken at peak flowering times at each site, which ranged from late April at the southern sites to mid-May at the northern sites. Figure 2 illustrates the latitudinal range of sites plotted against their PCA eigenvector values (Site Stress Index scores). (See Richardson et al. 2012 for additional information on the formulation of the PCA eigenvector values.)

Data were analyzed with R 2.15.1 using a generalized linear mixed effects model package that accommodates common error distributions associated with ecological data, such as zero inflation (package: glmmADMB. See Fournier et al. 2012 for more details). The percent cover data was transformed to integer values by multiplying all values by 100. Error distributions for each subset of data were identified based on lowest AIC_c scores for each respective best-fit model. Model selection was conducted with the dredge function. Best-fit candidate models within $\Delta 25$ AIC_c points were ranked and the top three candidate models for each subset of the data are included in Tables 2 and 3. Levels of significance (p-values) provided for treatment effects for each species at each site are the results of generalized linear models run with the R package glmmADMB.

Results

For all species across all sites, the count data identified two restoration treatments that resulted in significantly higher recruitment of the focal species (Figure 3). Both the Mow Burn Glyphosate treatment and the Poast Poast Burn treatment resulted in recruitment of the focal species that was highly significant ($p < 0.001$), while the estimate of the percent cover data showed weak support for the capacity of the Poast Poast Burn treatment to increase recruitment ($p = 0.042$), but did detect a significant decrease in cover of the focal species from the Mowing only treatment ($p = 0.026$)

Species-specific examination further highlighted the differences between the two forms of data analysis. Seedling count data were better able to differentiate between treatment effects for *A. millefolium*, *Danthonia spp.*, and *Lomatium spp.* than the count data, which largely showed no difference from the control, but indicated that treatment had no effect on the recruitment of *R. occidentalis*. The count and percent cover data were most similar for *E. lanatum*, and *P. congesta*. With the exception of *P. congesta*, treatment effects were not significant for any of these species when evaluated with the percent cover data. Cover data for *P. congesta* indicated that two treatments resulted in highly significant increases in germination response over the control treatment; Mow Burn Glyphosate and Poast Poast Burn, ($p > 0.001$ for both).

Model ranking for the each data type was consistently different. Based on the seedling count data, the best model for all species across all sites included site stress, treatment, and the interaction between the two (Table 2), while the highest ranked candidate model for the percent cover data included only site stress and treatment (Table 3). At the species level (pooled across all sites) for the seedling count data, four species included site stress in the highest ranked model, three of those models also included treatment. *Lomatium spp*. and *P. congesta* both had only treatment in the highest ranked model, while *R. occidentalis* had only site stress (Table 2). For the cover data, site stress was included in the highest ranked model for every species with the exception of *P. congesta*, for which treatment was strongest explanatory variable (Table 3). Species-specific and site-specific responses were extremely variable for both the seedling count data and the percent cover data and we did not carry the comparison of the data types to this level.

Discussion

Seedling counts and percent cover estimates were correlated when pooled across all species and all sites. This similarity diminished when comparing individual species pooled across all sites (Figures 3 and 4), with the exception of *P. congesta* and *Lomatium spp*. The model averaging points to distinct differences between the seedling count data and the percent cover (Tables 2 and 3). While the seedling count data indicated that the germination response to the Poast Poast Burn treatment and the Mow Burn Glyphosate treatment was consistently than the control, only one of the estimates of percent cover supported this conclusion. The explicit focus of the seedling count data on the recruitment response to treatment provided a higher level of resolution, though the small size of the subsampling location likely reduced the predictive power of the data set. Percent cover data is strongly affected by the life history stage of the focal species during the survey period, which changes quickly during the survey season; this potentially introduced a source of variation that may have decreased the capacity of the dataset to identify real differences between treatments.

