Invasive annual grass interacts with drought to influence plant communities and soil moisture in dryland restoration

Magda Garbowski1,2†, Danielle B. Johnston,3 Dirk V. Baker,4 and Cynthia S. Brown1,2

1Graduate Degree Program in Ecology, Colorado State University, 102 Johnson Hall, Fort Collins, Colorado 80523 USA
2Department of Agricultural Biology, Colorado State University, 307 University Ave, Fort Collins, Colorado 80521 USA
3Colorado Division of Parks and Wildlife, 711 Independent Ave, Grand Junction, Colorado 81505 USA
4Campbell Scientific, Inc., 815 W. 1800 N., Logan, Utah 84321 USA

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Abstract. Understanding the combined effects of drought and invasive species on plant community development and soil moisture could provide valuable insight into the mechanisms hindering successful native plant establishment in dryland restoration projects. We implemented a re-vegetation experiment at two sites in Colorado, USA (one each in the Western Great Plains and Cold Desert ecoregions) to investigate the effects of drought (66% reduction of ambient growing season rainfall), non-native Bromus tectorum seed addition (465 seeds/m2), and superabsorbent polymer soil amendment (25 g/m2) on plant community development and soil volumetric water content at 5 and 30 cm depth. Drought resulted in higher B. tectorum cover at the Western Great Plains site but lower B. tectorum cover at the Cold Desert site. These contrasting results suggest drought may interact with site-specific precipitation patterns to influence B. tectorum establishment. At the Western Great Plains site, drought reduced seeded forb cover and B. tectorum seed addition reduced seeded grass cover, highlighting how the effects of drought and invasive species may vary depending on which functional group is assessed. At the Cold Desert site, drought and B. tectorum seed addition each decreased seeded species cover from approximately 8% to 3%. Superabsorbent polymer effects were limited to slight increases in overall seeded grass cover at the Western Great Plains site from 2.2% to 4.9%. Both drought and B. tectorum seed addition reduced soil volumetric water content but in some cases effects depended on interactions between the two treatments, site, or soil depth. Notably, at the Cold Desert site the reduction in soil volumetric water content resulting from B. tectorum seed addition with ambient precipitation exceeded that of the drought treatment alone at 5 and 30 cm depth. Our results demonstrate that drought and invasive species both negatively influence native plant establishment and soil moisture, and in some cases may interact. Considering both abiotic and biotic stressors as well as their interactions in restoration planning could improve our understanding of native plant establishment and improve re-vegetation outcomes.

Key words: Bromus tectorum; climate change; drought; invasive annual grass; restoration; soil amendment; soil moisture.

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INTRODUCTION

Low precipitation and soil moisture hinder seedling recruitment and successful plant establishment in many environments including restored dryland systems (Booth et al. 2003, Hardegree et al. 2012, 2013, 2016). However, because distinct species phenologies may or may
not align with seasonal precipitation, impacts of low precipitation on plant establishment may be species or context dependent. Many invasive species have traits that allow them to be successful under changing climates, particularly under scenarios of higher atmospheric CO$_2$, greater resource availability, and increased global commerce (reviewed in Bradley et al. 2010). The effects of altered precipitation on invasive species success, however, remain more uncertain (Bradley et al. 2010).

Wolkovich and Cleland (2014) suggest that fast-growing invasive species and those with high phenological plasticity (Wainwright and Cleland 2013) are able to track climate changes more closely than native species. This may result in increased invasive species establishment during periods of high resource variability but low competition at the beginning and end of growing seasons. Furthermore, when they do successfully establish, invasive species can themselves exert strong influences on species interactions (La Forgia et al. 2020), species coexistence (Germain et al. 2018), vegetation structure (Wilson et al. 2018), and soil hydrological processes (Pyšek et al. 2012). For example, in the western USA invasion of annual grasses of the Bromus genus can lead to loss of deep-rooted and fibrous-rooting plant species (Wilcox et al. 2012) and alter the phenology of invaded plant communities (West and Yorks 2006). These changes could in turn influence infiltration and retention of water in specific soil layers to alter the amount of soil moisture available for native species establishment (Booth et al. 2003, Brown et al. 2008, Ryel et al. 2010).

