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Source: Rangeland Ecology & Management, 67(3):275-284.
Published By: Society for Range Management
DOI: http://dx.doi.org/10.2111/REM-D-12-00024.1
URL: http://www.bioone.org/doi/full/10.2111/REM-D-12-00024.1

Rangeland Ecol Manage 67:275–284 | May 2014 | DOI: 10.2111/REM-D-12-00024.1

A Comparison of *Bromus tectorum* Growth and Mycorrhizal Colonization in Salt Desert vs. Sagebrush Habitats

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Abstract

Cheatgrass (*Bromus tectorum*) has recently invaded marginal low-elevation salt desert habitats across the Great Basin. We tested the hypothesis that cheatgrass seed produced in populations from the more stressful salt desert vs. upland sagebrush habitats should grow differently in salt desert soils compared to adjacent upland sagebrush soil, and vice versa. We evaluated growth, incidence of flowering, and arbuscular mycorrhizal fungi (AMF) colonization of plants grown in the soils from which their seeds were collected vs. in the reciprocal soils from the nearest sagebrush or salt desert site in three large basins in northern Nevada. Simultaneously we measured nutrient cations, available nitrogen and phosphorus, percent carbon and nitrogen, texture, and dry-down characteristics in all soils. We found that salt desert soils were generally more nutrient poor and more saline than their upland (sagebrush) counterparts; salt desert soils also generally had a higher percentage of sand compared to their upland counterparts and were consistently drier. The most dramatic plant responses to soil and seed source were 1) lower aboveground biomass of mature plants in most salt desert soils compared to sagebrush soils, or lower biomass in plants grown from salt desert seed; 2) lower root:shoot ratios in plants grown in salt desert soil across two of three basins, irrespective of seed source; 3) a higher percentage of flowering individuals from salt desert seed sources at harvest, irrespective of soil source; 4) depressed AMF colonization of plants in salt desert soils; and 5) strong influence exerted by seed source on AMF, whereby sagebrush-originating plants grown in sagebrush soils had greater AMF colonization compared to salt desert soils but salt desert-originating seedlings had very low AMF colonization rates irrespective of soil source. These results suggest that both population level and soil-based controls are important as this widespread weed moves into marginal habitat.

Key Words: AMF, invader, maternal effects, seed source soil nutrients

INTRODUCTION

Plant invaders may expand their range into a broad array of sites by undergoing local adaptation (Parker et al. 2003) or by having broad environmental tolerances (e.g., the all-purpose genotype, Baker 1965). Most predictions of range expansions of invading species have been based on climate matching or climate envelope modeling, although the predictive power of this approach is low (Williamson 2006). Much less attention has been paid to the role of soils in the invasion and range expansion of introduced plants. Yet studies of plants on serpentine soils, for example, have demonstrated the important role of edaphic conditions in influencing species evolution and population persistence (Batten et al. 2006). Variation in soil nutrient availability (e.g., Huenneke et al. 1990) and soil microbial communities (as reviewed by Inderjit and van der Puttten 2010) have been shown to strongly influence invasion.

Cheatgrass (*Bromus tectorum* L.) is a primarily selfing annual grass introduced to western North America from Eurasia and northern Africa in the 1800s (Mack 1989). Its invasion into salt desert (SD) shrub communities, however, has been observed only since the late 1980s (Young and Tipton 1990; Hunter 1991). Novak and Mack (1993) argue that cheatgrass shows little genetic variation across its North American range, whereas others (Ashley and Longland 2009; Leger et al. 2009; Scott et al. 2010) have suggested that cheatgrass has developed genetic variation within and among invasive populations, particularly in marginal compared to more central habitats. Its presence in marginal SD habitats has been noted for three decades; it can become abundant enough to fuel large wildfires with negative and long-term impacts on the native vegetation (Haubensak et al. 2009). The degree to which invasion into SD habitats has selected for adaptations to that habitat is unknown, as is the extent to which mycorrhizal associations are present in cheatgrass populations across habitats and soil types. It is a facultative host of arbuscular mycorrhizal fungi (AMF), demonstrates little growth response to AMF presence (Allen 1984), and can reduce AMF in soils (Hawkes et al. 2006). Considered a poor host for AMF, its invasion and site dominance may affect recolonization and growth of resident species that may be AMF-dependent (Vogelsang and Bever 2009; Busby et al. 2012).

Research was funded by the US Dept of Agriculture–Agricultural Research Service.

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Manuscript received 24 February 2012; manuscript accepted 10 March 2014.

In this study we evaluated the response of cheatgrass seedlings grown from different seed sources to soils from under different vegetation types collected from three basins in northern Nevada where cheatgrass is abundant. In each basin, cheatgrass occurs in an upland big sagebrush (*Artemisia tridentata* Nutt.) shrubland as well as in basin-bottom SD shrubland, dominated by bud sagebrush (*Picrothamnus desertorum* Nutt.) and shadscale (*Atriplex confertifolia* [Torr. & Frém.] S. Watson). The SD communities are considered to be different from sagebrush (SB) communities due to lower rainfall and more saline soil (Billings 1949), yet the two habitat types typically occur in close proximity such that genetic exchange via transport of seed among cheatgrass populations is likely. SD sites are considered to be stressful for cheatgrass growth (Rice and Mack 1991a) and likely on the edge of its environmental envelope (Mack 2011). Nonetheless we do not know if there has been selection for plant traits favorable in the SD community, nor how plant growth and the degree to which cheatgrass associates with native AMF vary by soil type independent of climate.

We used a common garden approach to evaluate the performance of different seed populations of cheatgrass in response to soil. Plants were grown from seed collected from SB or SD communities and then planted into their own soil or that of the nearest other community type (SB or SD) using a simple paired reciprocal design. Plant performance variables included root elongation during initial seedling growth, root:shoot ratio of developing seedlings, proportion of individuals that reached flowering by harvest, maximum size reached at harvest (2 mo) and percentage of colonization of roots of mature plants by AMF. We hypothesized that SD soils would represent a more resource-limited environment and thus, root elongation would initially be more rapid in plants on SD soils and that these plants should subsequently have higher root:shoot ratios. Further, we predicted that more plants grown in SD soils would flower due to selection for rapid growth (Mack 2011) in what is presumed to be a more water-limited environment. We simultaneously predicted that if the SD soils are indeed harsher for plant growth, then all plants should grow smaller in SD soils irrespective of seed source. Finally, we predicted that colonization of cheatgrass roots by AMF should be lower in SD soils because of several possible mechanisms: increasing salinity, which is often inversely associated with mycorrhizal colonization (Evelin et al. 2009); less opportunity to form these associations due to rapid growth and flowering at a smaller size; or selection for limited mycorrhizal colonization due to increased carbon cost (Hoeksema et al. 2010).