The use of seedling count data in concert with percent cover data did highlight one interesting treatment effect. The seedling count data and the percent cover data identified two treatments where the effects detected in the seedling count data were opposite of those shown in the percent cover data for *Danthonia spp.* Seedling count data showed a significant increase over the control for the Mow Burn Glyphosate treatment and the Poast Poast Burn treatment while the percent cover data detected a reduction of mature *Danthonia* plants in treatments that included the herbicides glyphosate or Poast™. Glyphosate is targeted at broad-leaf weeds, but has been shown to affect grasses. *Danthonia spp.* have broad hairy blades that might cause it to be disproportionately affected by this herbicide in comparison to other, more narrow-leaved grass species. Poast™ (generic: sethoxydim) is marketed as a grass specific herbicide, and its application resulted in a reduction in the percent cover of *Danthonia spp.* in the two treatments where it was included, significantly so when the treatment also included burning ($p = 0.0002$). Seedling counts for *Danthonia* were higher in the treatment plots where percent cover was low, implying conspecific competition as potentially significant for the recruitment of at least one species, and suggesting that the reduction of established conspecifics may increase germination success for *Danthonia*.

While trends in treatment effects were consistently visible, if not significant, in the seedling count data, the percent cover data was rarely able to detect differences between treatments at the species level. Specifically, the unmanipulated vegetative control treatment was more likely to overlap with the effect size of the treatments for the percent cover data. Agreement between the two forms of data was highest for *P. congesta*. *P. congesta*, also known as sea blush, is an annual that was not currently present at any of our sites before being seeded there. As an fleshy annual, it grows quickly after germination making it more likely to contribute to the percent cover estimates than some perennial species for which seedlings may take a year or longer to move past the cotyledon stage, such as *Lomatium spp*.

Seedling count data for *R. occidentalis* showed statistically indistinguishable differences for all vegetative manipulation treatments and the control, demonstrating that it is a resilient species in terms of recruitment; if the seeds can get to a site, they are likely to be strong competitors for available resources.

The effect of treatment could have been calculated in several different ways for the percent cover data due to the comprehensive methods of data collection. Indeed the method that most frequently detected the significance of treatment effect was calculated by subtracting the pre-seeding percent cover for each plot, which was collected in spring 2006, from the post-seeding percent cover over the same area of each plot, which was collected in spring 2007. While this method made the most sense from a biological perspective (the same area of each plot compared at pre- and post-seeding time points), it was incomparable to the way the seedling count data set, which was collected at a single point in time in the spring of 2007. A re-examination and comparison of these data that includes the pre- and post-seeding percent cover estimates over the same area would increase the likelihood of agreement between the two types of collection methods.

Conclusions

At least for the methods used here to compare count data and percent cover, count data provided finer resolution in terms of distinguishing between the effects of treatment on the recruitment of the focal species, despite the small area sampled for each plot. Further, we recommend the collection of count data when conducting seed addition studies, as percent cover data directly contradicted the count data for at least one species and was unable to distinguish between the effects of treatment on recruitment for others. The collection and comparison of these two types of data may allow researchers to detect whether conspecific competition is inhibiting recruitment, or if the treatments being applied in the field are inhibiting the ability of focal populations to recover.

Despite the high quality of count data, collection of census data will remain impractical for most practitioners, who often need to balance the desire for sampling rigor with the necessity of speed in the race to collect data before the end of the sampling season.

Acknowledgements

Data collection for this project would not have been possible without the University of Washington Department of Biology Botany Fellowship. The Frye-Hotson-Rigg Writing Fellowship, also provided by the UW Department of Biology, supported the writing of this manuscript. The Northwest Conservation Fund of the Priscilla Bullitt

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Figure 1.

