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Variation in resource acquisition and utilization traits between native and invasive perennial forbs[1]

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Understanding the functional traits that allow invasives to outperform natives is a necessary first step in improving our ability to predict and manage the spread of invaders. In nutrient-limited systems, plant competitive ability is expected to be closely tied to the ability of a plant to exploit nutrient-rich microsites and use these captured nutrients efficiently. The broad objective of this work was to compare the ability of native and invasive perennial forbs to acquire and use nutrients from nutrient-rich microsites. We evaluated morphological and physiological responses among four native and four invasive species exposed to heterogeneous (patch) or homogeneous (control) nutrient distribution. Invasives, on average, allocated more biomass to roots and allocated proportionately more root length to nutrient-rich microsites than did natives. Invasives also had higher leaf N, photosynthetic rates, and photosynthetic nitrogen use efficiency than natives, regardless of treatment. While these results suggest multiple traits may contribute to the success of invasive forbs in low-nutrient environments, we also observed large variation in these traits among native forbs. These observations support the idea that functional trait variation in the plant community may be a better predictor of invasion resistance than the functional group composition of the plant community.

Key words: invasive species; functional traits; root foraging; spotted knapweed; yarrow.

Exotic plant invasions pose a serious global ecological and conservation threat to native plant communities (Vitousek, et al., 1996; Simberloff, 2005) and can induce serious economic costs. For example, in the United States, alone, the annual cost of nonnative plant species was estimated at $34 billion (Pimentel et al., 2005). Because of their potential negative impacts, ecologists and invasion biologists need to understand which traits makes one species more invasive than others. We know that some nonnative species, following their arrival to a new area, simply naturalize and become part of the resident plant community (Richardson et al., 2000). In contrast, other species rapidly expand their range and are considered invasive (Pyšek et al., 2004). Determining which traits contribute most strongly to the competitive ability of a nonnative organism is an essential first step in improving the prediction and management of the spread of invasive species.

In natural ecosystems, plant success depends on a suite of traits related to resource acquisition and use. For example, soil nutrients are heterogeneously distributed both spatially and temporally at the levels of the individual plant and the community (Hodge, 2006). In nutrient-limited systems, the ability of a species to exploit nutrient patches may be important in determining its growth, competitive ability, and survival. At the root-level, plants have developed foraging mechanisms that allow them to alter root architecture, allocation, morphology, and physiology in response to variable resource supply (Drew and

Saker, 1975; Jackson et al., 1990; Jackson and Caldwell, 1991; Aanderud et al., 2003; Ivans et al., 2003; Wang et al., 2006). These responses are expected to increase the efficiency and rate of resource capture in heterogeneous environments (Fransen et al., 1999). However, the magnitude of root responses to nutrient patches varies among species (Campbell et al., 1991; Wijesinghe et al., 2001). Differences in foraging ability among species may, in part, contribute to their success in heterogeneous environments, as the ability to exploit patches may influence plant establishment and competitive interactions. For example, under competitive conditions, plants that rapidly proliferate roots into nutrient patches capture more resources than plants that proliferate in patches more slowly (Hodge et al., 1999, 2000; Robinson et al., 1999). Because of the ephemeral nature of nutrient patches (Lamb et al., 2004), the ability to quickly proliferate roots may provide a competitive advantage. Thus, growth rate, root system size, and precision (i.e., the ability to selectively place roots in nutrient patches) together influence a plant's ability to capture heterogeneous soil resources.

Enhanced allocation to roots can result in greater resource acquisition (Aerts and Chapin, 2000), which in turn influences aboveground processes. For example, in a greenhouse study, grasses with more root biomass also had higher leaf nutrient concentrations (Fransen et al., 1998). As resource acquisition increases, so can photosynthetic rates and biomass accumulation. Photosynthetic rates depend, in part, on leaf N concentration (Field and Mooney, 1986; Evans, 1989), and with increased photosynthetic assimilation, more reduced carbon is available for biomass production. Carbon gain may be enhanced in plants with greater photosynthetic nutrient use efficiencies because higher photosynthetic rates can be obtained for a given unit of nutrient (Lambers et al., 1998).

The broad objective of this research is to quantify a suite of key above- and belowground traits related to resource acquisition and use in native and invasive forbs. We predict that invasive forbs will have a greater ability to forage for heterogeneously distributed nutrients than native forbs. Additionally, we predict

that invasive species not only will acquire more resources from patches than native species, but they will produce more biomass, have higher photosynthetic rates, and have higher nutrient use efficiency. Combined, this suite of traits could confer a greater competitive ability in these nonnative species.

MATERIALS AND METHODS

Study species—Four native and four nonnative perennial forbs that cooccur at our study site in eastern Oregon were selected for this experiment (Table 1). All four invasive species are listed as noxious weeds by states in the Intermountain West, and the native species selected are used widely in restoring weed infested areas in this region. Seed for all invasive species and for *Erigeron linearis* were collected from local populations in eastern Oregon. All other native seeds were purchased from a commercial source (Granite Seed, Lehi, Utah, USA). Prior to planting, seeds were vernalized for 2 weeks at 4°C. Due to its tough seed coat, *Sphaeralcea munroana* seeds were scarified by poking a small hole in the seed coat with a razor blade.

