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ASSESSING THE VALUE OF POTENTIAL “NATIVE WINNERS” FOR RESTORATION OF CHEATGRASS-INVADDED HABITAT

Rebecca S. Barak^{1,2}, Jeremie B. Fant², Andrea T. Kramer², and Krissa A. Skogen²

ABSTRACT.—Native plants that are able to persist and reproduce in highly disturbed habitats (i.e., “native winners”) may be useful to include in seed mixes when restoring similarly disturbed habitat. Establishing whether these plants produce viable seeds that germinate to a high degree under appropriate conditions is a first step to determining their utility as restoration species. We identified 10 potential native winners at sites degraded by cheatgrass (*Bromus tectorum*), an invasive annual grass ubiquitous in the Colorado Plateau. We assessed seed viability for each species to determine its potential to reproduce within a cheatgrass-invaded site, and conducted a series of germination and competition experiments to test how effective these species may be when restoring habitat invaded by cheatgrass. All species produced viable seed (ranging from 56% to 100% viability), and the seeds of many species had high germination under a range of fall conditions without cold stratification, which is thought to increase establishment potential in cheatgrass-dominated habitats. We selected the 5 species with the highest germination and conducted a greenhouse competition study to determine their response to cheatgrass presence. The growth of all 5 forb species was suppressed by cheatgrass. However results from germination and competition trials suggest that several species, in particular *Acmispon humistratus*, *Cryptantha fendleri*, and *Machaeranthera tanacetifolia*, may be beneficial for restoration of cheatgrass-invaded sites. These 3 species have higher percent germination (78%–100%) and germination tolerance (0.42–0.63), and were suppressed less by cheatgrass (relative interaction index of negative 0.28–0.49) than a commonly seeded restoration species, *Penstemon palmeri*. *Acmispon humistratus* and *M. tanacetifolia*, in particular, are also desirable candidates for use in restoration because of the ecosystem services they provide. In general, natives that grow, reproduce, and tolerate competition in degraded habitats are potential native winners and worthwhile candidates for use in restoration of similarly degraded sites.

RESUMEN.—Las plantas nativas capaces de persistir y reproducirse en hábitats altamente perturbados (es decir, ganadores nativos) pueden ser valiosas en las mezclas de semillas utilizadas para restaurar un hábitat similarmente perturbado. Un primer paso para determinar su utilidad como especies restauradoras es establecer si estas plantas producen semillas viables con un alto grado de germinación en condiciones apropiadas. Identificamos 10 posibles ganadores nativos en ubicaciones degradadas por *Bromus tectorum*, una planta invasora con ciclo anual que se encuentra en la meseta de Colorado. Evaluamos la viabilidad de las semillas de cada especie para determinar su potencial para reproducirse en una ubicación invadida por *B. tectorum*, y llevamos a cabo una serie de experimentos de germinación y competencia para probar el potencial de estas especies para restaurar el hábitat invadido por *B. tectorum*. Todas las especies produjeron semillas viables (oscilando entre un 56% a un 100% de viabilidad), y muchas especies presentaron una alta germinación bajo un rango de condiciones de caída sin estratificación en frío, que se cree aumentan el potencial para establecerse en hábitats dominados por *B. tectorum*. Seleccionamos a las 5 especies de mayor germinación y realizamos un estudio de la competencia en invernaderos para determinar su respuesta a la presencia de *B. tectorum*. El crecimiento de las 5 especies fue suprimido por la hierba. Sin embargo, los resultados de germinación y los ensayos de competencia sugieren que varias especies evaluadas, en particular *Acmispon humistratus*, *Cryptantha fendleri* y *Machaeranthera tanacetifolia*, pueden ser beneficiosas para restaurar zonas invadidas por *B. tectorum*. Estas tres especies tienen mayor porcentaje de germinación (78%–100%) y tolerancia de germinación (de 0.42 a 0.63), y fueron menos perturbadas por *B. tectorum* (índice relativo de interacción negativa 0.28–0.49) que *Penstemon palmeri*, una especie utilizada en la restauración comúnmente. *Acmispon humistratus* y *M. tanacetifolia*, en particular, también son candidatos comunes para la restauración debido a los servicios que proporcionan a los ecosistemas. En general, los ejemplares nativos que crecen, se reproducen y toleran la competencia en hábitats degradados son posibles ganadores nativos y candidatos que merecen ser utilizados en la restauración de zonas degradadas de manera similar.

Highly disturbed habitat often requires ecological restoration to reestablish functional native plant communities (Young et al. 2005). Native plant species are seeded or planted in the hopes that they will establish, persist, and reproduce at the restoration site. Research has shown that the most appropriate species for restoring disturbed habitat could be ruderal native species, or those adapted to early successional environments found at disturbed sites

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(Jones and Johnson 1998, Leger 2008). However, most of the native plant material available for ecological restoration is from late-seral species. Consequently, little is known of the early seral species that may perform best in disturbed habitat (Shaw et al. 2005, Herron et al. 2013).

