

Provenance, life span, and phylogeny do not affect grass species' responses to nitrogen and phosphorus

ERIC W. SEABLOOM,^{1,5} CARA D. BENFIELD,² ELIZABETH T. BORER,¹ AMANDA G. STANLEY,³ THOMAS N. KAYE,³ AND PETER W. DUNWIDDIE⁴

¹*Department of Ecology, Evolution, and Behavior, 100 Ecology Building, University of Minnesota, St. Paul, Minnesota 55108 USA*

²*Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA*

³*Institute for Applied Ecology, P.O. Box 2855, Corvallis, Oregon 97339-2855 USA*

⁴*School of Forest Resources, University of Washington, Seattle, Washington 98195 USA*

Abstract. Successful conservation management requires an understanding of how species respond to intervention. Native and exotic species may respond differently to management interventions due to differences arising directly from their origin (i.e., provenance) or indirectly due to biased representations of different life history types (e.g., annual vs. perennial life span) or phylogenetic lineages among provenance (i.e., native or exotic origin) groups. Thus, selection of a successful management regime requires knowledge of the life history and provenance-bias in the local flora and an understanding of the interplay between species characteristics across existing environmental gradients in the landscape. Here we tested whether provenance, phylogeny, and life span interact to determine species distributions along natural gradients of soil chemistry (e.g., soil nitrogen and phosphorus) in 10 upland prairie sites along a 600-km latitudinal transect running from southern Vancouver Island in British Columbia, Canada, to the Willamette Valley in Oregon, USA. We found that soil nitrate, phosphorus, and pH exerted strong control over community composition. However, species distributions along environmental gradients were unrelated to provenance, life span, or phylogenetic groupings. We then used a greenhouse experiment to more precisely measure the response of common grass species to nitrogen and phosphorus supply. As with the field data, species responses to nutrient additions did not vary as a function of provenance, life span, or phylogeny. Native and exotic species differed strongly in the relationship between greenhouse-measured tolerance of low nutrients and field abundance. Native species with the greatest ability to maintain biomass production at low nutrient supply rates were most abundant in field surveys, as predicted by resource competition theory. In contrast, there was no relationship between exotic-species biomass at low nutrient levels and field abundance. The implications of these findings for management of invasive species are substantial in that they overturn a general belief that reduction of nutrient supplies favors native species. The idiosyncratic nature of species response to nutrients in this study suggests that manipulation of nutrient supplies is unlikely to alter the overall balance between native and exotic species, although it may well be useful to control specific exotic species.

Key words: *colimitation; competition; exotic species; grasslands; invasion ecology; resource competition; restoration ecology; soil.*

INTRODUCTION

A primary goal of conservation and restoration management is to increase the abundance of native species and reduce exotic-species dominance. A variety of management interventions have been used to accomplish the goal of fractionating communities based on species provenance (i.e., native vs. exotic origin; Hobbs and Humphries 1995); however, the effectiveness of these interventions is difficult to predict a priori. As a result, many management plans are of necessity heuristic and idiosyncratic (Palmer et al. 1997, Seabloom et al.

2003c, Young et al. 2005). While management interventions are most frequently intended to selectively impact communities based on species' provenance (e.g., to reduce exotic cover or increase native cover), basic research in community and invasion ecology suggests that provenance is only one of at least three axes of species characteristics that may govern species performance in response to management (Brandt et al. 2009). Two other axes that have also been suggested as important determinants include life history and phylogeny (Brandt et al. 2009).

While species-specific methods exist to control exotic species (e.g., specialized biological control agents or hand-pulling), most management interventions are more broadly targeted (e.g., manipulation of burning regime, herbicide application, or generalist consumers), and are

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⁵ E-mail: seabloom@umn.edu

only effective if the members of the exotic community have a shared susceptibility to the management that is distinct from that of the native community (Shea and Chesson 2002, Mitchell et al. 2006, Parker et al. 2006, Orrock et al. 2008). In reality, most management actions, such as burning or altering nutrient supplies, variably impact a community based on species phenotypes, life history, or phylogeny, as opposed to provenance per se (Hobbs and Humphries 1995, Mitchell et al. 2006). For example, burning to remove invasive woody species or spraying taxa-specific (e.g., grass or broadleaf) pesticides can be effective for controlling exotic species only when the invasive community is biased towards species that are susceptible to burning (i.e., woody species) or narrow-spectrum herbicides (Ansley and Castellano 2006, Stanley et al. 2011). Similarly, manipulation of resource supply rates may alter the abundance of exotic species only if they differ systematically from natives in their resource use patterns (Tilman et al. 1999, Daehler 2003, Harpole et al. 2007, Perry et al. 2010). Greater clarity about the general effects of management actions will arise from a mechanistic understanding of the direct and indirect pathways by which management actions alter exotic dominance. Here we describe a framework for grassland management based on three plant characteristic axes: provenance, life history, and phylogeny.

Provenance is the plant characteristic most restoration activities seek to target and, in some situations, provenance may drive species responses directly. For example, exotic species may flourish in an introduced area because they are released from the pressure of natural enemies allowing them to allocate more resources to competition rather than defense (enemy release and evolution of increased competitive ability hypotheses; Mitchell et al. 2006). Biological control is an example of a management technique that directly targets an invasive plant's provenance by re-associating it with an effective enemy from its native range, thereby reducing its density and impact in the invaded community (McEvoy et al. 1991). Conversely, exotic species also may suffer disproportionately from enemies in their introduced range, because they have not had the time and opportunity to evolve effective resistance (new associations hypothesis; Mitchell et al. 2006). Exotic species also may be able to exploit unoccupied niches by accessing underutilized resources or create new niches by removing competitors through the release of allelopathic compounds (the novel niche and novel weapons hypotheses; Mitchell et al. 2006). On the other hand, native species may be better competitors in harsh environments, such as in sites where resources are limited (Daehler 2003, Perry et al. 2010), presumably because native plants have evolved to tolerate the stress of resource limitation (Vitousek et al. 1997). For example, many of the most successful grass invaders evolved in association with agriculture and hooved grazers and thus are particularly strong competitors in

areas with grazing or high nutrient supply rates (Mack 1989), and management strategies such as burning, C addition, and topsoil removal are employed to reduce nutrient availability and favor native species (Perry et al. 2010).

