ASSESSING RESTORATION POTENTIAL OF NATIVE FORBS FROM CHEATGRASS-DOMINATED HABITATS

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COMMENTS ON THESIS DEFENSE FOR MASTER OF SCIENCE IN PLANT BIOLOGY AND CONSERVATION
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on the date of Sept 7, 2012. The committee members have rendered the following decision:

☐ Pass with no revisions ☒ Pass with minor revisions

☐ Pass with major revisions ☐ Fail to pass

Committee members:

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Abstract: After large-scale disturbances such as fire, seeding can be necessary to reestablish a plant community and prevent soil erosion. While native plants are ideal for providing ecosystem services and supporting wildlife, currently seeded natives often fail to establish in disturbed landscapes. Further, reseeding with native plants is often hindered by *Bromus tectorum L*. (cheatgrass), a ubiquitous invader in the Colorado Plateau and throughout western North America. High seed viability and a high germination percentage early in the growing season are known to be key to the invasiveness of cheatgrass. Through life-history or local adaptation, native plants growing in cheatgrass-dominated habitats may share these characteristics of cheatgrass, and may tolerate or compete with the invader. A series of experiments was conducted to identify native forb species with viability and germination characteristics similar to those of cheatgrass and the ability to compete with cheatgrass, as these species would represent ideal candidates for use in reseeding projects. Ten native forb species growing in cheatgrass-invaded habitats in and around Zion National Park, UT and Montrose, CO were evaluated for germination response with and without pre-treatment (cold stratification and scarification), at four temperature regimes. Five species with high viability and germination rates were then included in two greenhouse competition experiments to determine their competitive effect on and response to cheatgrass neighbors. We identified seven species with viability that did not significantly differ from cheatgrass, and five species with germination percentages that did not significantly differ from cheatgrass under certain treatments. While all species were suppressed by cheatgrass competition, several species were identified that may represent improvements over those commonly seeded in the Colorado Plateau. These species represent promising candidates for use in restoration and should be considered in post-fire reseeding of sites where cheatgrass remains a concern.

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Introduction:

Invasive species accelerate declines in biodiversity and ecosystem services in habitats throughout the world (Sala et al. 2000, Charles and Dukes 2007). Invasive plants can degrade native habitats by altering fire regimes and nutrient dynamics, and reducing or eliminating populations of native species (D'Antonio and Vitousek 1992, Mack et al. 2000). Cheatgrass (*Bromus tectorum* L.) is an annual bunchgrass native to Europe, North Africa and Southwest Asia (Novak and Mack 2001), that has invaded approximately 40 million hectares throughout western North America, including the Colorado Plateau (Mack 1981, Rowe et al. 2009). Due to its dominance throughout the landscape, and tendency to alter both native habitats and fire regimes, cheatgrass has been referred to as "the quintessential invader" (Novak and Mack 2001) and "the invader that won the west" (Pellant 1996).

The invasiveness of cheatgrass is primarily determined by life-history characteristics, a tendency to increase fire frequency, and the ability to proliferate following fire. Cheatgrass can germinate, grow and reproduce in many habitats, due to high viability, a germination rate close to 100 percent and high seed production (Klemmedson and Smith 1964, Knapp 1996, Smith et al. 2008). Cheatgrass usually germinates in the fall and grows roots over the winter, providing plants with access to soil moisture early in the growing season. This allows cheatgrass to establish before most natives have begun germinating, and contributes to its competitiveness with native plants (Klemmedson and Smith 1964, Melgoza et al. 1990, Arredondo et al. 1998).

As cheatgrass senesces early in the season and adds significantly to fine fuel load, cheatgrass invasion increases the frequency, intensity, and size of wildfires, (Manakis et al. 2003, Hull 1965). Fire frequency has increased in parts of the Western US from every 60-110 years, to every 3-5 years due to cheatgrass invasion (Chambers and Pellant 2008). Unlike most native plants, cheatgrass spreads quickly after fire (Melgoza et al. 1990), and though the cheatgrass seedbank is depleted after fire, often a sufficient number of seeds remain to reestablish its dominance, if management actions are not taken (Meyer et al. 2007). Further, fire can remove larger, older plants that serve as barriers to cheatgrass dispersal, allowing cheatgrass to quickly invade new areas post- fire (Johnston 2011). The grass-fire cycle (positive feedback between cheatgrass and fire) impedes natural reestablishment of the native plant community following fire and hinders efforts to restore native plant biodiversity (D'Antonio and Vitousek 1992, Knapp 1996, Baker 2006).

The Colorado Plateau, a highly variable semi-arid ecoregion containing several habitat types found almost nowhere else in the world, is uniquely suited to a discussion of restoration of cheatgrass-dominated habitats (Padgett et al. 2010, Schwinning et al. 2008, Van riper III 2008). Cheatgrass invasion is a problem in the Colorado Plateau, particularly in burned areas (Getz and Baker 2008). However, cheatgrass invasion does not appear to be as well studied in the Colorado Plateau as in the adjacent Great Basin. Furthermore, climate change has the potential to significantly alter cheatgrass distribution throughout the Colorado Plateau. Under multiple climate models, parts of the Colorado Plateau will become more susceptible to cheatgrass invasion, while other areas will become less hospitable to cheatgrass due to increased summer precipitation (Bradley 2009). The precipitation change would decrease suitability for cheatgrass, and may favor native plants, providing an excellent opportunity for establishing native plant communities in these habitats (Bradley et al. 2009, Bradley and Wilcove 2009). On a decadal scale, altered cheatgrass densities due to climate change present an opportunity for reestablishing native plant communities in the Colorado Plateau.

On a more immediate and shorter time scale, fire also represents an opportunity for reestablishing native plant communities in cheatgrass-dominated habitats, as the cheatgrass seedbank is significantly depleted after fire. Post-fire ecological restoration has the potential to break the grass-fire cycle, reducing cheatgrass density and providing economic benefits, particularly by reducing fire risk (Thompson et al. 2006, Epanchin-Niell 2009). However, the best practices for species selection for restoration in the Colorado Plateau are in question. While there are policies in place to promote reseeding with native plants, much exotic seed is currently used in reseeding efforts, due in part to a belief that exotic plants may be better at stabilizing soil and competing with invasive plants (Richards et al. 1998, Peppin 2010). However, restoration using native plants rather than exotics could reduce erosion and invasion, while also providing additional benefits that include establishing native biodiversity, providing habitat and forage for pollinators and wildlife – including threatened and endangered species – and creating biotic communities that are more resilient in the face of future threats (Weltz et al. 2003, Harris et al. 2006, Thompson et al. 2006). Forbs (broadleaf herbaceous plants) are especially important in achieving many of these benefits and developing a diverse, functional native community, which may be more resistant to reinvasion (Elton 1958, reviewed by Levine and D'Antonio 1999).

In addition to their roles in forming a diverse plant community, forbs may be particularly well-suited in preventing reinvasion of cheatgrass in restoration sites, because they are both similar to, and different from, cheatgrass. Typically, annual and short-lived perennial forbs are among the first species to emerge after a disturbance in the intermountain west. However, in invaded communities, cheatgrass has become the first colonizer, by outcompeting emerging natives, or because cheatgrass-fueled fire destroys the native seedbank. As an annual grass, cheatgrass has few native analogs in the intermountain west (Kerns et al. 2006). If used in reseeding efforts, native ruderal forbs may fill the niche of cheatgrass and help prevent or reduce reinvasion. Furthermore, forbs exploit soil resources differently from cheatgrass. This resource portioning may allow forbs to avoid competition with cheatgrass (Melgoza et al. 1990, Parkinson et al. 2012).

While there are many benefits to including native forb species in reseeding efforts in the Colorado Plateau, there is also much room for improvement regarding their use (Shaw et al. 2005). Seeds of native forb species are often unavailable in the quantities needed for large-scale restoration efforts and are frequently absent from restoration sites (Richards et al. 1998, Dickson and Busby 2009), and those that are currently used tend to have low establishment (Kulpa et al. 2012). Low establishment of seeded forbs may be due to species selection, as well as other factors such as seeding method or timing (Herron 2010, James and Svejcar 2010, Stella et al. 2010). Furthermore, many forbs from this region are unstudied or understudied, and basic ecological data will help to identify potential forb species that would have greater establishment at restoration sites than species currently used (Forbis 2010, CPNPP 2011).

Seeds collected from pristine remnant populations have been considered the gold standard for use in ecological restoration (Broadhurst et al. 2008). However, when a restoration site is degraded by invasive species, seeds from pristine, or pre-disturbance habitat, may not be the most appropriate choice to meet restoration goals. Rather species adapted to the disturbance may perform better (Jones and Johnson 1998, Leger 2008). Recent studies (Mealor et al. 2004, Rowe and Leger 2011, Goergen et al. 2011) have shown that populations of native bunchgrasses in cheatgrass-dominated habitats have adapted to compete with the invader. This suggests that using seed from degraded rather than pristine habitats would help achieve restoration goals of establishing native plants in cheatgrass-invaded habitats. Similar patterns are expected for forbs, and other functional groups, but remain untested in the literature.

Community assembly theory predicts that over time, biotic interactions such as those between native plants and cheatgrass in invaded sites may shape the plant community, such that those natives present in an invaded community are those best suited to living with cheatgrass (Keddy 1992, Young et al. 2005). As high viability, early germination, high germination percent and competitive ability contribute to the invasiveness of cheatgrass, we hypothesized that native species with similar life-history characteristics would perform well in a cheatgrass-dominated habitat (Plummer 1943, Forbis 2010). These qualities would also promote establishment in restoration sites where cheatgrass seeds may be present in the seed bank or able to disperse from nearby habitats (Keeley and McGinnis 2007, Johnston 2011). However, absent historical or experimental information about invaded communities, we cannot establish whether native plants found growing in an invaded habitat are (1) competitors (able to suppress the invader), (2) tolerators (able to avoid suppression, or to grow and reproduce despite the invader) (Goldberg and Barton 1992), or (3) remnants (plants that will soon be outcompeted by cheatgrass, or whose population is declining) (Brooks 2000).

We seek to encourage the use of native forbs in post-fire restoration in the Colorado Plateau by identifying species with a high potential for establishment in restoration sites. To assess their potential value in restoration efforts, we tested the following hypotheses to determine if native forbs from cheatgrass-invaded habitats in the Colorado Plateau are competitors, tolerators, or neither: (1) forbs from cheatgrass-dominated habits produce seeds that have viability and germination rates similar to cheatgrass under early-season Colorado Plateau temperatures, (2) forb species with high viability and germination are also cheatgrass competitors, and (3) forb species will differ in viability, germination, and interaction with cheatgrass, and those with high viability, germination and competitive ability will be useful restoration species. To test these hypotheses we performed laboratory and greenhouse experiments on forb seed collected from cheatgrass-dominated habitats. We separately analyzed competitive effect – (the ability to suppress cheatgrass), and competitive response – (the ability to avoid suppression by cheatgrass) (Goldberg 1996), as both would be important traits for species seeded into cheatgrass-dominated sites.

Materials and Methods:

The Colorado Plateau

The Colorado Plateau overlaps the boundaries of four states, Colorado, New Mexico, Arizona and Utah, and is bounded by the Sierra Nevada Mountains on the west, and the Rocky Mountains on the east. The Colorado Plateau area covers 340,000 km^2, with 42 percent public land (BLM: 31 percent, NPS: 7 percent, USFS: 4 percent), and represents a highly variable habitat, including Piñon-Juniper woodlands (23 percent), shrub-steppe (11 percent) and grassland (8 percent, Schwinning et al. 2008, van Riper III 2008).

Seed Collection

Ripe fruits were collected from cheatgrass and 10 native forb species during summer and fall of 2010 from cheatgrass-invaded sites in Zion National Park, UT and Montrose, CO, which represent the western and eastern boundaries of the Colorado Plateau, respectively. The study species include: *Acmispon humistratus* (Benth.) D.D. Sokoloff (Fabaceae), *Chamaesyce albomarginata* Torr. & A. Gray (Euphorbiaceae), *Cryptantha fendleri* (A. Gray) Greene (Boraginaceae), *Eriogonum leptophyllum* (Torr. & A. Gray) Woot. & Standl (Polygonaceae), *Lupinus pusillus* Pursh (Fabaceae), *Machaeranthera tanacetifolia* (Kunth) Nees (Asteraceae), *Oenothera deltoides* Torr. & Frém (Onagraceae), *Penstemon palmeri* A. Gray (Plantaginaceae), *Sphaeralcea grossulariifolia* (Hook. & Arn.) Rydb. (Malvaceae), and *Symphyotrichum campestre* (Nutt.) G.L. Nesom (Asteraceae) (Table 1). Fruits were collected from a minimum of 50 haphazardly-selected maternal plants from throughout a population and were bulked in paper bags. Seeds were separated from dry fruits and stored in coin envelopes under laboratory conditions in the Reproductive Biology Lab at The Chicago Botanic Garden, Glencoe, IL until the start of experiments.

