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The relationship between invasive annual grasses and biological soil crust across Eastern Washington

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The Relationship Between Invasive Annual Grasses and Biological Soil Crust Across Eastern Washington

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A Thesis

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In Partial Fulfillment of the Requirements

for the Degree

Master of Science

By

Jarrett B. Cellini

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Thesis of Jarrett Bradley Cellini Approved by

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Dr. Suzanne Schwab, Graduate study committee member

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Dr. Stacy Warren, Graduate study committee member

Master’s Thesis

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Overall Abstract

Invasive annual grasses cause ecological and economic damage across the western US and are a focal point in restoration and management plans. Managing invasion resistance of natural areas is critical to maintaining their biodiversity and function. Climate change is expected to shift species interactions, including invasive annual grasses, and may alter invasion resistance. One component of invasion resistance is biological soil crust (biocrust), which has been shown to limit *Bromus tectorum* (cheatgrass) in arid regions. However, biocrust has been less studied in semiarid regions and its effects on other invasive annual grasses, such as *Ventenata dubia*, have never been studied. The goals of my project were to 1) determine how the relationship between invasive annual grasses and biocrust vary across a precipitation gradient and among different invasive annual grass species, 2) determine how patterns of biocrust and *Ventenata dubia* change over time (3 years), and 3) determine the effects of trampling on biocrust composition and species invasion over 3 years. I surveyed biocrust and invasive annual grasses in 168 plots across 21 sites along a precipitation gradient from arid to semiarid. I also resurveyed vascular plant species and biocrust across a series of transects that were located across a gradient from high to low *V. dubia* abundance three years after they were established. Finally, I resurveyed vascular plants and biocrust in a series of experimentally trampled and control plots after three years. Biocrust was surveyed using morphological and color groups. I found that the dominant invasive annual grass along the precipitation gradient in eastern Washington shifted from *B. tectorum* in arid regions to *V. dubia* in semiarid regions. Biocrust percent cover and lichen richness was negatively correlated with both invasive annual grasses across all sites. Soil depth and topography also affect distribution of invasive annual grasses. Looking at long-term patterns of *V. dubia* in a semiarid prairie, I found that biocrust abundance or composition did not affect *V. dubia*. Additionally, trampling applied 3 years ago appeared to have no impact on *V. dubia* or biocrust abundance. *V. dubia* abundance over 3 years of sampling was strongly correlated with spring water depth in vernal pond areas. My results can be used to help land managers better understand the relationship between biocrust and invasive annual grass, particularly in the face of climate change which may create more arid climates in the Inland Northwest. Additionally, land managers can focus management of *V. dubia* in locations where excess spring precipitation persists.

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Climate Effects on the Relationship between Invasive Annual Grasses and Biological Soil Crust in the Intermountain West

Abstract

Invasive annual grasses such as *Bromus tectorum* (cheatgrass) and *Ventenata dubia* are already a significant problem in the western U.S. and together with climate change can pose a serious threat to existing natural areas. One way to reduce invasion is to manage for decreased site susceptibility to invasion; however the factors that reduce susceptibility to invasion may vary in different climate zones. Biological soil crust (biocrust) can help reduce susceptibility to invasion by *B. tectorum* in arid regions but its impact in semiarid regions is less known, as well as its ability to reduce susceptibility to other species of invasive annual grasses, such as *V. dubia*. Past studies at Turnbull National Wildlife Refuge have shown that *V. dubia* can invade sites with biocrust in semiarid zones, but it is not clear how widespread this pattern is. To test this hypothesis, I documented biocrust and vascular plant species at 21 sites along a precipitation gradient in eastern Washington. I found that *B. tectorum* was more abundant in arid regions and *V. dubia* only appeared in more semiarid regions, where it was more common than *B. tectorum*. Additionally, biocrust and both invasive annual grasses were negatively correlated. Soil depth and heat index also were highly important variables in determining invasive annual grass abundance. My results suggest that land managers should protect biocrust in arid regions, avoid treating all invasive annual grasses the same, and recognize that *B. tectorum* may increase its range or abundance with climate change.

Introduction

Climate change is expected to shift species' ranges, phenology, productivity, and many other species-specific characteristics (D'Antonio and Vitousek 1992, Richardson et al. 2013, Hellmann et al. 2008). Examining these changes in individual species alone may not be sufficient to fully predict the impacts of climate change on communities. It will be necessary to understand how climate change impacts biotic interactions to effectively predict how communities will respond (Araujo and Luoto 2007, Tylianakis et al. 2008, Putten et al. 2010, Gilman et al. 2010). Invasive annual grass species are already an important problem in the Intermountain West and will likely become a larger issue under changing climatic conditions (Hunter 1991, Mayeux et al. 1994, Dukes et al. 2011, Prevey and Seastedt 2015). One approach for management of these species is to maintain and enhance community resistance to invasion (Richardson and Pysek 2006). In the Intermountain West, maintaining an intact biological soil crust (biocrust) layer has been shown to help communities resist invasive annual grasses (Belnap et al. 2001, Prasse and Bornkamm 2000, Root and McCune 2012) under a narrow set of climate conditions. Understanding how biocrust contributes to community resistance to invasive annual grasses under a broader set of climatic conditions is crucial for adaptive management of these ecosystems in the face of climate change.

The invasive winter annual grass, *Bromus tectorum* L. (cheatgrass), has caused serious economic and ecological problems in the western United States. This grass reduces native plant species, alters soil microbial communities and reduces habitat and forage for wildlife and livestock (O'Conner 1991, Kourtev et al. 2002, Clarke et al. 2005, Belnap et al. 2005, Simberloff 2005). Once established, these *B. tectorum* dominated landscapes are highly resistant to re-establishment by native perennials (Humphrey and Schupp 2004). As a winter annual grass, *B. tectorum* germinates in the fall, establishes a root system, and resumes growth once conditions are sufficient in the spring (Hironaka 1961), giving it an advantage over many native plant species that germinate in the spring.

The less studied *Ventenata dubia* (Leers) Cross. (wiregrass/North Africa grass) is an invasive winter annual grass in the intermountain west. *V. dubia* has been expanding in the region since it was first observed in the 1950s (Barkworth et al. 1993). It has since invaded sagebrush steppe, grasslands, CRP, and hay fields (Butler 2011, McCloskey et al. 2011, Wallace and Prather 2013). In some areas *V. dubia* has invaded ecosystems dominated by *B. tectorum* (Per. Com. Mike Rule, Tim Prather). As with other invasive annual grasses, *B. tectorum* and *V. dubia* outcompete native vegetation by using available moisture in the spring while native plants are still dormant (Melgoza et al., 1990). *V. dubia* in particular thrives in areas that receive excess moisture or are saturated in spring. An important aspect of managing these invasive annual grasses is understanding what drives community resistance to these species.

In arid regions, biocrust has been shown to reduce community susceptibility to invasive species (Prasse and Bornkamm 2000, Root and McCune 2012). Biocrust is a complex association between soil, moss, lichen, algae and cyanobacteria, and is an important component of arid and semiarid ecosystems where it can make up as much as 70% of the ground cover, making it more dominant than vascular plants (Belnap 1994). Biocrust is a strong driver of soil stabilization and can influence nutrient cycling, water storage, and soil microbe activity (Belnap et al. 2009, Maestre et al. 2005, Castillo-Monroy et al. 2015). Key factors that influence biocrust are soil depth, texture, and nutrients, grazing, precipitation, and shading by vascular plants. In arid regions, biocrust is inversely related to *B. tectorum* cover and is thought to reduce susceptibility to invasion by this invasive annual grass (Ponzetti et al. 2007, Prasse and Bornkamm 2000, Reisner 2010). Biocrust is thought to act as a barrier to germinating *B. tectorum* seeds while allowing native perennials to penetrate the soil with their deep roots (Boudell et al. 2002). Biocrust has been primarily studied in arid communities, which receive less than 300 mm/year rainfall. It is unclear whether biocrust plays the same role in semiarid regions (> 300 mm/year rainfall) or if biocrust reduces susceptibility to invasion by other invasive annual grasses, such as *V. dubia*.

The differences between arid and semiarid regions in the Inland Northwest are largely driven by precipitation and to some degree temperature. These factors affect vegetation communities primarily though their influence on soil moisture. Climate change models for the Inland Northwest predict higher mean annual temperatures in the coming decades, with the largest increase expected during the summer months (Karl and Melillo 2009, Kunkel et al. 2013). While models are not consistent in predicting a change in mean annual precipitation, a shift in timing is expected with increasing average precipitation in winter, spring, and fall and a decrease in the summer (Kunkel et al. 2013, Karl and Melillo 2009). An increase in temperature may cause more precipitation to fall as rain instead of snow, and will increase rates of evaporation. These conditions may favor invasive winter annual grasses as their lifecycle allows them to use early spring precipitation, and complete their lifecycles before drought conditions occur (Bradley 2009). Therefore it is important to understand the biological interactions with invasive annual grasses and to predict how these relationships may shift with respect to climate change.

Documenting vascular plants and biocrust over a large spatial scale and climate gradient can address two questions: 1) Does the relationship between biocrust and invasive annual grasses change along a precipitation gradient? And 2) Are *V. dubia* and *B. tectorum* driven by different factors? Understanding these interactions can help determine patterns of invasion with climate change, which will be critical for future management decisions.

Methods

Data collection

I sampled twenty one sites across an average annual precipitation gradient in Eastern Washington ranging from 195 to 461 mm/yr (**Figure 1 – Map of sites, with precipitation on map or on side**). Average annual precipitation was determined from 30-year averages (1981-2010), with a spatial resolution of 800 m (PRISM Climate Group 2014). Sites were chosen based on accessibility and disturbance history, with ownership primarily by the U.S. Fish and Wildlife Service or the Bureau of Land Management. Preference was given to sites with no tilling or development, limited roads and trail presence, and longer periods (> 3 years) since grazing or fire based on communication with agency staff. While all sites are considered shrub-steppe, one difference was sites in semi-arid regions contained Mima mounds. Mima mounds are hemispherical accumulations of soil surrounded by intermound regions, which can differ in vegetation (Bryant et al. 2013). I sampled all sites in June and July 2015, with drier sites sampled earlier to account for phenology differences across the precipitation gradient. Sites spanned a distance of 200 km with 2 km being the minimum distance between sites.

Eight plots (1 m^2) were sampled at each site for a total of 168 plots. Plots were located in a stratified random manner between invasive annual grass dominated areas and areas with minimal to no invasive annual grass. Plots were also stratified to account for slope and aspect. When Mima mounds were present, only intermound areas were sampled. Within the stratified sub-areas, I threw a Frisbee to determine specific plot location. Microhabitats that were not representative of the site were excluded (i.e. swales, cliff bases). In each plot I estimated absolute percent cover of all vascular plants species, and lichen and moss morphogroups (representing biocrust). Lichens were classified by morphology (crustose, areolate, gelatinous, squamulose, foliose, and fruticose) and color. Moss was classified by size (tall or short) and by color. I additionally collected location data (using a Trimble™ GeoXM 2003), soil depth (in sites where our permits allowed), slope, aspect, and ground cover percentages (duff, soil, rock, wood, and biocrust) for each plot. Soil depth was averaged in each plot from two corner measurements. To best account for plot topography, a unitless heat index was calculated for each plot using a combination of latitude, slope, and aspect (McCune 2002). This method uses a northeast-southwest relationship as the minimum and maximum heat load index.

Data analysis

To determine how the relationship between invasive annual grasses and biocrust changed across a precipitation gradient and accounting for other environmental variables, linear mixed-effects models were created using the *nlme* package in R (R 2013). Using a-priori variable selection and comparing AIC scores, the best model to explain invasive annual grass cover across all sites was created using incident radiation, native vascular plant cover, moss cover, moss frequency, lichen cover, lichen frequency, total crust cover, total crust richness, and precipitation. Models were also created in the same fashion using *B. tectorum* and *V. dubia* cover as the response variable. The model for *V. dubia* included only sites where *V. dubia* was observed (n = 7), as 350 mm average annual precipitation has been reported as the lower end of its range (Scheinost et. al 2008).

To examine changes in species composition across the precipitation gradient and associated with other environmental variables, nonmetric multidimensional scaling

(NMDS) ordinations of vascular plant species and biocrust composition were created using the *vegan* package in R (R 2013) for all sites. Vascular plant and Biocrust NMDS was created using 3 dimensions and Bray-Curtis dissimilarity indices with the maximum number of runs and iterations set at 200. *B. tectorum* cover, *V. dubia* cover, heatload index, precipitation, total biocrust cover, lichen richness, and total native cover were overlain on the vacular plant ordination and rotated so precipitation fitted along axis 1. *B. tectorum* cover, *V. dubia* cover, precipitation, total biocrust cover, lichen richness, moss richnes, rock cover, and soil cover were overlain on the biocrust ordination and rotated so precipitation was fitted along axis 1.

An additional NMDS was created using only sites where *V. dubia* occurred, using 2 dimensions and Bray-Curtis dissimilarity indices and 200 maximum runs and iterations. *V. dubia* cover, heatload index, total biocrust cover, lichen richness, total native cover, precipitation, and soil cover were overlain and precipitation fitted along axis 1.

Results

Modeling Total Invasive Annual Grass Cover

Of the 21 sites surveyed, *B. tectorum* was the most abundant invasive annual grass in 17. The four remaining sites were semiarid and had *V. dubia* as the most abundant invasive annual grass. *V. dubia* was present at a total of 7 sites, and was counted within plots at 6 of those sites. It was not abundant enough to have shown up in plots at one of the 7 sites.

The model that best predicted invasive annual grass cover included lichen richness, native cover, heatload index, biocrust cover, and precipitation as well as interactions between biocrust cover and precipitation, heatload index and biocrust cover, and lichen richnes and precipitation (Table 1). Soil depth was excluded as the 7 driest sites did not have this data and therefore would have been dropped in the model. The interaction between biocrust, precipitation and invasive annual grass was significant with the relationship between biocrust cover and invasive annual grass cover exhibiting a stronger negative correlation in more arid regions ($p = 0.0032$; Figure 2). The interaction between lichen richness and precipitation showed a similar pattern, though the relationship between lichen richness and invasive annual grass cover was slightly positive in sites in the middle precipitation group while negative in arid and semiarid precipitation groups ($p = 0.0094$; Figure 3). The interaction between biocrust cover and heatload index was nearly significant ($p = 0.0608$; Figure 4), with heatload index and invasive annual grass cover positive when biocrust cover was low and becoming negative as biocrust cover increased. Finally, native vascular plant cover was negatively related to invasive annual grass cover ($p < 0.0001$; Figure 5).

The final NMDS ordination for vascular plant species (Figure 6; Table 2) had a final stress value of 0.1745. Community composition varied across a gradient in precipitation that was associated with axis 1 ($R^2 = 0.0782$; $p = 0.003$). *B. tectorum* cover $R^2 = 0.1413$; $p < 0.001$) was associated with community composition along axis 2 and was negatively associated with native cover ($R^2 = 0.0472$; $p = 0.021$), biocrust cover ($R^2 = 0.0527$; $p = 0.015$) and lichen richness ($R^2 = 0.081$; $p < 0.001$) along axis 2. Lichen and moss cover had similar patterns to total biocrust cover and therefore were not split for this analysis. While not significant, the vectors showing the associations between heatload index ($R^2 = 0.0262$ $p < 0.093$) and *V. dubia* cover ($R^2 = 0.0149$; $p < 0.282$) with community composition were angled in the same direction as those for *B. tectorum* cover.

The final NMDS ordination for biocrust morphology/color (Figure 7; Table 3) had a final stress value of 0.1241. Species composition was associated with precipitation ($R^2 = 0.0837$; $p = 0.004$), moss richness ($R^2 = 0.0483$; $p = 0.035$), total biocrust cover ($R^2 = 0.0041$; $p = 0.047$), *B. tectorum* ($R^2 = 0.1184$; $p < 0.001$), and bare soil ($R^2 = 0.1171$; $p < 0.001$) along axis 1, with higher precipitation tending to be associated with higher moss richness and biocrust cover and lower amounts of *B. tectorum* and bare soil. Lichen richness ($R^2 = 0.1209$; $p < 0.001$) was also associated with species composition, and tended to be higher when *B. tectorum* cover was lower. *V dubia* ($R^2 = 0.0837$; $p = 0.715$) and rock cover ($R^2 = 0.0411$; $p = 0.068$) were not significantly associated with species composition.

Modeling Bromus tectorum Cover

The model used to best explain *B. tectorum* cover included heatload index, native cover, biocrust cover, precipitation and interactions of biocrust cover and precipitation, native cover and biocrust cover, and heatload index and native cover (Table 4; $R^2 = 0.71$). The relationship between biocrust and *B. tectorum* was negative in arid regions and became weaker with increasing precipitation (Figure 8; $p < 0.0001$). The relationship between native cover and *B. tectorum* can be characterized several ways depending on which interacting variable is used. When accounting for biocrust cover, the relationship between native cover and *B. tectorum* was negative when biocrust cover was low to absent, but became weaker with increasing biocrust cover (Figure 9; $p = 0.0454$). When accounting for heatload index, native cover and *B. tectorum* exhibited a negative relationship when heatload index was high, and became weaker and then positive with an increase in heatload index (Figure 10; $p = 0.0311$).

Ventenata dubia

When using data only from sites where *V. dubia* was present ($n = 7$, including the site where *V. dubia* was present but not contained in any of the plots), lichen richness, native cover, biocrust cover, heatload index, precipitation, soil depth, and the interaction of precipitation and soil depth were included (Table 5; $R^2 = 0.68$). Biocrust cover (Figure 11; $p = 0.0007$) and lichen richness (Figure 12; $p < 0.0001$) both exhibited negative relationships with *V. dubia* cover. Native cover and *V. dubia* were positively correlated (Figure 13; $p = 0.0197$). The interaction between precipitation, soil depth and *V. dubia* cover was significant, where precipitation and *V. dubia* cover didn’t have a relationship when soil depth was shallow (~5 cm) but became positive as soil depth increased (Figure 14; $p = 0.0013$). Heatload index created a better fitting model, though it was not significant ($p = 0.5254$).

The NMDS ordination of vascular plant species in sites containing *V. dubia* (Figure 15; Table 6) had a final stress of 0.2491. When overlaid across species composition, precipitation ($R^2 = 0.3253$; $p < 0.001$) and soil cover ($R^2 = 0.1472$; $p = 0.011$) were the only variables significantly associated with species composition. Both were correlated with axis one, but in the opposite direction.

Discussion

As I predicted, the relationship between biocrust and invasive annual grasses changed across a precipitation gradient (Figure 1) from strongly negative in arid regions to no relationship in semiarid regions (> 250 mm precipitation/yr). *B. tectorum* was most abundant in arid regions, while *V. dubia* was present and abundant in only the most semiarid sites.

The negative relationship I observed between *B. tectorum* and biocrust in my driest sites is consistent with other studies in arid areas (Ponzetti et al. 2007, McCune 2008). However, in semi-arid sites this pattern did not exist. To my knowledge, this study is the first to document the relationship between invasive annual grasses and biocrust with respect to aridity, and clearly shows that the pattern changes (becoming less negative) with increased precipitation. This may be caused by changes in growth patterns or species composition of both biocrust and invasive annual grasses in semi-arid sites. With *V. dubia,* the interaction of biocrust and precipitation did not contribute to the best model to explain *V. dubia* cover. This could be due to only having ventenata present in its lower range aridity range (320 – 450 mm/yr) as it has been documented to persist in areas up to 1,120 mm (Schienost et al. 2008). It also could be a result of *V. dubia* interacting differently with biocrust than with *B. tectorum,* as it has been documented to grow on areas dominated by biocrust (Anicito 2013).

V. dubia exhibited a negative relationship to biocrust cover and lichen richness, similar to what has been documented in *B. tectorum* (Belnap et al. 2006, Prasse and Bornkamm 2000, Root and McCune 2012). Looking at community composition ordination, this relationship may not be as strong in *V. dubia* compared to *B. tectorum*. Being a snapshot experiment, this can’t tell us whether biocrust is inhibiting *V. dubia* or if the areas where *V. dubia* was documented previously had more biocrust, or if *V dubia* is inhibiting biocrust. It would be necessary to study these relationships over time or through manipulation to understand these processes.

