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Impact of Native Grasses and Cheatgrass (*Bromus tectorum*) on Great Basin Forb Seedling Growth

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Abstract

Re-establishing native communities that resist exotic weed invasion and provide diverse habitat for wildlife are high priorities for restoration in sagebrush ecosystems. Native forbs are an important component of healthy rangelands in this system, but they are rarely included in seedings. Understanding competitive interactions between forb and grass seedlings is required to devise seeding strategies that can enhance establishment of diverse native species assemblages in degraded sagebrush communities. We conducted a greenhouse experiment to examine seedling biomass and relative growth rate of common native forb species when grown alone or in the presence of a native bunchgrass or an exotic annual grass. Forb species included bigseed biscuitroot (*Lomatium macrocarpum* [Nutt. ex Torr. & A. Gray] J.M. Coult. & Rose), sulphur-flower buckwheat (*Eriogonum umbellatum* Torr.), hoary aster (*Machaeranthera canescens* [Pursh] Gray), royal penstemon (*Penstemon speciosus* Douglas ex Lindl.), and Munro's globemallow (*Sphaeralcea munroana* [Douglas ex Lindl.] Spach ex Gray); and neighboring grass species included bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), Sandberg bluegrass (*Poa secunda* J. Presl); and cheatgrass (*Bromus tectorum* L.). Forbs and grasses were harvested after 6, 9, or 12 wk of growth for biomass determination and calculation of relative growth rates (RGR) of forbs. Neither bunchgrass reduced biomass of any forb. RGR was reduced for royal penstemon when grown with either native grass and for Munro's globemallow when grown with bottlebrush squirreltail. Although only assessed qualitatively, forbs with vertically oriented root morphologies exhibited no reduction in RGR when grown with native grasses, compared to forbs with dense lateral branching, similar to the root morphology of native grasses. Biomass of forbs was reduced by 50% to 91% and RGR by 37% to 80% when grown with cheatgrass. Understanding native forb interactions with native grasses and cheatgrass will aid land managers in selecting effective seed mixes and making better use of costly seed.

Key Words: invasive species, relative growth rate, restoration, revegetation, root morphology

INTRODUCTION

Historically, plant species selected to restore burned or degraded plant communities in the Great Basin have been primarily grasses and shrubs (Plummer et al. 1968; DePuit 1986). Although native forbs have a number of important ecological roles, they have been traditionally overlooked in revegetation plans because of our lack of understanding of their establishment and resource requirements and the limited availability of seeds (Shaw et al. 2005; Walker and Shaw 2005). Recent efforts to address seed availability and methods to enhance establishment (Shaw et al. 2005) are based on the recognition that grasses, shrubs, and forbs are all necessary to restore community structure and function and conserve biodiversity. They are also essential to meet the habitat needs of numerous organisms (Kufeld 1973; Gregg et al. 2008; Davies and Bates 2010). Pronghorn antelope (*Antilocapra americana* Ord), for example, forage primarily on grasses in spring and fall, and shrubs during the winter, but in summer months forbs may comprise up to 90% of their diet (Beale and Smith 1970). Along with shrubs, forbs are critical to maintaining pollinator populations (Gathmann and Tscharntke 2002). In healthy sagebrush (*Artemisia* spp.) plant communities, forbs and insects that depend on forbs provide the majority of the diet of sage-grouse (*Centrocercus urophasianus* Bonaparte) in spring and early summer (Drut et al. 1994; Gregg et al. 2008).

Because literature and practical experience pertaining to native forbs is scant, additional information on species phenology, relative growth rate (RGR), and root morphology can improve our understanding of species resource use in time and space. This will aid in selecting species and designing revegetation strategies to enhance partitioning of resources, thereby reducing competitive interactions among seeded species and increasing species richness of the established community (Pyke and Archer 1991; Schwinning and Ehleringer 2001).