Global climate models largely agree that drylands will experience increased aridity and variability in precipitation in the coming century, but predictions of soil moisture remain uncertain (Burke and Brown 2008, Orlowski and Seneviratne 2013). This is in part because precipitation and vegetation dynamics in drylands are tightly linked and can independently and synergistically affect soil moisture availability. Directly, increased variability in precipitation or longer and more intense droughts can affect soil moisture. Indirectly, climate-induced changes in vegetation can influence soil moisture availability via altered interception, uptake, and transpiration, all of which may have unique effects on moisture at different soil depths (Wilson et al. 2018).

While numerous studies have investigated the effects of drought and invasive species on ecosystem and plant community dynamics in intact systems, investigations of drought and invasive species effects on developing plant communities undergoing ecological restoration are limited. Furthermore, no studies have considered the effects of both drought and invasive species on soil moisture simultaneously in a restoration context. Understanding the combined effects of drought and invasive species on plant community development and soil moisture could provide valuable insight into the mechanisms hindering successful native plant establishment in dryland restoration projects. Such projects have dismal success rates between 5% and 10% (Kildisheva et al. 2016).

Fluctuations in seedbed microclimate resulting from variable precipitation may result in conditions that favor invasive species germination and establishment over that of native species (Roundy et al. 2007, Hardegree et al. 2010, 2013). Restoration ecologists often aim to improve seedbed microclimate and increase the availability of soil resources with soil amendments such as mulch or biochar (e.g., Chambers 2000, Zink and Allen 2003, Beesley et al. 2011). Superabsorbent polymers have been used for over 40 yr in agricultural settings to increase soil water retention (Hüttermann et al. 2009) but have rarely been used in ecological restoration. They are primarily advertised as a way to improve plant establishment in deficit water conditions, as they have been shown to promote crop seedling survival under drought (Akhter et al. 2004, Agaba et al. 2010), improve crop growth under limited irrigation (Hüttermann et al. 1999, Yang et al. 2014), and increase water-holding capacity of soil (Akhter et al. 2004). However, information about their efficacy in natural settings is limited, and effects on plant establishment in restoration projects have been inconsistent (e.g., positive impacts, Rubio et al. 1992, Mangold and Sheley 2007; no effect/variable results, Newhall et al. 2004, Lucero et al. 2010, Johnston and Garbowski 2020, Garbowski et al. 2020b). Understanding whether superabsorbent polymers incorporated into the first several centimeters of soil can ameliorate potential negative effects of drought and non-native species on native species establishment could provide valuable insight regarding their efficacy in ecological restoration.
Throughout the western USA, ongoing natural and anthropogenic disturbances including fire, recreation, and resource extraction have resulted in extensive degradation and effective restoration is needed to sustainably manage ecosystems in the region. Unfortunately, as in many dryland systems around the world, successful restoration in this region is hindered by both invasive species and variable precipitation. We established a study to investigate the interactive effects of growing season (April–September) drought, the invasive annual grass, *Bromus tectorum* L. (*B. tectorum* seed addition hereafter refers to treatment level), and superabsorbent polymers (SAP) on native plant community development and soil moisture at two climatically distinct dryland sites in Colorado. Specifically, we aimed to test the following hypotheses with this study:

1. Growing season drought will decrease native seeded species cover; increase *B. tectorum* cover; and decrease soil volumetric water at both sites across all years of the study
2. *B. tectorum* seed addition will decrease native seeded species cover and soil volumetric water content at 5 cm and 30 cm depth at both sites across all years of the study
3. Superabsorbent polymers (SAP) will ameliorate potential negative effects of drought and *B. tectorum* seeding on native seeded species establishment and soil volumetric water content across all years of the study

**Materials and Methods**

*Bromus tectorum*

The winter annual grass *B. tectorum* (cheatgrass or downy brome) has invaded over 2 million hectares of drylands in the western USA (Bradley and Mustard 2006). Because *B. tectorum* germinates in the fall, overwinters as a seedling and rapidly develops roots and shoots before native perennial species become active (Aguirre and Johnson 1991), it is able to preempt resources early in the growing season to outcompete native vegetation. In parts of its introduced range, *B. tectorum* invasion has resulted in decreased forage quality, altered nutrient cycles, and increased fire return intervals (e.g., Knapp 1996, Schaeffer et al. 2011). Most studies on *B. tectorum* have focused on its spread and impacts in Cold Desert ecoregions of the western USA, primarily the Great Basin (Brooks et al. 2016). Yet, *B. tectorum* readily invades disturbed areas across much of the western USA and several modeling (Bradley et al. 2009, Bradley et al. 2009, Abatzoglou and Kolden 2011) and empirical (Prevéy and Seastedt 2014, 2015) studies suggest that decreased summer precipitation may result in *B. tectorum* expansion throughout the Western Great Plains and Cold Deserts ecoregions outside of the Great Basin. With high levels of seed production (Johnston and Chapman 2014) and efficient dispersal in disturbed areas (Johnston 2011), *B. tectorum* is among the most problematic invasive species in restoration throughout the western USA.

