AN ABSTRACT OF THE THESIS OF

Jennifer M. Goodridge for the degree of Master of Science in Botany and Plant Pathology presented on September 5, 2001. Title: The Effects of Native Plants on Non-native Plant Abundance in a Restoration Setting: Differences Among Native Species and the Predictive Ability of Species Traits.

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Mark V. Wilson

Reducing the cover of non-native species is one of the challenges of ecosystem restoration. The goal of this study is to identify native species traits that will increase native species cover and reduce non-native species cover in the first growing season at upland and wetland prairie restoration sites.

Native and non-native prairie species were planted in the fall and harvested the following summer at both an upland and a wetland site. Native species traits, such as plant weight, leaf area, relative growth rate, leaf area ratio, leaf weight ratio, net assimilation rate, and specific leaf area were measured under laboratory conditions for 7- and 21-day old seedlings. Germination rate (laboratory) and phenology (field) were also measured.

At the upland site, species with a large 7-day plant weight and a high germination rate also had high native cover in the field ($P<0.001$, $R^2=0.83$). At the wetland site, high 21-day leaf area, low 21-day leaf weight ratio, and high net assimilation rate predicted

increased native cover in the field ($P<0.001$, $R^2=0.87$). An abundance of natives, as measured by native cover, native biomass, and number of individuals, likely results in fewer resources (light, nutrients, and water) available for the non-native species growth resulting in a reduction in the non-native cover.

Intrinsic traits of native species also predicted the field performance of non-native species, although the amount of variation explained was lower than the amount of variation explained in the models that predicted native cover. In the upland site, native species with high leaf weight ratio (21-day) tended to have lower non-native cover in their field plots ($P=0.087$, $R^2=0.23$). In the wetland site, the native species traits that predict non-native cover were low 21-day leaf area and high 21-day leaf weight ratio ($P<0.001$, $R^2=0.46$). These traits were similar to those that predicted native species cover at the wetland site.

This study demonstrates the ability of species traits to predict field performance. Predictive models were generated using native species traits to select species for restoration that will increase native cover and decrease non-native cover in the first growing season. Traits can be measured for species not included in this study and the models generated can be used to predict the field performance of species at similar sites.

The Effects of Native Plants on Non-native Plant Abundance in a Restoration Setting: Differences Among Native Species and the Predictive Ability of Species Traits

By

Jennifer M. Goodridge

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Dean of Graduate School

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THE EFFECTS OF NATIVE PLANTS ON NON-NATIVE PLANT ABUNDANCE IN A RESTORATION SETTING: DIFFERENCES AMONG NATIVE SPECIES AND THE PREDICTIVE ABILITY OF SPECIES TRAITS

INTRODUCTION

According to the Society for Ecological Restoration, ecological restoration is "the process of assisting the recovery and management of ecological integrity. Ecological integrity includes a critical range of variability in biodiversity, ecological processes and structures, regional and historical context, and sustainable cultural practices" (Society for Ecological Restoration 1998). Ecological restoration is important for restoring damaged or disturbed ecosystems, creating viable habitat for threatened or endangered species, and replacing an impacted community (such as in wetland compensation through mitigation). Unfortunately, ecological restoration projects often fail to meet their objectives. Common problems associated with restoration projects include poor native plant establishment, high cover by non-native species, inadequate hydrology, and limited site use by a targeted animal species (Clewell and Reiger 1997, Kusler and Kentula 1990, Malakoff 1998). Non-native plants that are competitive, aggressive, or invasive are concerns for restoration projects because colonization of restoration sites by non-native species interferes with site establishment by native species (Clewell and Reiger 1997, Ehrenfeld and Toth 1997). Conducting small scale research projects on reducing the success of non-native species will allow us to reach our larger goal of restoring biodiversity to entire ecosystems. This thesis focuses on the traits of native species that might allow them to reduce the establishment of non-native species in a restoration

setting. The first step in trying to reduce the establishment of non-native species is to understand why non-natives are so successful at restoration sites.

Once propagules are present, the success of non-native species, like any species, depends upon site conditions and plant traits. Restoration sites have often been graded to create the desired topography and vegetation has been cleared to prepare for planting. These activities are disturbances to the system and disturbed sites or bare ground are more likely to be invaded by competitive species (Crawley 1987, D'Antonio 1993) because these disturbances increase the availability of limiting resources, such as light, space, or nutrients (Hobbs 1991). In this way, disturbance can shift the balance of species to favor weedy, resource-demanding, non-native species.

Resource demanding, weedy non-native species are examples of ruderal or r-selected species. Intrinsic traits associated with ruderal or r-selected species include small seed size, rapid seed production, and short juvenile period. These traits are also associated with successful colonizing species (Rejmanek and Richardson 1996). Native species can also be ruderal, r-selected, and able to colonize well. If there are examples of native species that thrive in disturbed conditions because of specific traits, why not plant this type of native species in restoration projects? Perhaps the success of these natives would utilize abundant resources making them less available for non-native species.

However, it is difficult to select native species for restoration based on their intrinsic traits because the traits of native species are not widely known. This is particularly true in the upland and wetland prairies of the Pacific Northwest where there have been relatively few ecological restoration studies. For example, in his study of plant

traits, Grime (1988) identified the intrinsic traits of several species native to the British Isles, but very few of these species are also native to the Pacific Northwest.

Studies that use plant traits to predict ecological processes can provide useful information for ecosystem restoration. For example, seed size can be used to predict the depth of maximum seedling emergence rate (Bond et al. 1999) and thus calculate how deep seeds should be planted. Plant weight at 7 days can be used to predict seedling establishment rates (Clark et al. 2001) which may be helpful for estimating seeding density. To predict the success of an individual species at a site, certain traits have been found to correlate with specific types of environments. For example, species successful in highly productive environments also tend to have high relative growth rates (Grime 1975, Poorter and Remkes 1990). Increased information about the intrinsic traits of native and non-native species may enable ecologists to predict the outcome of ecological processes like competition and invasion (Pyke and Archer 1991). For example, light utilization (as measured by height and net assimilation rate) and early establishment (as measured by relative growth rate and initial propagule weight) predict competitive ability in experiments with cotton crops and weeds (Holt and Orcutt 1991). Information on plant traits not only would help in species selection during restoration planning, it would expand general ecological knowledge. A better understanding of these processes would also increase our ability to establish native species and exclude non-native species in restoration sites (Clewell and Reiger 1997). Quantification of the traits of native Willamette Valley prairie species will allow us to use species traits to predict which native species can reduce the establishment of non-native species during the first growing season.

Objectives

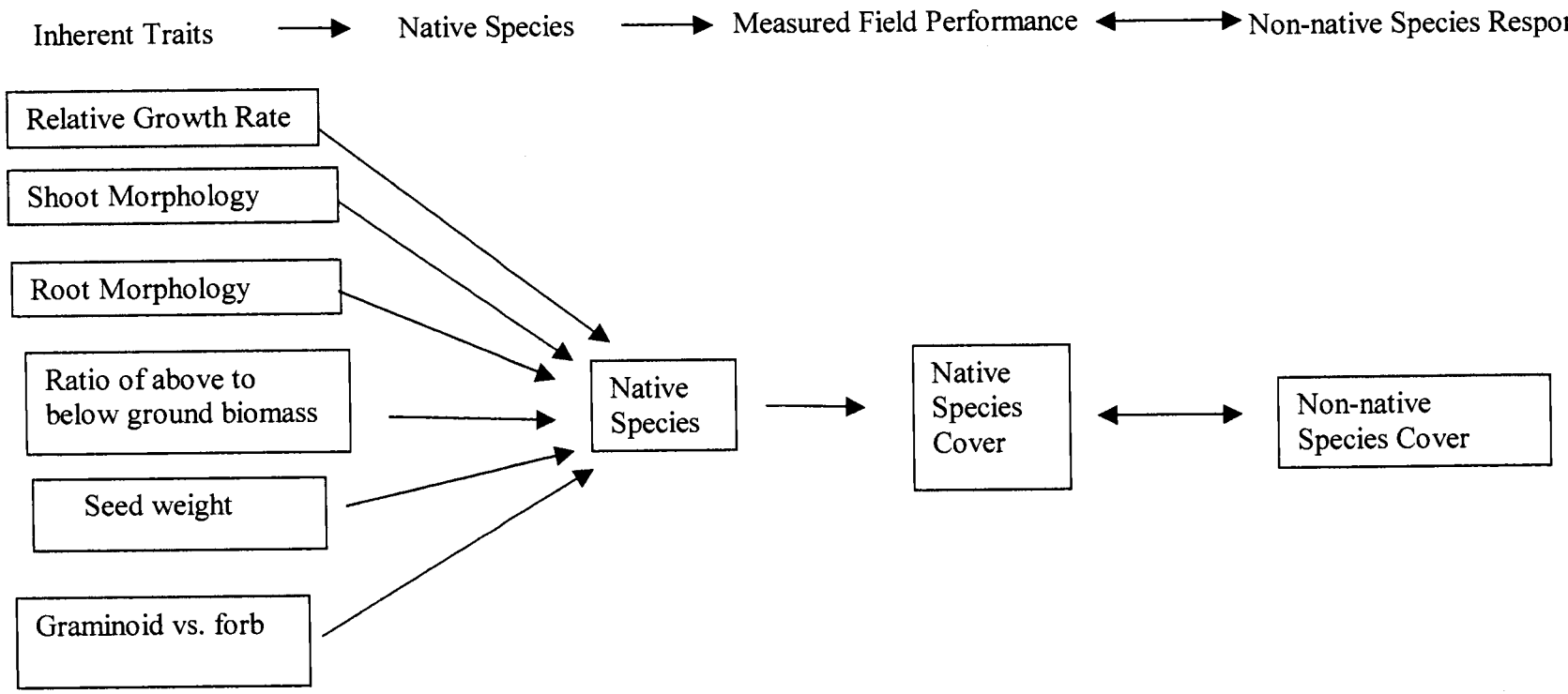
There were five objectives for this study:

1. To determine if there are differences among native species in their abilities to reduce the establishment of non-native species in the first growing season.
2. To quantify some of the intrinsic traits of Willamette Valley native prairie species.
3. To identify traits of native species that can be used to predict native species field performance.
4. To identify traits of native species that can be used to predict which native species will best reduce the establishment of non-native species.
5. To determine if intrinsic traits and field data explain different aspects of non-native field performance.

To investigate Objective 1, native species field performance was measured to assess native species ability to exclude non-native species. Native species were grown in the field with non-native species and cover and biomass were measured at the end of the first growing season. This experimental approach measured the response of non-native species as a result of the field performance of planted native species (Figure 1). Species performance beyond the first growing season was outside the scope of this project.

To investigate Objective 2, several intrinsic species traits were measured in the laboratory. Relative growth rate, shoot morphology (leaf thickness, leaf area, and growth form), allocation to leaves (leaf area per plant weight and leaf biomass per plant weight), phenology, germination rate, growth form (graminoid or forb), and seed weight were the intrinsic traits chosen for investigation. Trait selection was based on characterizing intrinsic ability to intercept light (shoot morphology, allocation to leaves), take up

Figure 1: Response Pathways



Objective 1: Native species (identity) → Non-native species response

Objective 2: Quantification of native species inherent traits

Objective 3: Inherent traits → Native field performance

Objective 4: Inherent traits → Native field performance → Non-native species response

Objective 5: Inherent traits vs. native field performance → Non-native species response

nutrients (allocation to roots), and grow (phenology, germination rate, relative growth rate). Intrinsic traits were measured on plants grown in the laboratory with the exception of phenology which was measured in the field. These intrinsic traits help determine a species's field performance (Figure 1).

