AN ABSTRACT OF THE THESIS OF

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Abstract approved:

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In ecological restoration, species that are sown to increase the native plant diversity range in establishment ability. Some species readily establish, while others rarely do. This study set out to investigate some of the potential processes influencing species establishment, as well as the traits that are associated with the success of species in restoration. Twenty-eight species native to upland prairies of the Willamette Valley of Oregon were sown in different seed mixtures in field plots in a former agricultural field. These species were divided into three *a priori* functional groups, annual forbs, perennial forbs, and grasses, to determine whether interactions among functional groups influenced the performance of functional groups and other measures of restoration success, including native species richness, cover, and biomass. There was no evidence of inter-group competition; rather, competition was greater within functional groups, particularly within annual forbs. Native cover and biomass increased significantly with the number of functional groups sown; however, the amount of variation explained by functional group diversity was less than 10%. Non-

native plant abundance was found to influence native performance much more than functional group richness. Sown native richness was not strongly influenced by either functional group richness or non-native abundance.

To look for correlations between species traits and performance, eleven different traits of each species were measured from both laboratory and field-grown plants. These were related to measures of field performance, including cover (%) and frequency of establishment using step-wise regression techniques. Models relating traits to measures of performance were strong, with traits explaining up to 56% of variation in cover, and 49% of establishment frequency. The relationship between traits and performance varied depending on functional group, and intergroup interactions among annual forbs also influenced cover within this functional group.

If these results were to be put into practice, a functionally diverse seed mix for greater native abundance would be recommended for greater native cover. The regression models should be tested using different species or at a different site to determine their predictive ability. The results presented here should be useful to land managers and from a general ecological sense as well.

Functional Groups, Traits, and the Performance of Species in Restoration

by
Rachael E. Roberts

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Rachael E. Roberts, Author

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Chapter 1 : Introduction

Using functional group interactions and traits to understand the performance of prairie plant species in restoration

Prairies once were a prominent ecosystem in Oregon's Willamette Valley, but much of the habitat formerly present has been lost. Conversion to agriculture, development, and succession have reduced these prairies to less than 1% of their former range (Titus et al. 1996). Much of the prairie that remains is heavily invaded by exotic plants, threatening the persistence of native species (Wilson and Clark 1998). Many species depend on these ecosystems, including the federally threatened Kincaid's lupine (*Lupinus sulphureus* ssp. *kincaidii*) and its associated federally endangered species Fender's blue butterfly (*Icaricia icarioides fenderi*) (Wilson et al. 1997, Schultz et al. 2003, Wilson et al. 2003). Restoration of prairie systems may be crucial to the survival of these and many other species (Schultz 2001).

Restoration projects may have different goals, but possibly the most common are related to native plant diversity and structure (Ruiz-Jaen and Aide 2005). The Society for Ecological Restoration International Primer on Ecological Restoration (2004) lists as its first attribute of restored ecosystems that they contain "a characteristic assemblage of the species that occur in the reference ecosystem and that provide appropriate community structure". Native cover is associated with a decrease in the abundance of exotic species (Wilson et al. 2004). A diverse native plant community provides habitat and resources for other native species (Schultz 2001). Native species richness provides ecosystem stability (Knops et al. 1999), and has even been shown to reduce the invasibility of a system (Kennedy et al. 2002), besides being aesthetically pleasing.

There is a wide range of variability in the performance of native species added in restoration (Howell and Kline 1994). Some readily establish, others rarely do, and still others are known to be aggressive and must be used in limited quantities. The reasons for this range in establishment ability are largely unknown, and could be due to a number of factors (Kline and Howell 1987). To look at some of the causes of this variability, I sowed seed mixtures in field plots to investigate some potential processes influencing species establishment. I also measured traits of these species to determine whether any are associated with the success of species in restoration.

The role of functional groups in restoration

One way of investigating the performance of species in restoration is by categorizing species into functional groups. Functional groups are organisms that respond similarly to the environment or are similar in morphology, life form, or resource use. From a practical standpoint, grouping species based on shared characteristics or behavior is a simpler way of studying plant communities than a species-by-species approach (Botkin 1975, Keddy 1990, Körner 1993, Grime et al. 1997a). Also, an ecological, rather than a taxonomic classification makes more sense when studying species interactions in natural systems (Westoby and Leishman 1997).

Functional groupings of plants have proven useful in predicting plant species' responses in various ecological settings (Keddy 1990, Solbrig 1993, Reich et al. 2003a, Reich et al. 2003b). Functional groups have been used to predict species' responses to global change (Díaz and Cabido 1997) as well as to disturbance (Lavorel et al. 1999). Functional groups in these circumstances can be considered "response guilds" (Keddy 1990), groups of species that respond similarly to environmental changes. These classifications are useful because they create generalizations that if proven predictive in one circumstance can be tested in other systems (Díaz and Cabido 1997).

Investigating functional groups makes sense in the context of prairie restoration because competition between functional groups is often implicated in the success of species in restoration. Often, grasses are associated with declining abundance and richness of forbs in prairie restoration (Howell and Kline 1994, Diboll 1997, Weber 1999). Sowing mixtures for restoration often recommend particular grass-to-forb ratios, with the warning that a mixture too heavy in grasses can reduce the abundance of forbs (Diboll 1997, Heritage Seedlings Inc. 2007). Little research has looked into competition between plant functional groups in a restoration setting, and until there is more controlled research into these interactions, it remains unknown how universal these recommendations should be. Do these sowing recommendations apply to all grasses? All prairie ecosystems?

The relationship between species' traits and performance

Traits are another potential means of forecasting the success of species in restoration. Simply, a plant trait is "any attribute that has potentially significant influence on establishment, survival, and fitness" (Reich et al. 2003b). These are characteristics that relate to a species' patterns of growth and allocation, and that evolved in response to abiotic environmental conditions and interactions with other species (Reich et al. 2003b). When the same traits are measured among many different species, they can be a useful tool for comparing these species (Grime and Hunt 1975, Hunt 1982).

Previous evidence indicates many traits that are related to establishment ability. Germination rate has been correlated with both seed mass and seedling relative growth rate (Grime et al. 1981). Establishment and other measures of seedling performance have also been related to seedling weight, growth form (Gross 1984), germination time and germination rate (Pywell et al. 2003), plant height, and DNA content (Leishman 1999). Research on prairie species in the Willamette Valley indicates seedling biomass, leaf area, leaf weight ratio, and unit leaf rate to be strong predictors of native plant performance (Clark et al. 2001, Goodridge 2002). Because the establishment and performance of seedlings is strongly related to the composition of resulting communities (Gross 1984), understanding what traits are related to the performance of species is the first step towards predictive models that can be an important tool in successfully restoring prairie systems.

Research objectives

In this thesis I address three primary objectives. In Chapter 2, I determine the effects of functional groups on the performance of other functional groups and on other measures of restoration success, including native species richness, cover, and biomass. I defined three *a priori* functional groups, based on differences in life history, physical structure, and widespread acceptance of these groupings. These functional groups are grasses, annual forbs, and perennial forbs. I sowed seven different combinations of these functional groups in an old agricultural field to answer two questions: Question 1: What is the effect of each functional group on the performance of other functional groups? Question 2: Does functional group richness positively influence total native cover, biomass, and sown species richness?

Chapter 3 addresses whether traits are related to species performance in restoration, whether the functional group identity of a species influences which traits are related to performance, and also whether the functional group identity of neighboring plants influences how traits are related to performance. Regression models were created using stepwise techniques that indicated which traits were best related to yield and frequency of establishment. These models, if later proven predictive, can be used by land managers to predict the performance of species prior to sowing, allowing managers to allocate their dollars towards species most likely to be successful.

Together, these studies increase understanding of the role that interactions between species and functional groups play in influencing the performance of native species, plant richness, and of restoration in general. The results should be useful to those practicing restoration and also shed some light on universal ecological processes.

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Chapter 2 : Competition or complementarity? Functional group interactions in prairie restoration

Introduction

The goal of many ecological restoration projects is to increase the abundance of native vegetation as well as the number of native plant species present at a site, often to achieve vegetation structure similar to historic communities (Howell and Jordan 1991, Lockwood 1997, Society for Ecological Restoration International Science & Policy Working Group 2004). The Society for Ecological Restoration International Primer on Ecological Restoration lists as its first attribute of restored ecosystems that they contain "a characteristic assemblage of the species that occur in the reference ecosystem and that provide appropriate community structure" (2004). Attempts to reintroduce all the desired plant species usually fail, however (Lockwood and Pimm 1999). Most prairie restorations never attain the diversity seen in prairie remnants, in part because only a fraction of native species may be sown, but also because many native species sown do not readily establish in restoration (Kindscher and Tieszen 1998, Sluis 2002, Ammann and Nyberg 2005, McLachlan and Knispel 2005, Polley et al. 2005). There is a wide range of variability in the performance of native species added in restoration (Howell and Kline 1994). Some readily establish, others rarely do, and still others are known to be aggressive and must be used in limited quantities. The reasons for this range in establishment ability are largely unknown, and could be due to a number of factors (Kline and Howell 1987).

One phenomenon often implicated in the success of prairie restorations is competition between sown species for limited resources such as light and nitrogen. This "prairie competing with the prairie" (Schramm 1992) can lead to dominance of a few aggressive species and decreased plant diversity in the restored community (Schramm 1992, Howell and Kline 1994, Diboll 1997, Lockwood 1997, Weber 1999). Many restoration practitioners give general recommendations on how to design a seed mix, which often consist of particular grass-to-forb ratios that are supposed to minimize the competitive effects of grasses (Schramm 1992, Diboll 1997, Weber 1999, Boyer 2006). Grasses are presumed to outcompete many forbs because of their aggressiveness, taller stature, dense, fibrous root systems, and tolerance of lower nitrogen levels (Diboll 1997, Howe 1999, Ammann and Nyberg 2005). Studies in which forbs and grasses are introduced sequentially have found that sowing forbs after grasses results in lower forb performance (Kindscher and Fraser 2000, Clark and Wilson 2005). However, few studies investigate the role of interactions between forbs and grasses sown simultaneously and their influence on the success of species in the resulting restored communities (Howell and Kline 1994).

Grasses and forbs can be considered functional groups, organisms that respond similarly to the environment or are similar in morphology, life form, or resource use. Grouping species based on shared characteristics or behavior is a simpler way of studying plant communities than a species-by-species approach (Botkin 1975, Keddy 1990, Körner 1993, Grime et al. 1997a). Also, an ecological, rather than a taxonomic classification makes more sense when studying species interactions in natural systems (Westoby and Leishman 1997). Functional groupings of plants have proven useful in predicting plant species' responses in various ecological settings (Keddy 1990, Solbrig 1993, Reich et al. 2003a, Reich et al. 2003b). Functional groups have been used to predict species' responses to global change (Díaz and Cabido 1997) as well as to disturbance (Lavorel et al. 1999). Functional groups in these circumstances can be considered "response guilds" (Keddy 1990), groups of species that respond similarly to environmental changes. These classifications are useful because they create generalizations that if proven predictive in one circumstance can be tested in other systems (Díaz and Cabido 1997).

Differences between functional groups should correspond to differences in resource use and resource capture from different areas in space or time, a phenomenon known as resource complementarity (Hooper 1998, Spehn et al. 2000). Functionally diverse plant communities are associated with greater productivity of species (Tilman et al. 1997, Reich et al. 2004), although this pattern is not always found (Hooper 1998). Because complementary functional groups can use resources more completely, fewer resources are available for invading plants, and invasibility decreases as functional group diversity increases, as has been found in several grassland systems (Fargione et al. 2003, Pokorny et al. 2005, Biondini 2007). Thus, the resource complementarity theory provides evidence that interactions between different functional groups may be beneficial to restoration.

This study was carried out to determine the effects that functional groups and functional group diversity have on measures of restoration success, including native species richness, cover and biomass. Twenty-eight species native to upland prairies in the Willamette Valley of Oregon were sown in experimental field plots. Species were divided into three functional groups: annual forbs, perennial forbs, and grasses. In this study I addressed two main questions: (1) What is the effect of each functional group on the performance of other functional groups? (2) Does functional group richness positively influence total native cover, biomass, and sown species richness? To answer question one I compared seed mix treatments containing one functional group to seed mix treatments with two functional groups to look at the effects of each functional group on the cover, biomass, and species richness of other functional groups. To answer question two I investigated how total native cover, biomass, and species richness is related to the number of functional groups sown.

Methods

Study site

The study site was located at the William H. Finley National Wildlife Refuge (hereafter, Finley NWR) (44°N, 123°W), approximately 10 miles south of Corvallis in the Willamette Valley of Oregon. The site was previously used to grow forage for wildlife, but the present goal is to restore upland prairie habitat, eventually sustaining populations of the federally threatened Kincaid's lupine (*Lupinus sulphureus* ssp. *kincaidii*) and its associated federally endangered species Fender's blue butterfly (*Icaricia icarioides fenderi*). A matrix of native grasses was sown in 2002 and an assortment of non-native grasses and forbs are also present. The exotic perennial grasses *Anthoxanthum odoratum* and *Agrostis stolonifera* are abundant, while exotic forbs such as *Hypochaeris radicata* and *Hypericum perforatum* are also common at the site. The soil type is mapped as Santiam silt loam, 2-8% slopes (NRCS 2007).

Species and functional group selection

Twenty-eight native species common to Willamette Valley upland prairies were used in this study (Table 2.1). Seeds were obtained from local native seed vendors.

