THESIS

RESTORING SEMI-ARID LANDS WITH SUPERABSORBENT POLYMERS UNDER REDUCED PRECIPITATION AND THREAT OF *BROMUS TECTORUM* INVASION

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2016

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ABSTRACT

RESTORING SEMI-ARID LANDS WITH SUPERABSORBENT POLYMERS UNDER REDUCED PRECIPITATION AND THREAT OF *BROMUS TECTORUM* INVASION

Restoration of arid ecosystems in the western United States (US) is often constrained by low and variable moisture and invasion by exotic species. After disturbance, variability in resources as well as inherent soil moisture and temperature regimes may influence the susceptibility of an ecosystem to exotic species invasion. The invasive winter annual grass, *Bromus tectorum* (*B. tectorum*), is particularly competitive in disturbed semi-arid areas, has invaded tens of millions of hectares throughout the western US, and its range is projected to expand under predicted climate scenarios. Increasing soil moisture and resources in restoration projects may decrease soil moisture variability and promote establishment of a native plant community that is resilient to disturbance and resistant to invasion of *B. tectorum.* With their ability to absorb moisture when it is abundant and slowly release it over time, superabsorbent polymers (SAP) may increase overall soil moisture and decrease soil moisture variability during restoration. In this study, we aimed to investigate the interactive effects of precipitation timing, drought, *B. tectorum*, and SAP on soil resources and developing restoration plant communities.

The study was established in 2014 at two climatically distinct sites: one site was located on the Eastern Slope (Larimer County) and one on the Western Slope (San Miguel County) of Colorado. Both sites fall under the mesic soil temperature regime and ustic-aridic soil moisture regime but vary in their susceptibility to invasion largely due to differences in seasonal precipitation patterns. While the Eastern Slope receives most of its growing season moisture in the early spring and summer, the Western Slope site receives most of its growing season moisture in the late summer and early fall. Two levels of three treatments (drought: exclusion of 66% of ambient rainfall or ambient rainfall; *B. tectorum* presence: 465 seeds m^{-2} or none; SAP: 26 g m^{-2} or none) were fully crossed in three blocks at each site resulting in a complete factorial experiment. After one year of monitoring soil moisture, plant available nitrogen (at the Western Slope site), and plant community responses, we observed significant effects of exclusion at both sites on soil resources and the developing plant communities. Independent and interactive effects of drought and SAP at the Eastern Slope site and drought and *B. tectorum* at the Western Slope site influenced plant communities and soil resources.

Overall *B. tectorum* establishment was low on the Eastern Slope and high on the Western Slope in the first year of the study. At the Eastern Slope site, drought limited seeded species recruitment late in the season and the positive effects of SAP on seeded species were apparent only under ambient precipitation conditions. Total and annual seedling densities were higher under SAP treatments at this site. At the Western Slope site, total seedling densities were lower in drought treatments, and native seedling densities were lower in drought treatments at the end of the growing season. The effects of *B. tectorum* on seeded annuals at the Western Slope site depended on date and precipitation treatment. Seeded annuals densities were highest in mid-summer in treatments without *B. tectorum* and ambient precipitation. Interestingly, at the Western Slope site, *B. tectorum* under ambient precipitation had a stronger negative impact on soil moisture at 30 cm depth than drought treatments regardless of level of *B. tectorum* or SAP. *B. tectorum* also decreased soil moisture at 5cm depth early in the season at the Western Slope site while exclusion treatments decreased soil moisture later in the growing season at both sites.

Our results demonstrate that drought negatively impacts soil resource availability and native plant community development in restoration. Techniques that improved water and nutrient availability especially under drought conditions are needed to promote native species establishment. While SAP did not improve soil moisture, higher seedling densities were found in SAP treatments at one site, especially under ambient conditions. This suggests that incorporating SAP into the soil may improve plant establishment, but effectiveness is likely affected by antecedent soil moisture and precipitation patterns.

In our study, *B. tectorum* negatively impacted soil moisture and native plant establishment at one site demonstrating the need for management of this species in restoration of semi-arid lands.

ACKNOWLEDGEMENTS

I would like to acknowledge the countless friends, technicians, family members, and students that together volunteered over 1,600 hours to develop and implement this study including but not limited to: Peder Englestad, Lindsay Ringer, Collin Petterson, Katharine Lynch, Garrett Stephens, Mary Cole, Shelby Ruettiger, Karen Holcomb, Tyler Keller, Nick Monzango, Jeaninne Nesky, Max Loeb, Anthony Kennedy, and Sunny Kearcher.

This research was supported by the Colorado Division of Parks and Wildlife (CPW). I would like to thank CPW for financial and logistical assistance in maintaing smooth field operations. Specifically, I would like to thank Murphy Jacox and Christine Harty for their never ending assistance and hositality.

I would also like to thank my family for their encouragement in this endeavour. In addition, I would like to thank Anthony for reminding me to stop to enjoy the flowers while I study them.

I would like to thank my committee members, Stuart Hardegree and Meagan Schipanski for their contributions to this study and guidance in conducting ecological research.

Most importantly, I would like to thank my advisors, Cini Brown and Danielle Johnston, for their support and mentorship throughout my research and academic pursuits. Completion of this project would not have been possible with out their encouragement, advice, and patience.

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CHAPTER 1: RESTORATION OF SEMI-ARID LANDS UNDER THREATS OF DROUGHT AND INVASION BY EXOTIC SPECIES

INTRODUCTION

Arid and semi-arid lands that cover over 40% of Earth's land surface and sustain over a third of the world's population are especially vulnerable to degradation due to high human population pressures and high sensitivity to disturbance (Millennium Ecosystem Assessment 2014). As ecosystem dynamics in arid systems are largely driven by precipitation (Noy-Meir 1973) climate changes including more variable precipitation can increase ecosystem sensitivity to disturbance and decrease resistance to invasion (Chambers et al. 2007). Reestablishing vegetation is vital for restoring structure, process, and function to degraded arid ecosystems. In the western United States (US), successful restoration of arid and semi-arid ecosystems is often constrained by low and variable moisture (Hardegree et al. 2012) and invasion by exotic species . Developing restoration methods that mitigate the negative impacts of water and resource fluctuations on plant establishment is imperative for directing these valuable ecosystems towards sustained recovery and stable functioning.

In the western US, millions of acres of land have been disturbed or degraded by development, grazing, natural resource extraction, fire, and/or climate change. Abrupt alterations to habitats can promote invasions (Vitousek and DAntonio 1992, Mack et al. 2000) by decreasing competition (Gross et al. 2005) and increasing nutrients (Burke and Grime 1996a). Exotic annual grasses are particularly competitive in disturbed areas (Hobbs and Huenneke 1992) and have established across much of the arid and semiarid Western US (Germino et al. 2016). While still an evolving area of research, the idea that a species' ability to invade is influenced by specific phenological and physiological attributes, the biotic and abiotic environment in which the species is introduced, and interactions between the two is generally accepted (Levine et al. 2003, Brown et al. 2008).

Spatial and temporal variability in resources (Davis et al. 2000) coupled with partitioning of resources among species (Rice 2009) can create ‘windows of invasion opportunity’ (or vacant niches) for exotic species (Drake et al. 2006). The distinct phenologies of many invasive species may allow them to exploit temporally vacant niches and pre-empt limited resources when competition from native species is low (Cleland et al. 2011). In addition to phenologically-based differences in resource use, physiological attributes including higher resource use efficiencies (Funk and Vitousek 2007, Cavaleri and Sack 2010), high growth (Mason et al. 2008) and root elongation rates (Larson et al. 2015), and flexible requirements for germination (Wainwright and Cleland 2013) may further benefit invasive species success in disturbed systems. Invasive species’ abilities to rapidly utilize scarce resources may result in a ‘priority advantage’ that can lead to increased establishment and dominance of invasives in a plant community (Wolkovich and Cleland 2014).

The winter annual grass, *Bromus tectorum* L. (cheatgrass or downy brome, hereafter, *B. tectorum)*, is a particularly troublesome exotic and has invaded tens of millions of hectares in the western US (Bradley and Mustard 2006). Native to Europe and southwestern Asia, since its introduction in the late 1800’s, *B. tectorum* has significantly transformed western US ecosystems by decreasing fire return intervals from centuries to decades (Vitousek and D'Antonio 1992), reducing forage for livestock and habitat for wildlife (Knapp 1996) and altering nutrient cycles (Evans and Belnap 1999) and soil properties (Belnap et al. 2005, 2016). *B. tectorum*’s success in the arid western US can be attributed to its life history and phenology. 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 and produces seed in the spring, completing its life cycle before native species are most active. In comparison to native perennial grasses, *B. tectorum* can germinate at lower temperatures and water potentials (Harris 1967, Hardegree et al. 2013), germinate more rapidly (Larson et al. 2015), and develop roots (Harris 1967) and shoots faster and earlier in the season (Aguirre and Johnson 1991). Because of these attributes, *B. tectorum* is able to utilize moisture and nutrients earlier in the season than seedlings of native perennial plants (Aguirre and Johnson 1991). These competitive advantages may be amplified under projected precipitation changes, as *B. tectorum* has been shown to compete more effectively when summer moisture is low (Bradley 2009) and when soil moisture is variable from year to year (Chambers et al. 2007).

B. tectorum's range is likely to expand under current and projected climate scenarios (Bradley and Mustard 2006; Bradley 2009). In addition to *B. tectorum*'s competitive traits, abiotic factors influence where and when *B. tectorum* is able to establish. Recently, soil temperature and moisture regimes have been integrated into broader concepts of ecosystem resilience to disturbance and resistance to invasion (R&R). Resilience is defined as an ecosystem's ability to reorganize and regain structure, function, and processes after disturbances such as fire or drought (Germino et al. 2016) while resistance refers to an ecosystem's ability to maintain ecosystem structure, processes and function despite stress. Chambers (2013) has ranked ecosystems throughout the western US on a spectrum of resilience and resistance: areas with colder temperature regimes (frigid/cryic) and wetter soil moisture regimes tend to have the highest potential R&R, while areas with warm (mesic) and dry (aridic) soil regimes have the lowest R&R. Ecosystem resistance to species invasions is influenced by both climate and interactions between the invader and the resident plant community (Chambers et al. 2013). As disturbances often remove much of the established vegetation, climate may be especially influential in determining where invasive species are able to establish following disturbance. Understanding how climate influences invasions and community development in disturbed ecosystems could greatly inform management and restoration of arid lands throughout the western US.

In addition to extreme climatic events, interannual as well as annual and seasonal weather fluctuations result in seedbed microclimate that is highly variable (Flerchinger and Pierson 1997) and potentially unfavorable to germinating and emerging native seedlings (Roundy et al. 2007, James et al. 2011) but favorable for *B. tectorum* establishment (Roundy et al. 2007, Hardegree et al. 2013). Improving seedbed microclimate and increasing the availability of soil resources at times when they are most limiting for native plants in arid-land restorations may improve native seedling establishment and decrease the window of opportunity for invasive species establishment. With their ability to absorb moisture when soils are wet and slowly release it over time (Agaba et al. 2010), superabsorbent polymers (SAP) may ameliorate the negative impacts of intermittent drought on native species establishment in restoration. In addition, SAP has been shown to retain nutrients in an agricultural setting (Islam et al. 2011), and could potentially bind nutrients early in the season reducing uptake by *B. tectorum.*

SAP has been utilized as a soil amendment for over 40 years primarily in agricultural settings to increase soil water retention, improve soil physical properties, and increase plant survival under periodic water stress (Murphy et al. 2010, Islam et al. 2011, Yang et al. 2014, Wang et al. 2016). Still, there have been relatively few studies of SAP treatments for vegetation, and effects on seedling establishment have been highly variable (Rubio et al. 1992, Newhall et al. 2004, Mangold and Sheley 2007, Lucero et al. 2010). In 2012, Johnston used SAP as a soil amendment in research focused on reestablishing vegetation to simulated oil well drilling pads. SAP was added at two sites in northwestern Colorado at rates of 6.7 g m^{-2} and 30.8 g m^{-2} in granulated form to drill-seeded rows of native wheatgrasses. *B. tectorum* was broadcast at a rate of 300 seeds m^{-2}. In the first year-post treatment, perennial grass densities were higher at both sites when SAP was added, although the effect at the site with the lower SAP addition rate was not statistically significant. In following years, no differences in perennial grass densities were observed with SAP, but densities of *B. tectorum* were significantly lower when it was present. Although a potentially promising restoration tool, information regarding interactions of SAP with precipitation variability, invasive species, and restoration of arid lands is limited.

