ENVIRONMENTAL EXTREMES DRIVE PLANT AND SOIL COMMUNITY DYNAMICS OF NATIVE AND DISTURBED GRASSLANDS

By

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Abstract: Environmental drivers such as precipitation and temperature are important predictors of changes in plant community composition. Anthropogenic disturbances also alter plant composition, often leading to the invasion by non-native plant species. Global climate change will lead to more extreme changes in environmental factors, therefore, it is important to understand how both native and disturbed plant communities will respond to rapid changes in important drivers like precipitation and temperature. We looked at the response of plant and soil community dynamics by conducting a greenhouse experiment and by modeling current plant community responses to the environment using field observations. Our greenhouse experiment examined the plant and soil feedback (PSF) response of both cool- and warm-season native and non-native grasses to elevated temperatures (ambient and +5° C) and drought (100% and 75% field capacity). We also used linear modeling and AICc weighted model averaging to determine the relationships between plant species richness and several environmental variables (annual precipitation, annual evapotranspiration, and annual mean, maximum, and minimum temperature) in both native and disturbed sites across an east-west gradient across the tallgrass prairie region. In the greenhouse study, we found that experimental increases in temperature and drought had a significant influence on the direction and strength of native and non-native PSF response compared the PSF response under ambient conditions. Our modeling data show significant linear correlations between plant species richness and temperature-related drivers in disturbed sites. However, linear models best explained plant species richness of native sites as precipitation, while results from AICc weighted model averaging indicated that the interaction between temperature and precipitation was the strongest driver of plant community composition. Understanding how climate drives plant community composition will become more urgent under climate change predictions, and our results suggest that future environmental models used to predict plant community changes should incorporate interacting terms. Our results also emphasize the importance of native plant influence on PSFs under warmer and dryer conditions in community resilience to non-native invasion.

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ABSTRACT

The plant-soil community feedback (PSF) framework allows researchers to target the interplay of plants and root-associated microbes and to determine the reciprocal effects of these interactions in biotic and abiotic contexts. The role of PSF in terrestrial ecology is well documented, but the strength and direction of PSFs as influenced by abiotic environmental factors, such as those predicted in current climate change scenarios, has yet to be fully explored in this important theoretical framework. Here we examined the PSF response of both cool- and warm-season native and non-native grasses to elevated temperatures (ambient and +5° C) and drought (100% and 75% field capacity). We found that experimental increases in temperature and drought had a significant influence on the direction and strength of native and non-native PSF response compared the PSF response under ambient conditions. Not in accordance with our predictions, PSF was driven primarily by differences of native plant growth, which benefitted the native under elevated temperatures and drought. We also found that these changes in PSF were not uniform across functional groups. Overall, our results

emphasize the importance of native plant influence on PSFs under warmer and dryer conditions in community resilience to non-native invasion.

INTRODUCTION

Biological diversity is a major driver of ecosystem productivity, stability, invasibility, and nutrient dynamics (Tilman et al., 2014). Therefore, it is important to understand the mechanisms that contribute to biological diversity. The interactions between plants and their soil microbial communities play a significant role in the maintenance of biodiversity. Microbial and fungal diversity can be especially important in the promotion of plant diversity in nutrient-poor environments and when there are higher levels of specification between plants and their associated fungal or microbial partners (van der Heijden et al., 2008; Wardle et al., 2004). Specifically, the symbiotic association of arbuscular mycorrhizal (AM) fungi with plant roots is an important driver of plant community diversity, as they form symbiotic association with about 80% of all terrestrial plant species (Smith & Read, 1997). A classic example of the importance of AM fungal diversity as a driver for plant diversity is a study of van der Heijden et al. (1998) which showed that plant diversity, nutrient capture, and productivity increase significantly with increasing AM fungal species richness. The interactions between plant species and their associated fungal partners is one mechanism that is likely to contribute to the maintenance of plant community diversity.