Functional groups were separated based on differences in life history, morphology, size in first year of growth, and potential competitive ability. First, species were divided into grass and forb functional groups. Much of the advice given on designing seed mixes for prairie restoration suggests different grass-to-forb ratios, which can vary depending on the location, goals, budget, and other factors (Diboll 1997). There is a common belief that these two groups of species differ in competitive ability and morphology (Schramm 1992, Diboll 1997, Kindscher and Fraser 2000). Previous restoration research within the Willamette Valley also indicates that a high grass-to-forb ratio can decrease the abundance of the native forbs sown (Schultz

2001). Nine grasses were used, all of which are perennial, as there are few native annual grasses that are commonly present in Pacific Northwest prairies.

Forbs were split into annual and perennial functional groups. Previous research at Finley NWR has shown annual forbs to have much greater cover than other functional groups in the first year (Clark and Wilson 2005). Because annuals must complete their life cycle in one year, they often grow rapidly and achieve greater height and cover over a shorter time span than perennial species. Many perennial forbs are very small in stature in their first year (pers. obs.). This above ground difference in size may relate to competition for light and thus affect community structure, and so the distinction between annual and perennial forbs was investigated. Nine annual forbs and ten perennial forbs were used.

Seed mixtures

The three functional groups were combined in seven different combinations: each functional group individually (1 FG), each pair-wise combination (2 FG), and all three functional groups together (3 FG) (Table 2.2). In each seed mix (also referred to as "treatment") nine species per replicate were sown together, and the species representing each functional group were chosen randomly. Thus, the one functional group seed mixes were comprised of either all grass (G), annual forb (A), or perennial forb (P) species (because there were only nine grass and perennial forb species the grass and perennial forb species in the one functional group seed mixes were not randomly chosen). The two functional group seed mixes contained four and five randomly chosen species per functional group (the number per functional group chosen randomly). In the three functional group treatment there were three randomly chosen species sown per functional group. An additional control treatment was established; in this treatment no seeds were sown, while all other procedures were kept the same.

The field experiment followed a complete randomized design. Each treatment was replicated eight times for a total of 64 quadrats. The treatment area was tilled prior to seed addition in early November 2005. Seed mixtures were sown within 1 m^2 quadrats, with 1 m buffers between them. Before sowing, quadrats were raked to remove any large clumps of remaining vegetation. Seeds were sown by hand and distributed approximately evenly across the quadrat. Quadrats were lightly raked after sowing to ensure greater seed contact with the soil. A pilot study in 2004-2005 was carried out to determine field establishment rates for each species (Appendix A). To achieve approximately equal numbers of seedlings per species, each species was sown in inverse relation to its 2005 field establishment rate.

The standard replacement series design was chosen for this study. This design keeps density constant while the species and functional group composition changes; thus, any differences in the abundance of the target species can be attributed to the change in composition rather than a change in overall density. Some have criticized the replacement series design because the results can be dependent upon the density chosen (Connolly 1986, Taylor and Aarssen 1989, Snaydon 1991); however, if the plants are sown at a density that attains final constant yield, then abundance becomes independent of density (Connolly 1986, Taylor and Aarssen 1989). Keeping the number of species constant while increasing the number of functional groups eliminates the effect of productivity will increasing with an increase in species diversity, as has been found in previous studies (Spehn et al. 2000).

A pilot study conducted in 2004-2005 was done to determine the density at which final constant yield can be attained in the field (Appendix A). Four representative species were chosen and sown in 1 m^2 plots at the study site at five different densities. The results from this pilot study indicated that the densities used were not great enough to attain constant final yield, thus a higher rate of approximately 1200 seeds/m^2 was used, which corresponds to a sowing rate of 8 lbs/acre. This rate is within the range suggested in the restoration literature for Willamette Valley Prairies (Ridgeline Resource Planning 1999, Heritage Seedlings Inc. 2007).

Single species plots

At the same time the treatment quadrats were sown, single species quadrats were sown to estimate the establishment rates for each species. These quadrats were placed in rows interspersed between the seed mixture treatments. One hundred seeds of each species were sown in 0.25 m^2 quadrats with 1 m buffers between these and the treatment quadrats. Although establishment rates were calculated for many of the species in the pilot study set up in 2004, not all species used in the 2005 study were sown in the pilot study. Species establishment rates are known to vary from year to year (pers. obs.), so the single species plots were also used to estimate establishment rates for the period of the 2005 study.

Data collection

In July of 2006 each quadrat was subsampled with a 0.5 m^2 square quadrat placed in the center. The cover (%) of each sown species was visually estimated with the aid of pre-measured templates. Also recorded were total native cover, which included non-sown native species, total non-native cover, and total cover (native and non-native). Sown species richness was measured as the number of sown species present in the subsample.

Following the cover measurements, two opposite edges of the 0.5 m^2 quadrat were randomly chosen. Within this quadrat all native above ground biomass, including the biomass of unsown native species, within a 10 cm distance from these edges was removed and was separated into functional groups. Biomass was dried for at least 48 h at 20 °C and then weighed to the nearest 0.1 g.

Data analysis

To determine the effect of seed addition on native abundance, the control treatment and the seven seed mixture treatments were compared. This was done using a one-way ANOVA with contrasts, which compared native cover, biomass, and sown species richness in the control treatment to the average values of the seven seed mixture treatments. The linear combination of group means was calculated as the difference between the control and the seven treatments, and the t-ratio was calculated based on the null hypothesis that the difference between the control mean and the treatment means was zero. To determine the effect of the different seed mixture treatments on native abundance, summary statistics were calculated for each measure of performance (cover, biomass, and sown species richness) within each treatment. Such summary results are useful to land managers who need to know which combinations of functional groups are most successful. ANOVAs were performed to determine whether there were any differences in native cover, biomass, and sown species richness between the seed mix treatments, excluding the control. When treatment differences were detected, pair-wise differences were tested with the Tukey multiple comparison method.

To answer question 1, whether one functional group had an effect on the performance of another functional group, actual values of cover, biomass, and species richness of the "response" functional group in the two functional group seed mix were compared to expected values based on the performance in its one functional group treatment. For example, $\tilde{B}_{AP}(A)$, the expected biomass of the annual forb (A) response functional group in the two functional group seed mix AP (annual forbs and perennial forbs) was calculated using the equation:

$$\tilde{B}_{AP}(A) = \left(\sum \frac{B_A(A)}{s_A(A)} \Big/ n \right) \times s_{AP}(A) \ ,$$

where $B_A(A)$ is the biomass of annual forbs in the annual forb seed mix, $s_A(A)$ represents the estimated seedling density in the annual forb seed mix, and n is the number of replicates of the annual forb seed mix; thus, the first half of the equation represents the biomass of annual forbs per seedling averaged over all replicates of that treatment. This was multiplied by $s_{AP}(A)$, the estimated seedling density of annual forbs in the annual forb-perennial forb seed mix, to calculate the expected biomass in the annual forb-perennial forb seed mix. Estimated seedling density in these equations was calculated as the seeding density of each species in the mix multiplied by the average species 2006 establishment rates in the single species quadrats.

Continuing with the previous example, to determine the effect of the perennial forb (P) functional group on annual forb biomass, I calculated $D_{AP}(A)$:

$$D_{AP}(A) = B_{AP}(A) - \tilde{B}_{AP}(A) \, ,$$

where $D_{AP}(A)$ is the difference between $B_{AP}(A)$, the actual biomass of annuals in the annual forb-perennial forb treatment, and the expected yield of annual forbs in the annual forb-perennial forb treatment. Under the null hypothesis, the expected biomass minus the observed biomass is zero, so $D_{AP}(A) = 0$. If $D_{AP}(A)$ is significantly higher than zero, this indicates that annual forbs have more growth when planted with perennial forb species then with planted with only other annual forb species.

Using the equations described above, the three response variables were used to calculate *D* for the cover, biomass, and sown species richness of each functional group in each two functional group seed mix. To determine whether each functional group had an effect on the performance of each other functional group, one-sided t-tests were performed to test the null hypothesis of no difference between *D* and zero. Statistical significance was established at the $\alpha = 0.05$ level.

To answer question two, whether there was a positive relationship between functional group richness and performance, simple linear regression models were created using functional group richness (excluding the control treatment) as the independent variable and cover, biomass, and sown species richness as the dependent variables. Likewise, the relationship between functional group richness and *D*, the difference between observed and expected values of performance, was examined using simple linear regression.

Results

Native plants were significantly more abundant where they were sown (in the treatment plots) than where they remained unsown (the control plots). These results were consistent whether abundance was measured as native cover ($t_{.05, 56}=-3.49$, $p<0.001$), biomass ($t_{.05, 55}=-2.52$, $p<0.01$), or sown species richness ($t_{.05, 56}=-15.1$, $p<0.0001$).

The performance of seed mixture treatments varied depending on the measure of performance. Native cover was not significantly different across any of the seed mix treatments ($F_{6, 49}$ = 2.08, p=0.07), nor was native biomass ($F_{6, 48}$ = 1.33, p=0.26) (Figure 2.1a, b). However, there were significant differences in sown species richness among the seed mix treatments ($F_{6, 49}$ = 5.81, p=0.0001) (Figure 2.1c). Out of a possible nine species sown, the annual forb treatment had the lowest number of sown species establish at 5.9, while the perennial forb-grass treatment had the highest with an average 8.8 sown species per plot.

Question 1: What is the effect of each functional group on the yield of other functional groups?

D, the difference between observed and expected measures, differed significantly from zero in two cases (Table 2.3). Annual forb cover was significantly greater than expected when sown with perennial forbs and with grasses. In most cases *D* was greater than zero, although the high amount of variability between replicate treatments obscured any significant differences between observed and expected measures of performance.

Question 2: Do native cover, biomass, and species richness increase with increasing functional group richness?

There was a positive relationship between both native cover and native biomass and functional group richness (Figure 2.2 a, b). Cover did increase significantly with increasing functional group richness, however the amount of variation explained by functional group richness was low (R^2=0.09, $F_{1, 53}$=5.38, p=0.01). Biomass showed a similar pattern, but the trend was weaker (R^2=0.06, $F_{1,53}$= 3.64, p=0.03). Sown species richness showed no relationship with functional group richness (R^2=0.00, $F_{1,54}$=0.14, p=0.35) (Figure 2.2c).

Similar relationships are evident between the number of functional groups added and the difference between observed and expected yield (*D*) (Figure 2.3). Observed cover increased more than expected with increasing functional group richness, but again the amount of variation explained by functional group richness was low (R^2=0.09, $F_{1, 54}$=5.25, p=0.01). Biomass shows a similar pattern (R^2=0.08, $F_{1, 53}$ =4.56, p=0.02). Species richness again shows no increase in *D* with functional group richness (R^2=0.00, $F_{1, 54}$=0.23, p=0.31).

Discussion

The goal of this study was to understand how interactions between commonly recognized functional groups affect the performance of native species in restored prairie communities. Regardless of any interactions, simply adding seed resulted in an increase in native abundance and diversity, making it apparent that native seed is limited at this site. This is in accord with other studies that have examined the abundance of native species before and after seed addition ((Turnbull et al. 1999, Seabloom et al. 2003). These results are an indication that seed addition is desirable if increased native abundance and diversity are desired at this site. In the seed addition plots, the average ratio of native cover to total cover was 0.38, putting these treatments in the range of a medium-quality prairie, as compared with other upland prairies in the Willamette Valley (Wilson 1996).

The contribution of the different functional group mixtures to native cover and biomass varied, although the lack of significant differences between treatments indicates that no treatment was a clear "winner" in terms of providing the greatest native abundance. The seed mixes containing annual forbs tended to have the highest cover and biomass, which is consistent with previous findings in the Willamette Valley (Clark and Wilson 2005). However, the seed mixture containing only annual forbs had significantly fewer species establish than the perennial forb seed mix and the perennial forb-grass mix, reflecting the competition among annual forbs that led to decreased abundance in this functional group.

Question 1: What is the effect of each functional group on the yield of other functional groups?

Contrary to observations in the Pacific Northwest and Midwest (Schramm 1992, Diboll 1997, Weber 1999, Schultz 2001), grasses did not reduce the yield of annual and perennial forbs. In fact, when grasses were sown with annual forbs, annual forb cover was significantly greater than expected. There are a few possible explanations for these results. First, the grasses that usually pose a competitive threat to diversity in Midwest prairies are warm-season, C4 grasses which reach an appreciable size (up to 2 m) and have dense root systems (Diboll 1997). Grasses in Pacific Northwest prairies, by contrast, are cool-season species, which do not reach the same size as those of the Midwest. Most grasses in this study were quite small when measured in their first year (median height < 10 cm). Furthermore, *Elymus glaucus,* one species which does typically grow larger and flower in its first year and which might have the potential to suppress forbs, failed to germinate in the field or in the lab.

The fact that annual forbs saw increased abundance when sown with grasses and perennial forbs relative to their yield in the one functional group mixtures indicates that overyielding may occur in annual forbs. Overyielding is defined as when "production in mixtures exceeds expectations based on monoculture yields"(Hooper and Dukes 2004), which is evident when crowding from intraspecific neighbors is more intense than crowding from interspecific neighbors (Trenbath 1974, Tilman et al. 1997, Hille Ris Lambers et al. 2004). Such a process is more likely to occur among species of differing functional groups, as they are presumed to use available resources differently (Fargione et al. 2003, Hooper and Dukes 2004), either by utilizing different resources, or by accessing them at different points in time or in space. Although the interactions of other functional groups in this study do not show a significant increase in yield, the overall trend of increased cover and biomass of functional groups when grown with different functional groups indicates that overyielding and complementary resource utilization may be occurring.

