Can native annual forbs reduce *Bromus tectorum* biomass and indirectly facilitate establishment of a native perennial grass?

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ARTICLE INFO

ABSTRACT

Restoration is challenging in systems invaded by competitive, disturbance oriented plants, but greater success may be achieved by mimicking natural successional processes and including disturbance-oriented natives in a seed mix. We asked whether seven native annual forbs from the Great Basin Desert, USA, were capable of reducing biomass of the invasive annual grass *Bromus tectorum*, and if competition between forbs and *B. tectorum* could indirectly promote establishment of the native perennial grass *Elymus multisetus*. Some annual forbs were highly competitive with *B. tectorum*. For example, in a field experiment, *Amsinckia tessellata* reduced *B. tectorum* biomass by 97%, and *Amsinckia intermedia*, *A. tessellata*, and *Descurainia pinnata* reduced seed output between 79 and 87%. Adding native forbs to interacting *B. tectorum* and *E. multisetus* increased *E. multisetus* seedling growth rates in the greenhouse, but had no significant positive effects in the field. Strong suppressive effects of native forbs on *B. tectorum* might lead to indirect enhancement of perennial native species in subsequent years. While native colonizing species are often themselves considered "weedy", they may be able to serve a transitory role in community recovery, allowing restoration in invaded systems to progress towards more desirable vegetation.

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1. Introduction

Restoration activities attempt to rebuild native community diversity, structure, and function, often from challenging starting points. A basic ecological understanding of plant community succession, assembly, and recovery after natural disturbance has led to management methods directly based on successional theory and plant competition (e.g. Westoby, 1980), and the recognition of the role of nexus species (species which strongly influence community composition during early successional stages, but are absent in later successional communities) in plant community development (Lockwood and Samuels, 2004). There is a growing literature supporting facilitation as an important component of plant interactions and seedling establishment (Callaway, 1995; Moro et al., 1997; Pugnaire et al., 1996). Facilitation, wherein an individual plant benefits from interacting with other plants, can be useful

when restoring degraded communities. Studies have demonstrated that the presence of nurse plants (larger, established plants that ameliorate growing conditions for younger plants) can increase establishment of desired species by improving microclimatic conditions (Armas and Pugnaire, 2009; Goergen and Chambers, 2011) or reducing herbivory (Soliveres et al., 2011).

Although modification of the abiotic environment by nurse plants may improve restoration success in some instances, in other situations where barriers to native recovery involve strong competitive interactions with invasive species, amelioration of the abiotic environment alone may not be sufficient to establish native species. In these situations, indirect facilitation, where one species improves the performance of a target plant by suppression of a shared competitor (Levine, 1999; Miller, 1994), may have potential to increase restoration success. Although less studied than cases of direct facilitation, indirect facilitation has been observed in a variety of systems. For example, the presence of *Arthrocnemum* buffered the competitive effects of *Monanthechloe* on several annual species in a salt marsh community (Callaway and Pennings, 2000). Similarly, competition by *Retama* in Mediterranean shrubland reduced the herbaceous understory vegetation, indirectly increasing oak seedling establishment (Cuesta et al., 2010), and in a greenhouse study, competitive pressure by native annual forbs

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with invasive species has been shown to improve performance of perennial species native to North American grasslands (Perry et al., 2009). The potential for indirect interactions to improve restoration may be important for restoration of diverse native communities in systems dominated by very competitive invasive species.

Arid rangeland ecosystems are undergoing drastic changes worldwide (Chambers and Wisdom, 2009; Verstraete and Schwartz, 1991). Pressures from a long history of grazing coupled with species invasions and climate change has led to dramatic changes in land cover. These changes are exemplified within arid rangelands of the Great Basin in the Western US, where more than 40 000 km^2 of shrubland have been converted to annual communities dominated primarily by the exotic annual grass *Bromus tectorum* (Bradley and Mustard, 2006). Increased fire frequency and intensity combined with reduced native seedbanks result in communities that often do not recover without intervention (Allen et al., 2008). After fires, vast areas of Western US rangelands are reseeded in an attempt to return communities to a desired state. Unfortunately, these large-scale restoration seedings often have only limited success (Beyers, 2004; James et al., 2011), due in part to the widespread presence of *B. tectorum*. This species is an excellent competitor for water and soil nutrients, produces abundant seeds, and displays earlier spring growth compared to native perennial grass seedlings (James, 2008). Restoration efforts are often unsuccessful because at the seedling stage, perennial grasses are not effective competitors against *B. tectorum* (Booth et al., 2003; Humphrey and Schupp, 2004).

Greater success may be achieved with seed mixes that mimic natural succession processes in Great Basin systems, which include native annuals as a key component of the post-disturbance community (Boyd and Svejcar, 2011; McLendon and Redente, 1990; Young and Evans, 1978). Native annual forbs are phenologically similar to *B. tectorum* and therefore may use similar resource pools (Forbis, 2010). Some native annual forbs have been shown to be highly competitive with annual grasses (including *B. tectorum*) in the Mojave desert (Abella et al., 2012). Competitive pressure by native annual forbs may indirectly improve establishment of native perennial grass seedlings (which are typically thought to use resources later in the growing season, e.g. Kulmatiski et al., 2006) by reducing early resource extraction by *B. tectorum*. If native annual forbs can limit *B. tectorum* growth and vigor without producing the same reduction in soil resources or changes in soil properties typically seen under *B. tectorum* monocultures, native annual forbs may be able to indirectly facilitate establishment by more desirable native perennial species (e.g. Perry et al., 2009, Fig. 1). Alternately, it is possible that the presence of native annual species could facilitate exotic annuals. Perennial nurse plants, which are associated with islands of fertility in desert systems (Garner and Steinberger, 1989) have been observed to facilitate the growth of exotic

annual grasses (e.g. Abella and Smith, 2013). Native annuals might also facilitate annual grass growth in shrub interspaces by ameliorating early growing season stress for seedlings, a process that has been observed between interacting annuals (e.g. Ariza and Tielborger, 2012).