My other goal was to determine whether *B. tectorum* and *V. dubia* are driven by different factors. Besides differences related to biocrust, *V. dubia* exhibited a positive relationship with native vascular plants, opposite of *B. tectorum*. I expected that *V. dubia* may behave similar to *B. tectorum* due to similar lifecycles (winter annual) and which make them better competitors compared to natives (DiTomaso 2000). As an invasive, it was thought *V. dubia* may also have other characteristics which make it a better competitor to natives, similar to which *B. tectorum* can alter soil conditions (Kourtev et al. 2002). It is possible that the positive relationship *V. dubia* had with native cover may be attributed to where sampling occurred in the semiarid mima mound sites, which made up 5 of the 6 sites with *V. dubia* within plots. In mima mound intermounds, both native and invasive vascular plants occur in lower amounts than on mounds, particularly if soils are shallow (Anicito 2013, Bryant et al. 2013). While the relationship was positive, documented cover for native and *V. dubia* were low, with no more than 25% cover of native species recorded. These abundances may not be enough for natives and *V. dubia* to experience competition.

The relationship *B. tectorum* had with native cover varied with heatload index. *B. tectorum* seems to favor drier slopes where *V. dubia* did not correlate with any particular slope or aspect. From what little information is available on *V. dubia*, it is noted that it may prefer south facing slopes (Old and Callihan 1987). It is possible that *V. dubia* within intermounds of eastern Washington do not conform to this pattern. The sample size of 6 sites with plots containing *V. dubia* may not be enough to capture a pattern if one does exist. Additionally, soil depth could not be collected for many sites containing *B. tectorum*, which may be more important than slope and aspect and alter relationships observed.

Soil depth proved to be a significant variable which interacted with precipitation to explain *V. dubia* cover (Figure 14). Only in deeper soils was *V. dubia* cover positively correlated with precipitation. As *V. dubia* may favor areas receiving spring moisture (Scheinost et. al 2008, Chapter 2 Cellini 2016), deeper soils receiving more precipitation could better support more *V. dubia*. It should be noted that this relationship was observed in the lower end of *V. dubia'*s precipitation zone and this relationship may change in other areas of its range.

As climate change alters soil moisture, plant communities and their interactions are bound to shift. Understanding biological relationships along a precipitation gradient can help guide management decisions as new regions are exposed to new climate conditions. An increase in annual precipitation may move *V. dubia* into new ranges, particularly where deeper soils occur. A decrease in annual precipitation may increase abundances of *B. tectorum* in its current range and even expand its range eastward in eastern Washington. Additionally, steep southwest facing slopes are at an even higher risk under these and predicted future conditions.

This study adds more support for the conservation of biocrust, particularly if *B. tectorum* poses a threat. Additionally, while the relationship between *B. tectorum* and biocrust may be less strong in more semiarid regions, with a shift in temperature and precipitation in the future, these semiarid regions could begin to act as current arid systems. Additionally, while “invasive annual grass” is used a term to lump particular species together, different species have very different interactions with the environment. An intact and diverse biocrust community may not be enough to prevent the establishment and spread of *V. dubia*. Variables such as soil depth are important to better understand how this invasive annual grass behaves. While research on *B. tectorum* is extensive (Knapp 1996, Chambers et al. 2007), more studies are needed focusing on *V. dubia* and factors that drive its abundance.

Tables

Table 1. ANOVA Table for the following linear mixed effect model for all sites: Invasive annual grass cover ~ lichen richness + native cover + heatload index + biocrust cover + average annual precipitation + (biocrust cover * precipitation) + (heatload index * biocrust cover) + (lichen richness * precipitation). The model's R^2 is 0.56.

	Num. DF	Den. DF	F-value	p-value
(Intercept)	1	138	92.1766	<.0001
Lichen Richness	1	138	87.19139	<.0001
Native Cover	1	138	10.39387	0.0016
Heatload Index	1	138	3.19509	0.0761
Biocrust Cover	1	138	38.26076	<.0001
Precipitation	2	18	17.16031	0.0001
Biocrust:Precipitation	2	138	5.98686	0.0032
Heatload:Biocrust	1	138	3.57426	0.0608
Lichen Richness:Precipitation.	2	138	4.83417	0.0094

Table 2. Vector table for environmental variables correlated with vascular plant community composition. NMDS1 and NMDS2 indicate the direction of each vector. R^2 indicates how well variables fit to species compositions.

	NMDS1	NMDS2	R^2	Pr(>r)
Lichen Richness	0.48835	-0.87265	0.081	0.001
Heatload	0.27397	0.96174	0.0262	0.093
Precipitation	1	0	0.0782	0.003
Biocrust Cover	0.60962	-0.7927	0.0527	0.015
Native Cover	-0.21812	-0.97592	0.0472	0.021
Ventenata Cover	0.54394	0.83912	0.0149	0.282
Cheatgrass Cover	-0.20043	0.97971	0.1413	0.001

Table 3. Vector table for environmental variables correlated with biocrust community composition. NMDS1 and NMDS2 indicate the direction of each vector. R^2 indicates how well variables fit to species compositions.

	NMDS1	NMDS2	R^2	Pr(>r)
Soil Cover	-0.99871	-0.05078	0.1171	0.001
Rock Cover	0.84821	-0.52965	0.0411	0.068
Lichen Richness	0.92883	-0.37051	0.1209	0.001
Moss Richness	0.8774	0.47976	0.0483	0.035
Precipitation	1	0	0.0837	0.004
Biocrust Cover	0.99197	0.12646	0.0424	0.047
Ventenata Cover	0.61525	-0.78833	0.0041	0.715
Cheatgrass Cover	-0.86337	0.50458	0.1184	0.001

Table 4. ANOVA table showing p-values for variables in the following linear mixed effect model : *B. tectorum* cover ~ heatload index + native cover + biocrust cover + average annual precipitation + (biocrust cover * precipitation) + (native cover * biocrust cover) + (heatload index * native cover). The model's R^2 is 0.71.

	numDF	denDF	F-value	p-value
(Intercept)	1	141	62.88573	<.0001
Heatload Index	1	141	14.21874	0.0002
Native Cover	1	141	45.3842	<.0001
Crust Cover	1	141	56.23511	<.0001
Precipitation	1	19	39.16255	<.0001
Biocrust Cover:Precip	1	141	21.49629	<.0001
Native Cover:Biocrust Cover	1	141	3.79013	0.0535
Heatload Index:Native Cover	1	141	4.67482	0.0323

Table 5. ANOVA Table showing p-valies for the following linear mixed effect model based on the sites where *V. dubia* was observed (n=7):. *V. dubia* cover ~ lichen richness + native cover + biocrust cover + heatload index + average annual precipitation + soil depth + (precipitation * soil depth). The model's R^2 is 0.68.

	numDF	denDF	F-value	p-value
(Intercept)	1	42	32.64793	<.0001
Lichen Richness	1	42	37.40606	<.0001
Native Cover	1	42	5.88398	0.0197
Biocrust Cover	1	42	13.27411	0.0007
Heatload Index	1	42	2.02439	0.1622
Precipitation	1	5	11.19647	0.0204
Soil Depth	1	42	0.41001	0.5254
Precipitation:Soil Depth	1	42	11.93425	0.0013

Table 6. Vector table for environmental variables correlated with community composition at sites where *V. dubia* was present. NMDS1 and NMDS2 indicate the direction of each vector. R^2 indicates how well variables fit to species compositions.

	NMDS1	NMDS2	R^2	Pr(>r)
Heatload Index	-0.13857	-0.99035	0.0061	0.856
Precipitation	1	0	0.3253	0.001
Biocrust Cover	0.4304	0.90264	0.0403	0.324
Native Cover	0.91517	-0.40307	0.0204	0.61
Ventenata Cover	0.75061	-0.66075	0.0644	0.198
Lichen Richness	0.08912	0.99602	0.0557	0.206

Figures

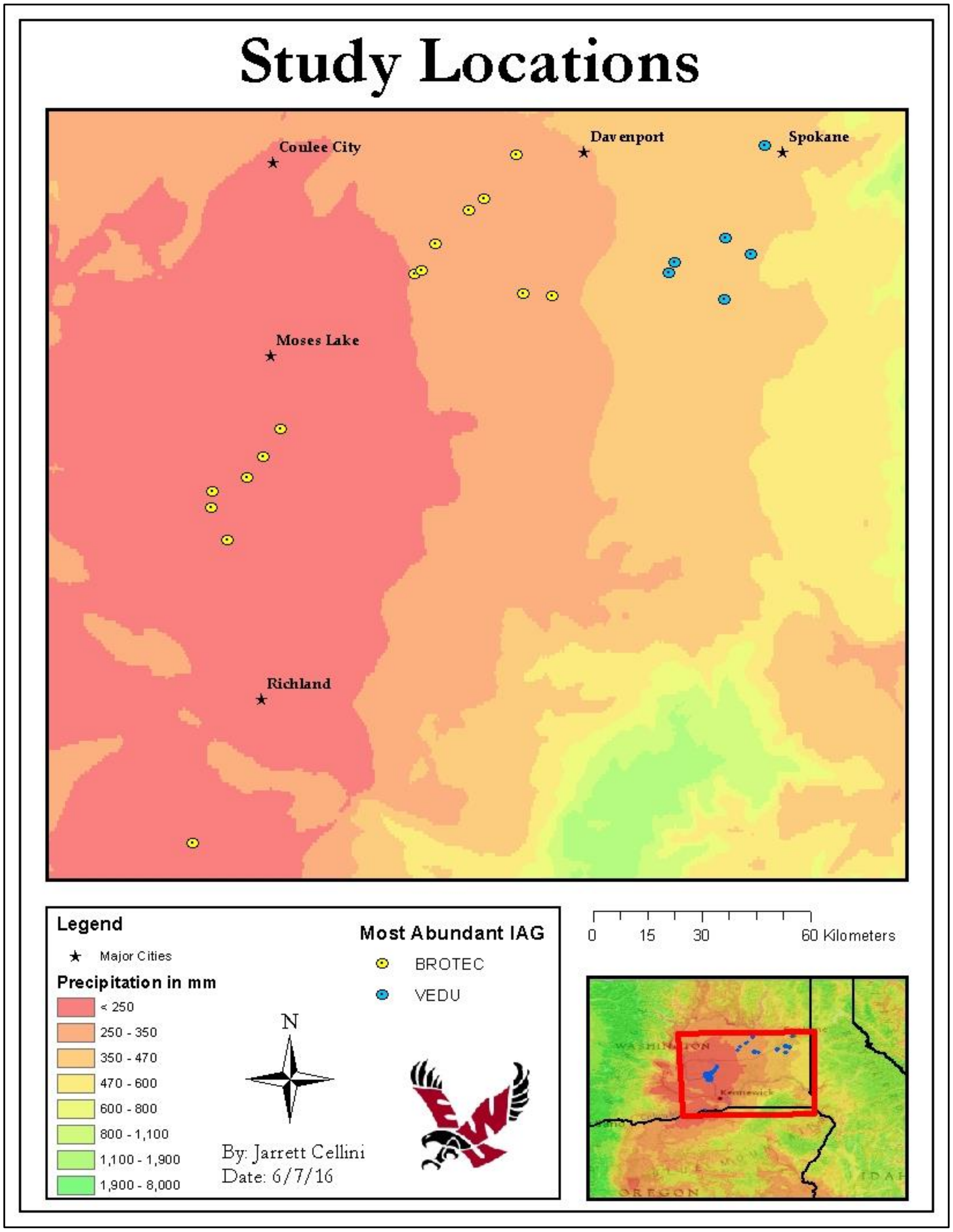

Figure 1. Location map of sites across eastern Washington

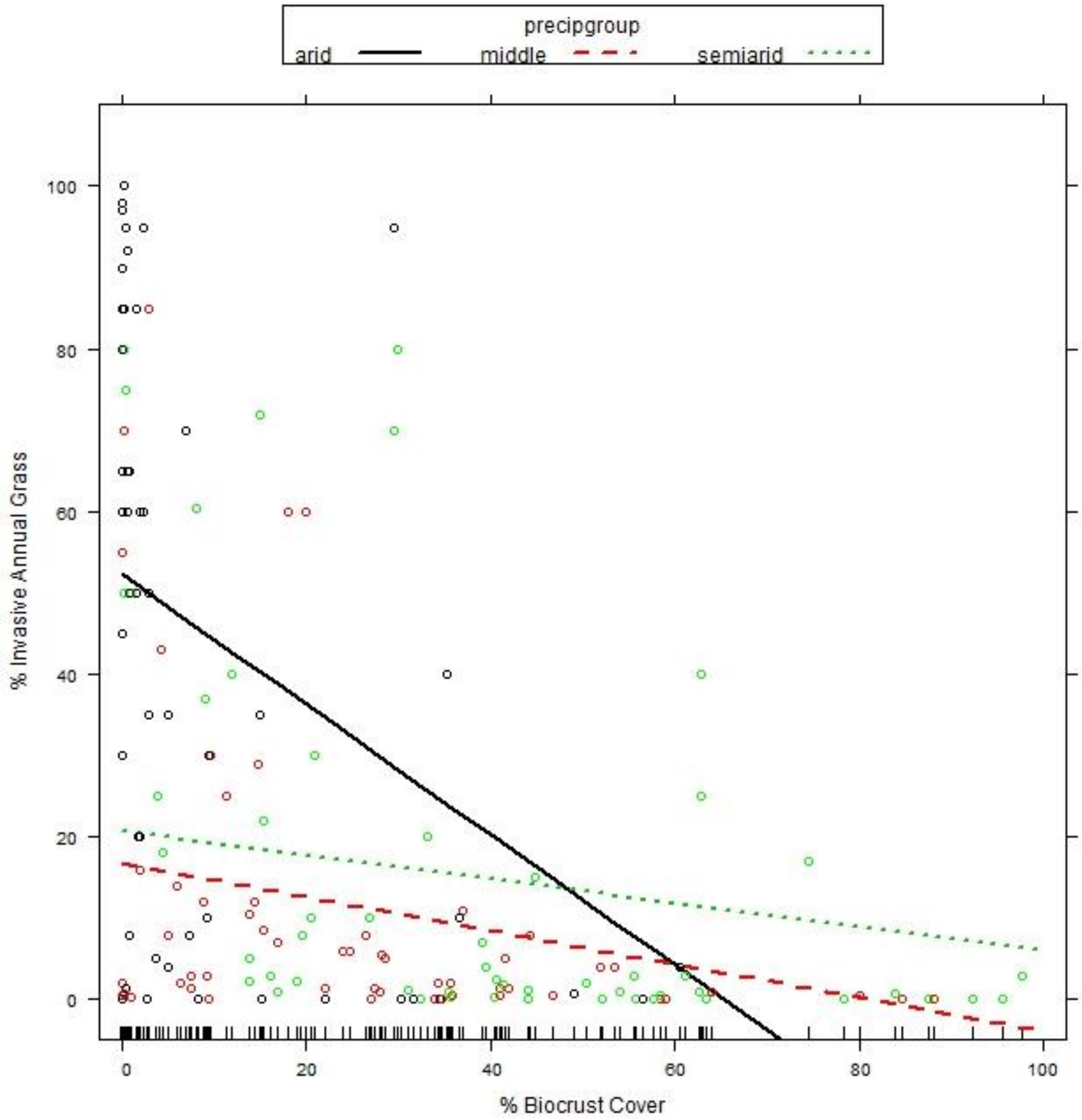

Figure 2. Interactive effect of biocrust cover and precipitation on invasive annual grass cover. Color of line and points represent aridity group (black: < 250 mm, red: 250 – 330 mm, green: > 330 mm) (Table 1; p = 0.0608).

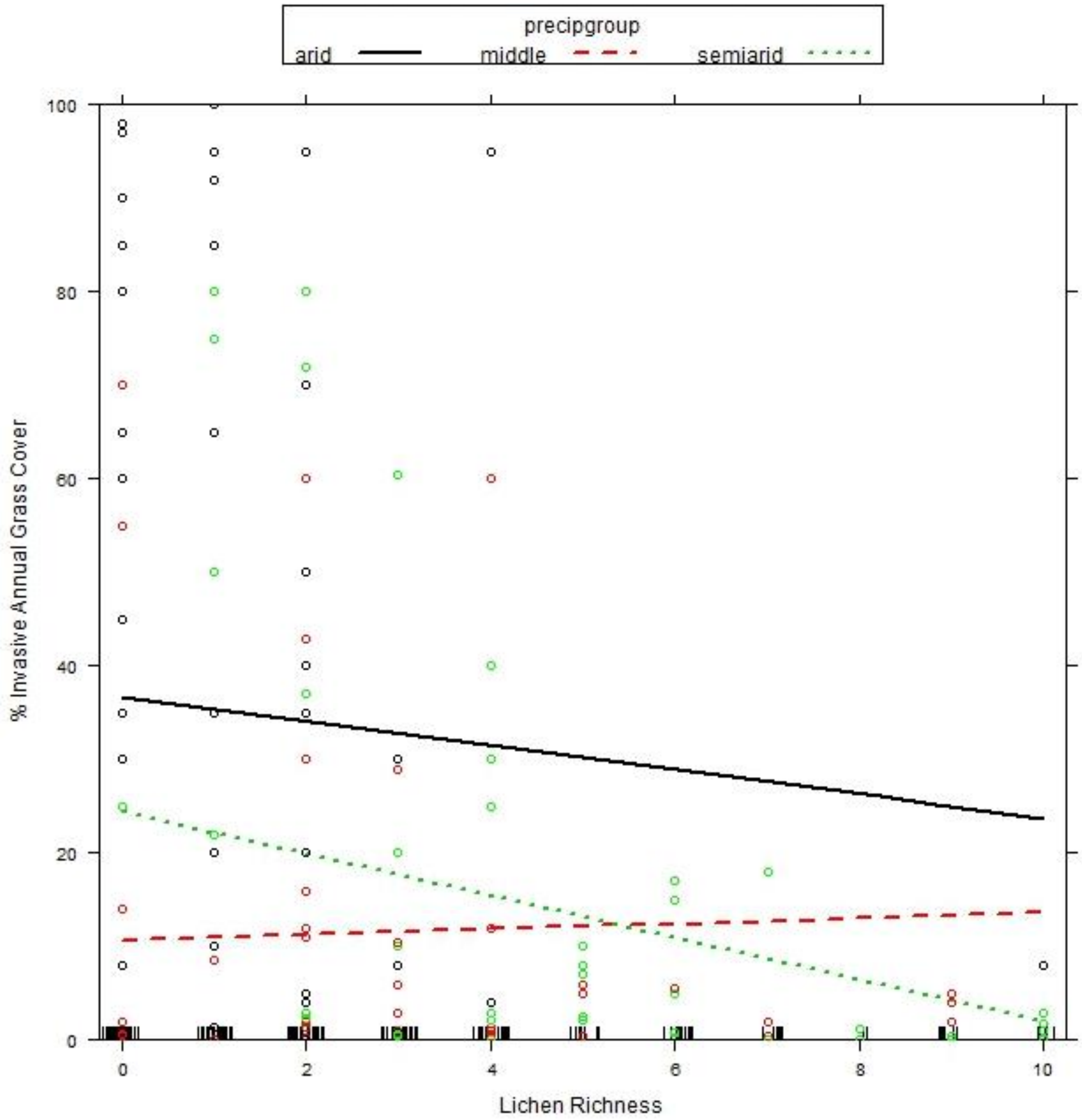

Figure 3. Interactive effect of lichen richness and precipitation on invasive annual grass cover. Color of line and points represent aridity group (black: < 250 mm, red: 250 – 330 mm, green: > 330 mm) (Table 1; p = 0.0094).