Question 2: How does functional group richness affect total yield?

Native cover significantly increased with functional group richness, as expected (Fig. 2.2 a, b). This pattern of increasing productivity with increased functional group richness is consistent with overyielding and resource complementarity (Hooper and Dukes 2004), and is in accord with the patterns observed in answering Question 1. When different species or functional groups are able to capture resources differently, more of the nutrients and other resources in a system are taken up, resulting in an increase in productivity (Hooper 1998, Spehn et al. 2000, Dukes 2001). This result was expected based on the differences in morphology and cover among these functional groups, assumed to underlie differences in resource utilization. However, the actual amount of variation in cover and biomass explained by functional group richness was low, at less than 10%. These results are similar to those of Tilman et al. (1997), who found functional diversity, while a significant predictor, explained only 9% of the variation in plant productivity. They concluded that functional group composition, in particular the presence of legumes and C4 grasses, to be better predictors of plant productivity than functional diversity.

In this study, while functional group richness influenced native plant productivity to some degree, other factors not included in the analysis played a much stronger role. One of these factors could be non-native cover. Non-native species often challenge the establishment of native plants (Society for Ecological Restoration International Science & Policy Working Group 2004, Wilson et al. 2004). The amount of non-native cover varied widely over the area where the experimental plots were located. To determine whether non-native cover played a role in influencing the abundance of native species in these treatments, regression analyses as described above were repeated, this time including the log of non-native cover as a predictor variable in addition to functional group richness. Non-native cover was strongly negatively related to native performance. Together, functional group richness and non-native cover accounted for 43% of variation in native cover ($F_{2, 53}$ =19.94, $p < 0.0001$), while non-native cover alone accounted for 38% ($F_{1, 54}$ = 32.85, $p < 0.0001$). An extra-sum-of-squares F-test indicated that the amount of variation in cover explained by functional group richess was still significant ($F_{1,53}$ =4.75, p=0.03). Non-native cover and functional group richness together explained 23% of the variation in native biomass ($F_{2, 52}$ = 7.63, p=0.001), and non-native cover alone explained 19% of the variation in native biomass ($F_{1, 53}$ = 12.48, p=0.0009). After accounting for exotic cover, functional group richness did not account for any more of the variation in native biomass ($F_{1,52}$=2.45, p=0.12). There was no relationship between non-native cover and sown species richness (R^2=0.03, $F_{2, 53}$ =0.96, p=0.39). Non-native cover was a statistically and biologically important constraint on native cover and biomass, and more important than functional group richness. However, neither functional group richness nor the amount of non-native cover had a bearing on the number of species sown that actually established.

One possible reason that functional group richness did not strongly influence native species abundance is that the *a priori* functional groups were not strongly different in allocation patterns, as assumed. To determine if this was true, a follow-up analysis was performed to determine whether the species in each *a priori* functional group did respond similarly to the seed mix treatments in terms of cover. A multivariate analysis of variance (MANOVA) was carried out to test for significant differences in mean cover values between species in the three functional groups. Average cover was calculated for each species (with the exception of *Elymus glaucus* and *Madia elegans*, two species that did not establish) at each of the three levels of functional diversity (1 FG, 2 FG, and 3 FG). Average cover values were log-transformed to attain a normal distribution of the data. The matrix for analysis was 26 rows × 4 columns, and contained the species in rows, mean cover for each level of functional diversity in three columns, and the functional group identity of each species in the 4^{th} column. Mean cover values at each level of functional group diversity were used as the dependent variables, while the functional group was used as the independent variable. Wilk's lambda (Λ) was used as the test statistic.

The MANOVA indicated there was no significant difference in cover between functional groups (Λ=0.71, $F_{6, 42} = 1.33$, $p = 0.26$). Wilk's lambda is the ratio of unexplained variability to total variability (Kline 2004). Thus, there is a large amount of variability in cover that is not explained by functional group, making functional group identity a poor indicator of above ground abundance. The problem with looking at functional group richness, as Petchey et al. (2004) state, is that "it assumes that species within groups are functionally identical" and that "all pairs of species drawn from different functional groups are equally different" (p. 848). In this case, species within functional groups were not identical in terms of above-ground resource allocation, and the variation in cover within functional groups was great. There was quite a bit of overlap among functional groups in their amount of cover, so it cannot be assumed that functional groups were utilizing space differently. The *a priori* groupings probably represent only weak complementarity.

Considering the results of these experiments, the functional groups defined here do not appear to be very useful in describing species effects on or response to seed mixture treatments. In this study, growth forms were used to define functional groups. While some inter-group competition was exhibited among annual forbs, and increased productivity was observed with functional group richness, growth forms were not strongly related to either of these patterns, indicating that they may not be useful as functional groups. However, functional groups can still be valuable. Functional groups can be useful when the goal is to reduce the number of species in a community to a smaller number of groups for study (Grime et al. 1997a). This may be desired when wanting to predict broad-scale patterns in plant communities, such as successional changes over time, responses to environmental changes (Díaz and Cabido

1997, Lavorel et al. 1999), or the function of species in a community (Boutin and Keddy 1993, Díaz Barradas et al. 1999, Wardle et al. 1999). Also, if groups can be identified on the basis of a few, easily measured traits, and these groups hold up over a range of environmental conditions, functional groups may be useful in predicting patterns of species performance (Díaz and Cabido 1997).

These results indicate that interactions between the functional groups described here do not necessarily have negative results for the success of restorations, at least in Willamette Valley upland prairies. However, I believe care must still be taken in the use of grasses in restoration, as a high grass:forb ratio can lead to reduced establishment of forbs (Schultz 2001). Grasses also been associated with lower forb abundance when sown before forbs (Clark and Wilson 2005). Grass densities may not have been high enough in this study to achieve a negative effect on forb yield. Also, this study only examined yield after one season's growth; different results may be expected over time, as perennial species take more time to reach full growth. Other studies in grassland have found that the relationship between diversity and productivity can vary between years (Hooper and Dukes 2004). However, overall, these results indicate that increased functional group diversity can lead to an increase in the cover and biomass of native species, which would be a positive development in the restoration of prairies in the Pacific Northwest. Possibly more important, however, is the reduction of non-native species at a site to be restored.

Table 2.1. Species used in this study, native to upland prairies in the Willamette Valley of Oregon. Common names are from USDA, NRCS (2007).

Scientific name	Common name	Family
Annual forbs		
Clarkia purpurea ssp. *quadrivulnera*	winecup clarkia	Onagraceae
Clarkia rhomboidea	diamond clarkia	Onagraceae
Collinsia grandiflora	giant blue eyed Mary	Scrophulariaceae
Collomia grandiflora	grand collomia	Polemoniaceae
Gilia capitata	bluehead gilia	Polemoniaceae
Lotus unifoliolatus var. *unifoliolatus*	American bird's-foot trefoil	Fabaceae
Lupinus bicolor	miniature lupine	Fabaceae
Madia elegans	common madia	Asteraceae
Madia gracilis	grassy tarweed	Asteraceae
Perennial forbs		
Achillea millefolium	common yarrow	Asteraceae
Agoseris grandiflora	bigflower agoseris	Asteraceae
Aquilegia formosa	western columbine	Ranunculaceae
Eriophyllum lanatum	common wooly sunflower	Asteraceae
Ligusticum apiifolium	celeryleaf licorice-root	Apiaceae
Lupinus albicaulis	sicklekeel lupine	Fabaceae
Potentilla glandulosa	sticky cinquefoil	Rosaceae
Potentilla gracilis	slender cinquefoil	Rosaceae
Prunella vulgaris var. *lanceolata*	lance selfheal	Lamiaceae
Sidalcea campestris	meadow checkerbloom	Malvaceae
Grasses		
Bromus carinatus	California brome	Poaceae
Bromus sitchensis	Alaska brome	Poaceae
Danthonia californica	California oatgrass	Poaceae
Elymus glaucus	blue wildrye	Poaceae
Elymus trachycaulus	slender wheatgrass	Poaceae
Festuca californica	California fescue	Poaceae
Festuca roemeri	Roemer's fescue	Poaceae
Koeleria macrantha	prairie Junegrass	Poaceae
Poa secunda	Sandberg bluegrass	Poaceae

Table 2.2. Seed mixture treatments used in this study. Sowing treatments consisted of either 1 functional group (1FG), two functional groups (2FG), or all three functional groups (3FG). Letters indicate which functional groups were sown in that treatment. A=annual forbs, P=perennial forbs, G=grasses.

1 FG	**2 FG**	**3 FG**
A	AP	APG
P	AG	
G	PG	

Table 2.3. Average values of *D*, the difference between actual and expected cover, biomass, and species richness in all seed mixture treatments. Numbers in parentheses indicate the standard deviation. Functional groups in seed mixtures are represented by the following letters: A=annual forbs, P=perennial forbs, G=grasses. Values of *D* are separated into three groups corresponding to the "response" functional group in parentheses. T-tests were performed to determine if *D* for the response functional group was significantly different from zero; *p<0.05.

	A	**P**	**G**	**AP**	**AG**	**PG**
D(A)						
cover	0.02			6.81*	12.55*	
	(9.66)			(6.78)	(11.26)	
biomass	0.01			5.73	4.34	
	(4.36)			(10.01)	(5.25)	
richness	0.00			-0.06	0.44	
	(1.36)			(0.95)	(0.85)	
D(P)						
cover		-0.21		0.78		2.22
		(6.03)		(5.49)		(5.93)
biomass		0.09		-0.25		0.77
		(3.79)		(2.06)		(3.19)
richness		0.00		0.19		-0.06
		(0.64)		(0.54)		(0.71)
D(G)						
cover			-0.01		1.65	1.76
			(9.90)		(4.78)	(7.12)
biomass			-0.01		-0.66	0.18
			(8.84)		(1.38)	(3.69)
richness			0.00		-0.25	0.40
			(1.04)		(0.77)	(0.72)

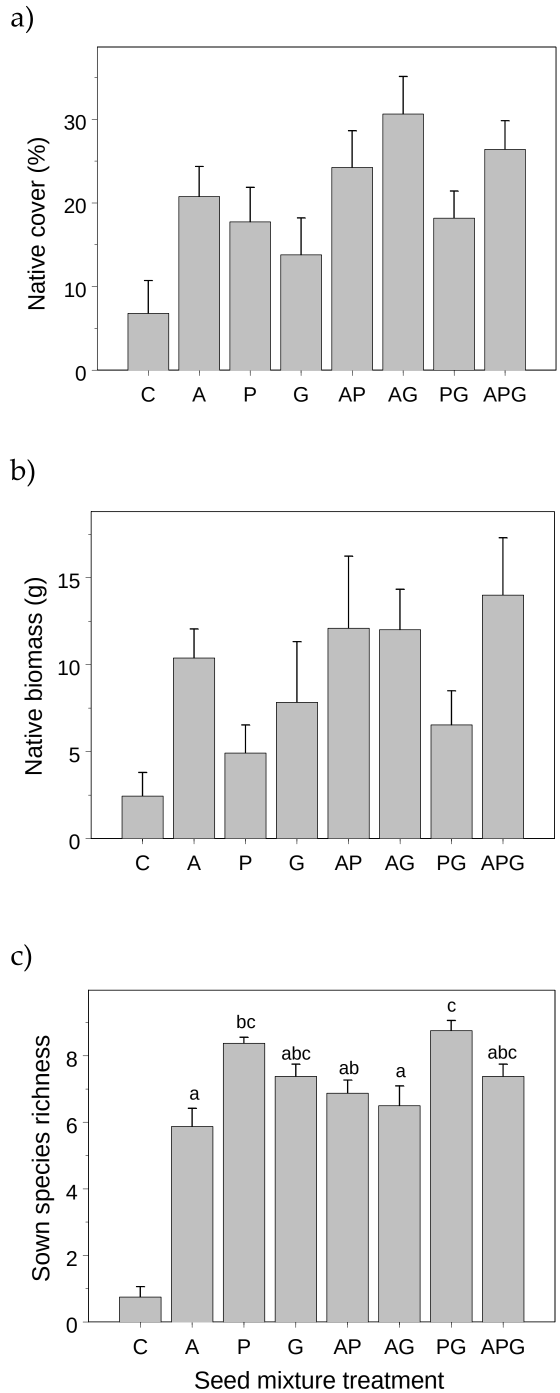

Figure 2.1. Average a) native cover, b) native biomass, and c) sown species richness in all seed mixture treatments (x axis). A=annual forbs, P=perennial forbs, G=grasses. Error bars indicate standard errors. Multiple comparison tests for differences in treatment means did not include the control treatment. Bars with different letters indicate significant differences in means.