We used greenhouse and field experiments to address two questions: (1) What are the direct effects of native annual forbs on *B. tectorum* performance? (2) What are the direct and indirect effects of native annual forbs on perennial grass seedling performance? To address the first question, we selected a suite of annual forbs that we observed growing in disturbed environments where *B. tectorum* was present, and grew these plants with *B. tectorum* in greenhouse and field conditions. To address the second question, we grew *B. tectorum* and native annual forbs in combination with the native perennial grass *Elymus multisetus*, an early successional species likely to establish at the same time as annual forbs under natural successional processes (Goergen and Chambers, 2009). *E. multisetus* and the closely related *Elymus elymoides* are species commonly used in restoration seed mixes because they are able to regenerate well from seed given adequate precipitation (Young et al., 2003) and compete well with *B. tectorum* once established (Goergen et al., 2011; Humphrey and Schupp, 2004).

2. Methods

2.1. Greenhouse experiments

We conducted two greenhouse experiments to examine the potential for native annual forbs to improve restoration of invaded rangelands, with seeds collected from semi-disturbed sites (affected by fires in the last 3–5 years, and experiencing moderate to high levels of grazing by livestock and feral horses) near Reno, NV, and Bordertown, CA, USA. One experiment was conducted to determine the effect of two annual forbs that grow in *B. tectorum* invaded communities, *Amsinckia tessellata* and *Mentzelia veatchiana*, on the performance of *B. tectorum*. While both forbs co-occur with *B. tectorum*, germination strategies are somewhat different. *A. tessellata* is capable of germinating in the fall without prolonged cold stratification, while *M. veatchiana* germinates best after a cold stratification, indicating a germination strategy typical of a spring emerging annual (Forbis, 2010). Individual target *B. tectorum* plants were planted with low (4) and high (8) competitors in the following combinations: (1) 4 *A. tessellata* + 1 *B. tectorum*; (2) 4 *M. veatchiana* + 1 *B. tectorum* (3) 4 *B. tectorum* + 1 *B. tectorum*; (4) 4 *A. tessellata* + 4 *M. veatchiana* + 1 *B. tectorum* (5) 8 *A. tessellata* + 1 *B. tectorum* (6) 8 *M. veatchiana* + 1 *B. tectorum* (7) 8 *B. tectorum* + 1 *B. tectorum*. Single *B. tectorum* were also grown as controls. Each treatment was replicated 15 times for a total of 120 pots.

In early spring 2009, ungerminated *B. tectorum* and *A. tessellata* seeds and germinated *M. veatchiana* seeds (germinated after experiencing a cold, wet stratification) were planted into deep tree pots (10 cm × 10 cm length and width; 36 cm depth, 2.83 L, Stuewe & Sons, Tanagent OR) filled with a Nevada topsoil/sand/compost mix, with no chemical fertilizers added. Pots were arranged into blocks containing one replicate of each treatment and grown in the USDA ARS greenhouse located at the University of Nevada, Reno. Forb seed availability was limited for this experiment, and overplanting was not possible. Final plant numbers for *A. tessellata* and *M veatchiana*, respectively, were 3.8 ± 0.1 standard error (SE) and 2.6 ± 0.2 SE in the 4 seed treatments and 7.1 ± 0.3 SE and 5.3 ± 0.6 SE in the 8 seed treatments; *B. tectorum* had 3.2 ± 0.2 SE and 7.5 ± 0.3 SE plants in the 4 and 8 seed treatments. Plants were watered 1–2 times per week, allowing pots to dry between watering, and harvested after approximately 3 months. Above-ground biomass of each target plant was harvested, separated into
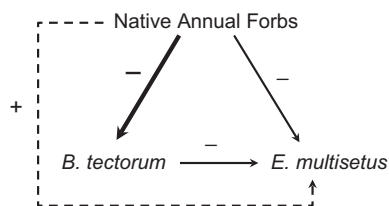

Fig. 1. Conceptual diagram and structural equation model depicting how the presence of native annual forbs could promote restoration of *B. tectorum* invaded rangelands via indirect facilitation (modified from Brooker et al., 2008). Solid lines represent direct effects, and the dashed line represents an indirect effect. In this diagram, we hypothesize that annual forbs will negatively affect *B. tectorum* more strongly than they affect *E. multisetus*, which results in an indirect positive benefit for *E. multisetus* when grown with both *B. tectorum* and annual forbs.

vegetative and reproductive structures, dried at 60 °C to a constant mass, and weighed. Not all of the *B. tectorum* flowered during the course of the experiment, but under both greenhouse (Goergen et al., 2011) and field conditions, seed production is highly correlated with biomass production in this annual grass. Seed production was estimated using the equation: seed production = (82.698*vegetative biomass) + 69.505, which was derived using linear regressions between seed production and dry biomass in a subset of 20 pots.

We used an additional greenhouse experiment to determine if the presence of native annual forbs could improve establishment of the native perennial grass *E. multisetus* in the presence of *B. tectorum*. Four commonly occurring native annual forbs were planted with target *E. multisetus* individually (*A. tessellata* or *M. veatchiana*) or as a mix (*A. tessellata*, *M. veatchiana*, *Cryptantha pterocarya*, and *Eriastrum sparsiflorum*). Target *E. multisetus* seedlings were planted with 2 levels of neighbors (4 or 8 seeds) in the following combination: (1) 4 annual forbs + 0 *B. tectorum* + 1 *E. multisetus*; (2) 8 annual forbs + 0 *B. tectorum* + 1 *E. multisetus*; (3) 4 annual forbs + 4 *B. tectorum* + 1 *E. multisetus*; (4) 0 annual forbs + 4 *B. tectorum* + 1 *E. multisetus*; (5) 0 annual forbs + 8 *B. tectorum* + 1 *E. multisetus*. Pots used in analysis had a full compliment of species present at the target number, obtained by planting additional seeds of any seedlings that failed to emerge during the first few weeks of the experiment. Single *E. multisetus* were also grown as controls. Each treatment was replicated 20 times for a total of 240 pots.

