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Small Mammals Matter? Linking Plant Invasion, Biotic Resistance, and Climate Change in Post-Fire Plant Communities

Rory Charles O'Connor
Brigham Young University - Provo

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Rory C. O'Connor

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Richard A. Gill, Chair
Samuel B. St. Clair
Brock R. McMillan

Department of Biology

Brigham Young University

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ABSTRACT

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Rory C. O'Connor
Department of Biology, BYU
Master of Science

The introduction and establishment of exotic species can profoundly alter ecosystems. Two exotic species drastically changing the landscape of deserts in western North America are *Bromus tectorum* L. and *Bromus rubens* L. Through the buildup of biomass and slow decomposition rates in deserts these two exotic annual grasses can alter fire regimes that change the plant and animal community dynamics in the ecosystems. To better understand the ecological mechanisms that could restrict or alter the patterns of invasive plant establishment we established a replicated full factorial experiment in the Great Basin and Mojave Desert. The combinations of factors being manipulated are burned or intact plant communities, and presence or exclusion of small mammals. Generally invasive species establishment is thought to be a result of competitive superiority or lack of natural enemies, but if that is the case then why do not all invasive species establish and become highly abundant in their new ecosystems? To understand why some invasive species establish and others do not we monitored three dominant exotic species from the Great Basin and the Mojave Desert, *B. tectorum*, *Halogeton glomeratus* (M. Bieb.) C.A. Mey., and *B. rubens*. We observed that the presence of small mammals create a biotic resistance to *B. tectorum, H. glomeratus,* and *B. rubens*. This pattern was observed in both intact and burned plant communities; however, it was most prevalent in the burned plant communities. The strength of the biotic resistance on these invasive species varied between species and the years sampled.

In deserts both plant and small mammal communities are tightly tied to precipitation. We wanted to understand how invasive species establishment is affected by small mammal presence after a fire disturbance, and manipulating total precipitation. Total precipitation was manipulated through three different treatments: 1) drought or 30% reduction of ambient precipitation; 2) ambient precipitation; 3) water addition or an increase of 30% ambient precipitation. We focused on *B. rubens* establishment in the Mojave Desert as our model organism by monitoring it beneath rain manipulation shelters nested in burned/intact and small mammal presence/absence full factorial plots. What we observed was that again small mammals created a biotic resistance on the density of *B. rubens* regardless of the burn or precipitation treatments. This biotic resistance also translated into decreasing *B. rubens* biomass and seed density. Under the drought and ambient precipitation treatments we found that small mammals kept the density and biomass equal but under increased precipitation the efficacy of biotic resistance on *B. rubens* density and biomass was lessened by the availability of the added water.

Keywords: Great Basin, Mojave Desert, biotic resistance, invasive species, fire, climate change, top-down and bottom-up effects

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Chapter 1. Biotic resistance success on invasive species establishment after fire

Abstract

Biotic resistance is a hypothesis that is commonly used to explain exotic plant establishment, but little work has explored how multiple invasive species are affected by native consumers after a disturbance. We explored the connections between invasive species establishment post-fire and how small mammals affect the establishment of multiple exotics in arid ecosystems. We designed a full factorial experiment in both the Great Basin and Mojave Desert where we had burned and intact plant community treatments crossed with the presence or exclusion of small mammals treatments. During each growing season in both deserts we monitored the density of three widespread invasive annual grasses (*Bromus tectorum, Bromus rubens, and Schismus arabicus*) and one invasive forb (*Halogeton glomeratus*). The effects of burning allowed for large increases of two- to four-fold in *B. tectorum, H. glomeratus,* and *S. arabicus* densities each year after the fire. *B. rubens* did not see a difference in density between the burned and intact sites. Small mammals created strong biotic resistance by decreasing the densities of *B. tectorum, H. glomeratus,* and *B. rubens* from one- to four-fold. *S. arabicus* was not directly impacted by small mammals because its density increased with the presence of small mammals. The interactions between burning and small mammal presence augmented the ability for small mammals to create the biotic resistance. This trend however was not noticeable in the intact plots with small mammal presence. Our findings support the biotic resistance hypothesis by demonstrating that small mammals can create consumer-mediated biotic resistance. It also shows that after a disturbance small mammals have a large role in determining the success of plants establishing in desert systems.

Introduction

Exotic species have the capacity to profoundly alter ecosystems, and yet understanding of the ecological mechanisms that can restrict or alter patterns of exotic plant establishment is still being sought after. Exotic plant species can establish in novel ecosystems by escaping natural enemies (enemy release hypothesis) and by increasing competitive advantage through possession of novel traits (novel weapons hypothesis). However, not all exotic species dominate the new environments (Pearson et al. 2012) and they can be presented with significant challenges for establishment (Williamson and Fitter 1996) such as biotic controls that limit success of establishing (biotic resistance hypothesis (Elton 1958)). Invasion success is highly variable between species, environments, and across space and time which implies that the strength of biotic resistance is dependent on multiple biological and environmental factors. While we understand some of the general mechanisms of invasion success we know far less concerning the biological factors that strengthen or weaken biotic resistance in invaded systems.

Biotic resistance can occur through antagonistic interactions between plant species (Levine et al. 2004, Mitchell et al. 2006) or can be mediated by animal consumers (Parker and Hay 2005, Pearson et al. 2012, Freestone et al. 2013, Connolly et al. 2014). Small mammals have been shown to be successful in creating strong top-down controls on native plants (Inouye et al. 1980, Brown and Heske 1990) through granivory (Davidson et al. 1985, Pearson et al. 2011, Connolly et al. 2014), and folivory ((Edwards and Crawley 1999, Maron and Kauffman 2006). A few studies have demonstrated consumer-mediated biotic resistance on weak invaders such as *Erodium cicutarium* (L.) L'Her. Ex Aiton, *Cirsium vulgare* (Savi) Ten., *Carduus nutans* L., *Tragopogon dubius* Scop. (Inouye et al. 1980, Pearson et al. 2011, 2012) but there is less evidence for biotic resistance against more aggressive invaders such as the *Bromus* species.

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Disturbances that occur in ecosystems give exotic species increased opportunities to acquire resources and expand their ranges(Allen et al. 2011). Such disturbances may modify the effectiveness of consumer-mediated biotic resistance through competitive release via reduction in vegetative cover of native species or a shift in native composition (Byers and Noonburg 2003). Alterations to the plant communities from disturbances have been shown to change the abundance and composition of small mammal communities that may have cascading effects on consumer-mediated resistance of exotic plant species (McGee 1982, Litt and Steidl 2011, Horn et al. 2012). Currently we are unaware of any studies that have directly investigated how disturbance, specifically fire, alters biotic resistance of invasion mediated by consumers.

The ability for small mammals to create biotic resistance on invasive species specifically in arid and semi-arid ecosystems should be dependent on the precipitation. Precipitation in arid and semi-arid environments dictates plant community structure and growth (Noy-Meir 1973, Ogle and Reynolds 2004, Adler and Levine 2007) That in time can affect the abundance of small mammal populations (Beatley 1976, Letnic et al. 2005). This close relationship between small mammal abundance and precipitation through plant productivity is a strong factor that should help determine the strength of biotic resistance to plant invasions over time.

The deserts of North America are undergoing large-scale plant invasions. The most prevalent are the invasive annual *Bromus* grasses, *Bromus tectorum L.* in the Great Basin and Columbia Basin and *Bromus rubens L.* in the Mojave Desert (D'Antonio and Vitousek 1992, Knapp 1996, Brooks et al. 2004). Both species increase biomass significantly during years with above-average precipitation creating a buildup of biomass in the inter-shrub space that when ignited carries fire through the shrub landscape (Beatley 1966, D'Antonio and Vitousek 1992, Knapp 1996, Brooks et al. 2004). The presence of these two annual grasses are indirectly altering

plant community composition allowing other invasive species to enter and establish after fire

disturbance through competitive release and opening new niche space (Abatzoglou and Kolden

2011, Brooks and Chambers 2011, Gabler and Siemann 2012). Two additional invasive species

that increase after disturbances are *Halogeton glomeratus* (M. Bieb.) C.A. Mey. an annual forb

in the Great Basin that is toxic to livestock (Dye 1956), and *Schismus arabicus* Nees in the

Mojave Desert that is also an annual exotic grass that contributes to fire.

In this study we monitored how small mammals in desert ecosystems could create

consumer-meditated biotic resistance to invasive species establishment post-fire. The following

questions were addressed during the experiment 1) is the recruitment success of *Bromus*

tectorum, *Bromus rubens*, *Halogeton glomeratus*, and *Schismus arabicus* impacted by small

mammal mediated biotic resistance? 2) What effects does fire have on the establishment success

of invasive species? 3) Does fire disturbance alter small mammal mediated biotic resistance to

plant invasion? To address these questions we measured the invasive plant species' density in

burned and intact plots where small mammals were either present or excluded over the course of

3 years after a fire.

Methods

Study Location

The studies occurred at two desert locations; the first is in Rush Valley located 80km

south west of Salt Lake City, Utah in the Great Basin Desert (12T 388784m E, 4438645m N)

with an elevation of 1660m. The experimental site is on public land managed by the Bureau of

Land Management where cattle and sheep grazing were present before the study was

implemented. There has not been fire recently as evidenced by mature sagebrush communities.

The site is a loamy soil (Soil Survey Staff 2014)with a mature stand of *Artemesia tridentata Nutt.*

var *wyomingensis* Beetel & Young as the dominant shrub; *Elymus elmoides* (Raf.) Swezey is the dominant perennial grass. *Bromus tectorum* L. and *Halogeton glomeratus* (M. Bieb.) C.A. Mey. are the two dominant annual exotic species in the study area. Long-term average annual precipitation between 1953 and 2012 was 269mm, with a mean annual temperature of 8.6 $^{\circ}$C (WRCC, Vernon Station 2014).