A major challenge in revegetating disturbed sites in the Great Basin is competition with cheatgrass (*Bromus tectorum* L.), which is present on more than 40 million hectares in this region (Young and Evans 1978; Knapp 1996). Limiting competition among seeded species and rapidly establishing vegetative cover is especially important given the risk of cheatgrass invasion and subsequent dominance (Mack and Pyke 1983). The competitive attributes of this winter annual are well documented. It uses more water earlier in the growing season than many native plants by initiating root and shoot growth at lower temperatures (Arredondo et al. 1998), and exhibits greater root and

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shoot relative growth rates (Cline et al. 1977; Aguirre and Johnson 1991). Mature perennial plants are more resistant to competition from annual grasses (Humphrey and Schupp 2004), and some communities, especially those with a perennial grass component, can suppress cheatgrass growth or even reduce its density (Booth et al. 2003; Beckstead and Augspurger 2004; Getz and Baker 2008; Leger 2008). In disturbance scenarios, however, the seedling stage of native species is vulnerable to competition from cheatgrass (Aguirre and Johnson 1991; Humphrey and Schupp 2004; Yelenik and Levine 2010). Cheatgrass densities as low as 10 plants m^{-2} in the first year following fire can increase to 10 000 plants m^{-2} within 3 yr (Young and Evans 1978), demonstrating that the window for seeded species to establish and persist can be quite narrow.

Constructing postdisturbance plant communities to maximize native species habitat and minimize exotic species invasion requires a strategy that uses highly competitive native species, but also accounts for establishment of a diverse mixture of species. Native grasses in sagebrush-steppe communities can increase resistance to invasion by nonnative species (Booth et al. 2003; Beckstead and Augspurger 2004; Chambers et al. 2007; Getz and Baker 2008; James et al. 2008), but those same grasses may either compete with or facilitate the recruitment of other species (Kindscher and Fraser 2000; Brown and Bugg 2001; Booth et al. 2003, Dickson and Busby 2009). Mature bottlebrush squirreltail plants (*Elymus elymoides* [Raf.] Swezey), for example, have a positive influence on diversity by increasing recruitment of sagebrush (*Artemisia tridentata*) seedlings and maintaining cheatgrass-free zones (Booth et al. 2003). However, grasses also reduce survival of forbs in restoration plantings (Kindscher and Fraser 2000; Brown and Bugg 2001; Dickson and Busby 2009), and therefore recommended protocols for revegetation strategies include 1) seeding forbs separately from grasses, 2) increasing forb seeding rates, or 3) reducing grass seeding rates to increase forb recruitment (Kindscher and Fraser 2000; Elstein 2004; Dickson and Busby 2009).

Because native forbs can improve community diversity and habitat values, a greater understanding of forb physiology and native grass effects on forb growth may provide useful information to reduce negative interactions among seeded species. In this study we examined the RGR of native forb species when grown with native perennial grasses or cheatgrass to assess their competitive abilities. Identifying forbs that maintain RGR in the presence of native grass seedlings will improve selection of effective native forb and grass restoration mixtures and seeding strategies for increasing establishment. Species that grow quickly at the seedling stage can reduce site availability for cheatgrass invasion, whereas slow-growing species may allow for a greater diversity of native forb establishment. Seed mixes therefore could be constructed with information on expected cheatgrass densities based on site history prior to the disturbance, burn intensity, and visual inspection (Young et al. 1976). Species identified as more vulnerable could be used in sites with little to no expected cheatgrass presence, whereas those species more resistant to cheatgrass competition could be seeded in sites with low to moderate background levels of cheatgrass. This will reduce the use of species at some sites that are not competitive with cheatgrass, preventing the waste of valuable forb seed.

In this study, we compared total biomass after 12 wk of growth, relative growth rates, and root mass ratios (RMR) and qualitative root morphology for five native Great Basin forb species under consideration as restoration species. Forb seedlings were grown either alone or with one of two native grasses to determine whether native grasses would facilitate or inhibit growth of each forb. Finally, native forbs were grown with cheatgrass, to determine whether they differed in their competitive response to this exotic grass. Competitive response is defined here as the "ability of an organism to avoid being suppressed by their companions," or have no to little reduction in growth with a neighbor compared to growth alone (Goldberg and Landa 1991). Given the lack of information on forb growth and forb response to grasses, we analyzed forb response to grasses, not grass response to forbs.