To investigate Objectives 3 and 4, I generated models that used either field performance or native species traits (measured in the laboratory) to explain the field variation in native and non-native species cover (Figure 1).

To investigate Objective 5, stepwise forward regression was used to determine whether species traits added additional explanatory power beyond field performance variables when field performance variables were fixed into a lower model and vice versa.

Hypotheses

In conjunction with the general objectives stated above, I developed five specific hypotheses about the effect of each intrinsic trait on the cover of non-native species. In addition, Hypothesis 6 relates native species cover to its ability to exclude non-native species.

Hypothesis 1: Growth rate. Sequestering of resources, such as light, nutrients, and water, by native species early in the growing season will make resources less available for resource-demanding non-native species. Therefore, plots sown with native species that have a high relative growth rate should have lower cover of sown non-native species.

Hypothesis 2: Seed weight. Life history theory suggests that species with light seeds (low seed weight) also tend to be species that grow rapidly. Species that grow

rapidly will sequester resources early in the growing season, therefore, plots sown with native species that have light seeds (low seed weight) should also have lower cover of non-native species.

Hypothesis 3: Leaf weight ratio. Species that invest more biomass in below-ground biomass in the first growing season may take up a lot of nutrients, but their reduced investment in above-ground biomass will leave bare ground and adequate light to allow for non-native species colonization. I hypothesize that non-native species respond more to available light than to soil resources. Therefore, plots sown with native species with a high leaf weight ratio (leaf biomass/plant biomass) should have lower cover of non-native species.

Hypothesis 4: Leaf area ratio. Species that invest in wider leaves will sequester more light resources allowing less light for sown non-native species establishment. Therefore, plots sown with native species with a high leaf area ratio (leaf area/plant biomass) should have lower non-native species cover.

Hypothesis 5: Germination rate. Species not sequestering resources (light, nutrients, and water) early in the growing season leave resources available for resource-demanding non-native species. Therefore, plots sown with native species that germinate earlier in the field should have lower non-native species cover.

Hypothesis 6: Native cover. Resource sequestering by native species throughout the growing season makes resources relatively unavailable for resource-demanding non-native species. Therefore, plots sown with native species that provide high cover (measured in the field) will have less cover of sown non-native species.

METHODS

Species selection

Eleven Willamette Valley native species were selected for use in this study: *Prunella vulgaris* var. *lanceolata* L., *Hordeum brachyantherum* Nevski, *Festuca roemeri*, *Wyethia angustifolia* Nutt., *Achillea millefolium* L., *Potentilla gracilis* var. *gracilis* Dougl., *Eriophyllum lanatum* Forbes, *Juncus tenuis* Willd., *Danthonia californica* Boland, *Carex tumilicola* Mack, and *Carex densa* Bailey. Species selection was based on importance in native prairies, feasibility of local collection, and representation of a range of intrinsic species traits based on existing information in the literature (Table 1).

Daucus carota L., *Holcus lanatus* L., and *Rumex acetosella* L. were chosen as representative non-native species because they were found growing near the field sites, have a range of germination dates, represent both forb/graminoid groups, were not considered noxious weeds (a request from Finley National Wildlife Refuge managers), and survive in mesic conditions so the same species could be used at both sites.

Seed Preparation

Collection

All species were collected locally (Table 2) with the exception of *Festuca roemeri*, which was purchased from Wild Garden Seed, Shoulder to Shoulder Farm, Philomath, Oregon. This company collects seeds from a native prairie in Philomath and

Table 1: Intrinsic traits used for native species selection.

Species	Relative growth rate (g/g day)	Seed weight (mg)	Forb/ Graminoid (Growth form)	Stratification increases germination	Source
Achillea millefolium	1.96	0.12 - 0.32	F	no	Guerrant and Raven 1995, Bourdot et al. 1985, Grime and Hunt 1975
Carex densa	–	0.893	G	yes	Guerrant and Raven 1995
Carex tumilicola	–	1.694	G	yes	Guerrant and Raven 1995
Danthonia californica	0.14	4.2 - 4.9	G	yes	Davis 1997, Guerrant and Raven 1995, Wilson et al. 1995
Eriophyllum lanatum	–	0.39 - 0.6	F	no	Guerrant and Raven 1995, Wilson et al. 1995
Festuca roemeri	–	–	G	–	
Hordeum brachyantherum	0.1	4.1 - 6.73	G	no	Guerrant and Raven 1995, Wilson et al. 1995, Davis 1997
Juncus tenuis	–	0.017	G	no	Guerrant and Raven 1995
Potentilla gracilis var. *gracilis*	–	0.32	F	yes	Guerrant and Raven 1995
Prunella vulgaris var. *lanceolata*	0.86	0.3 - 1.13	F	no	Grime and Hunt 1975, Winn and Werner 1997, Winn 1988, Guerrant and Raven 1995, Wilson et al. 1995
Wyethia angustifolia	–	9.5-13.65	F	yes	Guerrant and Raven 1995, Wilson et al. 1995

Table 2: Seed collection sites and dates, habitat of collection, and habitat of site planted.

Species	Collection			Site planted
	Site*	Date	Prairie type	
	Native Species			
Achillea millefolium	1	9/2/99	Mesic	Wetland
Achillea millefolium	2	8/15/99	Upland	Upland
Carex densa	1	7/28/99	Wetland	Wetland
Carex tumilicola	1	9/2/99	Mesic	Upland
Danthonia californica	3	8/26/99	Wetland	Wetland
Eriophyllum lanatum	3	8/11/99	Wetland	Wetland
Eriophyllum lanatum	2 and 4	9/11/99	Upland	Upland
Hordeum brachyantherum	1	7/28/99	Wetland	Wetland
Juncus tenuis	1	7/28/99	Wetland	Wetland
Potentilla gracilis var. *gracilis*	1	8/19/99	Wetland	Wetland
Potentilla gracilis var. *gracilis*	4	9/11/99	Upland	Upland
Prunella vulgaris var. *lanceolata*	1	7/28/99	Wetland	Wetland
Prunella vulgaris var. *lanceolata*	4	9/11/99	Upland	Upland
Wyethia angustifolium	3	8/26/99	Mesic	Upland
	Non-native Species			
Daucus carota	1	–	Mesic	Both
Holcus lanatus	2	7/16/99	Mesic	Both
Rumex acetosella	1	7/21/99	Mesic	Both

*Site numbers:

1. Willamette Floodplain Research Natural Area, William Finley National Wildlife Refuge, Benton County, Oregon
2. Baskett Slough National Wildlife Refuge, Marion County, Oregon
3. Royal Amazon South, Lane County, Oregon
4. Bald Hill, Benton County, Oregon

grows the seeds for commercial sale. *Festuca roemeri* was purchased commercially rather than collected because it is very difficult to identify the difference between *F. roemeri* and *F. rubra*. *F. rubra* has a fused leaf sheath, whereas, *F. roemeri* has an overlapping leaf sheath; however, the leaf sheaths can easily tear while they are being examined (Wilson 1999). The majority of the plants growing at Wild Garden seed have been correctly identified as *F. roemeri* by Dr. Barbara Wilson.

All seeds were collected in June – September 1999. Date of collection varied with each species depending on seed maturity (Table 2). Seeds were considered mature when they were firm, dry, generally a dark brown or black color, and almost ready to disperse.

Cleaning

Seeds were allowed to dry for at least two weeks at room temperature in a paper bag prior to cleaning. Seeds were separated from the inflorescence in a seed thresher. *Achillea millefolium* was air blown to separate chaff from filled seed.

Counting

All seeds were hand counted to ensure the correct number of seeds per plot and to discard unfilled seeds. *Juncus tenuis, Achillea millefolium,* and *Eriophyllum lanatum* were counted under a microscope to see the small seeds.

Field methods

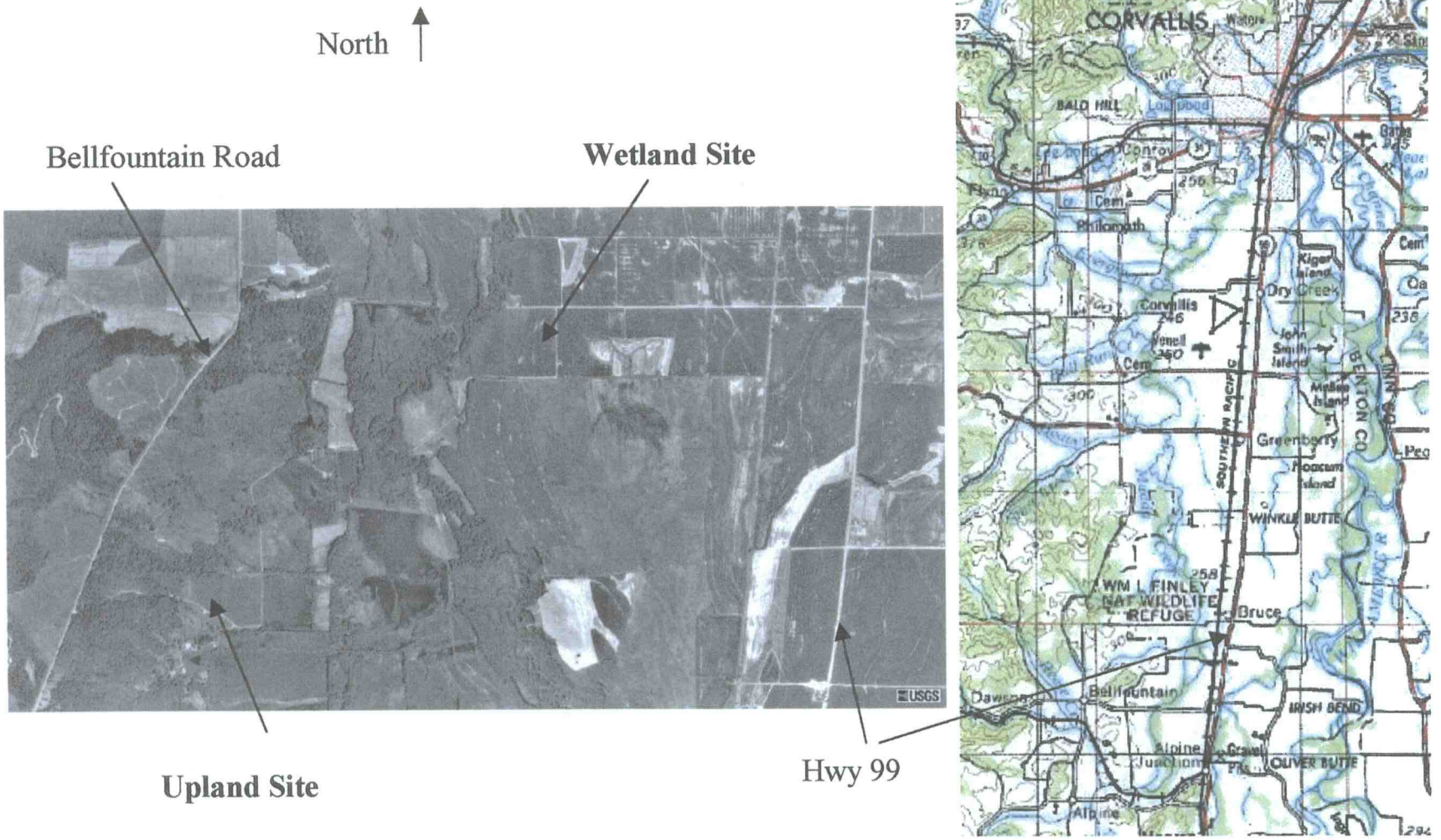
Study sites

Field studies were conducted at William Finley National Wildlife Refuge approximately 16 km south of Corvallis, Oregon (Figure 2). The climate of the Willamette Valley consists of mild, wet winters, and moderate, dry summers. The average annual precipitation in Corvallis, Oregon is 111 cm per year. Average January temperature is 7.9° C and average July temperature is 27° C (Oregon Climate Service, Hyslop Farm, 1971-2000).