Experimental approach—In April 2006, species and resource treatments (control or patch; described later) were assigned in a randomized block design with six blocks. There were six replicate pots of each treatment and species combination. Ten seeds were planted per pot (20 cm diameter, 30 cm deep; Nursery Supplies, Chambersburg, Pennsylvania, USA) in a 1:1 mixture of sand and fritted clay. For species with low germination (i.e., *E. linearis* and *Linum lewisii*), seedlings were germinated on moist filter paper and directly transferred to the pots. In each pot, 0.4 g N in the form of slow release nutrients (10·10·10 NPK, Miracle Gro Shake and Feed All Purpose, Marysville, Ohio, USA) was either thoroughly mixed within the top 5–15 cm of soil (control treatment) or distributed between two nylon bags (6 cm diameter, 10 cm height, 2 mm mesh size) that were buried in the 5–15 depth layer (patch treatment) (Fig. 1). The nutrient patches were placed at a 2.5-cm radius from the seeds. Similar bags filled with control soil were placed in control pots. The top 0–5 cm of soil was unfertilized. After approximately 2 weeks of growth, the seedlings were thinned to a common size, with one seedling remaining per pot. Seedlings were raised in a greenhouse at John Carroll University under ambient light conditions. To encourage germination, the pots were fertilized twice with one-tenth strength modified Hoagland's solution (Epstein, 1972) but thereafter were irrigated with tap water 2–3 times per week. While the rate of N release from the slow-release fertilizer is dependent on soil temperature and water, based on pot volume, soil bulk density and initial N concentration of the low N soil media, our N additions were expected to result in an average N supply rate of 0.4 mg·kg^{-1}·d^{-1}. This rate is well within the range of N mineralization rates documented in this system and is threefold lower than N mineralization rates documented following weed invasion in this system (Chen and Stark, 2000; Booth et al., 2003).

Photosynthetic assimilation rates (μmol·m^{-2}·s^{-1}) were measured under ambient light using a LI-6400 (Li-Cor, Lincoln, Nebraska, USA) over two consecutive weeks in June and July 2006. All leaves were rinsed and allowed to air dry before measurement to remove dust and other particulates. After equilibrium was reached inside the LI-6400 chamber, three subsamples for each plant were measured at 10-s intervals on two separate days at midday. The average photosynthetic photon flux density (PPFD) inside the chamber was 750 μmol·m^{-2}·s^{-1}, which is above saturation for this suite of perennial forbs (T. A. Monaco, USDA-ARS, unpublished data) and was representative of growing conditions during the experiment. For most plants, measurements were made on individual leaves. However, *L. lewisii* leaves were too small for the chamber, so measurements were made on entire shoot tips. Leaf area was determined for plants with small or dissected leaves (i.e., those that did not fill the chamber) using the program WinRHIZO (Régent Instruments, Quebec City, Quebec, Canada), and their photosynthetic rates were recalculated.

Harvest and measurements—After 12 wk of growth, all aboveground and belowground biomass was harvested. We analyzed 10 leaves from *L. lewisii* and *E. linearis* and three leaves from all other species for leaf area using WinRHIZO; this value was divided by their dry mass to determine specific leaf area. For all species, the youngest, fully expanded leaves were collected. Differences in leaf number measured were due to large differences in leaf size; *L. lewisii* and *E. linearis* had significantly smaller leaves than the other species. Specific leaf area then was used to determine photosynthetic nutrient use efficiency (described later). Following the harvest, aboveground biomass was triple-rinsed with deionized water, oven-dried at 60°C for 48 h, and then weighed. Belowground biomass was collected from two compartments—within the buried nylon bags and in the remaining portion of the soil column. The buried nylon bags carefully were removed from the surrounding soil, and any roots extending from the bag were cut and added to the remaining belowground biomass. Roots from within the nylon bags were collected and rinsed on a fine sieve (2 mm) and then were stored in deionized water at 4°C until further analysis (described later). After the bags were extracted, the remaining root system was washed gently and recovered over a sieve. Prior to weighing, all root mass was oven-dried for 48 h at 60°C.

Total root length of roots from the buried nylon bags was measured (WinRHIZO). These roots then were oven-dried and weighed to determine specific root length (root length per mass, km·kg^{-1}). Three *E. linearis* plants (two control replicates and one patch replicate) had so few roots in the nylon bags that reliable masses could not be obtained; these samples were omitted from the statistical analysis for specific root length. Root length density (root length per soil volume, km·m^{-3}) was determined based on total root length and the volume of the nylon bags. Root mass ratio, which indicates the amount of plant biomass allocated to belowground structures, was calculated as the total root mass divided by total plant mass.

Prior to nutrient analyses, all aboveground tissues (consisting almost entirely of leaf tissue) were finely ground. Total nitrogen was determined by micro-Dumas combustion. Samples for total phosphorus were dry-ashed and dissolved in 1 N HCl, then analyzed colorimetrically (Allen, 1989). Photosynthetic nutrient use efficiencies for nitrogen and phosphorus were determined as the photosynthetic assimilation rate per unit nutrient on an area basis (μmol CO$_2$·mol^{-1} N·s^{-1} or μmol CO$_2$·mol^{-1} P·s^{-1}, respectively).

Statistical analysis—Univariate ANOVA was used to compare differences in responses of native and invasive species to resource addition treatments (control vs. patch) (SAS Institute, 2002). Normality and equal variance were assessed using the Shapiro–Wilks test and Levene's test, respectively. When these assumptions were not met, the data were weighted by the inverse of the variance (Neter et al., 1990).