In February 2009, ungerminated grass and germinated forb seeds were planted into tree pots (10 cm × 10 cm × 36 cm) filled with a Nevada topsoil/sand/compost mix with no additional fertilizers. Pots were arranged into blocks with one replicate per treatment and watered 1–2 times per week. The number of green leaves on target *E. multisetus* plants was counted 9, 12, and 15 weeks after planting. From these numbers growth rate was estimated using the equation [Leaves$_{time\ 2}$ − Leaves$_{time\ 1}$]/time 2 − time 1. Growth rate was calculated between weeks 9–15, and between weeks 12–15, to determine if growth rate changed over time. Growth rates within treatments were similar between the two measures, so an overall growth rate from week 9–15 ([green leaves$_{wk\ 15}$ − green leaves$_{wk\ 9}$]/38 days) was used for final analyses. Plants were harvested in June 2009, when annual species were becoming senescent. Above-ground biomass of each target plant was harvested and dried at 60 °C to a constant mass and weighed.

2.2. Field experiment

To determine if similar results would be obtained under field conditions, we conducted a common garden experiment in Reno, NV. Five commonly occurring native annual forbs were examined (*A. tessellata*, *Amsinckia intermedia*, *M. veatchiana*, *Blepharipappus scaber*, and *Descurainia pinnata*). Annual forbs were chosen based on performance in the greenhouse experiments, knowledge of their dormancy/germination strategies (Forbis, 2010), and availability of seeds. Because we did not find a significant effect of annual forb number in greenhouse experiments, we used a single, larger number of competitors more comparable to field conditions for this study. Seed viability was assessed for each species using tetrazolium tests following the protocol of Forbis (2010), and seeding rates were adjusted for each species to produce 100 viable seeds per treatment. Target *E. multisetus* or *B. tectorum* seedlings were grown in the following combinations: (1) 100 viable seeds of a single annual forb + 1 target *E. multisetus* or *B. tectorum*; (2) 100 viable seeds of a single annual forb + 100 viable seeds of *B. tectorum* + 1 target *E. multisetus* or *B. tectorum*; or (3) 100 viable seeds of *B. tectorum* + 1 target *E. multisetus* or *B. tectorum*. Plots with a single *E. multisetus* or *B. tectorum* seed were also planted as

controls. Each treatment was replicated 10 times for a total of 240 plots.

Seeds of all species were sown into field plots (0.25 m × 0.25 m) on the University of Nevada, Reno (UNR) campus in October 2009. Average annual precipitation at the site between 2000 and 2009 was 182 mm (the Western Regional Climate Center's Reno, UNR Campus weather station is located directly adjacent to our research plot, www.wrcc.dri.edu). Over the course of this experiment (October 2009–June 2010), the site received ∼150 mm of precipitation. The site is an old-field formerly used for growing alfalfa, with soils classified as Orr sandy loam. Within each plot, seeds were sown in a 0.1 m × 0.1 m area in the center of the plot, with 100 seeds corresponding to a density of 10 000 seeds per m². Plots received only natural rainfall, and other non-planted species were removed by hand. The density of annual forb and *B. tectorum* competitors was counted in mid-March, and the number of green leaves of target *E. multisetus* plants were counted in April, May, and June 2010. Density of competitors was difficult to assess accurately after plants grew larger, so density was not measured in May and June. Plants were harvested in June 2010, when annual species were becoming senescent. Aboveground biomass of each target plant was harvested and placed in one bag and aboveground biomass of competitors was separated by functional group (annual forb or annual grass) and bagged separately. Tissue was dried to a common mass and weighed.

2.3. Data analysis

For the greenhouse experiments, differences in target (*E. multisetus* or *B. tectorum*) aboveground biomass, growth rate (*E. multisetus* only) or seed production (*B. tectorum* only) were analyzed using ANOVA. Analyses were first conducted without the single species pots to test for effects of competitor number (4 or 8 seeds) on target species performance with block as an additional random effect. Because competitor number did not affect target performance in either greenhouse experiment (all $P > 0.05$), final analyses were conducted on the entire dataset without competitor number in the model, but with competitor identity as a fixed effect and block as a random effect. For the field experiment, differences in target aboveground biomass, target growth rates (*E. multisetus* only), annual forb competitor density, and annual forb competitor biomass were analyzed using ANOVA with competitor identity as a fixed factor. Differences among competitor identity were examined using Tukey's HSD tests. In the field experiment, the final biomass of annual forb competitors and *B. tectorum* competitors was assessed across treatments, with a model that included competitor identity and target identity (*E. mulitsetus* or *B. tectorum*), analyzed separately for forb and *B. tectorum* biomass treatments. Additionally, we calculated the percent of total competitor biomass that was *B. tectorum* in the treatments that received seeding from 100 forbs and 100 *B. tectorum*, and used the same model (competitor identity, target identity) to compare *B. tectorum* competitor performance when grown with different annual forbs. All biomass values were transformed with the Box–Cox transformation to meet assumptions of ANOVA.

Increased performance of *E. multisetus* in experiments with *B. tectorum* and annual forbs present, relative to performance in treatments with *B. tectorum* without forbs (e.g. comparing treatments 3 and 4 in the second greenhouse experiment), would be interpreted as evidence of indirect facilitation by annual forbs. This was examined by using a one-sample *t* test to compare *E. multisetus* biomass or growth rate in the presence of forbs with the mean of biomass or growth rate, respectively, for *E. multisetus* when grown with only *B. tectorum*. Analysis was conducted with JMP 8.0.1 (SAS Institute, Cary, North Carolina), and all values are

presented in text and tables are means ± standard error of the means (SE).