Land use within William Finley National Wildlife refuge consists of fallow and active agricultural land, prairies, shrub and forested areas, gravel roads, an interpretive center, and recreational trails. There were two field study sites, an upland and a wetland site (Figure 2). The upland site is located near the western entrance to the refuge at approximately 330 feet above mean sea level. Until 1997 this area consisted of various cultivated crops, but since then it has been fallowed to restore it to native prairie conditions. To reduce weedy cover, it was covered with plastic from July through September 1998 and sprayed with Round-up in the spring of 1999. Weeds were scraped from the soil surface with a hoe prior to planting in the fall of 1999. The mapped soil type is the Hazelair complex which is a composite of moderate to well-drained silt loams and silty clay loams (Kneze Vich 1975). The soils at this site are moist throughout the winter, but the upland site is on a topographically high area that drains to an adjacent pond.

Figure 2: Field site locations, Finley Wildlife Refuge, Benton County, OR. Images courtesy of the USGS via Microsoft Terra Server (www.terraserver.com). Photos taken in 1994 by the National Aerial Photography Program.

Figure 2


North
Bellfountain Road
Wetland Site
Upland Site
Hwy 99
CORVALLIS
BALD HILL
Philomath
Dry Creek
Corvallis
Greenberry
WINKLE BUTTE
WM L FINLEY NAT WILDLIFE REFUGE
Bruce
Bellfountain
IRISH BEND
OLIVER BUTTE
Alpine
Alpine Junction
BENTON CO
SOUTHERN PACIFIC
USGS

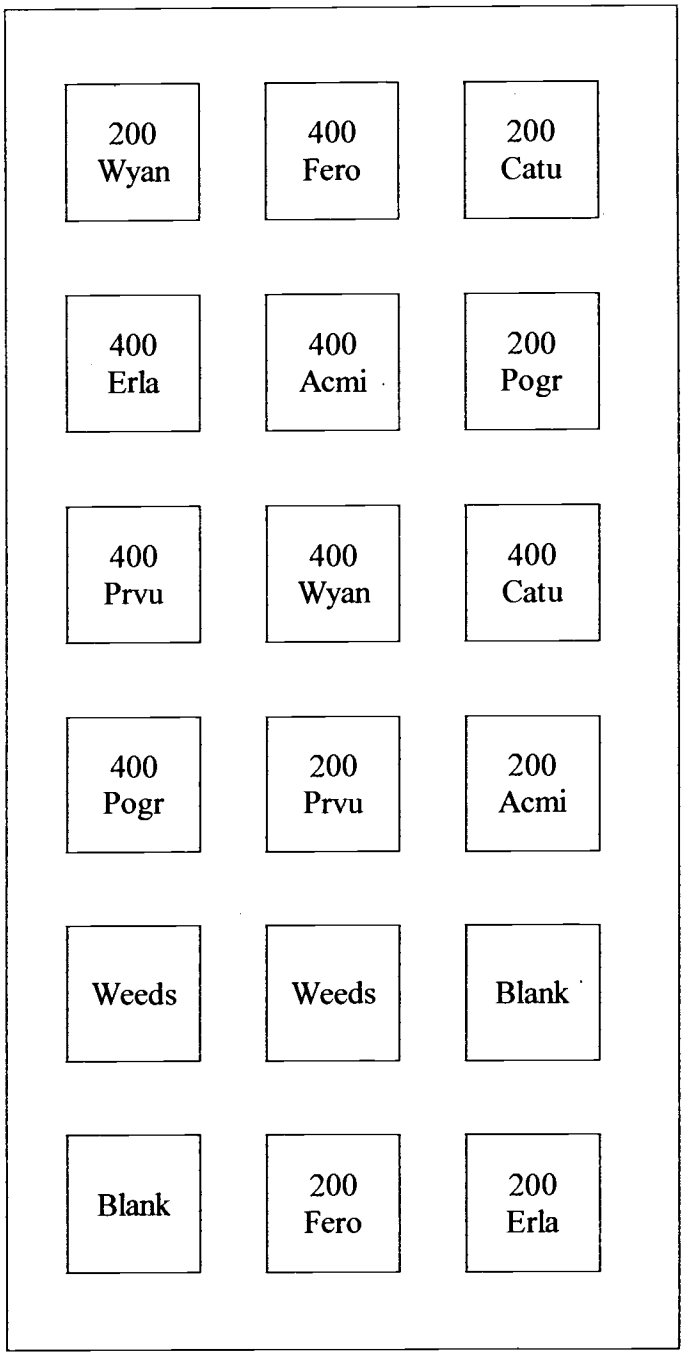
The wetland site is located near the eastern entrance to the refuge at approximately 255 feet above mean sea level. This site was used for annual ryegrass production until the fall of 1999 when it was burned and then plowed with a moldboard plow prior to planting this project. The mapped soil type is the Dayton silt loam which is a poorly drained, hydric soil (Kneze Vich 1975). The soils are saturated to the surface throughout the winter with ponding in some areas for a few weeks during the winter.

Experimental design and treatments

The study design consisted of a randomized complete block design with four replicated blocks at each site (Figure 3). Each block was 1 m by 2 m and contained 18 plots. Each plot was 25 cm by 25 cm with a 12.5 cm border in between each plot, a 0.5 meter border between each block, and a 1 meter border between the blocks and the surrounding ryegrass field.

One native species plus a mix of three non-native species were sowed within each plot. Native species were considered the treatment for each plot. Within each block, each species was planted at either 200 or 400 seeds per plot. Seed density was chosen based on the results of a pilot project the previous season that showed that the amount of non-natives in each plot may vary depending upon native seed planting density. Therefore, two different densities were used to isolate the effects of density so the effect of species traits would be clearer. At the low density there needed to be enough plants to exert an effect on non-natives. In the pilot project, some species had a field germination rate of less than 5%, so with 200 seeds there would be at least ten plants per plot. The

Figure 3: Example of a randomized complete block at the upland site. Each plot was 25 cm by 25 cm with a 12.5 cm border in between each plot. There was also a .5 meter border between each block and a 1 meter border between the blocks and the surrounding ryegrass field. The numbers represent seed density and the species are abbreviated by 4 letter codes (first two letters of the genus and first two letters of the species). Figure not to scale.



high density was chosen to avoid self-thinning. In the pilot project, it appeared that the establishment of *Prunella vulgaris* seedlings leveled off at 350 seeds, so 400 seeds per plot was chosen as the maximum density. Species were sown in the wetland or upland site based on the similarity to the habitat from which they were collected (Table 2).

Ten seeds of each of the three non-native species were sown in each plot with the native species. The number of seeds of each non-native species was chosen based on germination rates for *Daucus carota* and *Holcus lanatus* (Table 3). It seemed that with their high germination, there would be about 15 plants per plot, dense enough to interact with the sown native species. In addition, non-natives were the only species sown in two plots per block. This served as a way to assess block effects and the performance of the sown non-native species in the absence of interference by natives. In the upland site, there was one less native species so there was also one plot per block where nothing was sown to assess background levels of species recruitment to the site.

In order to minimize block effects, blocks were located within a relatively flat portion of the study site. Prior to seeding, the upland site was leveled with a hoe to remove lumps of dirt and existing vegetation. At the wetland site, the US Fish and Wildlife Service personnel used a backhoe to level the ground.

On September 23 and 24, 1999, native and non-native seeds were hand broadcast evenly across each plot at the upland and wetland sites, respectively. A thin layer of dirt (from nearby at the field site) was sprinkled over the plots to retain moisture for seed germination and to camoflauge seeds from predators. At the wetland site, recently overturned mole hole soil was used for this purpose.

Table 3: Characteristics reported in the literature for the sown non-native species.

Species	Germination rate	Stratification required?	Source
Daucus carota	39% – 56%	no	Pill 1994, Maret 1996
Holcus lanatus	90% - 95%	yes	Hayes 1976, Williams 1983
Rumex acetosella	–	–	–

Plots were visited once per month between October 1999 and May 2000 to record the phenology of native species germination. During those monthy visits, it was noted that agricultural ryegrass re-established at the wetland site at unexpectedly high rates. Therefore, ryegrass seedlings were weeded from the plots and clipped in the plot borders during the monthly visits. The clipped borders eliminated any effect of shading due to the ryegrass field surrounding the plots.

Sampling

In June 2000, average height, number of flowering stalks, cover, number of individuals, and biomass of the sown native species was recorded in each plot. Cover and biomass of sown non-native and unsown species was also recorded. Unsown species refers to those species that established in the plots from the seed bank and by dispersal to the site. In the wetland, ryegrass cover was included in unsown species cover. However, ryegrass plants were clipped and collected separately to calculate their biomass. Average height of the sown native species was estimated as the average canopy height from the ground surface. Cover was estimated by two observers using cover templates. Plants were clipped at the base, bagged, stapled, labeled, and brought to the laboratory for drying. Plants were dried in an oven at 75° C until plant weight no longer changed; plants were dry in 24 hours. When dry, bags of plant material were removed from the oven and immediately weighed to the nearest 0.01 gram. After weighing the plants plus the bag, plants were emptied from the bags and the bags were weighed.

Laboratory methods

Plant trait studies were conducted in the laboratory using procedures modeled after those by Hunt et al. (1993). Following consistent laboratory methods allows more direct comparison amongst plant-trait studies. However, changes were made in this study due to variation in the facilities and materials available, so the complete methods are described below. Different aspects of the laboratory studies were carried out in each of the following facilities: the U. S. Environmental Protection Agency Terrestrial Ecology Research Facility, Corvallis (growth chambers); the OSU Department of Forest Science Plant Physiology Laboratory (leaf area); and the Ecology and Forest Pathology Laboratory in the OSU Department of Botany and Plant Pathology (plant drying and weighing). The laboratory studies were conducted on twenty-two species including those species used in the field studies (Table 4). However, the methods and results presented in this paper will discuss only those species that were used in the field studies.

Seed stratification

Carex tumilicola, Carex densa, Eriophyllum lanatum, Potentilla gracilis, and *Wyethia angustifolium* have higher germination rates following cold stratification (Guerrant and Raven 1995). Therefore, the seeds of these species were cold stratified before they were placed in a growth chamber for germination. Twenty-five filled seeds were placed in a petri dish with filter paper moistened with distilled water; this was replicated five times for each species. Seeds were kept moist and placed in a dark refrigerator (or cold room) at approximately 5°C for 6 weeks.