**Site selection**

We conducted our study at two sites in Colorado both threatened by *B. tectorum* expansion: one within the Western Great Plains ecoregion in the northeastern corner of the state and another in the Cold Desert ecoregion in the southwestern portion of the state. The sites have similar land use histories and soil moisture and temperature regimes but vary in precipitation seasonality. The Western Great Plains site is located at a Colorado State University property in Larimer County (40°42′30.7″ N, 105°06′24.4″ W). The site receives approximately 390 mm of precipitation annually with about 270 mm falling during the growing season. Spring and early summer are the wettest portions of the growing season, with 170 mm of precipitation falling between April and June. The Cold Desert site is located at Dry Creek State Wildlife Area in San Miguel County (38°03′25.1″ N, 108°29′59.9″ W) and also receives approximately 390 mm of precipitation annually. Most of the growing season precipitation (160 mm of 220 mm) falls in the late summer and early fall between July and September. These averages are from local data ranging from 1983 to 2013 (NOAA). Soils at both sites are loams or clay loams with clay content ranging from 23% to 33%, and vegetation is a mixture of native and non-native species. Similarly to many other arid rangelands throughout the western USA, both sites were tilled and planted with *Agropyron cristatum* and other pasture grasses in the 1950s.

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or 1960s and were subsequently grazed by sheep or cattle periodically until c. 2000. B. tectorum is present at both sites but remains patchy at the Western Great Plains site, whereas it is a dominant part of the vegetation at the Cold Desert site.

**Study implementation**

At each site, three blocks were established between 50 and 200 m from one another within uniform vegetation and at minimal slope (<10°). A full factorial design was implemented in each block crossing the following three factors: (1) precipitation (ambient or 66% reduced [drought]); (2) B. tectorum seed addition (465 B. tectorum seeds/m² or none) and (3) SAP treatment (SAP 25 g/m² or none). This resulted in eight plots per block and 24 plots per site. Plots were 3.6 × 4.4 m and arranged in a check-board design with open spaces in between to minimize interactions among treatments.

Prior to study implementation, we removed sparse woody vegetation with a brush mower and applied glyphosate to remaining vegetation at a rate of 4,480 g ai/ha two or three times at each site over the course of several weeks. We tilled each experimental block with a rototiller to a depth of 5–10 cm. We undertook these pre-treatment actions to mimic heavy levels of disturbance such as those created by resource extraction in the region. These types of disturbances often result in substantial invasive species pressure, predominantly of invasive annual grasses such as B. tectorum (Johnston 2011, Chambers et al. 2014). After the initial tilling, we applied SAP (Stockosorb 660 Micro, 0.2–0.8 mm, Evonik Industries, Germany) to plots receiving this treatment at a rate of 25 g/m²: an application rate at a rate of reducing its movement and root growth between treatment and after ripened prior to being applied at a rate of c. 465 seeds/m² to B. tectorum seeded were dried and and applied glyphosate to remaining vegetation at a rate of 25 g/m² and applied glyphosate to remaining vegetation at a rate of 4,480 g ai/ha two or three times at each site over the course of several weeks. We tilled each experimental block with a rototiller to a depth of 5–10 cm. We undertook these pre-treatment actions to mimic heavy levels of disturbance such as those created by resource extraction in the region. These types of disturbances often result in substantial invasive species pressure, predominantly of invasive annual grasses such as B. tectorum (Johnston 2011, Chambers et al. 2014). After the initial tilling, we applied SAP (Stockosorb 660 Micro, 0.2–0.8 mm, Evonik Industries, Germany) to plots receiving this treatment at a rate of 25 g/m²: an application rate between amounts used in agricultural applications (1–10 g/m²; Ashkiani et al. 2013, Islam et al. 2020) and containerized experiments (60–600 g/m²; Agaba et al. 2010, Bakass et al. 2002). After broadcasting SAP, we cultivated study areas with a disk harrow to incorporate polymer to 5–10 cm deep.