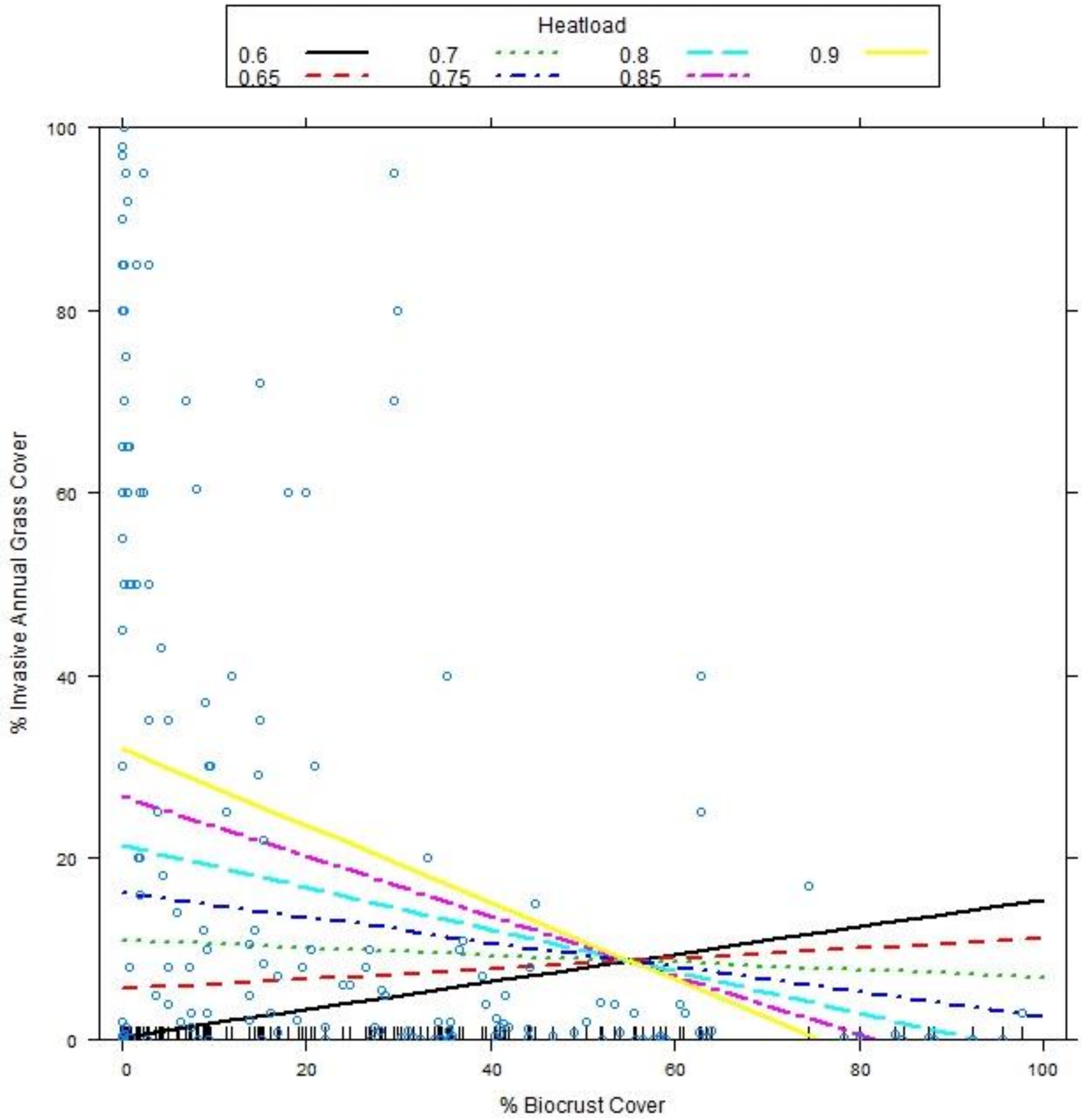

Figure 4. Interactive effect of biocrust and heatload index on invasive annual grass cover (Table 1; p = 0.0608). Line type/color indicate heatload index.

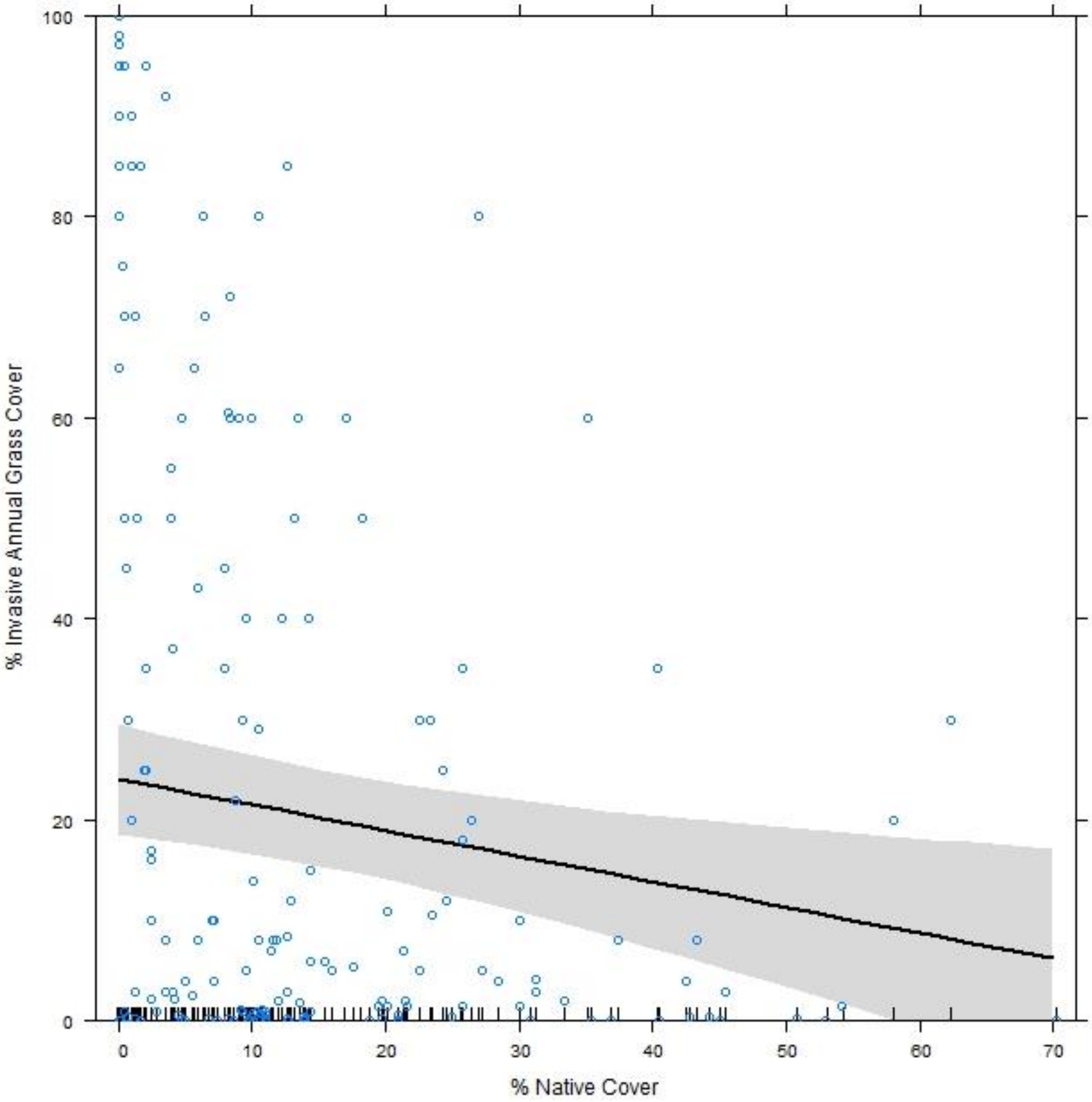

Figure 5. Relationship between percent native cover and percent invasive annual grass after accounting for other variables in the linear mixed effect model (Table 1; $p < 0.0001$)

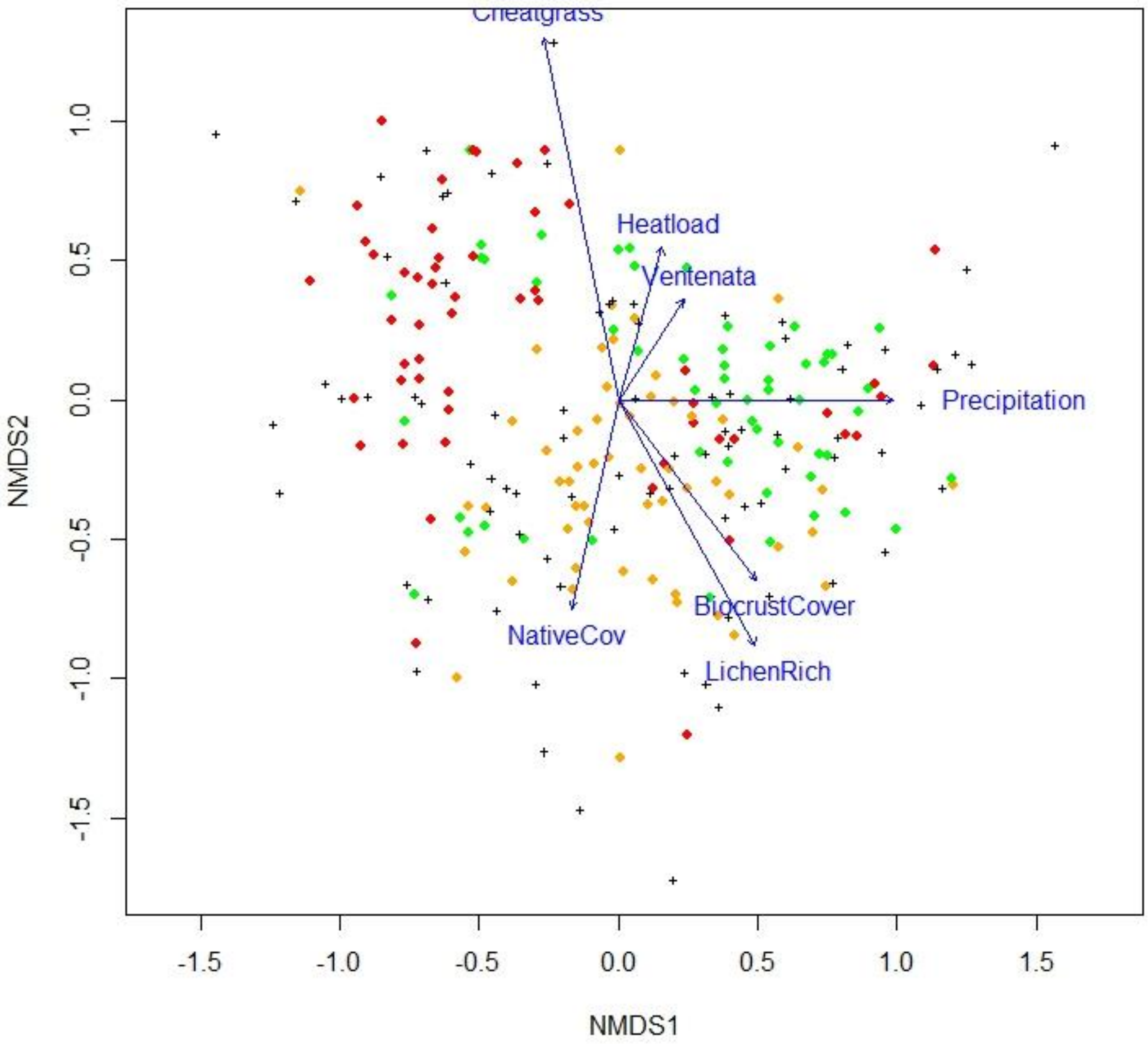

Figure 6. NMDS ordination based on vascular plant species composition of all sites (n= 21) with environmental and biological variables overlain using joint plot vectors (Table 2). Colored circles represent plot community composition and crosses indicate species. Color indicates amount of average annual precipitation in mm (red < 250, orange 250-330, green > 330 mm/year).

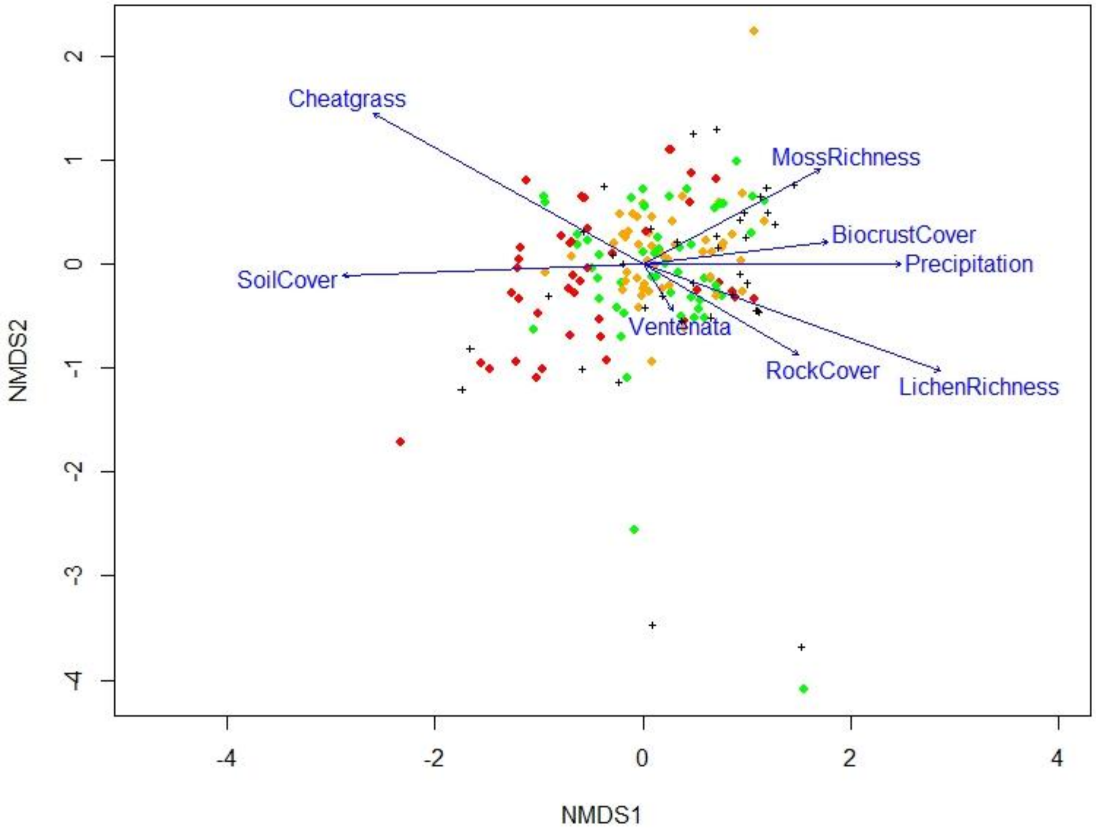

Figure 7. NMDS ordination based on biocrust morphology/color composition for all sites (n= 21) with significantly correlated environmental and biological variables overlain using joint plot vectors (Table 3). Colored circles represent plot community composition and crosses indicate species. Color indicates amount of average annual precipitation in mm (red < 250, orange 250-330, green > 330 mm/year).

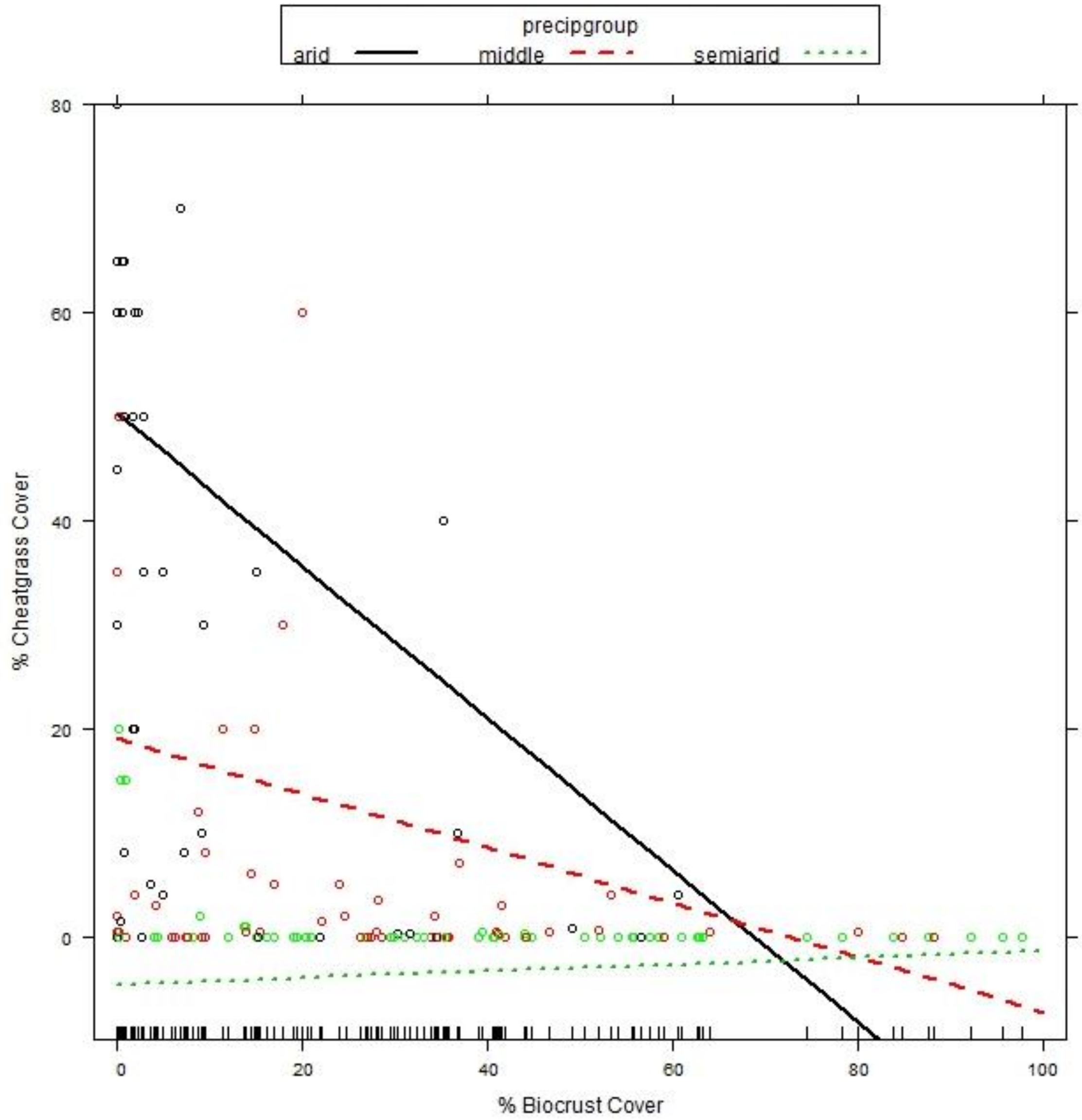

Figure 8. Interaction between biocrust, precipitation, and *B. tectorum* based on a linear mixed effect model (Table 4; $p < 0.0001$). Line type/color indicates precipitation group (black: < 250 mm, red: 250 – 330 mm, green: > 330 mm).

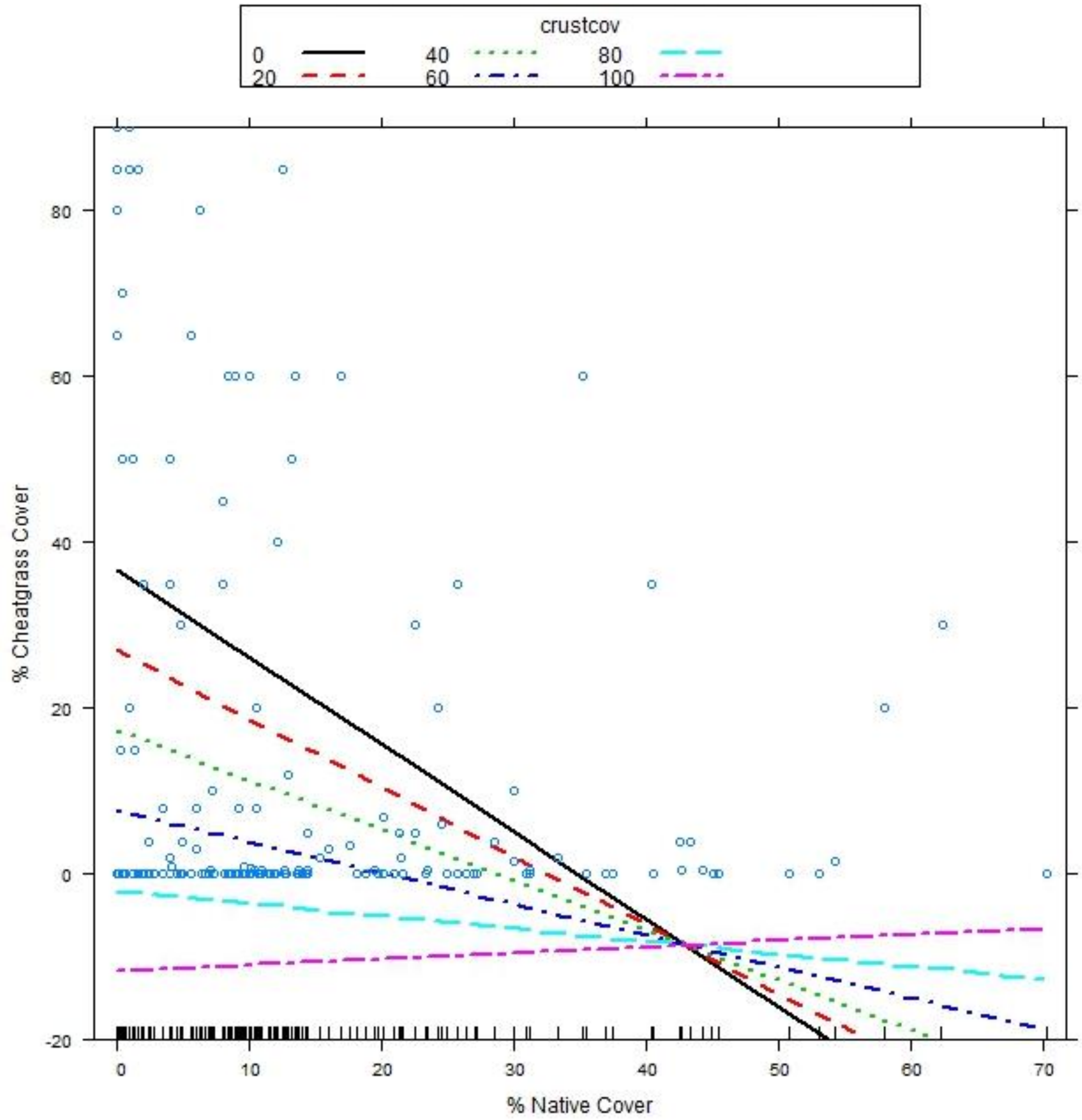

Figure 9. Interaction between native cover, biocrust cover, and *B. tectorum* based on a linear mixed effect model (Table 4; p = 0.0454). Line type/color indicate amount of biocrust cover.