In 2014 at two sites in Colorado, we established a study to investigate the interactive effects of SAP, precipitation timing and amount, and *B. tectorum* on developing seeded plant communities. Colorado's unique precipitation patterns together with the presence of the invasive annual grass *B. tectorum* provide an ideal model system to study the effects of precipitation and resource availability on native and invasive species establishment in restoration. While receiving similar amounts of precipitation annually, timing of precipitation differs between the two sites. The Eastern Slope site receives the majority of its moisture in the spring and early summer and is characterized by spring and summer moisture (mesic/ustic-aridic) (Figure 1) and moderate susceptibility to invasion by *B. tectorum* (Brooks et al. 2016). In contrast, the Western Slope site receives most of its moisture in the late summer and early fall. Located on the eastern edge of the Colorado Plateau, the Western Slope site is characteristic of the mesic soil temperature regime and ustic-aridic moisture regime, and has high susceptibility to invasion by *B. tectorum* (Brooks et al. 2016).

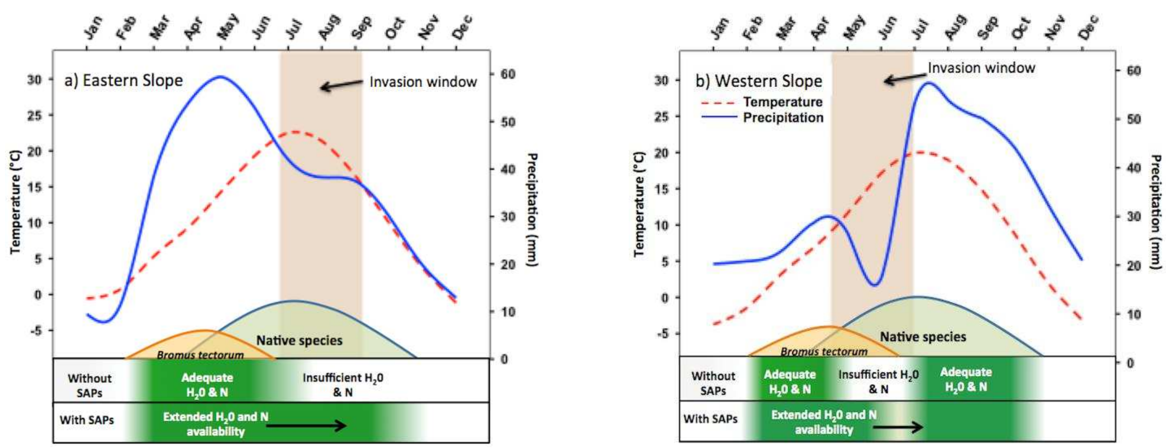

Figure 1 Thirty-year average temperature and precipitation for the a) Eastern Slope and b) Western Slope study sites. Resources are most limited during the warmest and driest months of the growing season at both sites: April-June at the Western Slope site and July-Aug at the Eastern Slope site. In disturbed areas, these resource-limited periods may provide 'windows of opportunity' for invasive species establishment. SAP will amplify and extended resource availability during stressful periods, improving native seedling establishment and survival and increasing competition from natives.

OBJECTIVES

1) Evaluate the impacts of exclusion of 66% ambient rainfall on native and *B. tectorum* establishment and soil resources (volumetric water content and nitrogen).

2) Evaluate the establishment and impacts of *B. tectorum* on native plant community development and soil resources.

3) Evaluate the effects of SAP amendments on native plant and *B. tectorum* establishment and soil resources.

4) Evaluate the interactions of precipitation amount and timing, *B. tectorum*, and SAP on plant establishment and soil resources in restored communities.

EXPECTED OUTCOMES

As moisture is a key factor limiting plant establishment in semi-arid areas, we expected to see decreased native seedling recruitment in rainfall exclusion treatments. We also anticipated lower native seedling densities in the presence of *B. tectorum* due to its ability to quickly invade disturbed sites and outcompete native species. We expected to see increased native seedling recruitment with SAP treatments due to increased soil volumetric water content especially at resource limited times and a shift in available plant nitrogen from early to late in the season (Figure 1). We anticipated the effects of SAPs to be most pronounced under exclusion because seedlings in these treatments would benefit most from improved soil moisture and nutrient availability. Furthermore, we anticipated increased soil moisture throughout the growing season and lower plant available nitrogen during the early portions of the season with SAP treatment. As a result of these shifts in moisture and nitrogen availability, we expected increased densities of native species that in turn would lead to lower densities of *B. tectorum.*

CHAPTER 2: RESTORATION OF SEMI-ARID LANDS WITH SUPERABSORBENT POLYMERS UNDER REDUCED PRECIPITATION AND THREAT OF *BROMUS TECTORUM* INVASION

INTRODUCTION

Restoration of arid ecosystems in the western United States (US) is often constrained by low and variable moisture (Hardegree et al. 2012) and invasion by exotic species (Chambers et al. 2007). As ecosystem dynamics in arid systems are largely driven by precipitation (Noy-Meir 1973), climate changes, including more variable precipitation, can increase ecosystem sensitivity to disturbance and decrease resistance to invasion (Chambers et al. 2007, Jiménez et al. 2011). Successful restoration hinges on reestablishing diverse, native, plant communities that are both resilient to future perturbations and resistant to invasion by exotic species.

Disturbances that remove resident plants can foster invasions by decreasing competition and increasing resources (Burke and Grime 1996b, Gross et al. 2005). In addition to phenologically-based differences in resource use, physiological attributes including higher resource use efficiencies (Funk and Vitousek 2007, Cavaleri and Sack 2010), high growth (Mason et al. 2008) and root elongation rates (Larson et al. 2015), and flexible requirements for germination (Wainwright and Cleland 2013) may further benefit invasive species success in disturbed systems. Invasive species' abilities to rapidly utilize scarce resources may result in a 'priority advantage' that can lead to increased establishment and dominance of invasives in a plant community (Wolkovich and Cleland 2014).

The winter annual grass, *B. tectorum*, exemplifies many of these invasive characteristics and has been highly successful in invading arid systems in the western US. *B. tectorum* has a phenology distinct from native species, germinating in the fall, remaining dormant throughout the winter, rapidly growing in the spring and completing its life cycle by the early summer (Rice et al. 1992) when native species are beginning to grow most actively. Additionally, the competitive advantage of *B. tectorum* may be improved during resource-limited times, as it has been shown to compete more effectively when summer moisture is low (Bradley 2009) or variable from year to year (Chambers et al. 2007).

Considering the influence of soil temperature and moisture regimes on ecosystem resilience and resistance (R&R) may greatly improve restoration planning and methods (Maestas et al. 2016). For example, as areas with warm (mesic) and dry (aridic) soil regimes have lower R&R compared to areas with colder temperature regimes (frigid/cryic) and wetter soil moisture regimes (Brooks et al. 2016), the threats of invasion post disturbance in the prior may be substantial and restoration plans should include aggressive invasive species management. In addition to regional soil temperature and moisture regimes, local seedbed microclimates can be highly variable (Flerchinger and Pierson 1997) and influence seedling establishment. Improving seedbed microclimate and increasing the availability of soil resources at times when they are most limiting may improve native seedling establishment and decrease the 'window of opportunity' for invasive species establishment.

With their ability to absorb moisture when soils are wet and slowly release it over time (Agaba et al. 2010), superabsorbent polymers (SAP) may ameliorate the negative impacts of intermittent drought on native species establishment in restoration. In addition, SAP has been shown to retain nutrients in an agricultural setting (Islam et al. 2011), and could potentially bind nutrients early in the season reducing uptake by *B. tectorum.* Johnston (2012) found SAP treatments improved perennial grass densities one year after incorporation and decreased *B. tectorum* cover in subsequent years in restoration of simulated oil drilling well pads in northwestern Colorado. Although a potentially promising restoration tool, information regarding the interactions of SAP with precipitation variability and invasive species in restoration of arid lands is limited.

In 2014 we established a study to investigate the interactive effects of SAP, precipitation timing and amount, and *B. tectorum* on developing plant communities at two sites in Colorado. Colorado's unique precipitation patterns together with the presence of the invasive annual grass, *B. tectorum*, provide an ideal model system to study the effects of precipitation and resource availability on native and invasive species establishment in restoration. While receiving similar amounts of precipitation annually, the Eastern Slope of Colorado is receives the majority of its precipitation in the spring and early summer and characteristic of mesic/ustic-aridic soil temperature and moisture regimes and has moderate susceptibility to invasion. The Western Slope of Colorado also falls under the mesic/ustic-aridic soil temperature and moisture regimes but in contrast receives most of its moisture in the late summer and early fall and is characterized as having high susceptibility to invasion (Figure 1).

The primary objectives of this study were to:

1) Evaluate the impacts of exclusion of 66% ambient rainfall on native plant and *B. tectorum* establishment and soil resources (volumetric water content and nitrogen) in a restoration setting.

2) Evaluate the establishment and impacts of *B. tectorum* on native plant community development and soil resources in a restoration setting.

3) Evaluate the effects of SAP amendments on native plant and *B. tectorum* establishment and soil resources in a restoration setting.

4) Evaluate the interactions of precipitation amount and timing, *B. tectorum*, and SAP on plant establishment and soil resources in a restoration setting.

METHODS

Study sites and climate characteristics

To investigate the effects and interactions of precipitation amount and timing, drought, and SAP on restored plant community development, we chose two sites in Colorado with similar management histories and total annual precipitation amounts but varied timing of precipitation. The two study sites are located in Colorado: one in the northeastern part of the state (Eastern Slope site) at the Colorado State Waverly property, in Larimer County, CO (Latitude: 40.708464, Longitude: -105.106834), USA and one on the Western Slope (Western Slope site) at Dry Creek Basin State Wildlife Area in San Miguel County, CO (Latitude: 38.060054, Longitude: -108.512885), USA. Since the 1950's, both sites had been tilled and seeded with pasture grasses and grazed by cattle or sheep, or both. Grazing ceased at the Eastern Slope site in the 1980s and at the Western Slope site in the mid-2000s. Soils at both sites are loams or clay loams with clay content ranging from 23 – 33%. Prior to establishing the study in 2014, various native and exotic species occupied the study areas. The weedy forb, *Convolvulus arvensis* L. (bindweed) and the native shrub, *Ericameria nauseosa* (Pallas ex Pursh) G.L. Nesom & Baird (rubber rabbitbrush), were common at both locations. Additional common species at the Eastern Slope site included *Helianthus annus* L. (annual sunflower), *Cleome serrulata* Pursh (Rocky Mountain bee plant), *Aristida purpurea* Nutt. (purple threeawn), *Agropyron cristatum* L. (crested wheatgrass) and *Pascopyrum smithii* (Rydb.) Á. Löve (western wheatgrass). Common species at the Western Slope site included *Sphaeralcea coccinea* (Nutt.) Rydb. (scarlet globemallow), *Alyssum simplex* Rudolphi (alyssum) and *Bromus tectorum* L. (cheatgrass or downy brome).