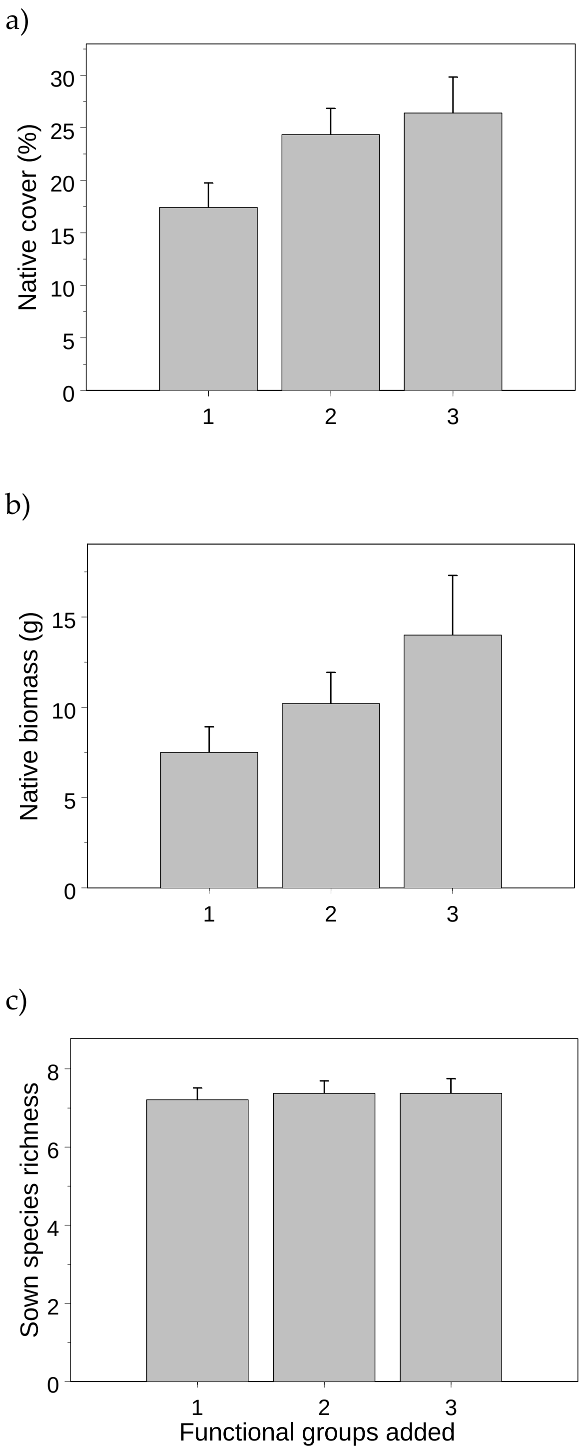

Figure 2.2. Mean total native a) cover, b) biomass, and c) sown specie richness with increasing functional group richness. Error bars indicate standard errors.

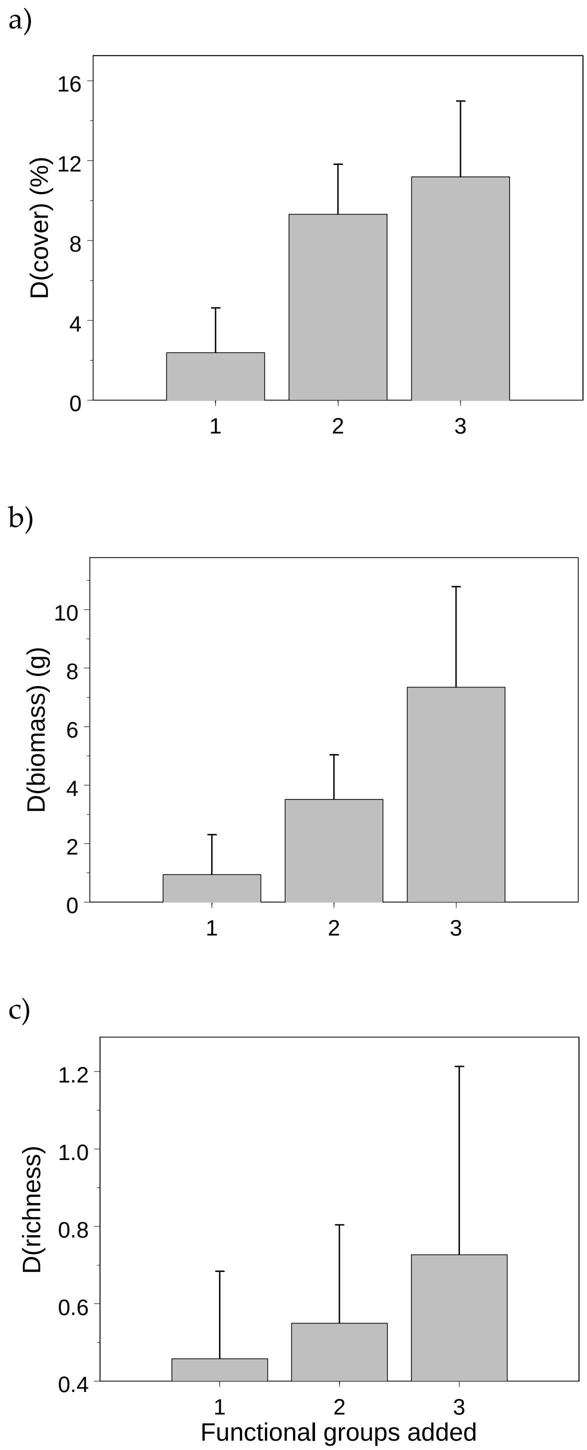

Figure 2.3. Difference between observed and expected (D) a) native cover, b) native biomass, and c) native sown species richness versus the number of functional groups added. Error bars indicate standard errors.

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Chapter 3 : Traits, neighbors, and species performance

Introduction

The goal of many ecological restoration projects is to increase the abundance of native vegetation and the number of native plant species present at a site, often to achieve vegetation structure similar to historic communities (Howell and Jordan 1991, Lockwood 1997, Society for Ecological Restoration International Science & Policy Working Group 2004). Because native seeds may be limited in degraded sites, it is often necessary to add seeds of the desired species (Turnbull et al. 1999, Seabloom et al. 2003). Species sown in restoration attempts show a range of establishment abilities, from dependable and easy to establish, to unable to establish at all (Howell and Kline 1994, Lockwood 1997).

Why some species are strong performers while others are more difficult to establish in a restoration is largely unknown (Howell and Kline 1994). A comparative analysis that examines the differences in traits between plant species is one way to investigate variation in performance (Grime and Hunt 1975, Keddy 1992, Grime et al. 1997b, Weiher et al. 1999). Simply, a plant trait is "any attribute that has potentially significant influence on establishment, survival, and fitness" (Reich et al. 2003b). These are characteristics that relate to species' patterns of growth and allocation, and that evolved in response to abiotic environmental conditions and interactions with other species (Reich et al. 2003b). When the same traits are measured among many different species grown under standardized conditions, they can be a useful tool for comparing these species (Grime and Hunt 1975, Hunt 1982).

There has been increasing interest in the use of plant traits for predicting the performance of species. Traits such as seed size, plant height, biomass, and relative growth rate have been correlated with the success of seedlings in greenhouse competition experiments, although the results often depend on the identity of neighbor plants (Goldberg and Landa 1991, Leishman 1999). Identifying traits that are associated with competitive success makes it possible to predict performance (Freckleton and Watkinson 2001, Moles and Westoby 2002), as well as look at the relationship between dominant traits and environmental variables between different sites (Díaz et al. 1999, Weiher et al. 1999). Traits have been correlated with plant strategies (Weiher et al. 1999, Craine et al. 2001, Carlyle and Fraser 2006); they can also determine species responses to particular environmental conditions such as shade and drought (Suding et al. 2003).

This study set out to determine whether traits, measured from both lab and field-grown plants, can be related to the performance of species in a restoration setting. Twenty-eight species native to upland prairies in the Willamette Valley of Oregon were sown in experimental field plots. Traits of each species were measured in field and laboratory-grown seedlings. I divided species into three functional groups: annual forbs, perennial forbs, and grasses. These *a priori* functional groups were identified to determine whether functional group identity is a trait related to performance and whether the relationship between traits and performance depends on functional group, as the relationship of traits to performance may vary depending on the life history or strategy of a species (Carlyle and Fraser 2006). The context in which a seedling grows can also affect performance (Leishman 1999, Symstad 2000, Fargione et al. 2003), so I also wanted to determine whether the functional group of neighbors influences what traits are related to performance. Species were sown into seven different mixtures representing all combinations of functional groups to test whether different neighbors influence what traits are associated with performance. In this study I addressed three main questions:

1) Are traits related to the performance of species in restoration?
2) Are the relationships between traits and performance consistent across functional groups?
3) Do the relationships between traits and performance depend on neighbor functional groups?

Performance for each species was assessed by cover (%) and frequency of occurrence in quadrats where sown. Using stepwise techniques, multiple regression analyses were used to relate traits, including functional group identity, and sowing treatment as predictor variables to performance in experimental quadrats. These models can be tested in future studies to determine their predictive power, and can potentially be useful in helping land managers understand field performance of species native to upland prairies in the Willamette Valley and perhaps elsewhere.

Methods

Study site

The study site is located at the William H. Finley National Wildlife Refuge (hereafter, Finley NWR) (44°N, 123°W), approximately 10 miles south of Corvallis in the Willamette Valley of Oregon. The site was previously used to grow forage for wildlife, but the present goal is to restore upland prairie habitat, eventually sustaining populations of the federally threatened Kincaid's lupine (*Lupinus sulphureus* ssp. *kincaidii*) and its associated federally endangered species Fender's blue butterfly (*Icaricia icarioides fenderi*). A matrix of native grasses was sown in 2002 and an assortment of non-native grasses and forbs are also present. The exotic perennial grasses *Anthoxanthum odoratum* and *Agrostis stolonifera* are abundant, while exotic forbs such as *Hypochaeris radicata* and *Hypericum perforatum* are also common at the site. The soil type is mapped as Santiam silt loam, 2-8% slopes (NRCS 2007).

Species and functional group selection

Three functional groups were defined *a priori*: grasses, annual forbs, and perennial forbs. Nine species were sown in both the annual forb and grass functional groups, and ten in the perennial forb functional group, for a total of 28 species sown in this study (Table 3.1). Seeds were obtained from local native seed vendors.

Functional groups were identified based on differences in life history, structure, and potentially competitive ability. Annual forbs, typically ruderal species, tend to have rapid growth, achieving a large amount of above-ground biomass in competition for light (Grime 1977). Previous research at Finley NWR has shown annual forbs to have much greater cover in the first year than other functional groups (Clark and Wilson 2005). The presence of annual forbs as neighbors may alter how traits are associated with cover and probability of establishment. Perennial forbs are usually much smaller in stature and slower growing than annual forbs (pers. obs.). Their differences in growth form and reproductive strategy indicates that they may be different in the traits that confer success. Grasses have a very different growth form from forbs and can be more abundant (Craine et al. 2001) and more competitive (Kindscher and Fraser 2000, Clark and Wilson 2005).

Seed mixture treatments

The three functional groups were combined in seven different seed mixtures (also referred to as "treatments"): each functional group individually (1 FG), each pair-wise combination (2 FG), and all three functional groups together (3 FG) (Table 3.2). In each seed mix nine species per replicate were sown together, and the species representing each functional group were chosen randomly. Thus, the one functional group treatments were comprised of either all grass (G), annual forb (A), or perennial forb (P) species (because there were only nine grass and perennial forb species the grass and perennial forb species in the one functional group treatments were not randomly chosen). The two functional group treatments contained four and five species per functional group (the number per functional group chosen randomly). In the three functional group treatment there were three species sown per functional group. An additional control treatment was established; in this treatment no seeds were sown, while all other procedures were the same.

The field experiment followed a complete randomized design. Each treatment was replicated eight times for a total of 64 quadrats. Seed mixtures were sown within 1 m^2 quadrats, with 1 m buffers between them. A pilot study in 2004-2005 was carried out to determine field establishment rates for each species (Appendix A). To achieve approximately equal numbers of germinants per species, each species was sown in inverse relation to its 2005 field germination rate. The treatment area was tilled prior to seed addition in early November 2005. Before sowing, quadrats were raked to remove any large clumps of remaining vegetation. Seeds were sown by hand and distributed approximately evenly across the quadrat. Quadrats were lightly raked after sowing to ensure greater seed contact with the soil.

The standard replacement series design was chosen for this study. This design keeps density constant while the species and functional group composition changes; thus, any differences in the abundance of the target species can be attributed to the change in composition rather than a change in overall density. Some have criticized the replacement series design because the results can be dependent upon the density chosen (Connolly 1986, Taylor and Aarssen 1989, Snaydon 1991); however, if the plants are sown at a density that attains final constant yield, then abundance becomes independent of density (Connolly 1986, Taylor and Aarssen 1989). Keeping the number of species constant while increasing the number of functional groups eliminates the possibility that productivity will increase with an increase in species diversity, as has been found in previous studies (Spehn et al. 2000).

A pilot study conducted in 2004-2005 was done to determine the density at which final constant yield can be attained in the field (Appendix A). Four representative species were chosen and sown in 1 m^2 plots at the study site at five different densities. The results from this pilot study indicated that the densities used were not great enough to attain constant final yield, thus a higher rate of approximately 1200 seeds/m^2 was used, which corresponds to a sowing rate of 8 lbs/acre. This rate is within the range suggested in the restoration literature for Willamette Valley Prairies (Ridgeline Resource Planning 1999, Heritage Seedlings Inc. 2007).

Single-species plots

At the same time the seed mixture quadrats were sown, single-species quadrats were also sown to monitor the performance of each species grown separately in the absence of interspecific competition and to measure field-based traits. These quadrats were situated in rows interspersed with the functional group treatments in a completely randomized design with four replicates per species. One hundred seeds of each species were sown in 0.25 m^2 quadrats with 1 m buffers between them.