Our experiment does not unambiguously test for local adaptation because we did not grow out seed populations for a full generation in the greenhouse prior to initiating the study. Nonetheless, maternal effects themselves are an interesting possible mechanism that may explain plant responses and tolerance of environmental heterogeneity, particularly in harsh environments (Roach and Wulff 1987). For example, Wehmeyer and Veirling (2000) have demonstrated the production and accumulation of heat shock protein in developing seeds, which later may function to protect seedlings from heat or desiccation stress (Sun et al. 2002; Wang et al. 2004).

METHODS

Study Sites

We located three basins in north-central Nevada in November 2002; both SB and SD plant communities were clearly delineated on an elevational gradient and in reasonably close proximity. SB sites were chosen on the basis of dominance by big sagebrush and were upland of SD sites. SD sites were chosen based on codomination by shadscale and bud sagebrush with other chenopod species (Bailey's greasewood [*Sarcobatus baileyi* Coville], winterfat [*Krascheninnikovia lanata* {Pursh} A. Meeuse & Smit], and fourwing saltbush [*Atriplex canescens* {Pursh} Nutt.]) variously present. SB sites were 1 448–1 553 m in elevation; SD sites were between 1 330 m and 1 377 m (Table 1). The three basins varied in soil origin and average rainfall and are named by various landscape features (Table 1); we will henceforth refer to the basins by these names. All sites were located within Major Land Resource Area-27 (US Department of Agriculture–Natural Resources Conservation Service 2006).

Soil and Seed Collection

In 2001 and 2002 dried mature seeds were collected and stored in brown paper bags in a humidity- and temperature-controlled laboratory in Reno, Nevada. Soils were collected in fall 2002, and stored until use in January 2003. Soils were collected from sites as close as possible to the seed collection points. At each site in an area of approximately 10 000 m^2, we haphazardly selected 40 intershrub locations and collected soils to a depth of 20 cm using standard shovels. Soils were bulked into barrels, brought back to the greenhouse where each site's soil was homogenized in a cement mixer and then dispensed into 11-L pots and 16-cm cone-tainers (Steuwe and Sons, Corvallis OR).

Soil Analyses

Homogenized soils were air-dried in the greenhouse, then subsamples of each soil were ground with a mortar and pestle and analyzed for total carbon (C) and total nitrogen (N) by combustion on a Carlo Erba NA 1500 CHN analyzer (Fisons Instruments, Beverly, MA). Separate aliquots of each soil were wetted to field capacity (–33 MPa) and dispensed into specimen cups for 14-d aerobic incubations to measure potential net N mineralization (Binkley and Hart 1989). Other subsamples of each soil were measured for manganese, iron, zinc, and copper by diethylenetriamenepentaacetic acid analysis (Blank et al. 2007). Calcium (Ca), magnesium, potassium (K), and sodium (Na) were measured by acetate analysis (Blank et al. 2007). Soil texture was measured by the hydrometer method. Soil dry-down curves were developed by measuring soils initially wetted to field capacity in pots with no plants and then followed over a 10-d drying period using time-domain reflectometry 20-cm probes placed into each pot . For each soil analysis $n=3$ except for net N mineralization and soil dry-down analyses where $n=5$.

Greenhouse Experiment

Five cheatgrass seeds were planted into each of 20 11-L pots and two seeds into each of 20 Ray Leach cone-tainers (2.5×16 cm, Stuewe and Sons) for the following treatments: seed from SD habitat planted into its own SD soil; SD seed planted into its

Table 1. Site, plant, and soil characteristics of three paired sagebrush and salt desert sites. Values are means ± 1 SE. Bold values demonstrate significant differences in sagebrush vs. salt desert paired *t* tests conducted in each basin separately (see Table 2).

	Seven Troughs		Poker Brown		Smoke Creek	
	Sagebrush	Salt desert	Sagebrush	Salt desert	Sagebrush	Salt desert
Elevation (m)	1 553	1 372	1 522	1 377	1 448	1 330
Dominant species	*Artemisia tridentata* subsp. *tridentata*, *Elymus elymoides*	*Atriplex confertifolia*, *Artemisia spinescens*	*Artemisia tridentata* subsp. *tridentata*	*Atriplex confertifolia*, *Artemisia spinescens*	*Artemisia tridentata* subsp. *tridentata*	*Sarcobatus baileyi*, *Atriplex canescens*
Latitude/longitude	lat 40°33′N, long 118°41′W	lat 40°28′N, long 118°41′W	lat 40°35′N, long 118°32′W	lat 40°28′N, long 118°19′W	lat 40°33′N, long 120°00′W	lat 40°30′78″N, long 119°49′94″W
Soil texture						
% Sand	67.1	68.1	**48.5**	**63.5**	**49.9**	**79.7**
% Silt	26.9	24.8	44.0	29.7	42.9	12.8
% Clay	6.0	7.1	7.5	6.8	7.2	7.6
Nutrient cations ($\mu g \cdot g^{-1}$)[1]						
Mn	**42.5 ± 3.1 SE**	**32.7 ± 9.1 SE**	**47.9 ± 6.1 SE**	**28.6 ± 4.2 SE**	**80.5 ± 14.6 SE**	**35.4 ± 0.73 SE**
Fe	**4.14 ± 0.38 SE**	**2.92 ± 1.09 SE**	**6.81 ± 0.59 SE**	**4.91 ± 0.28 SE**	**9.98 ± 1.03 SE**	**6.99 ± 0.25 SE**
Zn	**4.47 ± 1.20 SE**	**0.98 ± 0.04 SE**	**2.05 ± 0.25 SE**	**1.26 ± 1.12 SE**	**1.18 ± 0.17 SE**	**0.69 ± 0.03 SE**
Cu	**1.08 ± 0.11 SE**	**0.74 ± 0.30 SE**	**1.76 ± 0.29 SE**	**0.83 ± 0.08 SE**	**1.98 ± 0.28 SE**	**1.09 ± 0.03 SE**
Ca	1 963 ± 37.51 SE	1 876 ± 229.5 SE	**2 949 ± 244.3 SE**	**3 698 ± 563.2 SE**	5 764 ± 154.5 SE	5 521 ± 147.6 SE
Mg	**300.5 ± 5.13 SE**	**282.6 ± 86.78 SE**	**381.5 ± 10.70 SE**	**349.4 ± 16.22 SE**	**1 600 ± 397.6 SE**	**347.2 ± 5.34 SE**
K	636.9 ± 8.20 SE	621.0 ± 26.29 SE	**547.8 ± 193.0 SE**	**1 164 ± 168.6 SE**	**2 463 ± 312.2 SE**	**1 512 ± 19.45 SE**
Na	276.2 ± 64.9 SE	460.2 ± 88.89 SE	**218.9 ± 25.64 SE**	**137.2 ± 44.54 SE**	**62.67 ± 216.8 SE**	**754.2 ± 8.28 SE**
Bicarb-P	14.58 ± 3.50 SE	13.92 ± 3.47 SE	**35.25 ± 4.95 SE**	**19.54 ± 1.07 SE**	**135.2 ± 33.84 SE**	**29.56 ± 1.21 SE**
Total N (%)	**0.048 ± 0.007 SE**	**0.028 ± 0.001 SE**	**0.068 ± 0.001 SE**	**0.038 ± 0.001 SE**	0.129 ± 0.039 SE	0.035 ± 0.006 SE
Total C (%)	0.547 ± 0.092 SE	0.308 ± 0.003 SE	**0.860 ± 0.014 SE**	**0.501 ± 0.002 SE**	1.92 ± 0.658 SE	0.849 ± 0.143 SE
Net N mineralization[2]	1.13 ± 0.63 SE	1.20 ± 0.39 SE	1.17 ± 0.55 SE	0.39 ± 0.14 SE	**5.51 ± 1.58 SE**	**0.66 ± 0.22 SE**
Net nitrification[2]	2.34 ± 1.29 SE	2.73 ± 0.76 SE	2.30 ± 1.05 SE	0.48 ± 0.26 SE	**11.44 ± 3.16 SE**	**1.50 ± 0.43 SE**