The second axis of species characteristics that can be considered when selecting a management regime is life history, including life span, fecundity, seed size, dispersal rates, and resource requirements. Species with novel life histories have been shown to be more effective invaders (Fargione et al. 2003), and provenance may covary with life history. For example, in some areas exotic floras have a disproportionate frequency of certain life history groups such as annual or nitrogen-fixing species (Vitousek et al. 1987, Seabloom et al. 2006). Managers can exploit these life history biases to reduce exotic dominance. For example, species with an annual life span direct their energies to rapid above-ground growth to maximize reproductive output in a single season. In contrast, perennial species invest in belowground structures to maximize their resource capture abilities, enabling them to compete more effectively for water and nutrients (Grime and Hunt 1975, Jackson and Roy 1986, Garnier 1991, Holmes and Rice 1996). Because of the dependence of annual species on their yearly reproductive output, varying the frequency of disturbances such as mowing or burning can reduce the relative abundance of exotic annual species in native, perennial-dominated communities (D'Antonio and Vitousek 1992, Stromberg and Griffin 1996, Seabloom et al. 2003b).

Finally, the phylogenetic lineage from which a species has descended may determine its response to management (Cavender-Bares et al. 2009). Traits shared by closely related native and exotic species may cause them to have similar responses to management. On the other hand, if phylogenetic relatedness also means that species have strongly overlapping resource needs, then Darwin's naturalization hypothesis predicts that invaders most closely related to native species will be least successful at establishing in a novel location, or that a closely related native may be at highest risk of extinction (Mitchell et al. 2006, Strauss et al. 2006). Phylogeny can be a focal characteristic for managers. For example, the grass-specific herbicide Poast (active ingredient sethoxydim), to which some grass genera are resistant (Stanley et al. 2008, *in press*), is commonly used in grassland restoration.

Alteration of nutrient supply rates is an example of a perturbation that has been shown to lead to shifts in relative abundance of species that differ in terms of the three characteristics discussed above: provenance, life history, and phylogenetic lineage (Huenneke et al. 1990, Woo and Zedler 2002, Brewer and Cralle 2003, Seabloom et al. 2005, Siemann and Rogers 2007). For example, previous work suggests that increased nitrogen availability can confer a competitive advantage to invasive exotic species (Vitousek et al. 1987, Mack

1989, Huenneke et al. 1990), and there is correlative evidence that lower nitrogen levels can reduce competitive pressure from exotics (Daehler 2003, Lowe et al. 2003, Seabloom et al. 2003a, Harpole 2006). Manipulating the resource supply to favor a suite of desirable (i.e., native) species or reduce the abundance of the undesirable component (i.e., exotic species) of the community could form the foundation for an effective management technique, if growth response to nutrient supply could be predicted from measurable species characteristics (Harpole 2006). Furthermore, community theory provides a framework in which we can understand the effects of nutrient supply on community composition, because resource competition and spatial variability in resource supply rates form the core of some of the most well-known mechanisms governing species coexistence (e.g., the resource ratio theory [Tilman 1982] and the spatial storage effect [Chesson 2000]).

Here, we examined the role of nutrient availability in determining the composition of a suite of coexisting native and exotic Pacific Northwestern upland C₃ prairie grasses. Specifically, we looked for predictable relationships between the species characteristics of provenance, life span, and phylogeny in response to natural and constructed gradients of plant nutrients. We addressed the following questions: (1) Are changes in grass community composition along natural soil resource gradients predictable based on species' provenance, phylogeny, and life span? (2) Are changes in growth and biomass allocation of grass species along experimental resource gradients in greenhouse experiments predictable based on species' provenance, phylogeny, and life span? (3) Are species' distributions in the field predicted by their ability to maintain growth at low nutrient supply rates in greenhouse experiments? We used resource competition theory to link field and greenhouse results. Specifically, we predicted that the most competitive species will be those that are able to maintain the highest growth rate at the lowest nutrient supply rates (Tilman et al. 1982, Miller et al. 2005). Resource competition theory also predicts that the coexistence of many species only can occur along resource ratio gradients if there are trade-offs in the efficient use of multiple resources (Tilman et al. 1982, Miller et al. 2005). We tested for growth trade-offs between nitrogen and phosphorus use efficiency, a possible mechanism of coexistence among these grasses.

METHODS

Study system

The Willamette Valley–Puget Trough–Georgia Basin Ecoregion (WPG) is a 5.5 million ha area of coastal and intermontane alluvial lowlands that span a latitudinal gradient of 600 km in Oregon and Washington, USA, and British Columbia, Canada (Franklin and Dyrness 1973). The WPG is undergoing rapid conversion of natural areas to urban, agricultural, or production forestry (Altman et al. 2001, Floberg et al. 2004).

Prairies in the WPG are among the most endangered habitats in the U.S.; only 0.1% of the historical range of Pacific Northwest native prairies remains today (Noss et al. 1995). The enduring fragments are severely degraded by nonnative species and encroachment by woody vegetation (Altman et al. 2001, U.S. Fish and Wildlife Service 2008), and as such, are targets for ecological restoration. Pacific Northwest prairies differ from mid-continental U.S. prairies because of their Mediterranean climate characterized by cool, wet winters and hot, dry summers (Xu and Baldocchi 2004). As a result, all grass species in this study are C₃ (Smith and Brown 1973), as is typical of the grass flora along the Pacific coast. West Coast prairies experience lower nitrogen deposition than their Midwestern counterparts (0–2 kg N/ha vs. 2–3 kg N/ha; National Atmospheric Deposition Program 2007), and relatively low measures of plant-available nitrogen are recorded in Pacific Northwest prairie soils ($10.8 \pm 1.0 \mu\text{g NH}_4^+/\text{g soil}$ and $1.8 \pm 0.2 \mu\text{g NO}_3^-/\text{g soil}$ [mean \pm SE]; S. M. Griffith and M. Nelson, *unpublished data*; and 1.8 ± 0.3 – $9.1 \pm 0.3 \mu\text{g NH}_4^+/\text{g soil}$ and 0.7 ± 0.1 – $2.4 \pm 0.2 \mu\text{g NO}_3^-/\text{g soil}$; Pfeifer-Meister and Bridgman 2007). We focus on the grass portion of the flora because members of the family Poaceae have high natural diversity in Pacific Northwestern prairies (Sinclair et al. 2006), and species of this family receive considerable management attention because they are overrepresented as natural-area invaders (Mack 1989, Daehler 1998, Seabloom et al. 2006, Stanley et al., *in press*).