TABLE 1. List of eight species used in this study. Nomenclature follows USDA-NRCS PLANTS database 2007 (http://plants.usda.gov/index.html).

| Species	Species abbreviation	Common name	Family	Native range
Native forbs				
Achillea millefolium L. var. *occidentalis* DC.	ACMI	Common yarrow	Asteraceae	Widespread (invasive in southern hemisphere)
Erigeron linearis (Hook.) Piper	ERLI	Desert yellow fleabane	Asteraceae	Western USA
Linum lewisii Pursh.	LILE	Lewis flax	Linaceae	Western USA
Sphaeralcea munroana (Dougl. ex Lindl.) Spach ex Gray	SPMU	Munro globemallow	Malvaceae	Western USA
Invasive forbs				
Cardaria draba (L.) Desv.	CADR	Whitetop	Brassicaceae	Eurasia
Centaurea stoebe L.	CEST	Spotted knapweed	Asteraceae	Europe
Chondrilla juncea L.	CHJU	Rush skeletonweed	Asteraceae	Europe
Linaria dalmatica (L.) P. Mill.	LIDA	Dalmatian toadflax	Scrophulariaceae	Europe
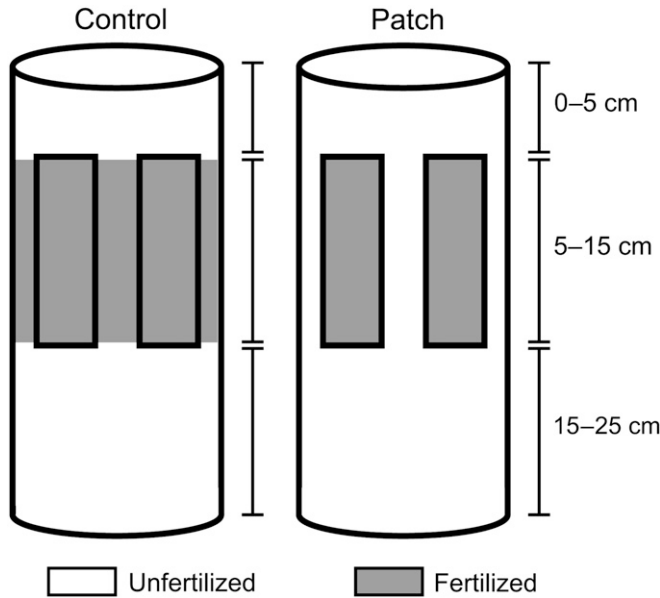
Fig. 1. Diagram of nutrient amendment in control (homogenous) and patch (heterogeneous) treatments. Gray shading indicates nutrient placement. All plants received equal nutrient addition.

RESULTS

Biomass and root morphology measurements—Invasive species, as a group, produced significantly more aboveground and belowground biomass than native species ($F_{1,87} = 45.06$, $P < 0.001$; $F_{1,87} = 73.07$, $P < 0.001$; respectively), but there was no significant main effect of treatment (control or patch) on aboveground ($F_{1,87} = 0.30$, $P > 0.05$) or belowground biomass ($F_{1,87} = 0.04$, $P > 0.05$) or interactive effect of plant origin (native or invasive) and treatment on aboveground ($F_{1,87} = 0.0.24$, $P > 0.05$) or belowground biomass production ($F_{1,87} = 0.10$, $P > 0.05$) (Fig. 2A, B). Additionally, invasive species allocated more of their total biomass belowground, having a significantly higher root mass ratio than did the native species ($F_{1,87} = 32.83$, $P < 0.001$) (Fig. 2C). Again, there was no significant main effect of treatment ($F_{1,87} = 0.00$, $P > 0.05$) or interactive effect of plant origin and treatment ($F_{1,87} = 0.02$, $P > 0.05$). There was, however, large variation in biomass responses among species within a group, with native species having coefficients of variation (CV) greater than 100 in both the control and patch treatments (Table 2). For example, among native species aboveground and belowground biomass varied 43- and 31-fold, respectively. Overall, *A. millefolium*, and to some extent, *S. munroana*, behaved more similarly to the invasive species in biomass accumulation than did the other two native species. Because of its low root biomass, *L. dalmatica* had the lowest root mass ratio of the invasive species, similar in magnitude to that observed in the native species.

Root morphology changed in response to resource availability. There were significant interactions between treatment (control or patch) and plant origin (native or invasive) for root length density ($F_{1,87} = 5.47$, $P = 0.022$) (Fig. 3A). As a whole, the invasive species were better foragers than were the native species. The native forbs *E. linearis* and *L. lewesii* produced very few roots, regardless of treatment. The other six species had higher root length density in nutrient patch soil than in control soil, with root proliferation of most species in the nutrient
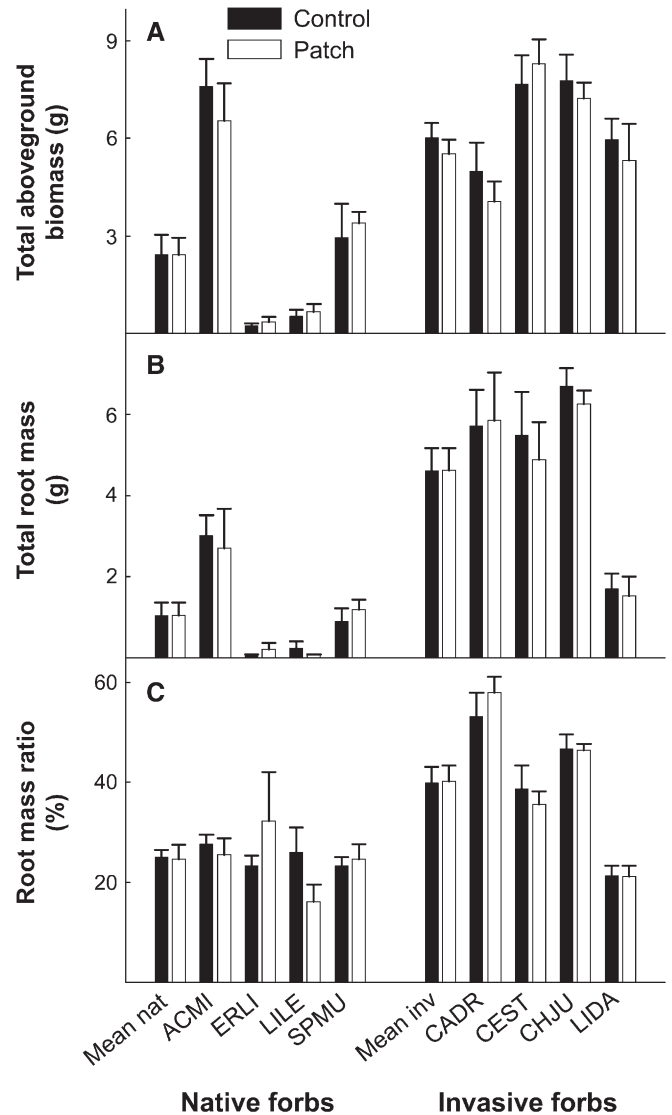