Forbs, especially early seral forbs, could play a particularly important role in ecological restoration because they support a variety of ecosystem services, including providing habitat and forage for pollinators and wildlife (Weltz et al. 2003, Wirth and Pyke 2003) and preventing the establishment of invasive species at disturbed sites (Abella et al. 2012). Diverse restored communities that include native forbs are demonstrably more effective at resisting invasion than grass monocultures (Sheley and Half 2006, Allen and Meyer 2014), by suppressing establishment and seed production of several invasive plants (Abella et al. 2012, Uselman et al. 2014).

Cheatgrass (*Bromus tectorum* L.) is an invasive bunchgrass, prevalent throughout western North America. Cheatgrass degrades native habitats by forming dense monocultures and increasing the frequency and intensity of large-scale wildfires (Mack 2011). In invaded habitats, cheatgrass is among the first to emerge because of rapid, early germination and because cheatgrass-fueled fire reduces native seed banks (Humphrey and Schupp 2001, Kerns et al. 2006, Mack 2011). But native ruderal forbs that also emerge rapidly following disturbance may serve as a “functional analog” for cheatgrass, reducing reinvasion and limiting invasive plant cover at disturbed sites, while also serving the restoration goal of increasing native biodiversity (Kerns et al. 2006, Shinneman and Baker 2009, Young et al. 2009, Herron et al. 2013). It is these ruderal forbs that may be most effective to use in restoration seed mixes at cheatgrass-degraded sites.

Despite the importance of native forbs to restoration, there are several barriers to their use in restoration seed mixes. First, establishment of seeded native forbs at restoration sites is often low, possibly due to mismatch between the successional stage of a restoration site (usually postdisturbance/early successional) and the species used (often later-seral, perennial species; Jones and Johnson 1998, Krueger-Mangold et al. 2006, Sheley et al. 2006,

Kulpa et al. 2012). Second, seeds of many forbs are commercially unavailable or prohibitively expensive; and third, forb species from the Intermountain West are typically understudied (Forbis 2010, Peppin et al. 2010, Herron et al. 2013). To address these challenges, several projects are underway to identify and develop forbs suitable for restoration following large-scale disturbances, including early seral species (Shaw et al. 2005, Padgett et al. 2010). Research into the biology of seeds and seedlings—such as seed viability, germination, early growth, and competition—with the goal of determining appropriate species for use in reseeding is an important first step in improving restoration outcomes throughout the Intermountain West (James et al. 2013).

Some native species persist even in heavily invaded habitats (Mealor et al. 2004). Community assembly theory predicts that biotic interactions—like those between natives and cheatgrass—shape the plant community. For example, native species that persist in invaded communities are best suited to living there (i.e., native winners), while unsuited species would be absent from the community after failing to survive and reproduce (Keddy 1992, Young et al. 2005). These potential native winner species may be more likely to tolerate cheatgrass competition and to have characteristics such as high seed viability and germination that make them useful as restoration species for cheatgrass-invaded habitats.

To identify which native forb species might be the most effective for restoring degraded habitat, we developed a 2-step framework. First, we performed laboratory experiments to determine whether native forbs found in cheatgrass-invaded habitats produce viable seeds that germinate to a high degree under a range of potential fall germination conditions without requiring cold stratification. These “fall germinators” have a similar germination pattern to cheatgrass, which can give these species a competitive edge when sown with cheatgrass (Forbis 2010, Leger et al. 2014). Forb species that met these criteria were then planted in a greenhouse competition study to test their ability to tolerate cheatgrass competition (sensu Goldberg 1996). Taken together, these results may help identify native winners to be used in restoration of cheatgrass-invaded habitats.

TABLE 1. Species information and collection sites for all 10 forbs studied.

Scientific name	Common name	Family	Life history ^a	Collection site ^b
<i>Acmispon humistratus</i>	Foothill deervech	Fabaceae	A	Z (37.267° N, 113.107° W)
<i>Chamaesyce albomarginata</i>	Rattlesnake weed	Euphorbiaceae	P	Z (37.271° N, 113.101° W)
<i>Cryptantha fendleri</i>	Sandstone cryptantha	Boraginaceae	A	Z (37.203° N, 113.065° W)
<i>Eriogonum leptophyllum</i>	Slenderleaf buckwheat	Polygonaceae	P	M (38.245° N, 108.002° W)
<i>Lupinus pusillus</i>	Rusty lupine	Fabaceae	A	Z (37.267° N, 113.107° W)
<i>Machaeranthera tanacetifolia</i>	Tansyleaf tansyaster	Asteraceae	A/B	Z (37.267° N, 113.107° W)
<i>Oenothera deltoides</i>	Birdcage evening primrose	Onagraceae	A/P	Z (37.341° N, 113.101° W)
<i>Penstemon palmeri</i>	Palmer's penstemon	Plantaginaceae	P	Z (37.271° N, 113.101° W)
<i>Sphaeralcea grossularifolia</i>	Gooseberryleaf globemallow	Malvaceae	P	Z (37.341° N, 113.101° W)
<i>Symphotrichum campestre</i>	Western meadow aster	Asteraceae	P	M (38.544° N, 107.690° W)

^aLife history: A = annual, B = biennial, P = perennial.

^bCollection site: Z = Zion National Park, Utah; M = Montrose, Colorado.