METHODS

Plant Materials

Perennial native forbs species used in our experiments included sulphur-flower buckwheat (*Eriogonum umbellatum* Torr.), bigseed biscuitroot (*Lomatium macrocarpum* [Nutt. ex Torr. & A. Gray] J.M. Coult. & Rose), hoary aster (*Machaeranthera canescens* [Pursh] Gray), royal penstemon (*Penstemon speciosus* Douglas ex Lindl.), and Munro's globemallow (*Sphaeralcea munroana* [Dougl. ex Lindl.] Spach ex Gray). All are insect pollinated. Seeds of the native grasses bottlebrush squirreltail and Sandberg bluegrass (*Poa secunda* J. Presl) were collected from plants growing at the Saylor Creek Range of southern Idaho, and seeds of the exotic annual cheatgrass were collected in the foothills around Boise, Idaho. Forb seed was collected in 2005 from the Snake River Plain of southern Idaho, at elevations less than 1 524 m, except for Munro's globemallow, which was collected in Uintah Co., Utah at 1 553 m (Table 1).

Experimental Design

Forb seed was stratified at 4.4°C for 2–12 wk in January–March 2007 (Parkinson 2008). In mid-March 2007, forb and grass seeds were transferred to Petri dishes lined with two layers of moistened Whatman no. 1 filter paper, sealed with Parafilm, and placed in a growth chamber set at a constant 24°C, with 14 h light and 10 h dark. Germinating seeds were planted in 16-cm-diameter × 45-cm-deep containers (Stuewe and Sons TP616) in growing media comprised of silt loam topsoil from Gallatin County, Montana, washed concrete sand, and peat moss (1:1:1, v/v/v). Forbs were grown alone or with one of the following grass neighbors: cheatgrass, bottlebrush squirreltail, or Sandberg bluegrass. Two to three germinants per species were planted to account for mortality, and seedlings were thinned to a single forb or a single forb and grass after 10 d of growth.

Containers were placed on benches in a Montana State University greenhouse in a completely randomized experimental design. With five forb species, four neighbor treatments, and 18 replicates there were 360 total sampling units. Greenhouse temperatures were between 18°C and 24°C and photoperiod, as

Table 1. Plant materials, seed characteristics, and location of seed collection sites.

Common name	Scientific name	Plant family	Seed · g^{-1}	Collection site location and elevation[1]
Bigseed biscuitroot	*Lomatium macrocarpum*	Apiaceae	99	lat 43°30′48″N, long 116°7′55″W; 946 m
Hoary aster	*Machaeranthera canescens*	Asteraceae	1 818	lat 43°13′60″N, long 115°54′53″W; 958 m
Munro's globemallow	*Sphaeralcea munroana*	Malvaceae	300	Uintah Co. Utah < 1 524 m
Royal penstemon	*Penstemon speciosus*	Scrophulariaceae	687	lat 43°23′13″N, long 116°01′13″W; 1 013 m
Sulphur-flower buckwheat	*Eriogonum umbellatum*	Polygonaceae	328	lat 43°28′06″N, long 116°05′22″W; 1 032 m

[1]All forbs collected in Snake River Plain of southern Idaho except Munro's globemallow.

controlled with supplemental lights, provided 14 h · d^{-1}of light. Plants were watered daily for the first 14 d, and every 2–3 d thereafter. After 6, 9, and 12 wk of growth, six containers of each treatment were destructively harvested to obtain root and shoot biomass. Containers were turned on their sides and root material was slid out carefully so as not to disturb or tear roots and to observe root orientation. Forb and grass root material were carefully separated by hand, cleaned, and dried at 65°C for 48 h, then weighed.

Data Analysis

Biomass differences among forb species after 6, 9, and 12 wk of growth were analyzed with one-way analysis of variance (ANOVA) on log-transformed total biomass (SPSS 2006), with Tukey multiple-comparison tests for the 6-wk data, and Games–Howell post hoc tests for 9- and 12-wk data, because these data failed Levene's test for homogeneity of variance (Leech et al. 2004). RMR is root mass divided by total (root plus shoot) biomass. Differences between species in RMRs after 6, 9, and 12 wk were tested with one-way ANOVAs for data from each harvest with Tukey multiple-comparison tests (α=0.05).