Structural Equation Modeling (SEM) was conducted using the program AMOS version 18 as an additional way to examine the indirect effects of annual forbs on establishment of *E. multisetus* in the presence of *B. tectorum*, as well as the direct effects of annual forbs on *E. multisetus* in the greenhouse and field (Grace, 2006; model illustrated in Fig. 1). Direct effects in this analysis are comparable to regression coefficients between continuous variables, describing, for example, the relationship between the biomass of *B. tectorum* and *E. multisetus*, while indirect effects are the relationship between two variables (e.g. annual forb biomass and *E. multisetus* biomass), mediated by additional factors (in our example, *B. tectorum*).

3. Results

3.1. Greenhouse experiments

3.1.1. Direct effect of annuals on B. tectorum performance

The presence of each annual competitor decreased *B. tectorum* vegetative biomass ($F_{4,114} = 19.39$, $P < 0.0001$) and seed production ($F_{4,114} = 23.29$, $P < 0.0001$, Fig. 2). Target *B. tectorum* biomass was lowest in the mixed forb and *A. tessellata* treatments, followed by *B. tectorum*, decreasing by 74–84% relative to growing alone (Fig. 2). *Mentzelia veatchiana* had the smallest effect on *B. tectorum* biomass, reducing it by 47%. Target *B. tectorum* seed production was reduced by 39–69% when grown with native annual forbs, with the greatest reduction observed in the *Amsinckia* and mixed forb treatments, where seed production was reduced to the level observed in the *B. tectorum* competitor treatment (Fig. 2).

3.1.2. Direct effect of annuals on E. multisetus performance

Annuals differed in their competitive effects on *E. multisetus* biomass ($F_{4,177} = 49.31$, $P < 0.0001$, Fig 3a). The presence of all annuals decreased *E. multisetus* biomass relative to monoculture, with biomass reductions ranging from 52% with *M. veatchiana* to nearly 90% when grown with *B. tectorum*. When grown with *A. tessellata* or the forb mixture, biomass decreased by 78–83%, and

Fig. 2. Direct effect of each annual species on target *B. tectorum* biomass and seed production under greenhouse conditions. Values are means and standard errors averaged across density treatments. Capital letters indicate significant differences in seed production and lower case letters indicate significant differences in biomass production between treatments based on Tukey's HSD tests ($P < 0.05$). AMTE = *Amsinckia tessellata*, BRTE = *Bromus tectorum*, MEVE = *Mentzelia veatchiana*. The forb mix included AMTE, MEVE, *Cryptantha pterocarya*, and *Eriastrum sparsiflorum*.

E. multisetus plants grown with only *A. tessellata* were not significantly larger than those grown with *B. tectorum*. The growth rate of *E. multisetus* decreased in the presence of all annuals ($F_{4,177} = 29.05$, $P < 0.0001$), but *E. multisetus* grown with native annual forbs grew significantly faster than those grown with *B. tectorum* (Fig 3b).

3.1.3. Indirect effect of annuals on E. multisetus performance

In the three-way interactions between *E. multisetus*, *B. tectorum*, and annual forbs, annual forb identity affected *E. multisetus* biomass ($F_{3,54} = 4.06$, $P = 0.011$, Fig 3c). Relative to *E. multisetus* growing with 4 *B. tectorum*, the addition of an additional 4 *B. tectorum* or *A. tessellata* or reduced *E. multisetus* biomass by an additional 30–52%. In contrast, the addition of the forb mix did not affect *E. multisetus* biomass, and the addition of 4 *M. veatchiana* seedlings increased *E. multisetus* biomass by 21%, though this increase was not significant (Fig 3c). The presence of annual neighbors affected *E. multisetus* growth rates, and there were differences among species ($F_{3,55} = 4.80$, $P = 0.005$, Fig 3d). Addition of *A. tessellata*, *M. veatchiana*, and the forb mix increased *E. multisetus* growth rates relative to growth rate with *B. tectorum* in the absence of native forbs.

3.2. Field experiment

Forbs differed in density during the March sampling ($F_{4,186} = 26.87$, $P < 0.0001$), with *A. intermedia*, *A. tessellata*, and *M. veatchiana* having significantly higher densities than *B. scaber* and *D. pinnata*. All annual forbs maintained similar densities across all treatments, regardless of whether they were growing with *E. multisetus* or *B. tectorum* targets, or with 100 *B. tectorum* competitors (averaged across all treatments, densities per 0.1 m^2 were: *A. intermedia*, 20.5 ± 1.5; *A. tessellata*, 24 ± 1.7; *B. scaber*, 4.2 ± 0.4; *D. pinnata*, 11.0 ± 1.6; *M. veatchiana*, 23.2 ± 2.4). Forbs also differed in final biomass production ($F_{4,186} = 26.87$, $P < 0.0001$, Table 1A), with *A. intermedia* and *A. tessellata* producing significantly more biomass than other species, followed by *D. pinnata*. *Blepharipappus scaber* and *M. veatchiana* produced significantly less biomass than the other three species, but did not differ in production from each other. All species maintained constant biomass across treatments except *B. scaber*, which had significantly lower biomass when grown with 100 *B. tectorum* than in other treatments (Table 1A).

3.2.1. Direct effects of annuals on B. tectorum performance

As in the greenhouse experiment, growing with other annuals reduced target *B. tectorum* biomass, and species differed in their effect on target *B. tectorum* performance ($F_{6,57} = 7.25$, $P < 0.0001$). Effects in the field were stronger than those observed in the greenhouse, and the greatest decrease in *B. tectorum* biomass occurred when target plants were grown with *A. tessellata* (97%), although *A. intermedia*, *B. tectorum*, and *D. pinnata* also caused large declines in *B. tectorum* biomass (84, 88, and 85%, respectively). The annual forb with the smallest effect on *B. tectorum* was *B. scaber* (38%), and an intermediate effect was observed for *M. veatchiana* (59%). Annual forbs also decreased target *B. tectorum* seed production, showing the same differences in competitive effects observed for biomass ($F_{6,57} = 9.57$, $P < 0.0001$, Fig 4a), with the greatest decrease of *B. tectorum* seed production observed in the presence of *A. tessellata* (87%).