Seed Viability Analysis

Seeds were analyzed via x-ray (Faxitron, model MX-W run for 20 seconds, 18 KV) to assess viability. Seeds that contained an embryo were counted as viable. Cut tests were performed on seeds that appeared partially filled in x-ray scans to determine if they contained a full embryo. The percent of seeds with an embryo for each species are reported as maximum percent viability. Three replicates of 50 seeds were analyzed for all species except *L. pusillus*, where sets of 25 seeds were analyzed due to insufficient seed. Viability experiments were conducted during January, 2012.

Germination Experiments

To determine percent germination under typical fall and spring temperatures in the Colorado Plateau, we incubated seeds in four day/night temperature treatments. Petri dishes containing seeds (see below) were placed in four incubators (Precision Scientific low temperature illuminated incubator, model 818) set to twelve-hour photoperiods and day/night temperatures of 11/1°C, 14/4°C, 17/7°C and 20/10°C. Daytime temperatures were based on mean monthly high temperatures for January, February and March, respectively, in Zion National Park (Western Regional Climate Center, wrcc.dri.edu). A final daytime temperature of 20°C was selected as it is considered an ideal germination temperature for Colorado Plateau species (Forbis 2010, Meyer and Kitchen 1994). This is slightly below the mean high for April of 22°C. Nighttime temperatures were 10 degrees below daytime temperatures to standardize temperatures shifts between incubators.

Seeds were placed on a 1.5 percent agar solution in a petri dish (60 mm x 15 mm, though three species with larger seeds – M. *tanacetifolia*, *S. campestre*, and cheatgrass were placed in larger, 100 mm x 15 mm petri dishes). A standard 5 x 5 grid printed on a transparent label was placed under each petri dish to ensure even spacing of seeds. For most species, 25 seeds were placed on a petri dish. Due to limited seed quantities 10 seeds of *C. albomarginata* were plated per dish. Three species were targeted for scarification (*A. humistratus*, *L. pusillus*, and *S. grossulariifolia*), as it increases germination in other species of these genera (Dreesen and Harington 1997, Jones et al. 2010, Pendry and Rumbauch 1993). For these three species, 12 or 13 out of 25 seeds per dish were scarified prior to plating. The 13th seed was randomly assigned to a scarification treatment. Scarification consisted of rubbing seeds with sandpaper for at least one minute to break the seed coat.

All temperature and scarification treatments were conducted with and without a cold stratification period to determine if such treatment was required to break dormancy. Seeds were plated and scarified as described above and either placed directly into the treatment incubators, or cold stratified prior to the 28-day incubation. For the cold stratification treatment, petri dishes were placed in cardboard boxes (rotated twice weekly to minimize position effects) in a refrigerator at 3 °C for 28 days before being transferred into treatment incubators for the remainder of the experiment. For both cold stratified and non-cold stratified seeds, four replicates of each species were incubated at each of the four temperatures. Petri dishes were arranged on two plastic trays, placed on two center shelves within each incubator in a stratified random design. Each stratum consisted of one petri dish for each species. Location of petri dishes was randomized for a total of two strata on each tray. Petri dishes were rotated one space within a tray, and trays were rotated within the incubators twice each week. Plates were checked twice weekly for germination, defined as radicle emergence of one mm. Percent germination of viable seeds (Percent $\text{germ}_{\text{viable}}$) was calculated using the following formula:

$\text{Percent germination}_{\text{viable}} = \text{Percent germ}_{\text{Plated}}/\text{Percent viability}_{\text{max}}$

Where Percent $\text{germ}_{\text{plated}}$ is the percent of all plated seeds that germinated, and Percent $\text{viability}_{\text{max}}$ is the maximum viability calculated from x-ray analysis.

Due to incubator malfunction, we do not report data on the 17/7 °C cold stratification treatment. Germination experiments were conducted between May and October 2011.

Competition Experiments

Five species with high viability and germination over 50 percent without cold stratification were used in two competition experiments to assess species interactions between each native forb and cheatgrass. These experiments were performed in the greenhouse at the Chicago Botanic Garden, Glencoe, IL, USA. Seeding densities of cheatgrass were based on low and high estimates of post-fire cheatgrass seedbanks (Smith et al. 2008, Beckstead et al. 2011). One cheatgrass seed per pot represents a field density of approximately 300 seeds/m^2.

In competition experiment I cheatgrass was the focal species. Cheatgrass was grown with interspecific and intraspecific and high- and low-density neighbors. Treatments consisted of a single cheatgrass plant grown: alone (control), with one cheatgrass neighbor (low-density intraspecific) with one of five forb neighbors (low-density interspecific), with four cheatgrass neighbors (high-density intraspecific) and with three cheatgrass neighbors, and one forb neighbor (high-density mixed competition, Figure 1). The mixed competition design was intended to determine if a single forb plant can suppress cheatgrass in the presence of “background” cheatgrass plants. Interspecific and mixed competition treatments were repeated with each of five forb species, for a total of 13 treatment-species combinations (three intraspecific, five low-density interspecific, five mixed).

In competition experiment II, each forb species was the focal species to determine the effects of low- and high-density cheatgrass neighbors on forb growth. Each of the five forb species was grown: alone, and with one (low-density) and four (high-density) cheatgrass neighbors in an addition series design, for a total of 15 treatment-species combinations (Figure 2).

The two competition experiments were planted together on January 18, 2012 in a randomized complete block design with 20 blocks (flats), each containing a 6.6 cm^2 by 8.2 cm pot with one of the 28 treatments and four pots with soil only, for a total of 32 pots per block. Each pot was filled with Fafard 3BC coir mix potting soil and seeds were planted to a depth of 1 cm. Two cheatgrass seeds and three forb seeds were planted at each position, and were thinned to the desired density within seven days after planting. Forb germinants were moved between trays and within treatments up to day 23 or until there was a forb in each replicate of that treatment. For the duration of the experiment, new germinants were pulled to ensure that no more than one forb was growing at each position. Flats were placed on a single bench in a greenhouse at Chicago Botanic Garden and rotated three times per week to reduce bench-position effects. Temperatures in the greenhouse were set between 16.5°C and 19°C but reached as high as 30°C during several unseasonably warm days. Flats were watered as needed, at least 5 times per week to keep soil moist during the duration of the experiments. Flats were treated with Azatin XL (OHP) against fungus gnat larvae on days 23, 30, 37, 44, 58, and 65 after planting.

Seedling emergence was scored three times per week for the first 30 days after planting and then once weekly until plants were harvested. The following data were recorded weekly for each cheatgrass focal plant: height (measured from the soil surface to the highest point when the plant was extended), leaf number and tiller (shoot) number, and for each forb focal plant: height, (H, from soil surface to the highest point of the unmanipulated plant), width A, (W_a, measured across the widest point of the forb) width B, (W_b, measured perpendicular to W_a) and leaf number. Volume was calculated from forb measurements using the formula for volume of an ellipsoid,

$$V = 4/3\,\pi abc,$$

Where a, b, and c are the elliptic radii, here calculated as:

$$V = 4/3\,\pi\,(H/2)(W_a/2)(W_b/2).$$

Pots were destructively harvested on day 85, 12 weeks after planting. Plants were clipped at the soil level and above ground biomass for focal plants and competitors were placed in separate envelopes labeled with the block and treatment. Belowground biomass was harvested from each treatment for three forb focal species – *A. humistratus, M. tanacetifolia, and P. palmeri*. Belowground biomass from all other species is not reported as focal plant roots could not reliably be separated from those of the cheatgrass plants growing in the pots. All biomass samples were dried in an herbarium drier for at least 48 hours before being weighed to the nearest 0.0001 g.

Analyses

All 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 (leaf number for cheatgrass, volume for forbs), and biomass to determine significant effects of factors. Global models were analyzed by model simplification of a linear model, or in the case of the growth data, linear mixed-effects models. In global models for germination and forb growth, data were relativized to the highest value for each species, in order to standardize for between-species comparisons. Viability, germination, emergence, growth and biomass data were square-root transformed, and belowground biomass data were log transformed to meet the assumptions of normality. For biomass and growth data, individual ANOVAs were performed on each forb species. Forb growth curves were analyzed further using model fitting. Each curve was fitted to a linear, exponential, logistic, and von Bertalanffy models, and AICc weights were calculated to determine the model that best described the curve. Tukey's honest significant difference tests with Bonferroni corrections were used in post-hoc analyses as noted. Relative interaction indices (RII) were calculated for each treatment in the competition experiments, following Armas et al. (2004) using the equation:

$$\mathrm{RII} = \frac{B_w - B_0}{B_w + B_0}$$

Where B_0 is the mean biomass of the focal plant in the control treatment and B_w is the mean biomass of the focal plant in an experimental treatment. Statistical tests were not performed on RII values. Because they were calculated using the means of each treatment, there is no variance in RII values. Values are shown to indicate patterns of interactions between species in the competition experiments.

Results:

Seed Viability

Viability differed between species (F_{10} = 75.89, $p<0.0001$). Cheatgrass seeds were 100 percent viable based on x-ray analysis. Seven forb species had maximum viability rates that did not significantly differ from cheatgrass ($p>0.05$, Figure 3).

Germination

Species differed in percent germination of viable seeds (“germination,” Table 2). Temperature and cold stratification had significant effects on germination in the overall model as did all two-way interactions between species, temperature and cold stratification. Cheatgrass germination was 100 percent under all treatments. Forb germination varied from zero to 100 percent (Table 3, Figure 4), depending upon species, temperature and pre-treatment. Temperature significantly increased final percent germination in seven species: *C. fendleri*, *E. leptophyllum*, *S. campestre*, *M. tanacetifolia*, *P. palmeri*, *S. grossulariifolia* and *C. albomarginata* (Table 3). Cold stratification significantly increased germination in *A. humistratus*, *P. palmeri* and *S. grossulariifolia*, while there was a significant interaction between temperature and cold stratification in *C. fendleri*, *E. leptophyllum*, *S. campestre*, *P. palmeri* and *S. grossulariifolia*.

Five species – *C. fendleri*, *A. humistratus*, *S. grossulariifolia*, *M. tanacetifolia* and *P. palmeri* had germination percentages that did not significantly differ from cheatgrass under certain conditions ($p>0.3$ in all cases). While *C. fendleri* reached maximum germination without pre-treatment, *M. tanacetifolia* and *P. palmeri* reached maximum percent germination following cold stratification and *A. humistratus* and *S. grossulariifolia* required cold stratification and scarification to reach maximum germination.

Competition experiments

The forb species seeded in the competition experiment – *A. humistratus*, *C. fendleri*, *E. leptophyllum*, *M. tanacetifolia*, and *P. palmeri* all had high viability, and germination of 50 percent or greater without cold stratification.

Emergence and mortality

Species differed in emergence timing of focal plants ($F_5 = 96$, $p <0.0001$, Figure 6), with cheatgrass emerging earliest. Out of 560 focal plants, 28 plants, (5 %) did not emerge. Of these, five were cheatgrass plants (four from the high-density mixed treatment with *A. humistratus*, and one from the high-density mixed treatment with *P. palmeri*), one was *C. fendleri* (from the control treatment), two were *M. tanacetifolia*, (both from the high-density cheatgrass treatment), two were *P. palmeri* (one from the low-density cheatgrass treatment, and one from the high-density cheatgrass treatment) and 18 were *E. leptophyllum* (10 from the control treatment, five from the low-density cheatgrass treatment, and three from the high-density cheatgrass treatment). In 28 cases, a neighbor plant did not emerge over the course of the experiment. These focal plants were excluded from the analysis.

Forty seven focal plants (8.4%), all of them forbs died over the course of the experiment. Of these plants, 33 were *C. fendleri* (14 from the control treatment, 12 from the low-density cheatgrass treatment and seven from the high-density cheatgrass treatment), six were *P. palmeri* (three from the control treatment, two from the low-density cheatgrass treatment and one from the high-density cheatgrass treatment), and eight were *E. leptophyllum* (three from the control treatment, three from the low-density cheatgrass treatment, and two from the high-density cheatgrass treatment). No cheatgrass, *M. tanacetifolia*, or *A. humistratus* plants died over the course of the experiment.

Competition Experiment I

Growth

Competition type ($F_{4,2702} = 539$, $p < 0.0001$), week ($F_{11,2702} = 1708$, $p < 0.0001$), and the interaction between these two variables ($F_{44,2702} = 34.12$, $p < 0.0001$) had significant effects on cheatgrass leaf number. Intraspecific competition significantly decreased leaf number ($F_{1,436} = 174$, $p < 0.0001$). Forb species had differing effects on leaf number in cheatgrass both in the low-density interspecific ($F_{4,965} = 31.30$, $p < 0.0001$), and in the mixed intra and interspecific treatment ($F_{4,939} = 6.36$, $p < 0.0001$). Growing with *A. humistratus* caused an increase in leaf number for cheatgrass, while growing with all other forbs reduced leaf number relative to the control treatment (Figure 7).

Biomass

Competition type, and the interaction between neighbor species and competition type had significant effects on cheatgrass biomass, while block, neighbor species, and additional two-way interactions were not significant (Table 4A). All intraspecific treatments differed significantly from one another ($p < 0.0001$ in all cases, Figure 8). Model selection dictated that low-density interspecific treatments (cheatgrass growing with one forb) remain separate in the model, indicating that different species of forb neighbor had differing effects on cheatgrass biomass. However, post-hoc analyses revealed that mean cheatgrass biomass after growing with any forb species did not differ from the control biomass (all $p > 0.05$). Within the forb interspecific treatments, biomass of cheatgrass growing with *M. tanacetifolia* (0.16 ± 0.01 g) was significantly lower than biomass of cheatgrass growing with *A. humistratus* (0.22 ± 0.01 g; $p = 0.002$). Cheatgrass biomass in the mixed- intra and interspecific treatments did not differ from the high density intraspecific treatment, or with regard to the identity of the forb neighbor ($p > 0.05$).