The interplay between plants and their associated soil, or plant-soil feedbacks (PSF), play an important role in the formation of plant communities (Kulmatiski et al., 2008; Mangan et al., 2010; Smith & Reynolds, 2015). Plant-soil feedback is the process whereby a plant influences the soil through root exudation, deposition and/or direct association with soil-borne microbial communities and the reciprocal influence of these microbes on the fitness of the plant itself, plus conspecific or heterospecific plants in the community (Bever et al. 2010). The direction of feedback can be either positive or negative, where fitness of the plant is increased or decreased, respectively. Coexistence is promoted when negative PSF occurs, creating or maintaining diverse plant communities, as the plant and associated soil community promote the growth of heterospecific plants over their own (Bever et al., 1997). Conversely, positive PSF occurs when the effects on the soil community promotes conspecifics over other species (Bever et al., 1997) which leads to a decrease in community diversity. Both biotic and abiotic factors can influence the strength and direction of PSF (Bever, 2002b; Ehrenfeld et al., 2005; Mangan et al., 2010; Smith & Reynolds, 2015). Previous research has shown that the promotion and accumulation of specific AM fungi with their associated plant species can result in negative PSF between competing plant species and their fungal partners, contributing to increased species coexistence (Bever, 2002b).

Previous research has shown that the presence of invasive plant species alters the density and composition of AM fungal communities, which may influence the feedback interactions that influences continued growth and establishment of both native and invasive species (Bever, 2002b; Reinhart & Callaway, 2006). This could potentially alter mutualistic interactions between the native plant and soil microbe communities, further influencing invasion. One way that invasive plant species have been shown to alter the soil communities are through reductions in the density of AM fungi. This can happen when the non-native plants' reduced dependence on native AM fungi, compared to native species, reduces the native soil community (Pringle et al., 2009). In California grasslands, it has been found that invasive plant species were less reliant on AM fungi, which reduced AM fungal densities and subsequently reduced native plant growth rates (Vogelsang & Bever, 2009). Alternatively, invasive species such as Old World Bluestems (e.g. *Bothriochloa spp.*) can be highly dependent on AM fungal species (Wilson & Hartnett, 1998) and can potentially disrupt the community though the alteration of the AM fungal identities. Indeed, competition by non-native *B. bladhii* resulted in reduced growth and AM colonization of native grasses (Wilson et al., 2012).

Alterations in soil microbial communities resulting from invasion of non-native grasses may further complicate grassland restoration efforts, and restoration of degraded soils may be advanced through restoration of native soil communities, particularly the AM fungal community. To assess potential effects of climate change on invasion dynamics, we conducted an experiment with the following objectives: 1) to assess the strength and direction of native and non-native grass PSFs under ambient conditions (well-watered and moderate temperatures) and 2) to assess the strength and direction of native and non-native grass PSFs under projected climate scenarios (drought conditions and elevated temperatures). We hypothesized that 1) soil alterations as a result of non-native species invasion will result in positive PSF under ambient conditions and 2) positive PSFs will be exacerbated under elevated temperatures and drought conditions, relative to ambient conditions. The expected exacerbation of positive PSFs under drought conditions and elevated temperatures are based on increases in non-native growth in elevated temperatures reported by Duell et al. (2016).

METHODS

Soil Collection: Native tallgrass prairie soil was collected from the Konza Prairie Biological Station, Manhattan, KS, USA. Soil was sieved through a 10mm sieve to remove non-soil material. Soil was then steam-pasteurized at 80 °C for 2 hours and transported to Oklahoma State University greenhouse facilities.