Question 1: Grass community composition along natural soil resource gradients

We sampled plant composition and soils in 10 intact, partially degraded, upland prairie fragments arrayed along a 600-km latitudinal transect running from the central Willamette Valley in western Oregon, USA, through the Puget Trough–Georgia Basin Ecoregion in Washington State, to the Cowichan Valley, British Columbia (Fig. 1). The data were collected from untreated control plots that were part of a larger experiment (see Stanley et al. [2008] for detailed experimental design; also Stanley et al. [*in press*]). We estimated percent cover of all plant species and ground cover (lichens, bryophytes, litter, rock, and bare ground) in four 1 \times 1 m quadrats nested within each of the four 5 \times 5 m control plots at each site between late April and mid May 2005 and 2006 for a total of 320 quadrats (10 sites \times 4 plots \times 4 quadrats \times 2 years). We averaged the percent cover data from all 32 quadrats and plots collected across two years at each site (4 plots \times 4 quadrats \times 2 years) to obtain values of mean cover for each of the 10 sites. We collected soil samples from three randomly selected positions within each plot. The soil cores, drawn from a 10–15 cm depth, were pooled and later analyzed at the USDA Agricultural Research Service (ARS) laboratory (Corvallis, Oregon, USA) for the percentage of soil moisture, pH, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$,

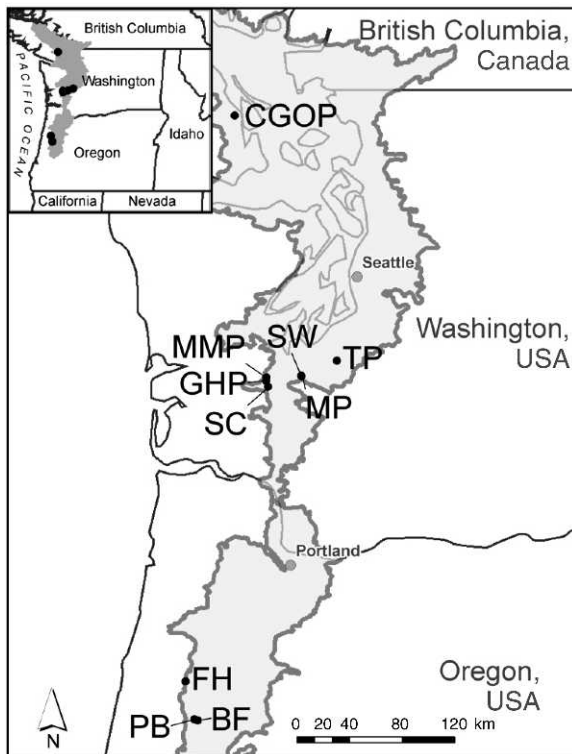


FIG. 1. Map of study sites in the Willamette Valley–Puget Trough–Georgia Basin (WPG) Ecoregion. From north to south: Cowichan Garry Oak Preserve (CGOP), The Nature Conservancy of Canada; Triangle Prairie (TP) (13th Division) and South Weir Prairie (SW), Joint Base Lewis-McChord, U.S. Department of Defense; Morgan Property (MP) (Tenalquot Prairie), The Nature Conservancy; Mima Mounds Preserve (MMP), Washington Department of Natural Resources; Glacial Heritage Preserve (GHP), Thurston County Parks/The Nature Conservancy; Scatter Creek Wildlife Area (SC), Washington Department of Fish and Wildlife; Fort Hoskins (FH), Benton County Natural Areas and Parks Department; Bellfountain (BF) and Pigeon Butte (PB), Finley National Wildlife Refuge, U.S. Fish and Wildlife. Figure and caption reprinted from Stanley et al. (2008), with permission from the authors.

total organic carbon, total nitrogen (N), and total phosphorus (P) (Table 2; S. M. Griffith and M. Nelson, *unpublished data*). We focused on N and P as these are general and interactive drivers of ecosystems (Elser et al. 2007), and we included pH because it has strong effects on nutrient availability (e.g., P availability declines with pH). We note that other micronutrients are important to many communities including Pacific coastal grasslands (Harpole et al. 2007, Harpole and Tilman 2007); however, we were not able to address these here.

We calculated the average percent cover across two years of data and arcsine square-root-transformed the species proportional cover data to improve normality. We then relativized the matrix by species maxima to equalize species' abundances (McCune and Grace 2002). In our analyses, we removed a rare species that only occurred in two plots at a single site, *Melica subulata*, as

this single occurrence did not provide information on species distributions along soil chemistry gradients.

Nonmetric multidimensional scaling (NMS) was used to ordinate sampling plots in terms of species abundance (Kruskal 1964, Mather 1976). The analysis, which was run with PC-ORD statistical software (version 5.04; McCune and Mefford 2006) on Autopilot set to "slow and thorough" using Sørensen's distance measure, began with a random starting configuration and ran through 250 iterations to find the single solution with the lowest stress and instability. The best dimensionality of the solution was assigned by PC-ORD and verified by a scree plot of final stress vs. dimensions of the solution.

Mantel tests were used to determine whether there was a correlation between the soil chemistry variables and the NMS ordination scores of sample units in species space to account for the inherently multivariate and covarying nature of soil chemistry and plant abundance data (Mantel 1967, McCune and Grace 2002). This method calculates the standardized Mantel statistic (r) as a measure of effect size, which is equivalent to the Pearson correlation coefficient between the corresponding elements of two matrices standardized by the variances in the two matrices. Monte Carlo randomization tests (1000 iterations) were used to evaluate the test statistic using PC-ORD (McCune and Mefford 2006).

We tested whether the species' distributions along environmental gradients in the field surveys were associated with their provenance, life history, or phylogenetic groupings using RLQ analysis. Specifically, we used RLQ analysis to test for co-structure between the soil variables sampled from the field observational plots (**R** matrix) and the life history, provenance, and phylogenetic groupings of the grasses observed there (**Q** matrix), using grass species cover observed in each plot (**L** matrix) as a link (Dolédéc et al. 1996). RLQ analysis is a co-inertia (i.e., eigenvalue based) method that searches for associations between environmental variability and species attributes by first ordinating the **R**, **L**, and **Q** matrices separately using principal components analysis (i.e., PCA on a correlation cross-products matrix) for the **R** and **Q** matrices and correspondence analysis on the **L** matrix, then using the resulting site and species scores to constrain the selection of a new set of axes which maximize the covariance between the **R** and **Q** tables. RLQ analysis takes into account only a fraction of the total variance in the **R**, **L**, and **Q** matrices because the structure of the individual matrices can only be partially optimized due to the constraints imposed by a joint analysis. A Monte Carlo permutation test was used to examine the significance of the co-structure between **R** and **Q**; the null hypothesis was that **R** and **Q** were independent. Rows of tables **R** and **Q** were shuffled and the total co-inertia value for 1000 iterations was compared to the observed value. The RLQ procedures were conducted with the ade4 package (Thioulouse et al. 1997, Dray and Dufour 2007) in R (version 2.7.0; R Development Core Team 2008).

Question 2: Growth and biomass allocation along experimental soil resource gradients

Eleven species of grasses, eight of which occurred in the field observational plots, were included in a greenhouse experiment to investigate whether response to nutrient supply in controlled conditions varied predictably with the general species characteristics of phylogeny, provenance, and life span. All 11 species are C_3 grasses that occur in Willamette Valley upland prairies and were selected for inclusion in the experiment because they include an exotic annual, an exotic perennial, and a native perennial species from each of four tribes of the grass family (Poaceae). There are so few native annual grasses in the WPG grasslands that we were unable to include them in the study. Congeneric to con-tribal groupings of species were selected to explicitly account for phylogenetic biases in our results when testing for the effect of provenance and life history (Felsenstein 1985, Agrawal et al. 2005, Brandt et al. 2009). The species used in the greenhouse experiment accounted for $32\% \pm 6\%$ of the grass cover in the field plots. Seed for all species was either collected from local prairie reserves or purchased from local seed producers (Table A2).