Relative interaction index

Cheatgrass had negative RII values when growing with low- and high- density cheatgrass neighbors and with *M. tanacetifolia* and *P. palmeri*, and positive RII values when growing with *C. fendleri*, *E. leptophyllum*, and *A. humistratus (*Figure 9).

Competition experiment II

Growth

In the overall model, species, competition type, week, and all two way interactions between these variables had a significant effect on forb volume (Table 5). Competition decreased volume in all forb species ($p < 0.05$), though only slightly in *A. humistratus* ($F_{1,663} = 3.1$, $p = 0.47$, Figure 10). *Eriogonum leptophyllum* growth in the control treatment was best described by a linear model, while all other species/treatment combinations were best described by a logistic model (appendix 1).

Forb aboveground biomass

Species, competition type, and the interaction between species and competition type all had significant effects on forb aboveground biomass while block and other two-way interactions were not significant (Table 4B). Competition reduced biomass in all forb species (Figure 11). *Eriogonum leptophyllum* biomass was not significantly reduced by low-density cheatgrass competition, ($p = 0.14$), but was reduced by high-density cheatgrass competition ($p = 0.01$). For *A. humistratus* and *C. fendleri*, all competition types differed significantly from one another, with high density cheatgrass competition resulting in the lowest aboveground biomass. For *M. tanacetifolia* and *P. palmeri*, competition with cheatgrass significantly decreased aboveground biomass relative to the control, but biomass in low- and high-density cheatgrass treatments did not differ.

Forb belowground biomass

Block, species and competition type, as well as the interaction between species and competition type and bock and competition type significantly affected belowground biomass in the three forbs for which belowground biomass data could be collected (Table 4C). Each species had significantly lower belowground biomass in competition versus control treatments ($p < 0.05$), however, belowground biomass under low and high density cheatgrass treatments did not differ for any of the forb species ($p > 0.05$, Figure 12).

Relative interaction index

All plants growing with cheatgrass neighbors had negative RII values (Figure 13). Of all forbs tested, *P. palmeri* had the lowest RII value when growing under low (-0.70) and high, (-0.83) cheatgrass competition.

Discussion:

Native forb species with life-history attributes similar to cheatgrass, and the ability to compete with cheatgrass may have increased potential for establishment, growth and reproduction in degraded habitats. We identified seven native forb species from cheatgrass-dominated habitats with seed viability as high as cheatgrass and five species with germination rates as high as cheatgrass under some conditions. Viability near 100 percent and high, rapid germination may contribute to the ability of these native species to establish, grow and reproduce in cheatgrass-dominated habitats. That forb seeds were viable, germinable, and produced plants that grew and survived over the course of the experiment suggests that forbs in cheatgrass-dominated habitats are reproductive individuals with the potential to persist in invaded habitats.

As a group, forbs collected from cheatgrass-dominated habitats did not significantly reduce the biomass of cheatgrass plants relative to controls (Goldberg and Barton 1992). Furthermore, forbs also had a weak competitive response to cheatgrass. Competition suppressed growth, above and belowground biomass for all forb species relative to controls. However, cheatgrass target plants were also significantly suppressed by cheatgrass competition in this study, and cheatgrass intraspecific competition has been documented extensively in the literature (Palmbald 1968, Sheley and Larson 1994, Lowe et al. 2003, Vasquez et al. 2008). Forb species differed from one another in their response to cheatgrass competition. Even though all forbs were suppressed by cheatgrass, we identified several species that may represent improvements over species currently used in reseeding projects in the Colorado Plateau and other parts of the intermountain west.

Of all the species tested in this experiment, *P. palmeri* is the only species commonly seeded in restorations (Meyer and Kitchen 1992), and is one of only two forb species used in post-fire reseeding at Zion National Park (Fuhrmann et al. 2008). *Penstemon palmeri* has been reported to have higher establishment than other seeded forbs in several studies (Brown and Paschke 2002, Winslow et al. 2007, Abella and Newton 2009). Nonetheless, *P. palmeri* had the weakest competitive response to cheatgrass in our study. *Penstemon palmeri* was suppressed by cheatgrass more than any other species, possibly because of its relatively late emergence timing. In another study, *P. Palmeri* was the weakest competitor with spotted knapweed, *Centaurea maculosa*, an allelopathic invader, of 23 species tested (Perry et al. 2005). We identified several species that may represent improvements over the "status quo" of *P. palmeri* in a restoration context. *Acmispon humistratus*, *C. fendleri* and *M. tanacetifolia* had germination percentages that were similar to or higher than *P. palmeri* at cool Colorado Plateau temperatures (Figure 4, 5), and were suppressed by cheatgrass to a lesser extent than was *P. palmeri* (Figure 13). In addition, *A. humistratus* and *M. tanacetifolia* had a similar final volume to *P. palmeri*, but grew more quickly than *P. palmeri* (Figure 10, appendix 1). These data suggest that *M. tanacetifolia*, *A. humistratus* and *C. fendleri* may be promising candidate species for use in reseeding efforts in the Colorado Plateau.

High performance native species

To further understand their restoration potential, the germination, growth and interaction with cheatgrass of *M. tanacetifolia*, *A. humistratus*, and *C. fendleri* need to be tested under field conditions, and results compared with the laboratory and greenhouse results reported here. Predicting field establishment and growth rates from greenhouse trials is difficult, and there have not been many published studies on cheatgrass competition that report both greenhouse and field results. In one case, Parkinson (2008) demonstrated that while forb growth was suppressed by cheatgrass competition in the greenhouse, several species were able to establish and grow in the field in spite of high level of cheatgrass competition.

Machaeranthera tanacetifolia suppressed cheatgrass growth more than any other forb studied (Figure 9). Considered an early seral, ruderal species (Busby et al. 2011), *M. tanacetifolia* is found in many habitat types, has grown even under heavy grazing in Colorado (Hart 2001) and is a forage plant for sheep in the Mojave desert (Philips et al. 1996). *Machaeranthera tanacetifolia* is currently on the priority list of early-seral forb species to be targeted for development by the Colorado Plateau Native Plants Program (A. Kramer, personal comm.), and appears to be a good candidate species for use in reseeding efforts.

Acmispon humistratus is a desirable species for use in restoration as it is a preferred food source for the federally threatened desert tortoise (*Gopherus agassizii*, Jennings 2007, fws.gov), which is found in Zion National Park (Crowe and McLuckie 2009). Germination response of *A. humistratus* in this experiment was much higher than previously documented (between 3 and 31%, as *Lotus humistratus*, Le Fer and Parker 2005), likely due to cold stratification and scarification treatments performed here. Scarification may be caused by fire in the field, as *A. humistratus* density has been shown to increase following fire (DiTomaso 2001). Despite possible benefits of using *A. humistratus* in reseeding efforts, in this experiment *A. humistratus* showed a very slight trend of facilitation of cheatgrass. This result is interesting, because although *A. humistratus* is a nitrogen-fixer and root-nodules were observed on the roots of plants growing in Zion National Park, no root nodules were found on the roots of greenhouse-grown plants in this experiment. This is likely due to a lack of appropriate rhizobial species in the soil mix. *Acmispon humistratus* may facilitate cheatgrass to a greater degree in the field, where native nitrogen-fixing bacteria are present, and root nodules are formed. This is a concern with the use of *A. humistratus* in restoration sites susceptible to reinvasion by cheatgrass. On the other hand, *A. humistratus* may also facilitate native plants. A field experiment found that on burned sagebrush steppe, legume *Lupinus argentus* increased biomass, but reduced emergence and survival of cheatgrass, while facilitating native *Elymus multisetus*, but had no effect on native forb, *Eriogonum umbellatum* (Goergen and Chambers 2012). Field studies are necessary to determine if the restoration potential of *A. humistratus* based on germination, growth and facilitation of native plants is eclipsed by its potential facilitation of cheatgrass.

Cryptantha fendleri had the highest germination percent of any forb species tested in this experiment, reaching 100 percent germination in the 17/7°C and 20/10°C treatments without cold stratification. Further, germination occurred rapidly, similar to cheatgrass (Figure 5). However, *C. fendleri* had low survival and growth throughout the greenhouse experiment. Of 47 individual forbs that died during the experiment, 33 (70 percent) were *C. fendleri*. This mortality was unrelated to competition from cheatgrass, as more plants died in the control treatment (14) as compared to the low-density (12) and high-density (seven) cheatgrass treatments. In all treatments, *C. fendleri* plants appeared to reach a maximum volume between weeks five and eight, and declined for the rest of the experiment (Figure 7). Rather, the observed mortality may have been related to moist soils in the greenhouse, as some plants appeared to be rotting during the experiment. Interactions between cheatgrass and *C. fendleri* may be quite different in the arid conditions of the Colorado Plateau. Additional research on *C. fendleri* in drier laboratory or field conditions are recommended to fully establish the restoration potential of this species.

Mechanisms of plant competition

Ecological theory predicts that competitive interactions between plants are stronger and more common under conditions of low abiotic stress, while facultative relationships form in high-stress habitats (Callaway and Walker 1997, Callaway et al. 2002, but see Maestre et al. 2005). The plants in this experiment were grown under greenhouse conditions, and likely received more water and nutrients than they would in their native habitats Zion and Montrose. Therefore, cheatgrass may actually suppress forbs to a lesser degree in the field, under conditions of higher abiotic stress.

In our experiments, the plants appeared to compete for space. Pots quickly became dominated by cheatgrass roots, which may explain why forb belowground biomass was reduced to a greater degree than aboveground biomass, and why there was not a significant difference between belowground biomass of forbs growing with one cheatgrass plant versus four (Figure 12). Cheatgrass can reduce belowground biomass of native plants in the field (Melgoza et al. 1990, Melgoza and Nowak 1991), however, differing root architectures may explain differences in forb response to competition with cheatgrass. Native plants with highly branched roots experience greater competition from grasses than do forbs with columnar roots, likely due to resource partitioning (Parkinson 2012). Forbs with root architecture different from cheatgrass may be able to access different soil resources from cheatgrass, reducing belowground competition (Melgoza and Nowak 1991, Parkinson 2012). The three forbs for which belowground biomass was isolated – *P. palmeri*, *M. tanacetifolia*, and *A. humistratus* all had branched roots. We are unable to conclude that root suppression was due to root structure, rather than pot size. Future research should utilize larger and much deeper pots, to adequately address the role of root architecture and belowground competition between native forbs and cheatgrass.

Future Directions - Assisted succession and post-fire restoration

Successional restoration has been suggested as a means to establish a diverse native plant community, stabilize soils, reduce reinvasion by cheatgrass and prevent future fire (Cox and Anderson 2004, Kruger-Mangold et al. 2006). One interpretation of successional restoration includes establishing stands of exotic plants like crested wheatgrass, *Agropyron cristatum* immediately after fire to prevent soil erosion and reinvasion, with the intent of planting native plants at a later stage (Cox and Anderson 2004, Hardgree and Van Vactor 2004). However, establishing native plants in crested wheatgrass stands has proved difficult (Fansler and Mangold 2011). More recently, native early seral species, in particular annual forbs have been proposed to fill the functional role of crested wheatgrass and other exotics, stabilizing soils and preventing cheatgrass reinvasion while providing ecosystem services such as pollinator attraction, forage and soil nutrients (Kruger-Mangold et al. 2006, Herron 2010). The low establishment of seeded species at restoration sites can result from a mismatch between the successional stage of a restoration site (usually post-disturbance/early successional) and the species seeded at the site (often later seral perennial species, Sheley et al. 2006). Planting early seral species may better mimic natural successional processes and facilitate the establishment of longer-lived perennial plants through natural dispersal, germination from a persistent seedbank, or additional seedings (Sheley et al. 2006, Brown et al. 2008).

Most of the species we collect from cheatgrass-dominated habitats were early seral species. Also, with few exceptions, the species with high germination percentages at early-season temperatures were early-seral annuals (*A. humistratus*, *C. fendleri* and *M. tanacetifolia*), or short-lived perennials (*P. palmeri*, Lessica and Cooper 1999, Meyer and Kitchen 1992, Busby et al. 2011, Le Fer and Parker 2005). *Eriogonum leptophyllum* was the only longer-lived perennial species with high germination percentages (at the highest temperature tested) and was also suppressed by cheatgrass competition less than any other native plant tested (Figure 13). Other annual and early seral species tested, such as *O. deltoides* and *L. pusillus*, had high viability but low germination rates in our experiment (Sheley et al. 2008). These plants likely had dormancy mechanisms that were not broken by the treatments in this experiment (Baskin and Baskin 2001).