Table 4: Complete species list for laboratory studies

Achillea millefolium
Agoseris grandiflora
Allium amplectens
Aster curtis
Aster hallii
Balsamorhiza deltoidea
Bromus carinatus
Carex densa
Carex tumilicola
Carex unilateralis
Clarkia amoena
Danthonia californica
Deschampsia cespitosa
Elymus glaucus
Eriophyllum lanatum
Festuca roemeri
Grindelia integrefolia
Hordeum brachyantherum
Juncus tenuis
Microseris lanatus
Potentilla gracilis var. *gracilis*
Prunella vulgaris var. *vulgaris*
Wyethia angustifolium
Zigadenus venenosus

Seed germination

Five replicates with twenty-five seeds of each species were placed on washed sand in petri dishes. Sand was moistened with Hoagland's basal salt growth solution (Table 5). Stratified and non-stratified seeds were put into a growth chamber with the following conditions for initiating germination: 134 $\mu mol/m^2s$ light, 20°C for 16 hr and no light, 10°C for 8 hr, with 60% relative humidity. Seeds were checked for germination daily and kept moist with distilled water.

Seedling growing conditions

Seeds were considered germinated when the cotyledons were visible. Once germinated, seedlings were transplanted into 50-ml pots filled with washed sand that was pre-moistened with distilled water. Pots were bottom-watered every other day with distilled water (enough so that there was some standing water in the tray – about 500 ml). On alternate days, plants were bottom-watered with 1.25 ml of growth solution per pot (90 ml per tray of 72 pots). A mix-up in the delivery of the growth solution resulted in two concentrations being used during the study. The growth solution was mixed at two different concentrations: high (10 times the concentration in Table 5) and low (as outlined in Table 5). The high concentration was used from the beginning of the study, 4 February 2000, until 20 February 2000. The low concentration was used from 23 February 2000 until the completion of the study, 25 March 2000. Therefore, some

Table 5: Contents of Hoagland's basal salt growth solution. Solution was mixed according to directions, then the pH was adjusted to 5.7 ± 0.1.

Components	mg/L
Ammonium phosphate monobasic	115.030
Boric acid	2.860
Calcium nitrate	656.4
Cupric sulfate pentahydrate	0.08
Ferric titrate	5.32
Magnesium sulfate anhydrous	240.76
Manganese chloride tetrahydrate	1.81
Molybdenum trioxide	0.0160
Potassium nitrate	606.6
Zinc sulfate heptahydrate	0.220

seedlings received only high, some only low, and some a mix of growth solutions (Table 6). Plants were put into a growth chamber with the following conditions: 120 $\mu mol/m^2s$ light (mix of incandescent and fluorescent bulbs), 22 °C for 14 hr and no light, 15 °C for 10 hr, and 50% relative humidity.

Potted plants were labeled with the species name, date planted, and 7 or 21 day. Plants were harvested at 7 or 21 days by removing the plant with the sand from the pot. Sand was washed from the roots with distilled water. The root and shoot were cut apart and the root was placed in a labeled envelope. The shoot was wrapped in cellophane for leaf area calculations.

Leaf area

Leaves were wrapped in cellophane to ensure that they were flat and then placed on a light table. The projected surface area of the leaf was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, WA). Camera sensitivity can be adjusted to improve the resolution of the image which varies slightly depending on the leaf thickness (both width and depth). Since this project involved calculating the leaf area of several different species, there was a range in the optimal calibration across leaf samples due to variation in leaf thickness. To keep the area consistent from day to day, the image recorder was calibrated daily against the same two pre-measured objects. In order to catch the whole image for very thin species, the outline of the plant was traced with a fine (0.2 mm) tipped pen. After the leaf area was measured, the cellophane was removed and the shoot was placed in a labeled envelope.

Table 6: Number of replicates for each species within each harvest period and growth solution concentration. Species names are abbreviated by the first two letters of the genus and the first two letters of the species. Up refers to upland and wet refers to wetland.

Growth before harvest	Growth Solution Code	Species											
		Acmi up	Acmi wet	Cade	Catu	Daca	Erla	Fero	Hobr	Pogr	Prvu up	Prvu wet	Wyan
7 days	Low	6	9	9	0	21	5	17	21	2	20	28	0
	Mix	0	6	6	3	0	1	0	0	3	0	0	0
	High	2	3	0	12	0	8	0	0	5	0	0	2
21 days	Low	1	3	2	0	0	2	1	1	0	0	1	1
	Mix	10	8	23	5	19	7	3	19	3	5	2	0
	High	13	11	1	5	0	0	22	0	2	8	14	0
Total		32	40	41	25	40	23	43	41	15	33	45	3

Biomass

Envelopes containing the roots and shoots were placed in an 70°C oven for 48 hours. Samples were removed from the envelopes and then weighed to the nearest 0.01 mg (Denver Instrument CD A-200DS balance) and recorded.

Statistical analysis

Field data

Biomass and cover data both measure plant abundance; cover emphasizes aboveground abundance and light capture. The biomass and cover data were highly correlated (Table 7 and Figure 4). Since my hypotheses were based largely on light capture, which is better reflected by cover, cover data were used for all of the analysis.

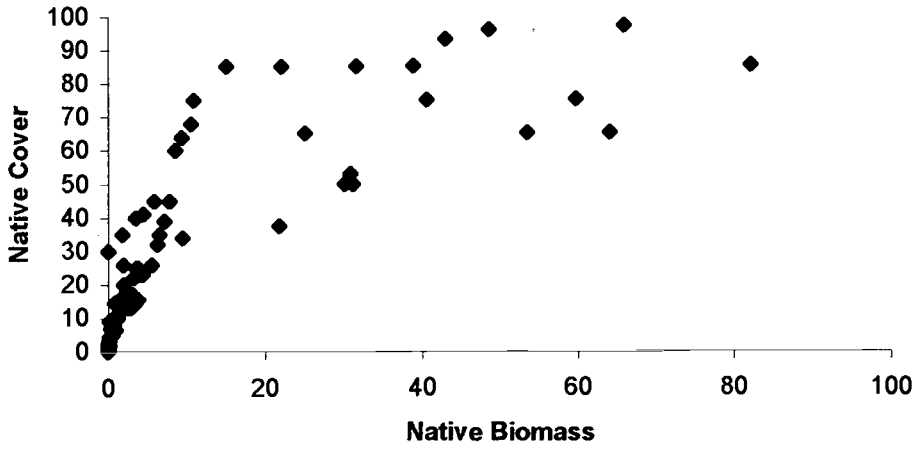
Analysis of variance (ANOVA) was used to determine whether the amount of sown non-native and unsown species varied by treatment (different native species). The protected Least Significant Difference (LSD), the most sensitive of the valid methods for representing group differences, was used to determine whether the means of the different groups differed significantly (Ramsey and Schafer 1997). S-PLUS 2000 was used for this analysis (MathSoft Inc. 1998-1999).

A linear regression model was used to test for treatment differences in the amount of remaining ryegrass in each plot. Biomass of ryegrass was log transformed (and 0.01 added) to meet the assumptions of the statistical tests and block and density were included in the model.

Table 7: Pearson correlation coefficients between cover and biomass data

Variables	Upland	Wetland
Native cover and biomass	0.93	0.91
Non-native cover and biomass	0.83	0.83
Unsown species cover and biomass	0.80	0.72

Figure 4: Correlation between native cover and native biomass (both sites combined).



Backwards stepwise regression was used to generate a linear model explaining the patterns in the field data. Stepwise regression in S-PLUS uses the Cp statistic as a measure of goodness of fit. This is a statistic which rewards accuracy while penalizing model complexity (MathSoft Inc. 1998-1999). The response variable in the wetland was log-transformed due to the funnel-shaped pattern of the residuals. Transformations of the remaining variables were not necessary. Five explanatory field variables were used in the full models of sown non-native plus unsown species cover: number of individuals, native cover, species identity, height, and number of inflorescences. Native species installment density and block, which are both field design variables, were fixed into the reduced models. S-PLUS 2000 was used for this analysis (MathSoft Inc. 1998-1999).

Laboratory data

The classical approach to growth analysis, as outlined in Hunt et al. (1993), was used for analysis of the laboratory data. Relative growth rate (RGR), leaf area ratio (LAR), net assimilation rate (NAR), leaf weight ratio (LWR), and specific leaf area (SLA) were calculated from the laboratory data (Table 8). The growth rates (RGR and NAR) are calculated with a log-transformation in their equation. The growth ratios (SLA, LAR, LWR) were calculated and then log-transformed for statistical analysis. Samples with both shoot and root weights that did not register on the scale (<0.005 mg) were removed from the analysis because a zero for plant weight cannot be log transformed or used in the denominator of the growth equations (n=3). The analysis for

Table 8: Rates and ratios used in this study.* All growth ratios were calculated for each plant then averaged separately for the 7 and 21 day samples for each species. W = plant weight, $\hat{W}$ = average plant weight, LA = leaf area, $\hat{A}$ = average leaf area, LW = leaf weight, ΔT = 21 day – 7 day.

Rates and Ratios	Definitions and interpretations	Equation	Units
Relative growth rate (RGR)	The relative increase in plant material per unit of time.	$= (\ln\hat{W}_{21}-\ln\hat{W}_7)/\Delta T$	day^{-1}
Leaf area ratio (LAR)	The amount of leaf area per unit of total plant biomass. A measure of the relative leafiness of the plant. A morphological index of plant form	$= LA/W$	cm^2/mg
Net assimilation rate (NAR)	The net gain in weight per unit of leaf area. A physiological index closely connected with the photosynthetic activity of the leaves; this also takes into account losses of respiration.	$= (\hat{W}_{21}-\hat{W}_7)(\ln\hat{A}_{21}- \ln\hat{A}_7)/(\Delta T)(\hat{A}_{21}-\hat{A}_7)$	mg/cm^2day
Leaf weight ratio (LWR)	The amount of leaf biomass per total plant weight; measures the plant allocation to leaves.	$=LW/W$	unitless
Specific leaf area (SLA)	The amount of leaf area per leaf weight; a measure of leaf thickness.	$=LA/LW$	cm^2/mg

*Table contents compiled from Vernon and Alison (1963), Radosevich et al. (1997), and Zobel (1998)

the growth rates and ratios was conducted on the data set for all twenty-two species resulting in 811 data points in the analysis.

The growth solution used for each growth period was converted into three categorical variables representing low, intermediate (a mix of high and low over the growth period), and high concentrations of growth solution. Regression analysis was used to determine whether or not the differences in growth solution had an effect on the response variables (plant weight, leaf area, LAR, LWR, and SLA). In S-PLUS, plant weight, leaf area, LAR, LWR, and SLA were used separately as response variables and day (7 or 21), growth solution code (low, intermediate, or high), and species were used as the explanatory variables to test the effects of the growth solution. Growth solution did have an effect on all of the response variables except leaf weight ratio (Table 9). Therefore, it was necessary to adjust the growth variables to a common growth solution.