We developed site-specific seed mixes that consisted of the similar numbers of pure live seeds (PLS) and proportions of native grasses (22%), forbs (46%), and shrubs (32%). Seed mixes were developed with species that were suitable to the climate at each site and for which seeds were commercially available (Appendix S1: Table S3). A total of 1200 PLS/m² were broadcast at the Western Great Plains site and 1344 PLS/m² were broadcast at the Cold Desert site. We based density of B. tectorum seeding on values reported in similar studies from the region: Johnston and Chapman (2014) reported propagule pressure between 0 and >1000 seeds/m² at sites in Western Colorado and Concilio et al. (2017) estimated B. tectorum densities of about 700 individuals/m² at sites on the Front Range of Colorado. We collected B. tectorum seeds within 6 km of both study sites. B. tectorum seeded were dried and after ripened prior to being applied at a rate of c. 465 seeds/m² to B. tectorum seed addition plots. Both native restoration and B. tectorum seeds were broadcast seeded and incorporated by hand raking. In accordance with recommendations for each area (NRCS 2011), seeding was completed at the Western Great Plains site in December 2013 and at the Cold Desert site in July 2014.

The drought treatment was based on projections of lower summer precipitation in the region (e.g., Archer and Predick 2008, Bradley et al. 2009). The drought we imposed excluded 66% of growing season (April–September) precipitation. We chose this drought scenario because recent research (Knapp et al. 2018) suggests that extreme manipulations of precipitation are needed to accurately assess community and ecosystem responses to climatic events. Although pronounced, in an average precipitation year, this reduction would still result in precipitation amounts within the 30-yr range of variability for both sites. Rainfall diversion shelters were modified from Yahdjian and Sala (2002). Our modifications included constructing plot-sized shelters (3.6 × 4.4 m) in an A-frame design with plastic rain-catchment troughs oriented toward prevailing winds (Appendix S1: Fig. S1). We installed plastic flashing around each plot to a depth of 45 cm to limit above- and belowground water movement and root growth between treatment areas and their surroundings. Each year we assembled shelters in early April and deconstructed them in late September or early October to allow for ambient winter precipitation. We monitored humidity and light interception outside of and under one shelter at each site throughout the course of the study and observed
no effect of shelters on these microclimate variables.

We measured vegetation cover at peak biomass in late June or early July at both sites: 2014–2017 at the Western Great Plains site, and 2015–2017 at the Cold Desert site. We measured cover by placing two cover data frames (1.5 × 1 m) with 96 evenly spaced intersections in plots and recorded point intercept cover hits at each intersection point for all canopy layers. Current year *B. tectorum* was recorded even if plants were senescing. Each year cover data were collected from the same areas within plots. At two of the blocks at each site, we installed soil moisture probes (5TM model probes, Decagon Devices, Pullman, Washington, USA) in treatment plots to assess effects of treatments on soil volumetric water content at shallow-depth (5 cm) and mid-depth (30 cm) soils throughout the 2015 and 2016 growing season. Continuous volumetric water content (m$^3$ water/m$^3$ soil) was calculated from the permittivity measured by the sensors using the Topp model (Topp et al. 1980).

**Data analyses**

We completed all statistical analyses in R (R Core Team 2014) for each site separately. We used repeated measures linear mixed effects models in the lme4 package (Bates et al. 2014) to analyze effects of treatments on plant cover for the following functional groups: *B. tectorum*, native seeded species (separated into forbs and grasses when sufficient observations of each permitted individual analyses), non-native annual forb species, and non-native perennial species. In these models, date and treatments were considered fixed effects, and block and plot were considered random effects to account for repeated measures across years.

Because of defective sensors and significant rodent damage, soil volumetric water content data from c. 25% of sensors were missing. The majority of failures occurred in plots with SAP, preventing us from conducting a repeated measures analysis of soil volumetric water content with SAP plots included. Therefore, we used only data from no-SAP plots for analyses of soil volumetric water content. The sensors we used have manufacturer-specified error of ±1 permittivity. This equates to between 2% and 5% volumetric water content; therefore, differences among treatments that fall within this error should be interpreted with caution. We used repeated measures linear mixed effects models (Bates et al. 2014) with time as the repeated measure to analyze effects of treatment on weekly averages of soil volumetric water content with date and treatments considered fixed effects and block and plot considered random effects. Analyses were completed separately for soil volumetric water content at 5 and 30 cm.

