Soil amendment interacts with invasive grass and drought to uniquely influence aboveground versus belowground biomass in aridland restoration

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Water-holding soil amendments such as super-absorbent polymer (SAP) may improve native species establishment in restoration but may also interact with precipitation or invasive species such as Bromus tectorum L. (cheatgrass or downy brome) to influence revegetation outcomes. We implemented an experiment at two sites in Colorado, U.S.A., in which we investigated the interactions of drought (66% reduction of ambient rainfall), B. tectorum seed addition (BRTE, 465 seeds/m²), and SAP soil amendment (25g/m²) on initial plant establishment and 3-year aboveground and belowground biomass and allocation. At one site, SAP resulted in higher native seeded species establishment but only with ambient precipitation. However, by the third year, we detected no SAP effects on native seeded species biomass. Treatments interacted to influence aboveground and belowground biomass and allocation differently. At one site, a SAP × precipitation interaction resulted in lower belowground biomass in plots with SAP and drought (61.7 ± 7.3 g/m²) than plots with drought alone (91.6 ± 18.1 g/m²). At the other site, a SAP × BRTE interaction resulted in higher belowground biomass in plots with SAP and BRTE (56.6 ± 11.2 g/m²) than BRTE alone (35.0 ± 3.7 g/m²). These patterns were not reflected in aboveground biomass. SAP should be used with caution in aridland restoration because initial positive effects may not translate to long-term benefits, SAP may uniquely influence aboveground versus belowground biomass, and SAP can interact with environmental variables to impact developing plant communities in positive and negative ways.

Key words: biomass allocation, Bromus tectorum, cheatgrass, drought, invasion, root biomass, soil amendment, super-absorbent polymer

Implications for Practice

• The effects of super-absorbent polymers (SAP) on native plant establishment may depend on environmental conditions such as invasive species or precipitation and vary by year, site, and plant community metric. Thus, they should be used with caution as a soil amendment in aridland restoration.
• Initial positive effects of SAP may not translate to long-term benefits as demonstrated by increased first-year native seedling densities but no effect on native plant biomass in the third year of our study.
• SAP may have variable and contrasting effects on aboveground and belowground biomass and allocation in restored plant communities. SAP amendment may result in lower aboveground and lower root biomass under drought conditions or in plant communities invaded by Bromus tectorum.

Introduction

In the western United States, successful restoration of arid and semi-arid ecosystems is often constrained by low and variable moisture (Hardegree et al. 2012) and invasion by nonnative species (Brown et al. 2008). Invasive annual grasses are highly competitive in disturbed areas (Hobbs & Huenneke 1992) and have established across much of the arid and semi-arid west (Germino et al. 2016). The annual grass, Bromus tectorum L. (cheatgrass or downy brome), is a particularly troublesome nonnative species and has invaded tens of millions of hectares in the western United States (Bradley & Mustard 2006). Unlike most native perennial grass, forb, and shrub species that have historically dominated these areas, B. tectorum usually germinates in the fall, overwinters as a seedling, and rapidly grows in the spring to complete its life cycle before many native species reach peak growth. Because of its mismatched phenology competitive in disturbed areas (Hobbs & Huenneke 1992) and have established across much of the arid and semi-arid west (Germino et al. 2016). The annual grass, Bromus tectorum L. (cheatgrass or downy brome), is a particularly troublesome nonnative species and has invaded tens of millions of hectares in the western United States (Bradley & Mustard 2006). Unlike most native perennial grass, forb, and shrub species that have historically dominated these areas, B. tectorum usually germinates in the fall, overwinters as a seedling, and rapidly grows in the spring to complete its life cycle before many native species...
compared to native perennials, *B. tectorum* is able to utilize moisture and nutrients earlier in the season than native plants (Aguirre & Johnson 1991). These competitive advantages may be amplified under projected precipitation changes, as *B. tectorum* has been shown to increase in abundance when summer moisture is low (Bradley 2009) and when soil moisture is variable from year to year (Chambers et al. 2007).

Interannual as well as annual and seasonal weather fluctuations result in seedbed microclimates that are highly variable and potentially unfavorable to germinating and emerging native seedlings but favorable for *B. tectorum* establishment (Roundy et al. 2007; Hardegree et al. 2010; Hardegree et al. 2013). Improving seedbed microclimate and increasing the availability of soil resources in aridland restorations may improve seeded species establishment resulting in greater competition from natives and lower *B. tectorum* establishment. However, increased soil resources may also benefit *B. tectorum* in the absence of competitors (Melgoza et al. 1990; Prevey et al. 2010). With their ability to absorb moisture when soils are wet and slowly release it (Agaba et al. 2010), super-absorbent polymers (SAP) may ameliorate the negative impacts of drought on species establishment in restoration but may also inadvertently promote establishment of nonnative species such as *B. tectorum* (Johnston & Garbowski 2019).