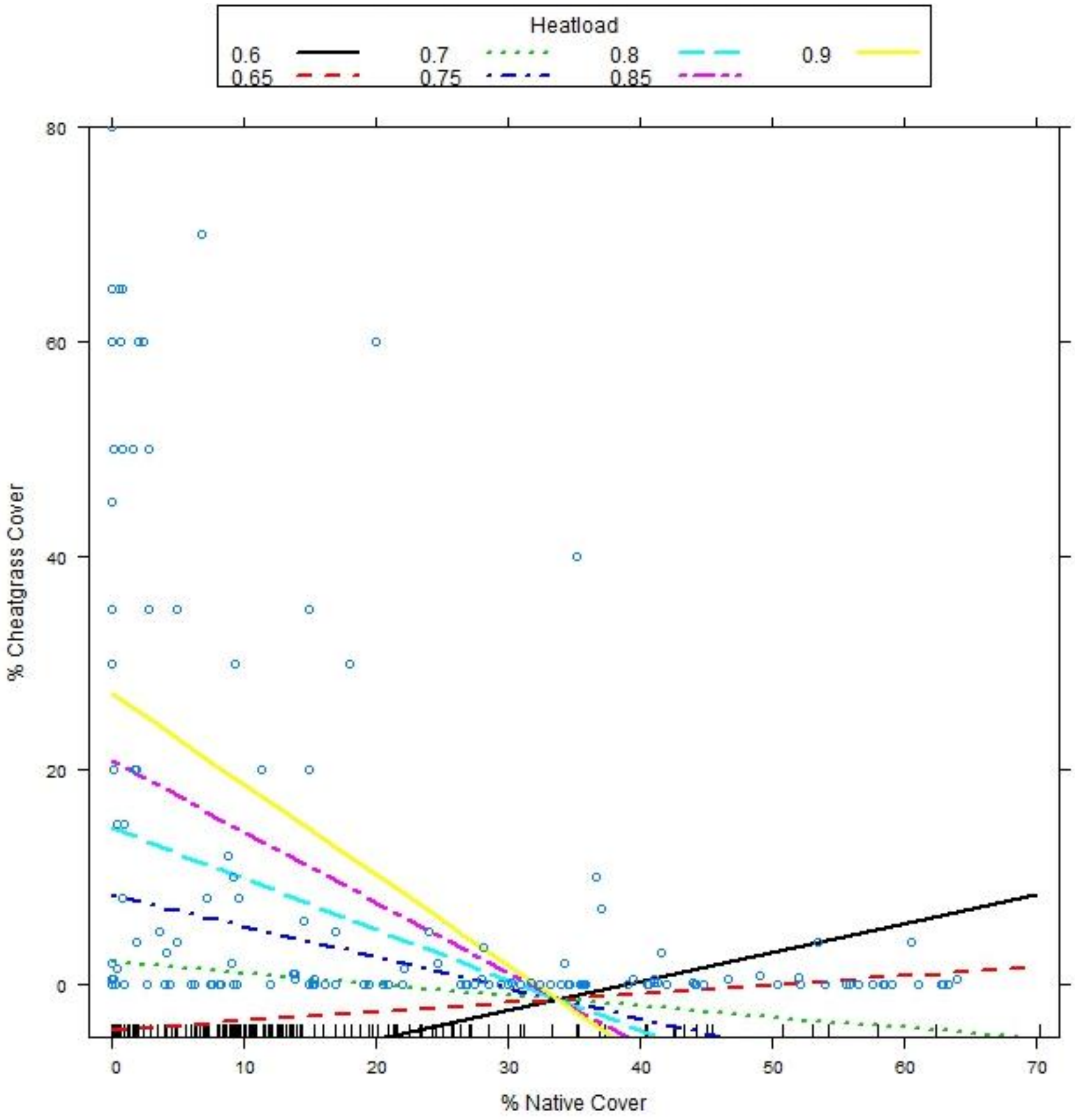

Figure 10. Interaction between native cover, heatload index, and *B. tectorum* based on a linear mixed effect model (Table 4; p = 0.0311). Line type/color indicate heatload index.

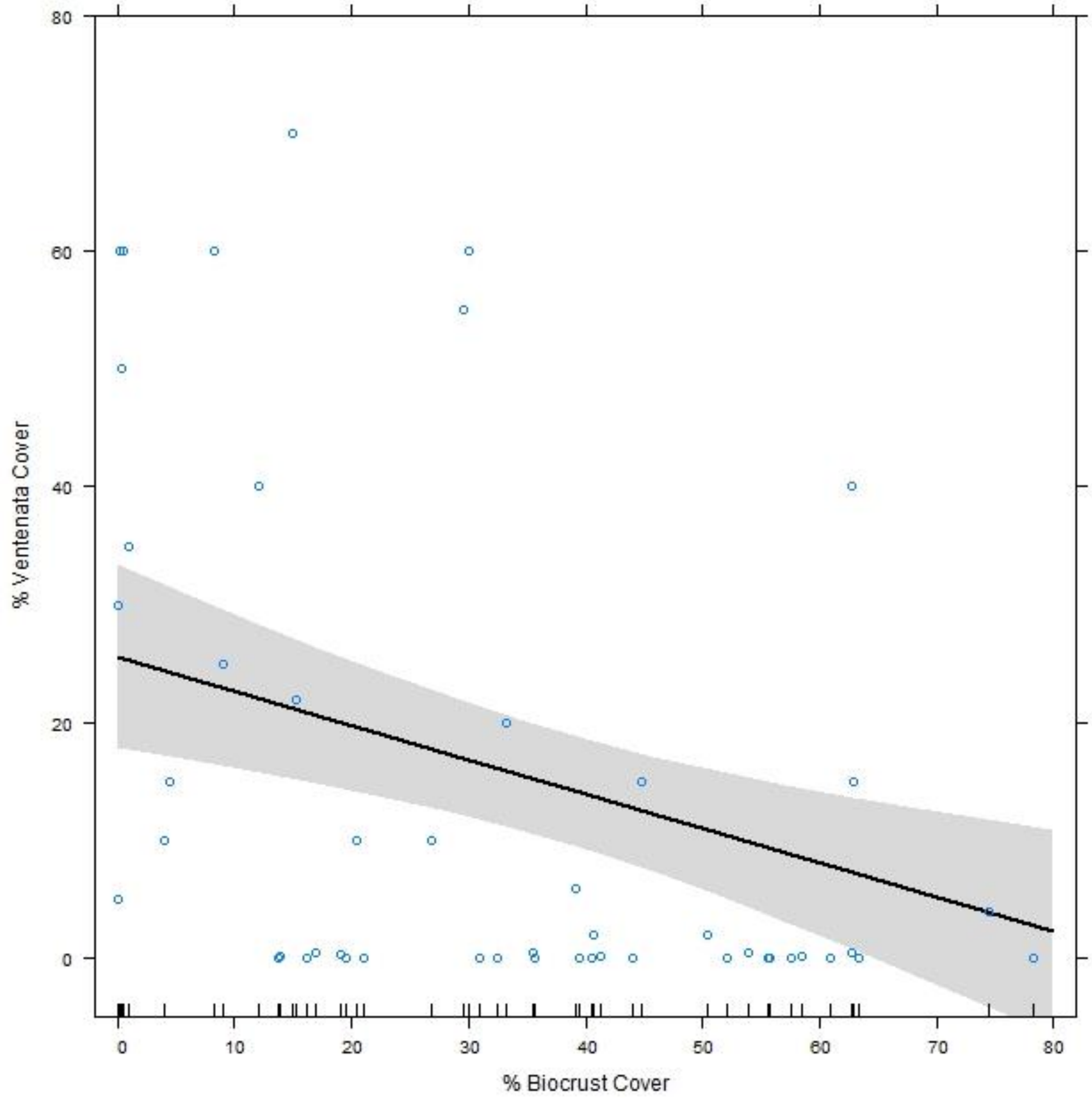

Figure 11. Relationship beteween biocrust cover and ventenata cover accounting for other variables based on the linear mixed effect model (Table 5; p = 0.0007).

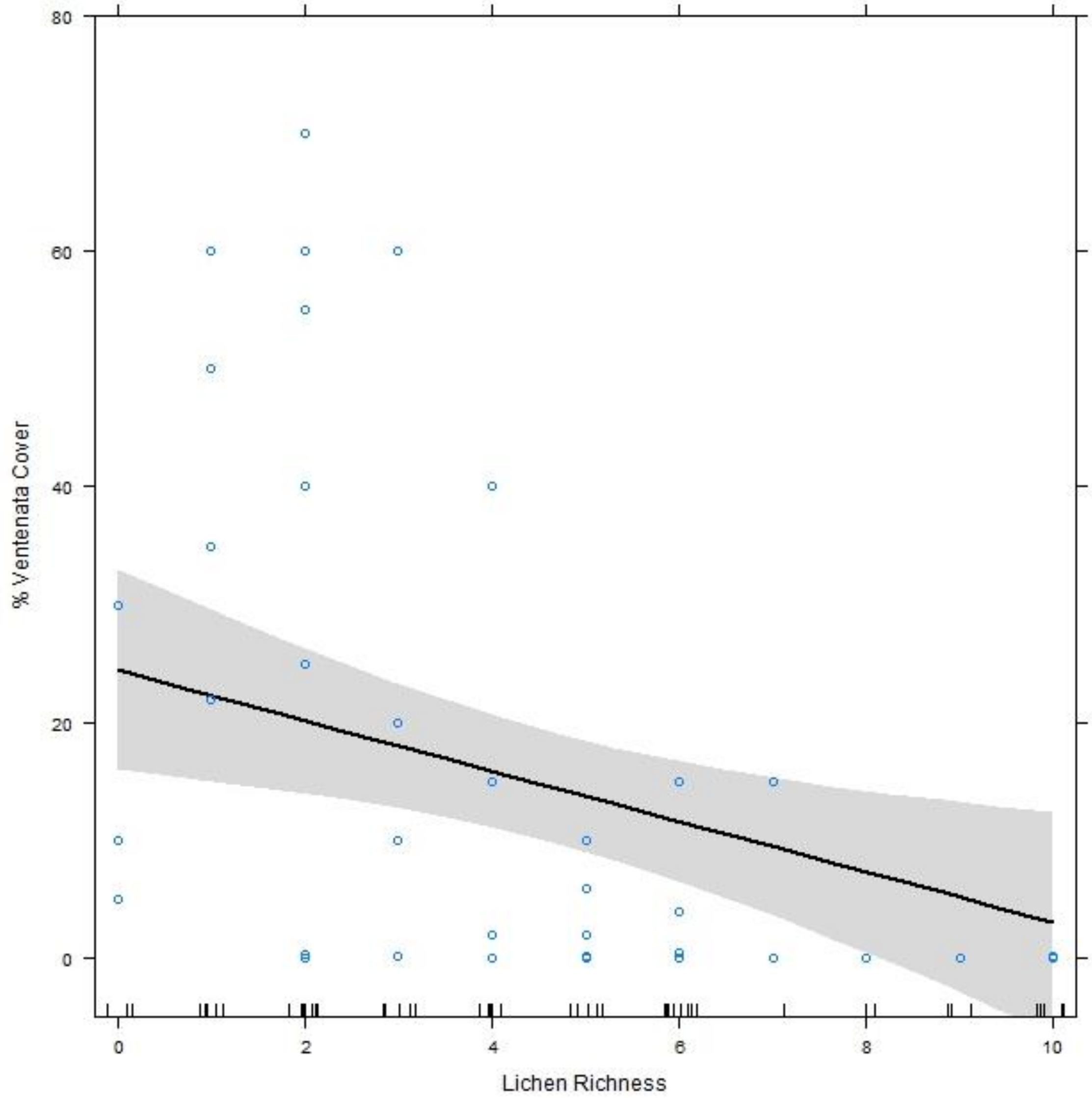

Figure 12. Relationship between lichen richness and ventenata cover accounting for other variables based on a linear mixed effect model (Table 5; $p < 0.0001$).

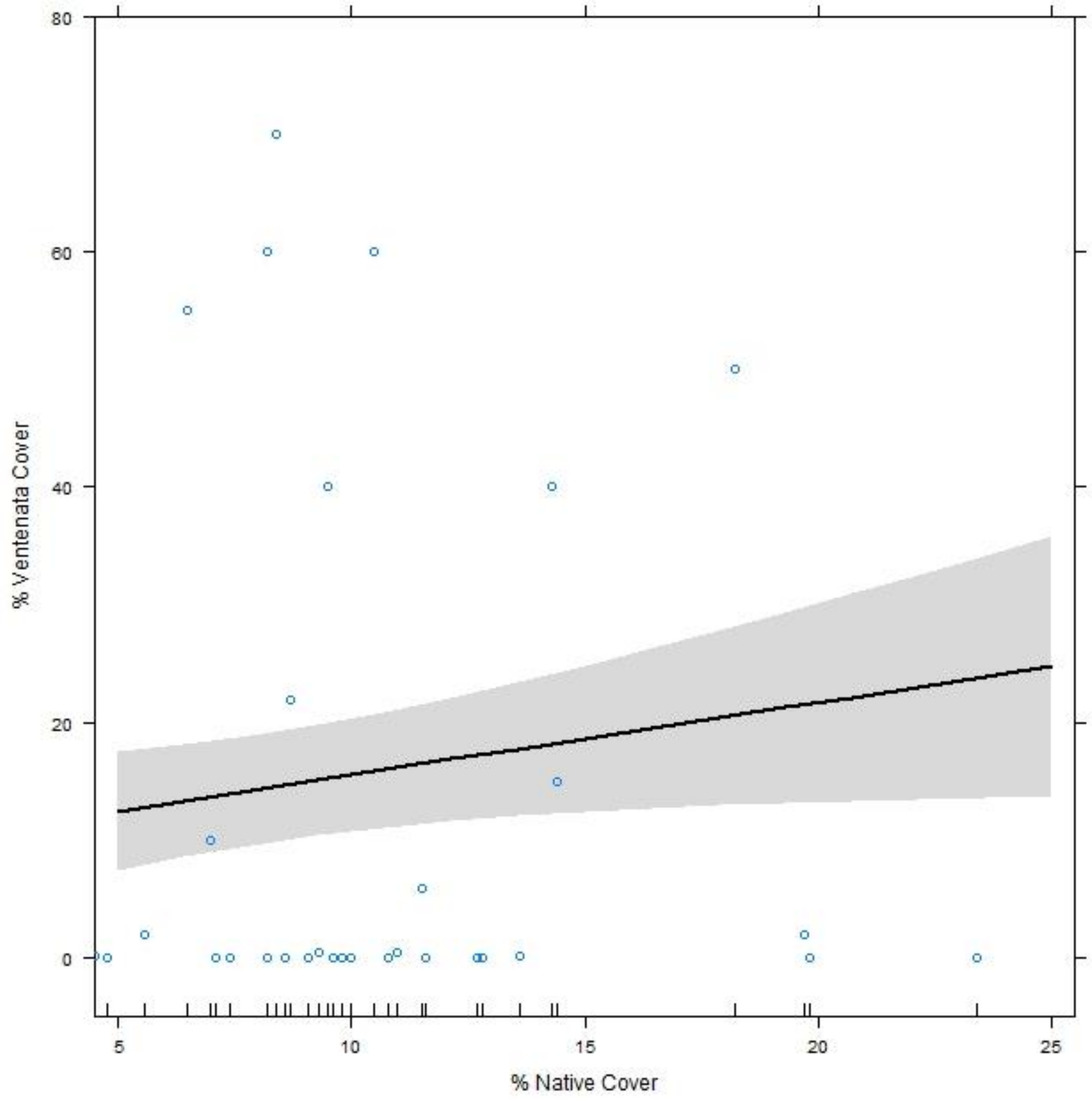

Figure 13. Relationship between native cover and ventenata cover accounting for other variables based on a linear mixed effect model (Table 5; p = 0.0197).

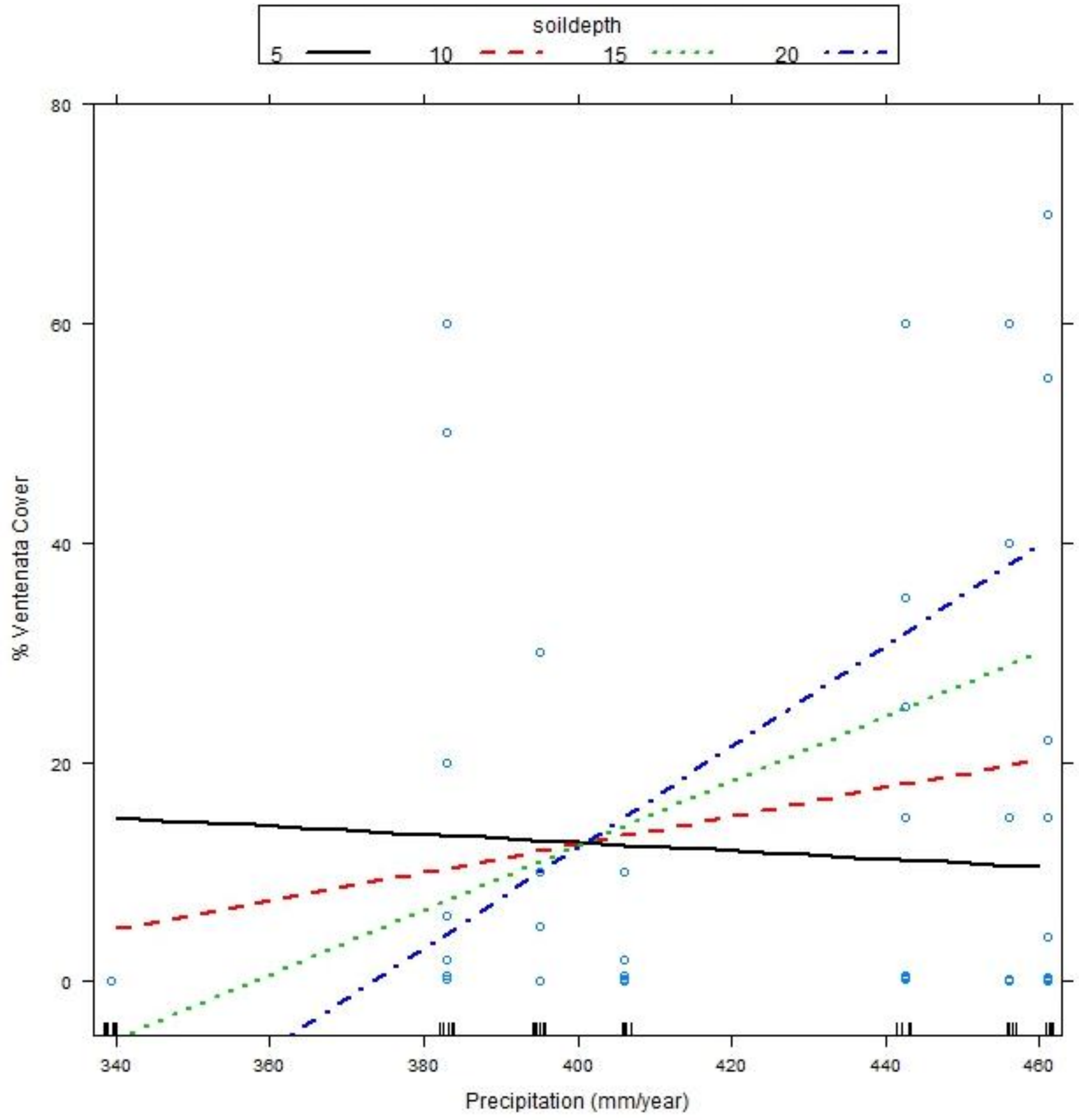

Figure 14. Interactive effect of average annual precipitation (mm/year) and heatload index on ventenata cover based on the linear mixed effect model (Table 5; p = 0.0013). Line type/color indicate soil depth.