The second study location is at the Lytle Ranch Preserve, a property owned by Brigham Young University and conserved in partnership with the Nature Conservancy. The experiment is located on a plateau in the Beaver Dam Wash of southwest Utah 57 km west of St. George Utah (765185m E, 4115523m N). The site has experienced historic cattle grazing but has been out of livestock production for over 20 years and there has not been a reported fire in the last 25 years at our experimental location. The soil is a sandy loam (Soil Survey Staff 2014)with desert pavement and the vegetation at the site is typical of a mid-elevation (915 m) Mojave Desert shrubland. It is dominated by *Yucca brevifolia* Engelm, *Larrea tridentata* (DC) Colville, *Coleogyne ramosissima* Torr, and *Ambrosia dumosa* (A. Gray) Payne, the herbaceous understory is dominated mostly by exotic annuals *Bromus rubens* L.*, Schismus arabicus* Nees*,* and *Erodium cicutarum* (L.) L'Hér. ex Aiton with the occasional native bunch grass *Aristida purpurea* Nutt. Long-term annual precipitation between 1988 and 2012 was 272mm with a mean annual temperature of 16 $^{\circ}$C for the ranch headquarters (WRCC, Lytle Ranch Station 2014).

Experimental design

In the summer of 2011, in both field locations, five blocks were established with a full factorial experiment between burn treatments and small mammal exclusion treatments within blocks (N = 20 per location). In Rush Valley the experimental burn treatment plots were burned in September 2011 (N = 10). Our site was a mature *A. tridentata var wyomingensis* stand which

had sparse lateral fuels to connect the shrub islands. To ensure that our fire burned uniformly straw was added and the fire burned uniformly through each designated burn treatment plot. The fire severity was high, consuming all vegetation to soil level. At Lytle Ranch we burned our experimental plots in June 2011 (N = 10). It was decided that there were enough lateral fuels to connect the *L. tridentata* shrub islands and no addition fuel was added. The fire severity was moderate, consuming all herbaceous vegetation and most all shrubs.

Each experimental plot mentioned is 30 m x 30 m surrounded by a wire mesh fence that is buried 0.35m and is 0.65m above ground level. Half of the plots have small mammals excluded by adding a 0.2m metal flashing to the top of the wire mesh fence and by trapping them out every three months (N = 10). All trapping data can be seen in Sharpe et al (2014).The small mammal access plots lacked metal flashing and had ground-level openings in the fence to allow small mammal movement between the plots and adjacent intact shrublands (N = 10).

Vegetation sampling

In August of 2012 in Rush Valley all *Halogeton glomeratus* plants were counted in the plots and in June of 2013 and 2014 to monitor the establishment of *Bromus tectorum*. The measurements occurred again in August in 2013 and 2014 to monitor *H. glomeratus*. The different monitoring times were established to account only for mature individuals of each species. At Lytle Ranch we sampled at the end of April or early May depending on the phonological maturity of the annual invasive plants in 2013 and 2014. At each study site we established four transect lines that were 25m long placed 2m in from the fence line to avoid any fence effect. The transect lines were spaced as evenly as possible along a perpendicular base line with a minimum distance of at least 2m apart. We used Daubenmire vegetation sampling frames (Daubenmire 1959) modified to be 25cm X 50cm to increase our ability to capture the variation

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of annual plant species. Along the transect lines we placed the vegetation frames every other meter for a total of 12 frames per transect line. The vegetation frames had a nested plot (10cm X 25cm) within to more accurately count the highly abundant annuals (*Bromus tectorum, Bromus rubens,* and *Schismus arbicus*) present in our study sites. Within the frames all plant species were identified and their density determined per square meter (m^2).

Statistical Analysis

Bromus rubens was the only plant species to meet the assumptions of normality for both years it was sampled and we proceeded to do an analysis of variance (ANOVA). We separated the data by year to look at the individual and combined effects of the different treatments to the response of plant establishment. We used our treatments of burn type and small mammal presence as our direct effects, and block as a random effect to account for spatial variability. No transformations were made to the data in either year. The statistical analysis was conducted in R Studio (R Core Team 2012) and all statistical tests levels of significance were set at $p < 0.05$ *a priori*.

Our other invasive species *Schismus arabicus*, *Bromus tectorum*, and *Halogeton glomeratus* all had wide variances that did not allow for any assumptions of normality to be met. We proceeded to use a mixed model with ranks procedure in SAS software (SAS 2013) to eliminate the issue of variance but still allowing for analysis of treatment effects. We separated the data by individual years and then ranked each species by year from one to twenty based off of increasing plant density, with one being the lowest density and twenty being the highest density. All ties in density were averaged and given the same average rank within species and year. We used block as a random effect to account for spatial variability between the different blocks. We also used least-square means to understand the differences between our treatments with significance set at $p < 0.05$ *a priori*.

Results

Small mammal effects on plant density

Small mammals had a large effect on the density of both *Halogeton glomeratus* and *Bromus tectorum* present at the Great Basin study site depending on the year.   Based off of the ranks *H. glomeratus* was significantly impacted by small mammal presence in both years 2012 and 2013 (table 1.1). In 2012 *H. glomeratus* had 50% more individuals per m^2 where small mammals were excluded; by 2013, there was a 10-fold difference due to small mammal exclusion (figure 1.1a). The rank data showed that small mammal presence only significantly affected *B. tectorum* rank in 2014. However, numerically we saw the same pattern of small mammal presence for *B. tectorum* in both years as in *H. glomeratus*. When small mammals were present there was a 65% decrease in *B. tectorum* for 2013 and in 2014 a similar decrease was observed with a 62% decrease in density (figure 1.1b).

In the Mojave Desert small mammals showed a similar trend as in the Great Basin based on year with its dominant invasive annual grass *Bromus rubens*. We found that small mammals significantly had a negative impact on *B. rubens* in 2013 but not in 2014 (table 1.2). When small mammals were present there was a decrease in *B. rubens* density by 28% in 2013 and a 16% decrease in 2014 (figure 1.1c). However, the other exotic annual grass *Schismus arabicus* had the opposite effect with small mammals compared to the other exotic species when small mammals were present. The rank data results had *S. arabicus* significantly impacted by small mammals present in 2013 but nothing significant in 2014 (table 1.2). With small mammals present we observed an increase in *S. arabicus'* density by 55% in 2013 compared to a 25% increase in 2014 (figure 1.1d).

Fire effects on plant establishment

Within the Great Basin we saw a strong difference between the burned and unburned plots with the density of invasive species establishing depending on the year since fire. The rank data has shown that for *H. glomeratus* in 2012 there was no effect but in 2013 there was a significant effect in the burned plots (table 1.1). In the burned plots *H. glomeratus* had a two-fold decrease from the unburned plots in 2012 (figure 1.2a). However, in 2013 we observed a shift to where there was a 62 fold increase in *H. glomeratus* in the burned from the unburned plots (figure 1.2a). *Bromus tectorum*'s rank data gave no significant effect to burning in 2013 but in 2014 burning did have a significant direct effect (table 1.1). There was a 6-fold increase in density in the burned plots compared to the unburned plots for 2013, and in 2014 *B. tectorum* had a 4-fold increase in the burned compared to the unburned plots (figure 1.2b).

The Mojave Desert's two invasive grass species had slightly different patterns to that seen in the Great Basin. *Bromus rubens* in our burned plots had a decrease in density by 20% compared to the unburned plots for 2013, and in 2014 it continued to have a decreased density of 28% in the burned plots compared to the unburned plots (figure 1.2c). While *B. rubens* decreased in density in the burned plots it was not statistically significant (table 1.2). *Schismus arabicus* in both years sampled saw a significant increase in burn plots compared to unburned plots based on the ranked data (table 1.2). In 2013 it had a four-fold increase in the burned plots compared to the unburned plots, and in 2014 there was a two-fold increase in density in the burned plots to the unburned plots (figure 1.2d).

Small mammal and fire effects on plant establishment

In the Great Basin we observed that there were no combined effects of small mammal presence and burning in either year for *H. glomeratus* and *B. tectorum* (figure 1.3; table 1.1). The same was true for the Mojave Desert invasive species *B. rubens* and *S. arabicus* (figure 1.4; table 1.2).

Discussion

Effectiveness of biotic resistance against invasive species recruitment

Our study confirms that small mammals can and will act as a biotic resistance for multiple aggressive invasive species. In the Great Basin and Mojave Desert our data demonstrated that when small mammals are excluded from an ecosystem exotic plant species that are trying to establish do so at high densities (figure 1.1). This is not the first time that biotic resistance has been shown to come from native consumers (Parker and Hay 2005, Pearson et al. 2012), but it is one of the first experimental demonstrations that small mammals can and do act as a biotic resistance on multiple invasive species (Pearson et al. 2011, 2012, Connolly et al. 2014).

Our study is unique in that we saw this pattern of biotic resistance in two desert systems with similar plant species *Bromus tectorum* and *Bromus rubens*. What is also novel about our results is that not only did we observe a significant reduction in the two annual grasses but we also saw a large reduction in *Halogeton glomeratus* a noxious weed to livestock (figure 1.1) (Young 2002). This halophyte forb can kill livestock (Dye 1956) but small mammals were not affected to our knowledge. We hypothesize that their not being influenced by the toxins has something to do with their gut microbial communities like what was observed in woodrats and *Larrea tridentata* (Kohl et al. 2014).

The effects of the small mammal biotic resistance in the Great Basin decreased all of the invasive species present, but in the Mojave Desert only affected *B. rubens* directly and *Schismus*

arabicus indirectly (figures 1.1c and d). We found that *S. arabicus* increased its density by more than 50% where *B. rubens* had decreased due to herbivory, this could be because *S. arabicus* was being competitively excluded by *B. rubens*. Often competitive exclusion is with exotic plants that are competing against the native plant species but in our study they are also competing against other exotic grass species that are trying to establishing (Oduor et al. 2013).

Effects of fire on invasive species establishment

Fire's effect on invasive species establishment was highly variable by species and by year. In the Great Basin both *H. glomeratus* and *B. tectorum* did not show any difference between the burned and the unburned plots for establishment in 2012 for *H. glomeratus* and 2013 for *B. tectorum*. However in 2013 for *H. glomeratus* and 2014 for *B. tectorum* we saw a huge difference where they were both prolific (figures 1.2 a and b). This pattern of delayed establishment success after a fire where *B. tectorum* had been present prior to the fire and *H. glomeratus* was not present prior to the fire demonstrates an open window of opportunity for restoration. Potential reasons for delayed germination in 2012 and 2013 for both of our Great Basin exotics could be due to climatic variables (i.e. temperature, precipitation) (Beatley 1966, Khan et al. 2001, Concilio et al. 2013), or granivory of the seeds through the small mammal community (Brown and Heske 1990, Connolly et al. 2014).