SAP have been utilized as a soil amendment for over 40 years primarily in agricultural settings to increase soil water retention and improve plant performance (reviewed in Hüttermann et al. 2009). They are predominantly marketed as a way to improve plant establishment inwater-limited situations as they have been shown to increase water-holding capacity of soil (Akhter et al. 2004; Abedi-Koupai et al. 2008), improve seedling survival under drought (Akhter et al. 2004; Agaba et al. 2010), and increase crop growth under deficit moisture conditions (Hüttermann et al. 1999; Yang et al. 2014). However, information about their interactions with precipitation in natural settings is limited, and effects on seedling establishment in revegetation projects have been variable (e.g. positive impacts: Rubio et al. 1992; Mangold & Sheley 2007; no effect/variable results: Newhall et al. 2009; Lucero et al. 2010; Johnston & Garbowski 2019). Although a potentially promising restoration tool, information regarding interactions of SAP with drought and invasive species in field settings is scarce. Additionally, as most SAP studies have focused on single species and aboveground vegetation responses, information about how SAP impacts multi-species plant communities and aboveground and belowground productivity is needed to better understand their practicality in ecological restoration.

To assess community development trajectories and restoration success, most restoration studies focus on aboveground responses such as plant density, height, and aboveground biomass. Optimal partitioning theory, which states that increases in soil resources should drive plants to allocate more biomass to aboveground structures (Bloom et al. 1985), is generally supported (e.g. Poorter & Nagel 2000; Poorter et al. 2012). However, plant communities may display decoupled aboveground and belowground responses to changes in precipitation (Wilcox et al. 2017) and soil nutrients (Hayes et al. 2017) and in water-limited systems plants may allocate more biomass to belowground structures in response to increases in precipitation (Bai et al. 2010) or soil nutrients (Benigno et al. 2012). As restoration ecologists often utilize soil amendments in revegetation projects to improve soil conditions, assessing belowground responses to drought and amendments is imperative to evaluating community development patterns and restoration success. By understanding how drought, invasive species, and SAP affect belowground biomass and allocation patterns, we may be able to develop a more thorough understanding of how plant communities in arid systems develop in response to variable environmental conditions and restoration practices.

We established a study to investigate the interactive effects of drought, *B. tectorum* seed addition, and SAP on restored native plant communities at two semi-arid sites in Colorado, U.S.A.: one in the Cold Desert (CD hereafter) and one in the Western Great Plains (WGP hereafter). Both sites are semi-arid, receiving approximately 400 mm of precipitation each year with similar growing season (March–October) precipitation (WGP site: 320 mm, CD site: 270 mm), but vary in their precipitation seasonality. The CD site receives most of its precipitation in the late summer and early fall, whereas the WGP site receives the majority of its growing-season precipitation in the spring and early summer. We sought to understand how drought, *B. tectorum* seed addition (BRTE hereafter), and SAP interact to affect initial native seeding and *B. tectorum* (hereafter the species name refers to response variable or species) establishment and longer-term aboveground and belowground biomass and allocation patterns at these two sites. We aimed to investigate the following hypotheses with our study:

1. In the absence of BRTE treatment, SAP amendment will increase first-year seeded species establishment and third-year aboveground biomass, and effects will be most pronounced under drought treatment.
2. In the presence of BRTE treatment, SAP amendment will have reduced positive effects on first-year seeded species establishment and third-year seeded species aboveground biomass regardless of precipitation.
3. Under all treatment combinations, SAP amendment will result in higher aboveground biomass, lower belowground biomass, and lower root mass fraction values.

**Methods**

**Study Sites**

Our two study sites have similar management histories and total annual precipitation but different precipitation patterns. The WGP site is located in northeastern Colorado at the Colorado State University Waverly property (latitude: 40.708464, longitude: −105.106834), U.S.A. This site receives most of its growing season precipitation (170 mm) between April and June. The CD site is located in southwestern Colorado (Dry Creek Basin State Wildlife Area; latitude: 38.060054, longitude: −108.512885), U.S.A., and receives the majority of its growing
season precipitation (200 mm) between July and September. Since the 1950s, both sites had been tilled and seeded with pasture grasses and grazed by cattle, sheep, or both until the mid-2000s. Soils at both sites are loams or clay loams with clay content ranging from 23 to 33%.