Both sites are semi-arid receiving approximately 400 mm of precipitation each year. Growing season (March – October) precipitation at the sites is similar (Eastern Slope: 320 mm, Western Slope: 270 mm) but the seasonal timing varies between the two sites. The Western Slope of Colorado receives most of its growing season precipitation (270 mm at the site) from Subtropical Pacific moisture in the late summer and early fall in a pattern known as the North American Monsoon (Cook and Seager 2013). The Eastern Slope site, on the other hand, receives the majority of its growing season precipitation (320 mm) in the spring and early summer from the Gulf of Mexico and subtropical regions of the US (Grantz et al. 2007).

Site preparation

To prepare sites for SAP incorporation and seeding, the study blocks at both sites were mowed with a brush mower to remove tall vegetation and shrubs (June 2013 at the Western Slope site and August 2013 at the Eastern Slope site) and then sprayed with a solution of glyphosate at a rate of 4.480 kg ai ha^{-1} (1 gal of 41% glyphosate acre^{-1}). Glyphosate was sprayed two times at the Eastern Slope site in the fall of 2013

(Oct 26, Nov 13). Glyphosate was sprayed at the Western Slope site twice (August, September 2013) and another two times in the spring (April, May 2014). Prior to seeding, experimental areas were tilled with a rototiller to a depth between 5-10 cm. Trenches were constructed around the perimeter of each plot to a depth of 45 cm and surrounded by two layers of 5 mm thick plastic to isolate treatment effects to appropriate plots and prevent root scavenging.

Experimental Design

Three blocks were placed at each site in areas that contained relatively uniform vegetation and were under 10° slope. Three treatments (exclusion, *B. tectorum*, SAP) were fully crossed in a 2 x 2 x 2 factorial design that resulted in eight treatment combinations per block. Treatment combinations were randomly assigned to 4.9 m x 3.7 m (18.13 m $^{-2}$) plots within each block in a checkerboard pattern to prevent treatments from interacting with one another (Figure 2).

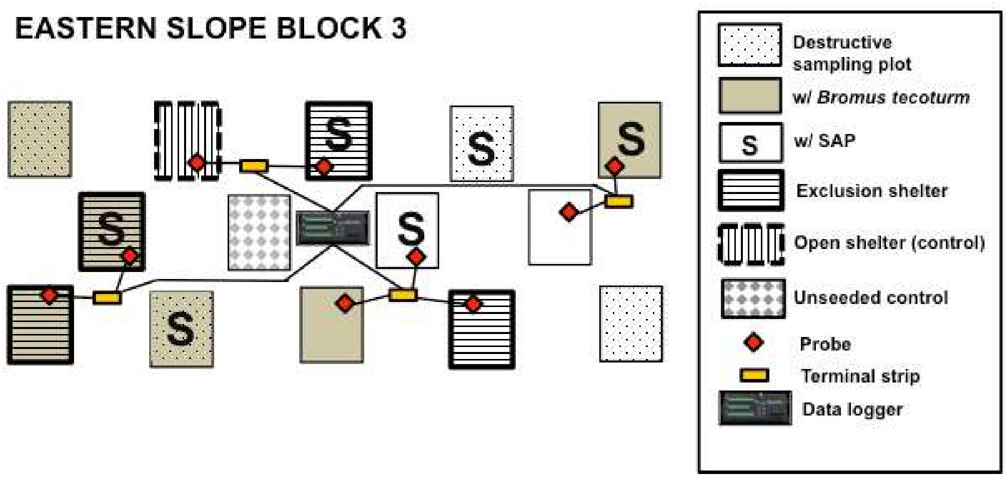

Figure 2 Schematic diagram of Block 3 at the Eastern Slope site illustrates treatments and soil moisture monitoring equipment.

Treatments

SAP addition: SAP (Stockosorb 660 Micro, 0.2-0.8 mm, Evonik Industries, Germany) was applied to appropriate plots by hand at a rate of 26 g m^{-2} and then the entire block area was disked twice to incorporate polymer to a depth between 5-10 cm. Plots without SAP addition underwent the same disking treatment.

B. tectorum addition: Approximately 465 *B. tectorum* seeds m^{-2} were broadcast on appropriate plots at the same time as broadcasting of native seeds. All seeds were raked into the soil after broadcasting and soil was packed down with a hand pushed cultipacker.

Figure 3 Completed exclusion shelter at the Western Slope site in July 2014.

Exclusion: To decrease growing-season precipitation in drought treatments we constructed rainfall exclusion shelters that deflected 66% of ambient precipitation from plots. We modified shelters from a design by Yahdjian and Sala (2002). In contrast to the shelters developed by Yahdjian and Sala that were one sided, supported by a metal frame and covered an area of 3.76 m $^{-2}$, our shelters were constructed as an "A-frame" made of wood that covered the whole plot are of 18.13 m $^{-2}$. 0.25 cm by 243.84 cm UV transparent plexiglass troughs (Plaskolite, Inc. OPTIX ® Acrylic) were placed across shelters to cover 66% of the plot area. Each shelter had two sides that were approximately 1 m from the ground surface, and rose to a height of approximately 1.7 m at the top of the A-frame roofline (Figure 3). At both sites, one of the sides closer to the ground was oriented perpendicular to the direction of prevailing winds in order to minimize rain from being blown in under the shelter. Shelter frames were installed in early April 2014 at the Eastern Slope and troughs were kept in place from April to late September 2014. At the Western Slope site, shelter frames were installed in early July 2014 and plastic troughs were kept in place from July to October 2014, and April to October 2015.

Seeding

Species and seeds in each functional group (grasses, forbs, and shrubs) were kept consistent, and number of *B. tectorum* seeds per plot was kept constant (465 seeds m^{-2}). *Artemisia tridentata* Nutt. was seeded only at the Western Slope site at a rate of 192 seeds m^{-2} (Table 1). *B. tectorum* seeds were collected within 6 km of each site and *Artemisia tridentate* seeds were collected for the Western Slope site from within 3 km of the study area. Native restoration seeds and *B. tectorum* seeds were broadcast on appropriate plots and incorporated by raking. After seeding, the soil surface was compacted with a lawn roller. Seeding was completed at the Eastern Slope site on 18 December 2013 and 25 July 2014 at the Western Slope site.

Table 1 Seed mixes at the Eastern Slope and Western Slope study sites.

Eastern Slope		Western Slope	
Shrubs			
Species	**Seeds m^{-2}**	**Species**	**Seeds m^{-2}**
Amelanchier alnifolia	48	*Artemesia tridentata*	192
Artemisia frigida	48	*Artemesia nova*	48
Artemisia ludoviciana	48	*Atriplex canecsens*	48
Cercocarpus montanus	48	*Atriplex confertifolia*	48
Atriplex canecsens	48	*Chrysothamnus viscidiflorus*	48
Krascheninnikovia lanata	48	*Ephedra viridis*	48
Ericameria nauseosa	48	*Ericameria nauseosa*	48
Yucca glauca	48	*Krascheninnikovia lanata*	48
Grasses			
Aristida purpurea	24	*Achnatherum hymenoides*	24
Bouteloua curtipendula	24	*Bouteloua gracilis*	24
Bouteloua dactyloides	24	*Ceratochloa carinata*	24
Nassella viridula	12	*Elymus elymoides*	24
Panicum virgatum	24	*Elymus trachycalus*	12
Schizachyrium scoparium	12	*Hesperostipa commata*	24
Achnatherum hymenoides	24	*Koeleria macrantha*	24
Pascopyrum smithii	12	*Leymus cinereus*	12
Koeleria macrantha	24	*Pascopyrum smithii*	12
Bouteloua gracilis	24	*Pleuraphis jamesii*	24
Elymus elymoides	24	*Poa fendleriana*	12
Elymus trachycalus	12	*Poa secunda*	24
Hesperostipa commata	24	*Sporobolus cryptandrus*	24
Forbs			
Dalea purpurea	36	*Achillia millefolium*	48
Oenothera speciosa	24	*Balsamorhiza saggitata*	36
Penstemon angustifolius	24	*Cleome serrulata*	36
Ratibida columnifera	48	*Erigeron speciosus*	36
Cleome serrulata	36	*Eriogonum umbellatum*	48
Heterotheca villosa	48	*Hedysarum boreal*	48
Linum lewisii	48	*Helianthus annuus*	36
Hedysarum boreal	48	*Heterotheca villosa*	48

Climate and Soil Moisture Monitoring Equipment Installation

At two of the blocks at each site, soil moisture and temperature probes (5TM model probes, Decagon Devices, Pullman WA) were installed in plots crossing SAP, *B. tectorum*, and exclusion treatments (Figure 2) at two depths: 5cm and 30cm. Probe cables were strung through PVC piping to prevent weather and animal damage and connected to data loggers (CR1000 model loggers, Campbell Scientific, Logan UT). Sensors to monitor shelter effects and ambient climate variables were installed at or near one randomly selected shelter at one block at each site. Precipitation (Campbell mo. #TE525) and wind speed and direction (Campbell mo. #03002-L10) sensors were installed outside the shelter. Air temperature, relative humidity (Campbell mo. #HC2S3-L50) and photosynthetically active radiation (Apogee mo. # SQ-110-L-15) sensors were installed both under shelters and adjacent to shelters. Cables from climate sensors were connected to data loggers. 20W solar panels (Campbell mo. #SP20-PW, Wel-Bilt, model # 25266) and batteries were installed at each site to continuously power data loggers.

Measurements

Wind speed and direction sensors (Campbell mo. #03002-L10) and rain gauges (Campbell mo. #TE525) were placed at both sites to measure wind and ambient precipitation. Temperature, and relative humidity (Campbell mo. #HC2S3-L50) and photosynthetic active radiation (Apogee mo. SQ-110: Sun Calibration Quantum Sensor), were measured outside and under one shelter at each site. Soil moisture at 5cm and 30 cm depth was measured every half hour throughout the growing season in treatment plots of two blocks at each site using Decagon 5TM probes. All climatic and soil moisture measurements were recorded automatically to a Campbell Scientific data logger (CR1000 model loggers, Campbell Scientific, Logan UT). At the Western Slope site in 2015, we used plant root simulator probes (WesternAg Innovations, PRS ® Technology) to measure the effects of treatments on plant available nitrogen. Four cation and anion probes were placed in treatment plots May – June, July –August, and September- October. WesternAg Innovations (Saskatoon, SK, Canada) analyzed inorganic nitrogen concentrations.

To measure plant community responses individual species seedling densities were counted. Within each plot, four 1 x 0.5 m^2 sampling quadrats (sampling frames) were placed one meter from each plot corner, ensuring at least a 30 cm buffer from plot edges. Individuals of all species were counted in each quadrat and averaged to the 1 m^2 scale for density analysis. Seedling densities were counted three times in the first growing season at each site: 17 May, 14 July, 2 September 2014 on the Eastern Slope, and 15 May, 17 July, 10 September 2015 at the Western Slope site.