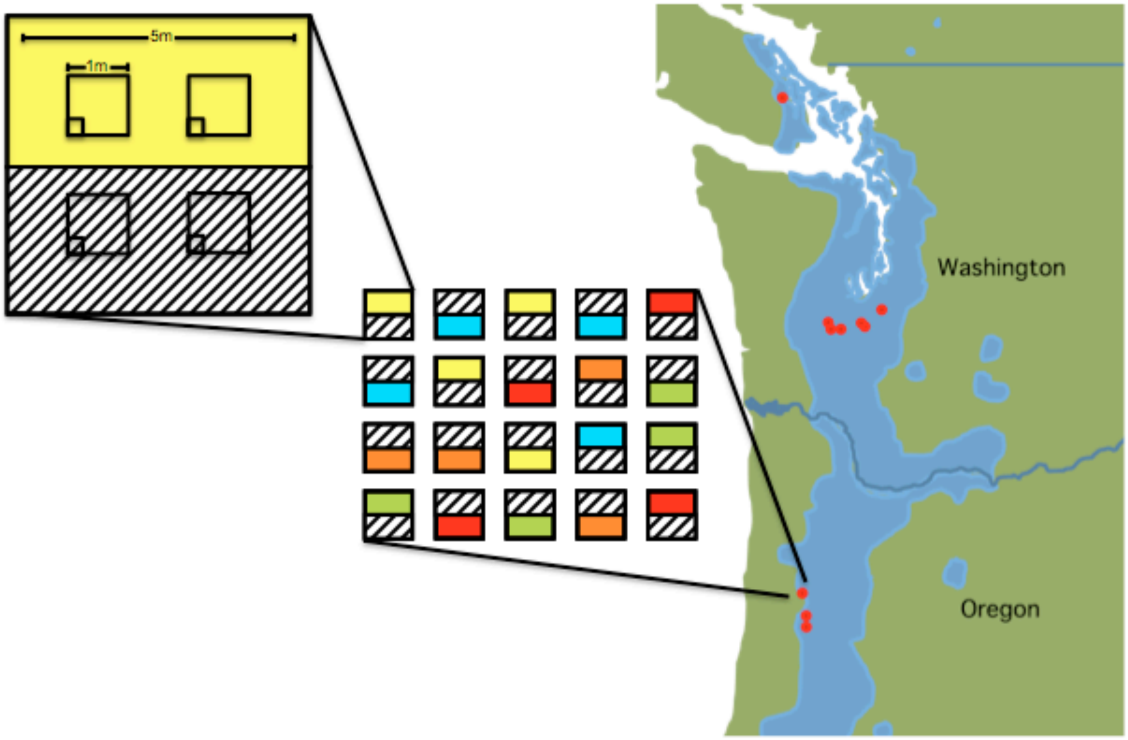

Figure 1. The location and arrangement of experimental sites. The sites were located on Vancouver Island, British Columbia, Canada, and in Washington and Oregon State, USA. Each site included four replicates of four treatments and a control for a total of twenty 5m^2 plots per site. One half of each 5m^2 plot was seeded and each 5m^2 plot had four 1m^2 subplots inset to avoid edge effects during sampling. A complete census of the focal species was conducted in the lower left corner of each 1m^2 subplot.

Figure 2.