Experimental Design
We designated three blocks at each site based on uniform vegetation and minimal slope (<10°) and implemented a full factorial design in each block crossing the following three factors: (1) precipitation (ambient or 66% reduced [drought]); (2) BRTE treatment (465 Bromus tectorum seeds/m² or none); and (3) SAP (25 g/m²) or none. This resulted in eight treatment combinations per block and 24 plots per site. We randomly assigned treatments to plots (3.6 m × 4.4 m) within the blocks in a checkerboard design with nontreated plot-sized areas separating experimental plots.

Study Implementation and Treatments
We developed site-specific seed mixes comprised of native grasses, forbs, and shrubs that were selected based on their suitability to the climate, presence in surrounding areas, and availability (Table S1). The number of pure live seeds (PLS) and species in forb, grass, and shrub functional groups was comparable among the two seed mixes (46% forbs, 15 species; 22% grasses, 13 species; 32% shrubs, 8 species). A total of 1,200 PLS/m² were used at the WGP site and 1,344 PLS/m² were used at the CD site. At both sites, we included diverse forb and shrub species in seed mixes because these functional groups are vital components of resilient and functionally diverse ecosystems yet are underused and understudied in ecological restoration (Gucker & Shaw 2019). In addition, prior research has identified positive effects of SAP primarily on grass species and information about how they impact forbs and shrubs is more limited (Johnston & Garbowski 2019). We collected B. tectorum seeds within 6 km of the study sites and seeding density was based on propogule pressure reported in similar systems (Concilio & Loik 2013; Johnston & Chapman 2014). A volume sufficient to provide 465 seeds/m² was prepared for each plot.

As SAP treatment needed to be uniformly incorporated into soil, we used a brush mower to remove tall vegetation and shrubs including Atriplex canescens, Sarcobatus vermiculatus at the CD site, and Ericameria nauseosa at both sites. We then sprayed remaining vegetation with a solution of glyphosate and water at a rate of 4,480 g ai/ha two or three times at each site to reduce re-sprouting from existing vegetation, primarily Convolvulus arvensis and Agropyron cristatum at both sites. After treatment with glyphosate, we tilled block areas with a rototiller to a depth of 5–10 cm and applied SAP (Stockosorb 660 Micro, 0.2–0.8 mm, Evonik Industries, Germany) to appropriate plots by hand at a rate of 25 g/m². We used a SAP application rate that was economically sensible and between amounts that have been used in containerized experiments (60–600 g/m²; Agaba et al. 2010; Bakass et al. 2002) and agricultural settings (1–10 g/m²; Ashkiani et al. 2013; Islam et al. 2011). We then disked complete block areas to incorporate polymer to 5–10 cm. These pre-study treatments were intended to simulate heavy levels of disturbance such as those created by oil and gas extraction, mining, or agriculture. We broadcast native restoration seeds and B. tectorum seeds on appropriate plots and incorporated them by hand raking. We then firmed the soil surface with a lawn roller. We completed these tasks according to recommended seeding dates for the two sites (Sharkoff & Taliga 2011) and prior to the onset of period with highest precipitation at each site: November/December 2013 at the WGP site and July 2014 at the CD site.

The drought treatment was based on forecasts of decreased summer precipitation in the region (e.g. Archer & Predick 2008; Bradley 2009). Rainfall diversion shelters were modified from Yahdjian and Sala (2002) and designed to have minimal effects on incoming light, wind speed, temperature, and humidity. We attached UV transparent plexiglass troughs to wooden shelter frames to intercept 66% of incoming precipitation from drought treatment plots. Shelters covered the whole plot area (3.6 m × 4.4 m) and we constructed four rainout shelters in each block, totaling 12 shelters at each site (Figs. S1 & S2). To prevent aboveground and belowground water movement between treatment areas and their surroundings, plastic flashing was installed around each plot to a depth of 45 cm and extended 10 cm above the soil surface. We constructed shelters in April 2014 at the WGP site and June 2014 at the CD site. We removed precipitation catchment “troughs” from shelters at the end of each growing season (late September/early October) to allow for ambient winter precipitation and reinstalled them during the first 2 weeks of April in subsequent years.

Measurements
Seedling Densities. We monitored seedling density three times throughout the first establishment season: 19 May, 14 July, and 1 September 2014 at the WGP site and 19 May, 25 July, and 30 September 2015 at the CD site. Four sampling frames (0.5 x 1 m) were placed 1 m from each plot corner, ensuring at least a 30 cm buffer from plot edges. We identified seedlings to species, averaged counts by functional group over sampling frames within plots, and converted them to the 1 m² scale for analyses.