Regression analysis was used to predict the values of the rates and ratios (plant weight, leaf area, LAR, LWR, and SLA) at the intermediate growth solution concentration for the 7 day and the 21 day harvests. *Wyethia angustifolium* was omitted from the predicted-values analysis and hence from the subsequent analysis of the laboratory results because three replicates were not enough to generate predicted values. Therefore, rates and ratios for *Wyethia angustifolium* are not adjusted to the intermediate growth solution. Extreme outliers, those data points with Studentized residuals greater than 3.8 and ratios (LAR and SLA) greater than 3, were removed to better meet the assumptions of the statistical tests. Removal of outliers resulted in eliminating 6 out of 811 entries for the LAR analysis, 3 out of 811 entries for the LWR analysis, and 17 out of 811 entries for the SLA analysis. Statgraphics Plus 4.0 (Statistical Graphics Corp. 1994-

Table 9: Effect of growth solution on plant weight, leaf area, leaf weight ratio, specific leaf area, and leaf area ratio. Amount of growth solution administered had a significant effect on all response variables except leaf weight ratio.

Response variable	Model F, R^2, *P*	Explanatory variables	df	MS	F	*P*
Plant weight	$F_{27,779}$=47.3, R^2=62%, *P*<0.001	Species	25	312.528	33.143	0.000
		Growth solution code	1	1384.398	146.811	0.000
		Day	1	2856.461	302.919	0.000
		Residuals	779	9.430		0.000
Leaf area	$F_{27,779}$=41.2, R^2=59%, *P*<0.001	Species	25	34.891	24.630	0.000
		Growth solution code	1	295.923	208.897	0.000
		Day	1	409.197	288.860	0.000
		Residuals	779	1.417		0.000
Leaf weight ratio	$F_{27,779}$=5.8, R^2=17%, *P*<0.001	Species	25	0.092	5.564	0.000
		Growth solution code	1	0.035	2.114	0.146
		Day	1	0.255	15.474	0.000
		Residuals	779	0.017		0.000
Specific leaf area	$F_{27,776}$=4.4, R^2=13%, *P*<0.001	Species	25	0.989	3.487	0.000
		Growth solution code	1	9.081	32.027	0.000
		Day	1	0.000	0.000	0.988
		Residuals	776	0.284		
Leaf area ratio	$F_{27,777}$=6.0, R^2=17%, *P*<0.001	Species	25	0.594	4.736	0.000
		Growth solution code	1	5.307	42.299	0.000
		Day	1	0.056	0.443	0.506
		Residuals	777	0.125		

1999) was used to identify outliers in this analysis and the predicted values for rates and ratios were generated in S-PLUS 2000 (MathSoft Inc. 1998-1999). Correlation coefficients between growth rates and ratios were generated in Statgraphics Plus 4.0 (Statistical Graphics Corp. 1994-1999).

Nine intrinsic native species characteristics were used to generate separate models for the patterns of native cover and sown non-native plus unsown species cover: RGR, LAR, NAR, SLA, LWR, laboratory germination rate, phenology (month of establishment in the field), seed weight, and growth form (graminoid or forb). Values for seed weight were obtained from the Geurrant and Raven (1995) study of Willamette Valley prairie species. Growth ratios can be determined for either the seven or the 21 day harvest period; therefore, both values were used in the model to determine which was more important for predicting field patterns. Forward regression in S-PLUS 2000 (MathSoft Inc. 1998-1999) was used to generate models predicting the variation in native cover and in sown non-native plus unsown species based on laboratory characteristics. Field design variables (block and density of installed native) were also fixed into these models.

Integrated models

Hierarchical models were used to determine which variables, species traits or field variables, better explained the variation in non-native plus unsown species cover. This was done by fixing the species traits with significant explanatory power into the model and adding the field variables to see if any field variables had additional explanatory

power. Then, the field variables with significant explanatory power were fixed into the model and the species traits were added to see if they had additional explanatory power. The field design variables (block and density of installed native) were fixed into all of these models. These models were generated for each site, upland and wetland, in S-PLUS 2000 (MathSoft Inc. 1998-1999). All ANOVA tables presented are Type 1 ANOVA tables.

Hypothesis

Pearson correlation coefficients were used to assess the hypothesized relationships between specific traits and sown non-native plus unsown species cover using S-PLUS 2000 (MathSoft Inc. 1998-1999).

RESULTS

Field plots

Cover of sown non-native plus unsown species

Sown non-native species cover ranged from 0% to 24% ($\bar{x}$=8.0) (upland) and from 0% to 38% ($\bar{x}$= 7.0) (wetland). All unsown species at the upland site were non-native species. At the wetland site, there were a few plots with a small amount of unsown native species; however, unsown native species were never the dominant unsown species in a plot. Unsown species cover ranged from 5.5% to 38% ($\bar{x}$= 17.0) (upland) and from 0.3% to 40% ($\bar{x}$= 18.0) (wetland). The ryegrass remaining after weeding did not vary by treatment (P=0.60, R^2=0.16)

Effects of treatments on non-native species

The non-native cover[i] varied by treatment in both the upland ($F_{8, 55}$= 2.7, P=0.012, Figure 5) and the wetland ($F_{8, 59}$=6.6, P<0.001 Figure 6) (Table 10). At the upland site, plots sown with *Wyethia angustifolia* and *Potentilla gracilis* had similar average (unadjusted means) non-native cover (32% and 29%, respectively), than plots sown with

[i] For the remainder of this paper non-native cover refers to the sum of sown non-native species cover and unsown species cover.

Figure 5: Unadjusted mean non-native cover and standard error at the upland site. Groups with the same letters are not significantly different (protected LSD with adjusted means).

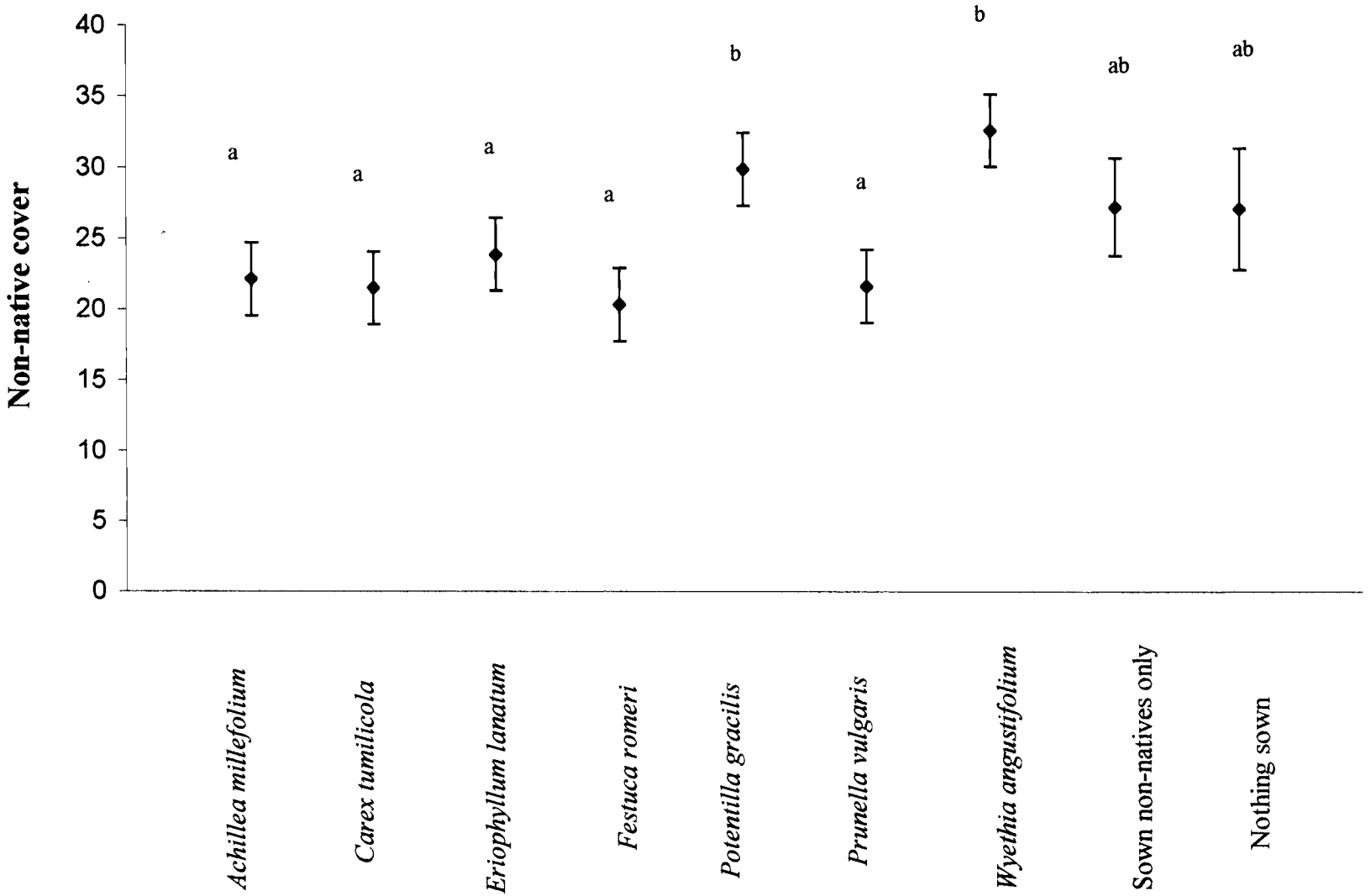


Figure 6: Unadjusted mean non-native cover and standard error at the upland site. Groups with the same letters are not significantly different (protected LSD with adjusted log transformed means).