Large-scale reseedings in the Colorado Plateau typically occur after fire (Peppin et al. 2010). Fire reduces the size of the cheatgrass seedbank by orders of magnitude (Humphrey and Schupp 2001, Meyer et al. 2007), providing a unique opportunity for reseeding. However, within 2-3 years of a fire, the cheatgrass seedbank of burned areas can be as large as that in unburned regions (Humphrey and Schupp 2001). This provides a short window for seeded species to germinate, grow and reproduce before cheatgrass becomes dominant (Kulpa et al. 2012). Species that germinate to high percentages without a cold stratification requirement may be optimal in this situation, as they can be seeded at the end of winter to germinate immediately, or seeded immediately after fire.

In a post-fire reseeding, seeded species will emerge along with cheatgrass seedlings emerging from any remaining seedbank, or dispersing into the site from adjacent habitats (Smith et al. 2008, Johnston 2011). In many greenhouse experiments, target plants were suppressed by cheatgrass when both were grown from seed, including hybrid and exotic grasses (Hull 1963, Aguirre and Johnson 1991), native grasses (Rafferty and Young 2002), and native forbs (Parkinson et al. 2012). However, competitiveness of native plants increases when natives are established prior to being exposed to cheatgrass (Humphry and Schupp 2004, McGlone et al. 2011). While a cheatgrass-free environment during the establishment period may not be possible, fast growing plants may have an opportunity to establish and reproduce during the two- to-three year window before cheatgrass would typically become dominant. Further, natives that compete with, or tolerate cheatgrass should persist even as cheatgrass seedlings emerge from the seedbank. In this way, native forbs with high viability and germination, rapid growth, and the ability to compete with cheatgrass may be able to help prevent cheatgrass dominance, while also contributing to a robust native community.

With few caveats, we suggest that invaded habitats represent a promising source of restoration material. First, since not all native forbs from such habitats are appropriate for use in restoration, we suggest that whenever possible data should be used to guide species selection for reseeding projects rather than convention (Wyant et al. 1995). Second, from this experiment, we cannot conclude whether the properties of forbs we observed represent species-level, or population-level effects. The species we collected from cheatgrass-dominated habitats may have an early-seral life-history, and therefore colonize, or persist in invaded habitats. If this is the case, restoration material could be collected from many potential populations, and plants could be grown on a large-scale for use in restoration. On the other hand, if the properties observed here are population-level effects, possibly adaptations to growing with cheatgrass (Mealor and Hild 2006, Rowe and Leger 2011, Goergen et al. 2011), source populations would be more limited, and large-scale seed growing operations may be more complicated. Further research comparing native forbs from invaded and non-invaded habitats may help distinguish between these two possible effects.

Applications:

Degraded habitats represent a promising seed source for restoration material in the Colorado Plateau. Due to innate life-history traits or adaptation to invasive plants or other features of degraded habitats, these plants may be uniquely able to establish and grow at a restoration site. Native forbs from cheatgrass-invaded habitats do not represent ecological “dead ends.” Rather they produce viable, germinable seeds that can grow with cheatgrass, and in some cases, suppress cheatgrass growth. Data about species from degraded habitats, and Colorado Plateau forbs in general is lacking from the literature, though several projects are now underway to identify promising restoration candidates among such species. Viability, germination, growth, interaction and fecundity data from the lab and field are useful tools for informing species selection in restoration planning, and meeting restoration targets. Previously underused or understudied species – particularly early seral species – may have improved establishment and growth in restoration sites over species that are currently widely used and widely available. Promising candidate species are recommended for use in post-fire reseeding activities.

Tables:

Table 1: Species information and collection site of forbs studied

Scientific Name	Common Name	Family	Life History	Collection Site
Acmispon humistratus	Foothill Deervetch	Fabaceae	A	Zion NP, UT– Right Fork (N37.267632 W113.107853)
Chamaesyce albomarginata	Rattlesnake Weed	Euphorbiaceae	P	Zion NP, UT – Grapevine (N37.271662 W113.101072)
Cryptantha fendleri	Sanddune Cryptantha	Boraginaceae	A	Zion NP, UT– Hop Valley (N37.203915 W 113.065167)
Eriogonum leptophyllum	Slenderleaf Buckwheat	Polygonaceae	P	Montrose, CO – BLMD7 (N38.24516 W108.00295)
Lupinus pusillus	Rusty Lupine	Fabaceae	A	Zion NP, UT – Right Fork (N37.267632 W113.107853)
Machaeranthera tanacetifolia	Tanseyleaf Tansyaster	Asteraceae	A/B	Zion NP, UT– Right Fork (N37.267632 W113.107853)
Oenothera deltoides	Birdcage evening Primrose	Onagraceae	A/P	Zion NP, UT – Wildcat (N37.34137 W113.10118)
Penstemon palmeri	Palmer's Penstemon	Plantaginaceae	P	Zion NP, UT – Grapevine (N37.271662 W113.101072)
Sphaeralcea grossulariifolia	Gooseberryleaf Globemallow	Malvaceae	P	Zion NP, UT – Wildcat (N37.34137 W113.10118)
Symphyotrichum campestre	Western Meadow Aster	Asteraceae	P	Montrose, CO – BCD3 (N38.54442 W107.69080)

A= Annual, B = Biennial, P =Perennial

Table 2: Final percent germination of *Bromus tectorum* and ten forb species after one month of incubation

	df	F	P
Block	391	0.16	0.688
Petri Dish	391	0.28	0.837
Species	10,357	40.12	<0.0001
Temp	1,357	37.28	<0.0001
ColdStrat	1,357	6.02	0.015
Species*Temp	10,357	2.26	0.015
Species*ColdStrat	10,357	2.71	0.003
Temp*ColdStrat	1,357	4.84	0.029

Linear model (analysis of variance) was performed on square-root transformed, relativized data

Table 3: Mean percent germination of viable seeds of *Bromus tectorum* and ten forb species after one month of incubation

		11/1 °C	14/4 °C	17/7 °C	20/10 °C
B. tectorum	Control	100^{a}	100^{a}	100^{a}	100^{a}
	Cold stratified	100^{a}	100^{a}		100^{a}
C. fendleri	Control	37^{a}	73^{b}	99^{c}	100^{c}
	Cold stratified	74^{c}	82		78
A. humistratus	Control	6^{a}	12^{a}	0^{a}	6^{a}
	Cold stratified	33^{b}	23^{b}		21^{b}
	Scarified	83^{c}	83^{c}	77^{c}	75^{c}
	Scarified and Cold stratified	92^{c}	88^{c}		90^{c}
M. *tanacetifolia*	Control	65^{a}	67^{ab}	72^{ab}	78^{b}
	Cold stratified	60^{a}	79^{ab}		85^{b}
P. palmeri	Control	7^{a}	17^{b}	45^{c}	64^{c}
	Cold stratified	56^{c}	77^{c}		61^{c}
E. *leptophyllum*	Control	3^{a}	19^{bc}	25^{cd}	50^{d}
	Cold stratified	10^{c}	17^{c}		31^{cd}
S. *campestre*	Control	5^{a}	38^{b}	38^{b}	53^{b}
	Cold stratified	33^{b}	31^{b}		36^{b}
L. *pusillus*	Control	0^{a}	15^{a}	17^{a}	17^{a}
	Cold stratified	6^{a}	4^{a}		8^{a}
	Scarified	12^{a}	17^{a}	17^{a}	13^{a}
	Scarified and Cold stratified	10^{a}	2^{a}		12^{a}
C. albomarginata	Control	0^{a}	0^{a}	0^{a}	11^{a}
	Cold stratified	0^{a}	0^{a}		3^{a}
S. *grossulariifolia*	Control	0^{a}	4^{ab}	8^{ab}	8^{ab}
	Cold stratified	0^{a}	15^{ab}		11^{ab}
	Scarified	0^{a}	11^{ab}	18^{ab}	14^{ab}
	Scarified and Cold stratified	7^{ab}	32^{b}		92^{c}
O. deltoides	Control	0^{a}	4^{a}	4^{a}	1^{a}
	Cold stratified	1^{a}	1^{a}		2^{a}

Within each species, different letters indicate significant differences ($p<0.05$) based on Tukey's HSD tests. All species were incubated at four different temperature regimes with no pretreatment, and following a one month cold stratification at 3°C. Half the seeds from three species, *A. humistratus*, *L. pusillus* and S. *grossulariifolia* were scarified before cold stratification and incubation.

Table 4: Aboveground biomass of *Bromus tectorum*, aboveground biomass of five forb species, and belowground biomass of three forb species from competition experiments I and II

	df	F	P
A. Competition experiment I: *B. tectorum*, Aboveground Biomass			
Block	232	0.55	0.460
Competition Type	236	101.71	<0.0001
Neighbor Species	231	0.01	0.183
Neighbor*CompType	227	3.84	0.010
Block*Neighbor	221	1.13	0.344
Block*CompType	227	0.63	0.639
B. Competition experiment II: Forbs, Aboveground Biomass			
Block	218	0.64	0.424
Species	229	11.84	<0.0001
Competition Type	228	86.10	<0.0001
Species*CompType	217	2.729	0.007
Block*Species	225	1.02	0.399
Block*CompType	225	0.39	0.677
C. Competition experiment II: Forbs Belowground biomass			
Block	162	4.42	0.037
Species	163	58.35	<0.0001
Competition Type	164	143.50	<0.0001
Species*CompType	157	6.41	<0.0001
Block*Species	161	3.53	0.0317
Block*CompType	159	0.71	0.497

Linear model (analysis of variance) performed on square-root transformed, relativized data for aboveground biomass in *B. tectorum* and forbs, belowground biomass data was relativized and log transformed. Block was a random factor. All other factors were fixed.

Table 5: Growth (volume) of five forb species measured over twelve weeks

	df	F	P
Block	1,18	1.09	0.310
Species	4,3076	355.67	<0.0001
Competition Type	2,3076	92.75	<0.0001
Week	1,3076	1459.80	<0.0001
Species*CompType	8,3076	16.85	<0.0001
Species*Week	4,3076	12.49	<0.0001
CompType*Week	2,3076	30.03	<0.0001
Block*Species	4,3076	01.13	0.343

Values calculated from a linear mixed effects model with block as a random factor and species, competition type, and week as fixed factors. Analyses conducted on relativized, square-root transformed data.

Table 6: Decision grid/Summary of data collected.

Species	Viability (%)	Max. Germination (%)	Emergence Day	Growth rate (mg/mo.)	RII Focal	RII CG
B. tectorum	100	100	5	59.9	-0.24	-0.24
A. humistratus	99	92*●	8.6	14.2	-0.30	0.09
C. albomarginata	93	11				
C. fendleri	97	100	8.1	3.1	-0.40	0.02
E. leptophyllum	89	50	14.3	4.5	-0.28	0.03
L. pusillus	100	17				
M. tanacetifolia	85	85	6.7	17.6	-0.49	-0.05
O. deltoides	95	4				
P. palmeri	95	77●	14.1	14.0	-0.70	-0.03
S. campestre	81	53				
S. grossulariifolia	56	92*●				

Mean viability, germination, emergence, growth, and species interaction data for all species tested. (*=Maximum germination percent reached after scarification ●= Maximum percent germination reached after cold stratification, germination percent corrected for viability, growth rate calculated from biomass). Colors represent recommendations for restoration – green: recommended, yellow: recommended with reservations, red: not recommended.

Figures:

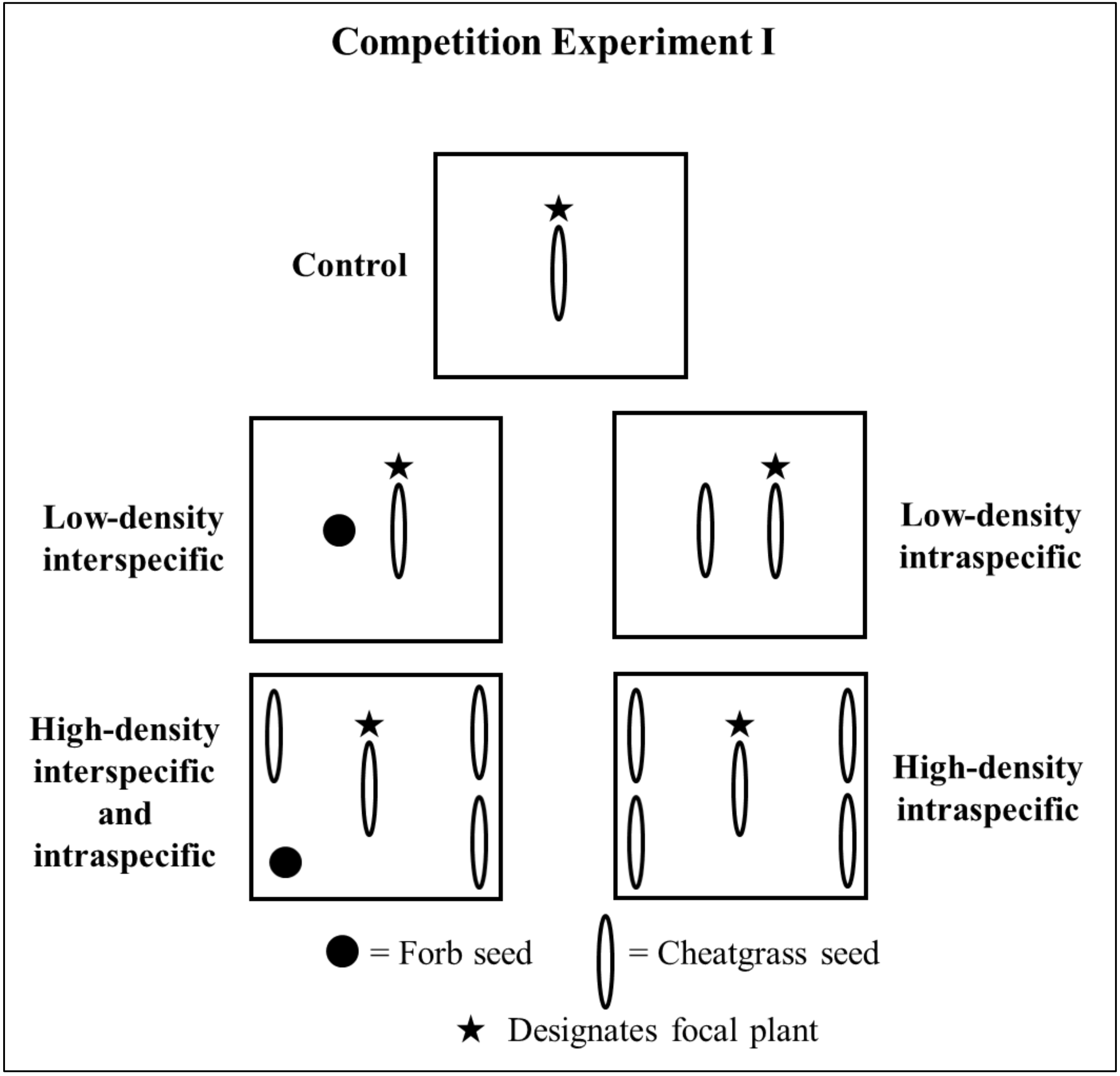


Figure 1: Competition experiment I design. *Bromus tectorum* focal plants were grown alone (control) with one other *B. tectorum* plant (low-density intraspecific), with four other *B. tectorum* plants (high-density intraspecific), with one forb (low-density interspecific) and with one forb and four *B. tectorum* plants (high-density mixed competition). Each treatment was repeated with each of five forb species and replicated 20 times.

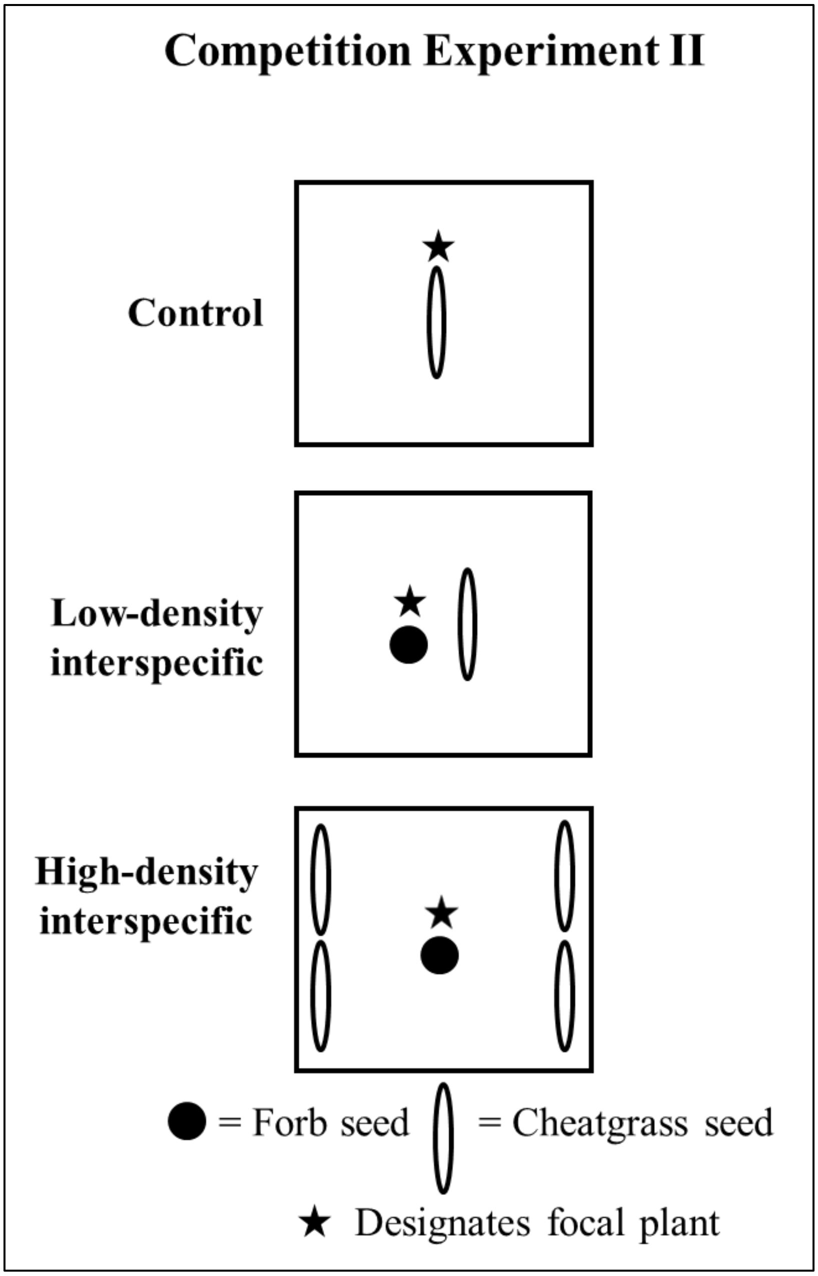


Figure 2: Competition experiment II design. Forb focal plants were grown alone, with one B. tectorum plant (low-density interspecific) and with four *B. tectorum* plants (low-density interspecific). Each treatment was repeated with each of five forb species and replicated 20 times.

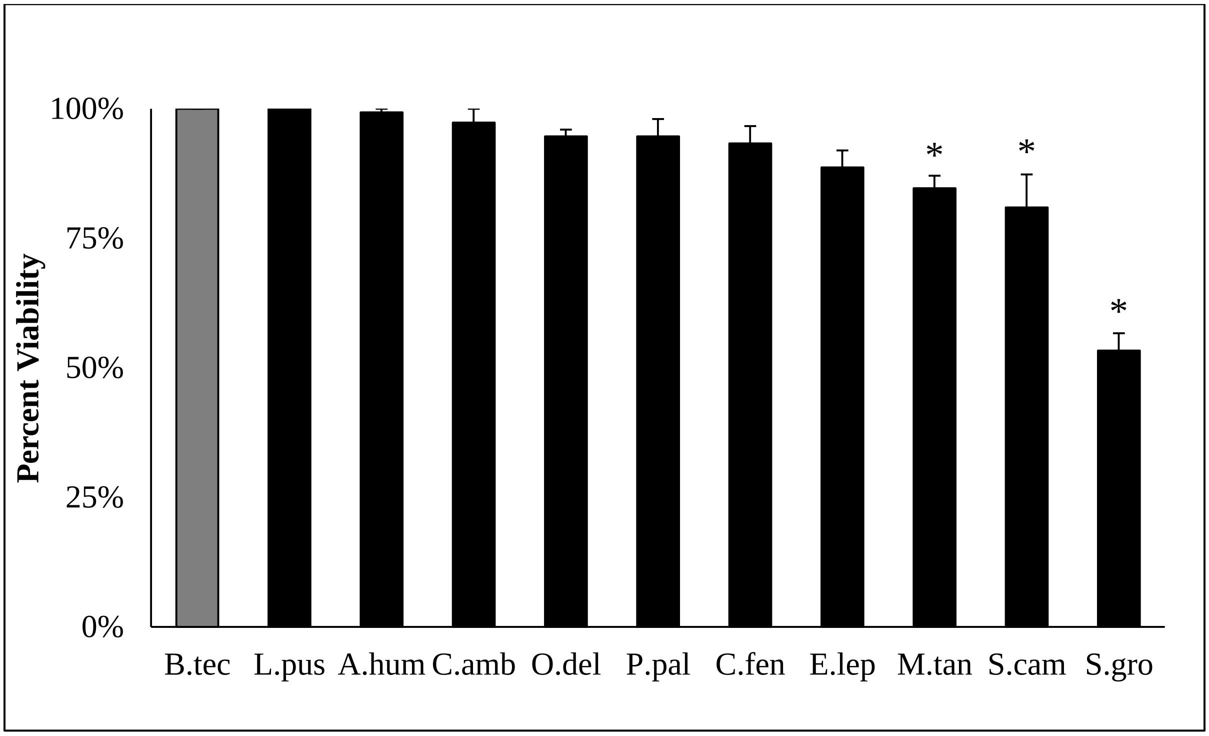


Figure 3: Maximum percent viability of *Bromus tectorum* (grey bar) and ten forb species (black bars, (Mean ± 1 SE). Viability estimated using x-ray analysis. Stared forbs have maximum percent viability significantly lower than *B. tectorum* ($p<0.05$), as calculated from Tukey's HSD tests.

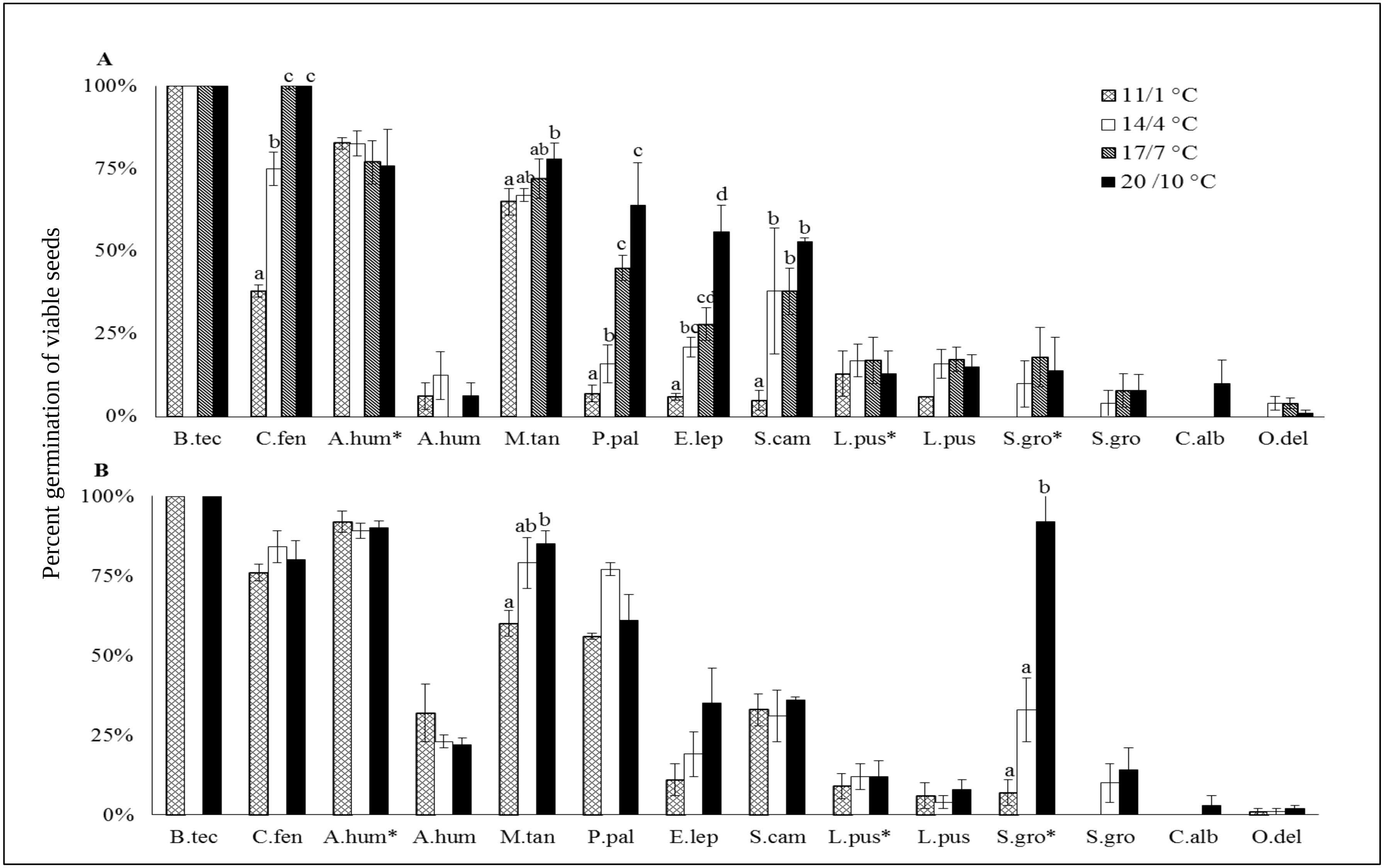


Figure 4: Percent germination of (A) non cold stratified seeds, and (B) cold stratified seeds of *Bromus tectorum* and ten forb species (Mean ± 1 SE). Values corrected for viability. * indicates scarified seeds. Analyses were performed on square-root transformed data, letters indicate significant differences between temperature treatments based on within species Tukey's HSD ($p<0.05$) comparison.