When grown in two-species mixtures of forbs and *B. tectorum* competitors, identity of the forb competitor also influenced target *B. tectorum* biomass ($F_{5,42} = 7.94$, $P < 0.0001$) and seed production ($F_{4,42} = 6.79$, $P = 0.0004$, Fig 4b). Annual forbs reduced target *B. tectorum* seed production by 15–58% relative to *B. tectorum* monocultures, except for *M. veatchiana*, which did not affect target *B. tectorum* seed production, and *B. scaber*, which increased seed
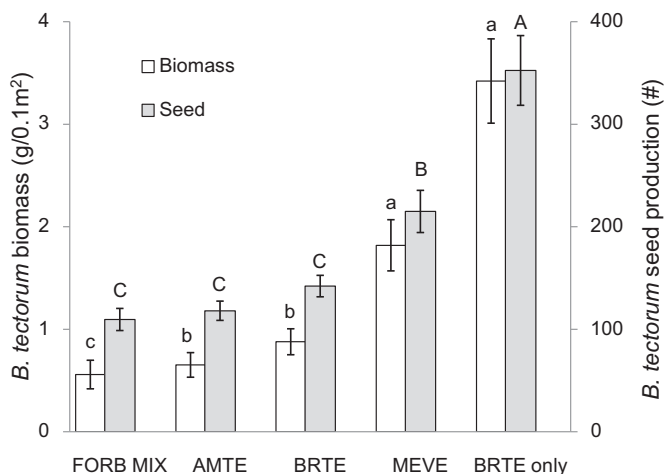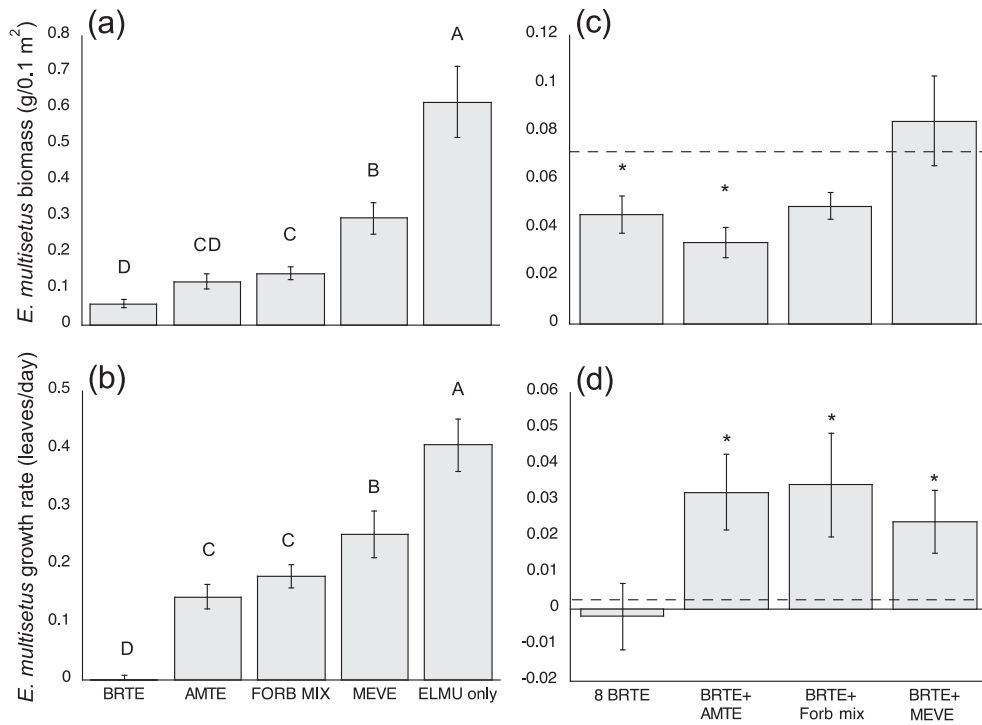
Fig. 3. Direct effect of each annual species on target *E. multisetus* (a) biomass and (b) growth rate and indirect effect on *E. multisetus* (c) biomass and (d) growth rate under greenhouse conditions. Different letters within (a) and (b) indicate significant differences ($P < 0.05$) among treatments based on Tukey's HSD tests. Values are means and standard errors averaged across density treatments. Dotted lines in (c) and (d) indicate *E. multisetus* biomass when grown with four *B. tectorum* (baseline); asterisks indicate significant differences ($P < 0.05$) between each treatment and baseline based on *t*-tests. AMTE = *Amsinckia tessellata*, BRTE = *Bromus tectorum*, ELMU = *Elymus multisetus*, and MEVE = *Mentzelia veatchiana*. The forb mix included AMTE, MEVE, *Cryptantha pterocarya*, and *Eriastrum sparsiflorum*.

production by 27% relative to monocultures of *B. tectorum*, though this increase was not significant (Fig 4b). In addition to affecting the biomass and seed production of *B. tectorum* targets, the identity of annual forbs also affected the total biomass of *B. tectorum* competitors ($F_{5,94} = 18.83$, $P < 0.0001$, Table 1B). In plots planted with

100 viable seeds of *A. tessellata* or *A. intermedia*, the biomass produced from the seeding of 100 viable *B. tectorum* seeds was reduced by 76–91% relative to plots with no annual forbs, and *B. tectorum* was a small percentage (<5.2%) of the total competitor biomass in the *Amsinckia* plots (Table 1B).