For all models, we examined residual and Q-Q plots to assess homogeneity of variance and normality. Cover values were square root transformed for all functional groups at both sites. We assessed the effects of treatments with *P* values < 0.05 for main effects and two-way and three-way interactions with *P* values < 0.1 by comparing estimated marginal means of treatment groups with Tukey HSD adjustment using the R package emmeans (Lenth 2016). Here, we discuss treatment interactions with significant effects within a given year. Results of treatment interactions with differences across years are provided in Appendix S1: Table S4.

**RESULTS**

Growing season precipitation (April–September) at the two sites varied considerably from year to year and deviated from 30-yr growing season averages (Western Great Plains 270 mm; Cold Desert 220 mm). At the Western Great Plains site, 227, 375, 154, and 278 mm of precipitation fell during the 2014, 2015, 2016, and 2017 growing seasons, respectively. A typical precipitation pattern of high rainfall early in the summer was only observed in 2015 and 2016 (Appendix S1: Fig. S2). At the Cold Desert site, below average precipitation of 193, 176, and 131 mm fell during the 2015, 2016, and 2017 growing seasons, respectively. At the Cold Desert site, a typical pattern of high rainfall late in the summer was not observed in any year of the study (Appendix S1: Fig. S3).

**Plant community development**

In general, *B. tectorum* cover was higher with *B. tectorum* seed addition, but specific results varied by drought treatment at the two sites. At the Western Great Plains site, *B. tectorum* cover was <2% in 2014 and we detected no differences
among treatments. In all subsequent years of the study, the *B. tectorum* seed addition resulted in higher *B. tectorum* cover (Fig. 1a; Appendix S1: Table S1) with the highest cover values in plots with *B. tectorum* seed addition and drought in 2015 and 2016. At the Cold Desert site, *B. tectorum* cover was higher in ambient plots compared to drought plots in the first growing season (2015), but effects of precipitation treatment were not detected in subsequent years (Fig. 2a; Appendix S1: Table S1). *B. tectorum* seed addition resulted in higher *B. tectorum* cover at the Cold Desert site in 2015 and 2016, but we detected no effects in the final year of the study (2017; Fig. 2b; Appendix S1: Table S1). *B. tectorum* cover was unaffected by SAP treatments at either site (Appendix S1: Table S1).

Seeded species cover was influenced by all treatments at the Western Great Plains site, but effects depended on year and functional group measured. Seeded forb cover was approximately 10% lower in drought plots compared to ambient precipitation plots regardless of *B. tectorum* seed addition and overall decreased throughout the course of the study (Fig. 1c; Appendix S1: Table S1). Seeded grass cover increased through time, but treatments effects were only evident in the final year of the study (2017) when cover was approximately 10% higher in plots without *B. tectorum* seed addition or drought compared to plots with *B. tectorum* seed addition, regardless of drought treatment (Fig. 1b; Appendix S1: Table S1). Across all years at the Western Great Plains site, seeded grass cover was higher in plots with SAP (4.9 ± 1.0%) compared to plots without SAP (2.2 ± 0.7%; Appendix S1: Fig. S4). At the Cold Desert site, seeded species cover was low across all years (approximately 5%) and was dominated by native annual forbs in the first year and perennial grasses in the later two years. The drought treatment reduced seeded species cover from approximately 8% to 3% (Fig. 2e; Appendix S1: Table S1). Similarly, *B. tectorum* seed addition reduced seeded species cover from 8% to 2%. We detected no SAP effects on seeded species at the Cold Desert site (Appendix S1: Table S1).

Non-native annual forb cover at the Western Great Plains site was lower in plots with *B. tectorum* seed addition across all years (Fig. 1f) but was unaffected by drought or SAP treatments (Fig. 1e, Appendix S1: Table S1). At the Cold Desert site, treatment effects on non-native annual forbs were limited to lower cover with drought treatment in 2015 (Fig. 2c; Appendix S1: Table S1). Non-native perennial cover was unaffected by treatments at either site but varied through time (Appendix S1: Tables S1, S4).