Inoculum Source: To assess the consequences of alterations in soil microbial communities, including AM fungal communities, soil inoculum was collected from a previous climate perturbation experiment (Duell et al. 2016) which investigated the effects of increased climate and drought on both native and non-native grasses. This experiment consisted of growing two warm-season grass species (one native [*Schizachyrium scoparium*] and one invasive [*Bothriochloa ischaemum*]) and two cool-season grass species (one native [*Pascopyrum smithii*] and one invasive [*Bromus inermis*])]) under two climatic regimes. Warm-season species were maintained at ambient (24° C) and elevated (29° C) temperatures and cool-season species were grown at ambient (17° C) and elevated temperatures (22° C). Temperature treatments were combined with two levels of soil moisture (field capacity and drought [35% less than field capacity]). Climate treatments were initiated following seedling establishment (Duell et al. 2016). The complete experimental design that produced our inoculum consisted of 6 treatment combinations: 4 plant species x 2 warming treatments x 2 drought treatments, arranged in a complete block design with 6 replications for a total of 96 pots.

Experimental Design: The experimental design of our current study was based on the feedback approach described in Bever (1994) with Duell et al. (2016) constituting the “training” portion of the study. Additionally, our study was separated into two components based on the differing photoperiods and temperature requirements of the selected warm- and cool-season grasses. Warm- and cool-season grasses were germinated in vermiculite. After 14-21 days (second-leaf stage) seedlings were transplanted into pots (6 cm diameter × 25 cm deep: DeePots; stuewe.com, Tangent, Oregon), filled with 600 g (dry wt) of soil partitioned into three layers: 400 g of steam-pasteurized soil, followed by 100 g of soil inoculum (see inoculum collection described above), followed by 100 g of steam-pasteurized soil to protect cross-contamination during the growing period.

One seedling was planted per pot and inoculated with soil conditioned by either the non-native or native grass that had been conditioned under all combinations of drought and temperature treatments in Duell et al. (2016) (described above). Seedlings were grown for 16 weeks. Our study consisted of a full factorial design with three factors (plant species, temperature, and soil moisture) each consisting of the two levels used in the initial experiment. In total, both the cool-season and warm-season experimental studies consisted of 392 pots (8 inocula x 2 plants x 2 temperature treatments x 2 soil moisture treatments x 6 replications + 8 sterile controls [no inoculum]), for a total of 784 pots.

Measurement and Harvest: After the 16-wk growing period the plants were harvested and roots were manually separated from soil. Soil was sub-sampled for soil analysis. Root and shoot biomass were collected and separated. Wet weights of roots were assessed and roots were sub-sampled and placed into a tissue cassette (Fisher

Scientific), submerged in water and stored until processed for AM fungal root colonization assessments. Shoots and remaining roots were dried at 70°C for 48 hours and weighed. Percent of roots colonized by AM fungi was assessed on sub-sampled roots. Roots were stained with trypan blue and scored for intra-radical AMF colonization using the magnified gridline intersect method (McGonigle et al., 1990). A digital microscope (200x) was used to measure the percentage of root length colonized by intra-radical hyphae, vesicles and arbuscules. All structures were combined for a total value of mycorrhizal colonization.

Statistical Analysis

Feedbacks were calculated for total biomass, aboveground biomass, root biomass, and percent AM fungal colonization. Using PROC-GLM in SAS we constructed a general linear model using log-transformed (for normalization of biomass data due to extreme values caused by drought) biomass and percent colonization as the dependent variables. Species identity, drought, and temperature treatments from the inoculum source and from the feedback study (6 total) were used as factors with all possible interactions. Analysis of the warm-season portion of the study was split by drought treatment due to low survival of water-limited warm-season plants and, therefore, only the well-watered plants were analyzed, resulting in a total of 5 factors (experimental temperature, experimental plants identity, soil temperature, soil watering treatment, soil plant identity) examined in the analysis. Feedback dynamics were detected using the "home vs. away" approach (Bever, 1994; Turkington & Harper, 1979), which assess pairwise comparisons between each plant identity in the current experiment and the soil legacy of both plants. For all significant pairwise interactions between current plant treatments and source treatments interaction coefficients were calculated using the formula (Eq. 1) described in Bever et al. (1997). Differences in biomass and colonization of plants under either watering or temperature treatments with significant feedback interactions were assessed using a two-way analysis of variance (ANOVA) and Tukey's Honest Significant Difference (HSD) in R version 3.2.3 (R Core Team, 2015). Biomass and colonization were analyzed using the PROC GLM procedure in (SAS Institute, Cary, NC, U.S.A.), version 9.4 of the SAS System for Windows.