Differences in instantaneous RGR were analyzed for all forbs except bigseed biscuitroot, which began to senesce in the greenhouse between Weeks 9 and 12. Instantaneous RGR was computed as the slope of the natural log of forb biomass regressed on weeks of growth. For each species, plants were ranked by total biomass at each harvest (from one to six) and paired with plants of equivalent rank from the 9- and 12-wk harvests to obtain six values for the RGR of each forb based on the three harvests. Ranking and pairing creates six RGR values (or slopes), allowing an assessment of variance within and among treatments as opposed to averaging the natural log of the six replicates from each harvest and using that to create one value for RGR. Differences among forb instantaneous RGRs were computed with the use of the Tukey multiple comparison test (α=0.05). Along with total RGR, the shoot and root RGR were computed separately. Additionally, to avoid the bias associated with pairing plants of similar size rank across harvest periods (Poorter 1989), differences in RGR among species were tested with the use of an ANCOVA of log-transformed biomass with harvest week as the covariate (SPSS 2006). The same RGR values (or slopes) were obtained as using the method above (ranking and pairing). Significant differences in RGR were identified by testing for an interaction between species and harvest week (time), which would indicate that at least one of the species differed in RGR (Poorter and Lewis 1986).

The effect of a grass neighbor on total biomass, total RGR, and shoot and root tissue RGR of each forb was tested with the use of one-way ANOVAs among neighbor treatments (alone, with cheatgrass, bottlebrush squirreltail, or Sandberg bluegrass). An ANOVA of RGR among neighbor treatments was not conducted for bigseed biscuitroot. The Tukey multiple comparison test (α=0.05) was used to determine which treatments differed.

RESULTS

Forb Biomass and Root Growth Without Grass Neighbors

Forbs exhibited large differences in total biomass after only 6 wk of growth (Table 2). Munro's globemallow was consistently the largest. By Week 12 its biomass was 7 and 16 times greater than the biomass of the next largest forbs, hoary aster and royal penstemon, respectively. Sulphur-flower buckwheat was intermediate and not significantly different from bigseed biscuitroot or royal penstemon at Weeks 6 and 9, but by Week 12 its biomass was five times larger than bigseed biscuitroot, but only one-third the size of royal penstemon.

Differences in RMR among species were apparent after 6 wk of growth and continued through Weeks 9 and 12 (Table 3). The RMR of bigseed biscuitroot exceeded that of the other species by an average of 4.2 times after 6 wk and by 1.7 to 3.6 times after 12 wk, respectively. Royal penstemon RMR was similar to that of Munro's globemallow, sulphur-flower buckwheat, and hoary aster after 6 wk of growth, but by Week 12 its RMR was 1.7 to 2 times that of the other three species, which exhibited similar RMRs throughout the 12-wk period.

Table 2. Total biomass (mean ± 1 SE) of forbs when growing alone after 6, 9, or 12 wk of growth. *F* and *P* values are from a one-way ANOVA of the log normal of total forb biomass of each species on each harvest date; df = 4,25. Letters indicate significant differences at each harvest week (within a column) based on Tukey's multiple-comparison test ($P < 0.05$).

	Total biomass (g)		
Common name	6 wk	9 wk	12 wk
Bigseed biscuitroot	0.022 ± 0.006 a	0.07 ± 0.003 a	0.08 ± 0.003 a
Sulphur-flower buckwheat	0.038 ± 0.006 ab	0.16 ± 0.04 ab	0.46 ± 0.12 b
Royal penstemon	0.067 ± 0.004 b	0.42 ± 0.10 b	1.50 ± 0.33 c
Hoary aster	0.395 ± 0.120 c	1.10 ± 0.09 c	3.38 ± 0.50 d
Munro's globemallow	1.987 ± 0.350 d	8.75 ± 0.92 d	24.09 ± 2.02 e
F value	72.4	139.40	145.62

Table 3. Root-mass ratios (mean ± 1 SE) of forbs when growing alone after 6, 9, or 12 wk of growth. *F* and *P* values are from a one-way ANOVA among species on the log normal of root-mass ratio at each harvest, df = 4,25. Letters indicate significant differences at each harvest week (within a column) based on the Tukey multiple-comparison test ($P < 0.05$).