Field measurements of performance

In July of 2006, at the peak of the growing season, each quadrat was subsampled with a 0.5 m^2 square quadrat placed in the center. The cover (%) of each sown species and each functional group was visually estimated and with the aid of pre-measured templates. Final cover for each species in each quadrat was calculated as the estimated cover minus the average background cover in the control plots. A species was determined to be present based on whether it was sown and present in the 0.5 m^2 subsample.

Plant trait measurements

Seedlings of each species were grown in a growth chamber to determine standardized plant traits of specific leaf area, leaf area, leaf weight ratio, above ground biomass, below ground biomass, relative growth rate, and unit leaf rate (Table 3.3). Seed mass was also measured. These traits are thought to influence establishment and the occupation of space (Weiher et al. 1999). Relative growth rate and unit leaf rate are considered "hard" traits, because they are difficult to measure, involving multiple measurements over a period of time. In contrast, seed mass, specific leaf area, leaf weight ratio, and measures of biomass are considered "easy" or "soft" traits, because they are easier to measure, but yet still are related to the biology of the species under study (Weiher et al. 1999, Díaz et al. 2004). They may be highly correlated with other hard traits, thus, they can stand in for more difficult measures of species performance.

For example, seed mass has been correlated with both seedling growth and longevity (Weiher et al. 1999), and because it is relatively easy to measure, it is a preferred trait for measurement.

Seeds were germinated on quartz sand in transparent germination boxes (11.8 x 11.8 x 2.8 cm) according to each species' requirements. As soon as possible after germinating, seedlings were transplanted and grown in a growth chamber under standardized conditions (Hendry and Grime 1993). Seedlings were planted into washed sand in individual cells (27.7 mL) of plug sheets (Landmark™ 98PSP vented) placed in plastic trays. A fine mesh material was placed at the bottom of each cell to prevent sand from escaping. Plants were fertilized 3 times a week with 5 mL of Hoagland's solution (either the 1938 or 1950 solution) (Hoagland and Arnon 1950). Additional water was added to the trays as necessary to prevent the sand from drying out. Light irradiance was 125 ± 10 μmol m^{-2} s^{-1} equivalent to 29 W m^{-2}. Other details of the growing conditions follow Hendry and Grime (1993).

Replicate seedlings of each species were grown for either 7 or 21 days and then harvested. Leaves were separated from the stem, placed flat on a transparency and scanned at a resolution of 600 dpi. Leaf, stem, and root biomass were separated and dried at 80 °C for at least 48 hours prior to weighing. Leaf area was measured using the image analysis software Assess (Lamari 2002).

The two field measurements of plant traits were carried out on plants in the single-species plots. Height in 1st year was measured in July 2006 at the peak of the growing season. Up to 4 plants were randomly selected from each single species quadrat for measurement. Average height was calculated for each quadrat and the mean of the quadrat averages was used in the final analysis. Exceptions were for *Agoseris*, which did not germinate in the single species plots; its height was measured where present in the treatment plots. *Elymus glaucus* usually germinates well in the field and lab, but failed to germinate at all in this experiment. Because of this abnormal behavior this species was removed from the analysis. *Madia elegans* did not germinate in either the single species or treatment plots, and had 100% mortality in the growth chamber, preventing calculation of its traits, so it was removed from the analysis. Field establishment rate was calculated as the total number of plants present in April 2006 per number of seeds sown.

Timing of germination was also monitored to determine what season established seedlings germinated. In December 2005, February 2006, and May 2006, the single species plots were monitored to look for fall, winter, and spring germinants, respectively. A 0.25 m^2 quadrat was placed in the center of the 0.5 m^2 quadrat and germinants were marked within this subsample. At each census, new germinants were marked with a colored toothpick, with different colors representing different seasons. At the final May census, all existing seedlings, considered established, were counted and the season when marked was noted. Time to germination was calculated as the average number of days after sowing that established seedlings germinated. Because some species failed to germinate in the single species quadrats, data was incomplete, so time to germination was not included in the analysis.

Data structure and analysis

S-Plus 7.0 (2005) was used for all analyses. The spreadsheet used for data analysis was constructed so that each row represented a single species in a single quadrat, and columns indicated the performance variables, treatment, and traits (similar to the abundance-environment-attribute list of Nygaard and Ejrnæs (2004)). In this way, treatment, traits, and species' abundances could be integrated in a single data sheet.

Two response variables were defined: species cover, when present, and presence/absence (1/0). This was done because the distribution of the cover data was bimodal, with a second peak indicating the replicates with zero cover. No transformations of the data created a normal distribution required for the analysis, so the positive cover values were separated and analyzed separately.

To determine which traits were most strongly related to the cover of species in restoration, traits, including functional group, and treatments were used as predictor variables in linear regression analyses, while cover of each species was the response variable. The same predictor variables were used to relate the frequency of occurrence with species traits, creating logistic regression models, using entire data set for analysis, and presence/absence as the response variable.

Prior to fitting the linear and logistic regression models, the distribution of each explanatory variable was examined to determine whether transformation was necessary to reduce skewness. The variables leaf area, above ground biomass, below ground biomass, seed mass, height, and field establishment rate were log-transformed. Because some species did not germinate in the single species plots, 0.1 was added to each value of field establishment rate so that values of zero could be log-transformed. For the linear regression analysis, after the positive cover values were separated the data was log-transformed to reduce skewness.

For both the linear and logistic models, preliminary steps were taken to reduce the possibility of collinearity between the explanatory variables, and thus reduced the number of terms in the saturated model. Because the values for 7- and 21-day-old were highly correlated for the traits specific leaf area, leaf area, and leaf area ratio, aboveground biomass, and belowground biomass, (Pearson's r=0.66-0.81), only the values for 7-day-old seedlings for these variables were used in the analysis.

The stepAIC procedure in the MASS library in S-Plus 7.0 was used to create linear regression models that related the strongest combination of predictor traits to the response variables. With stepAIC, a full model is specified which includes all candidate explanatory variables. Schwarz's Bayesian Information Criterion (BIC) was used to determine which variables were included in the final model. This criterion balances the increased explanatory power of more variables with a penalty for model complexity and sample size (Ramsey and Schafer 2002). The direction of the stepwise procedure was a combination of forward and backward.

Logistic regression was used to determine the probability a species will be present in the first spring following sowing. The full data set, with the exception of *Elymus glaucus* and *Madia elegans,* was used in the analysis. As in the multiple linear regression analysis, stepAIC was used to create the logistic regression models. After predictor variables were selected using this procedure, the generalized linear models were created using a quasi-likelihood approach, with a logit link function and variance μ (1-μ). The binomial distribution assumes that the variance in the deviance residuals is one, but if this variance greater than one, a model fit assuming a quasi distribution accounts for any extra-binomial variation by adjusting the standard errors of the parameters. Examination of the Pearson residuals revealed three data points with excessively large residual values, which were removed from the analysis. The model was then fit using the Design and Hmisc libraries in S-Plus, and the goodness of fit of the model was assessed using the le Cessie van Houwelingen-Copas-Hosmer unweighted sum of squares test, which tests the null hypothesis that the reduced model is correct. Wald's tests were used to test the significance of each parameter selected for the final model, and Nagelkerke's R^2 index was used to approximate the strength of the logistic regression model.

Analyses related to questions

For both the linear and logistic analyses, the following questions were posed and accompanying procedures were performed:

1) Are traits related to the performance of species in restoration?

To answer this question, traits were used as predictor variables in the stepwise regression. Indicator variables for annual forbs and perennial forbs were used to represent species in these functional groups. A "block" variable, representing each quadrat, was included to account for variation within each quadrat.

2) Are the relationships between traits and performance consistent across functional groups?

For this question, the indicator variables for annual forbs and perennial forbs were included in the model as interaction terms. If any interaction terms are selected by the stepwise procedure, this indicates that there is a different relationship between the trait and cover within species of that functional group that should be accounted for when predicting performance.

3) Do the relationships between traits and performance depend on neighbor functional groups?

To answer this question, indicator variables representing each one functional group and two functional group treatment (Table 3.2) were included in the model as interaction terms. Instead of including the block variable, as in the previous two models, a "replicate" variable was included to account for variation between replicates of each treatment.

Results

Species traits

The traits measured in this study were largely comparable to estimates found in previous studies (Table 3.4). The values of relative growth rate were similar to other estimates among herbaceous plants (Hunt and Cornelissen 1997). Overall, variation within groups was high. This high variation between species within *a priori* functional groups has also been seen in previous studies (Reich et al. 2003a). Average values for each species are listed in Appendix B.

Variation in the estimates of cover and frequency of establishment was also high (Table 3.5). Standard deviations of cover estimates for each functional group were greater than mean cover values for all functional groups. Annual forbs tended to have greater cover than perennial forbs and grasses, although establishment frequency was less among annual forbs than among species in other functional groups.

Traits related to cover

1) Are traits related to the performance of species in restoration?

In the linear regression analyses, stepwise regression indicated that several traits were related to performance. The variables height, field establishment rate, leaf weight ratio (7 and 21 days), seed mass, and the indicator variable for perennial forbs gave the lowest BIC, explaining 50.5% of the variation in cover (Table 3.6) ($F_{6,365} = 62.1$, $p<0.0001$).

2) Are the relationships between traits and performance consistent across functional groups?

When functional groups and their interactions were included in the full multiple regression model, the final model contained interaction terms between perennial forbs and leaf weight ratio (7 days) and seed mass (Table 3.6), indicating that the relationships between traits and performance are not consistent across functional groups. The final model explained 54.2% of the variation in cover ($F_{8, 363} = 53.6$, $p<0.0001$).

3) Do the relationships between traits and performance depend on neighbor functional groups?

Indicator variables for the annual forb and grass functional groups in the final model are a sign that the identity of neighbor species does influence cover (Table 3.6). The interaction term between leaf weight ratio (7 days) and the annual forb functional group indicates that the relationship between traits and cover also depends on the neighbor functional group present. The final model is very similar to the model created for Question 1, except the indicator variable for perennial forbs is removed and unit leaf rate was included. This model explained 56.3% of the variation in cover ($F_{9, 362}$ = 51.8, p<0.0001).

Traits related to establishment

1) Are traits related to the performance of species in restoration?

In the logistic regression analyses, the stepwise procedure indicated the traits establishment rate, unit leaf rate, leaf weight ratio (21 days), and the indicator variable for annual forbs were significant predictors of the frequency of establishment (Table 3.7). One outlier was removed from the analysis. The le Cessie van Houwelingen-Copas-Hosmer test statistic (Z) indicated that final model was well fit (Z=-1.32, p=0.188). All predictor variables were significant below the 0.05 level according to the Wald's statistics. These results indicate that traits are related to frequency of establishment.

2) Are the relationships between traits and performance consistent across functional groups?

Significant interaction terms between annual forbs and the variables unit leaf rate and relative growth rate indicate that trait relationships with establishment frequency are not consistent across functional groups. When interaction terms for annual forbs and perennial forbs were included in the full model, stepwise procedures indicated that relative growth rate and leaf weight ratio at 7 days should be included in the model, while the leaf weight ratio at 21 days should be removed (Table 3.7). The Nagelkerke R^2 value indicates this model is stronger than the model without interaction terms. The goodness of fit statistic also indicates that this model fits the data ($Z=-1.50$, $p=0.133$).

3) Do the relationships between traits and performance depend on neighbor functional groups?

When stepAIC was performed with the full model including interaction terms between traits and treatments, the variables selected for the final model were the same as those in the initial model containing no interaction terms (Table 3.7). Thus, there is no evidence to indicate that the identity of neighbors influenced establishment in this study.

Discussion

Questions

1) Are traits related to the performance of species in restoration?

Many of the traits measured on laboratory and field grown seedlings were strongly related to the performance of native species in the field. The amount of variation in cover explained by these traits was high—over 50% for all models. Several of the significant traits relating traits to cover in this study were also significant in explaining native cover in a previous study of Willamette Valley species (Goodridge 2002). In that research laboratory germination rate was significant in explaining upland species cover, while leaf weight ratio (21 days) and unit leaf rate were significant predictors of the cover of wet prairie species. These traits were also included in the logistic model predicting establishment frequency. The fact that these traits have been repeatedly included in regression models indicates that these traits are likely to be reliable predictors of species performance in the field.

Perhaps not surprisingly, field germination rate is strongly related to both cover and frequency of establishment. The more seedlings of a given species establish, the more likely it is to both occur in a plot, and the greater cover that species will have. This pattern has been found in previous studies (Pywell et al. 2003). Several of the other variables in the models are related to aboveground biomass. A species' height in its first year was strongly related to cover. This may have to do with competition for light with neighbors. Leishman (1999) found height positively related to survival among adult neighbors, although in this case height was related to cover, not establishment rate. Leaf weight ratio, the ratio of seedling leaf weight to total weight, is a measure of the "leafiness" of a seedling; hence, the more a species allocates to its leaves, the more cover it will have in a given plot.

Height, establishment rate, and leaf weight ratio are all associated with the capture of light and above ground space (Weiher et al. 1999). These traits are associated with an early successional strategy (Huston and Smith 1987). A strategy of above ground resource capture is favored when light becomes abundant, such as following disturbance (Grime 1977). The study site was tilled prior to sowing, providing the perfect conditions for competition for light. In the models relating traits with establishment frequency, the indicator value for annual forb functional group identity was highly significant. Annual forbs are often ruderal species which perform well following disturbance (Weiher et al. 1999), so the positive relationship between annual life history and establishment also makes sense in light of ecological theory.