METHODS

Seed Collection

The Colorado Plateau covers 340,000 km² at the intersection between Colorado, New Mexico, Arizona, and Utah, USA. The plateau includes numerous unique habitats and is the focus of research on best practices for restoration with native plants (Schwinning et al. 2008, Padgett et al. 2010). Mature fruits of cheatgrass and co-occurring native forb species were opportunistically collected during summer and fall 2010 from cheatgrass-invaded sites in Zion National Park, Utah, and Montrose, Colorado, which are the western and eastern boundaries of the Colorado Plateau, respectively. Fruits were collected in bulk from ≥ 50 haphazardly selected plants from throughout a population and placed in paper bags. Seeds were separated from dry fruits and stored in coin envelopes at room temperature until experiments were initiated. In total, mature seed was collected from 10 species, each represented by one population (Table 1): *Acmispon humistratus* (Benth.) D.D. Sokoloff, *Chamaesyce albomarginata* Torr. & A. Gray, *Cryptantha fendleri* (A. Gray) Greene, *Eriogonum leptophyllum* (Torr. & A. Gray) Woot. & Standl, *Lupinus pusillus* Pursh, *Machaeranthera tanacetifolia* (Kunth) Nees, *Oenothera deltoides* Torr. & Frém., *Penstemon palmeri* A. Gray, *Sphaeralcea grossularifolia* (Hook. & Arn.) Rydb., and *Symphotrichum campestre* (Nutt.) G.L. Nesom (Table 1). All experiments were conducted at the Chicago Botanic Garden, Glencoe, Illinois, USA.

Seed Viability

Seed viability was analyzed via X-ray (Faxitron MX-W; Faxitron Corp., Tucson, Arizona, USA: 20 s, 18 KV). For native seeds stored for a relatively short time (2–3 years), X-ray viability testing has been shown to have similar results to viability testing using tetrazolium chloride (Riebkes et al. in press).

Three replicates of 50 seeds were analyzed. Seeds containing full, visible embryos were counted as viable. Cut tests were performed on seeds that appeared partially filled in scans to verify viability counts. Percentage of seeds containing an embryo is reported as maximum percent viability.

Germination

Experiments were conducted to determine germination potential of cheatgrass and forbs under a range of potential fall conditions. Seeds were placed in 4 incubators (Precision Scientific low-temperature illuminated incubator, model 818; Precision Scientific Instruments, Inc., Buffalo, New York, USA) set to 12-h photoperiods and day/night temperatures of 11/1 °C, 14/4 °C, 17/7 °C, and 20/10 °C. Daytime temperatures were based on the potential range of high temperatures between October and December in Zion National Park (Western Regional Climate Center 2012; see Barak 2012 for additional details). Nighttime temperatures were set at 10 °C below daytime, to standardize temperature shifts between treatments.

In May 2011, 25 seeds were plated onto each of 4 replicate petri dishes filled with 1.5% agar for each species (except *C. albomarginata*, where only 10 seeds per dish were used because of limited seed quantities), and the dishes were sealed with Parafilm ("M," BEMIS flexible packaging). A 5 × 5 grid was used for all petri dishes to ensure seeds were evenly spaced. Three species (*A. humistratus*, *L. pusillus*, and *S. grossulariifolia*) were also scarified, which increases germination in congeners (Pendry and Rumbaugh 1993, Dreesen and Harrington 1997, Jones et al. 2010). For these species, half of the seeds per dish (determined randomly) were scarified with fine-grained sandpaper prior to plating. Petri dishes were randomly arranged on 2 transparent trays and placed on central shelves within treatment incubators. Dishes were rotated within trays, and trays were rotated within incubators twice weekly. Seeds were inspected twice weekly for germination, defined as radicle emergence of 1 mm. For each species, percent germination of viable seeds was calculated as the percent of plated seeds that germinated divided by maximum percent viability.

For each species, we also calculated Levins' B (Levins 1968, Feinsinger et al. 1981) as an estimate of germination tolerance range:

$$B = 1/R \sum_i p_i^2,$$

where p_i is percent germination at temperature i (mean of 4 petri dishes/replicates) and R is the number of temperatures tested (in this case, $R = 4$). B has a range of 0–1. Species

with a value close to 1 have a wide tolerance range (germinate over a large range of temperatures or have more flexible temperature requirements), while those with a value near 0 have a narrow tolerance range (germinate over a smaller range of temperatures or have more rigid temperature requirements).

Competition

The 5 species with highest germination in fall conditions were planted in a competition study to assess their interactions with cheatgrass. To determine their ability to tolerate cheatgrass competition, each forb species was grown as a focal plant in 3 treatments: alone, and with 1 (low-density) and 4 (high-density) cheatgrass neighbors. To test for intraspecific competition, cheatgrass was also grown as a focal plant under these 3 treatments. Seeding densities were based on low and high estimates of postfire cheatgrass seed banks (Smith et al. 2008, Beckstead et al. 2011). One seed per pot represents approximately 300 seeds · m⁻². Seeds were planted in January 2012 in a randomized complete block design with 20 blocks (flats), each containing a 43.6-cm² × 8.2-cm pot with one of the 18 treatment-by-species combinations. Each pot was filled with Fafard 3BC coir mix potting soil (Sun Gro Horticulture, Agawam, MA). Two cheatgrass and 3 forb seeds were planted 1 cm deep at each position for all treatments, and thinned to treatment densities within 7 d of planting. Because not all forbs germinated, germinants were moved between trays and within treatments until there was a forb in each replicate through day 23. After day 23, any new germinants were pulled within 1 week of emerging. Flats were placed on a single greenhouse bench and rotated 3 times per week. Temperatures were set between 16.5 °C and 19 °C but reached 30 °C during several unseasonably warm days. Flats were watered as needed, ≥5 times per week to keep soil moist. Flats were treated with Azatin XL (OHP, Inc., Mainland, PA) against fungus gnat larvae on days 23, 30, 37, 44, 58, and 65.