Common name	6 wk	9 wk	12 wk
Bigseed biscuitroot	0.60 ± 0.06 a	0.75 ± 0.01 a	0.83 ± 0.01 a
Royal penstemon	0.13 ± 0.02 b	0.25 ± 0.03 b	0.48 ± 0.02 b
Hoary aster	0.17 ± 0.02 b	0.23 ± 0.02 bc	0.29 ± 0.01 c
Sulphur-flower buckwheat	0.15 ± 0.02 b	0.17 ± 0.02 cd	0.23 ± 0.02 c
Munro's globemallow	0.13 ± 0.01 b	0.13 ± 0.01 d	0.24 ± 0.02 c
F value	46.4	174.15	198.16

Root morphology varied considerably among species. Bigseed biscuitroot was tap-rooted, with no lateral branches developing from the main root after 12 wk of growth (Fig. 1). In the first 6 wk, hoary aster was also tap-rooted, and developed lateral roots only between Weeks 9 and 12. Roots of sulphur-flower buckwheat were not tap-rooted; instead, all roots were extremely fine (< 1 mm diameter), with minimal branching, only two or three lateral branches within 3–5 cm of the soil surface, which were oriented vertically. In contrast, roots of royal penstemon and Munro's globemallow were densely branched, distributed laterally as much as vertically, and had considerable branching near the soil surface and throughout the depth of the container.

Forb Relative Growth Rates Without Grass Neighbors

Because bigseed biscuitroot grew very little between Weeks 9 and 12, consistent with the growth patterns of Great Basin *Lomatium* spp. in the field (H. Parkinson, personal observation, spring 2005–2007 field seasons), RGR was only calculated for the other forb species. The slopes of the natural log of total forb biomass by harvest time differed between species ($F_{3,20}=3.34$; $P < 0.05$). The slope of royal penstemon was greater than that of hoary aster, and slopes for sulphur-flower buckwheat and Munro's globemallow were intermediate and not different than either royal penstemon or hoary aster (Fig. 2). Separating plant growth rates by root and shoot tissue revealed that RGR of shoot tissue did not differ between species ($F_{3,20}=0.60$); however, the RGR of root tissue varied among species ($F_{3,20}=11.42$, $P < 0.0001$). The RGR of royal penstemon root tissue (0.72 ± 0.06) was significantly greater than that of Munro's globemallow (0.53 ± 0.06), sulphur-flower buckwheat (0.48 ± 0.08), and hoary aster (0.48 ± 0.10); the latter three forbs were not different from each other.

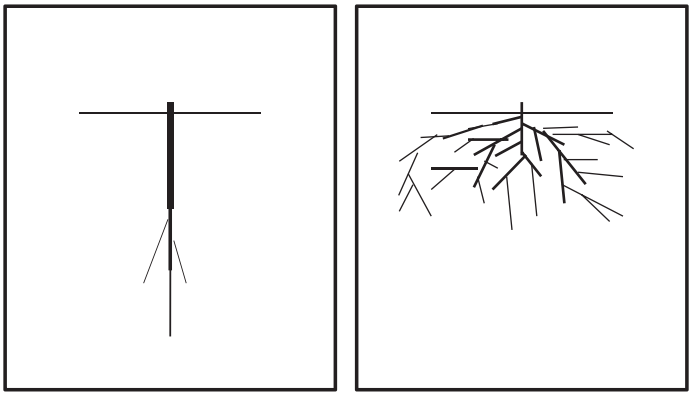

Figure 1. Diagram of forb root morphology types: **A,** Vertically oriented root morphology of bigseed biscuitroot, hoary aster, and sulphur-flower buckwheat. **B,** Dense lateral branching of Munro's globemallow and royal penstemon.