In the Mojave Desert the pattern that fire gave in the Great Basin with delayed establishment was much different after the prescribed fire. The invasive grass *B. rubens* was well established in our plots prior to the fire and after the fire their density was lowerer in the burned plots compared to the unburned plots which was unexpected (figure 1.2c). While *B. rubens* decreased S. *arabicus* increased in the burned plots (figure 1.2d). This dramatic increase is most likely brought on by the competitive release from *B. rubens* for space and nutrients

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(Esque et al. 2010, Brooks 2012). We know that the weather patterns had changed with the growing season temperatures and precipitation being very different for those two years potentially influencing the germination successes of both exotic species (Beatley 1966).

Combined effects of small mammals and fire on exotic establishment

Small mammals' ability to create resistance to invasive plant establishment after a fire disturbance could give greater insight into the patterns of invasion. We found that even though the direct effects of small mammals and fire influenced the establishment of invasive species in both deserts, albeit differently, they still give a picture of how invasive species establish (figures 1.1 and 1.2). The combined effects of small mammals and fire did not show direct interactions as expected for each year sampled (figure 1.3). We believe that the reasons we did not see any strong effects is that both deserts have been at or below average precipitation for the years sampled since the prescribed fires in 2011(Western Regional Climate Center Staff 2014). If we had several years of average or above-average precipitation the results could be different. The reason for this is that small mammals have periods where they are highly abundant due to above-average precipitation (Beatley 1976, Letnic et al. 2005, Letnic and Dickman 2010, Previtali et al. 2010). If small mammals had high abundance in the deserts after our prescribed fires it could be possible that combined the fire and the small mammals would create a strong resistance effect on establishing invasive species (Pearson et al. 2012). In 2012, the first year after the fire, we did see a decrease in *H. glomeratus* in the small mammal present plots that were burned which was the first year following an average precipitation year in the Great Basin (figure 1.3a and b). In Sharp et al (2014) they measured the small mammal abundance at our site for the years 2012 to 2014 and showed that the abundance of small mammals was higher in 2012 than in 2013 or

2014. This data with ours further supports the idea that after fire disturbance small mammals can influence the establishment of invasive species in a desert ecosystem.

Conclusion

Fires are increasing around the world and especially in our arid and semi-arid ecosystems of the Western United States (Liu et al. 2010, Abatzoglou and Kolden 2011). These fires in the Western United States are the result of fuel buildup caused by the *Bromus spp.* exotic annual grasses (D'Antonio and Vitousek 1992, Brooks et al. 2004). The disturbance by fire in desert ecosystems allows for new exotic species to enter and establish further changing the native plant community (Suazo et al. 2011). Even with changes in plant communities the small mammals of deserts are a strong shaper of the plant communities whether in uninvaded or invaded plant communities (Brown and Heske 1990, Pearson et al. 2011). By adding disturbances such as fire into the ecosystems the small mammal communities do change species dominance (Horn et al. 2012) which could have rippling effects on plant establishment and especially on invasive plant establishment after a fire disturbance. Based on the results of our study we conclude that small mammals can and do reduce the establishment success of multiple invasive species in the Great Basin and Mojave Deserts through herbivory. The strength of the biotic resistance provided by the small mammals is heavily tied to fire disturbance and the few years after the fire. The ability for small mammals to act as a biotic resistance should be taken under consideration in planning restoration efforts for post-fire disturbance.

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Chapter 1 Tables

Table 1.1. Mixed model rank sum test results for *Bromus tectorum* and *Halogeton glomeratus* by burn treatment, small mammal treatment, and combined burn and small mammal treatment interactions. Potential significance defined as $p < 0.07$. Statistically significant defined as: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

Source	2012			2013			2014		
	Df	F Value	Pr(>F)	Df	F Value	Pr(>F)	Df	F Value	Pr(>F)
Bromus tectorum									
Burn Treatment				1	0.45	0.513	1	9.22	0.010**
Small Mammal Treatment				1	2.64	0.130	1	6.12	0.029*
Burn Treatment : Small Mammal Treatment				1	0.51	0.489	1	2.48	0.141
Halogeton glomeratus									
Burn Treatment	1	0.00	1.000	1	29.31	<0.001***			
Small Mammal Treatment	1	6.09	0.029*	1	13.72	0.003**			
Burn Treatment : Small Mammal Treatment	1	3.97	0.069˙	1	2.03	0.179			

Table 1.2. ANOVA test result for *Bromus rubens* and a mixed model rank sum test result for *Schismus arabicus* by burn treatment, small mammal treatment, and combined burn and small mammal treatment interactions. Potential significance defined as •p < 0.07. Statistically significant defined as: *p < 0.05; **p < 0.01; ***p < 0.001.