Seedling emergence was scored 3 times per week for the first 30 d and then once weekly until harvest. Leaf and tiller (shoot) numbers were recorded weekly for each cheatgrass focal plant, and the following data were recorded for each forb focal plant: height, width A , (measured across the widest

point of the forb), and width B, (perpendicular to width A). Volume (an approximation of the space taken up by each forb) was calculated using the formula for the volume of an ellipsoid,

$$V = 4/3(A/2)(B/2)(C/2),$$

where A, B, and C are width A, width B, and height, respectively.

Pots were destructively harvested after 12 weeks. Aboveground biomass was clipped at soil level for all species. Belowground biomass was harvested from each treatment for 3 forb focal species—*A. humistratus*, *M. tanacetifolia*, and *P. palmeri*, but not for other species because roots could not reliably be separated. Samples were dried in a herbarium drier for 48 h and weighed to the nearest 0.0001 g. Relative interaction indices (RII) were calculated for each treatment in the competition study (low- and high-density cheatgrass), following Armas et al. (2004) using the equation

$$\text{RII} = \frac{B_w - B_0}{B_w + B_0},$$

where B_0 represents control aboveground biomass, and B_w is aboveground biomass from each competition treatment. Relative interaction indices values range from -1 to 1 . A negative RII reflects competition (i.e., aboveground biomass of the target plant is negatively affected by the presence of cheatgrass), while a positive RII reflects facilitation (i.e., aboveground biomass of the target plant is positively affected by the presence of cheatgrass).

Statistical Analysis

Analyses were completed in R version 2.14.0 (R Core Team 2012). Global models were performed for each response variable—viability, germination, emergence, growth (volume for forbs, leaf number for cheatgrass), and biomass (above and belowground)—and analyzed by linear model simplification, or for growth data, a linear mixed-effects model. Where data for multiple species were compared (germination, forb growth, or biomass), data were relativized to the highest value for each species. Forb and cheatgrass growth were analyzed separately because of differences in growth measurements. Viability, germination, emergence, growth, and aboveground biomass data were square-root transformed, and

belowground biomass data were log-transformed to meet assumptions of normality. For biomass and growth data, ANOVAs were performed for each forb. Tukey's HSD tests with Bonferroni corrections were used in post hoc analyses.

RESULTS

Seed Viability

Viability differed significantly between species ($F_{10} = 75.89$, $P < 0.0001$). All species had maximum viabilities above 80%, except *S. grossulariifolia* ($53 \pm 3.3\%$; Table 2).

Germination

Species differed significantly in percent germination of viable seeds ($F_{10} = 40.12$, $P < 0.0001$). Temperature ($F_3 = 37.28$, $P < 0.0001$) had a significant effect on germination in the overall model, as did interactions between species and temperature ($F_{10} = 2.26$, $P = 0.015$). Cheatgrass germination reached 100% under all treatments, while forb germination varied from 0% to 100%, depending upon species, temperature, and pretreatment (Fig. 1). Higher temperature significantly increased final percent germination in *C. fendleri*, *E. leptophyllum*, *M. tanacetifolia*, *P. palmeri*, and *S. campestris* (Fig. 1). Scarification significantly increased percent germination in *A. humistratus* ($F = 333.8$, $P < 0.0001$), and *S. grossulariifolia* ($F = 12.7$, $P = 0.0008$), but not *L. pusillus* ($F = 2.119$, $P = 0.15$).

Germination tolerance range varied by 3 orders of magnitude, from 1.00 for cheatgrass, indicating that cheatgrass germinated to 100% over all temperature treatments, to 0.001 for *O. deltoides*, which had very low germination at all temperatures (Fig. 1, Table 2). Forbs with the highest germination tolerance ranges were *A. humistratus* (scarified seeds), *M. tanacetifolia*, and *C. fendleri* (0.633, 0.500, and 0.415 respectively).

The 5 species (*A. humistratus*, *C. fendleri*, *M. tanacetifolia*, *P. palmeri*, and *E. leptophyllum*) with the highest percent germination (Fig. 1, Table 2) were tested further in a competition study. These 5 species had germination percentages $>55\%$ under fall temperatures.

Competition

EMERGENCE AND MORTALITY.—Study species differed in emergence timing ($F_{5,532} = 96$,

TABLE 2. Viability, germination, and growth of cheatgrass and 10 native forb species. Mean viability, germination, tolerance range, emergence, growth, and species interaction data for all species tested. Maximum germination is the maximum germination reached in ≥ 1 temperature treatment (* = after scarification), corrected for viability; emergence day was calculated as average days to germination in the greenhouse competition experiment; growth rate was calculated from biomass in the control treatment after 12 weeks of growth in a greenhouse; RII is relative interaction index, reduction in aboveground biomass after growing with one cheatgrass neighbor. Germination tolerance range and RII were calculated as described in the methods. Empty cells denote species that were untested in the greenhouse competition experiment.