Ungerminated seeds were planted into 6.4 cm diameter by 25 cm depth, 656-mL pots (Stuewe and Sons, Corvallis, Oregon, USA) containing a moistened mixture of 1:1:1 washed sand, perlite, and vermiculite. The seeds were allowed 5–10 d to germinate, and then germinants were thinned to the desired density of 1 or 10 plants per pot. Every pot was assigned to one of 18 possible treatments representing a full factorial combination of the following factors: nitrogen addition (0.2%, 1%, or 10% of half-strength Hoagland's nutrient solution), phosphorus addition (0.2%, 1%, or 10% of half-strength Hoagland's nutrient solution), and density (1 or 10 individuals per pot; Appendix: Table A3). We present the full composition of our Hoagland's solution in Appendix: Table A3. After germination and thinning, the pots were arranged in randomized positions on greenhouse benches (Corvallis, Oregon, USA) and were maintained at a natural daylight regime supplemented by irradiance from 500 W metal halide and 1000 W high pressure sodium bulbs at a $21^\circ\text{C}/16^\circ\text{C}$ temperature regime and 16 h/8 h day/night cycle.

All pots were treated semiweekly with a 50-mL fertilizer treatment alternating with a weekly watering of 50-mL reverse osmosis-treated water. The fertilizer solutions were modified from a half-strength Hoagland's nutrient solution (Hoagland and Arnon 1938, Downs and Hellmers 1975). The fertilizer solutions were modified to be nitrogen and phosphorus deficient, then NO_3^- -N and NH_4^+ -N as NH_4NO_3 and PO_4^{3-} -P as KH_2PO_4 were provided in a factorial combination at 0.2%, 1%, or 10% of the concentration prescribed in a half-strength Hoagland's recipe to yield nine possible fertilizer combinations (Table A3). The lowest levels of N and P used in our solutions provided the minimum

level of these nutrients for survival but not growth, based on a pilot study that included nitrogen and phosphorus levels as low as 0.1% of the concentration prescribed in a half-strength Hoagland's recipe (Benfield 2009).

Destructive samples of above- and belowground biomass were collected after 20 weeks of growth. Shoot samples were oven dried to constant mass at 60°C , and then weighed to the nearest 0.1 mg. Root samples were washed free of potting media under a stream of deionized water before they were dried and weighed. The procedure was repeated four times between September 2006 and June 2008, constituting four "runs," or time blocks.

We tested a suite of explanatory variables from the greenhouse nutrient limitation experiment using multiple regression with backward selection following Crawley (2005) to examine whether patterns of biomass addition and allocation to roots and shoots could be predicted on the basis of phylogeny, provenance, and life span. The biomass and root : shoot ratio data were limited to individuals that survived to the end of the experiment (i.e., 20 weeks); plants that died before the end of the experiment were not considered in the analysis. The response variables of total biomass and root : shoot ratio were logarithmically transformed to meet the assumptions of linear regression. Starting with a model containing all possible explanatory variables: temporal block, fertilizer N concentration, fertilizer P concentration, density, tribe, functional group (a combination of provenance and life span: exotic annual, exotic perennial, and native perennial), and all two- and three-way interactions, we used a stepwise model selection procedure to select the multiple linear regression models with the smallest Akaike's Information Criterion. All model selection and fitting procedures were performed in R (version 2.7.0; R Development Core Team 2008).

Question 3: Relationship between field distributions and response to experimental resource gradients

We summarized species responses to resource gradients in the greenhouse by calculating their ability to produce biomass in the most resource-limiting conditions, low nutrient addition rates, and high planting density. In each case, we calculated the biomass when the other nutrient was at high rates (i.e., low N with high P and low P with high N) to determine the effect of limiting only the target nutrient. We also calculated the biomass for each species at low N and low P as a metric of the ability to sustain growth when both nutrients were limiting. We tested for trade-offs between N and P use efficiency by testing for negative correlations between biomass at low N and low P. We also tested whether species able to maintain biomass at low N and P were more frequent (i.e., were present at a higher number of sites) or had higher cover in the field survey data.

TABLE 1. Phylogenetic group (tribe), life span, provenance, abundance, frequency in the field, and correlation (r) with field soil variables for the 22 grass species observed.

Species	Tribe, type	Life span	Provenance	Cover (%)	Frequency ($n = 11$)	Correlation with cover, r		
						NO ₃ ⁻	NH ₄ ⁺	Total P
<i>Agrostis</i> spp.	Poeae, Aveneae	perennial	exotic†	12.22 ± 4.1	9	-0.055	-0.331	-0.021
<i>Aira caryophyllaea</i>	Poeae, Poeae	annual	exotic	1.42 ± 1.1	5	0.145	-0.940	0.004
<i>Anthoxanthum odoratum</i>	Poeae, Aveneae	perennial	exotic	4.44 ± 3.5	4	0.968	0.510	0.958
<i>Arrhenatherum elatius</i>	Poeae, Aveneae	perennial	exotic	6.74 ± 4.9	4	-0.673	-0.204	0.586
<i>Bromus carinatus</i>	Bromeae	perennial	native	1.15 ± 0.8	4	0.997	0.990	0.936
<i>Bromus hordeaceus</i>	Bromeae	annual	exotic	2.51 ± 0.8	2	NS	NS	NS
<i>Bromus secalinus</i>	Bromeae	annual	exotic	0.92 ± 0.5	2	NS	NS	NS
<i>Bromus sterilis</i>	Bromeae	annual	exotic	5.97 ± 5.7	2	NS	NS	NS
<i>Cynosurus echinatus</i>	Poeae, Poeae	annual	exotic	0.31 ± 0.1	3	-0.079	0.405	-0.994
<i>Dactylis glomerata</i>	Poeae, Poeae	perennial	exotic	5.91 ± 5.4	2	NS	NS	NS
<i>Danthonia californica</i>	Danthonieae	perennial	native	0.57 ± 0.3	4	0.039	0.115	-0.550
<i>Danthonia spicata</i>	Danthonieae	perennial	native	0.84 ± 0.2	5	-0.355	0.129	-0.629
<i>Elymus glaucus</i>	Triticeae	perennial	native	1.13 ± 0.8	3	0.363	0.763	-0.943
<i>Festuca arundinacea</i>	Poeae, Poeae	perennial	exotic	0.95	1	NA	NA	NA
<i>Festuca roemerii</i>	Poeae, Poeae	perennial	native	3.38 ± 1.5	7	0.030	0.878	0.131
<i>Holcus lanatus</i>	Poeae, Poeae	perennial	exotic	1.45 ± 0.5	8	-0.638	-0.219	0.768
<i>Koeleria macrantha</i>	Poeae, Aveneae	perennial	native	0.25 ± 0.1	4	0.411	0.678	0.670
<i>Melica subulata</i>	Meliceae	perennial	native	0.28	1	NA	NA	NA
<i>Poa compressa</i>	Poeae, Poeae	perennial	exotic	0.47 ± 0.3	2	NS	NS	NS
<i>Poa pratensis</i>	Poeae, Poeae	perennial	exotic	2.16 ± 1.3	7	0.864	0.690	0.780
<i>Vulpia bromoides</i>	Poeae, Poeae	annual	exotic	0.36	1	NA	NA	NA