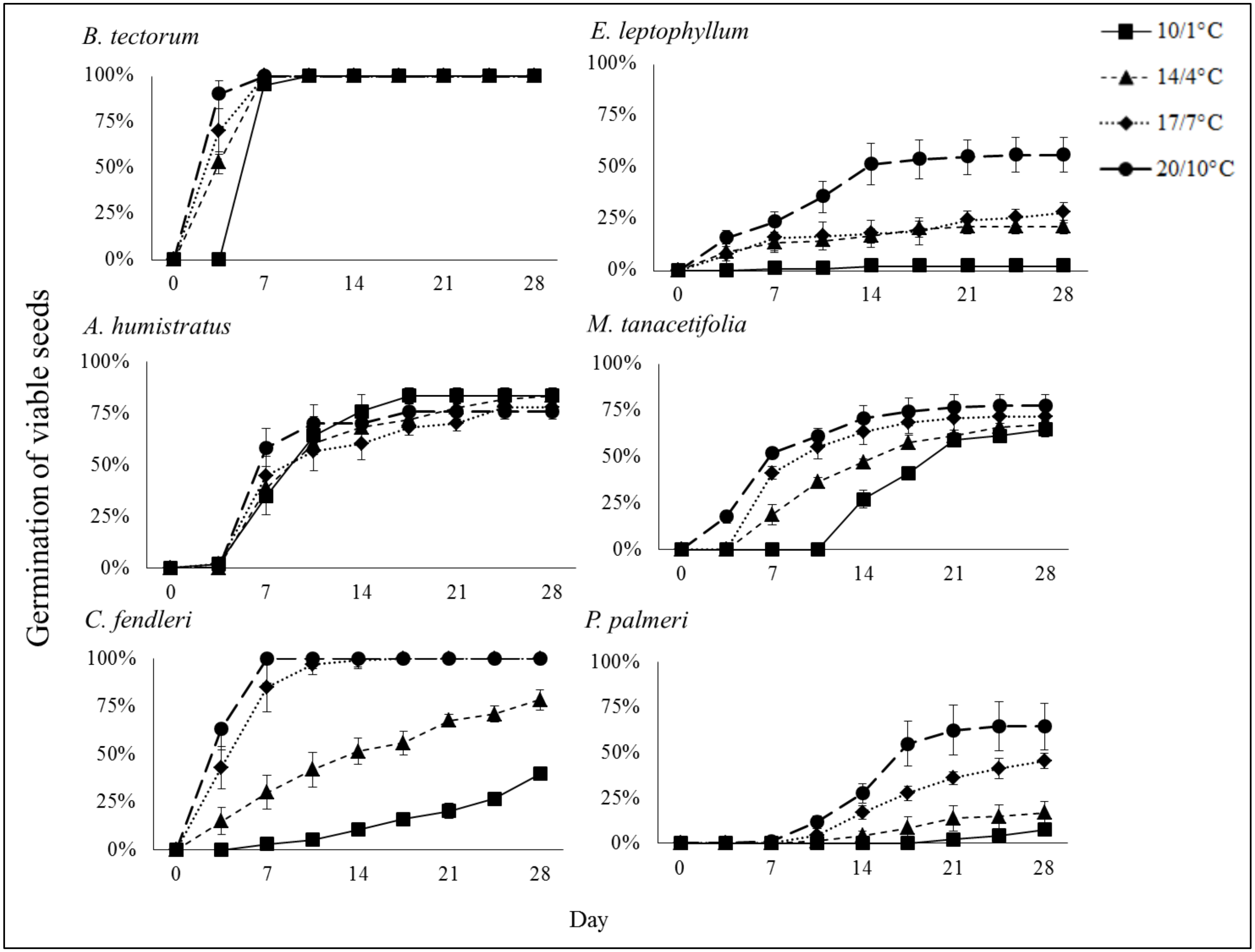


Figure 5: Germination time series of Bromus tectorum and five forb species seeded in the competition experiment.

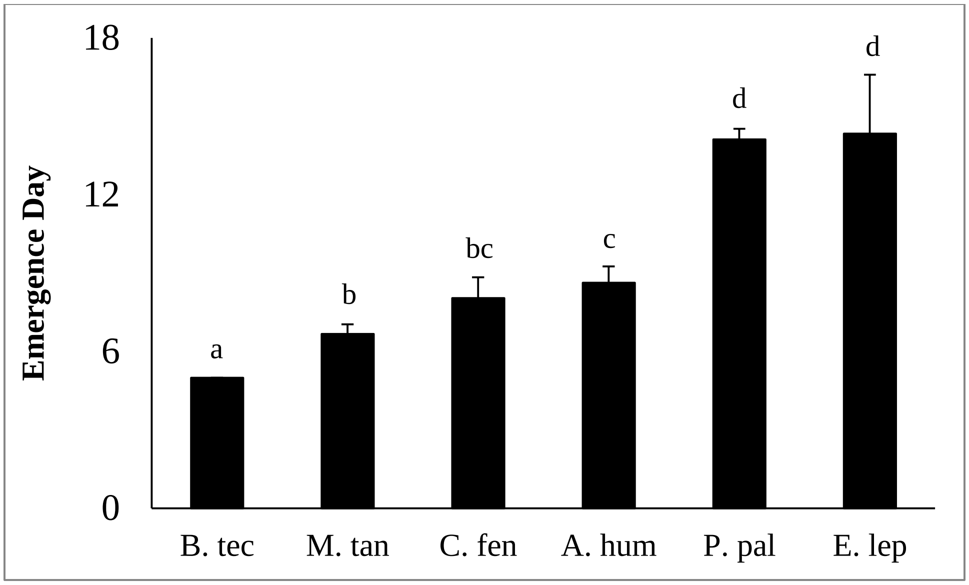


Figure 6: Emergence day of *Bromus tectorum* and forb focal plants from competition experiments I & 2. Emergence day (mean ± 1 SE) varied with species. Different letters indicate significant ($p < 0.05$) differences in Tukey's HSD tests.

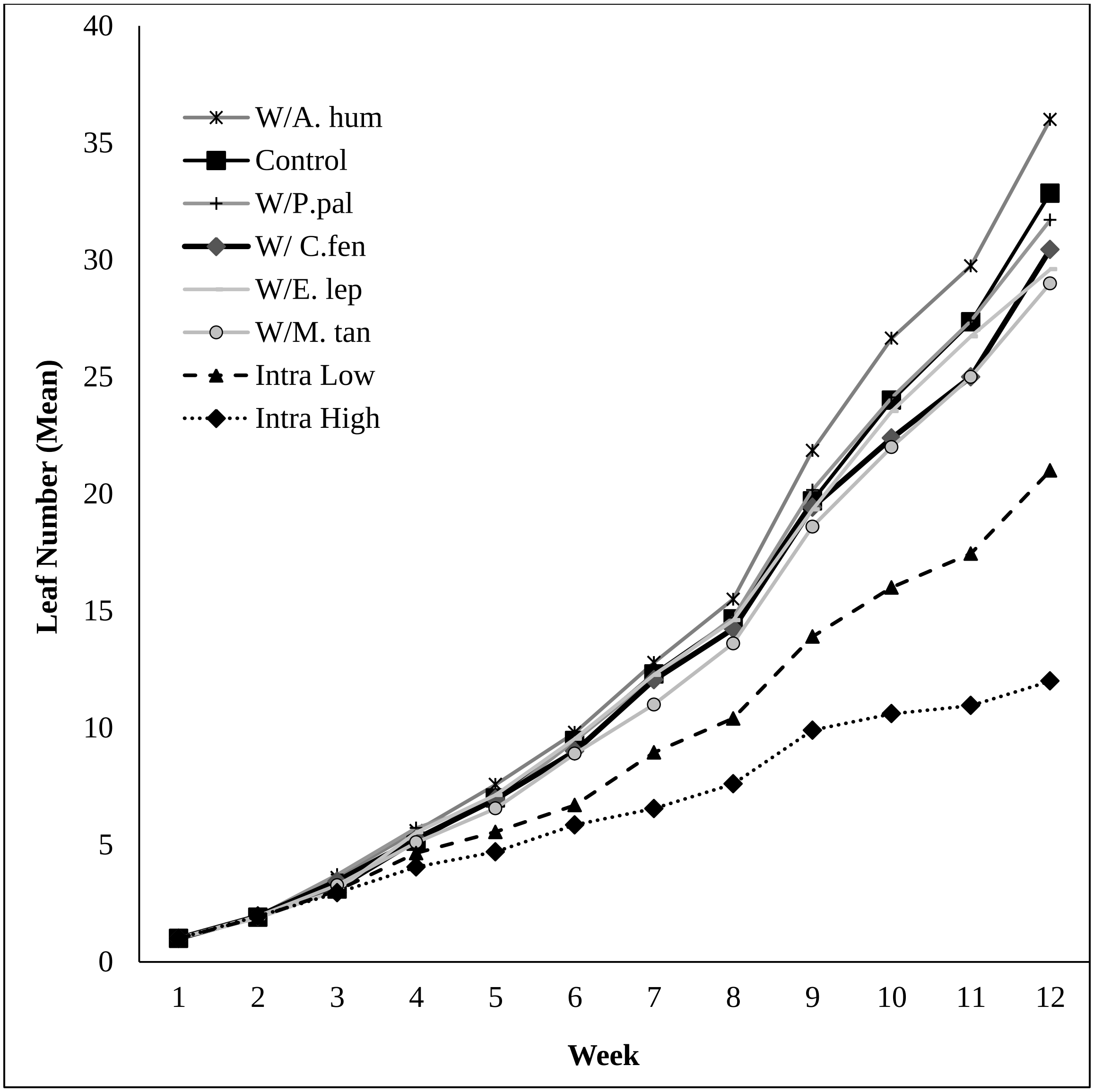
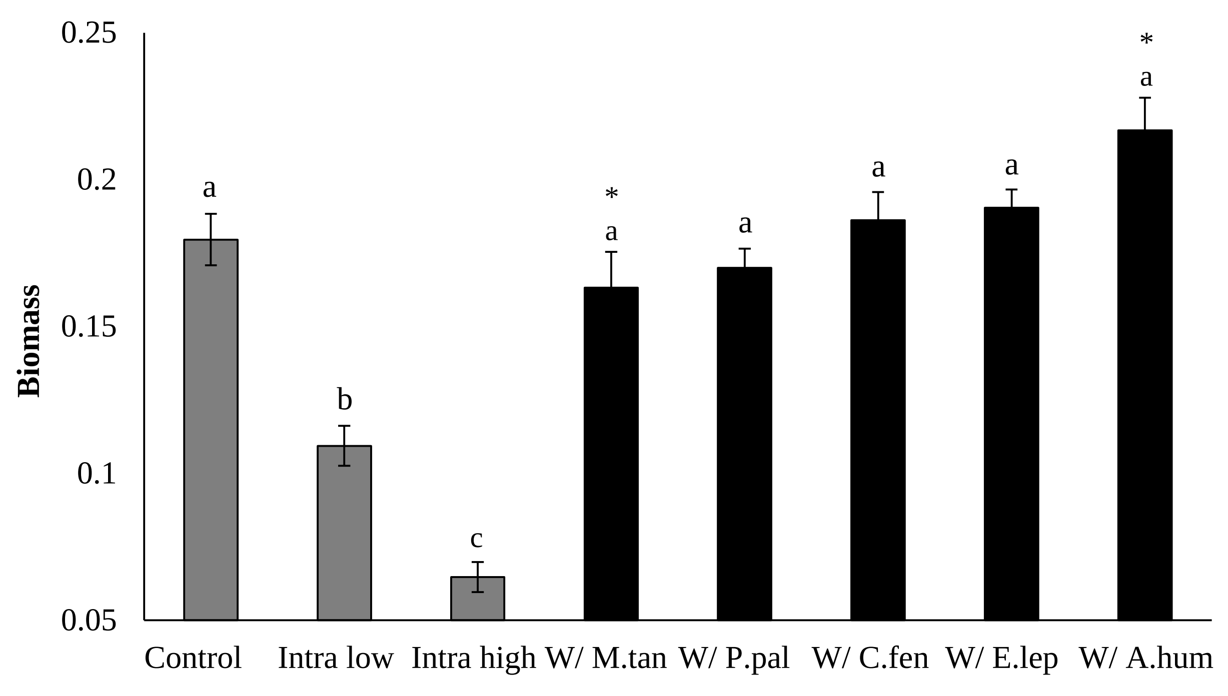


Figure 7: Mean leaf number of *Bromus tectorum* focal plants growing with *B. tectorum* and forb neighbors. Competition and week, and the interaction between these variables had a significant effect on leaf number (p<0.0001). Forbs species had differing effects on *B. tectorum* leaf number (p<0.0001). Analyses performed on square-root transformed data. (Error bars not shown).



F**igure 8:** Mean aboveground biomass of *Bromus tectorum* focal plants growing with *B. tectorum* (grey bars) and forb (black bars) neighbors (grams, mean ± 1 SE). Analyses performed on square-root transformed, relativized data. Different letters indicate significant ($p<0.05$) differences in Tukey's HSD tests. Biomass of interspecific treatments did not differ from the control in post-hoc tests, however the mean final biomass of *B. tectorum* plants growing with *M. tanacetifolia* differed significantly from those growing with *A. humistratus*.