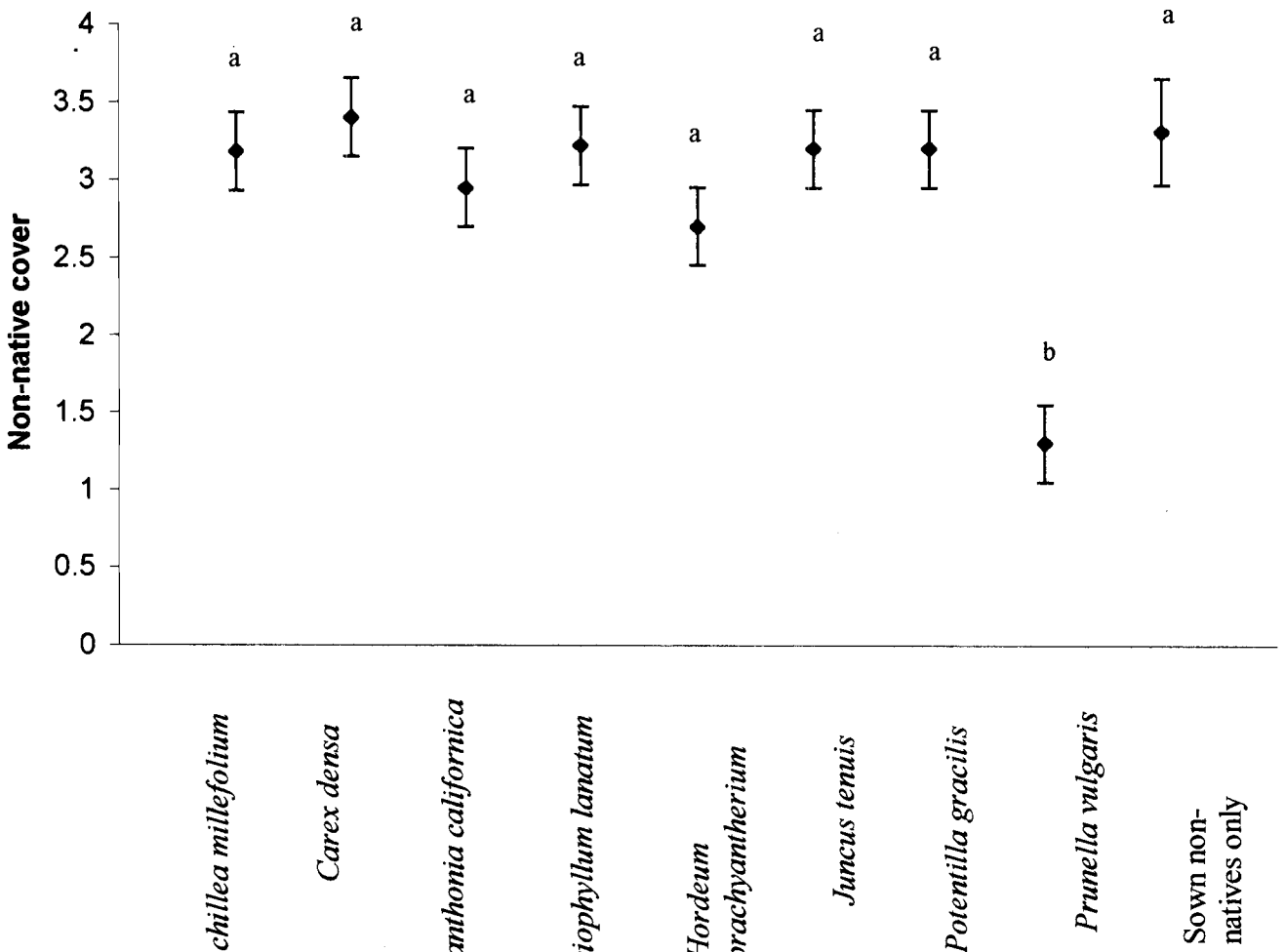


Table 10. Unadjusted means and standard error for non-native cover at both sites.

Species	Mean non-native cover	Standard error
Upland		
Achillea millefolium	21.61	2.03
Carex tumilicola	20.97	2.53
Eriophyllum lanatum	23.34	2.56
Festuca roemeri	19.81	2.32
Potentilla gracilis	29.34	2.73
Prunella vulgaris	21.09	1.83
Wyethia angustifolia	32.09	3.14
Sown non-natives only	29.41	2.26
Nothing sown	29.25	3.82
Wetland		
Achillea millefolium	25.13	3.26
Carex densa	34.38	5.39
Danthonia californica	22.75	5.58
Eriophyllum lanatum	28.63	5.75
Hordeum brachyantherum	15.38	1.88
Juncus tenuis	28.44	4.87
Potentilla gracilis	27.88	5.63
Prunella vulgaris	5.10	1.18
Sown non-natives only	39.56	7.14

non-natives only (29%) and the unsown plots (29%). Plots sown with *Festuca roemeri* had the lowest average non-native cover (20%). At the wetland site (Figure 6), the plots sowed with non-natives only had the highest non-native cover (39%). Plots sown with *Prunella vulgaris* had the lowest average non-native cover (5%).

Field variables predicting non-native cover

At the upland site, stepwise backward regression selected number of individuals, producing a model that explained 19% of the variability in non-native cover ($F_{5, 62}$=2.9, P=0.021, Table 11). At the wetland site, stepwise backward regression selected native cover and number of inflorescences, producing a model that explained 56% of the variability in non-native cover ($F_{6, 65}$=14.0, P<0.001, Table 12).

Native cover, number of individuals, and native species biomass were all inversely correlated with non-native cover at both sites, but the correlation coefficients were higher at the wetland site (Table 13). Number of inflorescences and height were strongly negatively correlated with non-native cover at the wetland site, but not at the upland site. Native species installation density was not strongly correlated with non-native cover at either site.

Species traits

Average germination rates for the eleven species ranged from 0% for *Juncus tenuis* to 95% for *Hordeum brachyantherum* (Table 14). Since *Juncus tenuis* did not germinate in the laboratory studies, it was not included in the analysis of laboratory traits.

Table 11. Parsimonious model of non-native cover at the upland site. Stepwise backward regression selected the single variable Number of individuals. The field design variables (Block and Sowing density) were forced into the model. $F_{5, 62}$=2.9, P=0.021, R^2=19% for the model.

Source	df	MS	F	P
Model				
Block	3	11.809	0.213	0.887
Sowing density	1	298.561	5.391	0.023
Number of individuals	1	462.692	8.355	0.005
Residuals	62	55.381		

Table 12. Parsimonious model of non-native cover at the wetland site. Stepwise backward regression selected the single variable Number of individuals. The field design variables (Block and Sowing density) were forced into the model. The response variable was log-transformed. $F_{6, 65}$=14.0, P=0.000, R^2=56% for the model.

Source	df	MS	F	P
Model				
Block	3	0.492	1.227	0.307
Sowing density	1	2.552	6.369	0.014
Number of inflorescences	1	26.707	66.658	0.000
Native cover	1	2.951	7.366	0.009
Residuals	65	0.401		

Table 13: Values represent Pearson correlation coefficients between field variables and non-native cover at each site. Non-native cover was log transformed at the wetland site. This data set includes the unsown plots at the wetland and the plots sown with with non-native species only at both sites. *Wyethia angustifolium* and *Juncus tenuis* are also included in these analysis.

Field variables	Upland	Wetland
Density	-0.11	-0.13
Height	-0.04	-0.51
Number of inflorescences	-0.08	-0.73
Native cover	-0.27	-0.71
Number of individuals	-0.38	-0.53
Biomass native	-0.27	-0.57

Table 14: Means ± standard deviation for germination rates (%) determined under laboratory conditions (n=125).

Achillea millefolium (upland)	82.4 ± 1.8
Achillea millefolium (wetland)	78.4 ± 1.5
Carex densa	91.2 ± 1.1
Carex tumilicola	12.8 ± 1.8
Danthonia californica	52.8 ± 3.1
Eriophyllum lanatum (upland)	28.0 ± 5.0
Eriophyllum lanatum (wetland)	20.8 ± 2.6
Festuca roemeri	44.8 ± 3.1
Hordeum brachyantherum	95.2 ± 1.3
Juncus tenuis	0.0
Potentilla gracilis (upland)	24.0 ± 2.1
Potentilla gracilis (wetland)	19.2 ± 2.5
Prunella vulgaris (upland)	75.2 ± 2.7
Prunella vulgaris (wetland)	94.6 ± 1.8
Wyethia angustifolia	19.2 ± 0.8

The values for growth rates and ratios reported in this section are those fitted to an intermediate level of growth solution (see Methods for details). *Achillea millefolium* (wetland) (0.18/day) had the highest RGR and *Wyethia angustifolium* (0.06/day) had the lowest RGR (Table 15). *W. angustifolium* had the highest 21 day total plant weight (20.0 mg), followed by *H. brachyantherum* (12.5 mg) and *Prunella vulgaris* (6.9 mg upland and 8.5 mg wetland). However, *P. vulgaris* had a larger leaf area at 21 days than *W. angustifolium*. *W. angustifolium* also had the thickest leaves as represented by specific leaf area and *P. vulgaris* had the thinnest leaves. There was less variation among species in leaf weight ratio 21 days (0.663 to 0.890) than in other traits such as plant weight (0.94 mg to 20.0 mg), leaf area (0.21 cm^2 to 3.7 cm^2), relative growth rate (0.06/day to 0.18/day), and leaf area ratio (0.176 cm^2/mg to .452 cm^2/mg). Growth ratios for the 7 and 21 day harvest were significantly correlated for all traits (Table 16). Relative growth rate was highly correlated with seven day leaf area ratio (r=0.84) and specific leaf area (r=0.86), but those correlations were weaker for the 21 day values (r=0.33 and r=0.36), respectively (Table 16). Leaf area was positively correlated with all traits except net assimilation rate (Table 16).

Species traits predicting field performance

Native species performance

The native species traits that best explained the field patterns in native cover differed at each site. In the upland site, stepwise forward regression selected the

Table 15: Predicted values for plant size, growth rates, and ratios under an intermediate growth solution (see Methods and Table 8). Values for plant size and ratios have been back-transformed.

	Plant weight 7 day (mg)	Plant weight 21 day (mg)	Leaf area 7 day (cm^2)	Leaf area 21 day (cm^2)	Relative growth rate (per day)	Net assimilation rate (mg/cm^2day)
Achillea millefolium (upland)	0.288	3.382	0.104	1.119	0.176	1.035
Achillea millefolium (wetland)	0.191	2.691	0.105	1.017	0.189	0.890
Carex densa	0.172	0.943	0.026	0.409	0.086	0.791
Carex tumilicola	0.380	1.135	0.034	0.205	0.078	1.131
Danthonia californica	1.510	5.007	0.297	1.327	0.086	0.726
Eriophyllum lanatum	0.676	3.421	0.148	1.323	0.116	0.732
Festuca roemeri	0.441	2.724	0.069	0.537	0.130	1.429
Hordeum brachyantherum	1.913	12.466	0.457	2.337	0.134	1.309
Potentilla gracilis	0.328	1.722	0.064	0.477	0.118	0.968
Prunella vulgaris (upland)	1.138	6.898	0.349	2.930	0.129	0.679
Prunella vulgaris (wetland)	1.107	8.554	0.319	3.721	0.146	0.768
Wyethia angustifolia	8.655	20.010	0.972	3.515	0.060	0.820

Table 15, Continued

	Leaf area ratio 7 day (cm^2/mg)	Leaf area ratio 21 day (cm^2/mg)	Leaf weight ratio 7 day (unitless)	Leaf weight ratio 21 day (unitless)	Specific leaf area 7 day (cm^2/mg)	Specific leaf area 21 day (cm^2/mg)
Achillea millefolium (upland)	0.351	0.340	0.790	0.821	0.443	0.416
Achillea millefolium (wetland)	0.346	0.385	0.837	0.874	0.425	0.442
Carex densa	0.148	0.406	0.760	0.663	0.194	0.427
Carex tumilicola	0.094	0.185	0.543	0.717	0.175	0.260
Danthonia californica	0.187	0.265	0.791	0.833	0.234	0.282
Eriophyllum lanatum	0.221	0.382	0.833	0.822	0.266	0.464
Festuca roemeri	0.149	0.205	0.742	0.793	0.199	0.261
Hordeum brachyantherum	0.227	0.187	0.758	0.829	0.296	0.225
Potentilla gracilis	0.198	0.283	0.817	0.772	0.244	0.367
Prunella vulgaris (upland)	0.291	0.438	0.748	0.785	0.385	0.562
Prunella vulgaris (wetland)	0.274	0.452	0.814	0.780	0.333	0.585
Wyethia angustifolia	0.105	0.176	0.950	0.890	0.111	0.197

Table 16: Numbers represent Pearson correlation coefficients between growth rates and ratios.