Fig. 2. Total aboveground biomass (A), total root mass (B), and root mass ratio (C) for all experimental native and invasive forbs grown in pots with nutrients distributed homogeneously (Control) or heterogeneously (Patch). Data are means ± SE ($N = 6$). In this and other figures, mean values for native (Mean nat) and invasive (Mean inv) species within both control and patch treatments are presented for comparison purposes. ACMI = *Achillea millefolium*; ERLI = *Erigeron linearis*; LILE = *Linum lewisii*; SPMU = *Sphaeralcea munroana*; CADR = *Cardaria draba*; CEST = *Centaurea stoebe*; CHJU = *Chondrilla juncea*; LIDA = *Linaria dalmatica*

patches, at a minimum, double the root proliferation in the control soils. However, overall, invasive species had greater root length density than native species, especially in the patch treatments. Specific root length was greater overall in the native species than in the invasive species ($F_{1,84} = 8.21$; $P = 0.005$), and most species had greater specific root length in the patch than the control treatment ($F_{1,84} = 7.76$; $P = 0.007$) (Fig. 3B). There was no significant interactive effect of plant origin and treatment ($F_{1,84} = 0.01$; $P > 0.05$). The magnitude of these responses varied by species; in fact, *L. dalmatica* had a specific root length more similar to the native species than to the invasive species. This large variation among species within a group (either native or invasive) is apparent when comparing CVs, with native species

TABLE 2.   Coefficient of variation (CV) for resource use and acquisition traits measured for native and invasive forbs grown in pots with nutrients distributed homogeneously (Control) or heterogeneously (Patch).

	Native		Invasive	
Trait	Control CV	Patch CV	Control CV	Patch CV
Total aboveground biomass (g)	120.4	107.7	35.4	38.8
Total belowground biomass (g)	132.1	151.9	52.9	57.3
Root mass ratio (%)	28.0	57.7	37.4	37.1
Root length density (km·m^{-3})	90.5	108.1	58.3	48.3
Specific root length (km·kg^{-1})	51.0	27.5	99.2	63.2
Leaf N (g·kg^{-1})	16.2	13.9	21.2	15.3
Leaf P (g·kg^{-1})	25.3	22.8	47.2	30.5
A (μmol·m^{-2}·s^{-1})	65.1	71.4	23.5	30.1
PNUE (μmol·mol^{-1}·s^{-1})	106.6	79.5	36.9	39.3
PPUE (μmol·mol^{-1}·s^{-1})	103.4	76.6	53.1	48.0

Notes: A, photosynthetic assimilation rate; PNUE, photosynthetic nitrogen use efficiency; PPUE, photosynthetic phosphorus use efficiency. (N = 19–24)

having higher CVs for root length density but lower CVs for specific root length compared to the invasive species (Table 2)

Leaf-level physiology—At the leaf level, leaf N was 1.1-fold higher in native species than in the invasive species ($F_{1,81}$ = 7.22; P = 0.009) but did not differ between patch or control treatment ($F_{1,81}$ = 0.34, P > 0.05) (Fig. 4A). However, leaf P was not significantly different between treatments (control or patch) ($F_{1,81}$ = 1.92, P > 0.05) or plant origin (native or inva-

Fig. 3.   Root length density (A) and specific root length (B) of native and invasive species grown in pots with nutrients distributed homogeneously (Control) or heterogeneously (Patch). Data are means ± SE (N = 4–6). See Fig. 2 for definitions of abbreviations.

sive) ($F_{1,81}$ = 0.00, P > 0.05) (Fig. 4B). CVs for both leaf N and P were lower than those observed for other traits, ranging from 13.9 to 47.2 among the different plant origin and treatment combinations. Photosynthetic assimilation rates were 1.3-fold higher in the invasive species than native species ($F_{1,87}$ = 7.88; P = 0.006) (Fig. 5A). Although photosynthetic nitrogen use efficiency(PNUE) and photosynthetic phosphorus use efficiency (PPUE) were 1.4- and 1.3-fold higher in the invasive species, only PNUE was significantly higher in the invasive species ($F_{1,77}$ = 5.93, P = 0.017 and $F_{1,77}$ = 3.23; P = 0.076, respectively, for PNUE and PPUE) (Fig. 5B). There was no significant main effect of treatment (PNUE: $F_{1,77}$ = 0.38, P > 0.05; PPUE: $F_{1,77}$ = 0.06, P > 0.05) or interactive effect of plant origin and treatment (PNUE: $F_{1,77}$ = 0.02, P > 0.05; PPUE: $F_{1,77}$ = 0.29, P > 0.05) on either measure of photosynthetic nutrient use efficiency. Overall, variation in photosynthetic assimilation rates, as well as photosynthetic nutrient use efficiency, was higher among the native species than the invasive species in both the control and patch treatments.