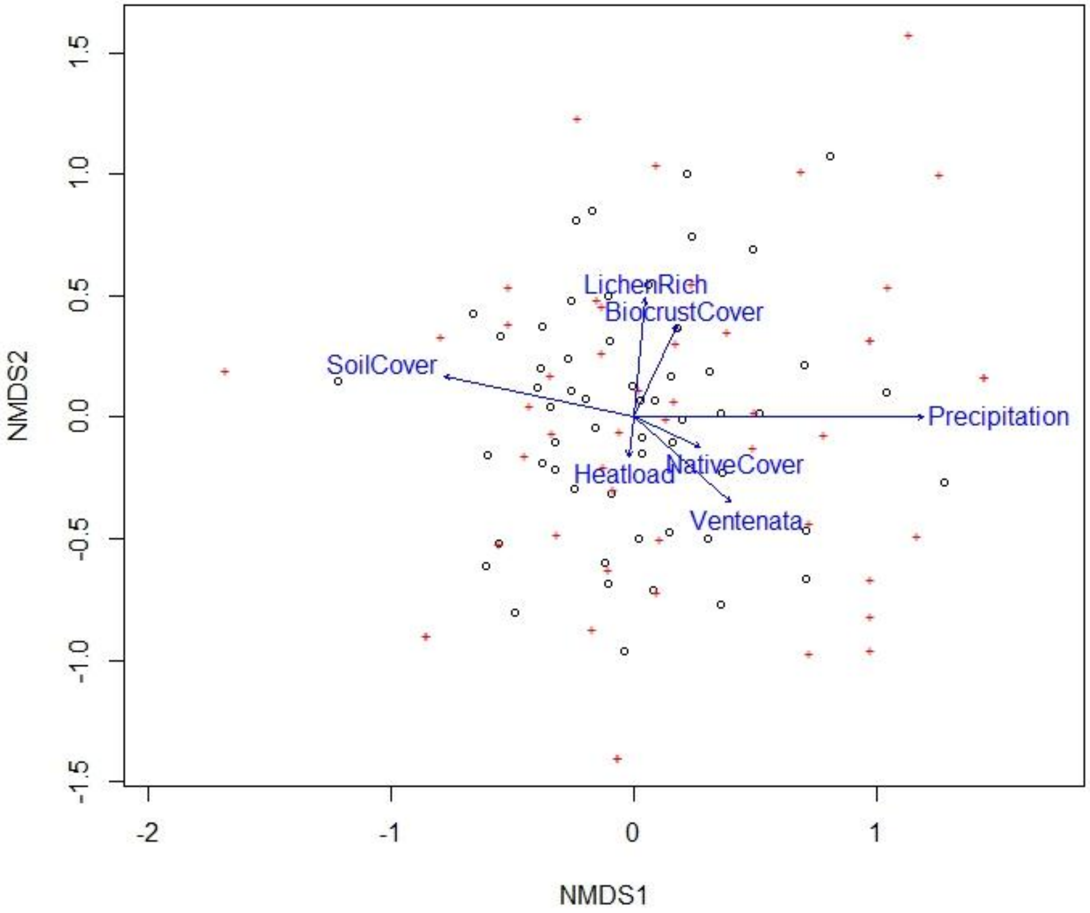

Figure 15. NMDS ordination of vascular plant species composition for all sites where *V. dubia* was observed (n= 7). Environmental and biological variables are overlain over ordination and rotated to fit precipitation along axis 1 (Table 6). Circles indicate vegetation plots, and crosses indicate species.

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Long-term *Ventenata dubia* patterns at a Turnbull National Wildlife Refuge in Eastern Washington

Abstract

The invasive winter annual grass, *Ventenata dubia* (ventenata), has recently become a serious problem throughout shrub-steppe ecosystems in the Inland Northwest. Research on *Bromus tectorum* (cheatgrass), another invasive winter annual grass, may serve as a starting point for managing *V. dubia*. Cheatgrass invasion has been shown to be limited by biocrust in the arid regions of Utah and central Washington, but it is unknown whether this effect extends to semiarid regions or to other invasive annual grass species. The purpose of this study is to document long-term (4 year) changes in *V. dubia* and biocrust at Turnbull National Wildlife Refuge (TNWR), a semiarid prairie in eastern Washington. I also examined the effect of disturbance and spring precipitation on this relationship. I resampled stratified plots on transects that crossed a gradient from high *V. dubia* to low *V. dubia*, to documented biocrust and vascular plant species. The transects were originally sampled in 2012; I resampled them in 2015. I also resampled plots (in 2015) where biocrust had been disturbed by human trampling (in 2012). Finally, I documented spring moisture at these locations to correlate with *V. dubia* abundance. While *V. dubia* cover at TNWR in 2015 was 63% lower than in 2012, this does not appear to be related to biocrust abundance or composition. Human trampling did not appear to have any impact on *V. dubia* or biocrust. Spring precipitation was positively correlated with *V. dubia*. While spring moisture availability is driving *V. dubia* abundance, biocrust seems to be resilient to infrequent surges of *V. dubia*. If spring precipitation patterns change, a different response would likely be observed. It is

important for land managers to pay close attention to spring precipitation and areas containing standing water, as these can be indicators of potential *V. dubia* invasion.

Introduction

Invasive plant species have been a major focus of land managers across the world as they are widespread and cause ecological and economic damage (Vila et. al 2011, Pimentel et al. 2005). Rapid growth, high seed production, alternative life histories, pathogen escape, and competitive ability are all characteristics that have been attributed to the success of these invaders (Rejmanek and Richardson 1996, Keane and Crawley 2002, Melgoza et al 1990). A group of species which use all of these characteristics to their advantage is invasive winter annual grasses. In the western U.S., these grasses germinate in fall, senesce during winter, and then fully develop in early spring (Rice et al. 1992). This winter phenology provides a competitive advantage over natives that begin to germinate in spring. While *Bromus tectorum* (cheatgrass) has been the most prevalent and most studied invasive annual winter grass in the western U.S., new species, particularly *Ventenata dubia* (ventenata) and *Taeniatherum caput-medusae* (medusahead) have recently begun to pose a problem. It’s critical to understand how these recent invaders interact with the environment to manage them effectively. Studies based on *B. tectorum* may serve as a starting point for learning how to best manage these new invasive winter annuals.

B. tectorum, has caused serious economic and ecological problems across the western United States. This grass has been shown to reduce native plant species, alter soil microbial communities, reduce habitat and forage for wildlife, and play a role in species extinction (O’Conner 1991, Kourtev et al. 2002, Clarke et al. 2005, Belnap et al. 2005, Simberloff 2005). *B. tectorum*, introduced in 1861, is estimated to occupy between 20 and 40 million hectares of the western U.S, an area larger than the state of Washington, and is expected to increase without active management (DiTomaso 2000). In the Western U.S., the presence of *B. tectorum* is modifying ecosystem properties such as increasing fire frequency, speeding up nitrogen cycling, and reducing soil moisture in early spring, all of which benefit *B. tectorum* and are detrimental to native persistence and re-establishment (Kerns et al 2006, Stark and Norton 2015, Booth et al 2003). Once established, these *B. tectorum* dominated landscapes are highly resistant to re-colonization by native perennials (Humphrey and Schupp 2004). Preventative management is preferred over reactive management because it can reduce long-term management costs (Leung et al. 2002). One preventative management approach is to reduce a community's susceptibility to invasion (Hooper et al. 2005), that is to reduce the likelihood of invasive species establishing and/or spreading through an ecosystem.

In arid climates (< 250 mm annual precipitation), biological soil crust (biocrust) has been shown to reduce community susceptibility to invasion by vascular plant species (Prasse and Bornkamm 2000, Deines et al. 2007, Root and McCune 2012). Biocrust is a complex association between soil, moss, lichens, algae and cyanobacteria, and is an important component of arid and semiarid ecosystems where it can make up to 70% of the ground cover, making it more dominant than vascular plants (Belnap 1994). Biocrust is a strong driver of soil stabilization, even more so than vascular native plants in a Colorado semiarid prairie (Belnap et al 2009). Biocrust species composition and richness have a strong influence on nutrient cycling, water storage (Maestre et al. 2005), and subsoil microbial activity (Castillo-Monroy et al. 2015). Biocrust species can be used as environmental indicators as they can vary greatly with respect to grazing disturbance, air pollution, and precipitation (Ponzetti et al. 2007, Coe et al. 2012, Zaady et al. 2014).

Grazing impacts on biocrust are particularly detrimental as the physical force can break apart crust species and cause vascular plants to establish and shade out crust species (Belnap et al. 2001, Belnap 2003, Chamizo et al. 2011). At high intensities, grazing can significantly reduce biocrust species diversity (Martinez et al 2006). Vehicle traffic over biocrust has similar physical impacts and additionally can disperse invasive species from long distances (Gelbard and Belnap 2003).

Most studies examining the relationship between invasive annual grasses and biocrust have been in arid regions (Prasse and Bornkamm 2000, Belnap 2003, Deines et al. 2007, O'Bryan et al. 2009), with only a handful in semiarid regions (250 – 500 mm/yr) Root et al 2011, Root and McCune 2012). Additionally, most of these studies have focused primarily on *B. tectorum* and none have examined the relationship between *V. dubia* and biocrust.

In the semiarid regions of the Intermountain West, areas dominated by biocrust are now being invaded by *V. dubia* (Anicito 2013). *V. dubia* is an emerging invasive annual grass that was first documented in the U.S. in Washington State in 1952 and is now found throughout the northwestern U.S. (Scheinost et al. 2009). Compared to *B. tectorum*, less is known about *V. dubia*, though preliminary studies indicate *V. dubia* may be outcompeting areas dominated by *B. tectorum* (T. Prather 2014 personal communication, 2014). Additionally, *V. dubia* has high silica content (2.7% more than desired foraging grasses), making it unpalatable to cattle, and is severely threatening timothy hay fields (Wallace and Prather 2013). To compound the issue of unpalatability, this unconsumed litter increases *V. dubia* emergence and growth (Wallace and Prather 2013). *V. dubia* persists in areas with shallow soil that are inundated in early spring but dry out later in the season (Anicito 2013, Scheinost et al. 2008), though this has not been tested directly. These shallow soils happen to be the same habitat where biocrust is found in greater abundance (Belnap 1994).

One area where biocrust communities have been relatively undisturbed in the Intermountain West is at Turnbull National Wildlife Refuge (TNWR), located approximately 5 miles south from Cheney, WA (Figure 1). Within the refuge, substantial amounts of biocrust are located at prairie sites between Mima Mounds. Mima mounds are hemispherical aggregations of soil up to 2 m tall and 30 m in diameter surrounded by intermound areas with shallow soil. At TNWR, the Mima mounds are underlain by alluvial gravels deposited during the Missoula Floods or basalt bedrock (Bryant et al. 2013). Vernal pools in eastern Washington have been documented to occur frequently around Mima mounds in the intermound areas (Bjork and Dunwiddie 2004). Cattle grazing was halted at TNWR in 1993, and the refuge has undertaken other land management practices (controlled burns, weed management) to maintain native plant communities. Nevertheless, the mima mound prairie community has been experiencing an increase in *V. dubia* since first being documented in 1990. *V. dubia* at the refuge appears to behave differently than other invasive annual grass species, as it does not appear to be inhibited by intact biocrust present in the intermound areas (Anicito 2013). Understanding how *V. dubia*, environmental variables such as standing water and biocrust relate and respond to each other is critical for understanding how to effectively manage ecosystems where both occur.

To understand how biocrust and *V. dubia* relate, Anicito (2013) examined the change between *V. dubia* and biocrust along established transects at TNWR. She found tall moss to be more associated with *V. dubia* and squamulose white lichen to be negatively associated with *V. dubia.* She also recorded a reduction in *V. dubia* from 2012 to 2013 across all transects. To better understand resistance to invasion, she experimentally trampled biocrust to determine effects on invasion by *V. dubia*. She found that *V. dubia* decreased from 2012 to 2013 along the transects and that trampling did not appear to impact *V. dubia* abundance. A limitation of her study was its short, one-year time frame, which may not have been enough time to assess long-term impacts of trampling or changes in plant communities. My objective is to understand how these disturbances and biotic relationships change over a longer period of time (3 years). Additionally, in collaboration with Rachael Hamby, I will document how standing water in intermounds relates to *V. dubia* abundance.

Methods

Study Location

Turnbull National Wildlife Refuge is located within Eastern Washington's Channeled Scablands, approximately 5 miles south of Cheney, WA (Figure 1 – Location Map). Of the approximately 18,000 acres at TNWR, the main concentration of open prairie Mima mound communities is located in the 380 acre Stubble Field Tract and Public Use Area in the southwest portion of the refuge and is underlain by both basalt and alluvium. This area has a dry-summer continental climate with the hottest months in July and August (13 degrees C low average to 28 degrees C high average) and coolest in December (-5 degrees C low average to 0 degrees C high average). The average annual precipitation is 432 mm, with most received in the winter and the least during the summer months, which makes it a semi-arid (250 mm- 500 mm) climate.

Data collection

To document change in *V. dubia* populations, seven transects, each with four 1 m^2 plots (28 total) were established, sampled, and marked with metal stakes by Kristin Anicito in 2012. These transects were placed only in the intermound areas on basalt bedrock (Figure 1). These transects were stratified from high to low/none *V. dubia* cover. The ends of the transects without *V. dubia* were primarily biocrust with few vascular plants. Twenty six of the 28 plots were relocated and resampled in 2013 and 2015. Two plots could not be relocated in 2013 and 2015 as the metal stakes were missing, possibly due to ungulate disturbance. Sampling in 2012 and 2013 took place in late June through early July, and 2015 sampling took place in mid-June though late June due to an early onset of vegetation emergence and senescence.

To test the impacts of trampling on biocrust's role in inhibiting *V. dubia*, six control and ten trampled 1 m^2 plots were established and sampled in 2012. These plots were also located in the intermounds on basalt bedrock. On December 3, 2012, Anicito (2013 Thesis) trampled biocrust by stomping in parallel lines within the boundaries of each plot for one minute. Five control and nine trampled plots were relocated and resampled in 2013 and 2015. Sampling in each year took place in mid-June through early July.

For each plot I estimated percent cover of all vascular plant species and biological crust morphotypes. Lichens and moss were recorded for biocrust. Lichens were classified by morphology (crustose, areolate, gelatinous, squamulose, foliose, and fruticose) and color. Moss was classified as tall or short (Rosentreter et al. 2007). If *V. dubia* was present, a stem count was completed within 0.04 m^2 (20 cm x 20 cm) of the southeast corner. Percent ground cover (litter, rock, soil) and soil depth (average of 2 corners) were also recorded for each plot.

To investigate the role spring moisture retention plays in *V. dubia* abundance, Rachael Hamby and I sampled plot characteristics related to standing water and saturation for the seven established transects mentioned previously (26 plots). Sampling occurred on March 9 and April 3, 2016. In each plot I estimated percent cover of standing water, depth of standing water, and percent of the plot that was saturated.

Data analysis

To document the changes in *V. dubia* cover and stem count, moss cover, and lichen cover along the established transects over time, I used a mixed effect model with repeated measures using the lme package in R (R Core Team 2013). I examined the effect of time and plot (high to low *V. dubia*) on *V. dubia* count and cover, moss cover, and lichen cover. Lichen cover data from 2012 and 2013 was relativized to 100 % as cover estimates were much larger than documented in 2015. To determine how *V. dubia* related to moss and lichens between years, I performed a mixed effects model under the lme package in R (R Core Team 2013).

To investigate the effects of trampling, I compared the effect of trampling and time since disturbance on *V. dubia* cover and stem count, moss cover, lichen cover, lichen richness, and squamulose white lichen cover using an ANOVA in R (R Core Team 2013). Lichen cover data from 2012 and 2013 was relativized to 100 % as cover estimates were much larger than documented in 2015.

To understand what role spring moisture plays in *V. dubia* abundance, I examined the effect of average standing water, water depth, and plot saturation in 2016 on *V. dubia* cover from 2012, 2013, and 2015 using a mixed effect model using the lme package in R (R Core Team 2013).

Results

V. dubia movement across biocrust

In 2012, there was 59% average cover difference (Figure 2; $p<0.001$), and a 205.9 average stem count difference (Figure 3; $p<0.001$) between the high and low *V. dubia* ends of the transects. However, this difference did not persist in 2013 ($p > 0.99$) and 2015 ($p=0.99$) because *V. dubia* cover was lower in all plots than 2012, resulting in all plots across the transect exhibiting the same *V. dubia* cover (Figure 2). Stem count data yielded similar results, with the only difference in *V. dubia* along the transects occurring when they were established (Figure 3).

For biocrust, there was no difference in moss cover among any plots within and among years (Figure 4). Lichen cover was not significantly different in any plots within and among years, except for the low *V. dubia* plot in 2013 which was higher than all other plots during that year (Figure 5).

V. dubia and moss cover were positively correlated, but only in 2012 (Figure 6; $p=0.015$, $R^2= 0.17$). No relationship was observed in 2013 or 2015. *V. dubia* cover and lichen cover were negatively correlated in 2012 (Figure 7; $p < 0.001$, $R^2 = 0.66$) with a similar relationship observed in 2013 ($p = 0.042$, $R^2 = 0.12$) and 2015 ($p = 0.032$, $R^2 = 0.14$).

Trampling impacts to biocrust

Trampling did not affect *V. dubia* cover (Figure 8; $p = 0.88$) or stem count (Figure 9; $p = 0.13$) during any of the years examined. There was a roughly 62% decrease in cover documented from 2012 to 2013 (control and trampled: $p < 0.001$) and a decrease in stem count for the same years (control: $p = 0.24$, trampled: $p < 0.001$) but this occurred relatively equally between control and trampled plots. Additionally, there was no impact on moss (Figure 10) or lichen (Figure 11) cover among treatments for any of the years sampled. Lichen species richness was also unaffected throughout the study (Figure 12). Additionally, there was no difference in squamulose white lichen cover between years or treatments (Figure 13).

Spring moisture and V. dubia abundance

Spring moisture characteristics documented in 2016 were positively associated with *V. dubia* cover documented in 2012, 2013, and 2015. The proportion of the plot that was saturated (Figure 15; $p < 0.001$, $R^2 = 0.50$), standing water depth (Figure 14; $p < 0.001$, $R^2 = 0.47$), and percent of the plot that contained standing water (Figure 16; $p < 0.001$, $R^2 = 0.31$) all showed positive relationships with *V. dubia* cover in all years sampled.

Discussion

V. dubia has been recently invading natural and agricultural habitats in the Inland Northwest, even out-competing *B. tectorum* (Prather 2009). Turnbull National Wildlife Refuge (TNWR) in eastern Washington saw a 15-fold increase of *V. dubia* from 2009 to 2013 raising concerns about how much worse this problem could become (Reynecke 2012, Anicito 2013, pers. comm. Mike Rule). *V. dubia* still remains on the refuge where it ranged from 0 to 95% cover in plots sampled in 2015, though overall its abundance has been greatly reduced since 2012.