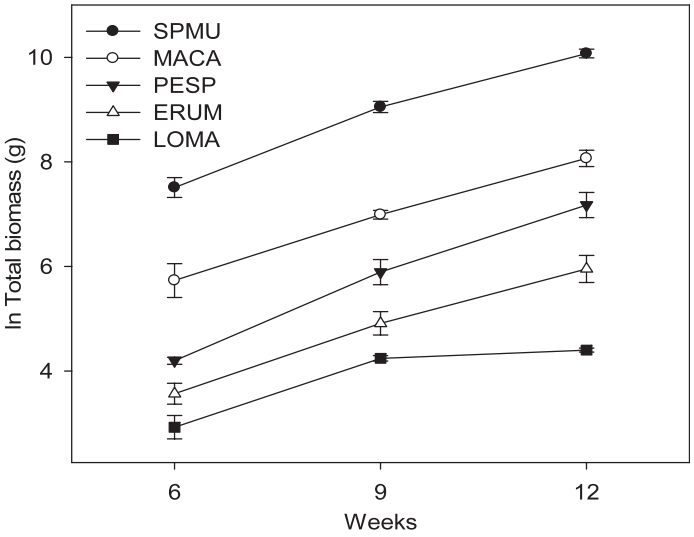

Figure 2. Natural log of total forb biomass (± 1 SE) when growing alone in a greenhouse for 6–12 wk. SPMU=Munro's globemallow; MACA=hoary aster; PESP=royal penstemon; ERUM=sulphur-flower buckwheat.

Forb Growth With Grass Neighbors

Total grass biomass averaged across all forb neighbors was 1.8 ± 0.22 g for Sandberg bluegrass, 7.3 ± 0.54 g for bottlebrush squirreltail, and 24.0 ± 0.52 g for cheatgrass. After 12 wk of growth, total biomass of all forbs when growing with a native grass was not different from growing alone (Table 4). In contrast, the total biomass of all forbs was reduced when growing with cheatgrass relative to growing alone. Compared to growth alone, reductions in forb biomass ranged from 50% for bigseed biscuitroot to 91% for royal penstemon.

Although a native grass neighbor did not affect forb biomass, values for total RGR were reduced when growing with a neighbor versus growing alone (Parkinson 2008). Both native grasses reduced the total RGR of royal penstemon by 25%; bottlebrush squirreltail reduced the total RGR of Munro's globemallow by 18% (data not shown). Cheatgrass reduced the total RGR of all forbs, with the reductions ranging from 37% for Munro's globemallow to 80% for royal penstemon.

Sandberg bluegrass and bottlebrush squirreltail reduced the root RGR of royal penstemon by an average of 20% compared to growth alone (Fig. 3). Native grass neighbors did not impact root growth rate of sulphur-flower buckwheat, hoary aster, or Munro's globemallow. Cheatgrass reduced the root RGR of sulphur-flower buckwheat by 42% and royal penstemon by 74% (Fig. 3), but did not affect RGR of hoary aster or Munro's globemallow. Shoot RGR (Fig. 3) was not impacted by Sandberg bluegrass; however, bottlebrush squirreltail reduced shoot RGR of royal penstemon by 35% and Munro's globemallow by 20%, but did not affect shoot RGR of hoary aster or

Table 4. Total forb biomass (mean ± 1 SE) among neighbor treatments after 12 wk of growth. *F* and *P* values are from one-way ANOVAs comparing forb biomass among neighbor treatments, df = 3,20. Letters indicate significant differences within a column ($P < 0.05$) based on Tukey multiple-comparison tests. Nontransformed data are presented; log-transformed data were used for analysis.