2) Are the relationships between traits and performance consistent across functional groups?

The significant interaction terms between perennial forbs and both seed mass and leaf weight ratio indicate the relationship between traits and performance differs depending on the functional group of a species. For example, considering all traits, leaf weight ratio was less strongly related with cover among perennial forbs than among annual forbs and grasses (Figure. 3.1), suggesting that this trait may be less important for land managers to consider if wanting to produce more perennial forb cover in the first year of restoration. Perennial forbs also had a more negative relationship between seed mass and cover relative to other functional groups (Figure 3.2). When looking at the relationship between traits and frequency of establishment, differential patterns were found depending on whether the species was an annual forb.

Among annual forbs, increasing both unit leaf rate and relative growth rate means a decrease in the frequency of establishment, relative to perennial forbs and grasses. It is difficult to interpret the relationship between individual traits and abundance, since many of these traits are partially correlated and cannot be separated from each other. However, the different patterns found may point to differences in strategies between functional groups. The same trait may have different value depending on whether a species must flower and set seed soon, or whether it must grow roots to survive the dry season (Pywell et al. 2003).

3) Are the relationships between traits and performance consistent across neighbor functional groups?

While the identity of neighbor species was not found to influence which traits predict establishment, the functional group identity of neighbor species did play a role in the relationship between traits and cover. When treatments, representing the functional groups present, are added as interaction terms to the linear regression model, it appears that annuals and grasses growing with individuals of their own functional group showed a decrease in cover compared with other treatments. This greater intragroup competition has been found in previous field research (Fargione et al 2003). Annual forbs with a greater leaf weight ratio at 7 days have a leg up over other annual forbs, perhaps because they are able to capture more resources at an early stage than annual forb species that allocate less to leaves at this stage.

Relationships between traits and performance

Other studies have also been successful in relating species traits and performance. Many studies looking at the relationship between traits and performance using simple linear regression models have found the variance in abundance explained by individual traits to vary widely, with R^2 from 0.03 to 0.88 (Reader 1998, Leishman 1999, Austrheim et al. 2005, Fargione and Tilman 2006). Fewer studies have tried to find the best combination of traits that relate to performance, as in this study, however Reader (1998) found three traits together explained 99% of the variance in relative abundance. The predictive ability of models such as these are not often tested; however, models that have been tested have shown that traits can have strong predictive power (Freckleton and Watkinson 2001, Moles and Westoby 2002). There has been little research relating traits to performance in restoration (Pywell et al. 2003). However, there is increasing interest in using traits to aid in restoration and conservation planning, as attested by the number of trait databases now available for this purpose (Fitter and Peat 1994, Knevel et al. 2003, Gachet et al. 2005, Wilson 2006, Koike 2007).

Implications for further work

This research is a first step towards the creation of models that can be used to predict the performance of species in restoration. Next, these models should be tested on an independent data set to determine how well they predict the cover and establishment probabilities of other species and at other sites. Different sites may favor different traits, as conditions such as precipitation, temperature, pH, and nutrient levels may influence what traits are successful (Kahmen & Poschlod 2004). Year to year variation in temperature and precipitation can have dramatic effects on the performance of species, and may affect different species in different ways (pers. obs.) I encourage other researchers to carry out similar research at other sites so that the relationships between traits and species performance can be better understood.

Table 3.1. Species used in this study, native to upland prairies in the Willamette Valley of Oregon. Common names are from USDA, NRCS (2007).

Scientific name	Common name	Family
Annual forbs		
Clarkia purpurea ssp. *quadrivulnera*	winecup clarkia	Onagraceae
Clarkia rhomboidea	diamond clarkia	Onagraceae
Collinsia grandiflora	giant blue eyed Mary	Scrophulariaceae
Collomia grandiflora	grand collomia	Polemoniaceae
Gilia capitata	bluehead gilia	Polemoniaceae
Lotus unifoliolatus var. *unifoliolatus*	American bird's-foot trefoil	Fabaceae
Lupinus bicolor	miniature lupine	Fabaceae
*Madia elegans**	common madia	Asteraceae
Madia gracilis	grassy tarweed	Asteraceae
Perennial forbs		
Achillea millefolium	common yarrow	Asteraceae
Agoseris grandiflora	bigflower agoseris	Asteraceae
Aquilegia formosa	western columbine	Ranunculaceae
Eriophyllum lanatum	common wooly sunflower	Asteraceae
Ligusticum apiifolium	celeryleaf licorice-root	Apiaceae
Lupinus albicaulis	sicklekeel lupine	Fabaceae
Potentilla glandulosa	sticky cinquefoil	Rosaceae
Potentilla gracilis	slender cinquefoil	Rosaceae
Prunella vulgaris var. *lanceolata*	lance selfheal	Lamiaceae
Sidalcea campestris	meadow checkerbloom	Malvaceae
Grasses		
Bromus carinatus	California brome	Poaceae
Bromus sitchensis	Alaska brome	Poaceae
Danthonia californica	California oatgrass	Poaceae
Elymus glaucus	blue wildrye	Poaceae
Elymus trachycaulus	slender wheatgrass	Poaceae
Festuca californica	California fescue	Poaceae
Festuca roemeri	Roemer's fescue	Poaceae
Koeleria macrantha	prairie Junegrass	Poaceae
Poa secunda	Sandberg bluegrass	Poaceae

*0% field germination and mortality in lab prevented determination of traits.

Table 3.2. Seed mixture treatments used in this study. Sowing treatments consisted of either 1 functional group (1FG), two functional groups (2FG), or all three functional groups (3FG). Letters indicate which functional groups were sown in that treatment. A=annual forbs, P=perennial forbs, G=grasses.

1 FG	**2 FG**	**3 FG**
A	AP	APG
P	AG	
G	PG	

Table 3.3. Traits measured, their relevance to establishment and performance, the sources indicating each trait's relevance, and how traits were measured or calculated. *A* = area, *W* = dry weight, *L* = leaf, *R* = root, *S* = shoot (leaf + stem), *T*=total plant; subscripts 1 and 2 indicate initial time (7 days) and time 2 (21 days) of measurement, respectively. *Indicates traits measured for both 7- and 21-day-old seedlings.

Trait	**Relevance**	**Citation**	**How measured**
	Growth chamber measurements		
Seed mass	Seedling resources	Leishman 2001	Mean seed mass (measured in batches of 20-100)
Specific Leaf Area* (SLA)	Quickly grown, low density tissue	Craine et al. 2001	$\frac{L_A}{L_W}$
Leaf area* (LA)	Light interception	Goodridge 2002	L_A
Leaf Weight Ratio* (LWR)	Biomass allocation to leaves; light capture	Goodridge 2002	$\frac{L_W}{T_W}$
Above ground biomass*	Light capture	Weiher et al. 1999	S_W
Below ground biomass*	Nutrient uptake	Boot 1989	R_W
Root:shoot ratio*	Nutrient uptake	Boot 1989	$\frac{R_W}{S_W}$
Relative growth rate (RGR)	Rate of resource acquisition	Grace 1990	$\frac{\log_e T_{W_2} - \log_e T_{W_1}}{t_2 - t_1}$
Unit leaf rate (ULR)	Photosynthetic efficiency	Goodridge 2002	$\frac{T_{W_2} - T_{W_1}}{t_2 - t_1} * \frac{\log_e L_{A_2} - \log_e L_{A_1}}{L_{A_2} - L_{A_1}}$
	Field measurements		
Height in 1st year	Light interception	Weiher et al. 1999	Measured at time of flowering
Field establishment rate	Colonization ability	Pywell et al. 2003	Counted in spring in monoculture plots

Table 3.4. Average trait values of annual forbs, perennial forbs, and grasses. Numbers in parentheses indicate standard deviations. See Table 3.2 for trait descriptions.

Trait	**Annual forbs**	**Perennial forbs**	**Grasses**
Seed mass (mg)	1.64 (1.38)	4.63 (9.93)	3.18 (2.28)
SLA 7 (mm^2/mg)	34.3 (17.1)	43.1 (21.4)	36.2 (12.6)
SLA 21 (mm^2/mg)	43.2 (12.2)	50.9 (19.1)	35.0 (7.5)
Leaf area 7 (mm^2)	28.1 (23.9)	47.6 (73.3)	33.3 (33.6)
Leaf area 21 (mm^2)	360.7 (243.4)	484.9 (396.3)	461.9 (443.6)
LWR 7 (mg/mg)	0.64 (0.09)	0.67 (0.10)	0.66 (0.11)
LWR 21 (mg/mg)	0.73 (0.05)	0.78 (0.05)	0.79 (0.09)
Above ground biomass 7 (mg)	1.00 (0.87)	3.26 (7.80)	0.89 (0.68)
Above ground biomass 21 (mg)	8.60 (5.34)	15.17 (21.14)	12.46 (10.84)
Below ground biomass 7 (mg)	0.28 (0.21)	0.74 (1.53)	0.35 (0.27)
Below ground biomass 21 (mg)	2.16 (1.48)	3.41 (4.18)	2.51 (1.76)
Root-shoot ratio 7 (mg/mg)	0.41 (0.24)	0.47 (0.23)	0.50 (0.18)
Root-shoot ratio 21 (mg/mg)	0.28 (0.07)	0.24 (0.08)	0.24 (0.11)
RGR (mg/mg*day)	0.164 (0.046)	0.167 (0.050)	0.171 (0.032)
ULR (x 1000) (mg/cm^2*day)	0.46 (0.08)	0.53 (0.16)	0.71 (0.18)
Height (cm)	29.66 (19.20)	10.01 (8.55)	18.67 (23.51)
Field establishment rate (%)	5.72 (4.26)	4.43 (5.40)	4.06 (3.99)

Table 3.5. Mean cover (when present) and establishment frequency for annual forb, perennial forb, and grass species in the seed mixture plots (excluding control). Numbers in parentheses indicate standard deviations.

	Annual forbs	Perennial forbs	Grasses
Cover (%)	6.01 (6.73)	1.84 (2.12)	1.88 (2.62)
Frequency	0.65 (0.48)	0.88 (0.33)	0.86 (0.35)

Table 3.6. Coefficients for the 3 linear regression models relating traits with cover (log transformed). ns: variable not present in final model. --- : variable not part of the analysis. AF=annual forb, PF=perennial forb; *p<0.05, **p<0.01, ***p<0.001, ****p<0.0001. See Table 3.3 for trait descriptions.

	Coefficient		
Variable	**No interactions (R^2=50.5%)**	**FG interactions (R^2=54.2%)**	**Treatment interactions (R^2=56.3%)**
Intercept	- 3.68****	- 2.13*	- 2.76****
Log(Height)	0.97****	0.93****	0.91****
Log(Field establishment)	0.44****	0.44****	0.41****
LWR 7	5.17****	4.66****	4.55****
Log(Seed mass)	- 0.19***	- 0.15**	- 0.17***
ULR	ns	ns	- 0.84*
LWR 21	- 3.15**	- 4.66****	- 2.80**
PF	0.26***	1.56**	ns
LWR 7*PF	---	- 1.89*	---
Log (Seed mass)*PF	---	- 0.15**	---
Grass treatment	---	---	- 0.56***
AF treatment	---	---	- 6.60****
LWR 7*AF treatment	---	---	8.63****
Variables not included in models (excluding interactions)			
SLA 7	ns	ns	ns
Log (LA 7)	ns	ns	ns
Log (Above ground bio. 7)	ns	ns	ns
Log (Below ground bio. 7)	ns	ns	ns
RGR	ns	ns	ns
Root:shoot 7	ns	ns	ns
Root:shoot 21	ns	ns	ns
Perennial forb treatment	---	---	ns
AF+Grass treatment	---	---	ns
AF+PF treatment	---	---	ns
PF+Grass treatment	---	---	ns
Block	ns	ns	---
Replicate	---	---	ns

Table 3.7. Coefficients for the 3 logistic regression models relating traits with frequency of establishment. ns: variable not present in final model. --- : variable not added to full model. * p<0.01, **p<0.001, ***p<0.0001.