DISCUSSION

As hypothesized, native and invasive species differed in functional traits related to nutrient acquisition and use. Overall, the suite of invasive species had greater root foraging precision (i.e., greater root length density in resource patches than in control soils) (Fig. 3A), and they invested a substantial portion of their total biomass (>40%) into roots (Fig. 2C). Comparing the mean root mass ratios of the invasive species and the two fast-growing native species (*A. millefolium* and *S. munroana*), the invasive species allocated 15% more of their biomass into belowground structures. Although greater root mass ratios often are associated with species adapted to low resource environments, high root allocation also has been observed in fast-growing species from various habitats (e.g., heathlands, grasslands, old fields), potentially increasing nutrient acquisition (Aerts and Chapin, 2000). A comparison of eight herbaceous perennials documented that plants with larger root systems also had a high degree of root foraging precision, and these traits were more common in the introduced, fast-growing species studied (Rajaniemi and Reynolds, 2004). Thus, in both the previous (Rajaniemi and Reynolds, 2004) and current study, species with larger root systems also had higher precision. This combination of traits may enable invasive species to capture more resources disproportionate to their size, potentially promoting size-asymmetric competition belowground.

The greater root foraging precision observed in invasive vs. native species likely is correlated to faster growth rates in the invasive species (James and Drenovsky, 2007). In fact, higher growth rates may underlie fast-growing species' ability to obtain resources (Kembel and Cahill, 2005). Our data suggest that under competitive conditions the suite of invasive species would be able to preempt resources in nutrient patches because of faster interception (i.e., high relative growth rates and greater root foraging precision). Additionally, when plants are competing for resources, rapid root proliferation is predicted to be more effective than simply increasing uptake rates at the root surface (Robinson, 2001). Thus, the greater or more rapid root foraging ability observed in this study may further contribute to the ability of these invasives to exploit patchy soil resources in an otherwise nutrient-poor environment.
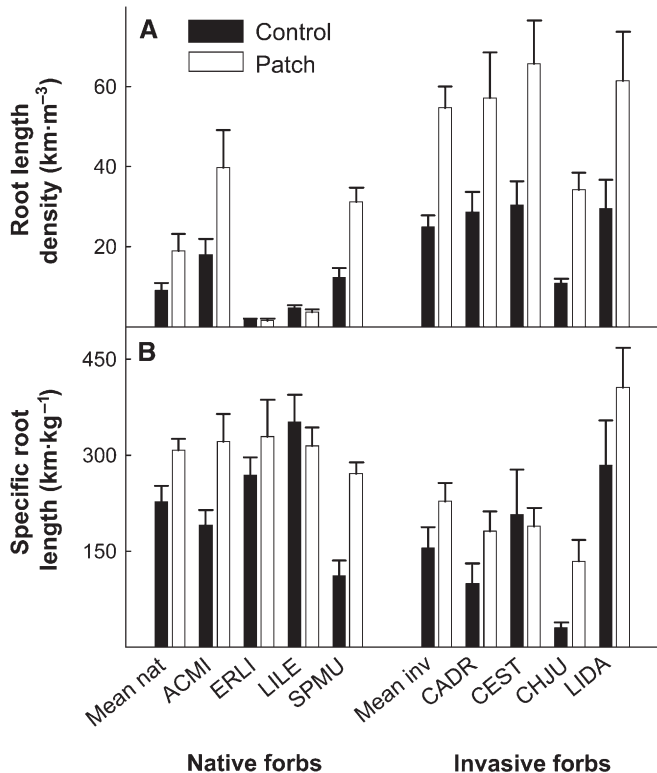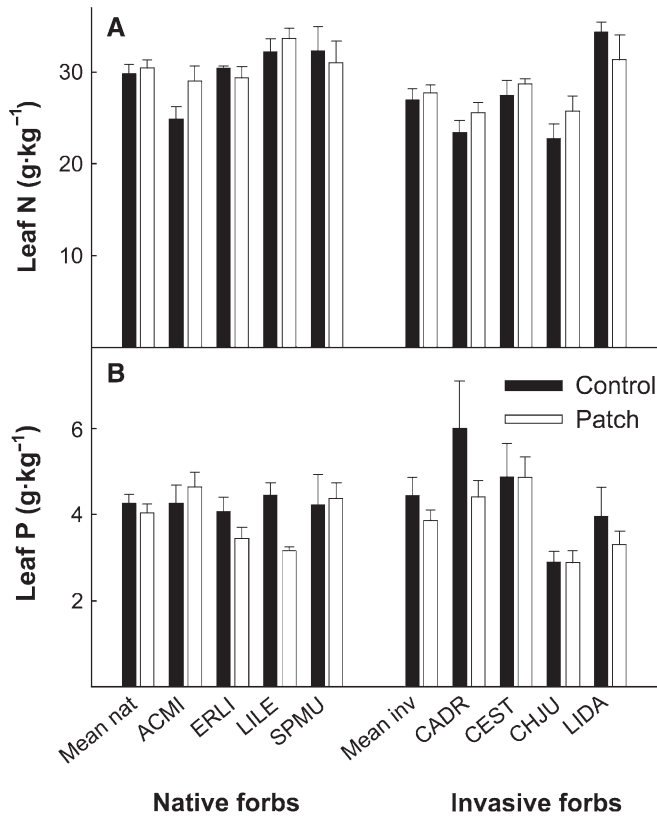
Fig. 4.   Leaf N and P concentrations in experimental plants grown in pots with nutrients distributed homogeneously (Control) or heterogeneously (Patch). Data are means ± SE (*N* = 3–6). See Fig. 2 for definitions of abbreviations.