Species	Viability (%)	Maximum germination (%)	Germination tolerance range	Emergence day	Growth rate (mg · month ⁻¹)	Relative interaction index
<i>Bromus tectorum</i>	100	100	1.00	5	59.9	-0.24
<i>Cryptantha fendleri</i>	97	100	0.415	8.1	3.1	-0.40
<i>Acmispon humistratus</i>	99	83*	0.633	8.6	14.2	-0.30
<i>Machaeranthera tanacetifolia</i>	85	78	0.500	6.7	17.6	-0.49
<i>Penstemon palmeri</i>	95	64	0.161	14.1	14.0	-0.70
<i>Eriogonum leptophyllum</i>	89	56	0.087	14.3	4.5	-0.28
<i>Symphotrichum campestre</i>	81	53	0.143			
<i>Lupinus pusillus</i>	100	17*	0.022			
<i>Sphaeralcea grossularifolia</i>	56	14*	0.016			
<i>Chamaesyce albomarginata</i>	93	11	0.003			
<i>Oenothera deltoides</i>	95	4	0.001			

$P < 0.0001$; Table 2). All cheatgrass plants emerged by day 5 (days after planting, mean \pm SE), followed by *M. tanacetifolia* (6.7 ± 0.4), *C. fendleri* (8.1 ± 0.8), *A. humistratus* (8.6 ± 0.6), *P. palmeri* (14.1 ± 0.4), and *E. leptophyllum* (14.3 ± 2.3). Of 360 focal plants, 23 (6.4%) did not emerge. One was *C. fendleri* (control), 2 were *M. tanacetifolia* (high-density), 2 were *P. palmeri* (1 low-density, 1 high-density), and 18 were *E. leptophyllum* (10 control, 5 low-density, 3 high-density). Focal plants with a neighbor that did not emerge (28) were excluded from analysis. Forty-seven focal plants (all forbs) died during the study. Of these, 33 were *C. fendleri* (14 control, 12 low-density, 7 high-density), 6 were *P. palmeri* (3 control, 2 low-density, 1 high-density), and 8 were *E. leptophyllum* (3 control, 3 low-density, 2 high-density).

FORB GROWTH.—Species ($F_{4,3076} = 355.67$, $P < 0.0001$), cheatgrass neighbor density ($F_{2,3076} = 92.75$, $P < 0.0001$), and interactions between species and neighbor density ($F_{8,3076} = 16.85$, $P < 0.0001$) had significant effects on forb volume in the overall model. Competition decreased volume in all species ($P < 0.05$), though only slightly in *A. humistratus* ($F_{1,663} = 3.1$, $P = 0.047$; Fig. 2).

FORB ABOVEGROUND BIOMASS.—Species ($F_{4,217} = 11.94$, $P < 0.0001$), neighbor density ($F_{2,217} = 91.42$, $P < 0.0001$), and interaction between species and neighbor density ($F_{8,217} = 2.73$, $P = 0.007$) affected aboveground biomass, while block and other two-way interactions were not significant. Competition decreased biomass in all species (Fig. 3). *Eriogonum leptophyllum* biomass was reduced by high- ($P = 0.01$), but not low- ($P = 0.14$) density competition.

FORB BELOWGROUND BIOMASS.—Species ($F_{2,154} = 64.19$, $P < 0.0001$), neighbor density ($F_{2,154} = 251.96$, $P < 0.0001$), and block ($F_{1,154} = 5.04$, $P = 0.03$), as well as interactions between species and neighbor density ($F_{4,154} = 6.50$, $P < 0.0001$) and species and block ($F_{2,154} = 3.78$, $P = 0.02$), affected belowground biomass in the 3 forb species. Competition decreased belowground biomass in all species ($P < 0.05$), but no difference was detected between low- and high-density cheatgrass treatments ($P > 0.05$).

CHEATGRASS GROWTH AND BIOMASS.—Leaf number decreased with increasing density of cheatgrass neighbors ($F_{2,2726} = 886.95$,