RESULTS

Warm-season: In the drought assessment component of the warm-season experiment, we observed a significant PSF interaction between temperature of the source soil (inoculum) and the experimental temperature for root biomass ($p<0.05$) (figure 1) and a significant interaction in total biomass ($p=0.05$) (figure 2). Plants grown under ambient temperatures were characterized by slightly negative (ambient source soil) and neutral (elevated source soil) PSF, while elevated temperatures lead to both positive and negative PSF, depending on source temperature (figures 1 and 2). Ambient source temperature led to positive PSF and elevated source temperatures lead to stronger negative PSF, compared to any other combination of experimental temperature and source soil temperature. While there were strong negative feedbacks in both root and total biomass, under the elevated experimental temperature and elevated source soil interaction the feedback was slightly stronger for root biomass, as compared to the total biomass.

Strong negative PSF in root and total biomass under elevated temperatures with elevated source soil was driven by significantly more *S. scoparium* biomass production in

B. ischaemum source soil than soil collected from the congener; whereas no difference was observed in *B. ischaemum* production with soil from either plant species (figures 3 and 4). There were significant trends in total biomass for the warm-season grasses, however, no other significant differences in root biomass or total biomass between congeners in the other three temperature combinations of experimental temperature and soil source temperature [ambient/ambient (figures 5 and 6), ambient/elevated (figures 7 and 8), elevated/ambient (figures 9 and 10)] were observed.

Cool-season: In the cool-season component of this experiment, there was a significant interaction between the temperature of the source soil and the experimental drought treatment for percent AM fungal colonization (figure 11) in each host plant. The combination of soil from ambient temperatures and experimental well-watered conditions led to a positive interaction, while the combination of soil from elevated temperatures and well-watered conditions led to a negative interaction (figure 11). Soil collected from plants grown under well-watered conditions inoculated with source soil collected from plants grown under ambient temperature led to a positive interaction, while soil collected from elevated temperatures resulted in a negative interaction. The opposite trend occurred under experimental drought conditions with a negative interaction occurring with soil from ambient temperature and a positive interaction occurring with soil from elevated temperature (figure 11).

The positive interaction observed under experimental well-watered conditions with soil from ambient temperature were the result of a marginally significant (p=.0935) promotion of *P. smithii* colonization in congener sourced soil (figure 12). However, no difference in colonization was observed between *B. inermis* grown in soil from *P. smithii* and in soil from *B. inermis* (figure 12). The positive interaction observed under experimental drought conditions with soil from elevated temperature were the result of a significant ($p<0.05$) decrease in *B. inermis* colonization in soil from *P. smithii*, compared to similar colonization of *P. smithii* in both soil from its congener and soil from *B. inermis* (figure 13). There were no significant differences in colonization under well-watered treatment with soil from elevated temperature (figure 14) or under experimental drought conditions with soil from ambient temperatures (figure 15).