3.2.2. Direct effect of annuals on E. multisetus performance

All annual competitors decreased *E. multisetus* biomass and growth rate relative to growing alone ($F_{6,44} = 11.87$, $P < 0.0001$ and $F_{6,44} = 14.33$, $P < 0.0001$ for biomass and growth rate, respectively, Fig 5a,b), with effects again stronger than those observed in the greenhouse. The magnitude of suppression differed among species. The presence of *A. tessellata* and *A. intermedia* decreased *E. multisetus* biomass and growth rate by 97–99%. *Bromus tectorum*, *D. pinnata*, and *M. veatchiana* had intermediate effects on *E. multisetus* biomass and growth rate, while *B. scaber* had the smallest effect on *E. multisetus* growth rate and did not affect *E. multisetus* biomass (Fig 5a,b).

3.2.3. Indirect effect of annuals on E. multisetus performance

When grown in the presence of *B. tectorum*, forb identity significantly influenced *E. multisetus* biomass ($F_{4,26} = 6.69$, $P = 0.0011$, Fig 5c). Similar to results in the greenhouse, the addition of *M. veatchiana* seedlings increased *E. multisetus* biomass by 71% relative to *E. multisetus* growing with *B. tectorum* only, though this effect was highly variable and non-significant. The addition of *B. scaber* did not affect *E. multisetus* biomass but the additions of *A. tessellata*, *A. intermedia*, and *D. pinnata* decreased *E. multisetus* biomass by 60–95%, with the addition of *A. tessellata* having the greatest negative effect. A similar but non-significant pattern was observed for *E. multisetus* growth rate ($F_{4,26} = 1.53$, $P = 0.23$, Fig 5d).
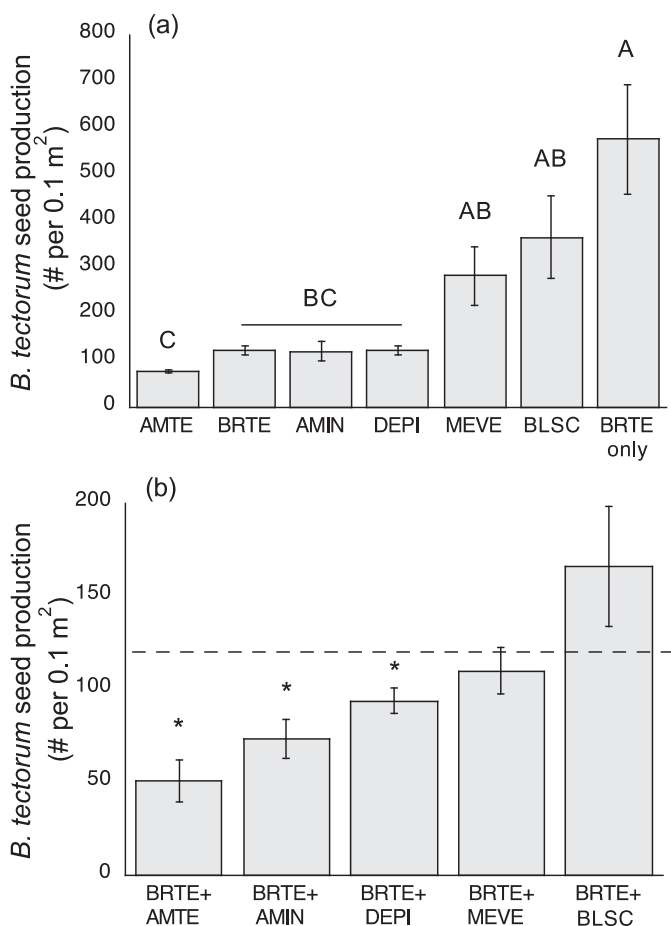
Table 1
Biomass (grams per 0.1 m²) of **A)** annual forb competitors and **B)** *B. tectorum* competitors from field experiment. Values are means and standard errors (in parentheses) of final field biomass of competitors after planting 100 viable seeds. Letters indicate significant differences (within rows, A, or columns, B, from Tukey's HSD comparisons. In **B)**, values are averaged from treatments with and without an additional *E. multisetus* seedling, as the presence of this perennial grass did not affect *B. tectorum* biomass in any of the forb treatments. Percent of total biomass is the percentage of total competitor biomass (BRTE + annual forbs) that is *B. tectorum*. AMTE = *Amsinckia tessellata*, AMIN = *Amsinckia intermedia*, BLSC = *Blepharipappus scaber*, BRTE = *Bromus tectorum*, DEPI = *Descurainia pinnata*, ELMU = *Elymus multisetus*, and MEVE = *Mentzelia veatchiana*.

A) Competing species	1 ELMU + annual forb	1 BRTE + annual forb	100 BRTE + annual forb	1 ELMU + 100 BRTE + annual forb
AMIN	86.9[a] (12.1)	71.6[a] (10.2)	80.4[a] (9.3)	61.6[a] (4.1)
AMTE	75.3[a] (9.2)	77.2[a] (4.9)	89.9[a] (13.3)	86.7[a] (7.8)
BLSC	2.1[ab] (0.3)	5.3[a] (1.2)	4.0[ab] (1.8)	1.0[b] (0.3)
DEPI	53.5[a] (7.6)	47.3[a] (14.4)	28.2[a] (9.0)	21.0[a] (5.6)
MENT	21.5[a] (6.4)	16.4[a] (8.1)	9.3[a] (3.8)	11.6[a] (4.1)

B) Competing species	Biomass of 100 BRTE	% of total biomass
AMIN	3.9[a] (0.9)	5.2[d] (1.1)
AMTE	1.5[a] (0.3)	2.9[d] (1.0)
No forb	16.2[b] (2.4)	–
BLSC	17.3[b] (2.1)	87.0[a] (3.5)
DEPI	11.5[b] (2.2)	40.7[c] (9.3)
MENT	14.7[b] (1.7)	61.1[b] (4.6)

Fig. 4. Under field conditions, the (a) direct effect of annual species on target *B. tectorum* seed production (different letters indicate significant differences, $P < 0.05$, among treatments based on Tukey's HSD tests) and (b) effect of each annual mix on *B. tectorum* seed production. Dotted line in (b) indicates *B. tectorum* seed production when grown in monoculture (baseline). Asterisks indicate significant differences ($P < 0.05$) between each treatment and baseline based on *t*-tests. AMTE = *Amsinckia tessellata*, AMIN = *Amsinckia intermedia*, BLSC = *Blepharipappus scaber*, BRTE = *Bromus tectorum*, DEPI = *Descurainia pinnata*, ELMU = *Elymus multisetus*, and MEVE = *Mentzelia veatchiana*.