Statistical analyses

We used repeated measures linear mixed effects models to analyze the effects of exclusion, *B. tectorum*, and SAP treatments on plant available nitrogen and plant densities for the following plant functional groups: all perennials, seeded perennials, all annuals (excluding *B. tectorum*), seeded annuals and *B. tectorum*. In seedling density and nitrogen analyses, date (the repeated measure or within subject factor) and treatments were considered fixed effects, and block was considered random. Functional group densities were either square root or log transformed before analysis to meet assumptions of equality of variance and backwards selection was used to retain the simplest model in all cases. ANOVA models were used to analyze the effects of exclusion, *B. tectorum*, and SAP treatments on volumetric water content (VWC) at 5 cm and 30 cm depth at weekly intervals. In analysis of VWC, and treatments were considered fixed effects, and block was considered random. Analyses were completed for both sites individually. All analyses were completed in the statistical program R (R Development Core Team 2012).

RESULTS

Weather

During the 2014 growing season, overall precipitation and temperature at the Eastern Slope site were average with the site receiving 307 mm of precipitation March – September (30-year average: 327mm) and observing temperatures between 5.7°C and 22.3°C. Typical of this area, the spring (March – June) was the wettest part of the year, though less precipitation fell than usual; the site received 155 mm of precipitation compared to the 30-year average of 209 mm. Slightly higher than average precipitation, 152 mm compared to the 30-year average of 119 mm, fell from July through the end of September at the Eastern Slope site (Figure 4c). Average temperatures (5.4°C - 22.2°C) and annual precipitation (280 mm compared to the 30-year average of 270 mm from March - September) were observed at the Western

Slope site during the first growing, but timing of precipitation was atypical for the area. The area usually receives around 110 mm of precipitation in the spring (March – June) but in 2015 during this period, the site received 190 mm of precipitation, 82 mm of which fell in the first ten days of June. Generally, the late summer and early fall are the wettest parts of the year with, on average, 160 mm of precipitation falling July – September. But in 2015, only 70 mm of precipitation fell during this period (Figure 5c).

Plant community

There were great differences in plant community responses between the two study sites. The plant community responses and densities reported below do not include *B. tectorum*, unless mentioned explicitly. Annuals dominated at both sites comprising 64% of the community (108 plants m^{-2}) on the Eastern Slope site and 78% of the community at the Western Slope site (129 plants m^{-2}). On the Eastern Slope the annual community was 86% native and dominated by two species, *Cleome serrulata* and *Helianthus annuus,* which accounted for 62% and 9% of all annual forbs, respectively. The annual community at the Western Slope site was dominated by non-native species, primarily *Alyssum simplex* and *Salsola tragus* L. (Russian thistle), which comprised 64% and 16% of the annual community, respectively. Compared to annuals, perennial establishment was low at both sites accounting for 34% of the community at the Eastern Slope site (71 plants m^{-2}) and 22% of the community at the Western Slope site (39 plants m^{-2}). Seeded native perennials accounted for 14% (9 plants m^{-2}) and 8% (3 plants m^{-2}) of the perennial communities at the Eastern and Western slope sites, respectively. *Convolvulus arvensis* was the most prevalent perennial species at both sites, accounting for 78% and 89% of the perennial community on the Eastern Slope and Western Slope, respectively. *B. tectorum* establishment was high on the Western Slope, reaching a maximum of 289 plants m^{-2} late in the season and accounting for 63% of the total plant community in plots were *B. tectorum* was seeded. In contrast, *B. tectorum* establishment on the Eastern Slope was low, reaching a maximum of only 2 plants m^{-2} and accounting for less than 2% of the total plant community. *Convolvulus arvensis* was prevalent at both sites, accounting for 78% of the perennial community on the Eastern Slope and 89% of the perennial community of the Western Slope.

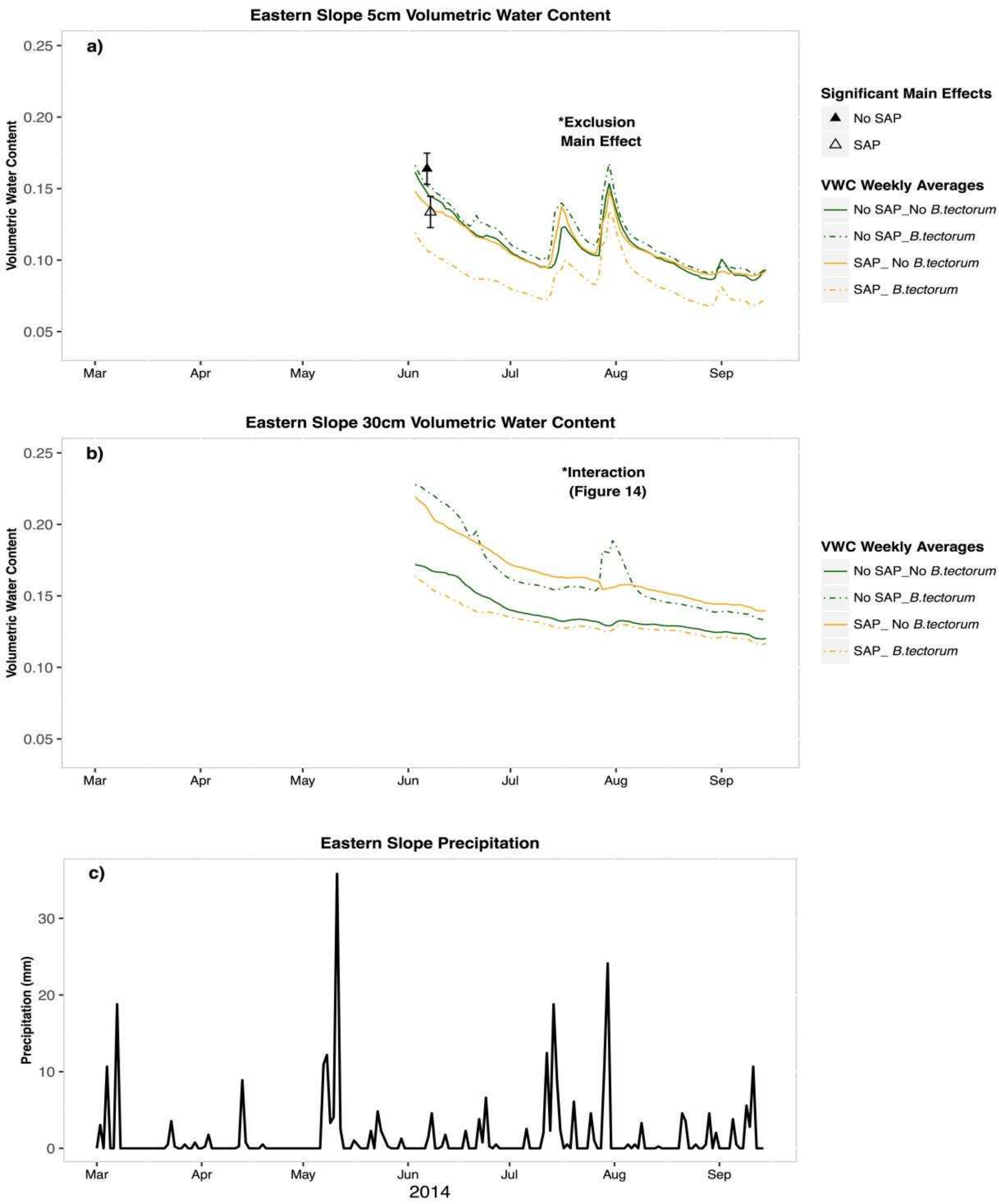

Figure 4 a) Soil volumetric water content (VWC) at 5cm depth and b) 30 cm depth at the Eastern Slope site. Lines depict weekly averages under SAP and *B. tectorum* treatments, averaging over exclusion treatment. Symbols denote significant ($p<0.1$) differences in means of main effects, averaging over other treatments. a) * Indicates a significant main effect of exclusion at 5cm on July 27, 2014. b) * Indicates a 3-way interaction between SAP, *B. tectorum*, exclusion existed (Figure 12) on July 27, 2014. c) Daily average precipitation in 2014 on the Eastern Slope. Data from Colorado Agricultural Metrological Network station FTC01.

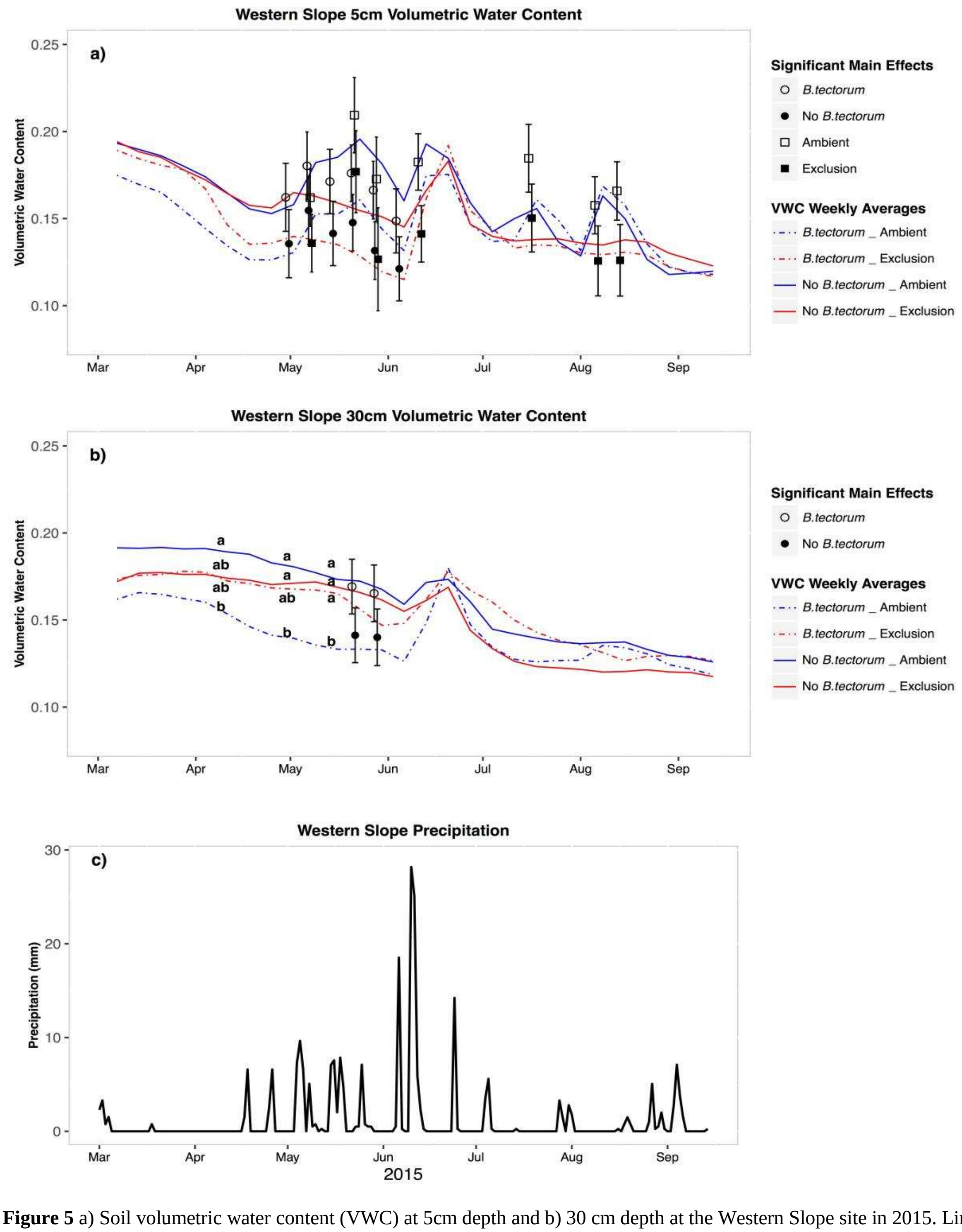

Figure 5 a) Soil volumetric water content (VWC) at 5cm depth and b) 30 cm depth at the Western Slope site in 2015. Lines depict weekly averages under exclusion precipitation conditions and *B. tectorum* treatments, averaging over SAP treatment. a) Symbols denote significant ($p<0.1$) differences in means of main effects, averaging over other treatments. b) Letters denote significant ($p<0.1$) differences in means. c) Daily average precipitation in 2015 at the Western Slope site. Data collected on site.