While maintaining an intact biological soil crust may be a successful management goal for limiting the invasion and spread of *B. tectorum*, it appears this may not be the case for *V. dubia* (Root and McCune 2012, Belnap 2000, Anicito 2013). Despite a diverse and abundant layer of biocrust species, the intermound areas within the Mima mound prairie at TNWR experienced *V. dubia* cover estimates up to 80% in 2012 (Anicito 2013). Even though *B. tectorum* and other *Bromus* species along with *V. dubia* were found on the mounds, only *V. dubia* was able to invade the biocrust rich intermound areas (Anicito 2013). I had hypothesized that *V. dubia* would further invade biocrust along my intermound transects, but this did not occur. Instead, *V. dubia* cover and stem counts were greatly reduced when resampled in 2013 and 2015 (Figure 2 & 3). However, I do not think that biocrust was repelling invasion by *V. dubia.* Rather, I suspect this reduction can be attributed to reductions in spring rainfall rather than rapid growth of biocrust.

Despite the rise and fall in abundance of *V. dubia*, moss and lichen species' covers remained basically unchanged throughout the study (Figure 4 & 5). The decrease in lichen cover observed in 2015 could possibly be attributed to either climate change, or differences in surveying between samplers. It remains unclear how biocrust responds after prolonged years of *V. dubia* abundance. I hypothesize that similar to other invasive annual grasses, *V. dubia* can outcompete biocrust for light and alter microhabitat conditions (Facelli and Pickett 1991) in ways that could be detrimental (Belnap 2006). Prather et al. (2012) have shown that persisting *V. dubia* litter acts as a positive feedback loop to increase the germination rate of *V. dubia* seeds, though this pattern was not observed at TNWR.

Past studies have shown that disturbance by intense grazing or vehicle traffic has negative impacts on biocrust communities, which in turn leads to an increase in invasive annual grasses (Lass and Prather 2007, Root et al. 2011). While this has been shown with *B. tectorum*, the same does not appear to hold true for *V. dubia* in this study, as human trampling treatments had no clear impact on *V. dubia* cover or stem counts (Figure 7). One reason that no impact was documented could be attributed to the amount of moisture present or the community type where the disturbance took place (Belnap 1994). Recovery estimates vary, but it is thought that areas which are moist following disturbance, as well as cool desert communities, often recover faster than dry hot desert biocrust communities (Belnap 2003). While I saw a large decrease in *V. dubia* from 2012 to 2013 which continued into 2015, this pattern matches all other data at TNWR indicating a site wide reduction in *V. dubia,* which indicates there may be no impact by trampling. It is entirely possible that the method for trampling was not forceful enough, or that trampling must be recurrent for it to have an effect, and results could be different with intense grazing by cattle or vehicle disturbance (Belnap 2003).

Two important unanswered questions remain. 1) Why is *V. dubia* able to thrive in biocrust dominated intermound areas while other invasive annual grass species do not? 2) What is driving the extreme rise and fall in *V. dubia* abundance between years? It is evident from sampling across TNWR that *V. dubia* is one of the few species able to inhabit intermound areas previously dominated by biocrust, despite other invasive annual grasses being present on the Mima mounds (Reyneke 2012, Anicito 2013). A few characteristics of *V. dubia* may help explain this. *V. dubia* biomass and root length are much smaller (10-16mm) than other invasive annual grasses (James 2008) which may allow them to persist in shallow soils. *B. tectorum* has larger roots (91 cm, Hironaka 1961) which may limit it from these shallow soil conditions. In a study by James (2008), *V. dubia* biomass, relative growth rate, specific leaf area, leaf mass ratio, and root length were all unaffected when grown in low N conditions indicating that perhaps *V. dubia* is able to tolerate low nutrient environments as well. Additionally, there may be some level of pathogen escape occurring which allows *V. dubia* to survive in environments where other invasive annuals have been excluded (Reinhart and Callaway 2006).

Along with tolerating shallow soils, perhaps the most notable characteristic of *V. dubia* is that is seems to prefer areas which collect precipitation in the spring (Scheinost et al. 2008, Anicito 2013, Personal observation across eastern Washington). These areas can act as vernal pools where standing spring water persists into spring depending on precipitation during that year. Vernal pools in eastern Washington have been documented to occur frequently with Mima mounds and appear to support a high amount of annual species (65% of the 85% native species recorded; Bjork and Dunwiddie 2004). *V. dubia* at TNWR was found to be positively correlated with plot saturation (Figure 14), standing water depth (Figure 13), and to some degree percent of standing water (Figure 15). Regardless if *V. dubia* cover was high (2012) or lower (2013 & 2015), these relationships remained. I expect an even stronger relationship to data that will be collected during the same growing season (2016). While there is a relationship between spring moisture and *V. dubia* abundance, there are many unanswered questions related to the timing, amount, and persistence of this moisture, as well as how this standing water impacts biocrust.

No observable pattern was found to exist between biocrust abundance or composition, indicating that biocrust may not inhibit *V. dubia*, as it does with *B. tectorum* (Belnap et al. 2001, Chamizo et al. 2011). Additionally, biocrust abundance or composition appears to be unaffected by the presence of *V. dubia*. When *B. tectorum* has become established, it has been documented to shade out and reduce biocrust (Belnap et al. 2001, Ponzetti et al. 2007). A major difference in the pattern of *V. dubia* at TNWR is that high amounts of *V. dubia* do not seem to persist for numerous years (Anicito 2013, Mike Rule pers. Comm.). Additionally, biomass and root length of *V. dubia* is significantly less than that of *B. tectorum* (James 2008) which may allow *V. dubia* to establish on top of biocrust, and also result in less shading compared to *B. tectorum*. Reduced shading and lack of persistence may explain why *V. dubia* did not significantly impact biocrust communities at TNWR. Together with the data suggesting that biocrust disturbed by human trampling does not increase amounts of *V. dubia*, these biocrust communities may be more resilient to fluxes in *V. dubia* than expected.

This does not however account for the preliminary results which suggest a strong correlation between spring moisture and *V. dubia* abundance. This appears to show the strongest link to what is driving the patterns observed of *V. dubia* at TNWR. With climate change expected to shift precipitation in the Inland Northwest to more falling in winter and spring and less in summer (Karl and Melillo 2009, Kunkel et al. 2013), this could have significant impacts on *V. dubia* at TNWR. If we were to see more years with greater standing water in the spring and higher *V. dubia* abundance, we may not see the same relationship with biocrust that has been previously documented. Many questions remain related to timing, amount, and persistence of spring moisture to *V. dubia*. These should be investigated to better understand what years *V. dubia* may pose the largest threat. Land managers may tailor yearly management dependent on spring indicators and allow resources to be distributed more efficiently. Additionally, biocrust should continually be examined, in order to capture changes that may result from consecutive years with heavy *V. dubia* abundance.

Figures

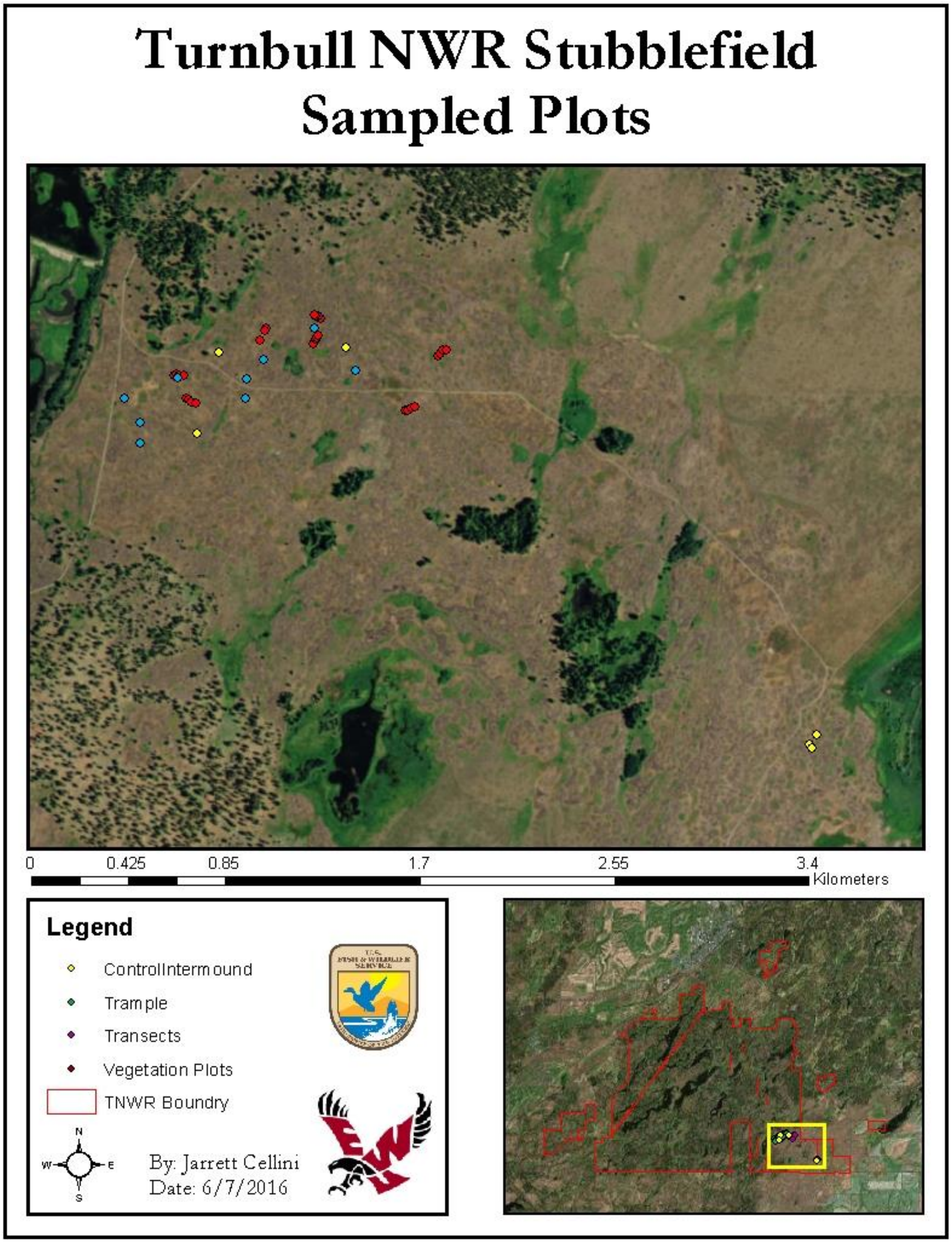

Figure 1. Transect, control and trampled plot locations at the Stubblefield Area in Turnbull National Wildlife Refuge.

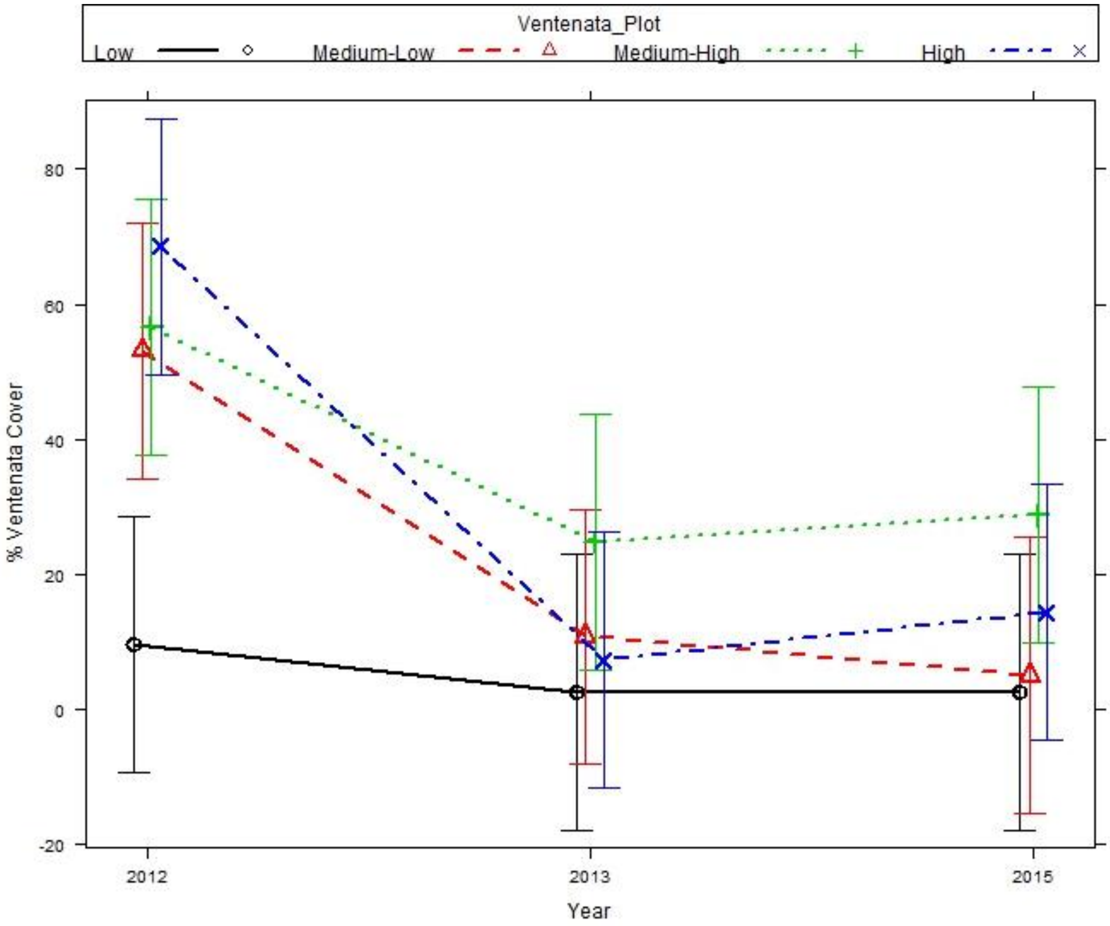

Figure 2. *V. dubia* percent cover on stratified transects across years. Established plot type (Ventenata_plot) along the transects are represented by color/line type. These plots correlate to the abundance of ventenata when first established in 2012. Error bars represent + SE.

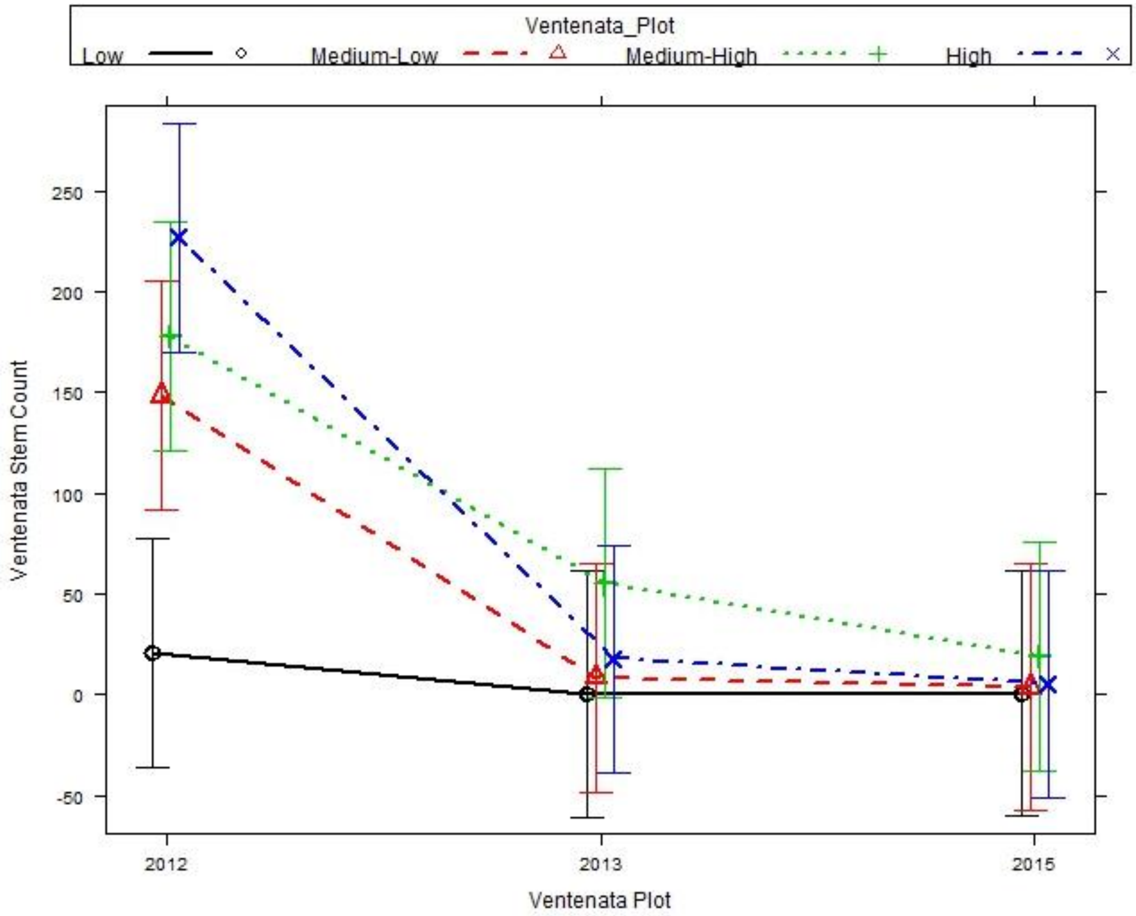

Figure 3. *V. dubia* stem count on stratified transects across years. Established plot type (Ventenata_plot) along the transects are represented by color/line type. Ventenata_Plot indicates plot position on the transect with respect to ventenata abundance in 2012. Error bars represent ± SE.

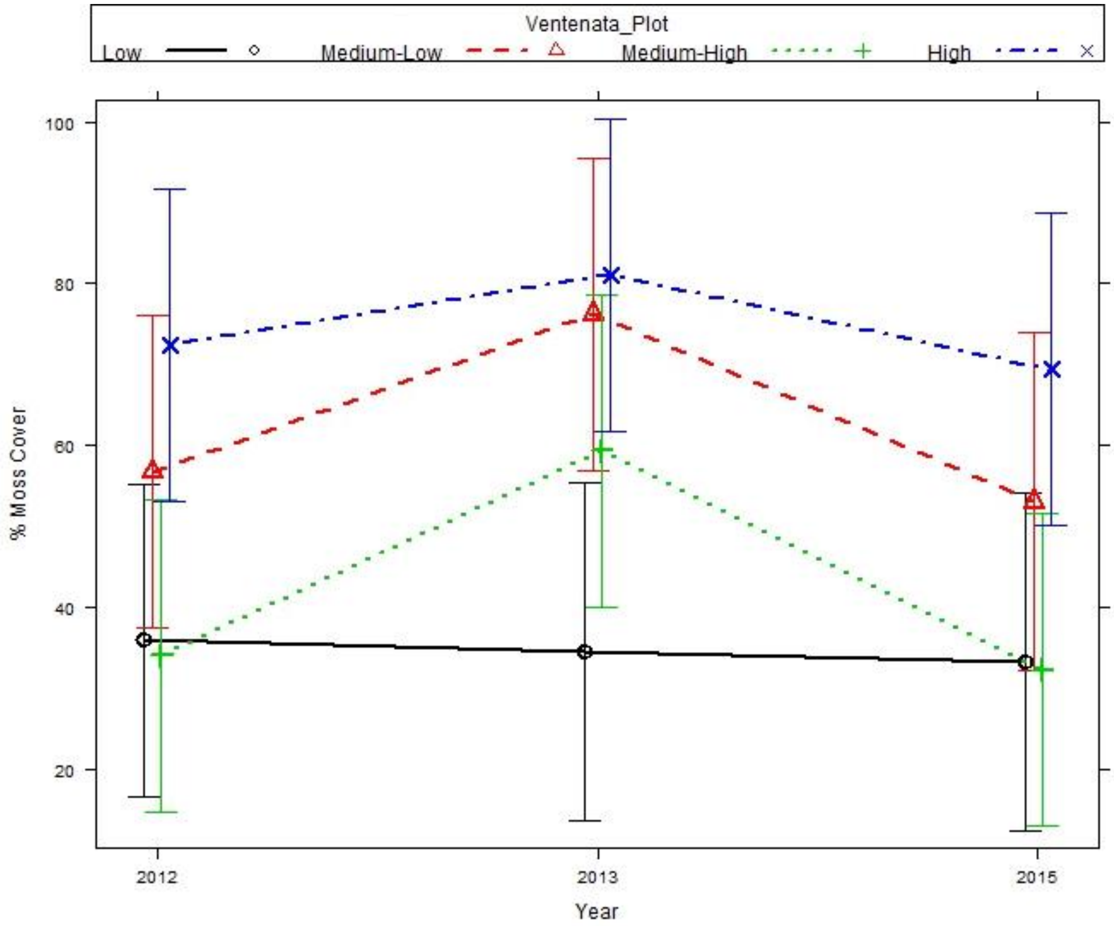

Figure 4. Moss cover on stratified transects across years. Established plot type along the transects are represented by color/line type. Error bars represent ± SE.