	Forb species				
Neighbor treatment	Bigseed biscuitroot	Sulphur-flower buckwheat	Royal penstemon	Hoary aster	Munro's globemallow
Alone	0.08 ± 0.003 a	0.46 ± 0.12 a	1.49 ± 0.33 a	3.38 ± 0.50 a	24.09 ± 2.02 a
Sandberg bluegrass	0.06 ± 0.01 ab	0.51 ± 0.09 a	0.70 ± 0.08 ab	5.30 ± 1.26 a	22.13 ± 2.38 a
Bottlebrush squirreltail	0.05 ± 0.01 ab	0.29 ± 0.11 ab	0.78 ± 0.23 ab	5.50 ± 0.40 a	23.77 ± 2.51 a
Cheatgrass	0.04 ± 0.01 b	0.10 ± 0.02 b	0.13 ± 0.02 b	0.75 ± 0.17 b	8.76 ± 1.44 b
F value	3.03	6.24	21.59	20.13	20.59
P value	0.05	0.004	< 0.001	< 0.001	< 0.001

sulphur-flower buckwheat. Cheatgrass reduced shoot RGR of all forbs by an average of 60%, ranging from 45% for Munro's globemallow to 81% for royal penstemon.

DISCUSSION

Re-establishing native plants to restore ecosystem function, structure, and diversity following disturbance is a high priority in the Great Basin. In particular, it is of critical importance to establish plant communities that will be resistant to weed invasions and resilient to future disturbances. Because the relative growth rates of sulphur-flower buckwheat and hoary aster were not reduced when they were grown with a native grass neighbor, our results challenge previous suggestions that forbs should be seeded separately from grasses, or that forb seeding densities should be reduced to increase forb recruitment (Kindscher and Fraser 2000; Elstein 2004; Dickson and Busby 2009). These two forb species may grow well when seeded with native grasses. In contrast, the decline in RGR of royal penstemon when grown with either native grass and of Munro's globemallow when grown with bottlebrush squirreltail is consistent with other research demonstrating the potential for native grasses to reduce the establishment of specific native forbs (Brown and Bugg 2001; Dickson and Busby 2009; McCain et al. 2010).

Although only qualitatively observed, differences in root morphology may partially explain why native grasses did not reduce RGR of two of the forbs. Both sulphur-flower buckwheat and hoary aster had a columnar and vertically oriented root morphology, and both exhibited no reduction in total RGR when grown with either native grass. The root morphologies of royal penstemon and Munro's globemallow were densely fibrous, with high lateral branching, increasing spatial overlap with grasses, which shared this root morphology. Designing seed mixes to increase heterogeneity of root characteristics could result in increased species richness, and planting forbs with a columnar, vertically oriented root morphology with native grasses may be a tool to reduce niche overlap and increase species and life-form diversity (Stubbs and Wilson 2004).

Differences in forb growth patterns and response to native-grass neighbors implies that considering all forb species as a single functional group ignores important variation in both morphology and growth rate that could be used to design diverse native seedings. For example, increasing the density of all forb species in a seed mix without an adequate understanding of this could potentially increase interspecific competition among forbs and reduce forb diversity, considering the large differences in forb biomass in the first 12 wk of growth. Likewise, reducing grass seeding rates without considering the identity and characteristics of the forb species included in the mixture could preclude an opportunity to increase invasion resistance.

Because cheatgrass densities can be high enough to preclude natural recovery of native plants (Knapp 1996), identifying