Aboveground and Belowground Biomass. We sampled peak aboveground biomass in four 0.1 m² subplots in July of the third year post-seeding (2016 at the WGP site and 2017 at the CD site). Aboveground biomass was clipped at ground level, sorted to species, dried for 48 hours at 60°C, and weighed. Aboveground biomass was converted to the 1 m² scale prior to data analyses. We collected belowground biomass (i.e. root biomass) from the same four subplots from which aboveground biomass was collected by extracting 7.6 cm diameter soil cores at two depths: 0–10 cm and 10–20 cm. Samples from each depth were combined in bags and frozen until they could be cleaned and measured. We thoroughly mixed soil and roots from each plot at each depth and collected three subsamples of 1,000 cm³ for
analyses following methods described by Schroth and Kolbe (1994). We collected roots by first sieving soil through a #20 soil sieve (0.85 mm screen) and then manually separating roots from soil, rocks, and other detritus. We then weighed roots after drying them for 48 hours at 60°C. Subsamples from each plot and depth were converted to the 1 m² scale prior to analyses. Similar methods have been employed in undisturbed ecosystems to estimate root biomass and aboveground to belowground biomass ratios (e.g. Mueller et al. 2013).

Data Analyses

We completed all statistical analyses in R version 3.5.1 (R Core Team 2014). Data from the two sites were analyzed separately. We used repeated measures linear mixed effects analysis of variance models (“lme4” package; Bates et al. 2014) to analyze effects of treatments on seedling densities, aboveground biomass, and belowground biomass. We analyzed seedling densities and aboveground biomass for the following functional groups: B. tectorum, seeded species, nonnative annual forb species, and nonnative perennial forb species. In seedling density models, we considered date and treatments as fixed effects, and block and plot as random effects to account for repeated measures over time. Because of low B. tectorum seedling densities in 2014 at the WGP site, we averaged counts across the whole season and removed date as a fixed effect for B. tectorum density analyses. In aboveground biomass models, we considered treatments as fixed effects and block as random. In the analysis of belowground biomass, we considered treatments and depth as fixed effects and block and plot as random effects to account for repeated measures by depth. As we were interested in all interactions, we retained all variables in statistical models. In all models, we checked residuals for normality and variance homoscedasticity by assessing quantile–quantile and residual versus predictor plots and applied appropriate transformations to data when needed. We investigated differences in means among treatments when interactions resulted in a p value of <0.1 or main effects resulted in a p value of <0.05. To determine differences between means of treatments with more than two levels, we performed Tukey’s HSD adjusted pairwise comparisons using the “lsmeans” package (Lenth 2016).

Results

Seedling Densities

At the WGP site, in the first establishment year (2014) date was significant for all functional groups that included date in the model, usually resulting in the highest densities of plants later in the season (Tables S2 & S3A). BRTE treatment resulted in higher Bromus tectorum densities (BRTE: 2.3 ± 0.6 plants m⁻²; No-BRTE: 0.1 ± 0.1) (F = 47.58; p < 0.01; Table S2). BRTE treatment led to the lowest densities of nonnative annual forbs, but only in the absence of SAP (BRTE × SAP interaction, F = 6.53; p < 0.01; Tables S2 & S3A). A precipitation × SAP interaction influenced seeded species density such that seeded species densities were over two times higher in treatments with ambient precipitation and SAP than in other treatments (Precip. × SAP interaction, F = 3.46; p = 0.07; Fig. 1A; Table S2). Across all treatments seeded species density in the first establishment year was greater than 30 plants/m² and was primarily comprised of annual and biennial forbs, including Cleome serrulata, Helianthus annuus, and Machaeranthera tanacetifolia. Nonnative annuals, primarily Salsola tragus, and nonnative perennials, primarily Convolvulus arvensis, also established at substantial densities of 6 plants/m² and 14 plants/m², respectively.

At the CD site, in the first establishment year (2015) a BRTE × precipitation × date interaction influenced total seedling density (BRTE × Precip. × Date interaction, F = 3.14; p = 0.06; Table S2). Across the season, ambient precipitation resulted in greater total seedling density, but only in BRTE plots. This trend was largely driven by differences at the September sampling date when B. tectorum densities were highest (Tables S2 & S3B). B. tectorum densities tended to be higher in ambient precipitation plots compared to drought plots, but the trend was only significant within BRTE treatment and only at the September sampling date (Tables S2 & S3B). Nonnative annual forb densities (i.e. Alyssum simplex, Descurainia sophia, and Sisymbrium altissimum) were lower overall in drought plots (8.12 ± 10.04 plants/m²) compared to ambient plots (65.81 ± 189.78 plants/m²) (F = 13.08; p < 0.01; Table S2). Seeded species density was lower in BRTE plots (2.82 ± 0.83 plants/m²) compared to no-BRTE plots (5.18 ± 2.91 plants/m²) (F = 12.29; p < 0.01; Table S2). Date influenced seeded species density and nonnative perennial forb density such that densities were highest at the mid-sampling date for both functional groups (F = 11.1; p < 0.01; Tables S2 & S3B). Seeded species density in the first establishment year at the CD site was quite low (<5 plants/m²) and comprised primarily of annual forb Helianthus annuus and perennial grass Pascopyrum smithii.
C. arvensis was the most common nonnative perennial species and was found at approximately 15 plants/m².