**Volumetric water content**

At the Western Great Plains site, the magnitude and direction of drought effects on soil volumetric water content at 5 cm depth varied over time. At this site, soil moisture was higher with drought early in the growing season and lower with drought later in the growing season (Fig. 3a,b; Appendix S1: Table S2). In addition, *B. tectorum* seed addition decreased seasonal soil volumetric water content at 5 cm in 2016 (Fig. 3d, Appendix S1: Table S2) but not in 2015 (Fig. 3c; Appendix S1: Table S2). At 30 cm, soil volumetric water content was higher in plots with *B. tectorum* seed addition and ambient precipitation than in all other treatment combinations in both 2015 and 2016 (Fig. 3e,f; Appendix S1: Table S2). At the Cold Desert site, *B. tectorum* seed addition and drought treatments interacted to influence seasonal soil volumetric water content at 5 and 30 cm in 2015 and at 30 cm in 2016 (Fig. 4a–d; Appendix S1: Table S2). In 2015, seasonal soil volumetric water content at 5 cm was highest in plots without *B. tectorum* seed addition or drought. However, somewhat surprisingly, regardless of drought treatment, plots with *B. tectorum* seed addition had lower soil volumetric water content than plots with drought alone (Fig. 4a; Appendix S1: Table S2). A similar pattern was observed at 30 cm in 2015: seasonal soil volumetric water content was higher in plots without *B. tectorum* seed addition or drought. However, somewhat surprisingly, regardless of drought treatment, plots with *B. tectorum* seed addition had lower soil volumetric water content than plots with drought alone (Fig. 4a; Appendix S1: Table S2). A similar pattern was observed at 30 cm in 2015: seasonal soil volumetric water content was higher in plots without drought or *B. tectorum* seed addition compared to plots with drought alone or with *B. tectorum* seed addition and ambient precipitation (Fig. 4c; Appendix S1: Table S2). In 2016, seasonal soil volumetric water content at 5 cm was lower in plots with *B. tectorum* seed addition and drought than all other treatments (Fig. 4b; Appendix S1: Table S2). No treatment effects on soil volumetric water content at 30 cm depth were detected in 2016 (Fig. 4d; Appendix S1: Table S2) at this site.
Fig. 1. (a) Bromus tectorum and (b) seeded grasses under B. tectorum seed addition and precipitation treatment (ambient vs. drought) at the Western Great Plains site. Seeded forbs (c and d) and non-native annual forbs (e and f).
DISCUSSION

Changes in climate such as lower or more variable precipitation may facilitate the spread of non-native species (Cleland et al. 2007, Abatzoglou and Kolden 2011, Prevéy and Seastedt 2014, 2015) and hamper restoration efforts. In our study, drought and invasive species both negatively influenced native plant establishment and soil moisture, and in some cases interacted.

We hypothesized that drought would result in higher B. tectorum cover at both sites, but this trend was observed only at the Western Great Plains site in two of the four study years (Fig. 1a). Brooks et al. (2016) suggest that consistent summer precipitation in the Western Great Plains results in high competition from native species and unfavorable conditions for B. tectorum invasion. If summer precipitation is reduced, B. tectorum is predicted to increase in this region (Bradley 2009). The higher cover of B. tectorum we observed in drought plots at the Western Great Plains site in 2015 and 2016 is consistent with these predictions and other research from the area. In studies investigating the effects of seasonal shifts in precipitation on plant communities along the Front Range of Colorado, Prevéy and Seastedt (2014, 2015) observed higher abundance of winter-active, exotic grasses (2014) and higher population growth rate of B. tectorum with increased winter precipitation (2015). While our drought treatment did not alter winter precipitation—all plots in our study received ambient precipitation from October to March—the reduction in summer rainfall in our study resulted in proportionally more rainfall in the winter similar to Prévey and Seastedt (2014, 2015). Because growing season precipitation differed significantly in these two years (375 mm in 2015 vs. 154 mm in 2016) it is likely that proportional changes in seasonal precipitation rather than total precipitation amount resulted in conditions that favored B. tectorum establishment over native species establishment.

The imposed summer drought in our study may have created a vacant temporal niche (i.e., a period during which other species are inactive) for B. tectorum to exploit before native species became established at the Western Great Plains site. Wolkovich and Cleland (2014) suggest that fast-growing and plastic species like B. tectorum (Mack and Pyke 1983) may be well suited to track changing climate patterns to take advantage of periods of variable resource availability and low competition at the beginning and end of growing seasons. Given that soil volumetric water content was counter-intuitively higher in drought plots early in the growing season at the Western Great Plains site, it is possible that B. tectorum experienced particularly favorable conditions for growth before native species became active under drought treatment.