Seedling counts

Different experimental treatments had the greatest influence on the divergent plant communities at our two sites: SAP and exclusion drove patterns on the Eastern Slope and *B. tectorum* and exclusion drove patterns on the Western Slope. The densities reported for both sites do not include *B. tectorum* seedlings. In the first growing season (2014) at the Eastern Slope site, total seedling densities were 60% higher (82.38 ± 29.41 plants m^{-2}) with SAP treatment than without SAP (52.33± 29.41 plants m^{-2}) though this trend was not significant (p=0.10). This was primarily driven by over a three-fold increase in annual seedlings in May, from 14 plants m^{-2} in plots without SAP compared to 49 plants m^{-2} with SAP (Table 2, Figure 6). Seasonal seeded annual densities were three times greater in SAP treatments with 13 plants m^{-2} compared to 41 plants m^{-2} without SAP, but this trend was not significant (p = 0.11) (Table 2). In addition, densities of seeded species under ambient conditions increased steadily throughout the season (May: 37.9 plants m^{-2}, July: 44.6 plants m^{-2}, September: 52.6 plants m^{-2}) but increases under exclusion conditions were smaller and no significant increase was observed in the later part of the summer (May: 16.3 plants m^{-2}; July: 20.8 plants m^{-2}; September: 22.3 plants m^{-2}) (Figure 7). Overall, SAP treatments improved establishment of all seeded species under ambient conditions (13 plants m^{-2} to 77 plants m^{-2}, p = 0.09) but not under exclusion conditions (17 plants m^{-2} to 23 plants m^{-2}, p = 0.99) (Figure 8). Interactive effects of exclusion, SAP, and *B. tectorum* affected seeded perennial densities. Seeded perennial densities were lower in exclusion treatments in all cases except in treatments with *B. tectorum* and no SAP. *B. tectorum* seedling densities were low overall, reaching only three plants m^{-2} (Figure 9). Perennial seedling counts under this treatment combination (*B. tectorum* and no SAP) did not vary

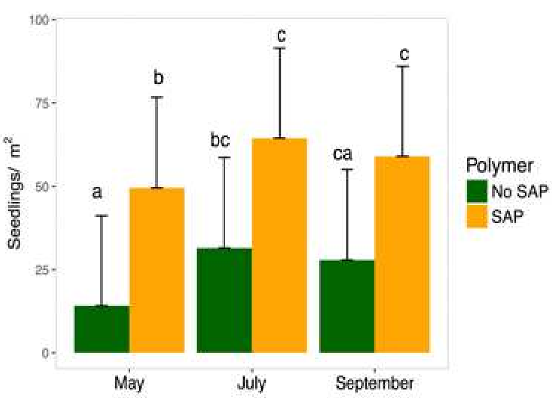

Figure 6 Seasonal trends of 2014 annual species densities with and without SAP at the Eastern Slope site. Data are averaged over exclusion and *B. tectorum* treatments. Bars are means of untransformed data ± standard error of the mean. Letters denote significant differences between means of transformed data (p < 0.1).

between ambient (4.5 plants m^{-2}) and exclusion (5.1 plants m^{-2}) conditions (Table 2, Figure 10).

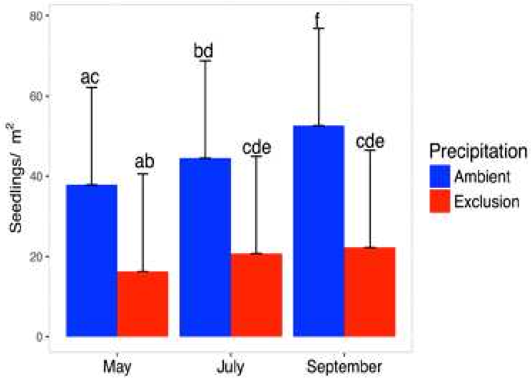

Figure 7 Seasonal trends of 2014 annual species densities under ambient and exclusion precipitation conditions at the Eastern Slope site. Data are averaged over SAP and *B. tectorum* treatments. Bars are means of untransformed data ± standard error of the mean. Letters denote significant differences between means of transformed data (p < 0.1)

At the Western Slope site total seedling densities were over two times greater in ambient precipitation treatments (82.51 ± 31.2 plants m^{-2}) than in exclusion treatments (28.86 ± 30.42 plants m^{-2}). Annual species densities were three times greater in ambient treatments (67.62 ± 29.10 plants m^{-2}) than in exclusion treatments (14.69 ± 28.25 plants m^{-2}) and drove this overall trend (Table 2). After reaching their highest densities in July (12.92 ± 2.43 plants m^{-2}), native seedling densities in ambient plots remained higher at the end of the season (10.77 ± 2.43 plants m^{-2}) than early establishment (May), but densities in exclusion plots returned to spring levels (5.43 ± 2.39 plants m^{-2}) (Figure 11). *B. tectorum* treatments had varied effects on different plant functional groups. Total seedling densities were higher with seeded *B. tectorum*, 67.27 ± 30.03

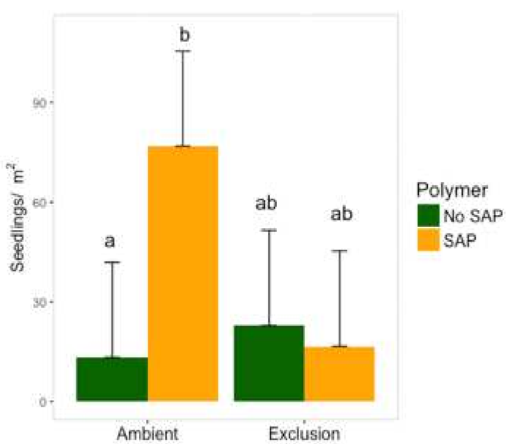

Figure 8 2014 seedling densities of seeded species at the Eastern Slope site. Data are averaged over *B. tectorum* treatments. Bars are means of untransformed data ± standard error of the mean. Letters denote significant differences between means of transformed data (p < 0.1).

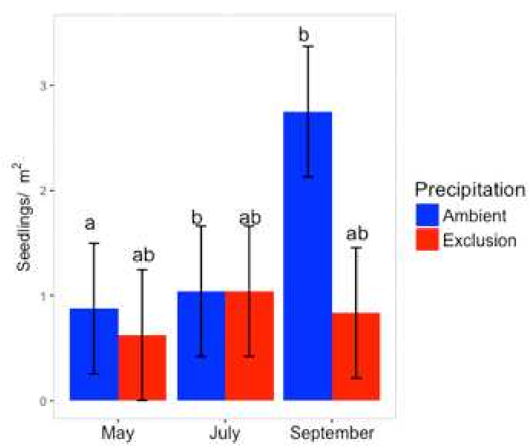

Figure 9 *B. tectorum* seedling densities in 2014 at the Eastern Slope site. Data are averaged over SAP treatments. Bars are means of untransformed data ± standard error of the mean. Letters denote significant differences between means of transformed data (p < 0.1).

plants m^{-2} compared to 44.10 ± 31.75 plants m^{-2} without seeded *B. tectorum*, and once again this trend was primarily driven by increases in annual seedling densities (54.62 ± 27.85 plants m^{-2} with *B. tectorum*, 27.71 ± 29.69 plants m^{-2} without *B. tectorum*) (Table 2). However, densities of all seeded species were lower with *B. tectorum* (Table 2). Densities of all seeded species with *B. tectorum* reached 2.79 ± 0.83 plants m^{-2} compared to 5.13 ± 0.85 plants m^{-2} without *B. tectorum.* Seeded annual densities were also greater without *B. tectorum* though differences varied by date and precipitation treatment. Seeded annual densities in plots with ambient conditions and without *B. tectorum* were greater than densities with

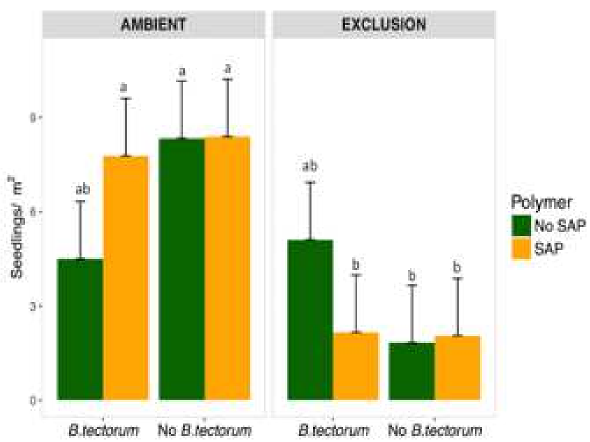

Figure 10 2014 seedling densities of seeded species at the Eastern Slope site. Data are averaged over *B. tectorum* treatments. Bars are means of untransformed data ± standard error of the mean. Letters denote significant differences between means of transformed data ($p < 0.1$).

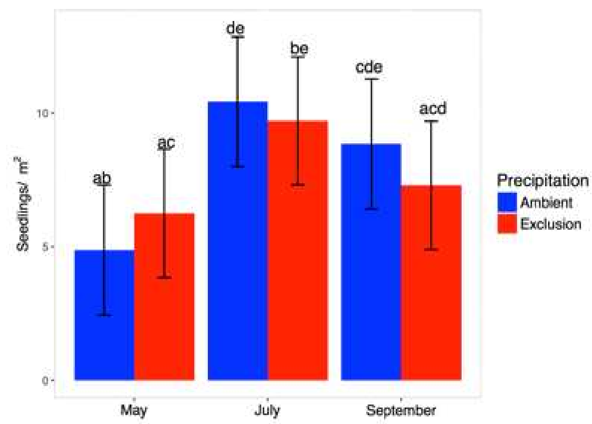

Figure 11 Native seedling densities in 2015 at the Western Slope site. Data are averaged over *B. tectorum* and SAP treatments. Bars are means of untransformed data ± standard error of the mean. Letters denote significant differences between means of transformed data ($p < 0.1$).

exclusion and *B. tectorum* in July and September, as well as treatments under ambient precipitation with and without *B. tectorum* in September (Table 2, Figure 12). The lower densities of *B. tectorum* seedlings under exclusion treatments was primarily driven by differences between treatments in the fall with 476.52 ± 157.7 seedlings m^{-2} under ambient conditions compared to 0.52 ± 153.24 seedlings m^{-2} under exclusion (Table 2, Figure 13).

Table 2: Analysis of variance results for main effects and interactions of *B. tectorum*, exclusion, and superabsorbent polymer (SAP) treatments for densities of different plant functional groups at the Eastern and Western slope sites. P values less than 0.1 are in bold. Degrees of freedom (df) are for the numerator and denominator (num,den), F and p values from selected models.