3.3. Modeling direct and indirect interactions

In results from the SEM analysis, the direction and magnitude of both direct and indirect effects of native annual forbs on *E. multisetus* performance mirrored ANOVA results in the greenhouse and field experiments. With the exception of *A. intermedia*, direct, standardized effects of native annual forbs on *E. multisetus* growth rate were positive (ranging from 0.128 to 0.352, with the highest value for *M. veatchiana*), whereas effects on biomass were mostly negative (ranging from 0.053 for *M. veatchiana* to −0.318 for *A. intermedia*). Indirect standardized effects were largely positive for both biomass (ranging from 0.018 for *A. tessellata* to 0.400 for *B. scaber*) and growth rate (ranging from 0.014 for the forb mix to 0.470 for *B. scaber*). High variability in responses among the different forb species resulted in non-significant SEM models (results not shown).

4. Discussion

Direct and indirect interactions among species are a main factor directing community development and composition after disturbance, and the use of direct facilitation in restoration is becoming a more common practice in arid systems (Gomez-Aparicio, 2009; Pueyo et al., 2009; Yoshihara et al., 2010). In sagebrush systems, low success of restoration attempts is influenced by environmental constraints, but also by competitive interactions with exotic species (Bakker et al., 2003; James et al., 2011). Because of the overlap in phenology and similar affinity for disturbance, there is increasing interest in using native annuals as part of restoration in arid systems (e.g. Abella et al., 2012). Our results show that some native annual forb species from the Great Basin were highly effective at suppressing the growth and seed production of *B. tectorum*, and could therefore be important for overcoming biotic limitations and facilitating restoration in invaded systems. *A. intermedia*, *A. tessellata*, and *D. pinnata* were the most effective suppressors, reducing target *B. tectorum* seed production between 79 and 87% in the field, and biomass up to 97% (*A. intermedia*). Many of the forbs were highly tolerant of competition, maintaining their biomass even when growing with high densities of *B. tectorum*, exemplified by the *Amsinckia* species dominating the total competitor biomass production in field plots.

There was some evidence for indirect benefits of annual forbs to *E. multisetus* via increased growth rates in the greenhouse study, though the effects were small and did not lead to significant increases in biomass. Many of the forbs were highly competitive with seedlings of *E. multisetus*, exerting strong direct negative effects in the field and greenhouse, but the addition of one species, *M. veatchiana*, to plots with *B. tectorum* was associated with non-significant increases in *E. multisetus* biomass in the field and greenhouse. Our studies lasted for only one growing season, but it is possible that positive indirect effects could become stronger over time. Seeding these early seral forbs immediately after disturbance may reduce *B. tectorum* seed production, which would result in reduced competition from this exotic grass in subsequent years. Because annual forbs tend to be common after disturbance but decline over time (Boyd and Svejcar, 2011; Goergen and Chambers, 2009), the strong direct effects of competitive annuals on perennial seedlings may decrease over time. Combined with the observation that the competitive ability of perennial grasses in their second year is vastly greater than that of first-year seedlings (Ferguson, 2012), seeding native annuals may result in better long-term plant community outcomes, even though they are very competitive with first year seedlings. Longer-term studies would be useful for determining if native annual forbs would decline in density over time in restoration seedings, perhaps persisting in the seed bank but yielding above-ground dominance to native perennials.