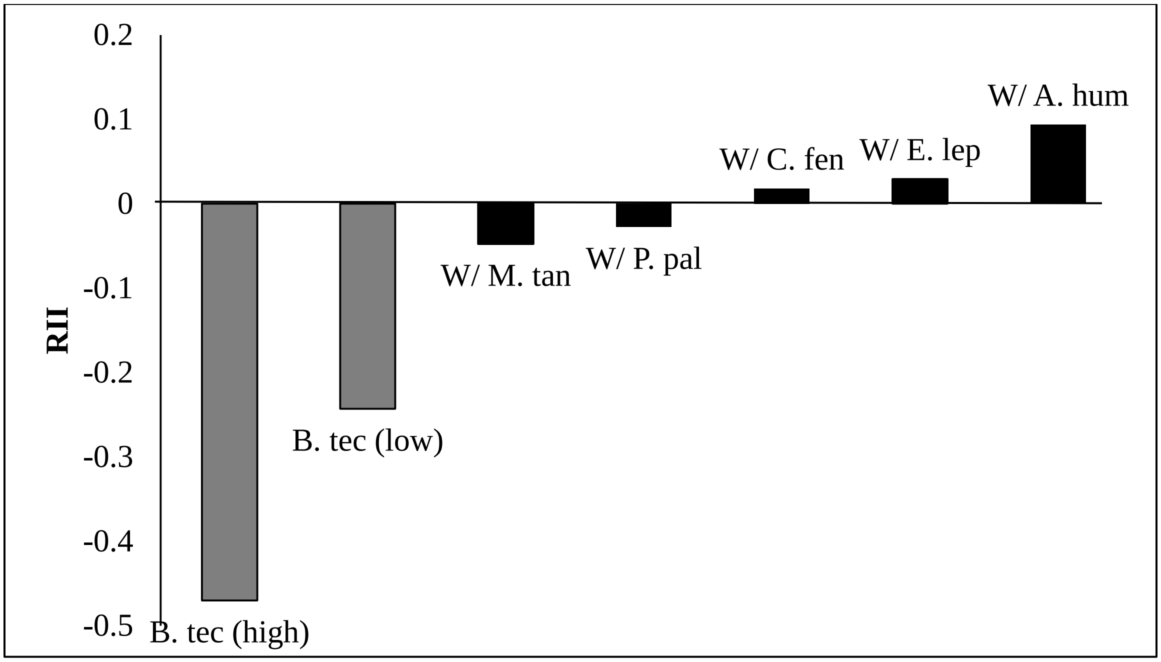


Figure 9: RII (relative interaction index) of *Bromus tectorum* plants growing with *B. tectorum* (grey) and forb neighbors (black). Forb data are from low-density interspecific treatments. Statistical tests were not performed on these data, but they are included to show the interaction between *B. tectorum* and interspecific and intraspecific neighbors.

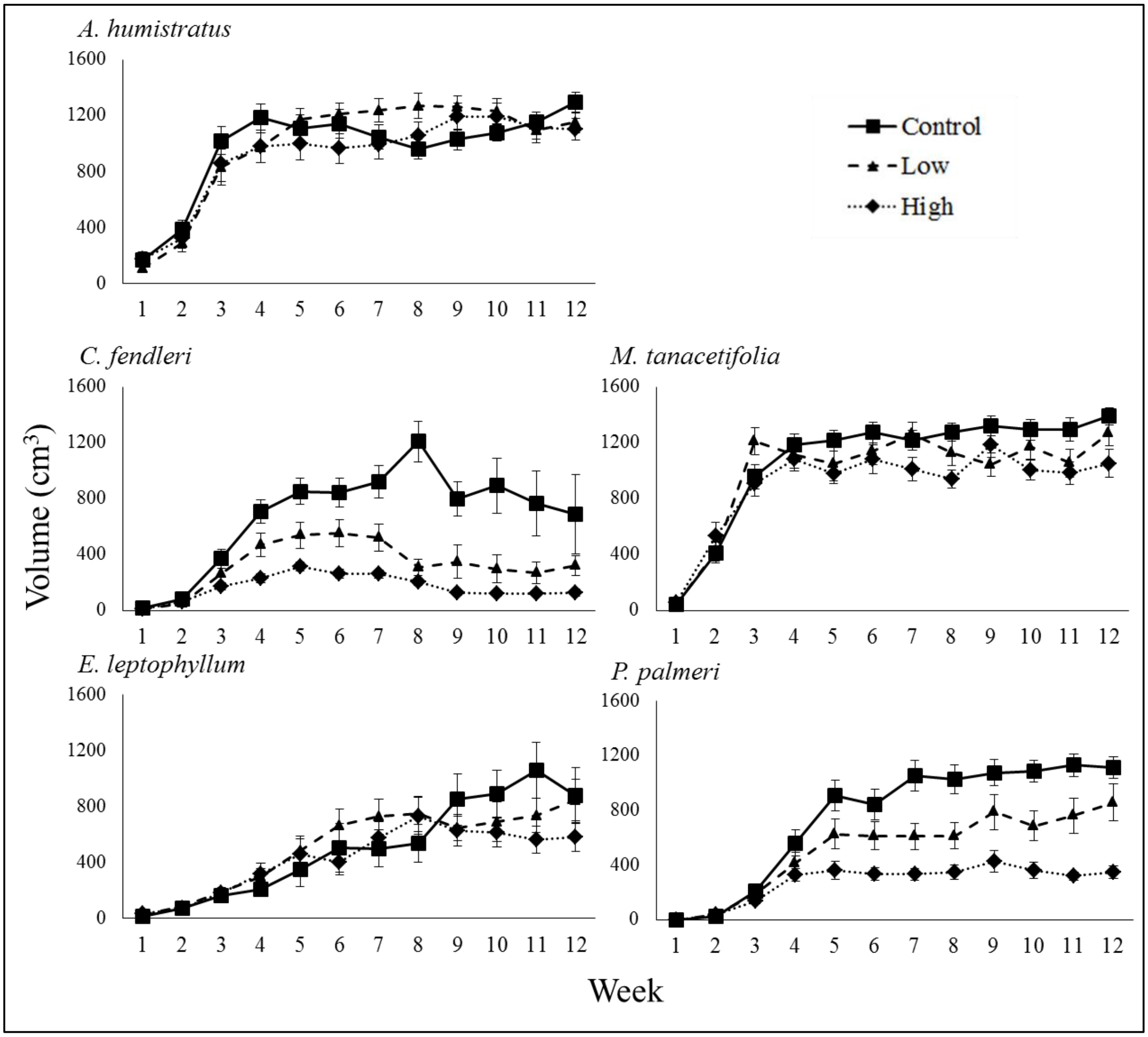


Figure 10: Volume of forbs under low- and high-density *B. tectorum* competition, measured over twelve weeks. Competition significantly decreased ($p<0.05$) volume in all forb species.

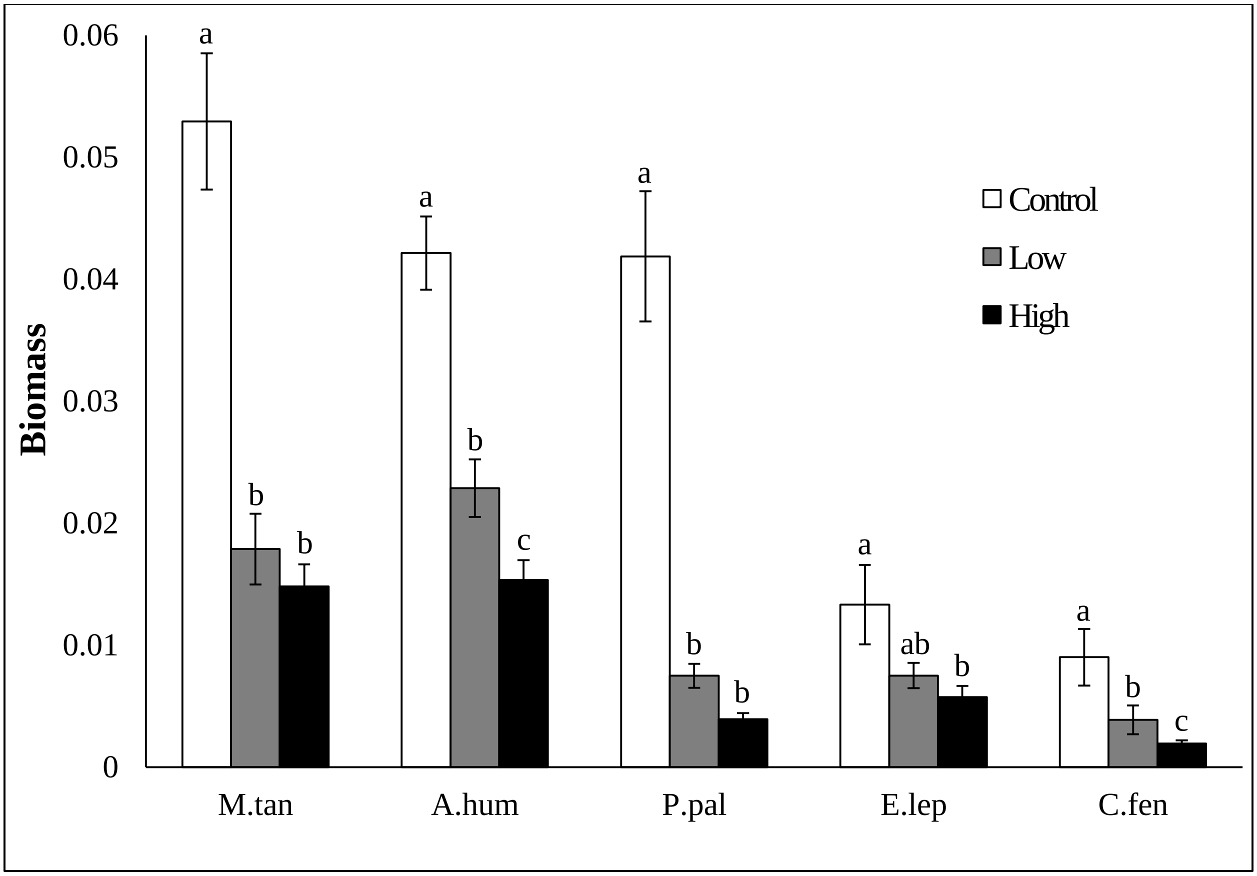


Figure 11: Mean aboveground biomass of forbs growing under low- and high density *Bromus tectorum* competition (grams, mean ± 1 SE). Analyses performed on square-root transformed data. Different letters indicate significant differences ($p<0.05$) in within-species Tukey's HSD tests.

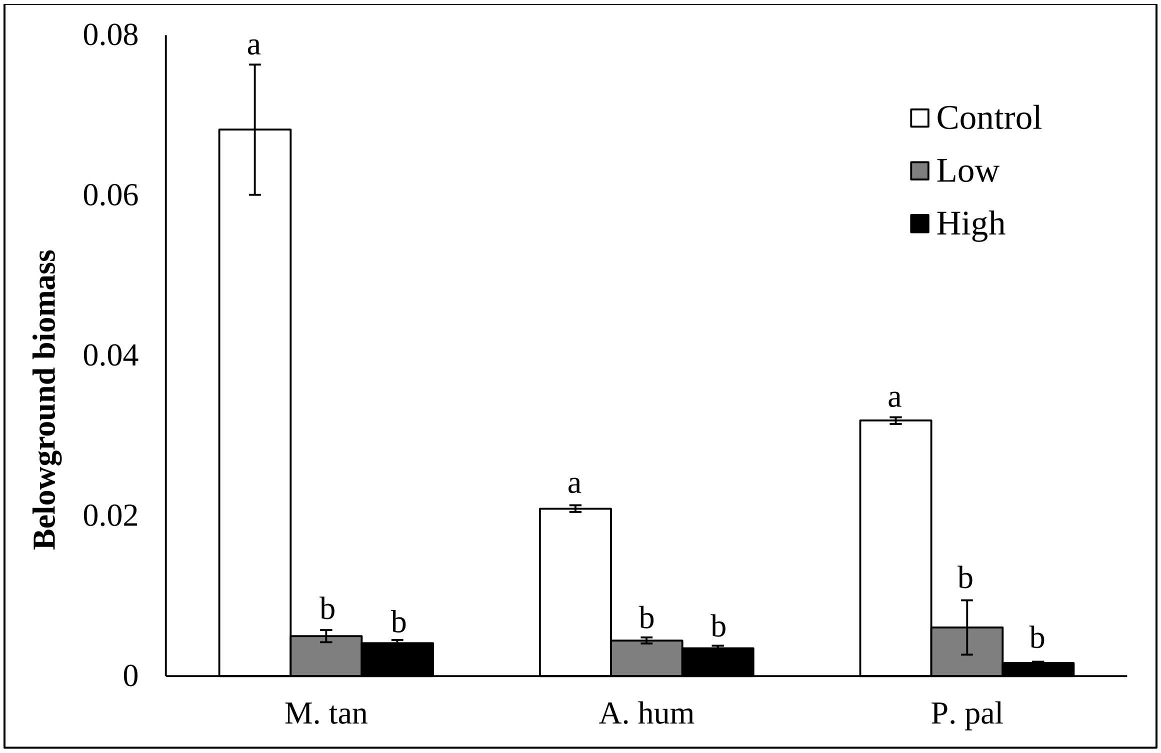


Figure 12: Mean belowground biomass of forbs growing under low- and high-density *Bromus tectorum* competition (grams, mean ± 1 SE). Analyses performed on log transformed data. Different letters indicate significant differences ($p<0.05$) in within species Tukey's HSD tests.