Functional Group Aboveground Biomass

At the WGP site, BRTE seeding resulted in higher aboveground B. tectorum biomass (BRTE: 171.28 ± 6.57 g/m², No-BRTE: 17.93 ± 1.92 g/m²) (F = 80.69, p < 0.01), lower aboveground biomass of all other species (BRTE: 64.54 ± 3.20 g/m²; No-BRTE: 188 ± 64.54 g/m²) (F = 11.97, p < 0.01), and lower aboveground biomass of nonnative annual forbs (BRTE: 17.93 ± 1.92 g/m²; No-BRTE: 124.38 ± 6.57 g/m²) (F = 31.52, p < 0.01) in the third year of the study (Tables S4 & S5). We detected a precipitation × BRTE interaction that resulted in an apparent trend for higher B. tectorum biomass in BRTE plots with drought (221.18 ± 30.13 g/m²) than all other treatment combinations (range: 6.28 ± 3.61 to 121.38 ± 28.06 g/m²) (precipitation × BRTE interaction, F = 4.17, p = 0.06; Tables S4 & S5). Seeded species aboveground biomass was higher with ambient precipitation than with drought but only in the absence of SAP (Table S4 & Fig. 1B). By the third year of the study, seeded species biomass was >20 g/m² at the WGP and dominated by perennial forbs and grasses including Linum lewisii, Ratibida columnifera, P. smithii, and Elymus trachycaulus.

At the CD site, BRTE treatment resulted in higher aboveground B. tectorum biomass (BRTE: 41.24 ± 12.49 g/m²; No-BRTE: 22.91 ± 9.95 g/m²) and lower aboveground biomass of all species, excluding B. tectorum (BRTE: 51.38 ± 7.97 g/m²; No-BRTE: 93.03 ± 13.11 g/m²) (Tables S4 & S5B). We detected a BRTE × SAP interaction that resulted in an apparent trend for higher B. tectorum biomass in BRTE plots compared to no-BRTE plots but only in plots without SAP (BRTE × SAP interaction, F = 3.47, p = 0.08) (Tables S4 & S5B). No treatment effects (p < 0.05) were detected on other functional groups at the CD site. Seeded species biomass was approximately 14 g/m² and primarily comprised of perennial grasses Ceratocloa carinata, P. smithii, and Elymus trachycaulus.

Total Aboveground and Belowground Biomass and Allocation

At the WGP site, a three-way precipitation × BRTE × SAP interaction influenced several third-year (2016) community-level metrics: aboveground biomass (F = 6.80, p = 0.02) (Tables 1 & S6; Fig. 2A), total biomass (F = 13.83, p < 0.01) (Tables 1 & S6), and root mass fraction (F = 11.79, p < 0.01) (Tables 1 & S6). Overall, no differences in these response variables were detected in BRTE plots (Tables 1 & S6; Fig. 2A). In no-BRTE plots, total biomass (aboveground and belowground) was highest in ambient plots without SAP (control) (417.74 ± 49.47 g/m²) and significantly greater than all other precipitation × SAP treatment combinations (ranging from 264.20 ± 16.06 to 300.7 ± 37.26 g/m²) (Tables 1 & S6). SAP treatment and drought treatment each independently resulted in lower total aboveground biomass than control, but only in no-BRTE plots (Table 5; Fig. 2A). SAP with ambient precipitation resulted in higher root mass fraction (largest proportion of biomass in roots) (0.5 ± 0.03) than all other treatment combinations (ranging from 0.25 to 0.32) besides plots with only drought (0.042 ± 0.01) (Tables 1 & S6). Belowground biomass was influenced by two interactions: precipitation × SAP and precipitation × BRTE (Table S6; Fig. 2B & C). Total belowground biomass was 33% lower with SAP compared to without SAP but only under drought treatment (Fig. 2B). The precipitation × BRTE interaction influenced belowground biomass such that belowground biomass was lower in BRTE plots than no-BRTE plots but only with ambient precipitation (Fig. 2C).
Amendment–drought–invasive grass interactions

Figure 2. Western Great Plains site 2016 (A) aboveground biomass under precipitation (Ambient, Drought), Bromus tectorum seed addition (BRTE), and super-absorbent polymer (SAP) treatments. Darker segments correspond to B. tectorum biomass and lighter segments correspond to biomass of all other species. Belowground biomass under (B) precipitation and SAP treatments averaged over BRTE treatments and (C) precipitation and BRTE treatments averaged over SAP treatments. Lighter segments correspond to shallow (0–10 cm) root biomass and darker segments correspond to deep (10–20 cm) root biomass. Different letters denote differences in (A) total aboveground, and (B) and (C) belowground biomass means that are statistically significant at the $\alpha = 0.05$ level. Error bars represent +SE.