DISCUSSION

Plant and soil feedbacks play a large role in the development and diversity of plant communities with negative feedbacks promoting plant diversity and positive feedbacks leading to losses in diversity (Bever et al., 2010). Additionally, alterations to the soil microbial community and their associated process are predicted to have strong impacts on plant community and ecosystem reactions to environmental change (Singh et al., 2010). Mutualistic associations with mycorrhizal fungi help to shape the strength and direction of these feedbacks, and are also impacted by anthropogenic environmental changes. Plant associations with mycorrhizal fungi can substantially reduce the plant's resource needs, effectively reducing that plants R*, which influences the outcomes of competitive interactions with other plants (Van Der Heijden, 2002). In a warmer, dryer world, the associations with beneficial mycorrhizal fungi can effectively reduce plant requirement for water, which in turn impacts overall plant and soil feedbacks within the system. Feedback interactions then have the potential to have more influence in scenarios predicting reductions in water availability. Our results suggest that predicted climate environmental extremes (Pachauri et al., 2014) will have the most significant and strongest impacts on the feedback dynamics of native and non-native grasses in warm-season grasslands and impact local adaptation of fungal interactions in cool-season grasslands.

There is increasing evidence that a rapidly changing climate will impact mycorrhizal communities (Drigo et al., 2008; Johnson et al., 2013; Rillig et al., 2002; Singh et al., 2010), which will in turn impact microbial feedback dynamics. However, little is known about importance or direction of these feedback responses to global change (Johnson et al., 2013; Singh et al., 2010). We know that abiotic factors, such as light availability, can influence the strength and direction of feedback interactions (Smith & Reynolds, 2015), but it is not known how changes in environmental drivers such as precipitation and temperature will also alter the strength and direction of plant and soil feedback interactions. We found that elevated temperatures, combined with a soil legacy of elevated temperatures, lead to strongly negative PSF between native and non-native warm-season grasses. This was in contrast to the slightly negative to positive feedback exhibited in other experimental temperature and altered temperature soil legacy combinations. However, this pattern was not consistent in the PSF of native and non-native cool-season grasses; we did not find significant PSF in plant biomass, but rather found that environmental drivers influenced the strength of local adaptation of mycorrhizal fungi to their host plant. Our findings suggest that changes in environmental drivers will impact the strength and direction of PSFs and that these changes will also impact the interactions of plants and their associated mycorrhizae. The differences in observed PSF under these conditions between the cool- and warm- season studies also shows that the impact of these drivers will depend on the identity of the species.

Despite our hypothesis that increases in temperatures and reduction in water-availability would result in strong positive feedbacks, we found the opposite occurred. Our hypothesis was based on a combination of observations that non-native *B. ischeaemum* currently invades into grasslands, and Duell et al. (2016) reported elevated temperatures led to increases in the non-native's growth. Additionally Greer et al. (2014) reported exudation of allelopathic chemicals for *B. ischeaemum*, and these allelopathic chemicals can restrict growth of both conspecifics and heterospecifics. The presence of allelopathic chemicals could potentially contribute to the observed negative feedbacks if the negative effects of the allelopathy inhibited congener growth more than the native grass' growth. If this were driving the PSF, we would expect a decrease in biomass in *B. ischaemum* in its own soil compared to when grown in native soil.

However, we observed the alternative scenario, in that the biomass of the non-native was not influenced, while the biomass of *S. scoparium* was greater in non-native soil compared to when grown in congener soil. While we do not suggest that the non-native soil generally promotes native growth, we propose that these results may be contributed to two mechanisms. The first mechanism is that the changes in the AM fungal community contributed to the negative PSF observed (Bever, 2002a). Changes to the fungal community were more pronounced due to the greater growth of the non-native grass relative to the native grass in Duell et al. (2016) (the source of our inoculum) under elevated temperatures. Warm-season grasses, such as *B. ischaemum*, readily associate with AM fungi (Wilson & Hartnett, 1998) and can have impacts on the soil community. Native *S. scoparium* might have taken advantage of the changes in the fungal community composition more effectively than the non-native species.

Alternatively, the accumulation of host specific pathogens could explain the increase in *S. scoparium* biomass in *B. ischaemum* soil in elevated temperatures with soil from elevated temperature. Plants in their native communities can accumulate host specific pathogens that contribute to negative feedback and to community succession (Bauer et al., 2015; Mills & Bever, 1998). These host specific pathogens inhibit the growth of the host paving the way for colonization of other plant species. The release of *S. scoparium* from its host specific pathogens would also result in the increase in *S. scoparium* growth in the non-native soil that lead to the observed negative PSF. Either mechanism indicates that the native is able to utilize soil communities altered by the non-native, relative to the non-native grass, under elevated temperatures or following a soil legacy of elevated temperatures.