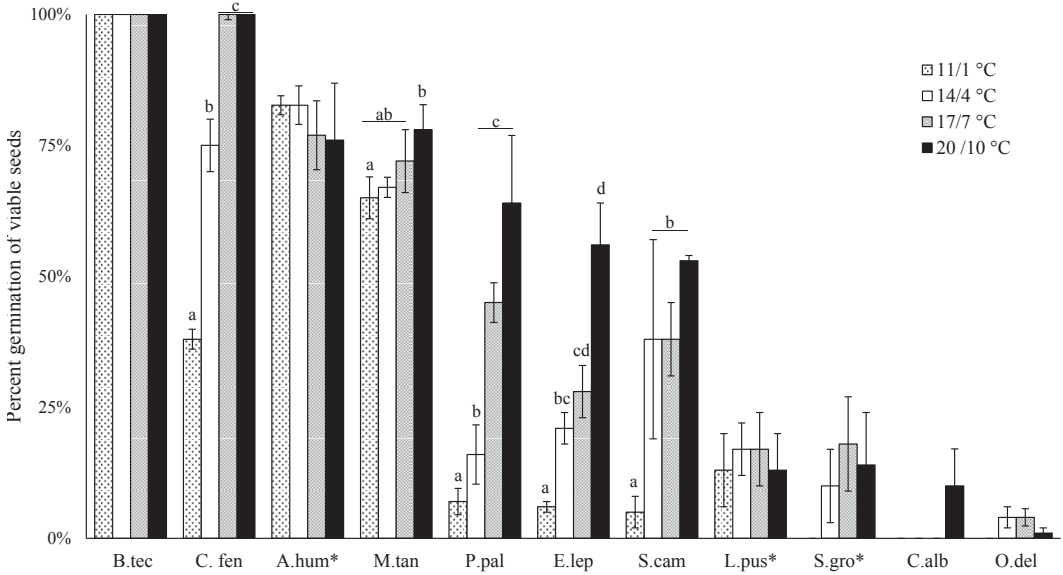


Fig. 1. Percent germination of seeds of cheatgrass and 10 forb species (mean \pm 1 SE). All values are corrected for viability. Values for scarified seeds are shown for species marked with an asterisk (*). Analyses were performed on square-root-transformed data; letters indicate significant differences between temperature treatments (Tukey's HSD test, $P < 0.05$) within species. Where no letters are shown, no significant differences between temperatures were detected.

$P < 0.0001$). Increasing neighbor density ($F_{2,226} = 231.33$, $P < 0.0001$) decreased cheatgrass biomass from 0.18 ± 0.0088 g in the control treatment, to 0.11 ± 0.0068 g in the low-density, and 0.065 ± 0.0051 g in the high-density competition treatment.

RELATIVE INTERACTION INDEX.—All plants, including cheatgrass, were suppressed by low and high densities of cheatgrass neighbors (Fig. 4, Table 2). Two forbs, *E. leptophyllum* and *A. humistratus*, were suppressed by cheatgrass to a similar degree as cheatgrass itself. In fact, *E. leptophyllum* was suppressed less by high-density cheatgrass competition than was cheatgrass itself. *Penstemon palmeri* was most suppressed by both low and high densities of cheatgrass.

DISCUSSION

Native forb species with high viability and germination under a range of potential fall temperatures, and the ability to compete with cheatgrass (i.e., native winners), should have increased potential for establishment, growth, and reproduction in degraded habitats where cheatgrass is present. We identified 10 potential native winners growing in

cheatgrass-dominated habitats, and 5 of them produced viable seeds with high germination under fall conditions. When these 5 species were exposed to competition from cheatgrass in the greenhouse study, all were suppressed by cheatgrass (in some cases to the same degree as cheatgrass suppressed itself; as in Palmblad 1968). However, species were suppressed to different degrees, which may have implications for restoration. Three study species in particular—*A. humistratus*, *C. fendleri*, and *M. tanacetifolia*—may be useful additions to currently seeded species in restoration of cheatgrass-degraded sites because they had high viability and high germination tolerance, and were less affected by cheatgrass than other species.

All 10 species included in this study are native to the Intermountain West, but only *P. palmeri* is commonly seeded in restorations (Meyer and Kitchen 1992), and it is one of only 2 forbs used in postfire reseeding at Zion National Park (Fuhrmann 2008). Although *P. palmeri* has been reported to have higher establishment than other seeded forbs (Abella and Newton 2009), in our study it was suppressed by cheatgrass more than any other forb, possibly because of its relatively late