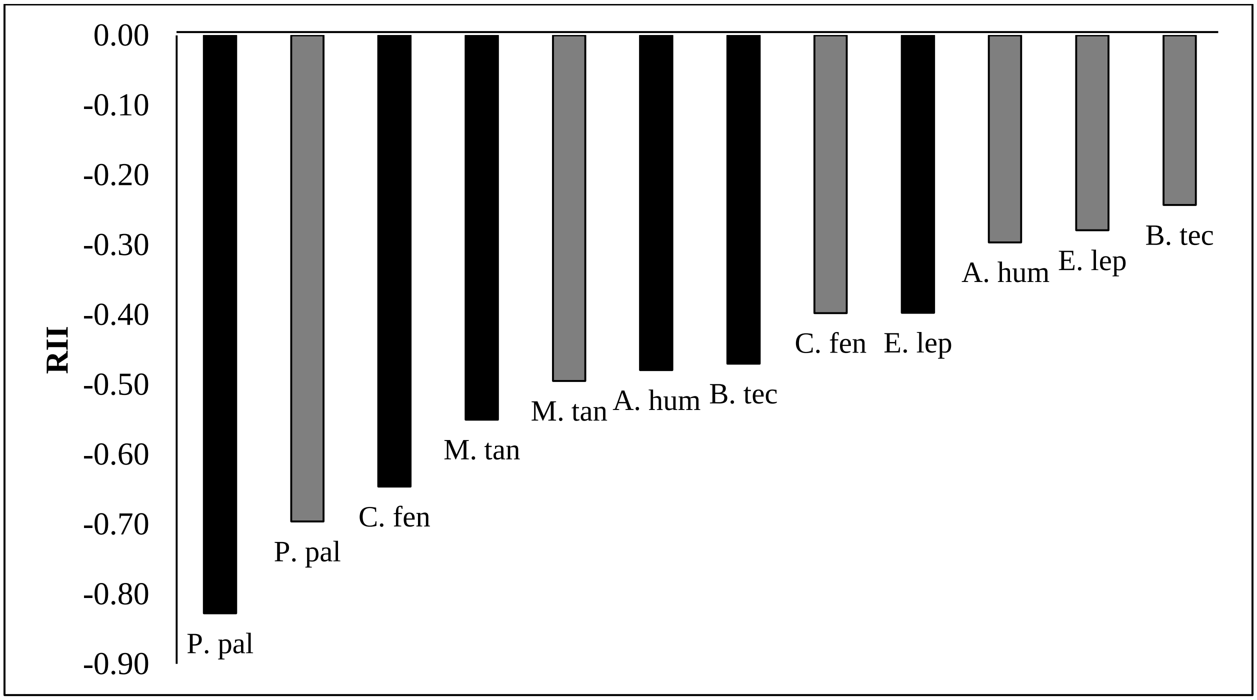


Figure 13: RII (relative interaction index) of focal plants growing under low- (grey) and high- (black) *Bromus tectorum* competition. Statistical tests were not performed on these data, but they are included to show the interaction between target plants and *B. tectorum* neighbors. All plants were suppressed by low and high densities of *B. tectorum*.

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Appendix 1: Forb growth curve data

Table A1: Model selection for forb growth curves

	linear		**exponential**		**logistic**		**Von Bertalanffy**	
Species	AICc	weight	AICc	weight	AICc	weight	AICc	weight
A. humistratus								
Control	172.3	0.00005	173.5	0.00003	152.7	0.984	161.0	0.016
Low	173.6	0.011	176.1	0.0003	142.5	0.596	153.8	0.394
High	166.5	0.0001	169.2	0.00003	148.6	0.815	151.6	0.185
C. ambigua								
Control	173.7	0.0008	175.8	0.0003	159.6	0.950	165.6	0.050
Low	163	0.011	163.4	0.009	154.3	0.855	158.1	0.125
High	147.9	0.098	148.0	0.097	143.7	0.804	-	-
E. leptophyllum								
Control	146.2	0.631	156.8	0.0032	148.0	0.264	150.0	0.101
Low	153.4	0.0002	160.8	5.74x10^{-6}	136.7	0.995	147.4	0.005
High	153.6	0.003	159.1	0.0002	141.9	0.936	147.4	0.061
M. tanacetifolia								
Control	173.6	6.87x10^{-9}	176.2	1.90x10^{-9}	136.1	0.993	145.2	0.007
Low*								
High	171.3	1.25x10^{-6}	172.5	6.72x10^{-7}	144.5	0.834	147.7	0.166
P. palmeri								
Control	165.8	7.0x10^{-6}	172.9	2.0x10^{-7}	142.1	0.999	156.0	0.0010
Low	154.0	0.011	161.1	0.0003	146.0	0.600	146.8	0.400
High	148.1	4.05x10^{-6}	151.0	9.52x10^{-7}	123.3	0.999	136.8	0.001

Table A2: Asymptote and time to inflection point calculated from logistic models

Species	Asymptote (Volume)	Time to inflection point (Weeks)
A. humistratus		
Control	1112.7	2.2
Low	1204.1	2.6
High	1079.6	2.4
C. ambigua		
Control	875.0	3.2
Low	402.6	2.7
High	196.4	2.2
E. leptophyllum		
Control	1061.3	6.9
Low	743.1	4.3
High	615	4.1
M. tanacetifolia		
Control	1285.0	2.4
Low		
High	1032.6	2.0
P. palmeri		
Control	1070.4	4.0
Low	720.2	3.8
High	355.4	3.1

Appendix 2: R Code for statistical analysis

Germination Experiments

#Effects of species on viability

```
Via.M1<-aov(via$PercentFilled~via$Species.Code)

Via.M2<-aov(via$PercentFilled~1)

anova(Via.M1,Via.M2)

TukeyHSD(Via.M1)
```

 # Determining significance of factors on percent germination of viable seed (final percents, after 28 days)

```
Germ.aov.a<-
aov((sqrt(GV$PercentOfViable)~(GV$SpeciesCode+GV$ColdStrat+GV$Tray+GV$PlateLetter
+GV$Temp+GV$SpeciesCode*GV$ColdStrat+GV$Tray+GV$SpeciesCode*GV$Temp+GV$C
oldStrat*GV$Temp)))
Summary(Germ.aov.a) #model simplification to identify significant effects and interactions.
```

#Next, made individual models for each species to determine effects of cold stratification, scarification and temperature on percent germination of viable seed (example shown below for *A. humistratus*):

```
MFD.a<-
aov(sqrt(PercentOfViable)~as.factor(Scarified)+as.factor(ColdStrat)+as.factor(Temp)+as.factor(
ColdStrat)*as.factor(Temp)+as.factor(Scarified)*as.factor(ColdStrat)+as.factor(Scarified)*as.fac
tor(Temp), data = GV[GV$SpeciesCode == "FD",])

## Model simplification by dropping terms to identify significant effects and interactions.

MFD.e<-
aov(sqrt(PercentOfViable)~as.factor(Scarified)+as.factor(ColdStrat)+as.factor(Scarified)*as.fact
or(ColdStrat), data = GV[GV$SpeciesCode == "FD",]) #final model
TukeyHSD(MFD.e)
```

Competition Experiment I

#Effects of focal species on emergence day

```
Emer.aov<-aov(sqrt(focal$EmergenceDay)~focal$Species)

TukeyHSD(Emer.aov)
```

#Effects of factors on cheatgrass leaf number (growth)

```
CG.leaf.a<-lme(sqLeafNumber~as.factor(CompType)+as.factor(Week)+as.factor(CompType)*as.factor(Week), random = ~ 1|Tray, data = CGG)
```

```
anova(CG.leaf.a)
```

##used linear mixed effects model on leaf number data. Also analyzed cheatgrass growing in interspecific, mixed, and intraspecific treatments separately (example below):

```
CG.leaf.il<-lme(sqLeafNumber~as.factor(Neighbor)+as.factor(Week)+as.factor(Neighbor)*as.factor(Week), random = ~ 1|Tray, data = CGG[CGG$CompType == "InterLow",])
```

#Determining effects of factors on cheatgrass biomass

```
CG.bio.a <-lm(sqrt(RelativeAbMass)~CompType+Tray+Neighbor+CompType*Neighbor+CompType*Tray+Neighbor*Trat, data = CG)
```

##Used model simplification (dropping terms) to determine significant effects

#Determining effects of specific treatments on cheatgrass biomass.

##Created “levels” with different treatments to determine if, for instance, individual forb species should be kept separate or “lumped” in the final model (example below).

```
M2<-lm(sqrt(CGComp$RelativeAbMass)~(as.factor(CGComp$Treat)+CGComp$Tray)) #Full model with all treatments separate.
```

```
ForTog<-factor(CGComp$Treat) #creating a list of all interspecific low density treatments
```

```
levels(ForTog)
```

```
levels(ForTog)[c(2,6,8,10,12)]<-“InterLow”
```

```
M3<-lm(sqrt(CGComp$RelativeAbMass)~(ForTog+CGComp$Tray)) #M3 has all "interlow" (1 CG 1 forb) lumped
```

```
anova(M2,M3) #M2 and M3 were different, so forb species were kept separate in the overall model. This type of analysis was also performed on all intraspecific treatments (sig.) and all “mixed” treatments (interintra, not sig.). At the end, a tukey’s HSD test was performed on the model.
```

```
M4a<- aov(sqrt(CGComp$RelativeAbMass)~(IITog))
```

```
TukeyHSD(M4a)
```

Competition Experiment II

#Comparison of volume of forbs using linear mixed effects model

```
Forb.lme<-lme(sqrt(as.numeric(ElliVol))~Species+CompType+Week+Species*Week+Species*CompType+Week*CompType+Species*Tray, random=~1|Tray, data = GF)
```

#Next, did a mixed effect model on each species to see if competition treatments differed from one another.

```
CR.lme<-lme(sqrt(as.numeric(ElliVol))~as.factor(CompType)+as.factor(Week)+as.factor(Week)*as.factor(CompType),random=~1|Tray, data = F1G)
```

#Model selection for forb growth curves

##Compared fit of linear, exponential logistic and von Bertelanffy models to means of forb volume data. Used AIC weights to determine best model fit.

```
## Used AICc (in qpcR package) instead of AIC for smaller sample sizes.
## Added several pacakges for von Bertelanffy analysis
##Example below for A. humistratus control data (FDC).

####Linear Model####
FDC.lm<-lm(FDC$Vol~FDC$Week)
summary(FDC.lm)
AICc(FDC.lm)

#####Logarithmic Model#####
FDVol<-FDC$Vol
FDWeek<-FDC$Week
FDC.log<-nls(FDVol~SSlogis(FDWeek, Asym, xmid, scal))
AICc(FDC.log)

######Von Bertelanffy Model ######

install.packages(c("FSA", "ncstats"))
library(FSA)
install.packages("nlstools")
library("nlstools")
install.packages("FSA")
vb<-vbStarts(Vol~Week, data = FDC)
unlist(vb) # to get starting value estimates for von B function.
```

```
vbTypical <- Vol~Linf*(1-exp(-K*(Week-t0)))
FDC.vb<- nls(vbTypical,data=FDC,start=vb)

overview(FDC.vb)
AICc(FDC.vb)

#######Exponential Function##########

FDC.exp<- nls(Vol ~ I(exp(1)^(a + b * Week)), data = FDC, start = list(a = 0,b = 1))
summary(FDC.exp)
AIC(FDC.exp)

####logistic is the best fit for FD, control.

###To get AIC weights, make a list of all AICc & use:
AIC.PPL<-c(AICc(PPL.lm), AICc(PPL.exp), AICc(PPL.log), AICc(PPL.vb))
akaike.weights(AIC.PPL)
```

#Determining significance of factors on relativized biomass of forbs

```
Forb.bio.a <-
lm(sqrt(RelativeAbMass)~Species+CompType+Tray+Species*CompType+Species*Tray+Comp
Type*Tray, Data = Forbs) #aboveground

Forb.below.a <-
lm(log(RelBelow)~Species+CompType+Tray+Species*CompType+Species*Tray+CompType*
Tray, data = Bel) #belowground

##Used model simplification (dropping terms) to determine significant effects (note, in some
cases, couldn’t have all interaction terms in one model due to “zero at backsolve” issues & had to
include interaction terms in different models, and do anova on these models as part of model
simplification).
```

#Determining effects of specific treatments on forb biomass

##Conducted separate tests on each species to determine the effects of competition type on biomass (example below for *A. humistratus*).

```
FD.above<-aov(sqrt(F2$RelativeAbMass)~F2$CompType)
summary(FD.above)
TukeyHSD(FD.above)

FD.below<-aov(log(RelBelow)~CompType, data = BF2)
summary(FD.below)
TukeyHSD(FD.below)
```