Notes: Assignment to taxonomic group follows Soreng et al. (2009). The most rare of these species, *Melica subulata*, was not included in the ordination analysis. Note that "NS" indicates correlations that were not significant at the $P = 0.05$ level, and "NA" indicates species present at a single site. Values for cover are means ± SE.

† Samples at a few sites may have contained very small amounts of the indistinguishable native *Agrostis pallens*.

RESULTS

Question 1: Grass community composition along natural soil resource gradients

The most abundant grass species observed in the field plots were *Agrostis* spp. (mix of *A. tenuis* and *A. pallens*), *Arrhenatherum elatius*, *Bromus sterilis*, and *Dactylis glomerata*, while the least abundant species were *Cynosurus echinatus*, *Melica subulata*, and *Koeleria macrantha* (Table 1). The most widespread species, those present at the highest number of sites, were *Agrostis* spp., *Holcus lanatus*, *Festuca roemerii*, and *Poa pratensis*, whereas *Schedonorus phoenix*, *M. subulata*, and *Vulpia bromoides* only occurred at one site each (Table 1). Of these species, only *Festuca roemerii*, *Melica subulata*, and *Koeleria macrantha* are native. Most of the sites had soils with low soil nitrogen typical of this region (Agriculture Water Quality Alliance 2009) and a narrow range of slightly acidic pH (Appendix: Table A1).

There were many strong species-specific correlations between cover and soil nutrients. For example, the cover of the perennial grasses *Anthoxanthum odoratum*, *Bromus carinatus*, and *Poa pratensis* was positively correlated with soil nitrate (Table 1). Cover of *B. carinatus* and *Festuca roemerii*, two native perennial species, was positively correlated with soil ammonium, while the exotic annual, *Aira caryophyllaea*, was negatively correlated with ammonium (Table 1). Two perennial species, *A. odoratum* and *B. carinatus*, were most strongly positively correlated with soil total phosphorus, while *C. echinatus* and *Elymus glaucus*

were strongly negatively correlated with total phosphorus (Table 1).

The nonmetric multidimensional scaling (NMS) ordination of samples in species space had a three-dimensional solution that accounted for 86.5% of the distance in the original data set (Monte Carlo test, $P = 0.0196$; final stress = 11.67, final instability = 0.00001 in 139 iterations). Axis 1 explained 41.7%, axis 2 explained 15.2%, and Axis 3 explained 29.6% of the variation in distance in the original data set. Mantel tests for correlation between soil chemistry variables and ordination scores of sample units in species space indicated that nitrate, total phosphorus, and pH were the most strongly positively associated with grass community composition and abundance, while ammonium was weakly positively associated (Table A4). We note that the effects of pH on the grass community are likely indirect through the effects of pH on phosphorus availability. While there were strong relationships between the grass community structure and local soil chemistry, the RLQ analysis did not reveal a significant association between soil chemistry variables and the higher order species groupings of phylogeny, provenance, and life span ($P = 0.109$; Monte Carlo permutation test).

Question 2: Growth and biomass allocation along experimental soil resource gradients

Total biomass was significantly affected by all individual variables examined in the greenhouse fertilizer study except phosphorus (Table 2). Nitrogen ($P <$

TABLE 2. Results of a regression model of per plant biomass (root + shoot) of 11 grass species grown for 20 weeks in a greenhouse under experimental gradients in nitrogen, phosphorus, and plant density.

Parameters	df	Deviance	F^\dagger	P
Run	1	19.14	241.38	<0.0001
Nitrogen	1	110.16	1389.23	<0.0001
Density	1	81.88	1032.54	<0.0001
Tribe	3	1.59	6.68	0.0002
Functional group	2	1.07	6.73	0.0013
Nitrogen \times density	1	4.15	52.36	0.0000
Nitrogen \times tribe	3	1.00	4.22	0.0057
Nitrogen \times functional group	2	0.61	3.87	0.0214
Tribe \times functional group	5	4.16	10.49	0.0000
Nitrogen \times tribe \times functional group	5	5.20	13.11	0.0000
Density \times tribe \times functional group	10	3.02	3.81	0.0001

† Total df = 757, and error df = 723.

0.001) and planting density ($P < 0.001$) were the two strongest main effects (Table 2). Nitrogen had significant two-way interactions with planting density, functional groups, and phylogeny (i.e., tribe membership; Table 2). Total biomass for plants planted at a density of 1 plant per pot increased more with nitrogen addition than plants planted at a density of 10 plants per pot (Fig. 2A). On average, an individual plant increased 10-fold between the lowest and highest level of fertilizer, but when growing with conspecifics, it only increased five-fold. There were also significant interactions between functional group membership and tribe, indicating that responses were species specific rather than being consistent among groupings (Table 2). For example, the species with the highest biomass were in different functional groups in each tribe: the exotic perennial in the Aveneae and Poeae tribes and the native perennial in the Bromaeae tribe (Fig. 2B).

Root:shoot ratio was affected by nitrogen, tribe membership, and functional group membership ($P < 0.001$). Interactions between nitrogen level and planting density ($P < 0.001$) and tribe and functional group membership ($P < 0.001$) also significantly affected root:shoot ratio. For plants planted singly, roots attained approximately three times the mass of shoots at the lowest level of nitrogen, twice the mass at the mid-level of nitrogen, and about one-and-a-half times the mass at the highest level of nitrogen (Fig. 3A). Plants planted at a density of 10 plants per pot had slightly lower root:shoot ratio than plants planted singly at the lowest and mid-level of nitrogen, but had a greater root:shoot ratio at the highest level of nitrogen used in the study (Fig. 3A). The native perennial representatives of the Aveneae tribe (*K. macrantha*) and Triticeae tribe (*E. glaucus*) had greater root:shoot ratios than species from other functional groups within those tribes while the exotic perennial representatives of the Bromaeae tribe (*B. inermis*) and Poeae tribe (*S. phoenix*) were the species with the greatest root:shoot ratios in their tribes (Fig. 3B).