Source	2013			2014		
		F			F	
	Df	Value	Pr(>F)	Df	Value	Pr(>F)
Bromus rubens						
Burn Treatment	1	4.16	0.064•	1	3.88	0.072•
Small Mammal Treatment	1	9.11	0.010**	1	1.19	0.295
Burn Treatment: Small Mammal Treatment	1	1.44	0.252	1	0.79	0.391
Schismus arabicus						
Burn Treatment	1	45.25	<0.001***	1	20.73	<0.001***
Small Mammal Treatment	1	9.04	0.010**	1	1.23	0.288
Burn Treatment: Small Mammal Treatment	1	1.41	0.258	1	0.44	0.517
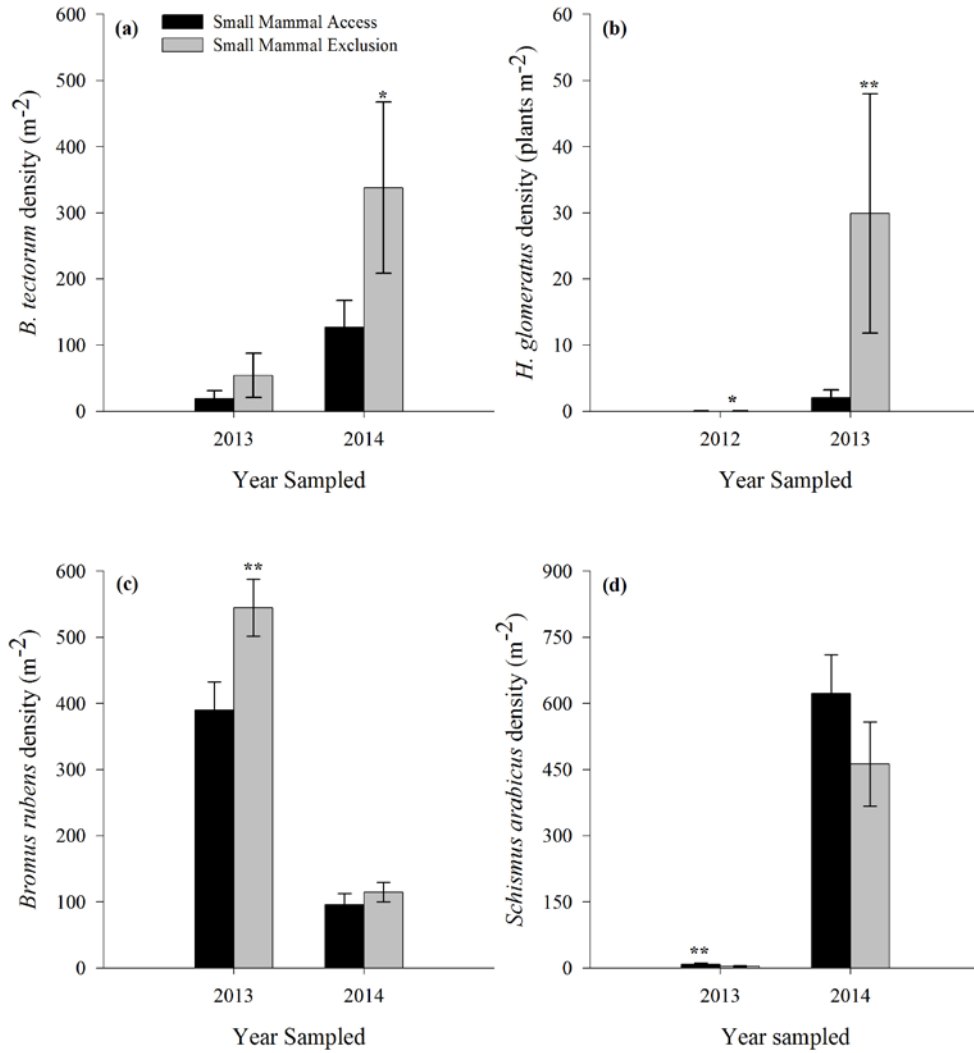
Figure 1.1. The effects of small mammal presence on *Bromus tectorum, Halogeton glomeratus, Bromus rubens,* and *Schismus arabicus* on their mean (±SEM) plant densities. The main effects for each species and year are shown (see tables 1.1 and 1.2). Panels follow as (a) *B. tectorum* (b) *H. glomeratus* (c) *B. rubens* (d) *S. arabicus*. It should be noted that *H. glomeratus* was sampled in 2012 and 2013, while the other species were sampled in 2013 and 2014.
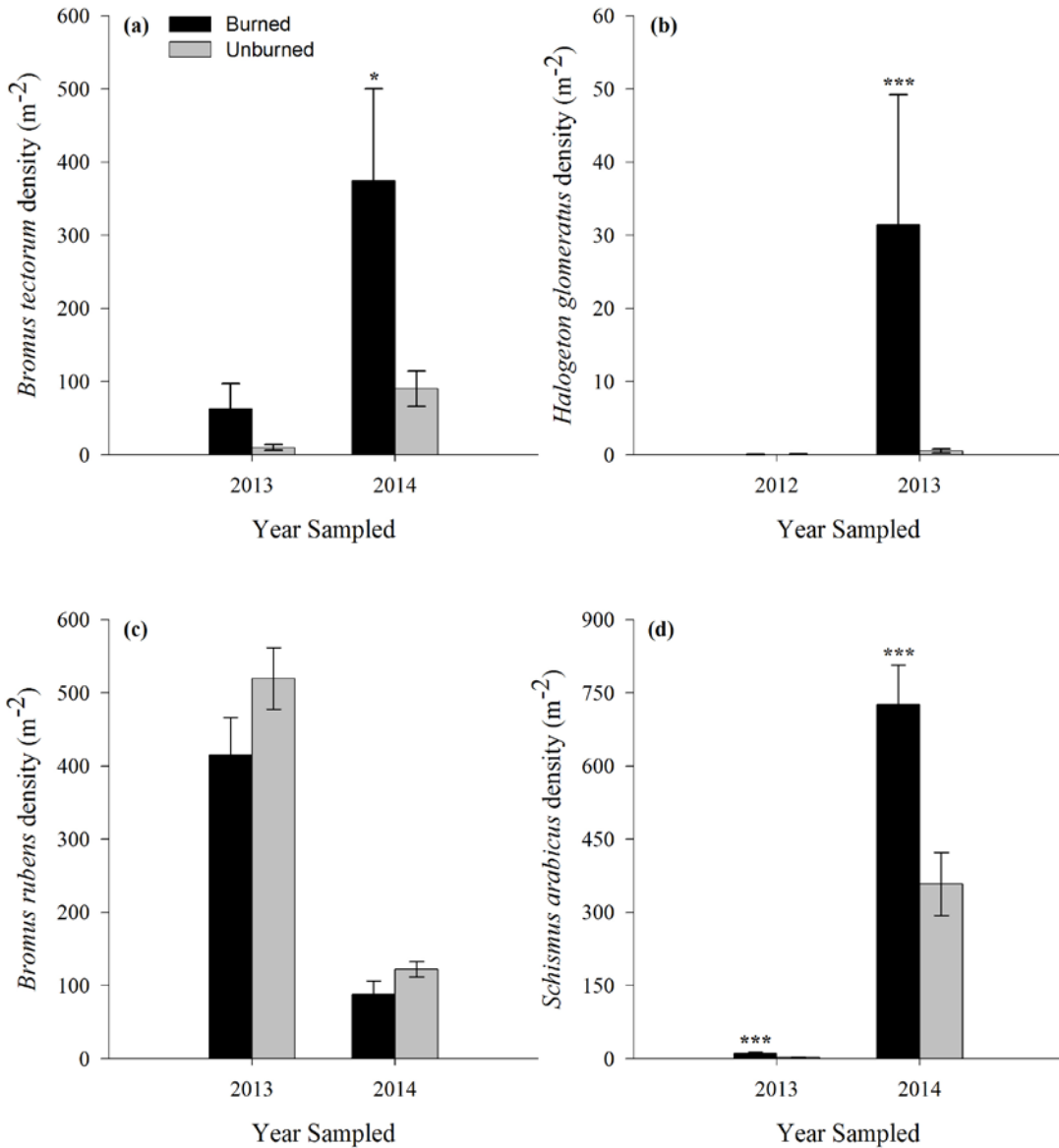
Figure 1.2. Burn effects on *Bromus tectorum, Halogeton glomeratus*, *Bromus rubens,* and
Schismus arabicus on their mean (±SEM) plant densities. The main effects for each species and
year are shown (see tables 1.1 and 1.2). Panels follow as (a) *B. tectorum* (b) *H. glomeratus* (c)
B. rubens (d) *S. arabicus*. It should be noted that *H. glomeratus* was sampled in 2012 and 2013,
while the other species were sampled in 2013 and 2014.
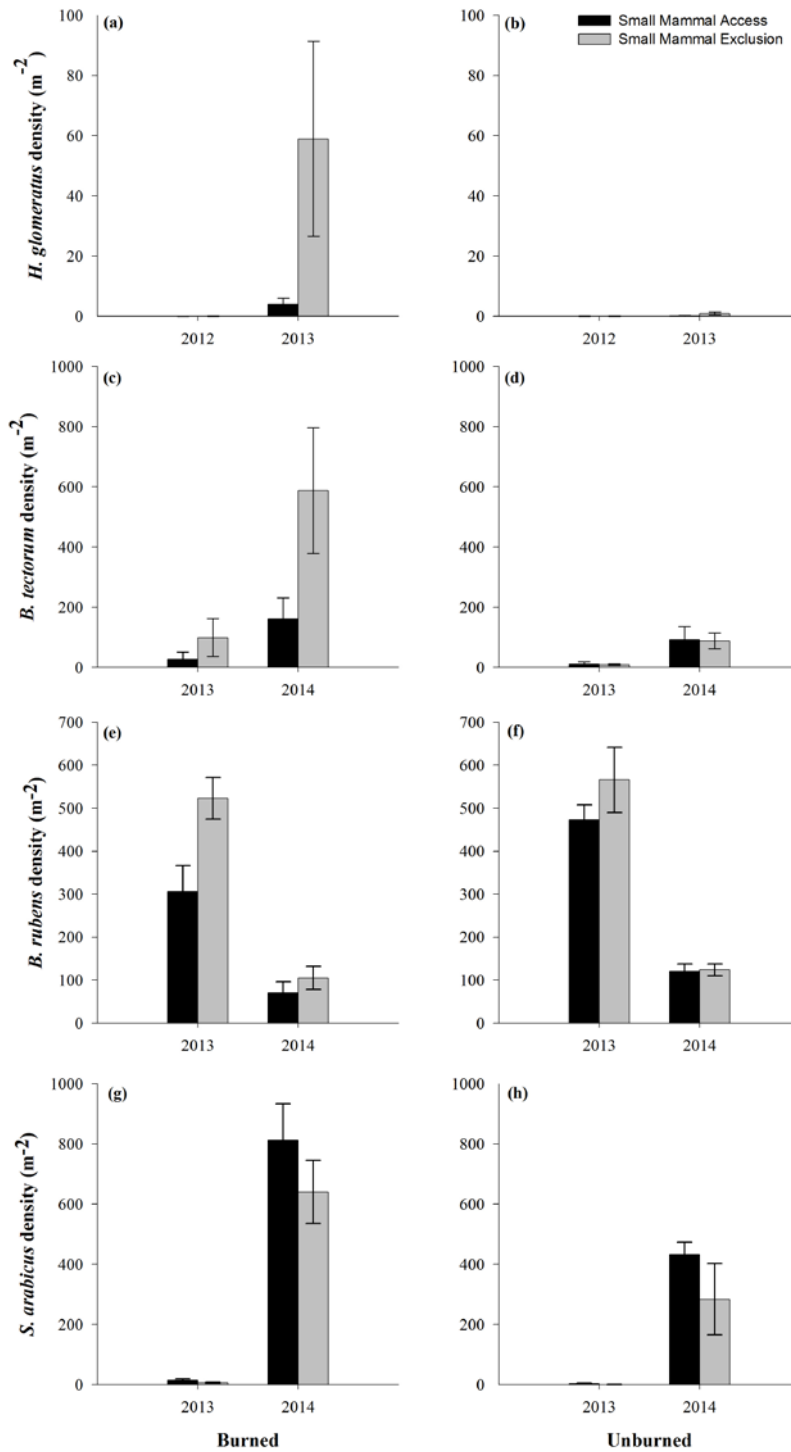
Figure 1.3. Combined burn and small mammal interactions on *Halogeton glomeratus*, *Bromus tectorum,* *Bromus rubens,* and *Schismus arabicus* on their mean (±SEM) plant densities. The combined effects of burn type and small mammal presence for each plant species, by year are shown (see tables 1.1 and 1.2). Panels follow as species type in burned treatment and unburned treatment respectively (a and b) *H. glomeratus, (c and d) B. tectorum,* (e and f) *B. rubens,* (g and h) *S. arabicus*. It should be noted that *H. glomeratus* was sampled in 2012 and 2013, while the other species were sampled in 2013 and 2014.

Chapter 2. Precipitation and herbivory thresholds for *Bromus rubens* establishment post-fire

Abstract

Precipitation and herbivory are two explanations for how plants establish in dryland ecosystems. These two paradigms tend to be acknowledged separately and rarely combined to describe invasive species establishment. In the Mojave Desert *Bromus rubens* is altering the native plant community by shortening the fire return intervals. We implemented a nested full factorial experiment that observes how *B. rubens* establishes under different precipitation regimes and how small mammal predation affects its establishment in burned and intact plant communities. For two growing seasons we monitored *B. rubens* density (m^{-2}), biomass (g m^{-2}), and seed density (m^{-2}). We observed that small mammals do create a top-down pressure on *B. rubens'* establishment in both burned and intact plant communities. The greatest effect of small mammals is during years of average precipitation where they reduce up to 50% of *B. rubens'* density. During droughts and severe droughts their top-down effects are negligible. As a result precipitation creates a threshold below which the efficacy of small mammal herbivory is not observed. Thus there is a tight relationship between top-down and bottom-up effects in dryland ecosystems where both have significant intertwined effects on exotic plant establishment.

Introduction

After decades of research community assembly rules are elusive and it remains challenging to develop theory-driven species prediction models. There are however two broad classes of explanations for how plants establish and persist in dryland ecosystems. The first group of explanations depends on soil resource availability and is commonly referred to as bottom-up effects. In arid and semi-arid ecosystems these bottom-up effects, specifically soil water availability, may regulate the establishment of plants and also determine which species

persist (Noy-Meir 1973, Beatley 1976, Schwinning and Sala 2004, Adler and Levine 2007). The other explanation that has formed is top-down pressures, generally through herbivory and granivory, which determines which plant species establish and persist in arid or semi-arid communities (Inouye et al. 1980, Brown and Heske 1990, Oduor et al. 2013). These two paradigms have shaped how we think about plant community assembly in arid and semi-arid ecosystems but there seems to be strong linkages between both that could be combined to create a unifying concept for plant establishment.

One of the fundamental applications of community assembly theory is understanding the processes controlling plant invasions. Invasive annual grasses are the dominant exotic species in dryland ecosystems and are drastically altering the native plant communities. The drastic changes in native plant communities arise from a conversion from shrubland to grassland. The change to grassland does not occur directly through competition but indirectly mainly from fire (D'Antonio and Vitousek 1992, Brooks et al. 2004). Exotic annual grasses are physiologically adapted to survive in a Mediterranean clime where a large majority of the yearly precipitation occurs from late fall to early spring (Bykova and Sage 2012). The available soil moisture from the fall to spring precipitation triggers germination events for both exotic and native species; however, the moisture requirement for the exotic annual grasses is lower than that of the native plants leading to an increased advantage in annual grass establishment (Beatley 1966, 1967, Brooks 1999). This advantage allows increased invasive grass establishment and growth that accelerates a buildup of litter allowing fire to spread eliminating the native plant community (D'Antonio and Vitousek 1992, Brooks et al. 2004). Ultimately, after a fire there is a release from competition and the annual grasses begin to dominate because they can acquire the soil resources more readily than native species (Boyd & Davies, 2012; Eskelinen & Harrison, 2013).

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One critical factor in the success of invasive annual grasses comes from their ability to use soil moisture from fall and early spring precipitation to establish.