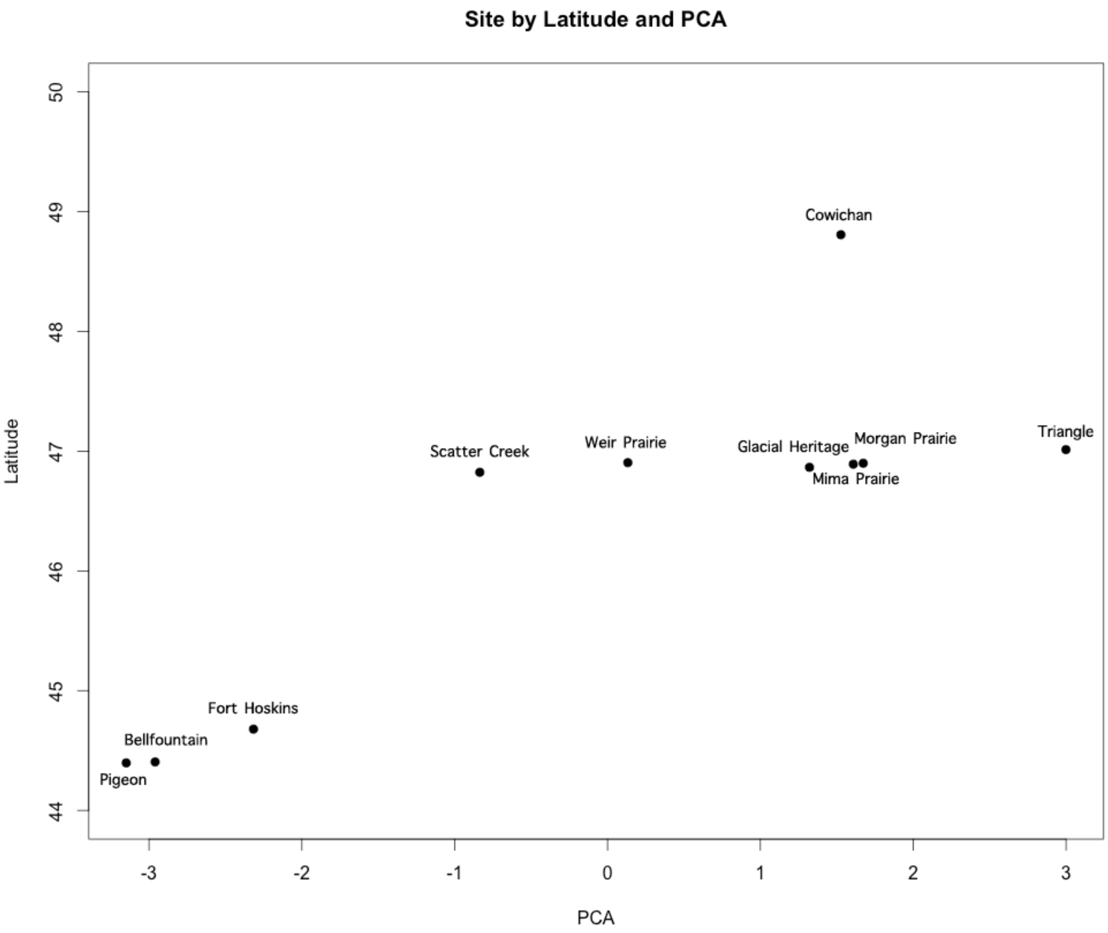

Figure 2. The relationship between latitude and the PCA score. Low PCA values indicated high stress score on the Site Stress Index (SSI), while high PCA values translated to low SSI scores. The lower latitude sites were estimated to have higher stress levels than high latitude sites.

Figure 3.