The trend for higher B. tectorum in drought plots was limited to the Western Great Plains site; at the Cold Desert site, B. tectorum cover was lower in drought plots in the first year of the study. Below average rainfall combined with drought treatment at the Cold Desert site may have negatively affected initial B. tectorum establishment. In a companion study, Garbowski et al. (2020a) observed lower B. tectorum establishment under drought throughout 2015, particularly in the fall. Survival and growth after fall germination are imperative for successful B. tectorum recruitment (Mack and Pyke 1983, Prevéy and Seastedt 2015, Bishop et al. 2019), and in warmer and drier regions, B. tectorum often requires favorable environmental conditions or high propagule pressure to successfully establish and persist (Meyer et al. 2001).

Our result of higher B. tectorum cover under drought at the Western Great Plains site is supported by prior research (Bradley et al. 2009, Chambers et al. 2014, Prevéy and Seastedt 2014), but our finding of lower cover at the Cold Desert
site suggests that summer drought can also hinder B. tectorum establishment. These contrasting results corroborate uncertainty identified in prior studies focused on understanding how precipitation affects B. tectorum establishment (Bradley et al. 2009, Chambers et al. 2014). Clarifying interactive relationships among invasive species, abiotic stress, and native plant establishment is essential to understanding community assembly in restored systems as effects of invasive species on native species may depend on abiotic conditions (e.g., La Forgia et al. 2020) and because competition may affect long-term coexistence to a greater extent than water limitation (e.g., Germain et al. 2018).

When it does successfully establish, B. tectorum may alter the extent and timing of soil moisture availability (Booth et al. 2003, Ryel et al. 2010, Prevéy and Seastedt 2014) and hinder recruitment of native species that depend

Fig. 2. (a) Bromus tectorum (a and b), seeded species (c and d) and non-native annual forbs (e and f) under drought (left panels) and B. tectorum seed addition (right panels) treatments at the Cold Desert site. Data are averaged over non-significant treatments in each case. Points are means of untransformed data and bars are ± standard error of the mean. Lowercase letters denote significant differences between means in that year, and uppercase letters denote significant differences between means across all years at $P < 0.05$. 
Fig. 3. Soil volumetric water content at 5 cm under precipitation treatment in (a) 2015 and (b) 2016 at the Western Great Plains site. Lines show means of weekly volumetric water content, and points show
on shallow soil moisture for germination and growth (Hardegree et al. 2013, Harris and Wilson 1970, Booth et al. 2003, Humphrey and Schupp 2004, Ryel et al. 2010). In our study, B. tectorum seed addition resulted in decreased seasonal soil volumetric water content at 5 cm at both sites. Notably, at the Cold Desert site in 2015, B. tectorum seed addition resulted in lower volumetric water content at 5 cm than our imposed drought of 66% reduced growing season precipitation. As B. tectorum has high transpiration rates (Harris 1967) and shallow roots (Kulmatiski et al. 2006), this result is unsurprising and reflects findings from other studies in dryland communities (Harris 1967, Cline et al. 1977, Booth et al. 2003, Ryel et al. 2010). However, the magnitude of the effect of B. tectorum seed addition on soil moisture is stark in comparison to drought.

As hypothesized, seeded species cover was negatively affected by drought and B. tectorum seed addition at both sites, but effects varied by site and, in some cases, by functional group. At the Cold Desert site drought and B. tectorum seed addition had comparable negative effects on seeded species, each decreasing seeded species cover by approximately 5%. At the Western Great Plains site drought reduced seeded forb cover and B. tectorum seed addition reduced seeded grass cover in ambient precipitation plots. The most abundant native forb species (i.e., Cleome serrulata, Helianthus annuus, Ratibida columnifera, and Machaeranthera tanacetifolia) at the Western Great Plains site are tap rooted and active late in the growing season. Because they likely depend on soil moisture from deep soil layers, these forbs may have been more impacted by pervasive dry conditions at 30 cm depth than shallow-rooted grasses. B. tectorum seed addition reduced cover of morphologically similar native grasses and phenologically similar early-season non-native annual forbs. As in other studies, our findings suggest strong competitive effects of B. tectorum on morphologically or phenologically similar species (Aguirre and Johnson 1991, Humphrey and Schupp 2004, Funk et al. 2008) and resource partitioning between B. tectorum and dissimilar forb species (Sheley and Larson 1994, Brown and Rice 2009, Parkinson et al. 2013).