At the CD site, third year (2017) total and aboveground biomass were influenced by two interactions: precipitation $\times$ BRTE and BRTE $\times$ SAP (Tables 1 & S6). When averaged over SAP treatments, total biomass (precipitation $\times$ BRTE interaction, $F = 12.09$, $p < 0.01$) (Tables 1 & S6) was higher in plots with ambient precipitation and without BRTE than all other treatments. Similarly, aboveground biomass was higher in plots with ambient precipitation and without BRTE than all other treatments (precipitation $\times$ BRTE interaction, $F = 13.17$, $p < 0.01$) (Table S6, Fig. 3B). Aboveground biomass was influenced by a SAP $\times$ BRTE interaction such that aboveground biomass was lower with BRTE, but only in the presence of SAP (Fig. 3A). Root mass fraction was also influenced by a SAP $\times$ BRTE interaction ($F = 4.64$, $p < 0.05$) such that plots with SAP and BRTE had a higher root mass fraction compared to no-BRTE plots with and without SAP (Tables 1 & S6). Drought resulted in lower belowground biomass (Table S6; Fig. 3D) and a BRTE $\times$ SAP $\times$ depth interaction resulted in belowground biomass at 0–10 cm that was higher in plots with SAP and BRTE than BRTE alone (Table S6; Fig. 3C).

Discussion

Seedling Densities

We predicted that SAP would increase seeded species establishment and biomass in the absence of BRTE treatment and that effects would be most pronounced under drought. However, positive effects of SAP on seeded species were limited to the WGP site and were not influenced by BRTE treatment. At the WGP site SAP initially increased seeded species densities by over 100% but, contrary to our hypothesis, effects were only detected with ambient precipitation. This positive effect was short-lived and by the third year of the study aboveground biomass of seeded species was highest in plots without SAP with ambient precipitation. Several studies have identified similar, short-term effects of SAP on plant establishment in restoration projects. Working with native shrub species in the western United States, Minnick and Alward (2012) observed higher short-term (4 month) transplant survival of native shrubs Artemesia tridentata, Ericameria nauseosa, and Atriplex canescens with SAP application, but effects were undetectable 4.5 years after transplanting. Similarly, working in...
tropical dry forests, Werden et al. (2017) observed increased initial transplant survival of various tree species with SAP application, but effects were not present after 2 years. In our study, it is possible that the positive influence of SAP on seeded annual establishment in the first year, primarily of Cleome serrulata and Helianthus annuus, prevented initial establishment of perennial species and thus influenced seeded species biomass 3 years later.

SAP effects on first-year seedling establishment were undetectable under drought conditions. Prior studies have found more pronounced SAP effects under deficit moisture conditions. For example, Eneji et al. (2013) found SAP to have the greatest effect on corn biomass under deficit water conditions. Although our results may seem to contradict Eneji et al. (2013), soil moisture conditions in our study differed from theirs. In Eneji’s study, the greatest deficit water treatment had soil matric potentials of 9 kPa pressure; 9 kPa of pressure in our loam/clay loam soils would translate to approximately between 29 (loams) and 38% (clay loam soils) volumetric water content. Even at their highest soil moisture content (approximately 23% volumetric water content), the soils in our study were far drier than the deficit irrigation conditions in Eneji’s study (Garbowski 2016). It is possible that beneficial effects of SAP are less likely to be observed below a threshold soil water content and that positive effects of SAP amendment observed in less water-limited agricultural settings may not translate to aridland restoration projects with low antecedent moisture conditions.

Soil texture may also be a driving factor influencing SAP effectiveness, as the swelling capacity and water retention of SAP may be less restricted in sandy soils than in heavy-textured clay or loam soils (Hüttermann et al. 2009; Agaba et al. 2010; Hussien et al. 2012; Guilherme et al. 2015). In fact, several studies have found stronger SAP effects in soils with relatively higher sand than clay contents. In agricultural settings, working with trees and tomatoes, respectively, Agaba et al. (2010)
and Gomez (2015) found that SAP application improved tree growth and total tomato yield more in sandy soils than in heavy-textured clay loam soils. Soils at both of our sites are loam/clay loam and, thus, SAP effects may have been limited due to their textures. SAP amendment in restoration settings may be most effective in soils with low water-holding capacity (i.e. sandy soils) but additional research is needed to clarify interactive effects of soil texture and SAP on developing plant communities.