[1]Mn indicates manganese; Fe, iron; Zn, zinc; Cu, copper; Ca, calcium; Mg, magnesium; K, potassium; Na, sodium; Bicarb-P, bicarbonate phosphorus; N, nitrogen; and C, carbon.
[2]Fourteen-day laboratory aerobic incubations (Binkley and Hart 1989).

paired upland (SB) soil; seed collected from SB habitat planted into its own SB soil; SB seed planted into its paired lowland (SD) soil. The large pots were used to allow plants to grow for approximately 2 mo, whereas the cone-tainers were used for examination of initial root growth. Two weeks after germination, seedlings were thinned to a single randomly chosen individual in the 11-L pots. Cone-tainer samples were thinned to a single randomly chosen individual immediately (within 2 d) after germination. Three replicates of all treatments were planted into cone-tainers. One set was harvested 3 d after germination, the second 7 d after germination, and the third 14 d after germination, in order to evaluate treatment effects on initial seedling growth and root elongation. Only 14-d results will be discussed hereafter because patterns of root growth were similar across all three time points.

Mycorrhizal Analysis

After the final harvest of greenhouse plants (those grown in 11-L pots), we used scissors to subsample 5–10-cm lengths of root mass from each plant to evaluate them for mycorrhizal colonization. Subsamples were placed in 7-mL plastic scintillation vials containing a 50% ethanol solution in deionized water and stored at room temperature until analysis.

The root fragments from each vial were heated at 90°C for about 1 h in a 5% w/v potassium hydroxidebath to remove host cytoplasm and most of the nuclei, making the vascular cylinder distinctly visible. Next, roots were rinsed in a 1% hydrochloric acid solution for 2 min followed by submergence in a 0.05% (w/v) trypan blue staining solution that was heated to 90°C for 15 min. A destaining solution identical to the lactoglycerol solution, without trypan blue, was applied to stained roots at 90°C for 15 min. Stained roots were cut into 1–4-cm fragments prior to being mounted in glycerin on 2-mm gridded microscope slides (Electron Microscopy Supply, Inc., Fort Washington, PA; Tenant 1975). Samples on the slides were covered with 22×22 mm cover slips and sealed with a compound of acetate and formaldehyde resin.

We sampled roots from 12 plants per treatment after determining that this sample size was adequate to achieve constant variance. For each sample, we also determined the minimum number of slides needed per individual plant to achieve a constant low level of variance (< 2%) and used that sample size ($n=5$) thereafter. To keep mounting consistent, a fragment was placed in each row of the grid box parallel, and in-between, the long axes of the gridlines (Tennant 1975).

Quantification of mycorrhization was performed according to the magnified intersection method of McGonigle et al. (1990). Colonization rate was calculated as the proportion of mycorrhizal intersections to the total number of root intersections along the slide gridlines. Colonization rate therefore represents the proportion of root length containing mycorrhizal structures. Fungal structures were quantified at ×200 magnification, and confirmed at ×400 magnification. At each root intersection, all mycorrhizal fungal structures were counted. If hyphae with a spore, vesicle, or arbuscule were intersected (regardless of being within the cortex of root) then it was considered part of a mycorrhization (McGonigle et al. 1990). The counts were recorded so that two observers could compare counts on a single slide. For each sample, the five colonization percentage values (measured on five slides) were averaged to produce one colonization value per pot.

Statistical Analyses

To compare nutrient cation concentrations in SD versus SB soils, each basin was analyzed separately and paired *t* tests were run on each soil variable. We did not have true replication to compare across basins because all samples of each soil type were from homogenized bins of soil from that site. N mineralization rates were also analyzed by basin, via one-way analysis of variance (ANOVA) with soil as a fixed main effect. To understand soil dry-down traits of each soil type, we applied a *t* test immediately after soil wet-up for each paired SB–SD soil, and at day 10.

In order to examine the effects of both soil and seed origin on plant growth attributes including mycorrhizal colonization, we initially used a three-factor mixed model ANOVA with basin as a random factor, and soil source and seed source as fixed main effects. Because basin was always significant ($P < 0.05$), we then analyzed each basin separately via two-factor ANOVA with soil source and seed source as fixed main effects, plus their interaction. Incidence of flowering was evaluated by counting the number of flowering plants in each soil–seed source combination and then performing χ^2 tests to determine whether seed or soil source (or their interaction) explained percentage of flowering. All statistical analyses were conducted with JMP 9 (SAS Institute Inc., Cary, NC).

RESULTS

Soils

The differences between SD and SB soils varied among the three basins we sampled, but with some exceptions SD soils generally had lower cation concentrations, and lower available N and phosphorus (P) compared to their SB counterparts (Tables 1 and 2). In two of the three basins (Poker Brown and Smoke Creek) SD soils had significantly higher Na compared to their upland SB counterparts, but at the third basin (Seven Troughs) there was no difference in Na between the two soil types. In the Smoke Creek basin SD soils were substantially lower in all cations except Ca, which did not differ between the two soil types. The SD soils in this basin also had significantly lower P and available N compared to their upland counterpart. At Poker Brown, SD soils also had lower concentrations of all cations with the exception of Ca and K, which were higher compared to the SB soils. Like Smoke Creek, the SD soils in Poker Brown also had significantly lower P concentrations, but there was no significant difference in available N between the two soil types. In the Seven Troughs basin, the SD soils had lower cation concentrations than the SB soils. In Seven Troughs, as in the Poker Brown watershed, there was no difference in net N mineralization rates between the SB and SD soils. Only Poker Brown had higher percentages of C and N in SB compared to SD soils; Seven Trough SB soils had a higher percentage of N compared to SD soils. In Smoke Creek there was no difference in percentages of C and N between the two soil types (Tables 1 and 2).