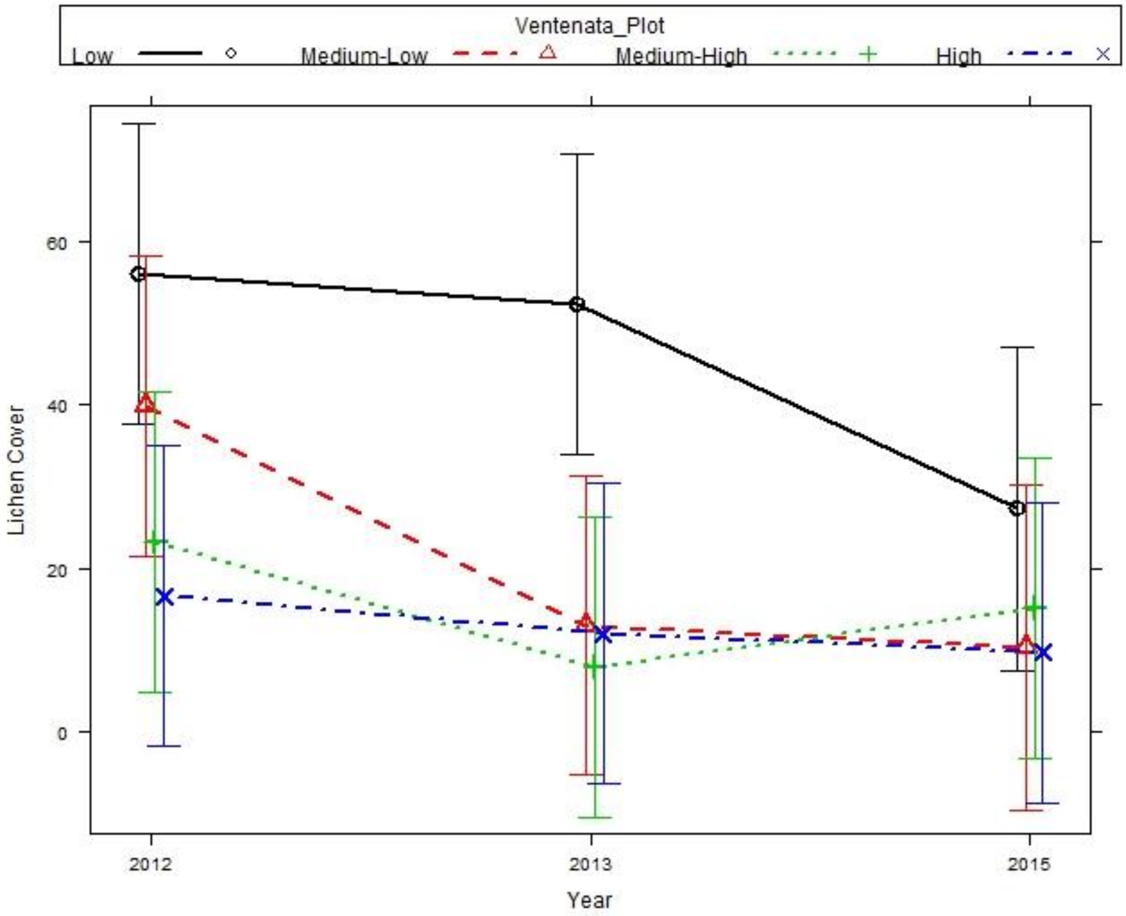

Figure 5. Lichen cover on stratified transects across years. Established plot type along the transects are represented by color/line type. Error bars represent ± SE.

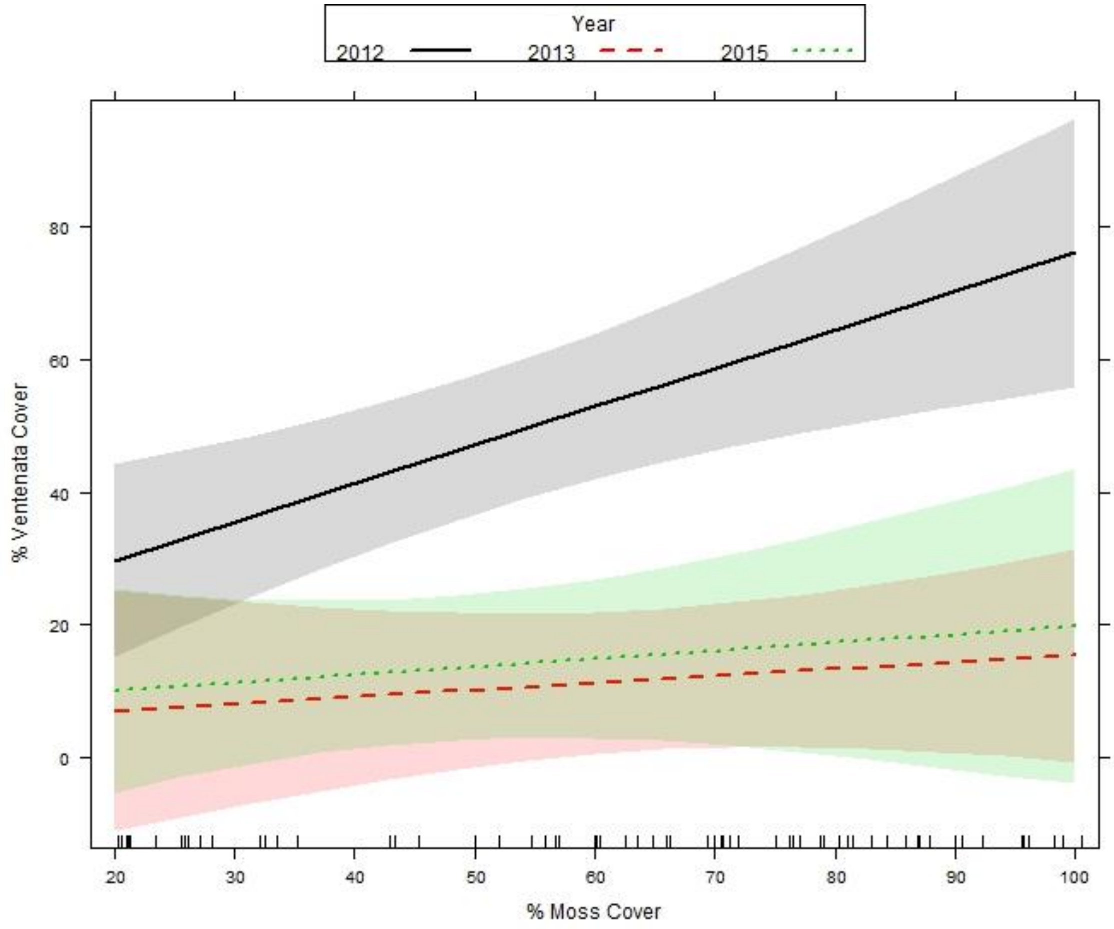

Figure 6. Relationship between moss cover and *V. dubia* cover on stratified transects over time. Year is represented by color/line type. Shading around each line represents 95% confidence interval.

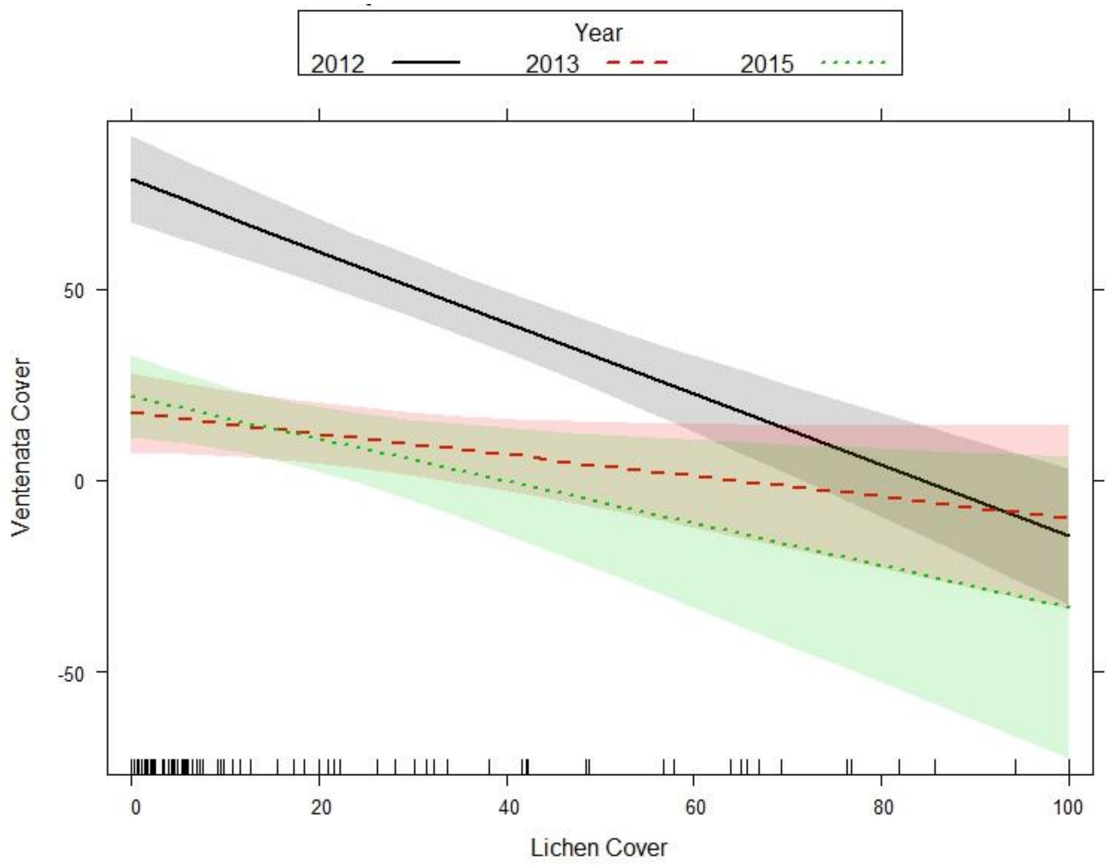

Figure 7. Relationship between lichen cover and *V. dubia* cover on stratified transects over time. Year is represented by color/line type. Shading around each line represents 95% confidence interval.

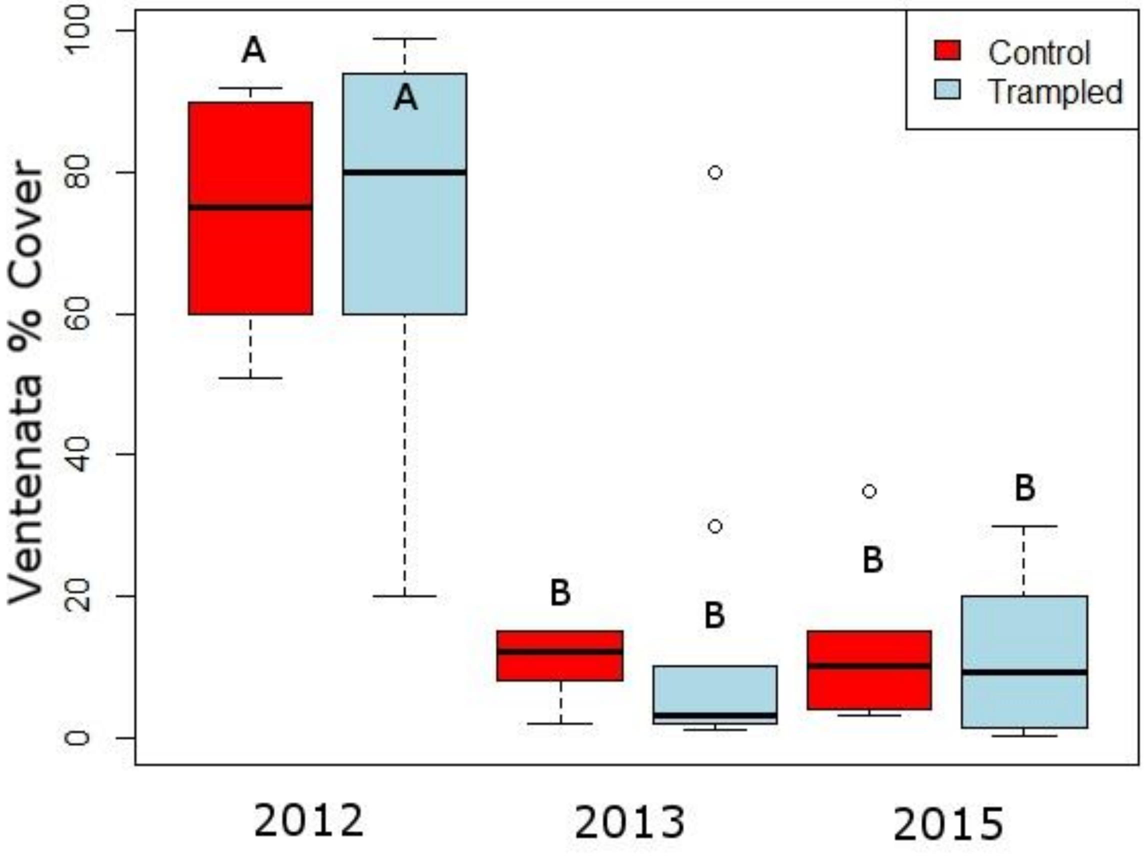

Figure 8. *V. dubia* cover between control (n=5) and trampled (n=9) plots. Bars with the same letter are not significantly different ($p < 0.05$). Color indicates control or trampled plots. Error bars represent + SE.

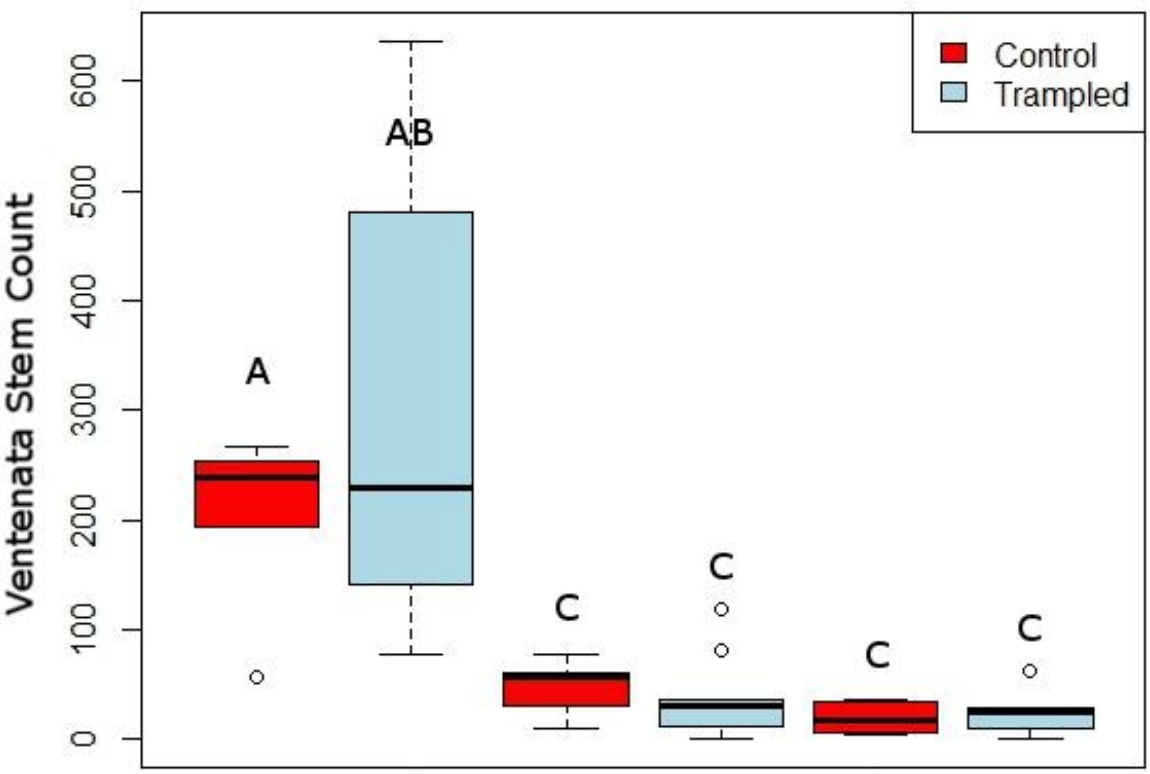

Figure 9. *V. dubia* count between control (n=5) and trampled (n=9) plots. Bars with the same letter are not significantly different ($p < 0.05$). Color indicates control or trampled plots. Error bars represent ± SE.

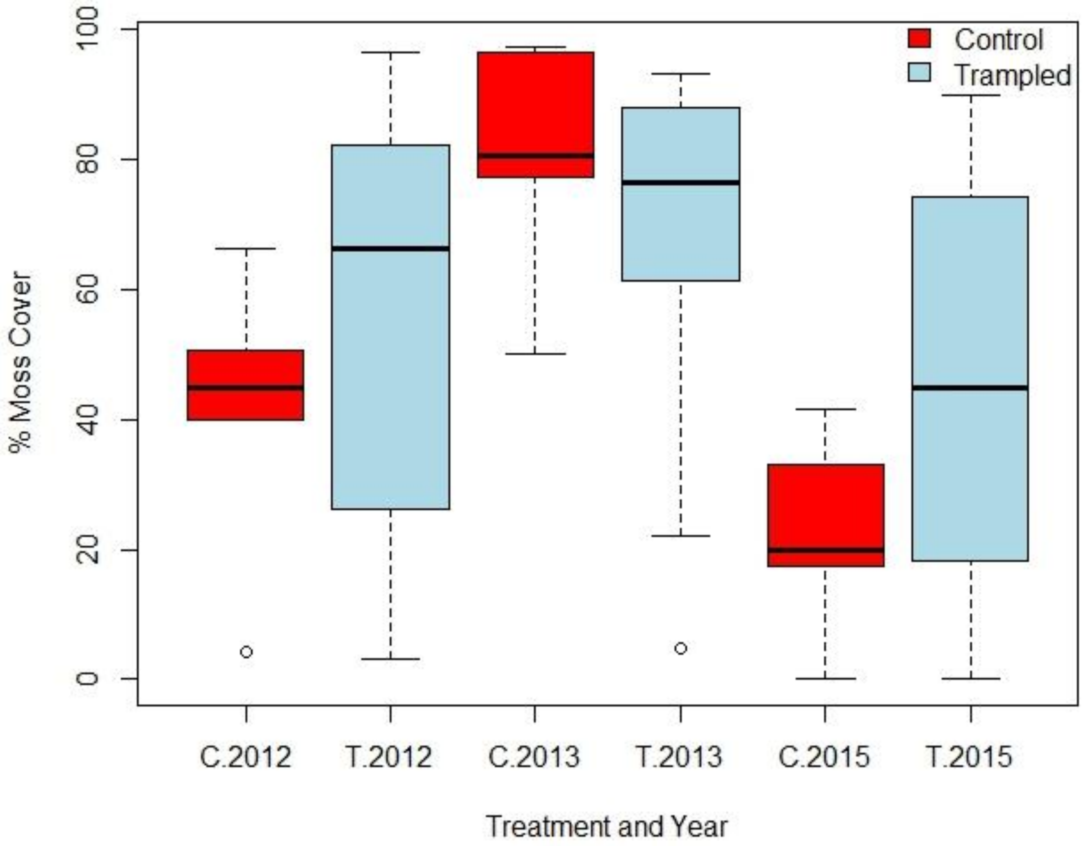

Figure 10. Moss cover between control (n=5) and trampled (n=9) plots. Different letters indicate significance ($p < 0.05$). The only significant difference is between control 2013 and control 2015. Color indicates control or trampled plots. Error bars represent ± SE.