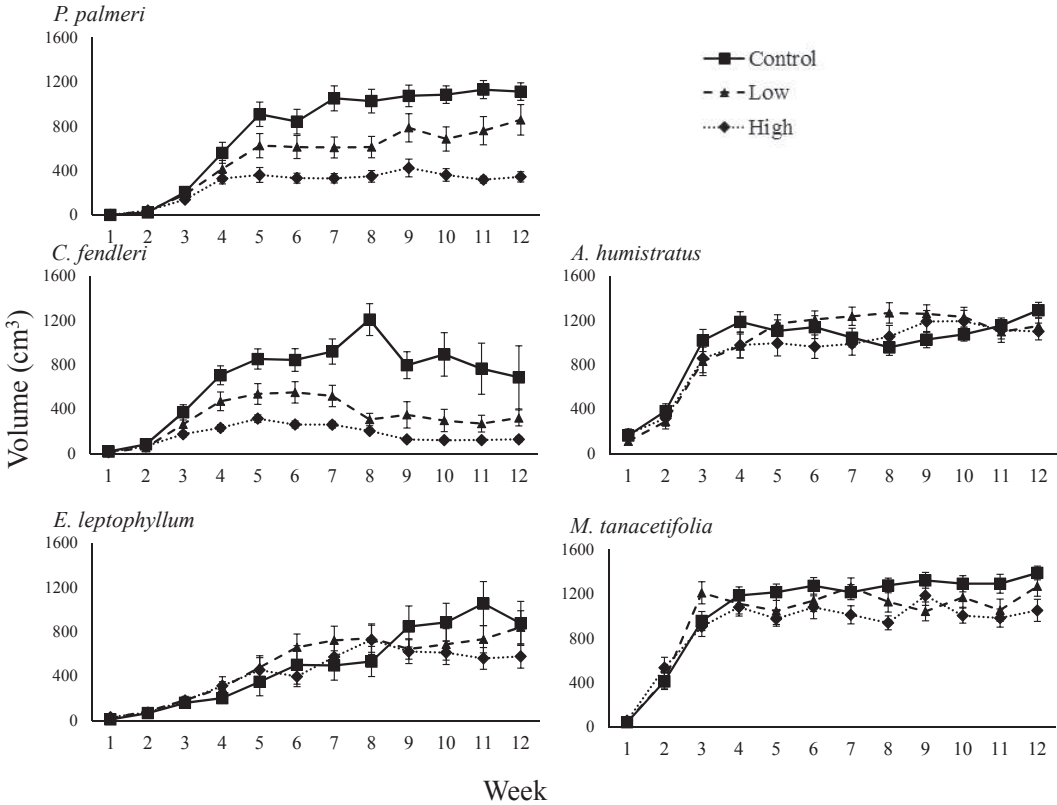


Fig. 2. Volume of forbs under control (no competition), low-density, and high-density cheatgrass competition, measured over 12 weeks (cm³, mean \pm 1 SE). Competition significantly decreased volume in all forb species by week 12 ($P < 0.05$).

emergence (14.1 d vs. 5 d for cheatgrass). *Acmispon humistratus*, *C. fendleri*, and *M. tanacetifolia* had germination percentages similar to or higher than *P. palmeri*. These 3 species also exhibited the largest germination tolerance ranges of all forbs tested under 4 potential fall germination temperatures. Fall germination is an important factor in the ability of native plants to reduce cheatgrass cover in the field (Leger et al. 2014). In addition, *A. humistratus* and *M. tanacetifolia* had growth rates similar to *P. palmeri*, but emerged earlier and grew more quickly. Both *A. humistratus* and *M. tanacetifolia* had high overlap in plant volume (but not biomass) between control and competition treatments, showing spatial growth even when biomass was limited in the presence of cheatgrass neighbors. *Cryptantha fendleri* had the highest and most rapid germination in germination trials (Barak 2012) but had low growth rates in the greenhouse. Because a majority of plants died in

the control treatment, the relatively poor performance of this species in the greenhouse may be due to low tolerance of moisture conditions in the greenhouse, rather than low competitive ability.

Acmispon humistratus and *M. tanacetifolia* may be valuable for use in restoration not only because of their ability to grow and produce seed in cheatgrass-degraded habitat, but also because of the ecosystem services they provide. *Acmispon humistratus* is a preferred food source for the federally threatened desert tortoise (*Gopherus agassizii*; Jennings 1997), and as a nitrogen fixer it may facilitate other native plants (Goergen and Chambers 2012). *Machaeranthera tanacetifolia* supports pollinators, grows in diverse habitats, and persists even under heavy grazing (Hart 2001, Tilley et al. 2013). For these reasons, both *A. humistratus* and *M. tanacetifolia* could be effective and valuable species for restoration of cheatgrass-degraded habitats.

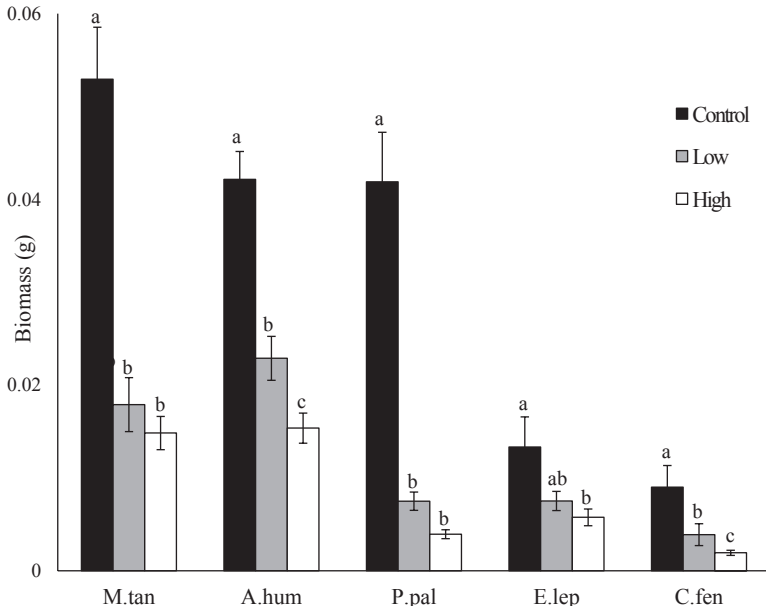


Fig. 3. Mean aboveground biomass of forbs growing under control (no competition), low-density, and high-density cheatgrass competition (grams, mean \pm 1 SE). Analyses performed on square-root-transformed data. Different letters indicate significant differences within-species (Tukey's HSD test, $P < 0.05$).