The idea of seeding competitive species as 'place-holders' to reduce recruitment of exotic species after disturbance has a long history in Great Basin restoration. For example, in an attempt to prevent recruitment by exotic annual species, cover crops of non-native species such as crested wheatgrass (*Agropyron cristatum*) are regularly seeded (Hulet et al., 2010) and annual grasses, sometimes sterile, have been seeded to reduce soil nutrients in disturbed communities (e.g. *Secale cereale*, Herron et al., 2001). While using non-native cover crops may reduce exotic recruitment, addition of these species can alter or even arrest natural succession within a community because native growth and survival can be depressed (Henderson and Naeth, 2005; Hulet et al., 2010). For example, attempts to restore native species diversity into monocultures of crested wheatgrass using mechanical, chemical, and seeding methods in both Oregon and Utah have had limited success due to intense competition from crested wheatgrass (Fansler and Mangold, 2011; Hulet et al., 2010). Additionally, "sterile" non-native annual grasses used in restorations have been documented to produce viable seeds (Morris and Schupp, 2009), and thus may persist in native communities. Native annuals may be able to serve the same function as these non-native cover crops,
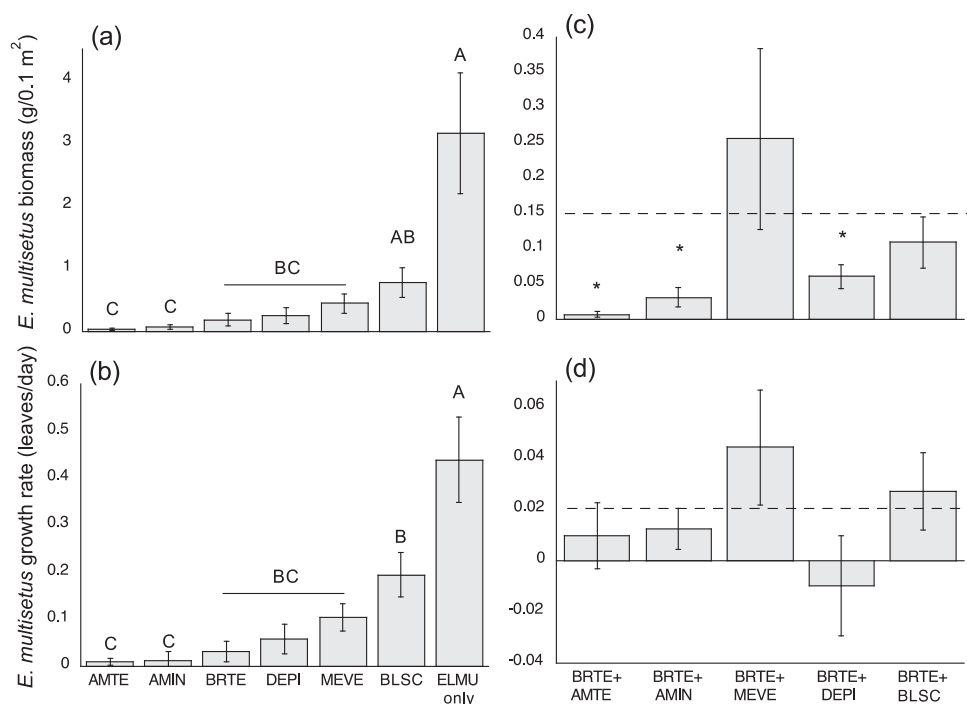
Fig. 5. Direct effect of each annual species on target *E. multisetus* (a) biomass and (b) growth rate and indirect effect on *E. multisetus* (c) biomass and (d) growth rate under field conditions. Different letters within (a) and (b) indicate significant differences ($P < 0.05$) among treatments based on Tukey's HSD tests. Dotted lines in (c) and (d) indicate *E. multisetus* biomass when grown with four *B. tectorum* (baseline); asterisks indicate significant differences ($P < 0.05$) between each treatment and baseline based on *t*-tests. AMTE = *Amsinckia tessellata*, AMIN = *Amsinckia intermedia*, BLSC = *Blepharipappus scaber*, BRTE = *Bromus tectorum*, DEPI = *Descurainia pinnata*, ELMU = *Elymus multisetus*, and MEVE = *Mentzelia veatchian*.

perhaps without undesirable long-term impacts on community composition.

Not all forb species were equally competitive with *B. tectorum*. The three species that were the most capable of suppressing *B. tectorum* in the field (*A. tessellata*, *A. intermedia*, and *D. pinnata*) all demonstrate seed germination strategies consistent with fall germination (Forbis, 2010), and thus are most likely to overlap with *B. tectorum* during its active fall growing season. *Mentzelia veatchiana* and *B. scaber*, which were less effective at suppressing *B. tectorum* biomass, have seed germination strategies most consistent with spring germination (both germinate best after a period of prolonged cold, wet stratification), and thus may not overlap as strongly in resource use. *Blepharipappus scaber* has the highest seed dormancy of all the annual species used in this study (Forbis, 2010), and showed the lowest emergence in our field study. While seed dormancy is an effective strategy for maintaining fitness in highly variable environments (Childs et al., 2010), it may result in reduced ability to compete with *B. tectorum* in restoration settings.

The mechanisms responsible for the observed indirect benefit of native annuals on *E. multisetus* growth rates in the greenhouse were not directly examined. Indirect facilitation is predicted to be most likely when plants are limited by more than one resource, such that direct competition between two species for a subset of resources frees up additional resources for a third species (Brooker et al., 2008). In this system, native annual forbs could obtain soil resources from a pool that overlaps more strongly in space and time with the needs of *B. tectorum* than with those of native perennials, excluding *B. tectorum* via competition for space, light, or upper soil profile resources while perennial species use other resource pools. Alternatively, annual species could compete most strongly for a common soil resource (for example, N), while native perennial species may be limited more by availability of different resource

(for example, water or P). This could indirectly facilitate *E. multisetus* by lowering N availability, potentially increasing the competitive ability of native species when grown with the nitrophylic *B. tectorum* (e.g. Lowe et al., 2003). Finally, it is possible that the presence of native annuals could mediate belowground effects of *B. tectorum* on soil biota that negatively impact native species (Wolfe and Klironomos, 2005). Further studies manipulating rooting depth, soil resource availability, aboveground interactions, and soil biota could differentiate among these alternative mechanisms for increased growth rates observed in the greenhouse.

Native annual forbs are often overlooked as restoration materials, in part because they are weedy, ruderal species. However, these same characteristics may result in pre-emption of space and resources, leading to reduced recruitment of exotic species like *B. tectorum*. An important difference between native annual forbs and other introduced annuals may be a shared evolutionary history with the more desirable native plants, and native annuals are themselves desirable for pollinator communities, other insects, and wildlife (Krausman et al., 1997; Pyle and Crawford, 1996). Unlike introduced invasive annuals, native annual forbs do not form large, persistent monocultures in disturbed systems; rather, they are a step in the successional pathway and decrease in abundance over time, remaining in the seed bank until future disturbance occurs (McLendon and Redente, 1990). As such, they may represent nexus species that are important to perennial community establishment, which may not be apparent from their low frequency in well-established communities. A critical next step is to determine how to increase these species for use in restoration, including developing methods for growing and harvesting these small-statured plants, and determining appropriate seeding rates in wild systems. These efforts are underway (e.g. Shaw and Pellant, 2013), especially for perennial forbs, but additional work is required to determine the feasibility and costs associated with annual forb

restoration. The incorporation of native annual forbs in restoration of seriously degraded systems could improve both short-term restoration success, as well as provide site resilience to future disturbances, via the creation of a seed bank of these competitive native annual species.

Acknowledgments

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