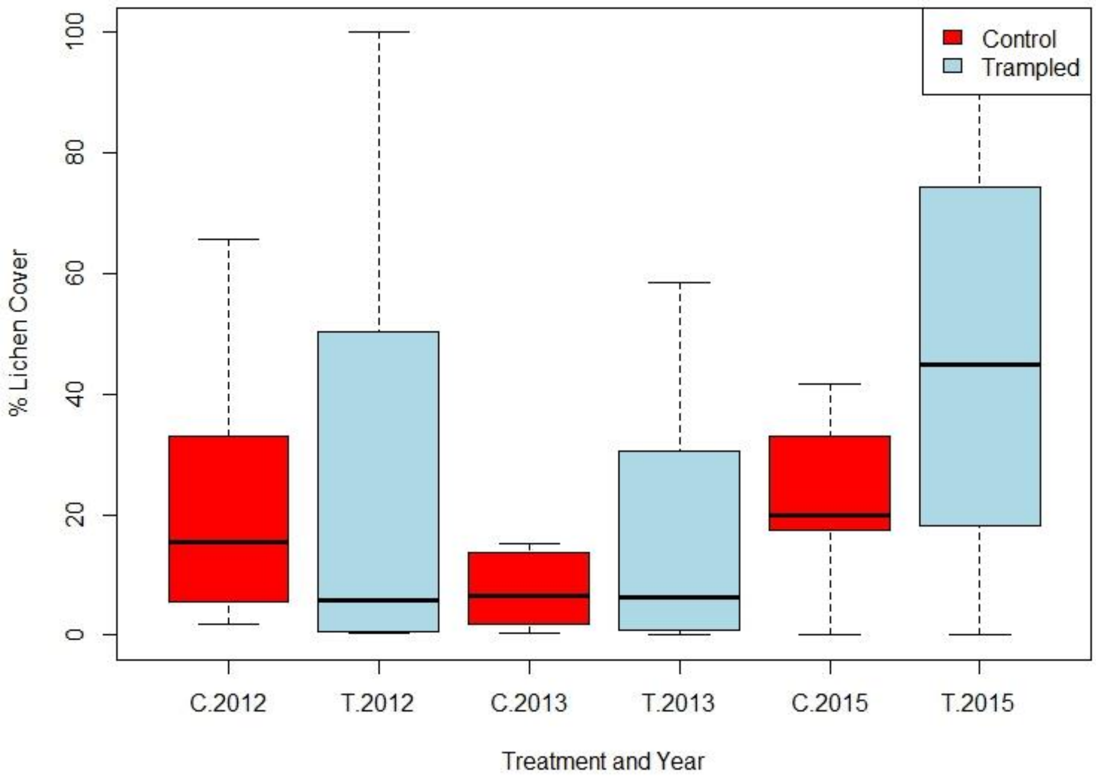

Figure 11. Total lichen cover between control (n=5) and trampled (n=9) plots. No difference between any year and treatment. Color indicates control or trampled plots. Error bars represent ± SE.

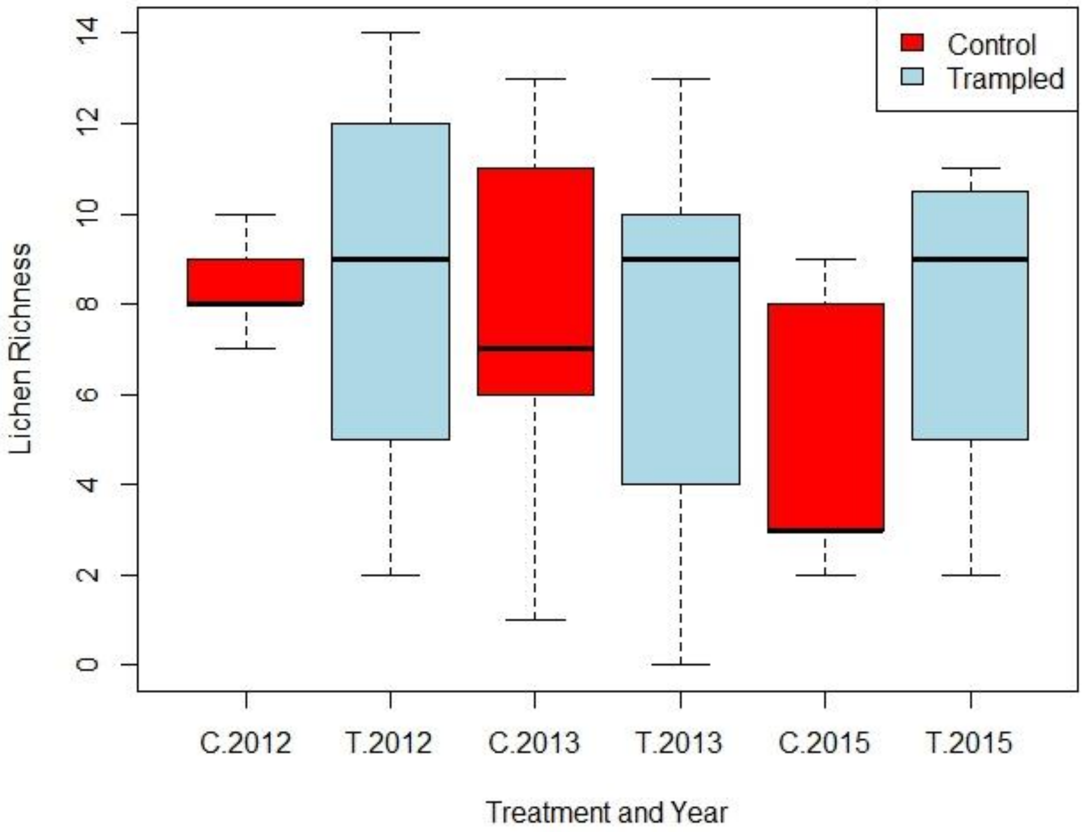

Figure 12. Total lichen richness between control (n=5) and trampled (n=9) plots. No difference between any year and treatment. Color indicates control or trampled plots. Error bars represent ± SE.

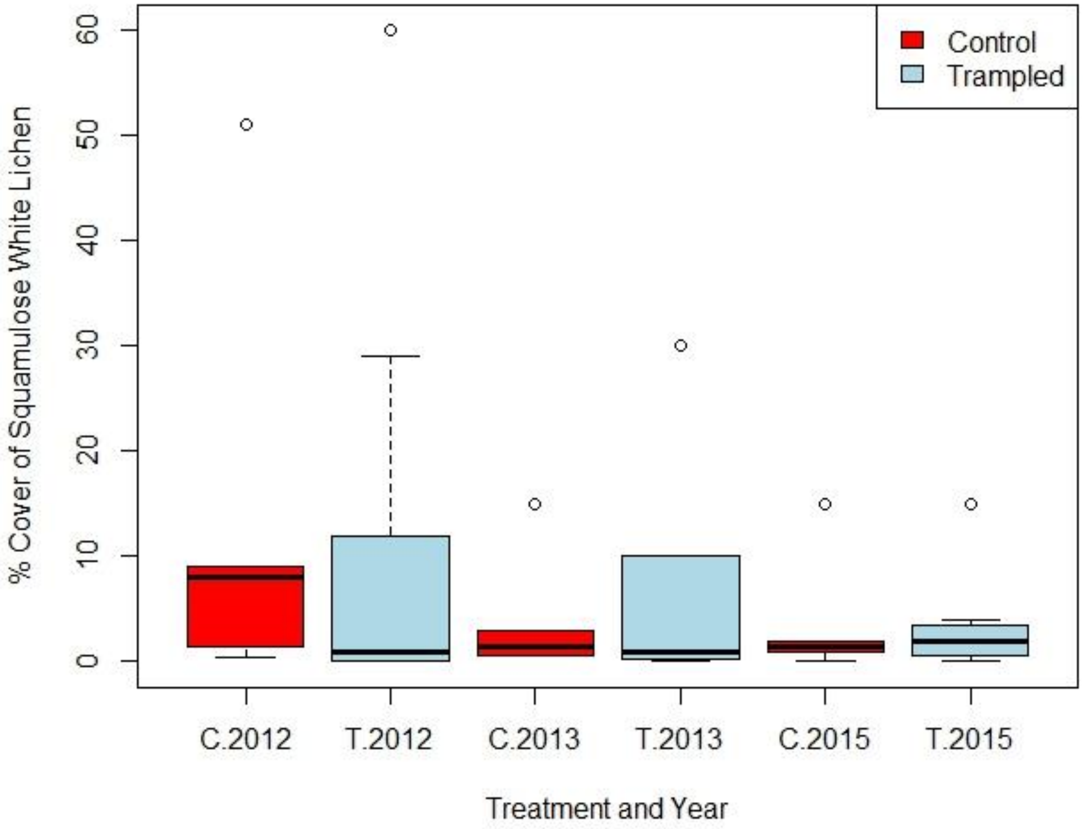

Figure 12. Total squamulose white lichen cover between control (n=5) and trampled (n=9) plots. No difference between any year and treatment. Color indicates control or trampled plots. Error bars represent + SE.

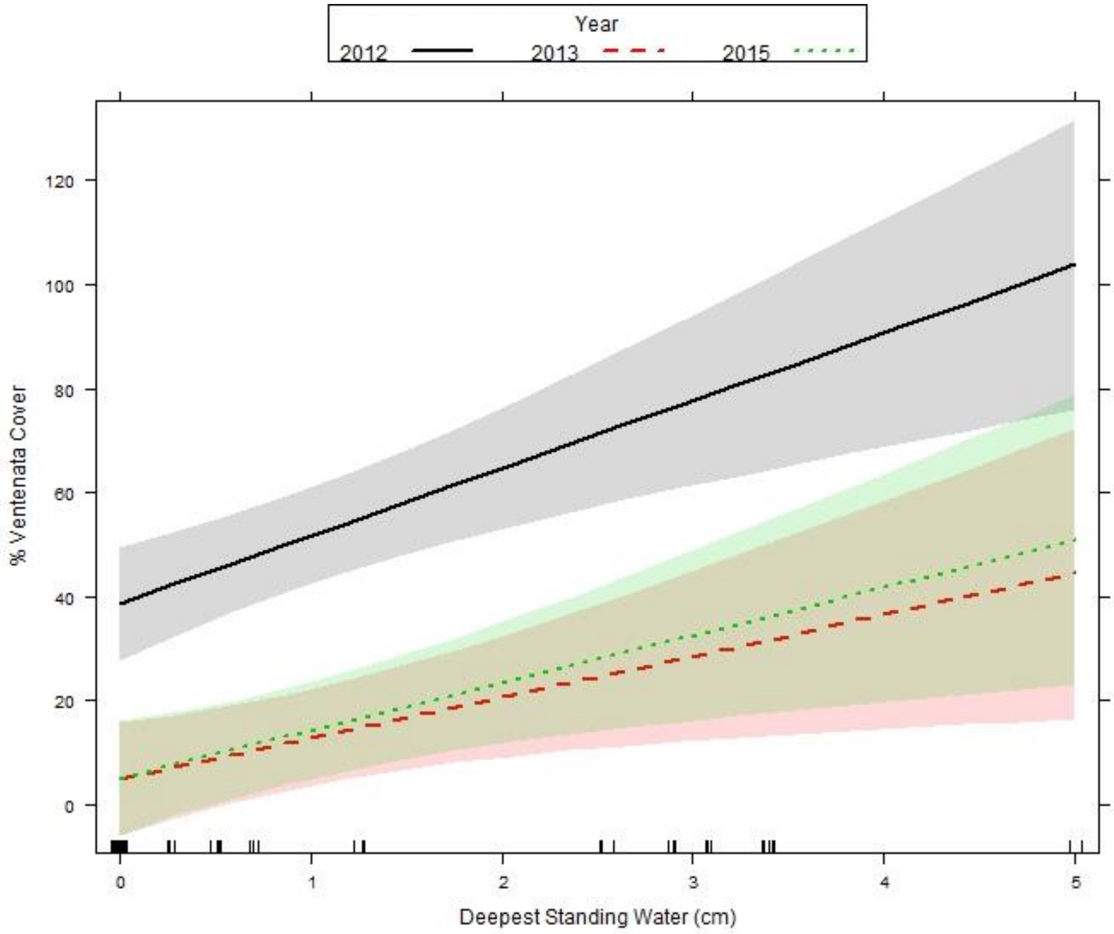

Figure 13. Relationship of standing water depth recorded in spring 2016 to *V. dubia* cover percent in 2012, 2013, and 2015 (p = .000131, R^2=.4732). Year is represented by color/line type. Shading around each line represents 95% confidence interval.

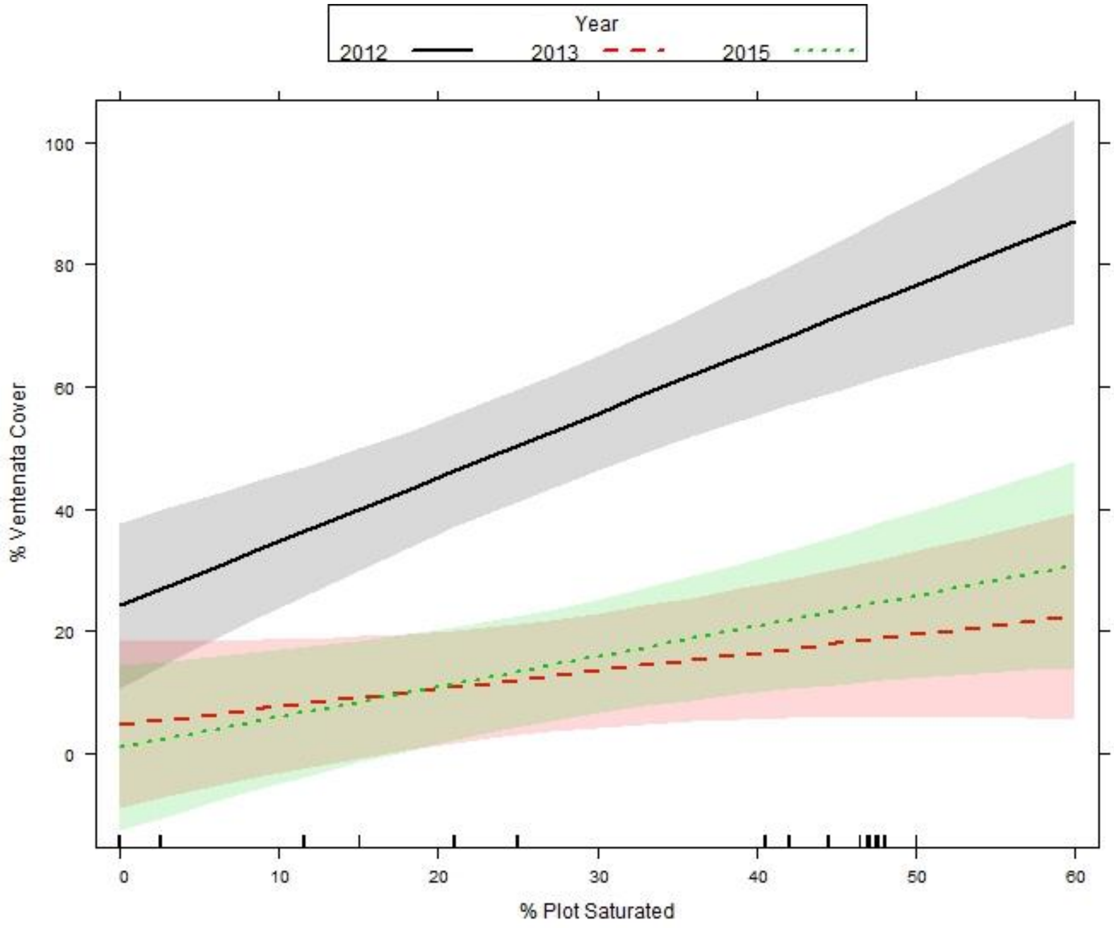

Figure 14. Relationship of saturation within plots recorded in spring 2016 to *V. dubia* cover percent in 2012, 2013, and 2015 ($p < .0001$, $R^2 = .50$). Year is represented by color/line type. Shading around each line represents 95% confidence interval.

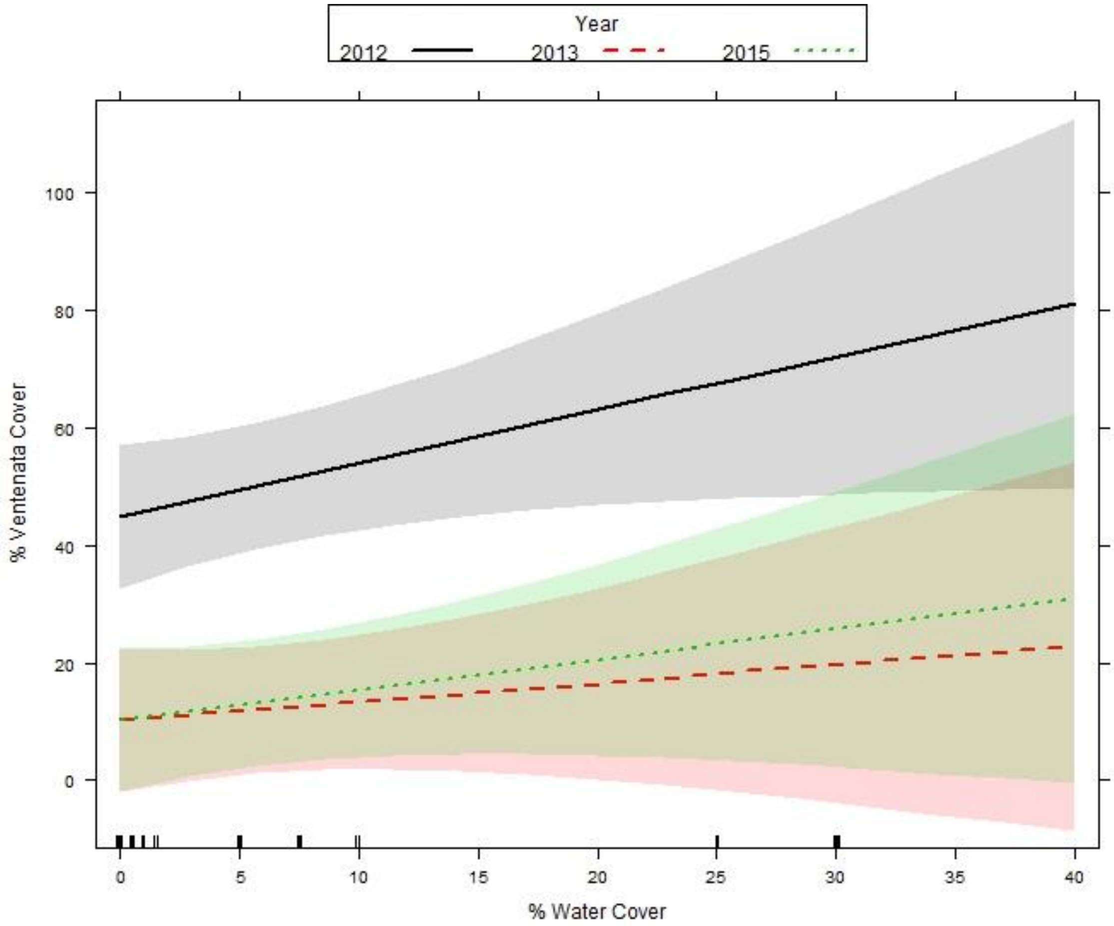

Figure 15. Relationship of percentage of water within plots recorded in spring 2016 to *V. dubia* cover percent in 2012, 2013, and 2015 ($p < .0001$, $R^2 = .50$). Year is represented by color/line type. Shading around each line represents 95% confidence interval.

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Conclusions and Management Recommendations

Both studies show that *B. tectorum* and *V. dubia* interact with biocrust differently and these relationships can change with environmental variables. The relationship between *B. tectorum* and biocrust became weaker with an increase in precipitation. While across the precipitation gradient biocrust and *V. dubia* exhibited a negative relationship, areas dominated by biocrust at Turnbull NWR were able to support high *V. dubia* abundances in certain years. At Turnbull it appears that timing of precipitation plays an even more important role in where and when *V. dubia* is more abundant.

With climate expecting to impact temperature and precipitation it is important to understand how these invasive species may respond. Warmer and drier summers may favor greater *B. tectorum* abundance in areas where it has been less prevalent. Maintaining an intact biocrust in these and other arid regions should be an important priority to decrease site susceptibility to invasion by *B. tectorum*. If precipitation is to shift to greater amounts in the spring, *V. dubia* may experience more years with higher abundances. Along with higher abundances of *V. dubia*, a loss in lichens may occur which highlights the importance of managing *V. dubia* around areas of lichen conservation.

More research is needed on *V. dubia*, particularly since it appears to behave differently that other invasive annual grasses and little is known about its interactions with its environment within its entire range. Additionally, the dynamic nature of its population at Turnbull points to the importance of completing long-term studies where yearly conditions can play a large role in abundances.

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