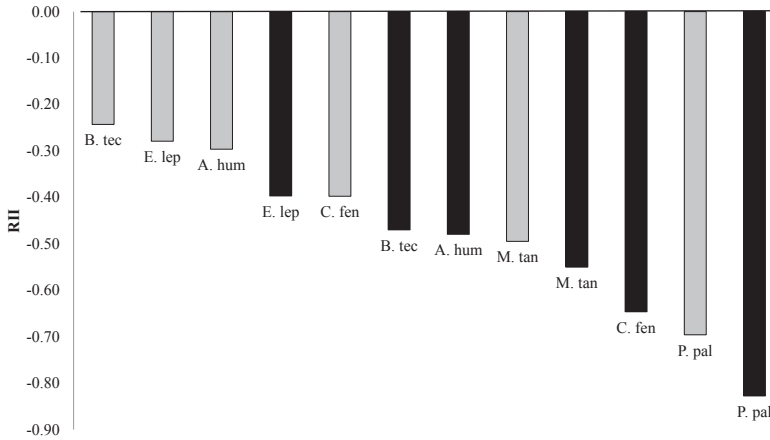


Fig. 4. Relative interaction index (RII) of focal plants growing under low-density (gray) and high-density (black) cheatgrass competition. More negative numbers (longer bars) indicate greater suppression of focal plant growth when grown with cheatgrass. Statistical tests were not performed on these data, but the data are included to show the interaction between focal plants and cheatgrass neighbors. All plants were suppressed by low and high densities of cheatgrass.

Research suggests that the competitive patterns observed under the benign conditions of a greenhouse may be similar or even less evident under the stressful conditions experienced in a restoration. This is because ecological theory predicts that competitive interactions increase under benign conditions, while facultative

relationships form under stress (Callaway and Walker 1997). Cheatgrass may suppress forbs less in high-stress native habitats than in the relatively benign greenhouse. Parkinson (2008) demonstrated that although forb growth was suppressed by cheatgrass in the greenhouse, several species established and grew under

cheatgrass competition in the field. To confirm that these patterns persist in field conditions and can positively influence the outcomes of a restoration in degraded habitat, future work should incorporate field trials using these potential native winners.

Management Applications

To address the hypothesized mismatch in successional stage between restoration sites and seeded species, ruderal species (particularly annual forbs) have been proposed to serve as colonizers. These early seral species could stabilize soils, reduce reinvasion, and prevent future fire, while providing ecosystem services such as pollinator attraction and forage (Jones and Johnson 1998, Krueger-Mangold et al. 2006, Herron et al. 2013). This model of assisted succession may facilitate later-seral species that disperse naturally, germinate from a persistent seedbank, or are seeded with or after the early seral species (Sheley et al. 2006, Herron et al. 2013). The proposed native winners from our study (*A. humistratus*, *C. fendleri*, and *M. tanacetifolia*) are ruderal annuals, and may be useful for the early stages of assisted succession. Other ruderal annuals tested (including *O. deltooides* and *L. pusillus*) had high viability but low germination, likely due to dormancy mechanisms not broken by our treatment conditions. On the other hand, a longer lived perennial (*E. leptophyllum*) was least suppressed by cheatgrass of all study species. In fact, it was suppressed only slightly more by cheatgrass than cheatgrass was by itself at low densities, and less suppressed than cheatgrass was by itself at high densities of cheatgrass. This suggests that *E. leptophyllum* may be an important species in midsuccessional stages of restoration.

Large-scale reseeding in the Intermountain West typically occur postfire (Peppin et al. 2010). Fire reduces cheatgrass seed banks by orders of magnitude, but only for 2–3 years, providing a short window of opportunity for the establishment of native species (Humphrey and Schupp 2001, Kulpa et al. 2012). In previous greenhouse studies, focal plants were suppressed by cheatgrass when both were started from seed, including hybrid and exotic grasses (Hull 1965, Francis and Pyke 1996), native grasses (Rafferty and Young 2002), and native forbs (Parkinson et al. 2013). However, competitiveness has been documented to increase when natives establish prior to cheatgrass exposure (McGlone et al.

2011, Orloff et al. 2013). All species tested here persisted under cheatgrass competition for the duration of the study. Furthermore, several of the species tested had high germination tolerance ranges—high percent germination over all fall temperatures tested. This could allow for flexibility in planting time and may also help these species establish and reproduce during the window before cheatgrass becomes dominant. Competitive natives with high viability, early germination, and rapid growth may prevent cheatgrass dominance while contributing to a robust plant community.

Species identified as native winners will require research to determine whether and how they can be grown for commercial seed production so they can be made available for large-scale restoration of degraded sites. Success of large-scale seed production may depend on whether native winners' properties—viability, germination, competitive response—are species- or population-level effects. If they are species-level effects, restoration material could be collected from many populations, and plants could potentially be grown on a large scale for restoration. On the other hand, if they are population-level effects—perhaps local adaptation to growing with cheatgrass (Mealor and Hild 2006, Goergen et al. 2011)—source populations may be more limited and large-scale growing operations more complicated. Further research comparing natives from invaded and noninvaded habitats may distinguish between these effects.

Conclusion

We identified potential native winner species growing in cheatgrass-dominated habitats on the Colorado Plateau. Our results suggest that native plants persisting in invaded communities are not ecological “dead ends,” but have the potential to be useful restoration tools in degraded habitats. We suggest that the identification of restoration species for degraded sites should begin by observing community-level phenomena in the degraded sites themselves. Native species persisting and reproducing in degraded sites may be ideal candidate species for restoration use.

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