Fig. 5.   Photosynthetic assimilation rate (A), photosynthetic N efficiency (B), and photosynthetic P use efficiency (C) of native and invasive species grown in pots with nutrients distributed homogeneously (Control) or heterogeneously (Patch). Data are means ± SE (*N* = 3–6). See Fig. 2 for definitions of abbreviations.

In addition to greater root foraging precision the invasive species were able to maintain higher photosynthetic rates (Fig. 5A) and obtain greater biomass than the native species (Fig. 2A, B), making them more nutrient use efficient (Fig. 5B, C). Higher nutrient use efficiency, in turn, should increase plant performance and, potentially, fitness (Aerts and Chapin, 2000). In a comparison of native and invasive species from low nutrient habitats, higher photosynthetic nutrient use efficiencies were documented in the invasive species, suggesting that greater nutrient use efficiency is one functional trait enhancing their competitive ability and success in these environments (Funk and Vitousek, 2007). Similar results were observed in photosynthetic trait comparisons of native and nonnative *Rubus* species in the Pacific Northwest (McDowell, 2002) and the evergreen understory species *Ilex aquifolium* (native) and *Rhododendron ponticum* (nonnative) at two European sites (Niinemets et al., 2003). Thus, higher photosynthetic nitrogen use efficiency may be an additional key trait allowing these invasives to invade nutrient poor systems (Funk and Vitousek, 2007).

While native and invasive species differed in a number of traits examined, there also was substantial trait variation within a functional group, and in a few instances some native forbs had patterns of root foraging and nutrient use that were comparable to invasives. For example, aboveground and belowground biomass, as well as root length density, varied widely among the native species (Figs. 2A, B, 3A; Table 2), with *A. millefolium* and *S. munroana* behaving more similarly to the invasive spe-
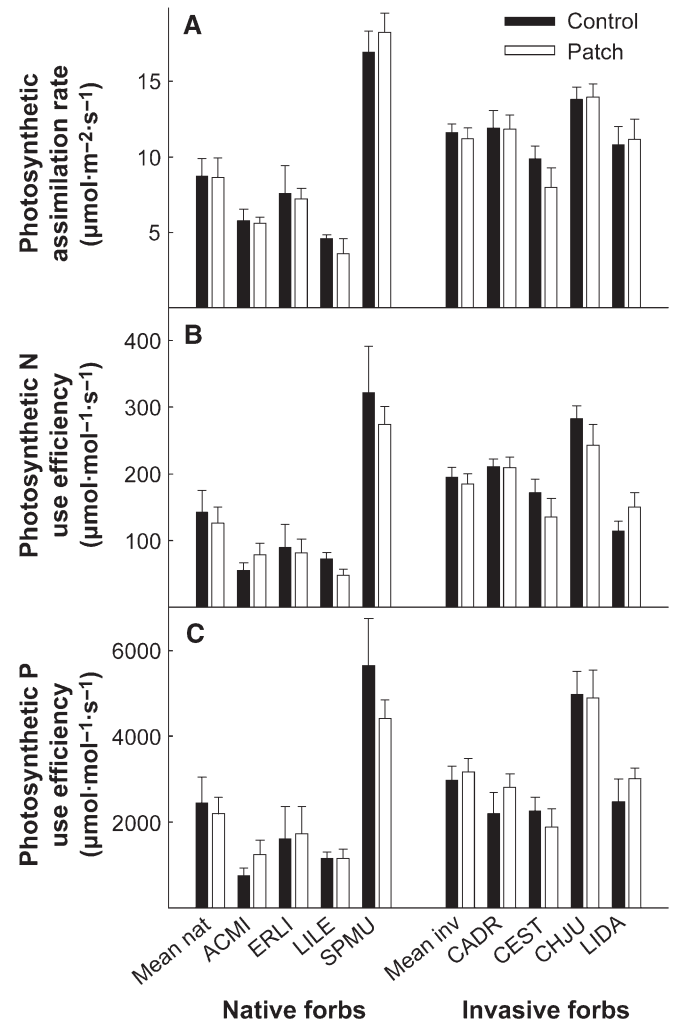
cies than to the other two native species. In contrast, the slow-growing, native species (i.e., *E. linearis* and *L. lewisii*) had low root foraging precision (Fig. 3A), photosynthetic rates (Fig. 5A), and shoot and root biomass production (Fig. 2A, B). Under competitive conditions, the potential consequences of this trait variation are large. For the slow-growing species, small root system size decreased their ability to obtain P, a highly immobile soil nutrient (Marschner, 1995); leaf P concentrations declined 15 and 29%, respectively, for *E. linearis* and *L. lewisii* in the patch relative to the control treatment (Fig. 4B). Under competitive conditions, these slow-growing species likely would be outcompeted due to resource preemption by their fast-growing, invasive counterparts. In contrast, the faster-growing native species would be more competitive with the invasive species, due to their greater root foraging ability.

One major hypothesis of invasion resistance is similarity in functional grouping between the biomass dominant and the invader (Emery, 2007). However, support for this hypothesis is mixed (Symstad, 2000; Dukes, 2001; Pokorny et al., 2005;

Emery, 2007). Much of this inconsistency may be related to the manner in which species are categorized into functional groups. Recent evidence suggests that categorizing species based on coarse differences in morphology or taxonomy may not adequately predict species effects on ecosystem processes (Wright et al., 2006). In support, our study suggests large trait variation may limit the ability to use conventional functional groupings to predict invasion resistance.