	Coefficient		
Variable	**No interactions (R^2=37.0%)**	**FG interactions (R^2=48.9%)**	**Treatment interactions (R^2=37.0%)**
Intercept	- 5.28*	- 9.81***	- 5.28*
Log (Field est.)	2.27***	2.63***	2.27***
Annual functional group	- 2.41***	9.76***	- 2.41***
ULR	- 3.07**	- 2.74*	- 3.07**
LWR 21	8.48**	ns	8.48**
RGR	ns	36.19***	ns
LWR 7	ns	7.16***	ns
ULR*Annual forb	---	- 11.07**	ns
RGR*Annual forb	---	- 31.01*	ns
Variables not included in models (excluding interactions)			
Log (Seed mass)	ns	ns	ns
SLA 7	ns	ns	ns
LA 7	ns	ns	ns
Root:shoot 7	ns	ns	ns
Root:shoot 21	ns	ns	ns
Log (Below ground bio. 7)	ns	ns	ns
Log (Above ground bio. 7)	ns	ns	ns
Log (Height)	ns	ns	ns
Perennial forb	ns	ns	ns
Perennial forb treatment	---	---	ns
Grass treatment	---	---	ns
Annual forb+Grass treatment	---	---	ns
Ann. forb+Per. forb treatment	---	---	ns
Per. forb+Grass treatment	---	---	ns
Block	ns	ns	---
Replicate	---	---	ns

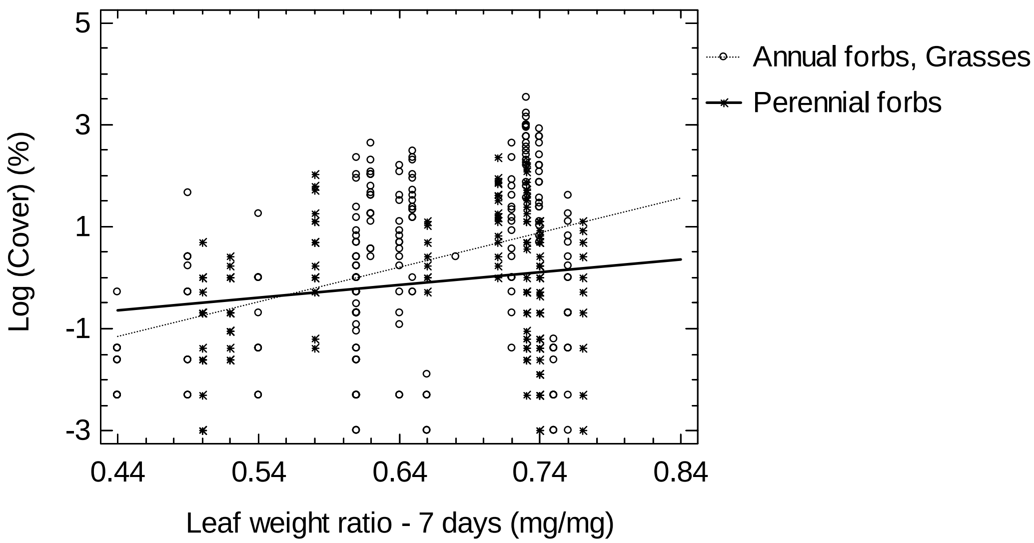

Figure 3.1. Simple linear regression plots showing the different relationship between leaf weight ratio (7 days) and cover between perennial forbs and both annual forbs and grasses in this study.

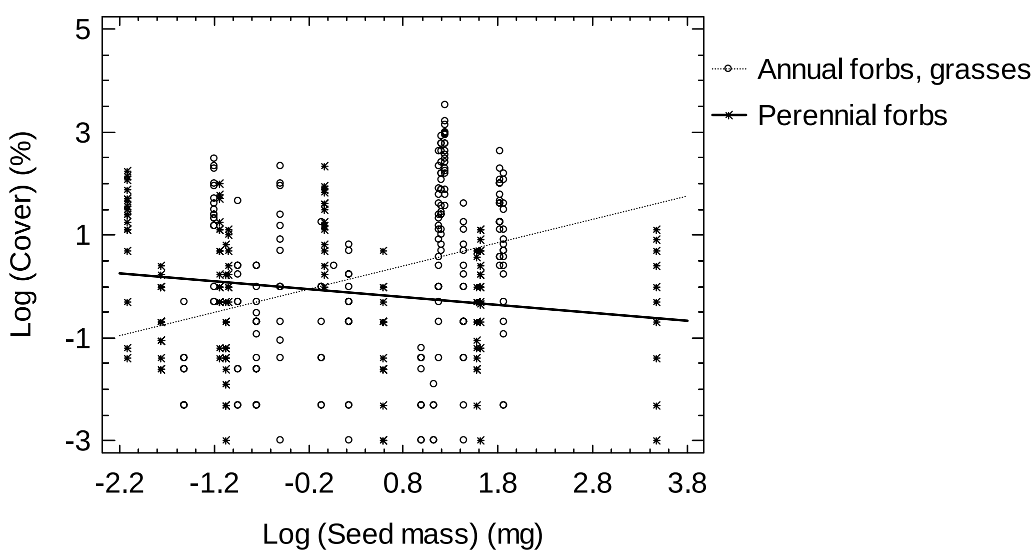

Figure 3.2. Simple linear regression plots showing the different relationship between seed mass and cover between perennial forbs and both annual forbs and grasses.

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Chapter 4 : Conclusions

This research was carried out to test ideas basic to restoration ecology and ecological theory. The results contradicted what many people carrying out and studying prairie restoration have found, which is that grasses can reduce the diversity of restoration plantings. I did not observe this, but I did see other evidence of competition within functional groups. There was also some evidence of overyielding within functional groups, which supports the theory that plant productivity should increase with increasing diversity.

Another goal of this research was to determine whether plant traits can be used to predict the performance of native species in restoration. Regression analyses did reveal several traits that are strongly related to plant cover and the frequency of establishment. These analyses also indicated that a species' functional group influences what traits are related to its performance, and that the functional group of the neighbors influences the traits related to performance. The research presented here should be useful for land managers and from a general ecological sense as well.

What do the results tell us about functional group interactions?

Contrary to expected, there was more competition within certain functional groups than between functional groups. Annual forbs in particular experienced a decrease in cover, biomass, and species richness when grown among each other than when grown with species from other functional groups. Grasses and perennial forbs showed a similar pattern, although the decreases were not as pronounced.

As the number of functional groups increased, and the number of species per functional group decreased accordingly, both total native cover and biomass increased. This pattern provides some evidence that competition within groups was greater than between groups. Native species richness, however, was unaffected by functional group richness. Biomass and cover both were greater than expected in the two and three functional group mixtures based on single functional group mixtures, a pattern that points to overyielding among functional groups (Hooper and Dukes 2004). While other studies have indicated that increasing species richness leads to greater productivity (e.g., Hille Ris Lambers et al. 2004, Roscher et al. 2005), this study also provides evidence that functional richness also plays a role, although small, in the relationship between productivity and diversity.

Post hoc analyses revealed that the amount of non-native cover had a strong negative effect on the amount of native cover and biomass, explaining 19-38% of the variation in native abundance, compared with less than 10% explained by functional group richness. Further analysis revealed that the *a priori* functional groups did not differ significantly in cover. This violated the assumption that functional groups utilized resources differently in space, and may explain why functional group richness did not show a stronger relationship with native cover and biomass.

What do the results tell about the relationship between traits and performance?

Multiple linear regression and logistic regression analyses gave strong evidence that traits measured in the lab and in the field are related to the performance of species in restoration. Although the mechanisms are still unknown, the traits related to performance can be used to investigate possible relationships between growth patterns, morphology, physiology, and performance. These models can also be tested against other data sets to determine their predictive ability. If proven successful, these models will make it possible to know with some degree of assurance how species will perform prior to sowing.

Regression analyses also revealed that within forb species the relationship between traits and performance depend on functional group. Higher leaf weight ratio and seed mass were related with lower cover in perennial forbs relative to annual forbs and grasses, while higher relative growth rate and unit leaf rate were related with lower establishment success in annual forbs. The functional identity of neighbors also influenced the cover of species. Annual forbs and grasses had less cover when growing with species of the same functional group than when growing with species of other functional groups; however, annual forbs with a higher leaf weight ratio did better when growing among other annual forbs. The fact that annual forbs had greater cover and biomass when growing among perennial forbs and grasses gives further support to the overyielding hypothesis found in Chapter 1.

What do the results tell about seed mixes in restoration?

For land managers wishing to increase the cover of native species, I recommend a seed mix that is functionally diverse. There are circumstances in which sowing only grasses or forbs is advantageous, but based on this study I recommend sowing all functional groups at once. This will give the greatest native cover and biomass, while species richness should be unaffected. The regression equations derived in Chapter 3 can be used to estimate which species will be more likely to establish and have greater cover. However, an approach which seeks to maximize cover by only sowing species predicted to have high cover could backfire by increasing above ground competition between these species, which may decrease the diversity in these sowings, such as was seen in the annual forb sowing treatments in Chapter 1.

Taken together, the research presented here indicates that functional group diversity in seed mixes is beneficial in restoration. Rather than finding negative effects of grasses on the performance of other species, I found that other functional groups increased in cover and biomass in the presence of grasses, although this increase was not always statistically significant. This may be due to the density at which grasses were sown. Other studies in the Willamette Valley have shown that grasses can have a negative effect on forb abundance; future work should look further at whether greater density of grasses influences the performance of other species.

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Appendices

Appendix A: Pilot studies

Pilot study 1: Field germination rates

Objective

The objective of this pilot study was to determine field germination rates of each species so that sowing densities can be calculated. I also wanted to know which species would not establish at the site, so that any failure of species to establish would not be contributed to competition from other native species, but would be due to some other mechanism, such as incompatibility of site conditions.

Methods

In the fall of 2004 seeds were sown to determine the germination rates of each species at the study site. The area sown was tilled prior to seed addition and the establishment of the single species plots. Quadrats were 0.5 m^2 and separated by 0.5 m buffers. The thirty single-species plots were placed in blocks five quadrats wide and six quadrats deep. Four blocks were established for a total of four replicates per species.

Seeds were sown in early November 2004. Immediately prior to sowing, the quadrats were raked to remove large clumps of existing vegetation on the seed bed. Seeds were sown by hand evenly into quadrats at a density of 125 seeds/m^2. After sowing they were lightly raked in to establish better contact with the soil and to reduce any possible predation.

Results

In May and June of 2005 the quadrats were visited and all of the seedlings of the sown species were counted. A few of the study species were present in quadrats where they were not sown. These included *Bromus carinatus*, *Elymus glaucus*, *Festuca roemeri*, and *Lotus micranthus*. The three grass species were sown previously at the site, while *Lotus micranthus* was not sown but occurs sporadically. To determine background levels, for each of these species four quadrats per block were randomly chosen and the number of individuals was counted. Average background levels were subtracted from average germination rates to calculate the final germination rate. The germination rates and the background rates for each species are shown in Table A.1.

Table A.1: Mean number of seedlings, mean number of background individuals, and germination rates for each species sown in 2004.

Species	Mean no. plants	Mean no. background plants	Germination rate (st. dev.)
Annual forbs			
Clarkia amoena	41.0		32.8 (10.7)
Clarkia rhomboidea	12.3		9.8 (5.9)
Collinsia grandiflora	23.0		18.4 (10.9)
Collomia grandiflora	2.5		2.0 (1.4)
Gilia capitata	11.3		9.0 (2.1)
Lotus micranthus	7.8	0.3	6.0 (2.1)
Lotus purshianus	6.3		5.0 (4.9)
Madia gracilis	27.0		21.6 (11.1)
Trifolium tridentatum	0.3		0.2 (0.4)
Perennial forbs			
Achillea millefolium	9.0		7.2 (3.1)
Agoseris grandiflora	2.0		1.6 (1.5)
Aquilegia formosa	6.3		5.0 (2.6)
Eriophyllum lanatum	29.5		23.6 (10.5)
*Erythronium oregonum**			
Ligusticum apiifolium	4.0		3.2 (2.1)
Lomatium utriculatum	7.3		5.8 (8.3)
Lupinus albicaulus	36.3		29.0 (4.0)
Potentilla glandulosa	6.8		5.4 (1.8)
Potentilla gracilis	17.5		14.0 (2.1)
Prunella vulgaris	56.0		44.8 (10.6)
Sidalcea campestris	11.0		8.8 (2.7)
*Symphyotrichum hallii**			
Graminoids			
Bromus carinatus	25.5	7.8	14.1 (9.7)
Bromus sitchensis	9.3		7.4 (3.7)
*Carex pachystachya**			
Danthonia californica	5.3		4.2 (1.4)
Elymus glaucus	5.5	1.5	3.2 (2.0)
Elymus trachycaulus	15.0		12.0 (1.7)
Festuca roemeri	17.0	0.6	13.1 (4.8)
Poa secunda	1.5		1.2 (1.0)

* Was unable to positively identify seedlings of these species.

Pilot study 2: Density-biomass relationships

Objective

The purpose of this pilot study was to examine the relationship between native biomass and sowing density, to calculate the density at which biomass becomes independent of density.

Methods

Four species were sown at five different densities. Two annual forbs, *Clarkia rhomboidea* and *Trifolium tridentatum*, one perennial forb, *Eriophyllum lanatum*, and one graminoid, *Bromus carinatus* were chosen for study. Each was sown at 50, 100, 250, 500, and 700 seeds/m^2. These densities were chosen because they represent the approximate range of seeding densities recommended by prairie restoration practitioners in the Willamette Valley (Ridgeline Resource Planning 1999, Heritage Seedlings Inc. 2007).

Seeds of each species at each density were sown into 4 1 m^2 quadrats, distributed over 4 blocks, for a total of 4 replicates. Quadrats were placed 4 wide and 5 deep, and had 1 m buffers between them.

Quadrats were harvested in mid-July 2005. At the time of sampling all species were in bloom or beginning to produce fruit. All sown species within the quadrat were clipped at soil level. Plants were placed in paper bags and then dried for at least

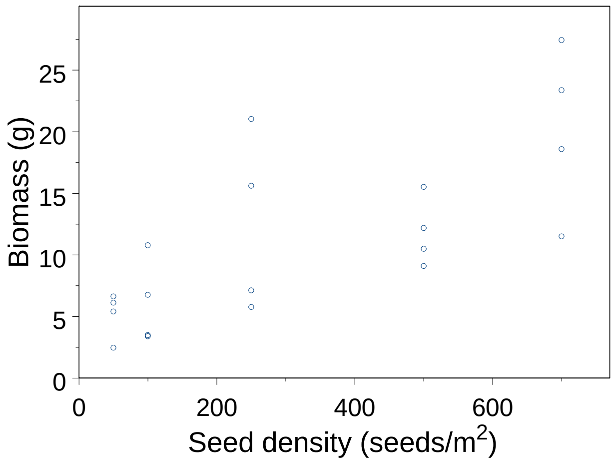
72 hours at 60 °C. A combination of an unseasonably warm late winter, followed by a cool, wet spring led to a late maturation and apparently less growth of seedlings than observed in previous years.