	Plant weight 7 day	Plant weight 21 day	Leaf area 7 day	Leaf area 21 day	Relative growth rate	Net assimilation rate
Plant weight 7 day	-					
Plant weight 21 day	0.84	-				
Leaf area 7 day	0.87	0.97	-			
Leaf area 21 day	0.69	0.92	0.93	-		
Relative growth rate	-0.16	0.38	0.30	0.45	-	
Net assimilation rate	-0.07	-0.04	-0.21	-0.36	0.11	-
Leaf area ratio 7 day	0.11	0.57	0.58	0.74	0.84	-0.33
Leaf area ratio 21 day	-0.18	0.07	0.14	0.45	0.33	-0.81
Leaf weigh ratio 7 day	0.06	0.38	0.41	0.56	0.52	-0.37
Leaf weight ratio 21 day	0.36	0.62	0.65	0.54	0.65	0.05
Specific leaf area 7 day	0.09	0.55	0.55	0.69	0.86	-0.28
Specific leaf area 21 day	-0.16	0.08	0.13	0.44	0.36	-0.75

Table 16, Continued

	Leaf area ratio 7 day	Leaf area ratio 21 day	Leaf weight ratio 7 day	Leaf weight ratio 21 day	Specific leaf area 7 day	Specific leaf area 21 day
Plant weight 7 day						
Plant weight 21 day						
Leaf area 7 day						
Leaf area 21 day						
Relative growth rate						
Net assimilation rate						
Leaf area ratio 7 day	-					
Leaf area ratio 21 day	0.61	-				
Leaf weight ratio 7 day	0.74	0.58	-			
Leaf weight ratio 21 day	0.66	-0.01	0.51	-		
Specific leaf area 7 day	0.97	0.54	0.54	0.64	-	
Specific leaf area 21 day	0.58	0.97	0.47	-0.03	0.55	-

variables plant weight (7 day) and germination rate, producing a model that explained 83% of the variability in native cover ($F_{6,41}$=34.3, P<0.001, Table 17). In the wetland site, stepwise forward regression selected the variables leaf area (21 day), leaf weight ratio (21 day), and net assimilation rate, producing a model that explained 87% of the variability in native cover ($F_{7,48}$=46.9, P<0.001, Table 18). Germination rate, leaf area, plant weight, leaf area ratio (7 day), and specific leaf area (7 day) were all positively correlated with native species cover at both sites (Table 19). Leaf area ratio (21 day) and specific leaf area (21 day) were also positively correlated with native species cover at the upland site, but not at the wetland site. Phenology was negatively correlated with native cover at both sites. There were no strong correlations between native cover and relative growth rate and leaf weight ratio (7 or 21 day) at either site.

Non-native species performance

The native species traits that best explained the patterns in non-native cover in the field differed at each site. In the upland, stepwise forward regression selected the variables leaf weight ratio (21 day) and seed weight, producing a model that explained 23% of the variability in non-native cover ($F_{6,41}$=2.0, P=0.087, Table 20). In the wetland, stepwise forward regression selected the variables leaf area (21 day) and leaf weight ratio (21 day) producing a model that explained 46% of the variability in non-native cover ($F_{6,49}$=7.0, P<0.001, Table 21).

There were no strong correlations between individual species traits and non-native cover in the upland site (Table 22). However, in the wetland site, germination rate, leaf

Table 17. The native species traits that best explain the field response in native cover at the upland site. $F_{6, 41}=34.3$, $P<0.001$, $R^2=83\%$ for the model.

Source	df	MS	F	*P*
Model				
Block	3	40.75	0.474	0.702
Density	1	1135.88	13.207	0.001
Plant weight (7 day)	1	14416.15	167.617	0.000
Germination rate	1	2045.77	23.786	0.000
Residuals	41	86.01		

Table 18. The native species traits that best explain the field response in native cover at the wetland site. $F_{7, 48}=46.9$, $P<0.001$, $R^2=87\%$ for the model.

Source	df	MS	F	*P*
Model				
Block	3	47.18	0.303	0.823
Density	1	12.87	0.083	0.775
Leaf area (21 day)	1	42148.20	270.523	0.000
Leaf weight ratio (21 day)	1	6484.45	41.620	0.000
Net assimilation rate	1	2342.25	15.033	0.000
Residuals	48	155.80		

Table 19. Values represent Pearson correlation coefficients between each species trait and native cover at each site.

Species Trait	Upland	Wetland
Forb or graminoid	0.29	-0.01
Germination rate	0.50	0.54
Phenology	-0.46	-0.65
Seed weight	0.16	0.39
Leaf area (7 day)	0.80	0.70
Leaf area (21 day)	0.65	0.84
Plant weight (7 day)	0.78	0.65
Plant weight (21 day)	0.79	0.80
Relative growth rate	-0.25	0.26
Net assimilation rate	-0.55	0.27
Leaf area ratio (7 day)	0.43	0.34
Leaf area ratio (21 day)	0.62	-0.09
Leaf weight ratio (7 day)	0.18	-0.17
Leaf weight ratio (21 day)	-0.14	0.15
Specific leaf area (7 day)	0.47	0.36
Specific leaf area (21 day)	0.64	0.03

Table 20. The native species traits that best explain the field response in non-native cover at the upland site. $F_{6,41}=2.0$, $P=0.087$, $R^2=23\%$ for the model.

Source	df	MS	F	*P*
Model				
Block	3	34.499	0.784	0.510
Density	1	8.459	0.192	0.663
Seed weight	1	158.895	3.609	0.065
Leaf weight ratio (21 day)	1	258.363	5.869	0.020
Residuals	41	44.023		

Table 21. The native species traits that best explain the field response in non-native cover at the wetland site. The response variable was log-transformed. $F_{6,49}$=7.0, P<0.001, R^2=46% for the model.

Source	df	MS	F	*P*
Model				
Block	3	0.623	1.190	0.323
Density	1	0.762	1.433	0.237
Leaf area (21 day)	1	16.270	30.610	0.000
Leaf weight ratio (21 day)	1	3.506	6.597	0.013
Residuals	49	0.532		

Table 22. Pearson correlation coefficients between species traits and field variation in non-native cover.

Species Trait	Upland	Wetland
Forb or graminoid	0.26	-0.15
Germination rate	-0.12	-0.32
Phenology	0.12	0.41
Seed weight	-0.23	-0.09
Leaf area (7 day)	0.07	-0.43
Leaf area (21 day)	-0.05	-0.58
Plant weight (7 day)	0.04	-0.38
Plant weight (21 day)	-0.06	-0.48
Relative growth rate	-0.17	-0.20
Net assimilation rate	-0.21	0.02
Leaf area ratio (7 day)	0.11	-0.28
Leaf area ratio (21 day)	0.16	-0.13
Leaf weight ratio (7 day)	0.21	-0.04
Leaf weight ratio (21 day)	-0.15	-0.07
Specific leaf area (7 day)	0.06	-0.28
Specific leaf area (21 day)	0.18	-0.23

area, and plant weight were negatively correlated with non-native cover. Phenology was positively correlated with non-native cover.

Comparing models

Hierarchical models were used to assess Objective 4, which was to determine whether the intrinsic species traits or the field variables have more explanatory power for predicting the non-native cover (see Methods).

Upland

No field variables added statistically significant explanatory power to models with the field design variables and the significant native species traits (seed weight and leaf weight ratio) (Table 20). Two of the native species traits (growth form and specific leaf area) added statistically significant explanatory power to models with field design variables and the significant plant field variables (number of individuals) (Table 23). Thus, intrinsic species traits appear to contribute additional explanatory power beyond field performance.

Wetland

The field variables (native cover and number of inflorescences) provided additional explanatory power beyond that of the native species traits (leaf weight ratio

Table 23. Native species traits selected from stepwise forwards regression with the upland field variables fixed and native species traits added. $F_{7,40}$=2.0, P=0.076, R^2=26% for the model.

Source	df	MS	F	P
Model				
Block	3	34.499	0.800	0.501
Density	1	8.459	0.196	0.660
Number of individuals	1	211.603	4.909	0.032
Growth form	1	160.734	3.729	0.061
Specific leaf area (7 day)	1	125.687	2.916	0.095
Residuals	40	43.104		

and leaf area) (Table 24). Native species traits did not add statistically significant explanatory power to models with the field design variables and the significant explanatory field variables (native cover and number of inflorescences) (Table 25). This model is slightly different from Table 11 because the analysis with the laboratory variables does not include the plots sown with *Juncus tenuis* or non-native species only.

Table 24. Variables selected from stepwise forwards regression with the native species traits fixed and wetland field variables added. The response variable was log-transformed. $F_{8,47}=10.8$, $P<0.001$, $R^2=65\%$ for the model.

Source	df	MS	F	*P*
Model				
Block	3	0.633	1.744	0.171
Sowing density	1	0.762	2.100	0.154
Leaf area (21 day)	1	16.269	44.843	0.000
Leaf weight ratio (21 day)	1	3.506	9.664	0.003
Number of inflorescences	1	6.629	18.273	0.000
Native cover	1	2.363	6.512	0.014
Residuals	47	0.363		

Table 25. Variables selected from stepwise forwards regression with the native species traits fixed and wetland field variables added. The response variable was log-transformed. $F_{6,49}=14.2$, $P<0.001$, $R^2=64\%$ for the model.

Source	df	MS	F	*P*
Model				
Block	3	0.633	1.752	0.169
Sowing density	1	0.762	2.110	0.153
Native cover	1	24.284	67.247	0.000
Number of inflorescences	1	3.841	10.636	0.002
Residuals	49	0.361		

DISCUSSION

Are there differences among native species in their abilities to reduce the establishment of non-native species in the first growing season?

The first objective of this study was to determine whether there were differences in the ability of native species to reduce non-native cover in the field. The species with lower non-native species cover (Table 10), such as *Festuca roemeri, Prunella vulgaris, Achillea millefolium, Carex tumilicola*, and *Hordeum brachyantherum,* would be good choices for restoration. Whereas, *Potentilla gracilis* and *Wyethia angustifolium* did not suppress non-natives at all so these species would be poor choices for site capture.

Some of the characteristics of native species field performance that corresponded to a reduction in non-native species cover were similar for both sites, although the patterns were stronger in the wetland (Table 13). At both sites, abundance of natives, as measured by native cover, native biomass, and number of individuals, resulted in a reduction of non-native cover. Presumably, the mechanism for the reduction in non-native cover was that increased use of resources by native species reduced the amount of resources (light, nutrients, and water) available for the non-native species growth. Ross and Harper (1972) also found that the occupation of biological space, as measured by the density of individuals, is the most important factor for reducing the establishment of future individuals. At the wetland site, height and more inflorescences also caused a reduction in non-native cover suggesting that native plant vigor also increases the use of resources such as nutrients and water. Increased use of resources by natives means fewer

resources are available by non-native species, resulting in a reduction in the non-native species cover when the natives in the same plot are flowering. Height and number of inflorescences were less important in the wetland, but this may be because there was a narrower range in the values for these parameters at the upland site compared to the wetland site (Table 26).

These results are consistent with the findings of Ross and Harper (1972). Native species use of resources appears to decrease the amount of resources available for non-native species growth resulting in a decrease in non-native cover in the first growing season. If intrinsic species traits can be used to predict the field performance of both native and non-native species, then these traits can be used to identify field performance of species not included in this study.