Question 3: Relationship between field distributions and response to experimental resource gradients

We found no evidence of a trade-off between the ability to tolerate low levels of N and P. There was a

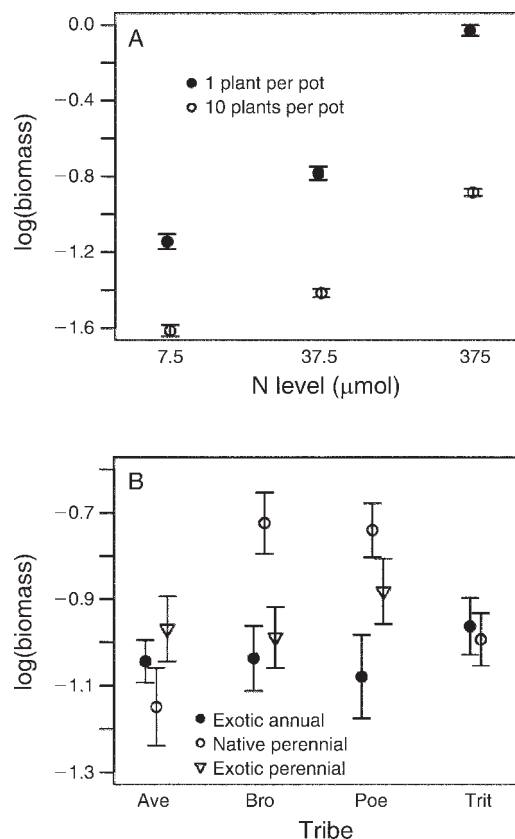


FIG. 2. Two-way interactions between the explanatory variables for total biomass in the greenhouse experiment. (A) Interaction between fertilizer nitrogen concentration and planting biomass at densities of 1 or 10 plants per pot. (B) Interaction between tribe membership and functional group. Biomass was originally measured in grams. Abbreviations are: Ave, Aveneae; Bro, Bromaeae; Poe, Poeae; and Tri, Triticeae). In all plots, error bars are \pm SE.

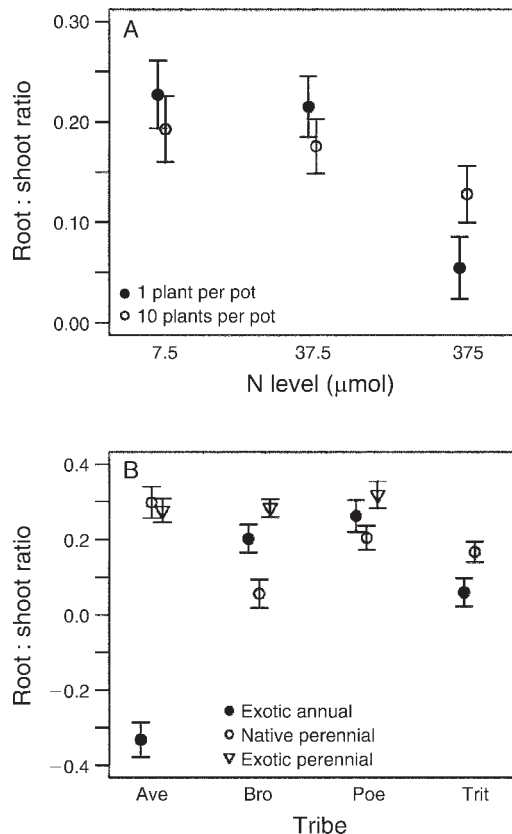


FIG. 3. Two-way interactions between the explanatory variables for root:shoot ratio in the greenhouse experiment. (A) Interaction between fertilizer nitrogen concentration and planting biomass. (B) Interaction between tribe membership and functional group. See Fig. 2 for abbreviations. In all plots, error bars are \pm SE.

positive, though nonsignificant, correlation between biomass at low N and biomass at low P ($r = 0.622$, $P = 0.099$). Across all species present in the greenhouse and field surveys, there was no evidence that the ability to sustain biomass production at low levels of N and/or P in the greenhouse could predict species abundance in the field, although all correlations were positive (though nonsignificantly so) as predicted by resource competition theory (Table 3). However, the lack of significance in the overall relationship arose from strong differences in the response of native and exotic grasses to resource limitation. For native species, correlations between biomass at low nutrient levels in the greenhouse and cover and frequency in the field ranged from 0.61 to 0.95, with the strongest and only significant relationship being between biomass when both N and P were limiting and mean cover in the field (Fig. 4). In contrast, correlations for exotic species were inconsistent (ranging from -0.42 to 0.87), and there was little variability in exotic biomass at low nutrient supplies. Only four native and four exotic species from our greenhouse studies were present in the field surveys, so only correlations greater than about 0.95 tested as significant.

DISCUSSION

Resource gradients, particularly nitrogen and phosphorus, shape the productivity and diversity of natural communities in terrestrial, freshwater, and marine systems (Elser et al. 2007, Hillebrand et al. 2007), and the interactions among plants within their nutrient resource environments has been an area active of investigation in invasion ecology (Huenneke et al. 1990, Daehler 1998, Seabloom et al. 2003c, Harpole 2006). Life history, provenance, and phylogeny are species characteristics that have been invoked to explain a plant species' predictable response to nutrients (Garnier 1991, Holmes and Rice 1996, Seabloom et al. 2003c). While it has been suggested that alteration of resource supply rates may provide a mechanism to reduce exotic abundances (Tilman et al. 1999, Corbin and D'Antonio 2004, Harpole 2006, Perry et al. 2010), we found that this approach would not be generally effective for restoration of Pacific Northwestern upland prairies.

Exotic and native species must have different growth responses to nutrient gradients for resource manipulation to be an effective tool to reduce exotic cover. We found that life history and provenance were highly confounded in the communities at our studies sites; for example, there were no native annual grasses found at any site. However, species responses to nutrient supply were not associated with provenance, life span, or phylogenetic groups in field surveys and greenhouse experiments. An important systematic difference between the native and exotic grasses was that native abundance in the field was highly correlated with the ability to maintain growth at low nutrient levels (R^*) as predicted by resource competition theory (Tilman 1982). In contrast, all exotic grasses were small and stunted at low nutrient levels, and there was no relationship between field abundance and R^* .

Resource competition theory provided a potential conceptual link between the field and greenhouse results by predicting, among other things, that species that can sustain growth at the lowest nutrient levels should be the dominant competitors in a community and that trade-offs must occur for variability in relative rates of resource supply to ease coexistence (Tilman 1982, Miller et al. 2005). Overall, there was no evidence of trade-offs in the ability to withstand low N or P supply rates, and there was little evidence that field distributions of these grasses were correlated with nutrient use patterns in the greenhouse studies.