EASTERN SLOPE SEEDLING DENSITIES															
	Seeded Perennials[a]			**Perennials**[a]			**Seeded Annuals**[b]			**Annuals**[b]			***B. tectorum***		
	df	F	p	*df*	F	p	*df*	F	p	*df*	F	p	*df*	F	p
B. tectorum	1,58	0.06	0.815	1,14	1.48	0.244	1,17	0.10	0.754	1,17	0.02	0.892	1,18	51.03	**<0.001**
Exclusion	1,58	31.69	**<0.001**	1,14	3.57	**0.080**	1,17	0.84	0.373	1,17	0.16	0.691	1,18	0.84	0.372
SAP	1,58	0.19	0.663	1,14	0.65	0.433	1,17	2.77	0.115	1,17	5.48	**0.032**	1,18	0.47	0.501
Date	2,58	63.77	**<0.001**	2,46	27.49	**<0.001**	2,46	17.02	<0.001	2,44	46.76	**<0.001**	2,44	5.02	**0.011**
B. tectorum : Exclusion	1,58	12.49	**<0.001**	1,14	0.47	0.504	-	-	-	1,17	2.22	0.155	-	-	-
B. tectorum : SAP	1,58	0.00	0.948	1,14	0.02	0.884	-	-	-	-	-	-	-	-	-
Exclusion : SAP	1,58	6.46	**0.014**	1,14	1.23	0.287	1,17	3.10	**0.096**	-	-	-	-	-	-
B. tectorum : Date	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Exclusion : Date	2,58	18.58	**<0.001**	-	-	-	-	-	-	2,42	3.13	**0.054**	2,44	4.38	**0.018**
SAP : Date	-	-	-	-	-	-	-	-	-	2,42	2.81	**0.072**	-	-	-
B. tectorum : Exclusion : SAP	1,58	8.52	**0.005**	1,14	4.58	**0.050**	-	-	-	-	-	-	-	-	-
WESTERN SLOPE SEEDLING DENSITIES															
	Seeded Perennials[a]			**Perennials**[a]			**Seeded Annuals**[a]			**Annuals**[a]			***B. tectorum***[b]		
	df	F	p	*df*	F	p	*df*	F	p	*df*	F	p	*df*	F	p
B. tectorum	1,17	1.19	0.290	1,17	1.33	0.265	1,16	11.52	**0.004**	1,18	3.30	**0.086**	1,16	41.54	**<0.001**
Exclusion	1,17	0.45	0.731	1,17	0.14	0.712	1,16	0.57	0.459	1,18	16.17	**<0.001**	1,16	10.44	**0.005**
SAP	1,17	0.12	0.512	1,17	0.15	0.705	1,16	0.26	0.617	1,18	0.16	0.696	1,16	0.61	0.445
Date	2,47	28.16	**<0.001**	2,47	28.24	**<0.001**	2,42	9.73	**<0.001**	2,48	1.77	0.181	2,41	0.07	0.931
B. tectorum : Exclusion	-	-	-	-	-	-	1,16	0.21	0.651	-	-	-	1,16	1.33	0.267
B. tectorum : SAP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Exclusion : SAP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B. tectorum : Date							2,42	1.22	0.305				2,41	2.25	0.119
SAP : Date	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Exclusion : Date	-	-	-	-	-	-	2,42	0.95	0.394	-	-	-	2,41	2.86	**0.069**
B. tectorum : Exclusion : Date	-	-	-	-	-	-	2,42	3.83	**0.030**	-	-	-	2,41	4.21	0.0218

[a] Transformation: sqrt(density) [b] Transformation: log(density+0.01) - Interactions not included in model

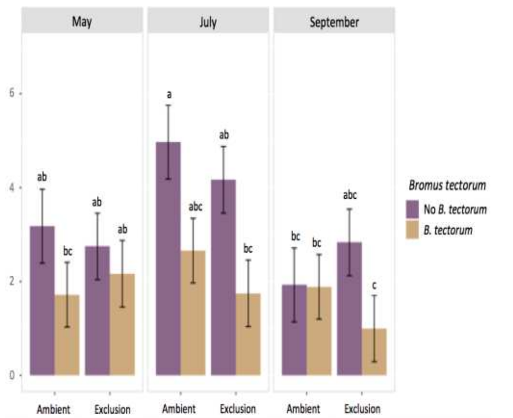

Figure 12 Seasonal trends of Western Slope seeded annual densities with and without *B. tectorum*, under ambient and exclusion precipitation conditions. Data are averaged over SAP treatments. Bars are means of untransformed data ± standard error of the mean. Letters denote significant differences between means of transformed data (p < 0.1).

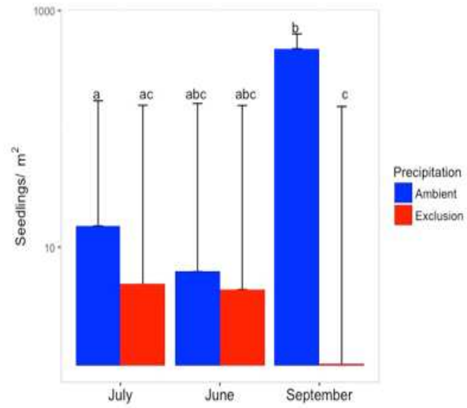

Figure 13 *B. tectorum* seedling densities in 2015 at the Western Slope site. Data are averaged over SAP treatments. Bars are means of untransformed data ± standard error of the mean. Letters denote significant differences between means of transformed data (p < 0.1).

Soil Volumetric Water Content

The effects of treatments on soil volumetric water content (VWC) varied by site, depth, and time. At the beginning of data collection at the Eastern Slope site on 3 June 2014, VWC at the 5 cm depth in plots with SAP was 20% lower (13.4 ± 1.1%) than in plots without SAP (16.4 ± 1.1%; p = 0.07) averaging over *B. tectorum* and exclusion treatments (Table 3, Figure 4a). On 27 July 2014, VWC at 5 cm in exclusion plots was 25% lower (11.9 ± 1.6%) than ambient plots (15.4 ± 1.6%; p = 0.057) (Table 3, Figure 4a). On 27 July 2014 the effect of SAP on VWC of soils at 30 cm varied with levels of *B. tectorum* and exclusion (Table 3). VWC in ambient plots without SAP and with *B. tectorum* was almost two times higher (21.91 ± 1.88%) than ambient plots with SAP and with *B. tectorum* (11.68 ± 1.88%; p = 0.08) and exclusion plots with SAP and without *B. tectorum* (9.56 ± 2.75%) (Table 3, Figure 14). In 2015 at the Western Slope sites, plots with *B. tectorum* had approximately 20% lower volumetric water content at 5 cm depth than plots without *B. tectorum* from 30 April 2015 to 4 June 2015 (Table 4, Figure 5a). Exclusion plots were drier than ambient plots at 5cm periodically from 7 May 2015 through 13 August 2015 (Table 4, Figure 5a). From 9 April 2015 through 14 May 2015, the effect of *B. tectorum* on VWC at 30 cm

Table 3: Analysis of variance results for dates at which main effects and/or interactions of *B. tectorum*, exclusion, and superabsorbent polymer (SAP) treatments on soil volumetric water content at 5 cm and 30 cm depth at the Eastern Slope site were significant (p<0.1). Each model at each date had one degree of freedom. Significant F and p values are indicated in bold.

EASTERN SLOPE 5 CM VOLUMETRIC WATER CONTENT										
	F	p	F	p	F	p	F	p	F	p
Date (2014)	**6/3**		**7/29**							
B. tectorum	0.62	0.449	0.03	0.874						
Exclusion	0.05	0.826	**4.51**	**0.057**						
SAP	**3.83**	**0.076**	2.88	0.118						
Block	**7.44**	**0.020**	2.18	0.167						
EASTERN SLOPE 30 CM VOLUMETRIC WATER CONTENT										
Date (2014)	**6/3**		**6/10**		**6/17**		**6/24**		**7/29**	
B. tectorum	0.00	0.991	0.00	0.985	0.04	0.852	0.25	0.631	0.84	0.394
Exclusion	0.21	0.655	0.66	0.437	0.41	0.539	0.01	0.931	3.54	0.109
SAP	1.19	0.301	1.65	0.228	2.22	0.167	1.28	0.284	2.16	0.192
Block	0.44	0.523	0.05	0.825	0.06	0.818	0.09	0.775	**11.48**	**0.015**
B. tectorum by Exclusion	-	-	-	-	-	-	-	-	0.01	0.922
B. tectorum by SAP	**10.15**	**0.010**	**7.11**	**0.024**	**5.33**	**0.044**	**3.95**	**0.075**	**6.16**	**0.048**
Exclusion by SAP	-	-	-	-	-	-	-	-	0.33	0.587
B. tectorum by Exclusion by SAP	-	-	-	-	-	-	-	-	**9.62**	**0.021**

- Treatment or interaction not included in model

depth varied with the level of precipitation. Under ambient conditions, VWC of soils with *B. tectorum* was on average 20% lower than in plots without *B. tectorum*. VWC of soils with ambient precipitation and *B. tectorum* throughout this period ranged from 13.4% ± 1.6% to 15.5% ± 2.5% as compared to soils with ambient precipitation and no *B. tectorum*, which ranged from 17.3% ± 1.6% to 20.7% ±3.8%. On two dates, 7 and 14 May, VWC at 30 cm in plots with *B. tectorum* under ambient conditions was 20% lower than in plots with exclusion treatments, regardless of level of *B. tectorum* within the exclusion treatment (Table 4, Figure 5b).

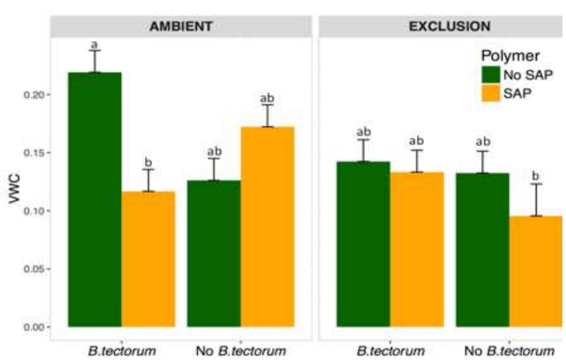

Figure 14 Soil VWC at 30 cm depth on 29 July 2014 at the Eastern Slope site. Bars are means of untransformed data ± standard error of the mean. Letters denote significantly (p < 0.1) different means.

Table 4: Analysis of variance results for dates at which main effects and/or interactions of *B. tectorum*, exclusion, and superabsorbent polymer (SAP) treatments on soil volumetric water content at 5 cm and 30 cm depth at the Western Slope site were significant (p<0.1). Each model at each date had one degree of freedom. Significant F and p values are indicated in bold.