Intrinsic traits of Willamette Valley native prairie species

The second objective of this study was to quantify the intrinsic traits of native prairie species. The range in values and correlations for species traits was comparable to other studies, which contributes to the validity of the values obtained for growth rates and ratios in this study. There was a two and a half-fold difference in leaf area ratio, and a three-fold difference in specific leaf area values, but there was less variation in leaf weight ratio (less than 2-fold). This suggests that among herbaceous Willamette Valley prairie species, there may be larger variation within leaf characteristics compared to the amount of variation in species allocation to roots.

There was a three-fold difference in relative growth rate values in this study which compares to those found in other studies (Poorter and Remkes 1990, Van der Werf

Table 26. Values for height and number of inflorescences at the wetland and upland site.

Field variables	Upland		Wetland	
	Range	Mean ±SD	Range	Mean ±SD
Height (cm)	0-8	2.66 ±2.50	0-40	8.45 ±12.14
Number of inflorescences	0-4	0.15 ±0.61	0-67	5.93 ±16.94

et al. 1998). Grime and Hunt (1975) found a twelve-fold difference in relative growth rate values, but that study involved herbaceous, shrub, and woody species. Within one growth form there may be less variation in relative growth rate and other growth parameters.

Relative growth rate was highly correlated with seven day leaf area ratio and specific leaf area (Table 16). Other studies have also found relative growth rate and leaf area ratio area to be highly correlated (Van der Werf 1998), suggesting that plant allocation to leaves results in more rapid accumulation of plant biomass (Poorter and Remkes 1990).

Once species traits have been quantified, they can form a basis for explaining differences in the field performance of the species.

Species traits predicting field performance

Native species performance

Intrinsic traits explained a large amount of the variation in native cover at both sites. At the upland site, species with a large 7-day plant weight and a high germination rate in the laboratory studies also had high native cover in the field (Table 27). This suggests that the more seeds that germinate in the field, the more seedlings that will survive which will lead to an increased establishment rate and increased native cover. Indeed, field establishment rate and native cover are also highly correlated ($r=0.81$). Clark et al. (2001) also found that 7-day plant weight in the laboratory predicted seedling establishment rates in the field.

Table 27: Native species traits and model coefficients that predict field performance.

Site	Native Cover		Non-native cover	
	Model coefficient	Trait	Model coefficient	Trait
Upland	33.55	Plant weight (7 day)	-9.26	Seed weight
	0.26	Germination rate	-80.90	Leaf weight ratio
Wetland	45.73	Leaf area (21 day)	-0.94	Leaf area (21 day)
	-165.86	Leaf weight ratio	3.53	Leaf weight ratio (21 day)
	34.48	Net assimilation rate		

At the wetland site, high 21-day leaf area (21 day), low 21-day leaf weight ratio, and high net assimilation rate predicted increased native cover in the field (Table 27). A large photosynthetic area allows capture of light resulting in increased growth and cover. Poorter and Remkes (1990) found leaf area ratio, which incorporates leaf area, to be the most important predictor of species function and they concluded that allocation to photosynthetic organs may lead to the most rapid accumulation of plant biomass[ii].

Leaf weight ratio is the only ratio used in this study that measures plant allocation to roots and acquisition of below-ground resources. Low leaf weight ratio, or increased allocation to plant roots, predicted higher native cover.

It might seem contradictory to have increased native cover with species that have high leaf area and large allocation to roots. This combination of traits suggests that large plant weight would be an important explanatory variable. Indeed, plant weight and native cover are strongly correlated, almost as much as leaf area (21 day) and native cover (Table 25). Large leaves and large allocation to roots can also occur in thin leaved plants. Indeed, specific leaf area is negatively correlated with native cover ($r = -0.36$).

High net assimilation rate also predicted high native cover, thus, net assimilation rate may be acting in concert with morphological capture of light to increase native cover. Roush and Radosevich (1985) also found net assimilation rate, along with leaf area ratio and plant weight, to predict species field behavior.

[ii] Poorter and Remkes (1990) did not include leaf area in their analysis.

Non-native species field performance

Intrinsic traits of native species also significantly predicted the field performance of non-native species, although the amount of variation explained was lower than the amount of variation explained in the models that predicted native cover (83% and 87% native cover vs. 23% and 46% non-native cover). This is to be expected since non-native cover depends upon other factors such as their germination rate and dispersal to the site, in addition to their response to native species use of available resources.

There were differences in the native species traits that explained non-native species cover in the upland and the wetland. In the upland site, native species with high leaf weight ratio (21 day) tended to have lower non-native cover in their field plots (Table 24). Thus capture of above-ground resources may be more important than capture of below-ground resources for reducing non-native cover at the upland site. Native species with heavy seeds also tended to have lower non-native cover in their field plots. Jurado and Westoby (1992) found that seedlings from heavier-seeded species were larger 10 days after soil wetting than seedlings with lighter seeds. Thus, it is possible that larger seeded species in this study became relatively larger seedlings resulting in increased resource uptake and decreased non-native cover.

In the wetland site, the native species traits that predict non-native cover were largely the same as those that predicted native species cover. This suggests that suppression of non-natives occurs because of specific native traits that produce large plants which usurp limiting resources from non-native plants. For example, native species with large leaves are intercepting light and reducing the establishment of non-native species. Within those species that have large leaves, those that also have a high

allocation to roots (or a low leaf weight ratio), would have increased nutrient and water uptake.

None of the specific hypothesis about the relationships between individual traits and non-native cover were supported in the upland site (Table 22). Although the directions of the interrelationships between species traits and non-native cover were consistent in the wetland site, the first four predicted hypothesis were not supported by strong correlations between individual species traits (Table 22). However, Hypothesis 5 and 6 were strongly supported in the wetland site. The significant positive correlation between phenology and non-native cover ($r = 0.16$ upland and $r = 0.43$ wetland) suggests that native species that germinate early in the growing season will reduce the resources available for non-native species growth. The negative correlation between native cover and non-native species cover ($r = -0.17$ upland and $r = -0.62$ wetland) suggests that increased native cover reduces the amount of light resources available for non-native species.

Comparing models

In the upland site, the combination of the laboratory variables seed weight and leaf weight ratio (21 day) explains a slightly larger amount of the variation in non-native cover (R^2=23%) than the significant field variable, number of native plants per plot (R^2=19%). Moreover, growth form and specific leaf area (7 day) explain additional variation in non-native cover beyond that of the number of native plants per plot. Growth form and 7-day specific leaf area were not selected as explaining the majority of the variation in the regression models. However, they must explain a different aspect of the

variation than the number of individuals, leaf weight ratio, and seed weight. The native graminoids (growth form) and thin leaved natives (specific leaf area) had less non-native cover growing in their plots.

In contrast, at the wetland site, significant native species traits were less successful in explaining patterns of non-native cover (R^2=46%) than were significant field variables (R^2=56%). In addition, species traits added no significant explanatory power when added to the model using field variables, but field variables did add additional explanatory power over just laboratory traits. This result is consistent with the very strong connection between laboratory traits and field cover (R^2=87%): laboratory traits largely determine field cover and once field cover is in the statistical model, laboratory traits did not offer much more explanatory power. But details of field conditions modifying field cover and vigor (as seen in the number of inflorescences) are important in determining the actual suppression of non-native cover.

Differences between upland and wetland site

Plant weight, leaf area, and germination rate were highly correlated with native cover at both sites (Table 19), however, the traits selected in predictive models varied at each site. Species traits that measure native species size and abundance (plant weight and germination rate) were better predictors of native cover in the upland site, whereas, specific aspects of resource capture (leaf area, leaf weight ratio, and net assimilation rate) were more important at the wetland site. These site specific differences may be due to pre-treatment site differences, or due to inherent differences between wetland and upland sites or species. This is difficult to determine because only one upland and one wetland

site were investigated. However, one inherent difference between uplands and wetlands is that wetlands are flooded throughout the winter; therefore, when water levels drop, there may be more immediate competition for resources. Thus, species with a large leaf area, high allocation to roots, and a high net assimilation rate early in their growing stages (7 and 21 days) may be able to gain cover and take up resources the most rapidly in the first growing season. In contrast, at the upland site, conditions allow plants to acquire resources in the winter (for fall germinating species) and in the early spring. Thus, number of individuals established is more important at the upland site than immediate competition for resources as water levels drop. If early competition is slight, native plants that establish in the fall to early spring have a competitive advantage over non-natives that are just beginning to establish in the late spring. This explanation is supported by the findings of other studies in which the early phenology of resource uptake confers a competitive advantage (Ross and Harper 1972, Goldberg and Miller 1990).

Meaning of results for ecological restoration

Currently, there are no predictive methods for selecting species for restoration. To choose species for restoration, restoration practitioners use species lists from reference sites; knowledge of the site such as its successional stage, landscape position, hydrologic regime, and historical condition; and species availability. Models that use species traits to predict native cover and/or non-native cover could be used in lieu of or in addition to current methods to select species for restoration. For example, the models generated in this study (Table 28) predicted 83% (upland) and 87% (wetland) of the variation in native

Table 28: Models using species traits to predict field performance.

Upland

Native cover = 33.55 (Plant weight$_{7\ day}$) + 0.26 (Germination rate)

Non-native cover = — 9.26 (Seed weight) — 80.90 (Leaf weight ratio$_{21\ day}$)

Wetland

Native cover = 45.73 (Leaf area$_{21\ day}$) — 165.86 (Leaf weight ratio$_{21\ day}$)

+ 34.48 (Net assimilation rate)

Non-native cover = 3.53 (Leaf weight ratio$_{21\ day}$) — 0.94 (Leaf area$_{21\ day}$)

cover. Choosing the right species though the use of these predictive models could double native cover compared to the use of average species. For non-native cover, these models predict 23% (upland) and 46% (wetland) of the field variation. These models suggest that native species with traits conferring increased light use may be most effective at reducing non-native species cover, presumably through light capture in the first growing season. Choosing the right species though the use of these predictive models could decrease non-native cover 12% in upland sites and 29% in wetland sites compared to non-native cover when average species are used.

To use the models for species selection during a restoration project, one would measure the traits that are in the model for several native species (following the methods in this paper). Then, one would plug in the values for the species traits measured and choose those species with the highest predicted values for native cover and/or those species with the lowest predicted values for non-native cover. As trait measurements accumulate, new laboratory studies may not be required. A database of species characteristics is being readied for public access (M.V. Wilson, pers. comm.), making existing information on species traits readily available. Of course, the models generated in this study should be field tested to see if the results are repeatable at other field sites and with other species before the models are widely applied.

Not all species traits are needed to improve species selection. Germination rate, an easily measured trait (and a trait that has already been measured for several species), predicted 50% (upland) and 54% (wetland) of the field variation in native cover. Thus, choosing species with a high germination rate should increase native species cover even though this was not one of the most important traits selected in the wetland models.

Because of the high correlation between phenology and non-native cover in the wetland, I recommend planting wetland restoration sites in the fall rather than the spring. However, planting date may also depend upon the hydrologic regime of a site and fall planting may be less appropriate for sites with a different hydrologic regime from this site, such as high water flow or deep inundation throughout the winter.

Selection of native species that have high cover and/or reduce the cover of non-native species should be an important step in restoring ecosystems. The more effectively native species can capture the resources of a disturbed restoration site, the more they can decrease non-native cover in the first growing season. Then, as the site matures, phased plantings of other native species could be installed to increase species diversity.

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