**Aboveground and Belowground Biomass and Allocation**

We predicted that SAP would result in higher aboveground biomass and lower belowground biomass and root mass fraction under all treatment combinations. However, we observed site-specific interactive effects among precipitation, BRTE, and SAP treatments on all components of community-level biomass. While we did not observe reduced effects of SAP on seeded species establishment and biomass with BRTE treatment as predicted, at WGP, BRTE treatment negated effects of SAP and drought on total aboveground biomass. In the absence of BRTE treatment, SAP and drought both resulted in lower aboveground biomass. At the CD site, BRTE and drought interacted to influence aboveground and belowground biomass in unique directions.

The variable results of SAP on aboveground plant biomass in our study mirror inconsistencies in the literature. Positive effects of SAP on plant biomass in containerized (e.g. El-Asmar et al. 2017) and agricultural (e.g. Agaba et al. 2010) settings have been found in several studies. However, Williamson et al. (2011) found negative effects of SAP on corn biomass under adequate irrigation. In a similar study in aridland restoration in Colorado, Johnston and Garbowski (2019) found SAP effects varied by site, year, and functional group. As most studies of SAP have been conducted in agricultural or glass-house settings (reviewed in Hüttermann et al. 2009), results may not translate to restoration settings in which many plants with varied species-specific responses to SAP (e.g. Rubio et al. 1992; Frantz et al. 2005; Johnston & Garbowski 2019) potentially compete for water held by SAP. Our result of higher *Bromus tectorum* biomass in no-BRTE plots with SAP suggests that SAP amendment may promote nonnative species in some cases and potentially increase competition against native species. Johnston and Garbowski (2019) observed a similar trend for higher *B. tectorum* cover with SAP amendment at one of two study sites. Additional studies that explicitly alter precipitation seasonality or focus on species-specific responses to SAP may further elucidate conditions under which SAP amendment may improve restoration outcomes.

Furthermore, most studies on SAP have focused on aboveground plant responses, even though soil amendments may uniquely influence belowground biomass and allocation patterns. At both sites root mass fraction was higher with SAP, but effects depended on other treatments. At the WGP site, root mass fraction was greatest with SAP and ambient precipitation. At the CD site, SAP resulted in a higher root mass fraction in BRTE plots. Theory predicts that an increase in soil resources should drive plants to invest more heavily in aboveground structures (Bloom et al. 1985; Poorter & Nagel 2000). Thus, it is surprising that SAP addition, which aims to increase soil resources, resulted in higher root mass fraction in our experiment. Similar results have been noted in several studies from dryland systems that found increased root proliferation resulting from addition of soil amendments aimed at increasing soil resources (e.g. Fuentes et al. 2010; Benigno et al. 2012) or under increased precipitation (Bai et al. 2010). As belowground biomass of grasses can be more responsive to nitrogen increase in water-limited systems compared to forbs (Bai et al. 2015), it is possible that grasses, which comprised 60% and 45% of our communities at the WGP and CD sites, respectively, contributed to the increase in root mass fraction with SAP. Because we were unable to separate roots by species, we cannot discern whether native or nonnative species caused these trends.

Belowground biomass was influenced by treatment interactions at both sites: SAP × precipitation and BRTE × precipitation at the WGP site and BRTE × SAP at the CD site. At the WGP site, the effects of drought on belowground biomass seemed to be exacerbated by SAP, resulting in lower root biomass in plots with drought and SAP than in plots with drought alone. Also, at the WGP site, BRTE treatment resulted in lower belowground biomass but only under ambient conditions. At the CD site, SAP resulted in higher root biomass but only in BRTE plots. As roots of many plant species (Hodge 2004), including *B. tectorum* (Mack & Pyke 1983), are highly plastic in response to variable environmental conditions, it is not surprising that treatments interacted to influence belowground biomass in our study. The reason why BRTE interactions with SAP and drought treatments varied by site remains unclear, although a shift in species composition offers a partial explanation.