Table 2. Results of paired Student's *t* tests for soil variables. $n=3$ for each soil type within watershed. Each watershed was analyzed separately. Bold values demonstrate significant differences between sagebrush and salt desert soils.

Soil	Seven Troughs			Poker Brown			Smoke Creek		
variables[1]	*t*	df	*P*	*t*	df	*P*	*t*	df	*P*
Mn	15.56	2.62	**0.001**	127.7	3.64	< **0.001**	30.11	3.13	< **0.001**
Fe	10.29	2.34	**0.005**	61.6	3.42	< **0.001**	10.69	3.08	**0.002**
Zn	4.87	2.02	**0.04**	3.57	3.29	**0.03**	12.12	3.38	**0.001**
Cu	17.49	3.87	< **0.001**	55.9	3.78	< **0.001**	27.48	2.18	**0.001**
Ca	1.73	3.08	0.17	−18.64	2.16	**0.002**	1.28	3.83	0.27
Mg	4.06	3.71	**0.02**	14.27	2.01	**0.005**	113.7	3.12	< **0.001**
K	1.03	2.75	0.38	−64.65	2.34	< **0.001**	9.65	2.16	**0.008**
Na	−7.47	2.03	0.17	14.97	3.35	**0.003**	−80.06	2.35	< **0.001**
P	0.135	2.03	0.91	12.37	2.25	**0.004**	30.78	2.55	**0.002**
Sand	−1.04	2.02	0.40	−6.8	3.01	**0.006**	−19.2	3.87	< **0.001**
Clay	−1.07	2.31	0.38	1.15	3.23	0.32	−0.91	2.49	0.44
Min N	−0.10	6.67	0.92	1.36	4.53	0.23	3.04	4.15	**0.04**
Nit N	−0.26	6.48	0.80	1.67	4.48	0.16	3.11	4.15	**0.03**
% C	2.23	4.00	0.09	26.03	4.00	< **0.001**	2.54	4.0	0.19
% N	5.68	4.00	**0.005**	25.68	3.50	< **0.001**	2.41	4.0	0.07

[1]Mn indicates manganese; Fe, iron; Zn, zinc; Cu, copper; Ca, calcium; Mg, magnesium; K, potassium; Na, sodium; P, phosphorus; N, nitrogen; and C, carbon.

The SB and SD soils did not differ with respect to percentage of clay in any of the three basins. However, Smoke Creek and Poker Brown SD soils had significantly more sand compared to their SB soil counterparts (Table 1). Differences were particularly dramatic in the Smoke Creek Basin. There were no differences in soil texture between soil types in the Seven Troughs Basin. SD soils also had significantly lower volumetric water content at field capacity at all sites, approximately 33% compared to approximately 44% (Fig. 1); Smoke Creek and Poker Brown SD soils also had lower soil moisture after 10 d of dry-down compared to SB soils (Fig. 1). Consistent with the similarity in soil texture between the two soil types at Seven Troughs, both SD and SB soils had similar dry-down patterns.

Plants

Seed Masses. Seed size varied both among basins and between soil types within basins. The largest seeds overall were from the Smoke Creek basin (2.1 mg ± 0.06 SE) but they were not different between the SB and SD collections. Poker Brown seeds averaged 1.7 mg ± 0.05 SE with no difference between SD and SB sites as well. Seven Troughs was the only basin with differences in seed size between the sites: the SB populations averaged 1.9 mg ± 0.05 SE whereas the SD seed was significantly smaller at 1.1 mg ± 0.04 SE ($t=11.62$, df$=90.6$, $P=0.001$).

Initial Seedling Growth. Fourteen days after germination in cone-tainers, the roots of seedlings from Smoke Creek and Seven Troughs had grown less in the SD soils, irrespective of seed source (main effect of soil, $F_{1,74}=4.91$, $P=0.001$ and $F_{1,72}=4.81$, $P=0.0001$ for Smoke Creek and Seven Troughs, respectively; Table 3). At Poker Brown, however, there was an effect of seed source on soil response: roots of seedlings from SB-derived seed grew longer in SD soil than in their own soil but roots from SD-derived seed were short on both soil types (soil × seed interaction, $F_{1,70}=8.397$, $P=0.005$). Shoot elongation was also strongly influenced by soil type across basins