Precipitation in deserts is highly variable from season to season and year to year. Any adjustments to the amount of precipitation will ultimately determine plant germination and reproduction that year (Noy-Meir 1973, Beatley 1974, Ogle and Reynolds 2004). With climate change occurring precipitation events are likely to become more variable (Hereford et al. 2006) resulting in changes of timing for plant establishment and species composition (Thomey et al. 2011, Báez et al. 2013). Because native dryland plant species often do not germinate or reproduce if soil moisture requirements are not met, below-average precipitation, higher evaporative rates, or longer dry periods give invasive grasses the opportunity to capitalize on the available soil resources for increasing biomass and reproductive output through seed production (Cipriotti et al. 2008, Suazo et al. 2011, Abatzoglou and Kolden 2011). As climate changes and exotic grass invasion expands it is crucial to understand how changes in seasonal precipitation quantity will affect the establishment, growth, and seed production of exotic annual grasses.

Precipitation's influence on dryland plant establishment creates a strong argument for bottom-up processes regulating invasive species establishment, but top-down pressures created from small mammal herbivory are highly influential in how plant communities establish, especially in arid and semi-arid environments. The classic study of Brown and Heske (1990) in the Chihuahuan Desert revealed that small mammals control which plant species establish depending on small mammal presence and herbivore species composition. Our current understanding is that with drought small mammal abundance is low, but during average or above-average precipitation years small mammal abundance increases which can exert some control over the plant community (Beatley 1969, 1976, Curtin et al. 2000, Letnic et al. 2005).

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However the majority of the studies on small mammal top-down pressures have been in intact, native systems. We have seen in the last several years several studies that have addressed top-down pressures and invasive species establishment but these have been in montane and prairie environments (Pearson et al. 2011, 2012, Connolly et al. 2014). With desert precipitation being highly variable within and from year to year, we would expect that small mammal herbivory should define a threshold where invasive species establishment is restricted based on the amount of precipitation received during the growing season.

Currently the Mojave Desert is experiencing an unprecedented increase in fire frequency because of the exotic annual grass *Bromus rubens L.* (Brooks and Matchett 2006). With the increased fire frequency and climate change, the Mojave Desert is undergoing a shift in plant community structure from shrubland to annual grassland. To understand the bottom-up factors influencing *B. rubens'* success in altering the structure of the plant community we established an experiment to observe how drought and increased precipitation post-fire influences the establishment of the annual grass. Also, we wanted to understand how top-down pressures from small mammal herbivory influences the establishment of *B. rubens* along with their interactions of herbivory with amount of precipitation post-fire.

We hypothesized that there will be an increase in establishment, growth, and reproductive success of *B. rubens* with an increase in the amount of precipitation received during the growing season after a fire disturbance, and where small mammals are present they will decrease the number of individuals that actually establish through herbivory. To help test this hypothesis we addressed three key questions to better understand the interactions between the bottom-up effects from fire and precipitation and the top-down herbivory effects from small mammals. 1) Does small mammal herbivory have an effect on biomass and density of *B. rubens* and does that effect

change depending on soil water availability? 2) Is there a threshold in soil water availability below which small mammal herbivory does not affect the reproductive success of *B. rubens*? 3) Does burning allow *B. rubens* to increase its biomass, density, and reproductive success regardless of precipitation treatment through competitive release?

Methods

Study Location

Our study is located on an upland Mojave Desert site at Lytle Ranch, a property owned by Brigham Young University and partnered with the Nature Conservancy in the Beaver Dam Wash of southwest Utah (37°08'54"N, 114°00'51"W). To our knowledge the site has not burned since settlement but has had historic cattle grazing. The soils at the site are a sandy loam (Soil Survey Staff, 2014) and desert pavement with the vegetation being typical of a mid-elevation (915 m) Mojave Desert shrubland dominated by *Larrea tridentata* (DC) Colville, *Coleogyne ramosissima* Torr, *Ambrosia dumosa* (A. Gray) Payne, and *Yucca brevifolia* Engelm. Much of the herbaceous understory vegetation is dominated by the exotic annuals *Bromus rubens* L*., Schismus arabicus* Nees*,* and *Erodium cicutarum* (L.) L'Hér. ex Aiton. The twenty year mean annual precipitation of the site is 264 mm with a mean annual temperature of 16°C (WRCC, Lytle Ranch Station). Our growing season (October to May) precipitation for 2013 and 2014 were 139.44 mm and 75.94 mm. As is typical of the Mojave Desert there was substantial variation in temperature and precipitation during the two years of our experiment (Figure 2.1).

Experimental design

In 2011, we established five blocks with a full factorial (2x2) design per block for a total of 20 plots to study the relationship between small mammals and vegetation recovery post-fire. Each plot was 30m x 30m surrounded by a wire mesh fence that was buried 0.35m and is 0.65m

above ground level. Half of the plots (N = 10) had small mammals excluded by adding a 0.2m

metal flashing to the top of the wire mesh fence and through trapping in April, July, and October,

the other half of the plots (N=10) have access holes cut into the fence to allow small mammals

entrance. In June 2011, half of the plots were burned as a treatment (N = 10) leaving the other

half of the plots unburned (N = 10). Each treatment present was randomly assigned within each

block prior to construction of the plots. Within each factorial plot, 2-3 precipitation shelters

were constructed and nested within to manipulate the annual rainfall. The three treatments

present for rainfall manipulation were drought, where we exclude 30% of the annual

precipitation (N = 20), a water addition of 30% of the 20 year long-term average (N = 20), and a

control rainfall (N = 10) for a total of 50 rainfall manipulation shelters. These shelters were

constructed to better understand how precipitation regulates plant growth and recruitment.

Precipitation shelter design and construction

Each rain manipulation shelter was 6 m^2; the shelters were centered over one *L.*

tridentata shrub. During construction of the shelters a 0.30 m deep trench was dug and the plot

was lined on all four sides with metal flashing to help eliminate lateral water flow. To eliminate

external water flowing into the "sheltered area," which term will be used throughout identifying

the area beneath the shelter, 0.05 m of metal flashing was added to the already buried flashing on

the uphill and side hill slopes. The downhill edge did not have the flashing to allow water to

move off of the sheltered area to eliminate pooling of water. The sheltered areas for the

treatments have an edge buffer of 0.4 m x 0.4 m to give a central plot dimension of 1.6 m x 2.6 m

where all plant sampling occurred so as to not be impacted by edge effects from the trenching or

construction of the shelter.

Shelters and their roofs were finished at the end of the spring of 2012 and covered the plots starting from the summer of 2012 to date. The aboveground structure consisted of six steel pipes, four corner posts and two in the center between the two long axes to add stability to the structure. Each post was set 0.5m in the ground and was cemented into place. The roof consisted of nine plastic slats ≈0.1m apart that either directed the water off into a gutter and away from the shelter or allowed water to enter the sheltered area. The roofs were 2 m from ground level sloping to 1.5 m from the ground. The shelters for drought treatments excluded 30% of the annual rainfall. The slats in the water addition and control shelters were turned upside down to allow the full amount of the annual rainfall to enter the sheltered area. The water addition shelters add 30% more water through the use of a gas pump irrigation spraying system. All water for the addition shelters comes from a well located on the Lytle Preserve property. The amount of water added to the sheltered areas change every month to follow the long-term monthly averages. The amount of water applied during each "precipitation event" is based off of a timed addition of water. The time duration for application of water was based off of timing how long it takes to spray water into a pre-determined volume container and calculating the amount of time needed to apply a predetermined amount of water to the sheltered area.

Vegetation monitoring

We measured *B. rubens* densities beneath each sheltered area using 0.01m^2 quadrats in the spring of 2013 and 2014. Measurements took place in two site locations beneath the sheltered area, the first beneath the shrub within the fertile island and the second location was in the inter-shrub space. At each location we made eight measurements corresponding to cardinal directions (N, NE, E, SE, etc.). At each cardinal direction we placed the 0.01 m^2 quadrat and counted the number of *B. rubens* tillers rooted within each quadrat. *B. rubens* was sampled this

way for all 50 shelters in the 20 plots. After sampling density beneath each sheltered area we then destructively harvested whole plants of *B. rubens* with a $0.025m^2$ frame on the north and south side of the shrub and inter-shrub space beneath each sheltered area. The harvested samples were then oven-dried at 60 °C for 24 hours and then weighed. The biomasses obtained from the dried samples allowed us to determine the effects that precipitation combined with the burned and small mammal treatments have on the growth of the established *B. rubens* individuals. After weighing whole plant samples we dissected the inflorescences to remove all filled seeds. The seeds were then counted and weighed to determine the differences in whole plant biomass, fecundity, and seed weight.

Small mammal trapping

Small mammal trapping was done in April, July, and October each year to ensure that the exclosures were effectively excluding small mammals. When small mammals were caught in the exclosures they were then removed. Each small mammal seasonal sampling period occurred over a three day period. Sherman live-traps were baited at dusk and retrieved around dawn. We recorded small mammal species, weight, and reproductive status as well as ear tagging the individual to avoid double counting of recaptures. These measurements were to maintain a record of the small mammal community present at our experimental site (data not presented see Sharp 2014).

Data Analysis

All data collected were averaged by shelter for use in the statistical analyses. All data were scaled from their sampling frame size to square meters for ease of interpreting the data. For our data analysis we used R Studio (R Core Team 2012) and the lme4 package (Bates et al. 2013) for all of our exploratory and final analyses. We analyzed the data using a nested repeated

measures mixed model analysis of variance with our response variables being *B. rubens* density (tillers/m^2), total aboveground biomass (g/ m^2), seed count (seeds/ m^2), and seed biomass (g/ m^2). The explanatory categorical variables used in all models were burn type (burned or unburned), small mammal treatment (present or excluded) and precipitation type (drought, control, or addition). We nested precipitation shelters with blocks and years to account for all spatial and temporal variation within our models. All response variables were transformed. Plant density, seed count, and seed weight were transformed using a square root transformation to achieve normality and homoscedasticity and red brome biomass was transformed using a log+1 transformation to achieve normality and homoscedasticity; all other assumptions required for ANOVAs were also met. All significant factors and interactions with more than three levels were tested with a least-square means pairwise comparison using the lsmeans package in R (Lenth 2014). Statistical significance was set at an alpha level of 0.05 prior to performing statistical analyses.