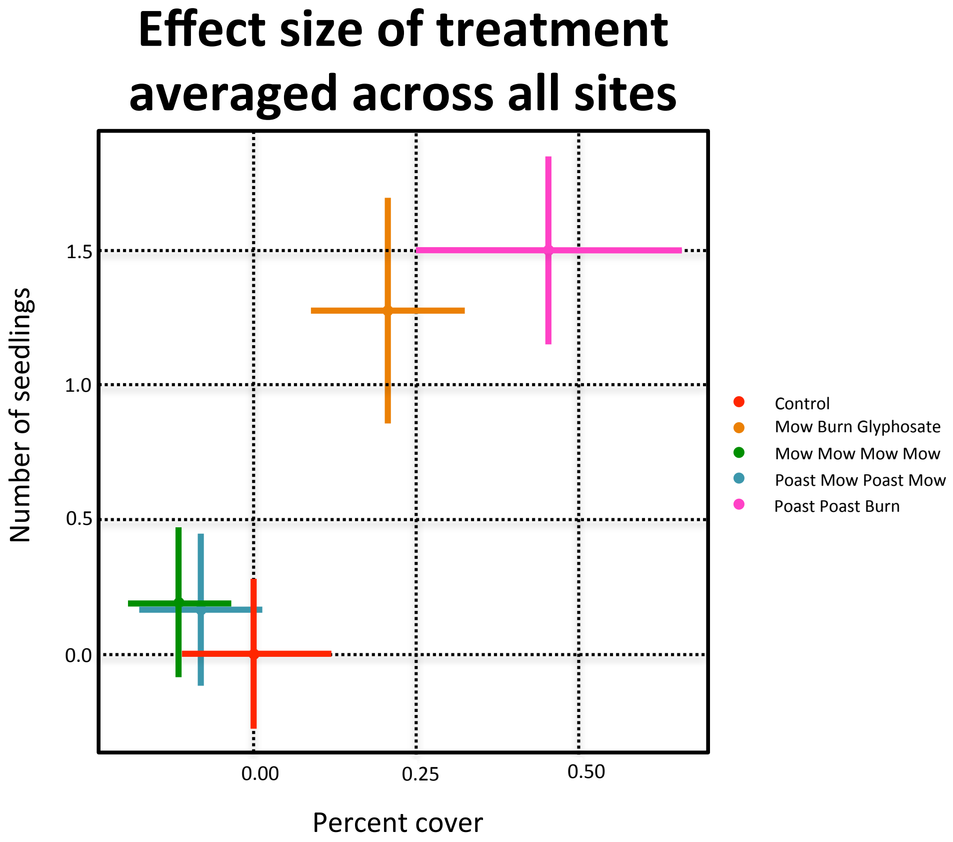

Figure 3. Simple effect size of treatment (the mean of each treatment – the mean of the control) (calculated from the effect size of seed addition) averaged for all species across all sites. The effect size of the count data is mapped to the y-axis while the effect size of the percent cover data is mapped to the x-axis.

Figure 4.