In the cool-season study, we did not find significant feedbacks in biomass production, but our analysis revealed evidence for changes in local adaptation of AM fungi to the non-native *B. inermis* resulting from combinations of soil temperature conditions and experimental drought conditions. We know that host plants play an active role in the formation of AM fungal communities (Ji et al., 2013). Here we saw that mycorrhizal root colonization was lower in *B. inermis* in heterospecific soil under drought conditions and soil from elevated temperature, showing that the fungal community from the *B. inermis* was better able to colonize it's congener than the fungal community from *P. smithii*. This suggests increased reliance on a locally adapted soil community for *B. inermis* under these extreme conditions. While mycorrhizal colonization does not necessarily indicate fitness, our results indicate that under extreme conditions the influence of native conditioned soil may become more important in resisting invasion because of the non-native's increased reliance on having locally adapted AM fungi available.

In both studies there is a common thread, which emphasizes the importance of native plant presence under extreme conditions. In both scenarios the influence of native soil became more important in either the promotion of natives or in decreases in mycorrhizal colonization of non-native species. In the warm-season study, under elevated temperatures native plants better utilized non-native soil communities conditioned under elevated temperatures than the non-native. In the cool-season study extreme conditions lead to the decreased mycorrhizal colonization of the non-native in native soil, which suggests that the non-native will become increasingly reliant on locally adapted fungi. There is already a wealth of knowledge on the stability of native plant communities against invasion (Fargione & Tilman, 2005; Tilman, 1997, 1999). Our findings suggest that the presence of native plant communities will only become more important in inhibiting non-native invasion under extreme conditions. We suspect that the presence of native plants will have a greater influence on the inhibition of non-native growth and establishment under predicted climate change scenarios. Unfortunately, we have seen that in grassland ecosystems consistent climatic drying has lead to a decrease in plant diversity, particularly impacting wildflower species (Harrison et al., 2015) Considering this, our research only emphasizes the importance of incorporating native plug and seed management strategies into non-native plant eradication efforts.

CONCLUSION

In sum, we have shown that changing environmental drivers influences PSF, but that this will depend on the plant community in question. Our results support the idea that the influence of native plants will become more important under extreme conditions caused by anthropogenic environmental changes. While this research does make valuable contributions toward understanding the impacts of climate change on PSF, our conclusions were based on pairwise interactions between specific native and non-native grasses. These are often dominant grasses in their respective ranges, but this greenhouse study only gives a glimpse of the feedback dynamics taking place in the field. Just as in experiments directly addressing competitive interactions, it becomes more difficult to accurately quantify interactions with every additional species added. We suggest that mesocosm studies, involving communities of native plants, designed with the same feedback approach will be valuable in that they will provide a better picture of the broader changes in PSF dynamics with changing climatic drivers.

CHAPTER II

VARYING UTILITY OF ENVIRONMENTAL ATTRIBUTES AS PREDICTORS OF PLANT SPECIES RICHNESS BETWEEN NATIVE AND DISTURBED GRASSLANDS

ABSTRACT

Environmental drivers such as precipitation and temperature are important predictors of changes in plant community composition. Anthropogenic disturbances also alter plant composition, often leading to invasion by non-native plant species. Global climate change will lead to more extreme changes in environmental factors, therefore, it is important to understand how both native and disturbed communities will respond to rapid changes in important drivers like precipitation and temperature. We used linear modeling and AICc weighted model building to determine the relationships among plant species richness and several environmental variables (annual precipitation, annual evapotranspiration, and annual mean, maximum, and minimum temperature) in both native and disturbed sites across an east-west gradient across the Tallgrass prairie region. Our data show significant linear correlations between plant species richness and temperature-related drivers in disturbed sites. However, linear models best explained plant species richness of native sites as precipitation, while results for AICc weighted model building indicated more complex models best explained native site plant species

richness. Understanding how climate drives plant community composition will become more urgent under climate change predictions, and our results suggest that future environmental models used to predict plant community changes should incorporate interacting terms, especially when predicting changes of later successional communities.