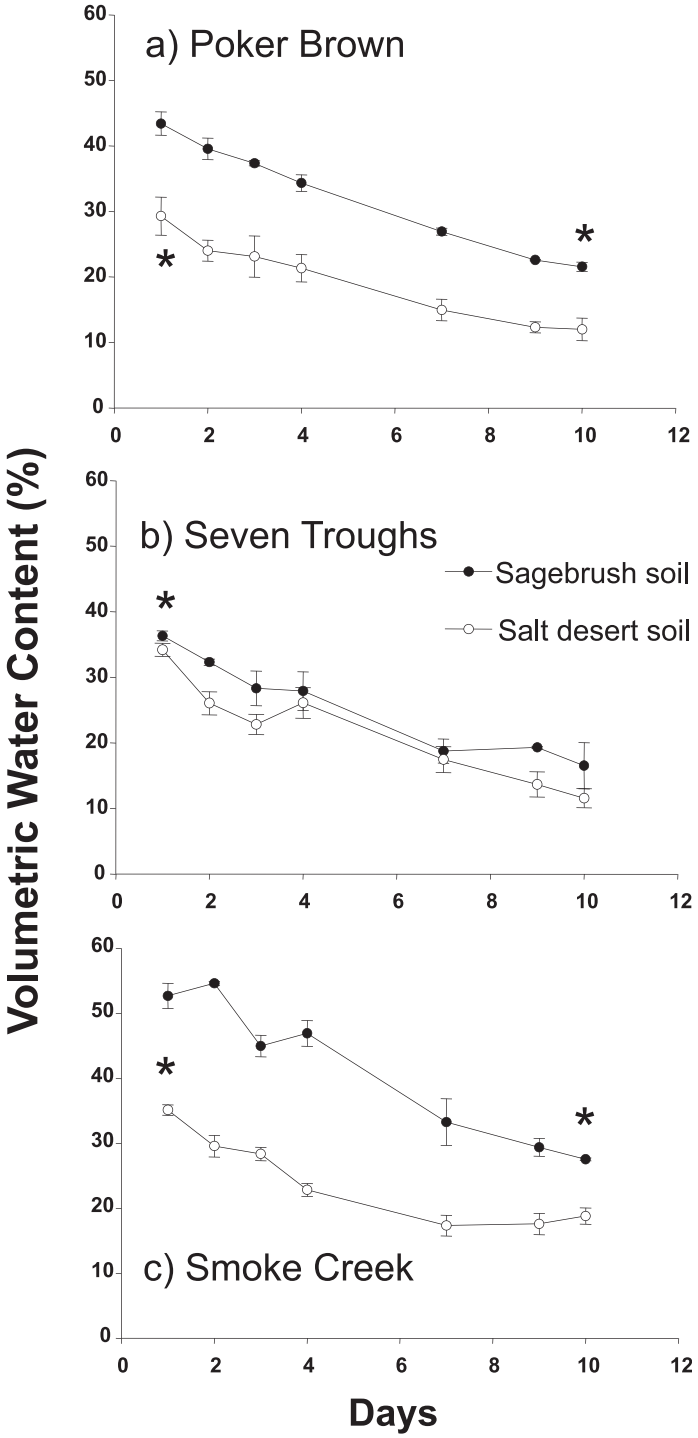

Figure 1. Soil dry-down curves for sagebrush and salt desert soils in **a,** Poker Brown, **b,** Seven Troughs, and **c,** Smoke Creek sites. Soils were wetted to saturation (≅ −3.3 MPa) then allowed to dry down over 14 d. Time-domain reflectometry measurements were taken to determine volumetric water content at days 2, 3, 4, 7, 9, and 10. Symbols are means of $n=3$ pots per soil per basin ± 1 SE. Asterisks indicate significant differences ($P<0.05$).

Table 3. Mean shoot and root length of cheatgrass seedlings 14 d after germination. Soils and cheatgrass seed were collected from sagebrush habitat and salt desert habitat in three sites. Values are means ± 1 SE. Shoots and roots were analyzed separately, within each site, via two-way analysis of variance with "soil source" and "seed source" as fixed main effects. Significant effects are indicated at bottom of each column in bold ($P < 0.05$).

		Seven Troughs		Poker Brown		Smoke Creek	
Soil source	Seed source	Shoot	Root	Shoot	Root	Shoot	Root
SD[1]	SD	16.5 ± 0.7 SE	20.7 ± 1.3 SE	12.5 ± 1.1 SE	13.9 ± 1.0 SE	16.7 ± 0.9 SE	24.3 ± 2.5 SE
SD	SB	16.1 ± 0.6 SE	21.4 ± 1.4 SE	12.7 ± 0.8 SE	14.6 ± 2.1 SE	15.6 ± 0.7 SE	27.5 ± 1.5 SE
SB	SD	14.1 ± 1.0 SE	14.4 ± 1.8 SE	20.5 ± 0.8 SE	22.5 ± 1.9 SE	19.7 ± 1.0 SE	16.1 ± 1.4 SE
SB	SB	14.2 ± 0.6 SE	14.5 ± 1.0 SE	16.4 ± 1.6 SE	15.9 ± 1.6 SE	19.8 ± 1.0 SE	18.2 ± 1.4 SE
		soil	**soil**	**soil**	**seed**	**soil**	**soil**

[1]SD indicates salt desert habitat; SB, sagebrush habitat.

(Table 3). Seedlings from all three basins grew taller in SD soils, irrespective of seed source (main effect of soil, $F_{1,70}=25.14$, $P=0.0001$; $F_{1,72}=8.512$, $P=0.005$; and $F_{1,74}=14.84$, $P=0.0002$ for Poker Brown, Seven Troughs, and Smoke Creek, respectively) (Table 3).

Final Harvest. After 2 mo of growth in 11-L pots, both the root and shoot biomass of seedlings grown from SD and SB seed sources had variable responses to the different soils across the three basins (Fig. 2). At Poker Brown, there was a significant seed×soil interaction for aboveground biomass ($F_{1,66}=4.645$, $P=0.035$), where SD populations were smaller in their own soil compared to their performance in SB soil while SB populations performed the same in both soils. Root biomass, however, depended only on soil type: seedlings from both seed sources had less root biomass in SD soils ($F_{1,74}=35.23$, $P=0.0001$). At Seven Troughs, there was a significant seed effect on shoot biomass: plants from SD seeds always were smaller regardless of soil type (seed effect, $F_{1,66}=4.54$, $P=0.037$). For root biomass, there were main effects of both soil and seed, where SD-originated seed and SD soil produced seedlings with lower root biomass (soil effect $F_{1,73}=6.49$, $P=0.13$; seed effect $F_{1,73}=6.882$, $P=0.011$). In Smoke Creek, the main effects of soil and seed source on shoot biomass were strong with no interaction: seedlings grown from SD seed had lower shoot biomass irrespective of soil type (seed effect, $F_{1,66}=6.45$, $P=0.01$), and seedlings grown in SD soil had lower shoot biomass, irrespective of seed origin (soil effect, $F_{1,66}=21.264$, $P=0.0001$) (Fig. 2). For root biomass, however, there was a significant soil×seed interaction ($F_{1,74}=5.11$, $P=0.03$) where SB seed produced plants with lower root biomass in SD soil compared to SD seed in SD soil.

Contrary to our initial predictions, final root:shoot ratios were significantly lower in SD soils irrespective of seed source in two of the three basins. Plants grown in SD soils at Poker Brown had much lower root:shoot ratios compared to their SB counterparts (1.41 ± 0.19 SE vs. 3.80 ± 0.56 SE, respectively) ($F_{1,64}=15.03$, $P=0.0003$). At Seven Troughs, however, root:shoot ratios were 1.48 ± 0.08 SE and this did not differ significantly by soil or seed source ($P > 0.05$). At Smoke Creek, the pattern was similar to Poker Brown, where SD soils produced plants with dramatically lower root investment ($F_{1,64}=42.41$, $P=0.0001$). SD soil root:shoot ratios were 0.68 ± 0.07 SE whereas SB soils were 2.90 ± 0.32 SE.

Flowering. Flowering of seedlings depended on seed source but not soil source across all three basins (seed effect, $\chi^2=10.44$, $P=0.01$ for Poker Brown; $\chi^2=16.78$, $P=0.001$ for Seven Troughs; $\chi^2=5.81$, $P=0.001$ for Smoke Creek). At the final harvest, approximately 50% of plants that originated from SD collected seeds had flowered (Fig. 3). By contrast, only 5% of the plants originating from SB soils had flowered regardless of soil type. There was no difference in incidence of flowering between the two soil types ($p > 0.05$ in all three basins).