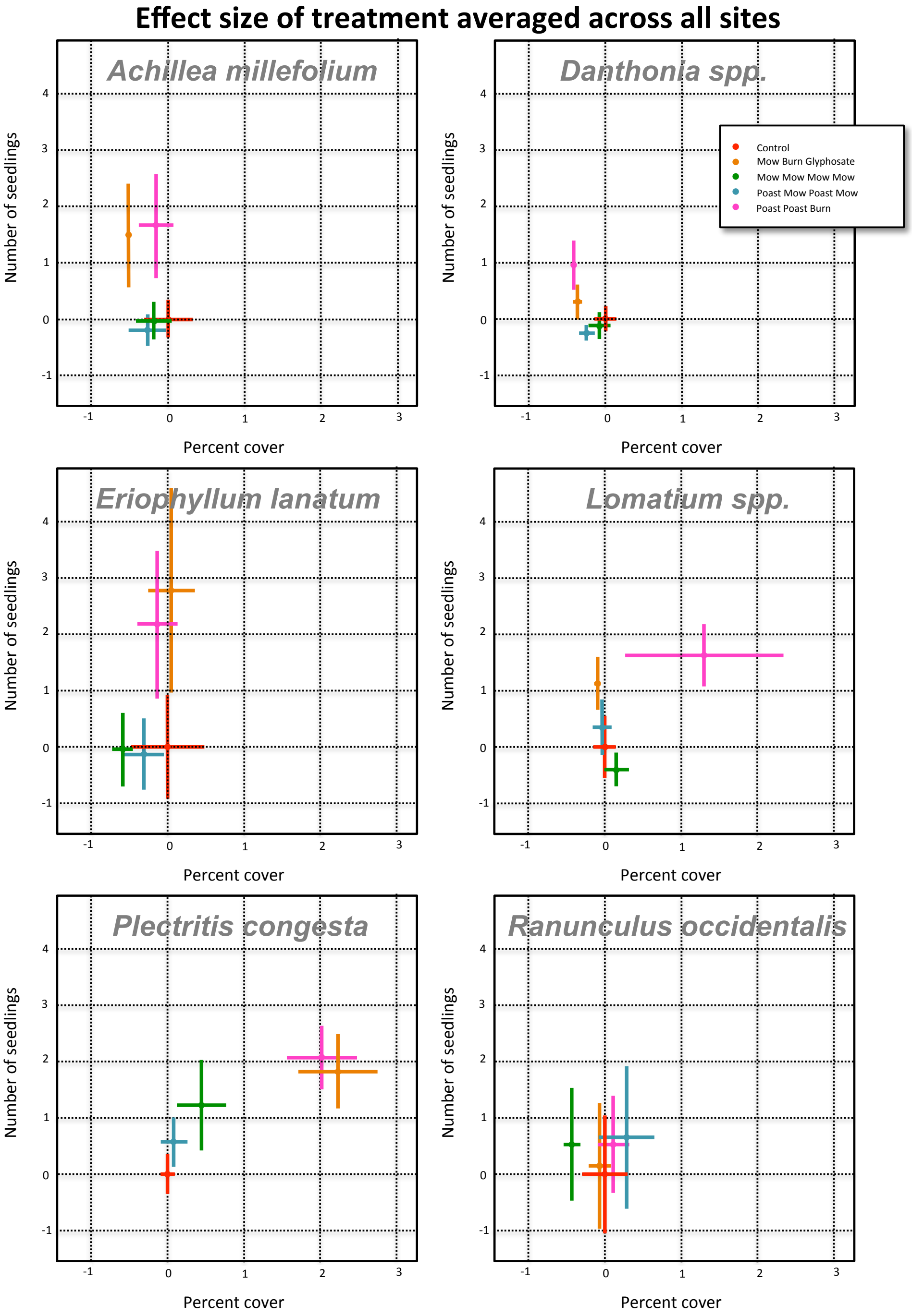

Figure 4. The simple effect size of treatment (the mean of each treatment – the mean of the control) (calculated from the effect size of seed addition) for each restoration treatment for each species averaged across all sites. The count data mapped to the y-axis and the percent cover data to the x-axis for each treatment.

Table 1.

	2005		2006	
Treatment	**Spring**	**Fall**	**Spring**	**Fall**
Control	No vegetative manipulation			
Mow Burn Glyphosate	Mow high			Burn/Glyphosate
Mowing Only	Mow high	Mow low	Mow high	Mow low
Poast Mow Poast Mow	Poast	Mow low	Poast	Mow low
Poast Poast Burn	Poast		Poast	Burn

Table 1. Treatment schedule as implemented in 2005 and 2006.

Table 2.

Recruitment	**Model Rank**			w_{ip}
ALL SPECIES COMBINED	**1**	**2**	**3**	
Site Stress	*	*	*	1.00
Treatment	*	*		1.00
Site Stress * Treatment	*			0.51
Δ_i	-	0.11	22.94	
W_i	0.51	0.49	0.00	
Achillea millefolium	**1**	**2**	**3**	
Site Stress	*	*	*	1.00
Treatment	*	*		1.00
Site Stress * Treatment		*		0.17
Δ_i	-	3.09	10.87	
W_i	0.83	0.17	0.00	
Danthonia spp	**1**	**2**	**3**	
Site Stress	*	*	*	1.00
Treatment	*		*	0.65
Site Stress * Treatment			*	0.07
Δ_i	-	1.01	4.17	
W_i	0.58	0.35	0.07	
Eriophyllum lanatum	**1**	**2**	**3**	
Site Stress	*	*	*	1.00
Treatment	*	*		0.98
Site Stress * Treatment		*		0.05
Δ_i	-	5.89	7.75	
W_i	0.93	0.05	0.02	
Lomatium spp	**1**	**2**	**3**	
Site Stress		*	*	0.41
Treatment	*	*	*	1.00