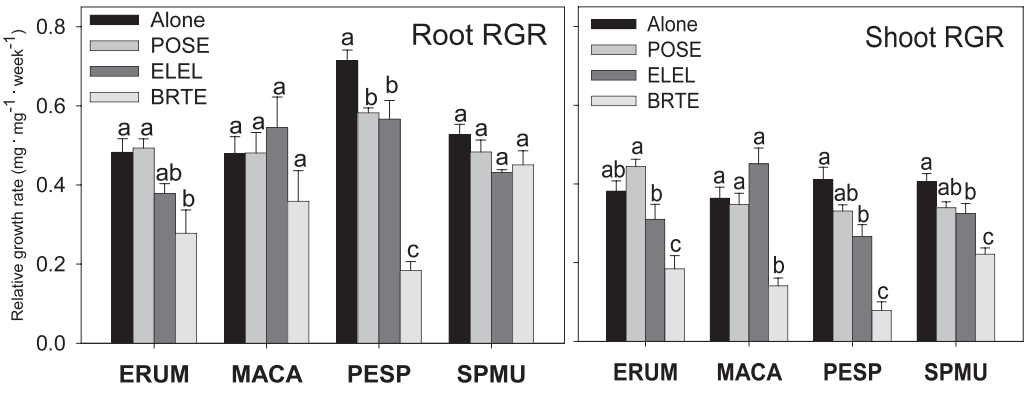

Figure 3. Forb root and shoot RGR ($mg \cdot mg^{-1} \cdot wk^{-1} \pm 1$ SE) among neighbor treatments (alone or with POSE [Sandberg bluegrass], ELEL [bottlebrush squirreltail], or BRTE [cheatgrass]). Different letters indicate significant differences within forb species based on Tukey multiple-comparison tests ($P < 0.05$). Forbs: ERUM = sulphur-flower buckwheat; MACA = hoary aster; PESP = royal penstemon; SPMU = Munro's globemallow.

how forb species vary in their competitive response to cheatgrass is important. The smallest forb in this study, bigseed biscuitroot, and the largest, Munro's globemallow, exhibited the least reduction in biomass when grown with cheatgrass (51% and 64%), illustrating that biomass alone is a poor indicator of ability to grow in the presence of cheatgrass. Identifying forbs that can establish and grow with cheatgrass could help design specific seed mixes to increase plant community resistance to cheatgrass invasion. In doing so, native forb species mixes should account for species differences in phenology to accommodate the life-history traits of cheatgrass. For example, as a facultative winter annual, cheatgrass may germinate in the fall, continue root growth throughout the winter, and initiate shoot growth earlier in spring than native plants, meaning it reduces soil water content and has a large size advantage over spring-emerging forb seedlings (Arredondo et al. 1998). Consequently, it is feasible that species that germinate early, such as bigseed biscuitroot and other species of biscuitroot grown for restoration (i.e., fernleaf biscuitroot [*L. dissectum*], nineleaf biscuitroot [*L. triternatum*], and Gray's biscuitroot [*L. grayi*]) (Scholten et al. 2009), will be less impacted by cheatgrass in early spring than species that germinate in mid-spring, approximately the time frame when cheatgrass begins to cause detectable differences in soil water content (Parkinson 2008).

The high cost of native seed and the decreasing likelihood of success with increasing cheatgrass densities are factors to be considered when designing a revegetation project. Although we cannot recommend that any of these species be seeded in areas expected to have high cheatgrass densities, our data suggest that species such as royal penstemon only be selected when the risk of cheatgrass invasion is anticipated to be very low. Because the presence of native grasses may reduce cheatgrass invasion, the inclusion of forb species that grow well with native grasses can enhance partitioning of resources, increase species richness of the established community (Pyke and Archer 1991; Schwinning and Ehleringer 2001), and potentially reduce invasion of exotic species.

IMPLICATIONS

The low survival and establishment that characterize many restoration seedings in arid environments like the Great Basin may be improved by defining variability among candidate restoration forb species for specific morphological and growth rate differences as well as competitive responses to cheatgrass. Previous research recommends that forbs be seeded separately from grasses to increase forb recruitment. Our research shows that such a broad generalization is not appropriate, as variation among forbs for relative growth rate and root morphology warrants independent consideration of species based on these characteristics. For example, forbs with densely fibrous root systems similar to those of grasses (e.g., Munro's globemallow and royal penstemon) encountered more interspecific competition from native grasses, potentially because of increased spatial overlap in the soil profile. Separating them spatially from native grasses, or seeding grasses at a reduced rate, may increase their survival. In contrast, the forbs with a tap root, or with roots oriented mainly vertically (i.e., bigseed biscuitroot [and other *Lomatium* spp.], hoary aster, and sulphur-flower buckwheat) may experience fewer restrictions when seeded with native grasses. Recognizing differences in root morphology, phenology, growth rates, and size will also allow managers to design species mixtures to reduce interspecific competition among seeded species. Although root growth patterns will vary in the field based on resource levels and interactions with other species, differences in root morphology may be used in future studies to investigate the potential for resource partitioning (Ray-Mukherjee et al. 2011). Combining the information on root morphology with observations on relative emergence dates and periods of primary growth among forbs and native grasses will likely increase our ability to select seeding strategies that minimize negative interactions among seeded species, while allowing for the development of plant communities more resistant to invasion by cheatgrass.

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