Mycorrhizal Colonization. Across all three basins, the effect of soil on AMF colonization was dependent on seed source (seed×soil interaction, $F_{1,50}=35.24$, $P=0.0001$ for Poker Brown; $F_{1,48}=13.72$, $P=0.001$ for Seven Troughs; and $F_{1,44}=10.10$, $P=0.003$ for Smoke Creek; Fig. 4). In all basins, cheatgrass plants from the SB habitat had higher AMF colonization when grown in their own SB soils (a range of 21–25% across sites), compared to cheatgrass individuals from the paired SD site grown in their own SD soil (a range of 12–24%; Fig. 4). Overall, plants grown from SB seed had lower AMF colonization when grown in SD soils, with particularly strong effects in Poker Brown and Smoke Creek (Fig. 4). SD populations, by contrast, had lower colonization regardless of the soil type they were grown in; their colonization rates were even depressed in the Seven Troughs SB soils compared to the SD soils (Fig. 4).

DISCUSSION

Although there was strong site-to-site variation, we found that in general plants grown from SD seed or grown in SD soil produced smaller plants that flowered more, with lower root:shoot ratios and less AMF colonization compared to their upland SB counterparts. Our data also support previous assertions that SD soils tend to be more saline and arid compared to the adjacent mesic SB upland habitat (Billings 1949). For the sites we analyzed, SD soils tended to have a higher proportion of sand, lower percentages of C and N, lower nutrient cation concentrations, and had lower volumetric water content after saturation than the SB soils. However, we also found that SD soils were not identical across watersheds, nor consistently different from their upland SB counterparts.

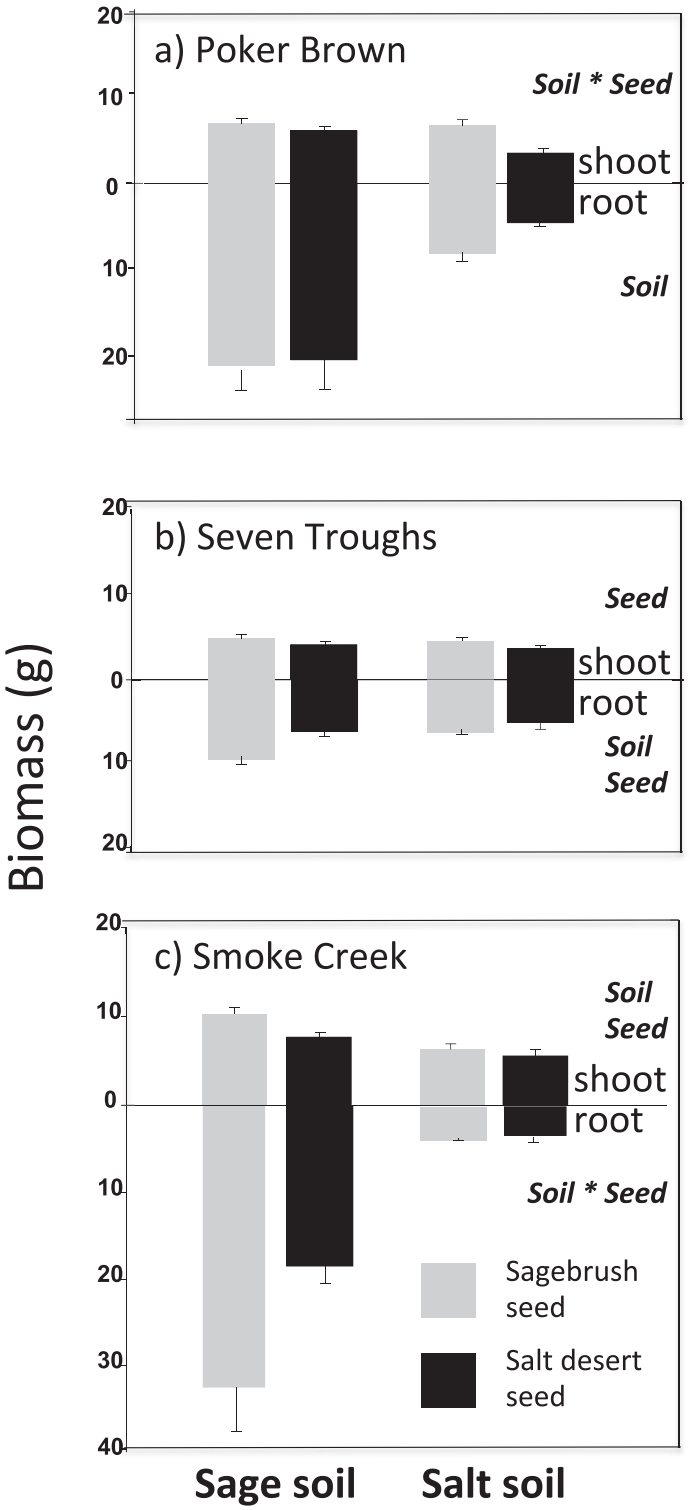

Figure 2. Mean shoot and root biomass of cheatgrass seedlings grown in pots after 8 wk in the greenhouse. Soils and cheatgrass seed were collected from sagebrush habitat and salt desert habitat in **a**, Poker Brown, **b**, Seven Troughs, and **c**, Smoke Creek sites. Bars are means $\pm$ 1 SE. Significant effect of "soil" or "seed" is indicated in bold font on each panel ($P < 0.05$).

Cheatgrass Growth Response to Seed and Soil Source

We found that cheatgrass plants responded to the different soil types: SD soils initially promoted greater root elongation but ultimately smaller plant size compared to plants grown in SB soils. Thus they may have initially been foraging for nutrients (longer initial root length) but some aspect of the soil ultimately dampened overall growth. The plants grown in SD soils also tended to have lower rates of AMF colonization, as we had predicted. In addition to this soil effect, the influence of seed origin was strong: 1) SD origin plants flowered more than SB origin plants regardless of soil type, and 2) SD origin plants had lower colonization rates of AMF when grown in SB soils. Still, one of the three basins we studied showed the opposite pattern for SD origin plants: in Seven Troughs plants had greater AMF colonization in SD soil compared to SB soil. These data suggest that seed populations differ from one another in terms of their capacity to respond to the environment, particularly in their ability to form mycorrhizal associations.