One limitation of our study was that we were unable to distinguish between traits of introduced, noninvasive species and traits of introduced, invasive species. Simple comparisons of native and invasive species cannot predict which characteristics are associated with invasiveness, per se, because species native to one area may become invasive in other areas if introduced (Burns, 2004). Although comparing invasive and noninvasive introduced species is a powerful comparison, this suite of species is not commonly found in the Great Basin. Namely, noninvasive, nonnative forbs do not tend to establish stable populations in the Great Basin. But given the inclusion of *A. millefolium*, an invasive weed in parts of the southern hemisphere (Pickering and Hill, 2007), we can make some inferences about the value of observed resource use and acquisition traits for an invader. As stated, *A. millefolium* behaved more similarly to the invasive species included in the experiment than to the other native species. This observation suggests that the measured resource use and acquisition traits are good indicators of invasibility and not just traits of nonnative species.

Overall, the ability of a species to capture N and P was influenced little by the different treatments. One interpretation of these results is that the patch treatments were potentially ineffective as a result of substantial nutrient movement out of the patches during the duration of the experiment. Such a scenario would have made the soils in the patch treatment relatively homogenous. This scenario is a possibility because there likely was some degree of nutrient diffusion and mass flow out of the patches. However, two lines of reasoning suggest nutrient movement from the patches was not a likely factor in our lack of treatment effect on plant nutrient capture. First, most species produced more root length in enriched patches compared to control patches, suggesting soil conditions in the two treatments differed enough to drive different root responses. Second, it has been fairly well demonstrated that the benefit of root proliferation in terms of plant biomass production and total nutrient capture is typically observed to the greatest degree when plants are in competition (e.g., Robinson et al., 1999).

Concluding remarks—Although as a group the native species had smaller root systems and lower root foraging precision, the responses among these native species were highly variable. *Linum lewisii* and *E. linearis* produced very little biomass and ineffectively foraged for nutrients, but the other two native species (*A. millefolium* and *S. munroana*) had biomass and root foraging traits more similar to the invasive species than to their native counterparts. Previous work has documented similar, and rapid, growth rates among *A. millefolium* and *S. munroana* and the suite of invasive species studied here (James and Drenovsky, 2007). Thus, although previous research has suggested native species of the same functional group as the introduced species may be more effective at resisting invasion (e.g., Pokorny et al., 2005), our data suggest that species from the same functional group may not share physiological and/or morphological traits. In fact, important functional traits were more variable within than between

groups of native and nonnative species. Recent research has suggested that the ability to link plant community composition to ecosystem function may depend heavily on understanding patterns of functional trait variation in plant assemblages and not simply how functional group diversity or composition is distributed in the plant community (Wright et al., 2006; Lavorel and Garnier, 2002). From a management perspective, focusing on native species with similar traits, rather than functional groups, as nonnative species may improve the ability to establish and maintain communities more resistant to invasion. Seed mixtures used to restore degraded or weed-infested communities typically are designed with the intent to maximize species diversity with the expectation that establishing diverse communities will maximize weed resistance. Results from this study and the ideas developed by Wright et al. (2006) and Lavorel and Garnier (2002) suggest restoration practitioners could gain more economic and ecological return on purchased seeds by designing species mixtures based on specific desired traits and not based solely on species diversity per se.

LITERATURE CITED

Aanderud, Z. T., C. S. Bledsoe, and J. H. Richards. 2003. Contribution of relative growth rate to root foraging by annual and perennial grasses from California oak woodlands. *Oecologia* 136: 424–430.

Aerts, R., and F. S. Chapin. 2000. The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advances in Ecological Research* 30: 1–67.

Allen, S. E. 1989. Chemical analysis of ecological materials, 2nd ed. Blackwell Science, Oxford, UK.

Booth, M. S., J. M. Stark, and M. M. Caldwell. 2003. Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub–steppe ecosystem. *Biogeochemistry* 66: 311–330.

Burns, J. H. 2004. A comparison of invasive and non-invasive dayflowers (Commelinaceae) across experimental nutrient and water gradients. *Diversity & Distributions* 10: 387–397.

Campbell, B. D., J. P. Grime, and J. M. L. Mackey. 1991. A trade-off between scale and precision in resource foraging. *Oecologia* 87: 532–538.

Chen, J., and J. M. Stark. 2000. Plant species effects and carbon and nitrogen cycling in a sagebrush-crested wheatgrass soil. *Soil Biology & Biochemistry* 32: 47–57.

Drew, M. C., and L. R. Saker. 1975. Nutrient supply and the growth of the seminal root system of barley. II. Localized, compensatory increases in lateral root growth and rates of nitrogen uptake when nitrate supply is restricted to only part of the root system. *Journal of Experimental Botany* 26: 79–90.

Dukes, J. S. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia* 126: 563–568.

Emery, S. M. 2007. Limiting similarity between invaders and dominant species in herbaceous plant communities? *Journal of Ecology* 95: 1027–1035.

Epstein, E. 1972. Mineral nutrition of plants: Principles and perspectives. Wiley, New York, New York, USA.

Evans, J. R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* 78: 9–19.

Field, C. B., and H. A. Mooney. 1986. The photosynthesis–nitrogen relationship in wild plants. *In* T. J. Givnish [ed.], On the economy of plant form and function, 25–56. Cambridge University Press, Cambridge, UK.

Fransen, B., H. De Kroon, and F. Berendse. 1998. Root morphological plasticity and nutrient acquisition of perennial grass species from habitats of different nutrient availability. *Oecologia* 115: 351–358.

Fransen, B., H. De Kroon, C. G. F. Kovel, and F. Ven Den Bosch. 1999. Disentangling the effects of root foraging and inherent growth

rate on plant biomass accumulation in heterogeneous environments: A modeling study. *Annals of Botany* 84: 305–311.

FUNK, J. L., AND P. M. VITOUSEK. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446: 1079–1081.