Where seeded, *B. tectorum* comprised about 80% and 45% of total aboveground biomass at the WGP and CD sites, respectively. At the WGP site, BRTE interacted with precipitation treatments such that belowground biomass was lower in plots with ambient precipitation and BRTE compared to ambient precipitation without BRTE. Based on aboveground values of *B. tectorum* biomass (>80% of aboveground biomass where seeded and <10% in unseeded plots), it is reasonable to assume that it comprised a similar proportion of belowground biomass at this site. As *B. tectorum* has high specific root length, low root density, and a lower root diameter than many native species (Ray-Mukherjee et al. 2011), it is possible that differences in root traits among dominant native species and *B. tectorum* drove differences in root biomass results at the WGP site. At the CD site, we observed higher root biomass in BRTE plots with SAP compared to BRTE plots without SAP. As *B. tectorum* relies on rapid root proliferation to quickly explore resources patches (Arredondo & Johnson 1999, 2011), it is possible that *B. tectorum* plants responded uniquely to “reservoirs of water” held by SAP within the soil (Wu et al. 2008; Zohuriaan-Mehr et al. 2010). Although untested, *B. tectorum* population differences may have influenced these site-specific results. *B. tectorum* populations from warm desert regions have been shown to allocate relatively more biomass to roots than populations from more
mesic areas (Meyer et al. 2016). Because locally collected seeds were used for BRTE treatments at both sites, it is possible that *B. tectorum* plants from the more variable CD site (Brooks et al. 2016) displayed more pronounced belowground responses to resource manipulations as an adaptation to variable environmental conditions (Venable & Brown 1988; Moles & Westoby 2004). Because we were unable to separate roots by species in our analyses, these interpretations remain speculative.

The result of lower root biomass with SAP and drought at the WGP site is unexpected and somewhat concerning. SAP application is often championed as a way to improve plant establishment and performance in deficit moisture conditions. But, because establishing plants in dryland communities often require deep and well developed root systems to access deep soil water (Padilla & Pugnaire 2007) or to quickly utilize pulse precipitation (Phillips et al. 2006; Bai et al. 2010), SAP application that may result in lower root biomass under deficit moisture could negatively impact long-term plant survival or future productivity (Doll et al. 2011).

Based on the seedling and biomass results presented here, it appears that the effects of SAP amendments in aridland restoration may be site specific and vary depending on what measure of the plant community is being assessed. Although SAP addition initially resulted in higher seeded species establishment at the WGP site, by the third year of the study SAP effects were undetectable, and no SAP effects on seeded species at the CD site were detected. Treatments interacted to influence all components of community-level biomass (total biomass, aboveground biomass, and belowground biomass) as well as the root mass fraction, but results were highly variable and often unique when assessing aboveground versus belowground metrics.

The variable results presented here reflect discrepancies related to SAP effects on plant productivity in the literature. As climate conditions in the arid and semiarid western United States are predicted to become more variable (Archer & Predick 2008) and invasive species will continue to hinder successful revegetation efforts (Brown et al. 2008), soil amendments such as SAP that can interact with environmental variables and can have long-term effects on the trajectories of restored plant communities (e.g. Paschke et al. 2005; Dietterich & Casper 2017) should be used with caution. As in other studies (Johnston & Garbowski 2019) SAP benefited both seeded species and *B. tectorum*. Future research in relation to SAP should therefore focus on competitive dynamics among invasive and seeded species. Furthermore, as root development and belowground productivity are important indicators of plant survival (Padilla & Pugnaire 2007) and future aboveground productivity (Doll et al. 2011) but may respond uniquely to restoration treatments, restoration ecologists and practitioners should consider the effects of soil amendments on belowground structures to develop a more thorough understanding of how restoration activities impact developing plant communities.

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Supporting Information
The following information may be found in the online version of this article:

Figure S1. Rainfall exclusion shelter used to impose drought treatments on plots.

Figure S2. Experimental block at Cold Desert field site in southwestern Colorado.

Table S1. Seed mixes for the Western Great Plains and Cold Desert study sites.

Table S2. Analysis of variance results for main effects and interactions of B. tectorum seeding (BRTE), precipitation (Drought), and super-absorbent polymer (SAP) treatments for densities of plant functional groups at the Western Great Plains and Cold Desert sites.

Table S3. Means (SE) for interactions of B. tectorum seeding (BRTE), precipitation (Drought) super-absorbent polymer (SAP) treatments, and date for seedling densities at the a) Western Great Plains and b) Cold Desert sites.

Table S4. Analysis of variance results for main effects and interactions of B. tectorum seeding (BRTE), precipitation (Drought), and super-absorbent polymer (SAP) treatments for aboveground biomass of various functional groups at the Western Great Plains and Cold Desert sites.

Table S5. Means (SE) for interactions of B. tectorum seeding (BRTE), precipitation (Precip.), and super-absorbent polymer (SAP) treatments for aboveground functional group biomass.

Table S6. Analysis of variance results for main effects and interactions of B. tectorum seeding (BRTE), precipitation (Drought), super-absorbent polymer (SAP) treatments, and date for total biomass (roots + shoots), aboveground biomass, root mass fraction (RMF), and belowground biomass.

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