Results

Small mammal herbivory on Bromus rubens establishment

When small mammals were present in the experimental plots they decreased the density of *B. rubens* tillers per m^2 ($F_{1,50}$ = 9.68, p = 0.003, table 2.1). The percent of tillers per m^2 that small mammals removed varied between ~15% in the unburned plots to ~46% in the burned plots, respectively, for the years 2013 and 2014 (figure 2.2). A reduction in *B. rubens* biomass was also detected by the presence of small mammals ($F_{1,50}$ = 4.98, p = 0.028, table 2.3) by ~25% in both the burned and intact plots for 2013 and 2014(figure 2.2).

Precipitations effects on Bromus rubens establishment

The density of *B. rubens* was also affected by the amount of precipitation received during the growing season ($F_{2,50} = 6.26$, $p < 0.001$, , table 2.1). We observed a two to three fold change in tiller density per m^2 ($p < 0.001$, table 2.2) between the drought treatments and the water addition treatments (figure 2.2). The control treatments had almost double the density of *B. rubens* tillers per m^2 than the drought treatments ($p = 0.004$, table 2.2), but between the control and water addition treatments there were no differences ($p = 0.065$, table 2.2). Tiller density of *B. rubens* saw no interactive effect with that precipitation and small mammal presence ($p = 0.098$).

For *B. rubens* biomass we saw an increase due to the precipitation treatments ($F_{2,50} = 7.62$, $p < 0.001$, table 2.3). The most noted increase was a two fold increase between the drought precipitation treatment and the water addition ($p = 0.001$, figure 2.2, table 2.4). Between the drought and control precipitation treatments we saw no differences ($p = 0.453$). We also saw no difference between the control and water addition precipitation treatments ($p = 0.153$). Additionally, *B. rubens* biomass had no interactions between precipitation and small mammal presence ($p = 0.194$).

Thresholds in reproductive success of Bromus rubens

The different precipitation treatments had a significant effect on the amount of *B.rubens* seed produced per m^2 ($F_{2,50} = 12.18$, $p < 0.001$, table 2.5). We observed that there was more than a two-fold difference between the drought treatments and water addition treatment ($p < 0.001$), the same two fold difference was observed between the control treatment and water addition treatment ($p = 0.049$, figure 2.3). There was however no difference between the drought and control precipitation treatments ($p = 0.318$). In observing the differences between precipitation

treatments and *B. rubens* seed densities per m2 we analyzed the individual weights of the *B. rubens* seeds and found that there were no differences with the average seed weight between precipitation treatment. The average seed weight across all treatments was 0.001 g (SE±0.0002).

The exclusion of small mammals did have an effect on the density per m^2 ($F_{1,50} = 6.46$, p = 0.012, table 2.5) and the interaction between small mammal exclusion and precipitation treatments was also significant ($F_{2,50} = 3.65$, p = 0.029, table 2.3). We observed that when small mammals are excluded there was a two-fold increase in seed count between the drought treatments and water addition treatments (p < 0.001, figure 2.3). We also saw a 43% to 67% decrease in seed density per m^2 between the small mammal treatments in the water addition plots (p = 0.009).

Burn interactions with precipitation and herbivory

Burning reduced the density of *B. rubens* by ~20-50% depending on the year (figures 2.1, $F_{1,50} = 0.014$, p = 0.014, figure 2.2, table 2.1). There were however no significant burn interactions for *B. rubens'* density with small mammals ($F_{1,50} = 0.28$, p = 0.747, table 2.1), precipitation ($F_{2,50} = 2.50$, p = 0.092, table 2.1), or a three-way interaction between the burn, small mammal, and precipitation treatments ($F_{2,50} = 0.35$, p = 0.706, table 2.1).

There was no burn effects on the amount of biomass produced by *B. rubens* ($F_{1,50} = 1.13$, p = 0.290, figure 2.4, table 2.3). The interactions between burn and small mammal treatments had no effect on *B. rubens'* biomass (F1,50 = 2.31, p = 0.131, table 2.3). However there was an interaction between burn and precipitation treatments where we observed a significant difference (figures 2.3, $F_{2,50} = 3.58$, p = 0.032, table 2.3). We observed more than a two-fold increase in biomass from the burned drought treatment to the unburned water addition treatment (p = 0.022,

table 2.4). There was also a doubling in biomass between the unburned drought and water addition plots (p < 0.001 table 2.4). All other interactions between burn and precipitation treatments for biomass were not significant (table 2.5). There was also no significant three-way interaction for biomass between burn, small mammal, and precipitation treatments ($F_{2,50} = 0.28$, p = 0.751, table 2.3).

The burn treatments did not have a significant effect on seed density ($F_{1,50} = 0.79$, p = 0.376, figure 2.4, table 2.5). However the burn treatments did have a significant interaction with the small mammal treatment on seed density ($F_{1,50} = 6.11$, p = 0.015, table 2.5). We observed a decrease of ~32% to ~67% of seeds per m2 in the burned plots with small mammals present compared to where small mammals were excluded (figure 2.4, p = 0.015). All other interactions between burn and small mammal treatments were not significant (table 2.6). The interaction between burn and precipitation treatments were not significant ($F_{2,50} = 2.14$, p = 0.123, table 2.5), along with the three-way interaction between burn, small mammals, and precipitation treatments ($F_{2,50} = 0.03$, p = 0.969, table 2.5).

Discussion

Small mammal direct effects on Bromus rubens

Our study found that the direct main effect of small mammal herbivory did have a strong effect on *B. rubens'* density, biomass, and seed density. We observed a 20 to 50 percent reduction in *B. rubens* density (figure 2.2), a 25 percent reduction in biomass (figure 2.2), and a two-fold reduction in seed density between the small mammal present plots and the small mammal exclusion plots (figure 2.3). Consumer mediated herbivory has been observed in other ecosystems but predominately on invasive annual forbs (Inouye et al. 1980, Pearson et al. 2011, 2012, Connolly et al. 2014).

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Few studies show that small mammals have a positive direct effect on the reduction of *Bromus* grasses (Connolly et al. 2014). Generally, it is reported that small mammals are negatively impacted by *Bromus* species, and this is mainly from a community analysis of species richness. However, Beatley (1966) showed that the kangaroo rat *Dipodomys microps* had negative interaction with *B. rubens* but that *Dipodomys merriami* showed no interaction with the annual grass, and Horn et al (2012) showed an increase in *D. merriami* in burned locations with *B. rubens*. It is possible that in bimodal desert ecosystems small mammals will take advantage of the early production of foliage and seed from invasive annual grasses until the native plant species become available.

Precipitation and small mammal interactions on Bromus rubens

Precipitation in the Mojave Desert comes during the winter and spring months with a monsoon season in late summer. During the two years of our study, the growing season precipitation (October to May) was 139.44 mm (2013) and 75.94 mm (2014), which were both below the 20-year long-term average of 214.12 mm for the site. This allowed our rain manipulations to mimic severe drought (minus 30% of current year precipitation), drought (control or current years precipitation), and an average (current year precipitation with 30% more water added from 20 year long-term average) year for precipitation. We observed in the water addition and control treatments that small mammals reduced *B. rubens* through a decrease in density, biomass, and seeds produced (figures 2.2, 2.3) (Brown and Heske 1990, Pearson et al. 2012). However during the minus water treatment small mammals had no effect on plant density, biomass, or seed density showing that there is a base threshold where *B. rubens* can survive without negative effects from small mammal herbivory.

There is another threshold where small mammal herbivory does not affect the reproductive success of *B. rubens*. We observed that during the mimicked years of severe drought and drought that the influence of small mammals is not noticed. In both 2013 and 2014 we saw this pattern but it is more pronounced during 2014. The 2014 growing season was very dry causing a significant difference to emerge between the water addition plots and the drought and control treatments in the production of seeds (figure 2.3). Because 2013 was wetter than 2014 the threshold is less noticeable between the control and water addition treatments. The large difference between the seed densities of 2013 and 2014 are likely related to the density of *B. rubens* in those years but it could also be attributed to the lack of early spring season precipitation that it needed for increased establishment, growth, and production (Concilio et al. 2013).

The combined bottom-up effects from precipitation and small mammal predation on *B. rubens* cannot explain fully the pattern that we observed between 2013 and 2014 with the large drop in tiller density and seed density (figure 2.2 and 2.3). We suspect that the drop in magnitude in plant and seed density was a result of heavy rains in November 2013 where 29.4 mm of precipitation was received causing a strong germination event (Beatley 1974, Brooks 1999, Salo 2004). This large amount of precipitation in November was followed by a dry December which only received 5 mm of precipitation, and also had several freezing events (figure 2.1). We hypothesize that these freezing events killed the majority of germinates and seedlings, leaving only the few surviving seedlings and the late germinating individuals to establish (Horn 2013). It is key for successful germination that winter annuals in the desert receive 25 mm of precipitation (Beatley 1974, Suazo et al. 2011), but other abiotic variables need to be studied in conjunction with precipitation to understand the requirements for establishment and persistence.

Burn interactions with precipitation and herbivory

Burning resulted in a decrease in density when compared to the intact plots (figure 2.4).

B. rubens biomass and reproductive output had no differences between the burned and unburned

plots or across precipitation treatments (figure 2.4).   We expected our burn treatments to show

similar results to that from previous studies where *B. rubens* density was high and had an

increase in biomass after a fire (Beatley 1966, Brooks 2002, Salo 2004, Esque et al. 2010). The

difference between our results and those of the other studies could possibly be related to our

prescribed burn. Our fire removed all fine fuels, grasses and forbs, but not all woody plants and

Yucca brevifolia making a heterogeneous burn pattern. It should be noted that our burn pattern

did not alter the direct effects that were observed on the treatments. Biomass did not have any

direct burn effects but it did have an interactive effect with precipitation (table 2.3). In both

years the average precipitation was considered to be at drought levels. The increased

establishment of *B. rubens* in the unburned control and water addition plots can be explained by

the retention of soil moisture beneath shrub canopies (Austin et al. 2004, Suazo et al. 2011). In

2014 the interactions between burning and precipitation were much less pronounced than in 2013

but the general pattern of increased biomass was still present in the water addition plots (figure

2.3).