However, the native and exotic species did differ. Intriguingly, patterns of field abundance of the native species were concordant with the predictions of resource competition theory (Tilman 1982). Natives that were better able to sustain growth at low resource levels were more abundant and widespread. This was not the case for the exotic species. While our statistical power was low, the large differences between the native and exotic flora suggest that interactions among native species may

TABLE 3. Correlations (r) between biomass at low nutrient level in greenhouse studies and local abundance (mean cover) and frequency of occurrence (number of sites with each species) of grass species in field surveys.

Species	Nitrogen level	Phosphorus level	Greenhouse biomass and field cover correlation	Greenhouse biomass and field frequency correlation
All species ($n = 8$)				
	low	high	0.366	0.695†
	high	low	0.364	0.502
	low	high	0.212	0.699†
Native species ($n = 4$)				
	low	high	0.832	0.613
	high	low	0.843	0.876
	low	high	0.952*	0.779
Exotic species ($n = 4$)				
	low	high	0.870	0.399
	high	low	0.073	0.159
	low	high	0.157	-0.419

Notes: All greenhouse metrics are estimated from high-density plantings. The only significant relationship (at $P < 0.05$) is between native-species field cover and biomass at low N and P due to low power of tests.

† Correlation significant at $P < 0.10$.

* Correlation significant at $P < 0.05$.

be of a fundamentally different nature than those between native and exotic species. Many exotic grasses have evolved in association with agriculture and grazing, and it is possible that their competitive success has been more tightly tied to general trade-offs other than efficient use of soil resources (Mack 1989), such as tolerance of herbivory, long-distance dispersal, or rapid

growth and resource preemption (Chesson 2000, Craine et al. 2005).

It is not surprising that gradients in nitrogen and phosphorus exert strong controls on community composition. These elements are vital for plant nutrition, and the soil N:P ratio creates a spatially heterogeneous environment controlling both plant composition and

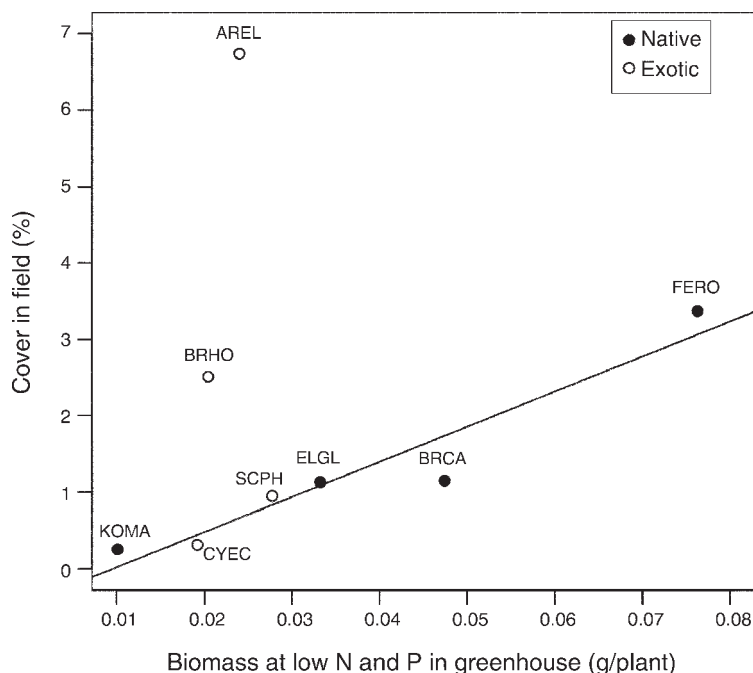


FIG. 4. Relationship between plant biomass at low nutrient levels in a greenhouse study and mean cover in field surveys of 11 natural grasslands. The regression line shows the relationship for native species; the regression was not significant ($P > 0.05$) for exotic species. Species codes are as follows: AREL, *Arrhenatherum elatius*; KOMA, *Koeleria macrantha*; BRHO, *Bromus hordeaceus*; BRCA, *Bromus carinatus*; CYNO, *Cynosurus echinatus*; SCPH, *Schedonorus phoenix*; FERRO, *Festuca roemerii*; and ELGL, *Elymus glaucus*.

productivity in wetland systems (Bedford et al. 1999), alpine tundra communities (Bowman et al. 1993), among herbaceous flora of serpentine soils (Huenneke et al. 1990, Harrison 1999), and in California central coast grassland flora (Gea-Izquierdo et al. 2007). The greenhouse experiments we used to isolate the specific effects of nutrient supply on plant growth response showed that grass biomass increased and allocation to roots decreased as additional nitrogen was delivered to greenhouse-grown plants, though phosphorus was never shown to significantly affect growth. The lack of a growth response to P reveals that our plants were not co-limited by N and P (N additions did not induce P limitations) at any of the N:P ratios supplied by the fertilizer, but were demonstrating the most efficient allocation of biomass for foraging for the limiting nutrient (Gleeson and Tilman 1992). We also did not find evidence of trade-off in the ability to tolerate nitrogen or phosphorus deprivation. The lack of a nitrogen-phosphorus trade-off may be expected, because these elements are tightly linked in plant tissues. N:P ratios are constrained across many plant taxa (Klausmeier et al. 2004, Niklas 2006, Reich et al. 2010), although they can vary systematically along global environmental gradients (Reich and Oleksyn 2004).

While abiotic conditions have been shown to correlate with species functional traits in a variety of natural systems including streams, coral reefs, and terrestrial fynbos (Thuiller et al. 2006, Bonada et al. 2007, de Voogd and Cleary 2007, Gea-Izquierdo et al. 2007), we did not find growth responses to field nutrient pools to be associated with the species characteristics of provenance, life span, or phylogenetic lineage for Pacific Northwestern prairie grass species. Total biomass and biomass allocation to growth, as measured in the greenhouse, varied among species, but concordant with the field response, this variation was not explained by the three plant characteristic axes of provenance, life span, and phylogeny; these characteristics do not provide strong a priori predictors for plant biomass and root : shoot allocation responses across a gradient of nutrient supply.

The conservative nature of trait evolution would be expected to impose a phylogenetic bias on trait associations (Cavender-Bares et al. 2009); however, we did not detect phylogenetic structuring within grass species' field abundance and/or biomass accumulation and allocation. Robust general patterns in plant growth response to nutrient additions also have failed to be detected within congeneric and confamilial groups in exotic invasive forbs (Hastwell and Panetta 2005, Muth and Pigliucci 2007) or between native and exotic terrestrial forbs of varying invasiveness (Leishman and Thomson 2005). However, the lack of a consistent phylogenetic response in the current study is in contrast to previous studies showing phylogenetic clustering of growth form and reproductive mode in woody Neotropical species (Chazdon et al. 2003) and rarity

within Canadian flowering plant assemblages (Cadotte and Lovett-Doust 2002). The traits examined in these studies (growth form and reproductive mode), are likely more highly conserved than the more plastic, and idiosyncratic, nutrient response that we tested. Ultimately, resolving the linkages between community processes, such as invasion and community assembly, and phylogeny requires a more general understanding of which species traits are both ecologically relevant and conserved (Cavender-Bares et al. 2009).