Our results suggest a correspondence between cheatgrass flowering and aridity of sites. Others have shown that cheatgrass from xeric lowland desert sites flowered earlier than plants originating from seeds of more mesic upland sites (Rice and Mack 1991b; Dyer et al. 2011). We found a similar pattern, where seeds collected from SD soil had a higher incidence of flowering across both soil types. Early flowering is a contingency measure against the possibility that favorable conditions will not continue through the growing season (Mulroy and Rundel 1977) or as an escape from seasonal drought (Franks et al. 2007). Dyer et al. 2011) suggest that postintroduction selection pressure on cheatgrass in more xeric habitat has resulted in a more fixed phenology that limits the capacity of plants to respond opportunistically to unpredictable resource availability such as late-season water availability.

We found that incidence of flowering varied strongly by seed source, yet many factors may be driving this intraspecific seed variation. For example, there is abundant evidence that seed size can affect germination characteristics, seedling and adult plant size, and competitive ability (Roach and Wulff 1987). Yet in our study seed mass was the same in both SD and SB habitat for two of our three basins; thus seed mass is unlikely to explain the differences we observed between the two seed origins for those basins. We cannot, however, explicitly rule out other environmental effects on the maternal tissue of seeds that might be important in our study, such as cold sensitivity during germination (Cal and Obendorf 1972) or heat-shock proteins produced in developing seeds in the more stressful SD environment from which the seeds were collected (Wehmeyer and Veirling 2000). Yet we found no differences in timing of emergence or germination rate, two factors that are primarily controlled by maternal tissues surrounding the embryo (Mayer and Poljakoff-Mayber 1982). Nevertheless, we cannot rule out the possibility that myriad other environmental factors (e.g., herbivory, fire, grazing pressure, drought, heat, soil chemistry, day length) could have affected the maternal plants as they were producing seed. These factors may have caused stress signals to be transferred to the seeds, resulting in effects on plant performance (Roach and Wulff 1987; Westoby et al. 1992; Sun et al. 2002).

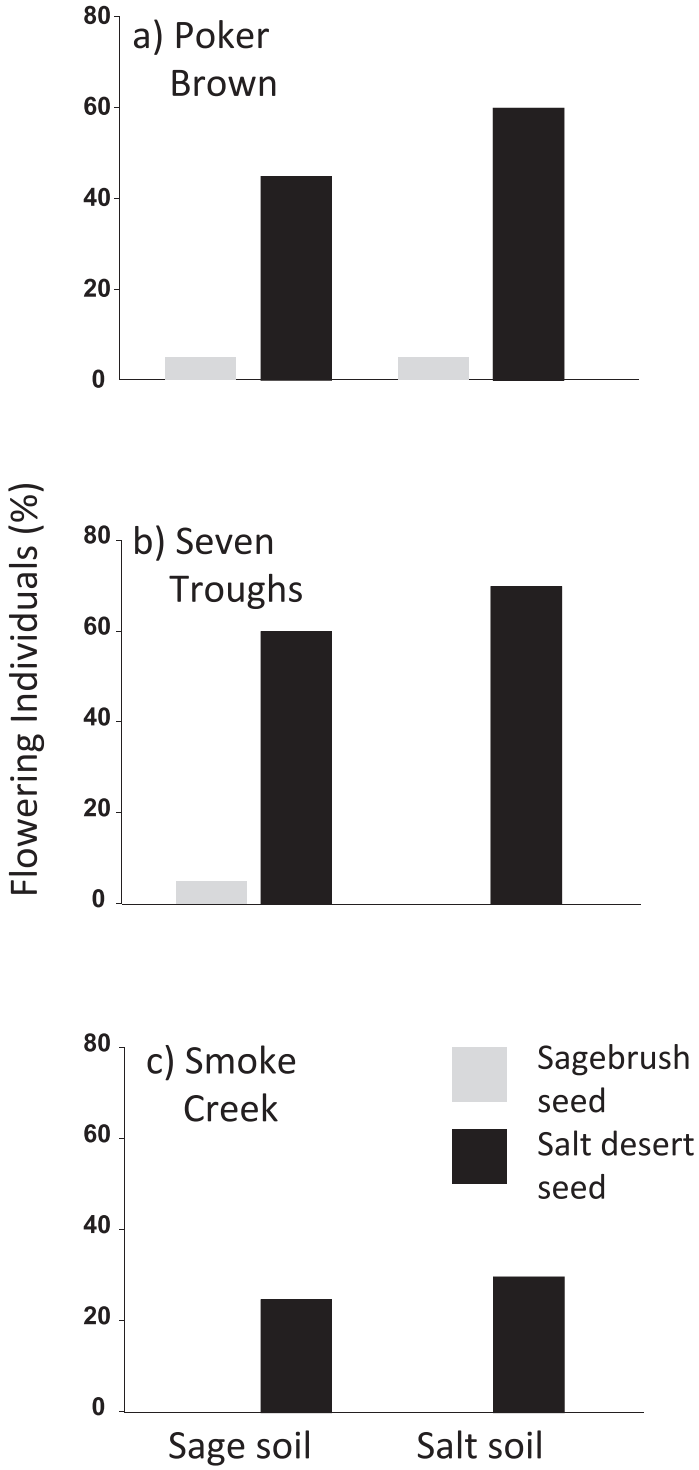

Figure 3. Percentage of flowering cheatgrass individuals (number of individuals that flowered divided by total sample size) grown in pots after 8 wk in the greenhouse. Soils and cheatgrass seed were collected from sagebrush habitat and salt desert habitat in **a,** Poker Brown, **b,** Seven Troughs, and **c**, Smoke Creek sites. Bars represent the number of individuals (out of $N=20$) that had flowered at the time of harvest.

Mycorrhizal Colonization of Cheatgrass Seedlings

Our results suggest that conditions in SD soil caused depressed AMF colonization in cheatgrass. Indeed, SB-originating plants were much more mycorrhizal on SB compared to SD soils, suggesting a strong level of soil control. However, seed origin was also important in determining AMF patterns: plants grown from SD-collected seeds had lower AMF colonization on SB soils than SB-originating seeds. In other words, plants originating from SD seed appeared to be limited in their ability to form the same level of mycorrhizal association that SB-originating plants achieved on the richer SB soils. As discussed above, the effect of seed source could result from either maternal effects or evolutionary changes in genotype among populations (Rice and Mack 1991a). As with the greater incidence of flowering that we observed in SD-seed-grown plants, we were able to rule out seed size (in at least two of the three basins) but cannot address other maternal effects. However, others have also demonstrated effects of soil and seed source (or population) on AMF colonization. For example, Pánková et al. (2008) showed that plants grown from seed originating from a soil with lower nutrient availability developed more AMF even when grown in soil with higher nutrient availability. Likewise, Johnson et al. (2010) demonstrated that *Andropogon gerardii* Vitman adapted to its local environment, particularly in resource-limited soils, by forming mycorrhizal associations that best maximized nutrient acquisition. In our study, the opposite pattern of mycorrhization with respect to soil nutrients was found. The SD soils, despite generally being more resource poor, produced plants with lower AMF compared to plants grown in SB soils (with the exception of Seven Troughs SD-originating seed, which produced high colonization on its own soil). Although this may not have implications for growth or colonization of cheatgrass, our data do suggest that cheatgrass is an ineffective host for AMF in SD soils, potentially reducing AMF availability for other plants in these sites (Vogelsang and Bever 2009; Busby et al. 2012).