Conclusion

It is well documented that growing season precipitation in arid and semi-arid systems

influences the abundance and growth of plants (Beatley 1974, Ogle and Reynolds 2004, Heisler-

White et al. 2008, Suazo et al. 2011) but when combined with small mammal herbivory we

observe that it can create thresholds that can control *B. rubens* establishment. However, this

changes when the Mojave Desert experiences average or above-average precipitation in the

growing season. Strong germination events caused by the increased precipitation inhibits the ability of small mammal herbivory to create a top-down control on *B. rubens* allowing it to escape, connecting shrub islands and building a continuous fuel load. We hypothesize that in those years where average and above-average precipitation occurs in the late fall (October and November) *B. rubens* escapes the top-down pressures from small mammal herbivory through increasing its density and biomass into the inter-shrub space and shrub canopies (Horn 2013). This escape from the top-down pressures of small mammals allows it to replenish the seed bank and build fuel to carry wildfires, which will perpetuate the cycle of invasive annual grasses.

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Chapter 2 Tables

Table 2.1. *Bromus rubens d*ensity Anova results. Statistically significant defined as p<0.05 = *, p<0.01 = **, p<0.001***.

Source	d.f.	MS	F	P
Burn	1,50	88.67	5.87	0.014*
Small Mammal	1,50	131.57	9.68	0.003**
Precipitation	2,50	354.05	6.26	< 0.001***
Burn*Small Mammal	1,50	1.42	0.28	0.7473
Burn* Precipitation	2,50	34.22	2.50	0.0929
Small Mammal* Precipitation	2,50	33.26	2.47	0.0983
Burn* Small Mammal* Precipitation	2,50	4.71	0.35	0.7067

Table 2.2. *Bromus rubens* density least-square means difference. Statistically significant defined as p<0.05 = *, p<0.01 = **, p<0.001***.

Source	estimate	SE	df	t.ratio	p.value
Precipitation					
control - minus	4.63131	1.33593	34.16	3.467	0.004**
control - plus	-3.11235	1.33593	34.16	-2.33	0.065
minus - plus	-7.7437	1.07233	34	-7.221	<0.001***

Table 2.3. *Bromus rubens* biomass Anova results. Statistically significant defined as
p<0.05 = *, p<0.01 = **, p<0.001***.

Source	d.f.	MS	F	P
Burn	1,50	0.62	1.13	0.2906
Small Mammal	1,50	2.82	4.98	0.028*
Precipitation	2,50	4.19	7.62	<0.001***
Burn*Small Mammal	1,50	1.27	2.31	0.1316
Burn* Precipitation	2,50	1.97	3.58	0.032*
Small Mammal* Precipitation	2,50	0.91	1.67	0.1943
Burn* Small Mammal* Precipitation	2,50	0.15	0.28	0.7519

Table 2.4. *Bromus rubens* biomass least-square means difference. Statistically significant defined as p<0.05 = *, p<0.01 = **, p<0.001***.

Source	estimate	SE	df	t.ratio	p.value
Precipitation					
control - minus	0.250691	0.20652	34.05	1.214	0.4533
control - plus	-0.39256	0.20652	34.05	-1.901	0.1539
minus - plus	-0.6433	0.16576	34	-3.881	<0.001***
Burn*Precipitation					
burned,control - unburned,control	-0.21679	0.338365	34	-0.641	0.987
burned,control - burned,minus	-0.00647	0.291569	34.03	-0.022	1
burned,control - unburned,minus	0.291061	0.291569	34.03	0.998	0.9153
burned,control - burned,plus	-0.20873	0.291569	34.03	-0.716	0.9787
burned,control - unburned,plus	-0.79319	0.291569	34.03	-2.72	0.0971
unburned,control - burned,minus	0.21032	0.291569	34.03	0.721	0.978
unburned,control - unburned,minus	0.507847	0.291569	34.03	1.742	0.5151
unburned,control - burned,plus	0.008059	0.291569	34.03	0.028	1
unburned,control - unburned,plus	-0.5764	0.291569	34.03	-1.977	0.3759
burned,minus - unburned,minus	0.297527	0.234426	34	1.269	0.7993
burned,minus - burned,plus	-0.20226	0.234426	34	-0.863	0.9527
burned,minus - unburned,plus	-0.7867	0.23443	34	-3.356	0.0221*
unburned,minus - burned,plus	-0.49979	0.234426	34	-2.132	0.2957
unburned,minus - unburned,plus	-1.0842	0.23443	34	-4.625	<0.001***
burned,plus - unburned,plus	-0.58446	0.234426	34	-2.493	0.1546

Table 2.5. *Bromus rubens* seed density Anova results. Statistically significant defined as p<0.05 = *, p<0.01 = **, p<0.001***.

Source	d.f.	MS	F	P
Burn	1,50	280.40	0.79	0.3763
Small Mammal	1,50	2346.80	6.46	0.0128*
Precipitation	2,50	4319.60	12.18	<0.0001***
Burn*Small Mammal	1,50	2167.70	6.11	0.0154*
Burn* Precipitation	2,50	760.10	2.14	0.1236
Small Mammal* Precipitation	2,50	1296.70	3.65	0.0299*
Burn* Small Mammal* Precipitation	2,50	11.10	0.03	0.9692

Table 2.6. *Bromus rubens* seed density least-square means difference. Statistically significant defined as p<0.05 = *, p<0.01 = **, p<0.001***.

| Source contrast	estimate	SE	df	t.ratio	p.value
Precipitation					
control - minus	7.700973	5.245202	34.06	1.468	0.3186
control - plus	-12.924	5.2452	34.06	2.464	0.0485*
minus - plus	-20.625	4.21009	34	4.899	0.0001***
*Burn*Small Mammal*					
burned,Small mammal excluded - unburned,Small mammal excluded	5.100893	5.374468	34	0.949	0.7787
burned,Small mammal excluded - burned,Small mammal present	18.6568	5.85133	34.49	3.188	0.0153*
burned,Small mammal excluded - unburned,Small mammal present	5.493134	5.85133	34.49	0.939	0.7843
unburned,Small mammal excluded - burned,Small mammal present	13.55591	5.85133	34.49	2.317	0.1139
unburned,Small mammal excluded - unburned,Small mammal present	0.392242	5.85133	34.49	0.067	0.9999
burned,Small mammal present - unburned,Small mammal present	-13.1637	5.953962	34	2.211	0.1407
*Small Mammal*Precipitation*					
Small mammal excluded,control - Small mammal present,control	7.412109	9.617195	35.56	0.771	0.9707
Small mammal excluded,control - Small mammal excluded,minus	11.77401	7.088591	34.48	1.661	0.5656
Small mammal excluded,control - Small mammal present,minus	11.04004	7.088591	34.48	1.557	0.6308
Small mammal excluded,control - Small mammal excluded,plus	-20.1657	7.088591	34.48	2.845	0.0738
Small mammal excluded,control - Small mammal present,plus	1.729765	7.088591	34.48	0.244	0.9999
Small mammal present,control - Small mammal excluded,minus	4.361905	8.291334	34.78	0.526	0.9947
Small mammal present,control - Small mammal present,minus	3.627932	8.291334	34.78	0.438	0.9978
Small mammal present,control - Small mammal excluded,plus	-27.578	8.29133	34.78	3.326	0.0235*
Small mammal present,control - Small mammal present,plus	-5.68234	8.291334	34.78	0.685	0.9824
Small mammal excluded,minus - Small mammal present,minus	-0.73397	5.953962	34	0.123	1
Small mammal excluded,minus - Small mammal excluded,plus	-31.94	5.95396	34	5.364	0.0001***
Small mammal excluded,minus - Small mammal present,plus	-10.0442	5.953962	34	1.687	0.5493
Small mammal present,minus - Small mammal excluded,plus	-31.206	5.95396	34	5.241	0.0001***
Small mammal present,minus - Small mammal present,plus	-9.31028	5.953962	34	1.564	0.627
Small mammal excluded,plus - Small mammal present,plus	21.8954	5.95396	34	3.677	0.0096**
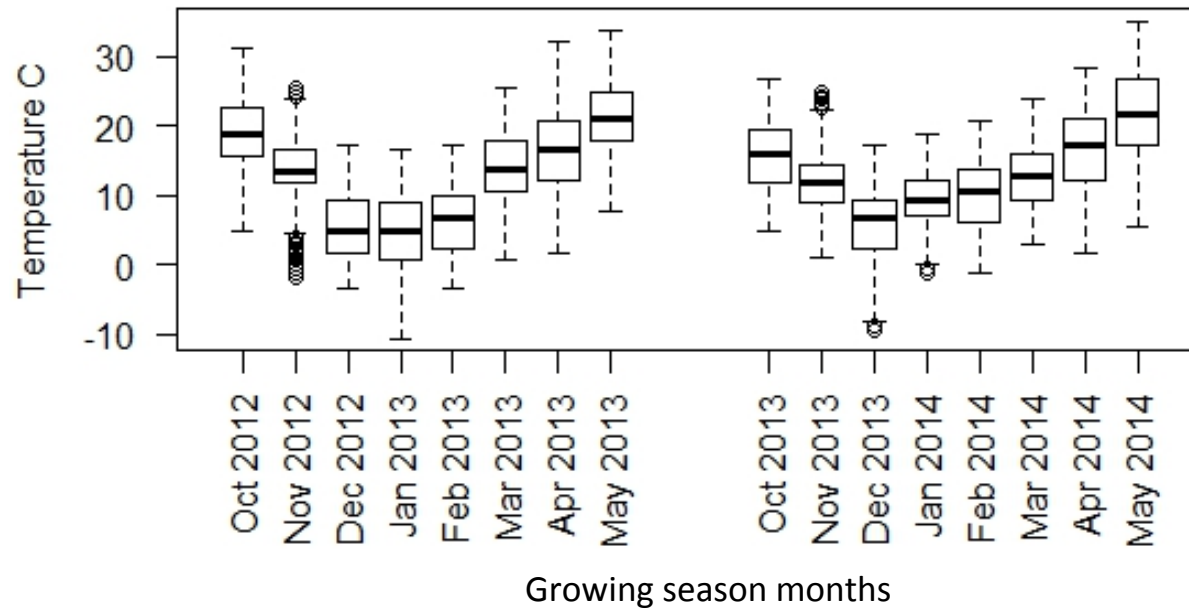
Figure 2.1. Growing season temperature for 2013-2014 taken from the Lytle Ranch weather station. We determined growing season to be from October to May based on the life history of *Bromus rubens*.
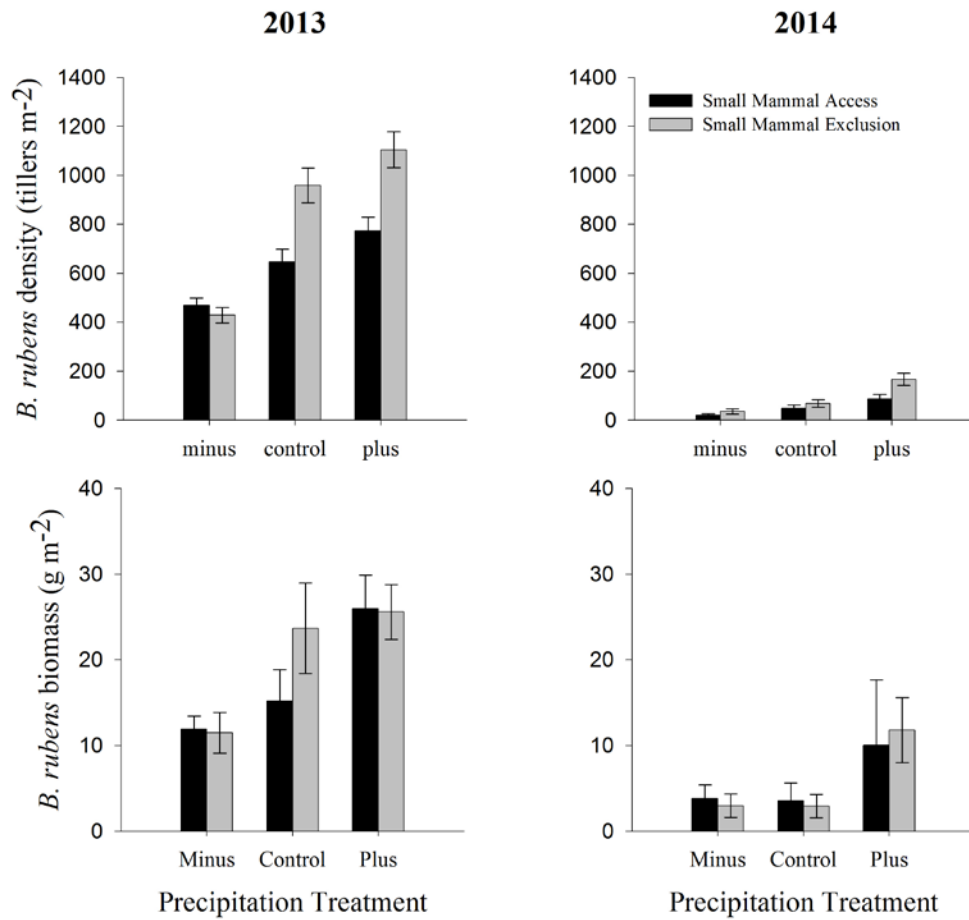
2013