Results

Because of very low germination of *Trifolium*, and very little biomass of *Clarkia*, these two species were not harvested.

The relationship between biomass and density for *Eriophyllum* and *Bromus* are presented in Figure A.1. As seen in Figure A.1, the densities that both species were grown at were not sufficient for biomass to become independent of density; that is, biomass continuously increased with density, and showed no indication at what density biomass would remain constant.

a)



b)

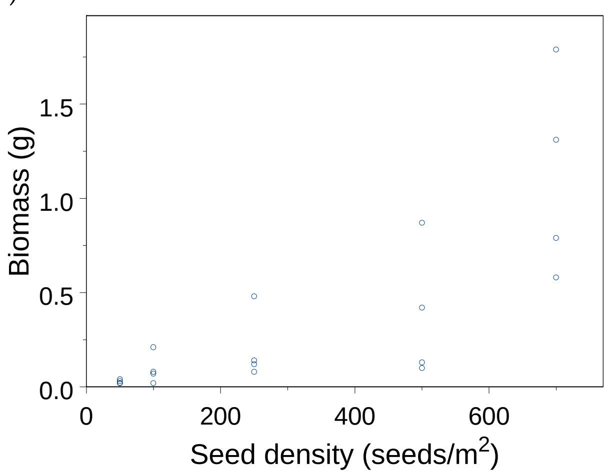


Figure A.1: Relationship between seeding density and biomass in a) *Bromus carinatus* and b) *Eriophyllum lanatum*.

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Appendix B: Species traits

Table B.1. Mean trait values for each species based on laboratory and field grown plants. Lab grown plants were harvested at either 7 or 21 days. Traits measured were leaf area (LA), specific leaf area (SLA), above ground biomass, below ground biomass, leaf weight ratio (LWR), root-shoot ratio, relative growth rate (RGR), unit leaf rate (ULR), seed mass, height in first year, field establishment rate in monoculture plots, and time to germination.

SPECIES	**LA 7 days (mm^2)**	**LA 21 days (mm^2)**	**SLA 7 days (mm^2/mg)**	**SLA 21 days (mm^2/mg)**
Achillea millefolium	17.74	548.59	62.22	51.36
Agoseris grandiflora	33.64	415.21	72.44	62.09
Aquilegia formosa	3.84	156.07	29.16	47.47
Bromus carinatus	103.13	1010.82	38.48	42.95
Bromus sitchensis	39.86	1194.43	32.50	38.92
Clarkia purpurea ssp. *quadrivulnera*	20.94	435.76	60.73	65.88
Clarkia rhomboidea	23.07	456.26	54.27	51.37
Collinsia grandiflora	2.70	105.83	24.27	39.28
Collomia grandiflora	14.63	263.03	11.01	32.79
Danthonia californica	21.80	151.91	24.46	35.92
Elymus glaucus	25.46	590.45	35.53	35.52
Elymus trachycaulus	72.82	791.62	43.50	36.52
Eriophyllum lanatum	12.68	169.12	42.91	64.28
Festuca californica	10.56	83.54	23.92	18.63
Festuca roemeri	6.39	106.67	21.34	27.34
Gilia capitata	3.01	121.54	20.95	44.93
Koeleria macrantha	7.18	75.00	45.21	38.91
Ligusticum apiifolium	25.29	215.40	19.91	38.71
Lotus unifoliolatus var. *unifoliolatus*	59.46	278.96	26.19	33.14
Lupinus albicaulis	248.29	1467.60	10.66	22.86
Lupinus bicolor	66.06	352.58	41.27	28.93
Madia elegans	---	---	---	---
Madia gracilis	34.79	871.94	35.90	48.90
Potentilla glandulosa	18.54	659.34	71.03	80.74
Potentilla gracilis	7.22	190.48	43.38	66.40
Poa secunda	12.54	152.27	60.84	39.86
Prunella vulgaris var. *lanceolata*	34.45	373.15	52.25	48.00
Sidalcea campestris	74.31	653.97	26.88	27.36

Table B.1 (continued). Mean trait values for each species based on laboratory and field grown plants. Lab grown plants were harvested at either 7 or 21 days. Traits measured were leaf area (LA), specific leaf area (SLA), above ground biomass, below ground biomass, leaf weight ratio (LWR), root-shoot ratio, relative growth rate (RGR), unit leaf rate (ULR), seed mass, height in first year, field establishment rate in monoculture plots, and time to germination.

Species	**Above ground biomass 7 days (mg)**	**Above ground biomass 21 days (mg)**	**Below ground biomass 7 days (mg)**	**Below ground biomass 21 days (mg)**
Achillea millefolium	0.38	11.12	0.14	2.58
Agoseris grandiflora	0.50	6.49	0.25	1.68
Aquilegia formosa	0.26	3.92	0.12	0.65
Bromus carinatus	2.27	23.76	0.92	4.12
Bromus sitchensis	1.16	30.75	0.61	5.55
Clarkia purpurea ssp. *quadrivulnera*	0.39	7.30	0.18	2.14
Clarkia rhomboidea	0.51	9.72	0.16	2.57
Collinsia grandiflora	0.12	2.44	0.08	0.49
Collomia grandiflora	1.51	6.69	0.27	1.08
Danthonia californica	0.94	4.57	0.39	2.68
Elymus glaucus	0.73	17.20	0.23	2.41
Elymus trachycaulus	1.56	21.32	0.45	4.12
Eriophyllum lanatum	0.23	3.53	0.18	1.18
Festuca californica	0.57	4.58	0.16	0.76
Festuca roemeri	0.32	3.74	0.16	1.44
Gilia capitata	0.19	2.21	0.10	0.19
Koeleria macrantha	0.27	2.40	0.11	0.52
Ligusticum apiifolium	1.20	5.58	0.42	0.97
Lotus unifoliolatus var. *unifoliolatus*	2.55	9.37	0.57	2.76
Lupinus albicaulis	25.26	71.20	5.08	12.94
Lupinus bicolor	1.78	12.58	0.64	3.89
Madia elegans	---	---	---	---
Madia gracilis	0.96	18.48	0.25	4.13
Potentilla glandulosa	0.29	8.41	0.09	1.35
Potentilla gracilis	0.18	3.00	0.14	0.94
Poa secunda	0.22	3.78	0.14	1.03
Prunella vulgaris var. *lanceolata*	0.72	9.00	0.33	2.63
Sidalcea campestris	3.53	29.50	0.66	9.20

Table B.1 (continued). Mean trait values for each species based on laboratory and field grown plants. Lab grown plants were harvested at either 7 or 21 days. Traits measured were leaf area (LA), specific leaf area (SLA), above ground biomass, below ground biomass, leaf weight ratio (LWR), root-shoot ratio, relative growth rate (RGR), unit leaf rate (ULR), seed mass, height in first year, field establishment rate in monoculture plots, and time to germination.

Species	**LWR 7 days (mg/mg)**	**LWR 21 days (mg/mg)**	**Root-shoot ratio 7 days (mg/mg)**	**Root-shoot ratio 21 days (mg/mg)**
Achillea millefolium	0.73	0.82	0.36	0.21
Agoseris grandiflora	0.66	0.76	0.51	0.31
Aquilegia formosa	0.50	0.80	0.79	0.20
Bromus carinatus	0.62	0.87	0.50	0.16
Bromus sitchensis	0.64	0.84	0.61	0.18
Clarkia purpurea ssp. *quadrivulnera*	0.65	0.72	0.48	0.30
Clarkia rhomboidea	0.61	0.74	0.30	0.25
Collinsia grandiflora	0.54	0.66	0.82	0.37
Collomia grandiflora	0.74	0.75	0.17	0.17
Danthonia californica	0.72	0.70	0.46	0.47
Elymus glaucus	0.77	0.87	0.32	0.14
Elymus trachycaulus	0.76	0.85	0.32	0.18
Eriophyllum lanatum	0.58	0.78	0.67	0.22
Festuca californica	0.75	0.86	0.36	0.17
Festuca roemeri	0.61	0.74	0.80	0.37
Gilia capitata	0.49	0.79	0.69	0.35
Koeleria macrantha	0.44	0.62	0.40	0.24
Ligusticum apiifolium	0.73	0.83	0.35	0.18
Lotus unifoliolatus var. *unifoliolatus*	0.73	0.67	0.21	0.28
Lupinus albicaulis	0.77	0.75	0.20	0.18
Lupinus bicolor	0.66	0.74	0.36	0.31
Madia elegans	---	---	---	---
Madia gracilis	0.68	0.80	0.24	0.22
Potentilla glandulosa	0.74	0.84	0.31	0.16
Potentilla gracilis	0.52	0.75	0.84	0.34
Poa secunda	0.61	0.78	0.72	0.28
Prunella vulgaris var. lanceolata	0.71	0.80	0.43	0.24
Sidalcea campestris	0.74	0.69	0.21	0.40

Table B.1 (continued). Mean trait values for each species based on laboratory and field grown plants. Lab grown plants were harvested at either 7 or 21 days. Traits measured were leaf area (LA), specific leaf area (SLA), above ground biomass, below ground biomass, leaf weight ratio (LWR), root-shoot ratio, relative growth rate (RGR), unit leaf rate (ULR), seed mass, height in first year, field establishment rate in monoculture plots, and time to germination.

SPECIES	**RGR (mg/mg*day)**	**ULR (mg/cm^2*day)**	**Seed mass (mg)**
Achillea millefolium	0.234	0.583	0.12
Agoseris grandiflora	0.171	0.299	0.35
Aquilegia formosa	0.179	0.644	1.78
Bromus carinatus	0.155	0.531	6.21
Bromus sitchensis	0.216	0.848	6.48
Clarkia purpurea ssp. *quadrivulnera*	0.200	0.444	0.30
Clarkia rhomboidea	0.208	0.587	0.61
Collinsia grandiflora	0.192	0.550	0.94
Collomia grandiflora	0.105	0.382	3.32
Danthonia californica	0.126	0.643	3.25
Elymus glaucus	0.215	0.768	3.77
Elymus trachycaulus	0.181	0.582	4.24
Eriophyllum lanatum	0.176	0.465	0.32
Festuca californica	0.142	1.069	2.68
Festuca roemeri	0.171	0.939	1.26
Gilia capitata	0.163	0.384	0.39
Koeleria macrantha	0.146	0.619	0.22
Ligusticum apiifolium	0.100	0.418	4.80
Lotus unifoliolatus var. *unifoliolatus*	0.097	0.420	3.45
Lupinus albicaulis	0.073	0.554	32.39
Lupinus bicolor	0.137	0.586	3.07
Madia elegans	---	---	---
Madia gracilis	0.209	0.661	1.07
Potentilla glandulosa	0.232	0.374	0.34
Potentilla gracilis	0.178	0.463	0.17
Poa secunda	0.186	0.561	0.47
Prunella vulgaris var. *lanceolata*	0.169	0.514	0.96
Sidalcea campestris	0.161	0.912	5.04

Table B.1 (continued). Mean trait values for each species based on laboratory and field grown plants. Lab grown plants were harvested at either 7 or 21 days. Traits measured were leaf area (LA), specific leaf area (SLA), above ground biomass, below ground biomass, leaf weight ratio (LWR), root-shoot ratio, relative growth rate (RGR), unit leaf rate (ULR), seed mass, height in first year, field establishment rate in monoculture plots, and time to germination.

Species	**Height (cm)**	**Field estab. (%)**	**Time to germ. (days)**
Achillea millefolium	10.5	2.50	167
Agoseris grandiflora	30.5	0.00	---
Aquilegia formosa	3.7	2.25	177
Bromus carinatus	72.5	11.00	103
Bromus sitchensis	30.2	2.75	131
Clarkia purpurea ssp. quadrivulnera	26.1	11.00	149
Clarkia rhomboidea	36.2	7.50	94
Collinsia grandiflora	14.1	6.75	112
Collomia grandiflora	29.0	3.50	120
Danthonia californica	10.2	10.50	177
Elymus glaucus	---	0.00	---
Elymus trachycaulus	16.5	0.50	177
Eriophyllum lanatum	16.8	3.25	168
Festuca californica	5.1	2.00	156
Festuca roemeri	8.2	3.75	163
Gilia capitata	33.3	1.50	92
Koeleria macrantha	4.0	2.75	170
Ligusticum apiifolium	5.5	4.50	177
Lotus unifoliolatus var. unifoliolatus	28.8	12.00	177
Lupinus albicaulis	13.3	3.75	149
Lupinus bicolor	1.6	2.50	177
Madia elegans	---	---	---
Madia gracilis	68.2	1.00	---
Potentilla glandulosa	2.5	2.00	177
Potentilla gracilis	3.1	5.00	177
Poa secunda	2.7	3.25	166
Prunella vulgaris var. lanceolata	7.6	19.25	165
Sidalcea campestris	6.8	1.75	113