Although unmeasured, differences in the depth from which B. tectorum and other plants utilize soil moisture may have contributed to contrasting effects of B. tectorum seed addition and drought treatment on soil moisture at 30 cm depth at the two sites. At the Western Great Plains site, it is possible that in ambient plots with B. tectorum seed addition, competition from B. tectorum prevented root elongation and water extraction from deeper soil layers, resulting in relatively high soil volumetric water content at 30 cm depth. In drought plots, reduced precipitation coupled with high B. tectorum cover may have restricted root growth of all species to shallow soil layers resulting in low infiltration to 30 cm. At the Cold Desert site, high cover of B. tectorum in ambient precipitation plots in 2015 may have resulted in greater utilization of soil moisture at 5 cm and decreased infiltration of moisture to 30 cm depth. Isotopic studies that investigate from where establishing invasive and native species extract water could help clarify competitive, albeit indirect, impacts of annual grasses like B. tectorum (e.g., Melgoza et al. 1990) on establishing vegetation in restoration settings. Further, with larger datasets, structural equation modeling could elucidate direct and indirect relationships between abiotic and biotic drivers
of community dynamics in restoration settings (Grace 2006).

We predicted that SAP would increase seeded species establishment under drought and *Bromus tectorum* seed addition at both sites, but SAP treatment did not interact with either of the other treatments. SAP had a positive effect on perennial grasses but only at the Western Great Plains site, increasing seeded grass cover from 2.2% to 5% across study years. This is a modest increase compared to findings from a similar study in the region: Johnston and Garbowsk (2020) observed c. 25% increased cover of perennial grasses with SAP. However, they also detected a negative effect of SAP on perennial forbs, which were dominated by taproot-developing species. As SAP was applied to between 5 and 10 cm depth in both studies, fibrous, shallow-rooting grasses may
have benefited more than deeper-rooted forbs or shrubs from SAP addition in both cases. In addition, beneficial effects of SAP may be limited in natural settings in which antecedent soil moisture conditions are lower than in agricultural settings. Even at its highest values of c. 23%, soil moisture content in our study was much lower than in agricultural studies in which positive effects of SAP have been documented (e.g., Eneji et al. 2013). Further, effects of SAP on native species establishment may differ from those presented here if SAP is applied closer to target species (e.g., drill seeding) and soil is not tilled prior to seeding. Additional data on soil moisture conditions in SAP plots would have further informed our findings, but because of soil moisture sensor failures in these plots, we were unable to adequately assess effects of SAP on soil moisture. Overall, soil amendments such as SAP may improve restoration outcomes, but additional research is needed to discern when application will be beneficial or detrimental and which functional groups are most likely to be affected.

CONCLUSION

Our results demonstrate that precipitation may interact with invasive species presence to influence plant community development and soil moisture in dryland restoration, but effects may be site specific. Drought resulted in both higher (Western Great Plains site) and lower (Cold Desert site) B. tectorum establishment in our study. At the Western Great Plains site, B. tectorum seed addition reduced perennial grasses cover, whereas drought reduced native forb cover. Given this, using forbs with dissimilar morphologies and phenologies from B. tectorum may allow for improved restoration outcomes in invaded areas (Barak et al. 2015). At the Cold Desert site, drought and B. tectorum seed addition reduced native plant cover by similar magnitudes. To offset the negative impacts of planting during drought periods, restoration practitioners may want to seed at multiple dates (Bakker et al. 2003, MacDougall et al. 2008) or use high richness seed mixes with species that emerge under a wide range of conditions (Groves and Brudvig 2019).

In addition to negatively influencing native plant establishment, B. tectorum seed addition and drought treatments also reduced soil moisture at both sites. Seedling survival during drought has been linked to plant tolerance to low soil moisture conditions (Ackerly 2004), the ability of seedlings to develop deep roots and access moist soil layers during establishment (Padilla and Pugnaire 2007), and root allocation and morphology (Atwater et al. 2015, Ferguson et al. 2015). Seedling survival in relation to B. tectorum competition has been linked to higher root-to-shoot ratios (Rowe and Leger 2010), earlier adult phenology (Rowe and Leger 2010), greater allocation to fine roots (Goergen et al. 2011), and rapid root growth (Leger et al. 2019). As both drought and B. tectorum seed addition in our study decreased soil moisture, it is possible that species that can tolerate or avoid low moisture conditions may be best suited to establish under both scenarios. Future studies that relate functional traits, particularly root traits, to ecosystem processes or plant performance (Suding et al. 2008, Laughlin 2014, Garbowskis et al. 2020b) may inform species selection for dryland restoration threatened by both drought and invasive species.

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Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3417/full