2014

Figure 2.2. *Bromus ruben*s density (tillers m-2) and biomass (g m-2) are reported here in this panel for the years 2013 and 2014. The treatments on the x-axis are the different precipitation treatments imposed from the rainout shelters. The black bars signify small mammals having access to the experimental plots while the grey bars are where small mammals were excluded from the experimental plots. Small mammals had a significant direct effect on both density and biomass of *B. rubens* (tables 2.1 and 2.3). The interactions between small mammals and precipitation treatment were not significant.
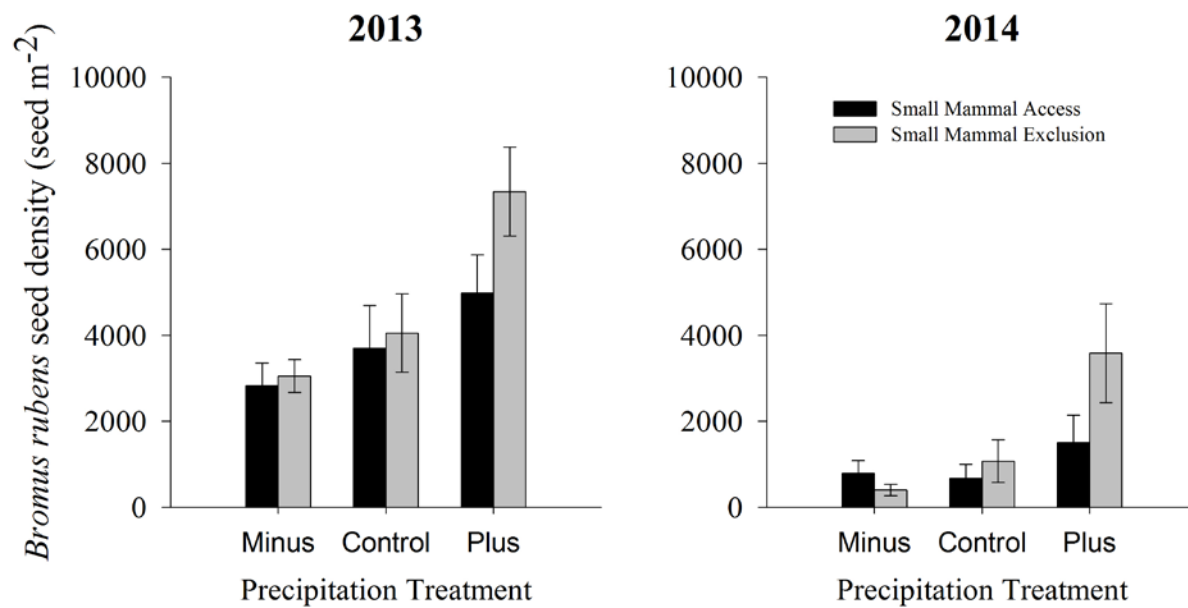
Figure 2.3. *Bromus ruben*s seed density (seed m-2) for the years 2013 and 2014. The main treatment was that of the rainout shelter precipitation manipulations. The black bars represent small mammals that have access to the experimental plots with the grey bars representing small mammals being excluded from the experimental plots. There was a two-fold difference between the minus treatment and the plus treatment for seed density where small mammals were excluded along with that same trend between the control and plus treatments with small mammals excluded but there was no difference where small mammals were present (tables 2.5 and 2.6).
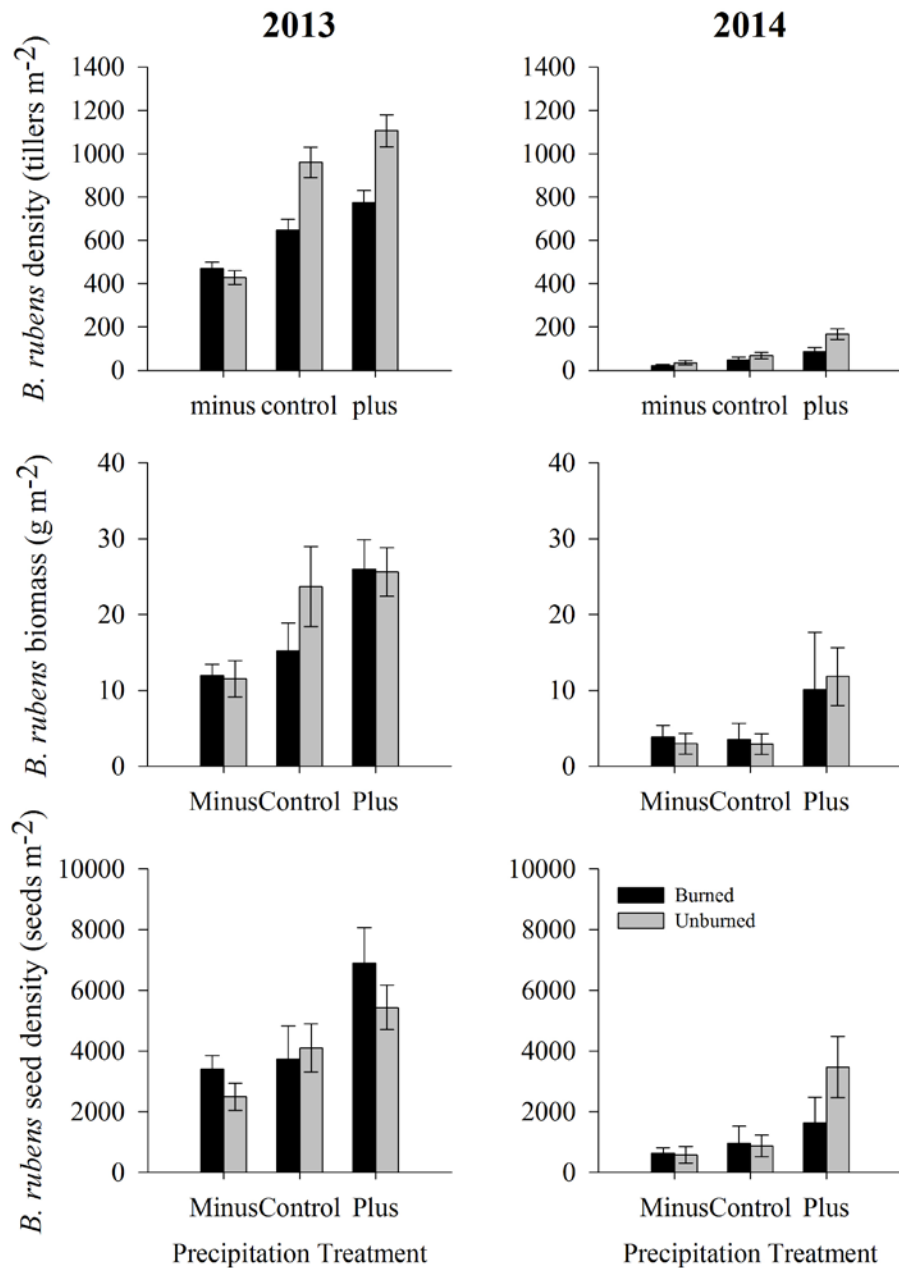
Figure 2.4. *Bromus ruben*s tiller density (m-2), biomass (g m-2), and seed density (m-2) with precipitation treatment factors on the x-axis. Black bars in all of the graphs represent the burned experimental plot and the grey bars represent the unburned experimental plots for the years 2013 and 2014. *B. ruben*s tiller density had a $20 - 50\%$ reduction in tillers both year in the burned plots with no other significant interactions with burning (table 2.1). *B. ruben*s biomass had no direct burn effect but did have a difference of a two-fold increase in biomass from the burned minus treatment with the burned plus treatment, and the burned minus treatment with the unburned plus treatment all other interactions were not significant (tables 2.3 and 2.4). There was no direct burn effect with seed density or its interactions with precipitation (tables 2.5 and 2.6).