Site Stress * Treatment			*	0.20
Δ_i	-	2.08	2.11	
$\mathbf{W_i}$	0.59	0.21	0.20	
Plectritis congesta	**1**	**2**	**3**	
Site Stress			*	0.31
Treatment	*	(null)	*	0.67
Site Stress * Treatment				0.05
Δ_i	-	1.63	1.72	
$\mathbf{W_i}$	0.54	0.24	0.23	
Ranunculus occidentalis	**1**	**2**	**3**	
Site Stress	*	*	*	1.00
Treatment		*	*	0.05
Site Stress * Treatment			*	0.02
Δ_i	-	6.00	7.53	
$\mathbf{W_i}$	0.93	0.05	0.02	

Table 2. The results of model selection and model averaging for generalized linear mixed effects models (glmms) of the probability of recruitment in site stress, treatment or the interaction between site stress and treatment for the seedling count data. Table 2 shows the three highest ranked candidate models where Δ_i is within twenty-five points of the top model and gives Δ_i for each model. Variables included in each model are indicated with an asterisk (*). Akaike weights (w_i) are the likelihood that a given model is the best of models considered (Burnham and Anderson 2002). Relative variable importance (w_{ip}) is the sum of w_i across all candidate models in which the variable appears. w_i does not sum to 1.00 in for some of the combinations included due to the exclusion of models deemed irrelevant (i.e., Δ_I > twenty-five points from top model).

Table 3.

Recruitment	**Model Rank**			**w_{ip}**
ALL SPECIES COMBINED	**1**	**2**	**3**	
Site Stress	*	*	*	0.99
Treatment	*		*	0.93
Site Stress * Treatment			*	0.05
Δ_i	-	5.05	5.84	
W_i	0.87	0.07	0.05	
Achillea millefolium	**1**	**2**	**3**	
Site Stress	*	*	*	1.00
Treatment	*		*	0.58
Site Stress * Treatment	*			0.52
Δ_i	-	0.42	4.19	
W_i	0.52	0.42	0.06	
Danthonia spp	**1**	**2**	**3**	
Site Stress	(null)	*		0.30
Treatment			*	0.26
Site Stress * Treatment				0.01
Δ_i	-	2.04	2.46	
W_i	0.54	0.20	0.16	
Eriophyllum lanatum	**1**	**2**	**3**	
Site Stress	*	*	*	1.00
Treatment	*	*		0.79
Site Stress * Treatment	*			0.40
Δ_i	-	0.11	1.26	
W_i	0.40	0.38	0.21	
Lomatium spp	**1**	**2**	**3**	
Site Stress	*	*	*	1.00
Treatment	*	*		0.88

Site Stress * Treatment		*		0.24
Δ_i	-	1.95	3.34	
W_i	0.64	0.24	0.12	
Plectritus congesta	**1**	**2**	**3**	
Site Stress		*	*	0.57
Treatment	*	*	*	1.00
Site Stress * Treatment		*		0.42
Δ_i	-	0.03	2.05	
W_i	0.43	0.42	0.15	
Ranunculus occidentalis	**1**	**2**	**3**	
Site Stress	*	*	(null)	0.85
Treatment		*		0.20
Site Stress * Treatment				0.01
Δ_i	-	2.87	3.53	
W_i	0.68	0.16	0.12	

Table 3. The results of model selection and model averaging for generalized linear mixed effects models (glmms) of the probability of recruitment in site stress, treatment or the interaction between site stress and treatment for the percent cover data. Table 3 shows the three highest ranked candidate models where Δ_i is within twenty-five points of the top model and gives Δ_i for each model. We include the top three models where Δ_i is within twenty-five points of the top model. Variables included in each model are indicated with an asterisk (*). w_i does not sum to 1.00 in for some of the combinations included due to the exclusion of models deemed irrelevant (i.e., Δ_I > twenty-five points from top model).

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