WESTERN SLOPE 5 CM VOLUMETRIC WATER CONTENT																				
	F	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Date (2015)	**4/30**		**5/7**		**5/14**		**5/21**		**5/28**		**6/4**		**6/11**		**7/16**		**8/6**		**8/13**	
B. tectorum	**4.48**	**0.058**	**4.18**	**0.066**	**6.30**	**0.029**	**7.44**	**0.020**	**10.65**	**0.008**	**5.42**	**0.040**	0.01	0.938	0.06	0.806	0.16	0.699	0.01	0.931
Exclusion	0.44	0.520	**7.51**	**0.019**	1.99	0.186	**15.78**	**0.002**	**6.05**	**0.032**	0.91	0.362	**4.47**	**0.061**	**4.93**	**0.053**	**4.18**	**0.071**	**7.66**	**0.022**
SAP	0.46	0.510	0.74	0.408	0.61	0.450	0.64	0.442	0.39	0.545	0.46	0.514	0.07	0.792	0.02	0.905	0.00	0.972	0.17	0.690
Block	2.51	0.141	2.16	0.170	3.53	0.087	**7.98**	**0.017**	**12.98**	**0.004**	**10.08**	**0.009**	2.78	0.126	**7.94**	**0.020**	**16.08**	**0.003**	**10.70**	**0.010**
WESTERN SLOPE 30 CM VOLUMETRIC WATER CONTENT																				
Date (2015)	**3/5**		**4/9**		**4/16**		**4/23**		**4/30**		**5/7**		**5/14**		**5/21**		**5/28**		**6/11**	
B. tectorum	1.92	0.196	**5.02**	**0.049**	**7.51**	**0.021**	**5.61**	**0.042**	**6.68**	**0.030**	**11.33**	**0.008**	**10.43**	**0.010**	**7.84**	**0.019**	**5.99**	**0.034**	1.21	0.303
Exclusion	0.15	0.708	0.07	0.792	0.39	0.547	1.33	**0.278**	**1.66**	**0.229**	2.85	0.126	2.76	0.131	0.07	0.790	0.08	0.787	0.22	0.652
SAP	**3.50**	**0.091**	1.85	0.204	1.23	0.293	0.44	0.523	0.56	0.474	1.16	0.310	1.37	0.272	0.23	0.643	0.07	0.799	1.95	0.200
Block	0.19	0.673	0.01	0.934	0.05	0.832	0.58	0.467	0.68	0.430	1.21	0.300	1.20	0.301	3.18	0.105	2.51	0.144	0.13	0.725
B. tectorum by Exclusion	1.57	0.238	**4.26**	**0.066**	6.07	**0.034**	4.83	**0.056**	**5.04**	**0.051**	**6.80**	**0.028**	**5.90**	**0.038**	1.05	0.330	1.23	0.294	**5.75**	**0.043**

- Treatment or interaction not included in model

Plant available nitrogen

At the Western Slope site where nitrogen measurements were taken in 2015, concentrations of soil total inorganic nitrogen, most of which was nitrate, varied by date and precipitation treatments (Figure 15, Table 5). In June 2015, total nitrate concentrations were twice as high (499.77 ± 46.52 mg m^{-2}) in exclusion treatments as in ambient treatments (144.72 ± 46.52 mg m^{-2}). This pattern reversed by September 2015, when concentrations of nitrate were over three times greater in ambient treatments (221.83 ± 46.51 mg m^{-2}) compared to exclusion treatments (69.33 ± 46.51 mg m^{-2}). Concentrations of soil ammonium varied based on precipitation and *B. tectorum* treatments (Figure 16). Without *B tectorum*, concentrations of ammonium were greater in treatments under exclusion (4.97 ± 0.49 mg m^{-2}) than ambient conditions (3.11 ± 0.49 mg m^{-2}), but no differences were observed in the presence of *B. tectorum.* Ammonium concentrations decreased throughout the season overall, while nitrate concentrations decreased only in exclusion treatments (Figure 15).

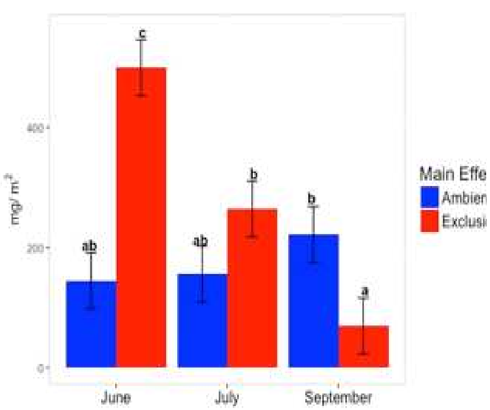

Figure 15 Seasonal soil nitrate concentrations under ambient and exclusion precipitation conditions. Bars are means of untransformed data ± standard error of the mean. Data are averaged over B. tectorum and SAP treatments. Letters denote significant (p<0.1) differences between means.

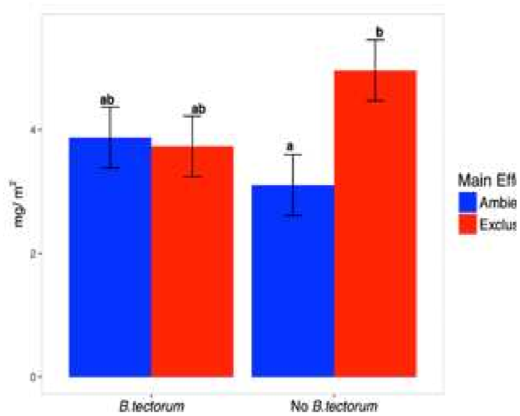

Figure 16 Ammonium concentrations under ambient and exclusion precipitation conditions with and without *B. tectorum.* Bars are means of untransformed data ± standard error of the mean. Data are averaged over SAP treatments. Letters denote significant differences (p< 0.1) between means.

Table 5: Analysis of variance results for main effects and interactions of *B. tectorum*, exclusion, and superabsorbent polymer (SAP) treatments for total plant available nitrogen, nitrate and ammonium concentrations in the soil. Degrees of freedom (df) are for the numerator and denominator (num,den), F and p values from selected models.

WESTERN SLOPE PLANT AVAILABLE NITROGEN									
	Total N			**NO_3^-**			**NH_4^-**		
	df	F	p	*df*	F	p	*df*	F	p
B. tectorum	1,18	1.339	0.262	1,18	1.334	0.263	1,17	0.294	0.595
Exclusion	1,18	0.063	**0.007**	1,18	9.207	**0.007**	1,19	4.108	**0.059**
SAP	1,18	9.290	0.805	1,18	0.057	0.814	1,17	1.082	0.313
Date	2,44	15.048	**<0.001**	2,44	14.823	**<0.001**	2,46	8.001	**0.001**
B. tectorum by Exclusion	-	-	-	-	-	-	1,17	5.583	**0.030**
Exclusion by Date	2,44	29.864	**<0.001**	2,44	29.864	**<0.001**	-	-	-

- Interactions not included in model

DISCUSSION

Drought – Plant community (Both sites)

Drought conditions (66% reduction of ambient rainfall) had significant effects on plant emergence and establishment at both of our study sites. At the Eastern Slope site, seeded species densities increased early in the growing season under both ambient and exclusion conditions, but recruitment through the end of the season was only observed under ambient conditions (Figure 7; compare differences May-July vs. July-Sept). This suggests that drought later in the growing season may limit plant recruitment, possibly as a result of competition for resources by annuals that established earlier in the season (Tilman 1997, Zimmerman et al. 2008). At the Western Slope site, total seedling densities, most of which were non-native annuals, under reduced precipitation were half that of ambient levels. After reaching their highest densities in July, native seedling densities in ambient plots remained higher at the end of the growing season than at early establishment (May), while densities in exclusion plots returned to spring levels (Figure 11). Post emergence seedling mortality is considered a key limitation to plant establishment in arid and semi-arid systems (Salihi and Norton 1987, Pyke 1990). Our results suggest that emerging native plants under drought conditions were particularly affected later in the growing season. At the Eastern Slope site native seedlings were unable to either germinate or emerge, while at the Western Slope site seedlings experienced a bottleneck in survival from emergence to establishment. Even though overall densities varied greatly, in the fall at both sites, exclusion limited densities of *B. tectorum*. As *B. tectorum* generally germinates in the fall, rainfall reduction during this time may have a large impact on the following year's generation of *B. tectorum* (Beckstead et al. 1996) and subsequent effects on the plant community (Prevéy and Seastedt 2015).

Although drought had large effects at both sites, it interacted with the other treatments differently at the two sites. At the Eastern Slope site, exclusion and SAP interacted to affect seedling densities, while at the Western Slope site, exclusion interacted with *B. tectorum* to affect soil resources and seedling densities. The two sites also differed in spring precipitation, *B. tectorum* establishment, and dominant annual forb species, which may have influenced treatment effects and plant responses. On the Eastern Slope, two large rainfall events occurred in May. Although we did not have soil moisture sensors in place at that site until mid-June, given the size of the rainfall events and the fact that smaller precipitation events were followed by increases in soil moisture at both sites (compare panels of Figures 4 and 5), it is reasonable to conclude that May soil moisture was high on the Eastern Slope in the Spring of 2014.

B. tectorum established readily on the Western Slope, but only at very low densities on the Eastern Slope, which may have been related to the timing of seeding at the two sites. The Eastern Slope site was seeded in December 2013, past the opportune fall germination window for *B. tectorum* (August-October) (Beckstead et al. 1996). As soil moisture in the spring was suspected to be high, cold temperatures (Chambers et al. 2007, Blumenthal et al. 2016) or the early germination of *Cleome serrulata* may have suppressed *B. tectorum* establishment at the Eastern Slope site. In contrast, seeding at the Western Slope site (July 2014) was followed by high fall precipitation (162 mm from July through September 2014) and resulted in high *B. tectorum* establishment the following spring. Finally, dominant annual forb species differed at the two sites, with large-statured *Cleome* dominating the Eastern Slope site, and small-statured *Alyssum* dominating the Western Slope site.

SAP + Drought x SAP – Plant community (Eastern Slope)

At the Eastern Slope site, SAP treatments increased establishment of total seedlings, most of which were the native annuals *Cleome serrulata* and *Helianthus annuus*. The higher numbers of annuals that emerged in SAP plots suggests that SAP application may improve establishment of some species more than others. Shorter hydrothermal periods needed for germination (Larson et al. 2015) or higher germination percentages (Wainwright and Cleland 2013) of annuals may explain why annuals but not perennials responded to SAP treatments. Interestingly, SAP treatments improved establishment of all seeded species (82% annual forbs) under ambient conditions but not under exclusion (Figure 8). Although significant interactions emerged between SAP, exclusion, and *B. tectorum* on seeded perennial densities, effects were largely driven by exclusion treatments and no significant differences of means were found for different levels of *B. tectorum* or SAP with each precipitation treatment (Figure 10). SAPs are primarily marketed as a way to improve plant establishment in water limited areas and have been found to improve germination and water use of plants in both agricultural and re-vegetation settings (Eneji et al. 2013, Yang et al. 2014, Mazen et al. 2015). Still, information about their interactions with precipitation amount is limited. In a study investigating water use and growth of corn in soils treated with SAP, Islam (2011) found that water-use efficiency and leaf-water potential improved under deficit irrigation but no differences were found under moderate or adequate irrigation treatments. In Islam's (2011) study, the greatest deficit water treatment had soil matric potentials set at 9 kPa pressure. 9 kPa of pressure in our loam/clay loam soils would translate to approximate volumetric water contents between 29% (loams) and 38% (clay loam soils). Even at their highest moisture content (~23% VWC), the soils in our study were far drier than the deficit irrigation conditions in Islam's study.

As the low matric potentials of SAP (Hüttermann et al. 1999) may result in rapid loss of water when demands by plants, surrounding soils, or the atmosphere are high (Yang et al. 2014), the effectiveness of SAP may depend on soil type and overall water availability. Agaba (2011) found that SAP application improved plant available water most in sandy soils and least in clay soils, and effects on tree seedling growth depended on soil type. It appears that SAP effectiveness is highly dependent on environmental conditions including soil and plant matric potentials as well as evaporative demand, and a window of plant available water may exist below which SAP may not be beneficial, especially for germinating and emerging seedlings, which are highly susceptible to environmental perturbations (James et al. 2011). The observation that SAP improved native seedling establishment under ambient but not drought conditions at our Eastern Slope site is consistent with this hypothesis. It is also possible that differences in dominant annuals or soil type drove the differences between sites. Regardless, it is clear that the effects of SAP on germination and plant water uptake are likely dependent on environmental conditions, antecedent water availability, soil type, and specific germination and growth requirements of different species.