Nutrient manipulations of natural systems frequently produce plant biomass or species abundance changes among provenance groups (native vs. exotic plant species; Huenneke et al. 1990, Woo and Zedler 2002, Brewer and Cralle 2003, Seabloom et al. 2005, Siemann and Rogers 2007), sometimes with the ultimate effect of shifting the community composition toward an alternate dominant functional group (Brewer and Cralle 2003, Siemann and Rogers 2007). However, studies that have positively identified differences in grass species response along lines of provenance (Seabloom et al. 2003b, Abraham et al. 2009), life span (Wilson and Tilman 1991, Abraham et al. 2009), and phylogenetic relatedness (Brandt et al. 2009) frequently examine suites of species in which a provenance bias exists, confounding exotic provenance with functional group and phylogenetic group. Thus, while previous work suggests that management via manipulation of nutrient pools may be effective (Perry et al. 2010), the work presented here suggests that effective management depends strongly on the covariation of plant nutrient responses with provenance. We designed our experimental work to provide a balanced, phylogenetically independent assessment of the role of provenance in regulating species growth responses.

While a species' invasiveness is frequently reported to arise directly from its exotic provenance (Daehler 2003, Mitchell et al. 2006), our results suggest that other species characteristics that are confounded with exotic provenance (i.e., functional group [provenance and life span] and phylogenetic group) may control an invader's success. Several authors also have recently cautioned against relying on provenance as a principal species property to determine performance in response to nutrient supply, as the groupings of "exotic" and "native" are confounded with other shared or disparate characteristics occurring between those groups (Thomson et al. 2006, Borer et al. 2009a, Brandt et al. 2009). Indeed, our combined results from field observations and greenhouse manipulations support the assertion that there is no set response that characterizes "exoticness" in our system, because provenance is closely interleaved with phylogeny and life span. The potential management approach we have investigated here (controlling exotic-species abundance via nutrient manipulations) may be more effective in systems where the exotic species are less related to the natives and/or where exotic provenance is known to covary with a plant trait that can be more directly influenced with the

application of a management technique. For example, establishment of seeded perennial grasses was most successful at fertile and productive sites in California grasslands (Seabloom 2010), where the perennial grass flora is biased toward a native provenance, but the annual grass flora is largely of an exotic provenance (Seabloom et al. 2006).

Our results demonstrate that intraspecific competition reduced biomass accumulation and altered the root–shoot allocation patterns across the N fertilization gradient; under controlled greenhouse conditions, nitrogen was the most important driver of grass biomass accumulation and allocation to roots and shoots, but these effects were both species specific and density dependent. Thus, the inclusion of a high-density growing condition is clearly important for assessing resource uptake patterns that are experienced under equilibrial growth dynamics, in contrast with more transient growing conditions experienced at lower densities (Tilman et al. 1982, Miller et al. 2005).

The nature of the nutrient response in the field was more difficult to determine, as the interaction of grass species with their resource environment was not driven by a single species or soil characteristic. The implications of these findings for grassland restoration and management are that manipulations of a single critical nutrient will likely fail to enhance native-grass diversity in a predictable manner. However, species differ from one another in their resource use patterns, and resource competition theory may supply the key to control or enhancement of specific species (Tilman et al. 1999, Harpole 2006). For example, carbon addition (to reduce N availability) reduced the biomass of *Centaurea diffusa* by 95% in northern mixed-grass prairies (Blumenthal 2009) and suppressed *Phalaris arundinacea* invasion in prairie pothole wetlands (Perry et al. 2004), while Na⁺-charged zeolite additions suppressed *Bromus tectorum* emergence and abundance in the intermountain west (Newingham and Belnap 2006). More generally, this work stands as a case study of the need for stronger linkages between basic community theory and the development of restoration and exotic-species management plans (Shea and Chesson 2002, Young et al. 2005).

The phylogenetic scale of this work has certainly influenced our findings. Our consideration of species from a single family, Poaceae, separated into groups along lines of provenance, life span, and phylogenetic relatedness, revealed only idiosyncratic, species-level responses. However, an expansion of the taxonomic scope and scale of species considered for resource use patterns (to more heterogeneous groupings of species) may reveal strong, predictable nutrient responses across phylogeny, provenance, or life span. Indeed, studies of grassland community biomass response in fertilized and natural systems have shown that a detectable response is dependent on the scale at which biodiversity is measured, whether at the species, functional group, or phylogenetic level (Reich et al. 2004, Cadotte et al.

2008). For example, in an examination of Florida plant communities, Cavender-Bares et al. (2006) reported reduced phylogenetic overdispersion when she expanded the scale of her consideration from one of a single phylogenetic lineage to more broadly include all seed plants within a community.

This work has demonstrated that, while there are strong responses of species to nutrient gradients, the responses tend to be species-specific and idiosyncratic relative to life span, provenance, and phylogeny. This result has important implications for managers: The success of nutrient manipulation to reduce community-level exotic dominance depends upon the covariation of species' provenance with competitive ability for nutrients; depending on the mixture of exotic species, nutrient manipulations may work to control specific problematic taxa. Furthermore, we found evidence that the importance of resource competition differed between the exotic and native grasses; native-grass abundance was well described by resource competition, whereas exotic-grass abundance was not.

We do not necessarily expect that the idiosyncratic response of the species in this system will be general. There are many cases where changes in burning regime, tilling frequency, consumer density, pathogen prevalence, or nutrient addition can fractionate a community based on provenance or life history (Huenneke et al. 1990, Woo and Zedler 2002, Brewer and Cralle 2003, Daehler 2003, Seabloom et al. 2005, 2009, Harpole 2006, Parker et al. 2006, Borer et al. 2007, 2009b, Siemann and Rogers 2007, Perry et al. 2010), but in many of these cases, provenance is confounded with phylogeny and life history. Recognizing the potential confounding between these species characteristics will improve management generally, as the effectiveness of resource manipulation in restoration depends upon the strength of the life history or phylogenetic biases in the native and exotic community members (e.g., invasive legumes into Hawaii [Vitousek et al. 1987] and mammals into New Zealand [Parkes and Murphy 2003]). Effective management will depend upon isolation of provenance effects per se from those effects that arise from biases in the composition of the exotic-species pool. This approach will lead to a more mechanistic basis for controlling exotic species, whose success may not be strictly linked to their origin. Our hope is that a more precise parsing of the effects of provenance, life history, and phylogeny will allow managers to more effectively generalize from their local successes in control of exotic species to novel sites and species.

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APPENDIX

Tables showing additional details on plant and soil characteristics and responses (*Ecological Archives* A021-096-A1).