HODGE, A. 2006. Plastic plants and patchy soil. *Journal of Experimental Botany* 57: 401–411.

HODGE, A., D. ROBINSON, B. S. GRIFFITHS, AND A. H. FITTER. 1999. Why plants bother: Root proliferation results in increased nitrogen capture from an organic patch when two grasses compete. *Plant, Cell & Environment* 22: 811–820.

HODGE, A., J. STEWART, D. ROBINSON, B. S. GRIFFITHS, AND A. H. FITTER. 2000. Spatial and physical heterogeneity of N supply from soil does not influence N capture by two grass species. *Functional Ecology* 14: 645–653.

IVANS, C. Y., A. J. LEFFLER, U. SPAULDING, J. H. STARK, R. J. RYEL, AND M. M. CALDWELL. 2003. Root responses and nitrogen acquisition by *Artemisia tridentata* and *Agropyron desertorum* following small summer rainfall events. *Oecologia* 134: 317–324.

JACKSON, R. B., AND M. M. CALDWELL. 1991. Kinetic responses of *Pseudoroegneria* roots to localized soil enrichment. *Plant and Soil* 138: 231–238.

JACKSON, R. B., J. H. MANWARING, AND M. M. CALDWELL. 1990. Rapid physiological adjustment of roots to localized soil enrichment. *Nature* 344: 58–60.

JAMES, J. J., AND R. E. DRENOVSKY. 2007. A basis for relative growth rate differences between native and invasive forb seedlings. *Rangeland Ecology and Management* 60: 395–400.

KEMBEL, S. W., AND J. F. CAHILL. 2005. Plant phenotypic plasticity belowground: A phylogenetic perspective on root foraging trade-offs. *American Naturalist* 166: 216–230.

LAMB, E. G., J. J. HAAG, AND J. F. CAHILL. 2004. Patch-background contrast and patch density have limited effects on root proliferation and plant performance in *Abutilon theophrasti. Functional Ecology* 18: 836–843.

LAMBERS, H., F. S. CHAPIN, AND T. L. PONS. 1998. Plant physiological ecology. Springer, New York, New York, USA.

LAVOREL, S., AND E. GARNIER. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology* 16: 545–556.

MARSCHNER, H. 1995. Mineral nutrition of higher plants, 2nd ed. Academic Press, London, UK.

MCDOWELL, S. C. L. 2002. Photosynthetic characteristics of invasive and non-invasive species of *Rubus* (Rosaceae). *American Journal of Botany* 89: 1431–1439.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied linear statistical models: Regression, analysis of variance and experimental design, 3rd ed. Irwin, Boston, Massachusetts, USA.

NIINEMETS, U., F. VALLADARES, AND R. CEULEMANS. 2003. Leaf-level phenotypic variability and plasticity of invasive *Rhododendron ponti-*

cum and non-invasive *Ilex aquifolium* co-occurring at two contrasting European sites. *Plant, Cell & Environment* 26: 941–956.

PICKERING, C., AND W. HILL. 2007. Roadside weeds of the Snowy Mountains, Australia. *Mountain Research and Development* 27: 359–367.

PIMENTEL, D., R. ZUNIGA, AND D. MORRISON. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288.

POKORNY, M. L., R. L. SHELEY, C. A. ZABINSKI, R. E. ENGEL, T. J. SVEJCAR, AND J. J. BORKOWSKI. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13: 448–459.

PYŠEK, P., D. M. RICHARDSON, M. REJMÁNEK, G. L. WEBSTER, M. WILLIAMSON, AND J. KIRSCHNER. 2004. Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. *Taxon* 53: 131–143.

RAJANIEMI, T. K., AND H. L. REYNOLDS. 2004. Root foraging for patchy resources in eight herbaceous plant species. *Oecologia* 141: 519–525.

RICHARDSON, D. M., P. PYŠEK, M. REJMÁNEK, M. G. BARBOUR, F. D. PANETTA, AND C. J. WEST. 2000. Naturalization and invasion of alien plants: Concepts and definitions. *Diversity & Distributions* 6: 93–107.

ROBINSON, D. 2001. Root proliferation, nitrate inflow and their carbon costs during nitrogen capture by competing plants in patchy soil. *Plant and Soil* 232: 41–50.

ROBINSON, D., A. HODGE, B. S. GRIFFITHS, AND A. H. FITTER. 1999. Plant root proliferation in nitrogen-rich patches confers competitive advantage. *Proceedings of the Royal Society of London, B, Biological Sciences* 266: 431–435.

SAS INSTITUTE. 2002. SAS/STAT user's guide, version 9.1. SAS Institute, Cary, North Carolina, USA.

SIMBERLOFF, D. 2005. Non-native species do threaten the natural environment! *Journal of Agricultural & Environmental Ethics* 18: 595–607.

SYMSTAD, A. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81: 99–109.

VITOUSEK, P. M., C. M. D'ANTONIO, L. L. LOOPE, AND R. WESTBROOKS. 1996. Biological invasions as global environmental change. *American Scientist* 84: 468–478.

WANG, L., P. P. MOU, AND R. H. JONES. 2006. Nutrient foraging via physiological and morphological plasticity in three plant species. *Canadian Journal of Forest Research* 36: 164–173.

WIJESINGHE, D. K., E. A. JOHN, S. BEURSKENS, AND M. J. HUTCHINGS. 2001. Root system size and precision in nutrient foraging: Responses to spatial pattern of nutrient supply in six herbaceous species. *Journal of Ecology* 89: 972–983.

WRIGHT, J. P., S. NAEEM, A. HECTOR, C. LEHMAN, P. B. REICH, B. SCHMID, AND D. TILMAN. 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters* 9: 111–120.