B. tectorum + Drought x B. tectorum – Plant Community (Western Slope)

The negative impacts of *B. tectorum* on establishment of seeded species at the Western Slope site exemplify the importance of managing this species in restoration projects. The effects of *B. tectorum* on seeded annuals depended on date and precipitation treatment. Seeded annual densities in plots with ambient precipitation and without *B. tectorum* were greater than densities in plots with exclusion and *B. tectorum* in July, but differences were not apparent in May or September (Table 2, Figure 12). As *B. tectorum* is capable of rapid use of shallow soil water (Melgoza et al. 1990) and has been shown to be an effective competitor when summer precipitation is low (Chambers et al. 2007), the effects of *B. tectorum* and drought may have compounded early in the season to hinder seeded annual establishment. Interestingly, in the fall we observed higher unseeded annual densities with *B. tectorum* possibly because the litter layer created by senesced *B. tectorum* altered microclimate conditions in a way that enhanced germination of the dominant species, *Alyssum simplex*.

Soil Resources (Both sites)

Drought independently and in combination with SAP and *B. tectorum* influenced volumetric water content (VWC) and plant available nitrogen at both sites. As nitrogen measurements were not taken and

VWC measurements did not begin until mid-June on the Eastern Slope, the following discussion is largely based on observations from the Western Slope site. At both sites, VWC in exclusion plots was lower at 5 cm depth than in ambient plots at different points throughout the season: on 27 July 2014 on the Eastern Slope and periodically from May through August 2015 on the Western Slope. As in other studies (e.g., Ogle et al. 2003, Prevéy and Seastedt 2014), at the Western Slope site, VWC at 5 cm depth in plots with *B. tectorum* was lower from April through early June 2015, indicating that *B. tectorum* was able to utilize shallow, early season moisture (Melgoza et al. 1990, Knapp 1996). Early in the season, VWC was lower in plots with SAP than plots without SAP ($p < 0.10$) at both sites: at 5cm depth on 3 June 2014 on the Eastern Slope and at 30cm depth on 5 March 2015 on the Western Slope. At the Eastern Slope site, higher densities of plants in SAP treatments likely drove down soil moisture early in the spring resulting in lower VWC. At the Western Slope site, SAP may have absorbed moisture from snowmelt in the top layers of the soil profile and prevented infiltration to deeper depths.

In addition to lowering VWC, exclusion treatments influenced soil nitrogen throughout the season on the Western Slope. Soil nitrate was higher in exclusion treatments in June and July but lower in September, suggesting that in the absence of moisture, plants were unable to acquire nitrate early in the season. In ambient plots, fall precipitation may have stimulated decomposition and microbial activity releasing nitrate and resulted in higher concentrations in these treatments. We found that in the absence of *B. tectorum*, ammonium levels in exclusion plots were higher than in ambient plots, but no differences were detected in the presence of *B. tectorum*. This suggests that *B. tectorum* is able to utilize ammonium under low soil moisture conditions. This is surprising because ammonium moves towards roots largely by diffusion and thus should be more difficult to acquire than nitrate, which moves mostly by mass flow (Belnap et al. 2016).

Drought Interactions – Soil Resources (Both sites)

At 30 cm depth, interactions between *B. tectorum* and SAP on the Eastern Slope and *B. tectorum* and exclusion on Western Slope site were observed. On the Eastern Slope on 27 July, VWC at 30 cm depth was influenced by interactions between all three experimental treatments. VWC in ambient plots with No SAP and *B. tectorum* was almost two times higher (21.91 ± 1.88%) than ambient plots with SAP and with *B. tectorum* (11.68 ± 1.88%; p = 0.08) and exclusion plots with SAP and no *B. tectorum* (9.56 ± 2.75%) (Table 3, Figure 14). Surprisingly, in the spring at the Western Slope site, VWC of soils at 30 cm in plots with *B. tectorum* under ambient conditions was over 20% lower than in plots with 66% precipitation reduction, regardless of the level of *B. tectorum* within the exclusion treatment (Figure 5c). As the effect of *B. tectorum* on deep soil moisture was more evident under ambient than reduced rainfall, and we saw trends for higher *B. tectorum* densities in ambient vs. drought plots, we find an apparent paradox by which higher precipitation leads to drier deep soil layers. Adequate precipitation seemed to allow increased establishment of *B. tectorum,* efficient sequestration of resources by *B. tectorum* in upper soil layers, and decreased infiltration of precipitation to deeper levels in the soil profile. The ability of *B. tectorum* to reduce moisture in deep soil layers may be a mechanism by which *B. tectorum* alters environmental conditions to the detriment of perennial grasses (Dyer and Rice 1999) or shrubs (Inouye 2006) that depend on moisture from deep in the soil profile.

The highly site-specific findings from our study, especially in relation to *B. tectorum* establishment, support previous research that links soil temperature and moisture regimes to ecosystem resilience and resistance to disturbance and *B. tectorum* invasion (Chambers et al. 2013, Maestas et al. 2016). Located on the western edge of the Great Plains, our Eastern Slope site has mesic soil temperature (8° C to 15° C) and aridic/ustic moisture regimes and is characterized by moderate susceptibility to invasion (Brooks et al. 2016). The low *B. tectorum* densities on the Eastern Slope were likely a result of seeding in December 2013, past the opportune fall germination window (Aug-Oct) for *B. tectorum.* As slightly below average precipitation fell in spring 2014, soil moisture, cold temperatures (Blumenthal et al. 2016) or the early germination of *Cleome serrulata* (observed emerging in late March) may have suppressed *B. tectorum* establishment at the Eastern Slope site. Our Western Slope site is located on the eastern edge of the

Colorado Plateau and is characteristic of the mesic soil temperature regime and ustic-aridic moisture regime (Brooks et al. 2016). These systems have low resilience and resistance and are highly susceptible to invasion (Brooks et al. 2016). At this site, high fall precipitation in 2014 (162 mm from July through September) resulted in high *B. tectorum* establishment in both exclusion and ambient treatments, though uncharacteristically low rainfall in fall 2015 (70 mm) hindered *B. tectorum* establishment in exclusion plots. Even though exotic species have been shown to have lower germination requirements and an ability to capitalize on warm temperatures, even under drought conditions (Wainwright and Cleland 2013), our results suggest that *B. tectorum* is at least partially limited by moisture during this period.

INFERENCES REGARDING RESEARCH OBJECTIVES

Our first objective was to evaluate the effect of 66% ambient rainfall exclusion on soil resources and plant establishment. We expected lower soil moisture and establishment of seeded species to be reduced in the exclusion treatment. During the first year of the study, exclusion of 66% of ambient rainfall significantly decreased soil moisture and seedling establishment at both sites, primarily in the later parts of the growing season. Our results in regard to our second objective, which was to evaluate the impacts of *B. tectorum* on soil resources and native plant community development, were limited to the Western Slope site where *B. tectorum* established well. We expected greater *B. tectorum* establishment would result in reduced success of seeded native species. At this site, *B. tectorum* had negative impacts on soil moisture and native plant community development, particularly early in the season when it was most active. Surprisingly, *B. tectorum* under ambient conditions had a stronger negative impact on soil moisture at 30 cm than drought treatments. Our third objective was to evaluate the effects of SAP on soil resources and plant community development. We anticipated that SAP would increase soil moisture over time and improve native species establishment. Significant SAP effects were primarily observed at the Eastern Slope site where SAP incorporation improved total and annual seedling establishment. Our fourth objective was to evaluate the interactions of precipitation amount and timing, *B. tectorum*, and SAP on plant establishment and soil resources. We anticipated the effects of SAP to be most pronounced under exclusion treatments because seedlings in these treatments would benefit most from improved soil moisture and nutrient availability. With improved native establishment we expected lower densities of *B. tectorum* in these treatments. Positive effects on seeded species were only evident under ambient precipitation conditions. In contrast to our prediction, it appears that SAP amplified resources at times when they were abundant rather than when they were most limiting. No interactions between SAP and *B. tectorum* were observed. Adequate early season precipitation at both sites interacted with *B. tectorum* on the Western Slope and SAP on the Eastern Slope to drive seasonal soil and plant community responses. This suggests that what happens early in the growing season may greatly influence the trajectory of the restored system during the first year of establishment. Improving establishment of desirable plants and managing invasives during this period may improve overall restoration success.

MANAGEMENT IMPLICATIONS

The effectiveness of SAP in our study was limited to one site, largely driven by annual species responses, and effects on seeded species were only evident under ambient precipitation. As discussed, this may be due to soil texture or inadequate soil moisture upon which SAP can act under the conditions of our study. It may also be due to the difficulty of applying SAP in sufficient quantities in field settings. Recommended application rates of SAP vary widely, from 22 kg ha^{-1} for field applications (equals 0.0039% by weight assuming incorporation to 5 cm and soil bulk density of 1.13 g cm^{-3}; John Wynne, Stockosorb product representative, *pers. comm.*), to 426 kg ha^{-1} for turf grass (0.075% by weight; BASF Luquasorb® brochure) up to 0.4% by weight in a containerized experiment (would equal 2,260 kg ha^{-1} for incorporation to 5 cm with soil bulk density of 1.13 g cm^{-3}; Agaba et al. 2011). The rate used in this study, 0.045% by weight (257 kg/ha) costs approximately $1,900 ha^{-1}, and is as high as would practically be used for dryland restoration. In addition, we found incorporation to 5 cm to be difficult; actual incorporation was closer to 10 cm, which led to a lower per-volume rate. Higher application rates may be more effective, but are impractical for the large areas relevant to dryland plant community restoration. Localized application either in direct contact with target seeds in drill seeded rows or incorporated into pellets with seed may improve target plant establishment. Furthermore, as with all restoration techniques, timing SAP application and seeding for optimal native but not exotic germination and establishment may improve the effectiveness of SAP and overall community development.

Overall the effects of SAP on plant emergence, soil resources, and *B. tectorum* establishment were site and precipitation dependent. Contrary to our hypothesis, SAP did not improve plant establishment under limited precipitation conditions or during the most water-limited times of the growing season. Rather, on the Eastern Slope site ambient precipitation throughout the growing season interacted with SAP to improve annual and seeded plant establishment. As *B. tectorum* did not establish well at the Eastern Slope, increased soil moisture from SAP may have been available for native plants to utilize in the early spring and summer. In contrast, SAP had no detectable effect on the plant community on the Western Slope and was unable to ameliorate the negative impacts of *B. tectorum* and reduced late-summer rainfall on soil resources. Furthermore, the effects of SAP on plant germination and establishment may be dependent on individual species germination and emergence requirements.

Rainfall reduction and *B. tectorum* presence had significant impacts on developing plant communities at our sites. As exclusion had negative impacts on *B. tectorum*, and both *B. tectorum* and exclusion decreased native seedling densities, concomitant effects of the two could influence the overall impact of exclusion on plant community development in later growing seasons. Further monitoring is essential to understand the long-term effects of these early treatment effects and plant responses. Developing restoration treatments and techniques that ameliorate the negative impacts of drought and invasive species is fundamental to establishing resilient and resistance plant communities. However, careful consideration of local weather patterns and plant germination and establishment requirements may help inform invasion potential, timing of restoration treatments, and appropriate species selection for restoring disturbed ecosystems throughout the west.

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