SD soils in our study were sandier with lower volumetric water content at field capacity compared to their upland counterparts. We speculate that in addition to direct selection for a short life cycle in the harsh edaphic and environmental conditions of the low-lying SD habitat, there may be additional selection pressure for plants to evolve limited AMF colonization due to their carbon cost in an environment that favors rapid reproduction (Hoeksema et al. 2010). Alternatively, because we generally observed lower allocation to root biomass in SD plants, AMF colonization may be low in response to lower substrate (root) availability (Bècard and Piché 1989), or in response to higher salinity in SD soils (Evelin et al. 2009). Cheatgrass associations with AMF also vary seasonally (Busby et al. 2012); the timing of our soil sampling may have coincided with low AMF inoculation levels.

The higher rates of AMF colonization in plants from Seven Troughs, however, suggest that these patterns may not be completely consistent or simple across SD soils. This variability is not surprising given that cheatgrass is a relatively recent invader of these soils, and the soils themselves are different across the landscape. Under this scenario, selection pressures would not be expected to be uniform.

IMPLICATIONS

SD soils were generally different from their upland SB counterparts and resulted in smaller cheatgrass plants with less mycorrhizal colonization despite consistent watering across

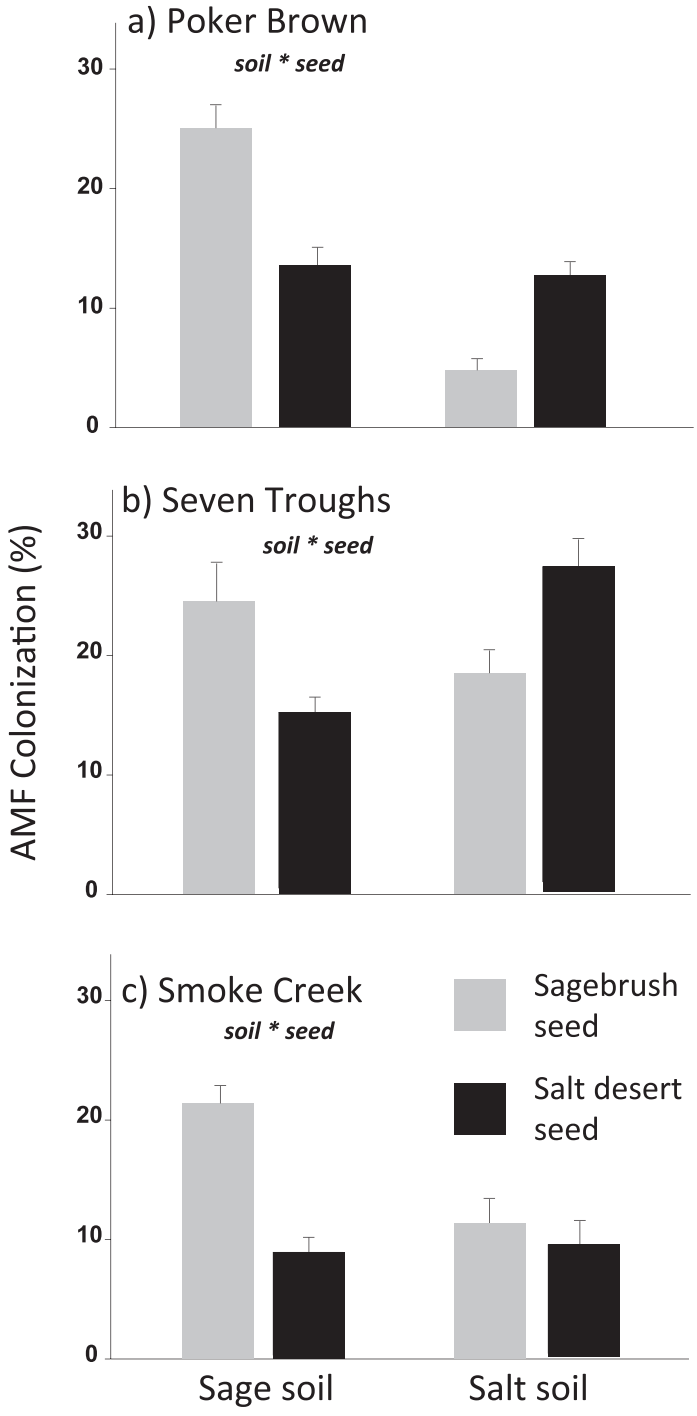

Figure 4. Mean percentage of AMF colonization of cheatgrass seedlings grown in pots for 8 wk in the greenhouse. Soils and cheatgrass seed were collected from sagebrush habitat and salt desert habitat in **a,** Poker Brown, **b,** Seven Troughs, and **c,** Smoke Creek sites. Bars are means $\pm$ 1 SE. Significant effect of "soil" or "seed" is indicated in bold font on each panel ($P < 0.05$).

all treatments in the greenhouse. Our results suggest that these soil controls on cheatgrass growth may slow invasion, contributing to sparse populations there (Mack 2011). On the other hand, plants grown from SD seed flowered more irrespective of soil source. Because seed output may be one of the primary advantages of cheatgrass in these environments, this population level control may override any soil control on invasion.

Seeds collected from plants in the SD appeared to reflect population-level differences expected in widespread species. Plants grown from these seed displayed traits that are advantageous in arid environments (i.e., rapid early root growth and higher incidence of flowering). Genetic variation in traits associated with rapid growth or flowering, such as reduced shoot investment and reduced mycorrhizal investment as our results suggest, may provide the material for natural selection as invaders move into marginal habitats. Our results also point to the importance of seed collection locality in determining plant growth characteristics. The importance of "local adaptation" or local seed collection is now widely recognized in restoration efforts (e.g., Gustafson et al. 2004; McKay et al. 2005; Bussell et al. 2006). Although we studied a widespread weed, our results suggest that understanding variation in plant performance requires separation of seed sources during experimentation.

ACKNOWLEDGMENTS

The authors gratefully acknowledge C. Clements for seed collection. H. Swartz, T. Jenkins, and D. Able assisted with soil collection.

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