INTRODUCTION

Variations in plant diversity are often seen along spatial and environmental gradients. One pattern that is well known is the latitudinal gradient of biodiversity, with species richness being greatest at the equator and falling with increasing latitude (Gaston, 2000). There are many theories that aim to explain this increase of species richness with increasing latitude, but often these theories rely on limited numbers of targeted organisms and explain only specific mechanisms; no one theory has been able to explain this pattern (Hillebrand, 2004). Increasing species diversity can also depend environmental gradients such as precipitation or soil-moisture gradients. Specifically, environmental properties such as soil moisture have been found to be key drivers of plant community composition (Roux et al., 2013). Precipitation and evapotranspiration rates drive many aspects that determine plant community composition. Additionally, mean annual precipitation has a strong and direct correlation with annual net primary production (ANPP) and is positively correlated with species richness, with rare species driving these trends (Cleland et al., 2013; Hsu et al., 2012). Future predictions of increased variation in precipitation events and of warmer and drier climates (Cook et al., 2014; Schwalm et al., 2012) will impact how these environmental drivers influence vegetation dynamics. Drier, more xeric areas will be more sensitive to variations in these climactic drivers (Cleland et al. 2013), whereas mesic grasslands have been shown to be more resilient to variation in moisture availability (Derner et al., 2011).

Losses in plant species richness that result from decreased mean annual precipitation and increased inter-annual variation in precipitation are documented to have direct correlations with ecosystem processes such as ANPP and decomposition rates that are nearly equivalent to or greater than other environmental drivers such as elevated CO2 levels and ultraviolet radiation (Hooper et al., 2012). Hector et al. (2010) showed that the biodiversity of grasslands have a stabilizing effect on the temporal variability of the aboveground ANPP. In addition to the benefits to associated fauna, the level of biodiversity in an ecosystem can also influence the ecosystems' resilience and resistance to invasion. Reductions in species richness and diversity can further accelerate invasion in vulnerable ecosystems (Fargione & Tilman, 2005; Fridley et al., 2007). As well as influencing ecosystem processes, greater species richness has been shown to confer greater community stability and resilience to invasion in both remnant and post-agricultural restored ecosystems (Foster et al., 2015; Tilman et al., 2014) with few exceptions at larger scales and with other covarying factors impacting invasion (Levine, 2000; Stohlgren et al., 2003; Stohlgren et al., 1999).

The functioning and sustainability of ecosystems are threatened through disturbances that increase invasibility (Burke & Grime, 1996; Hobbs & Huenneke, 1992; Naeem et al., 2000; Tilman, 1999). In grasslands specifically, invasion by non-native species is one of the major causes of native rangeland loss (Watkinson & Omerod, 2001). Compounding the impacts of disturbances on the invasibility of an ecosystem, projected changes in climate are expected to increase rates of invasion in the future (Diez et al., 2012). Other environmental properties can also influence the susceptibility of a community to non-native plant invasion as well. There is evidence that more stressful environments are less invaded than more moderate ones (Zefferman et al., 2015) presumably due to either lack of propagule pressure or the harsh abiotic factors in the environment. Stohlgren et al. (2002) has shown in large-scale studies that invasion was more strongly correlated with conditions favoring overall plant growth and is less correlated with native species abundance. Conversely in a long-term total stand replacement event, invasive plants dominated in warmer and drier sites than more moderate, wetter areas (Dodson & Root, 2015).

With such a strong tie between soil moisture, or mean annual precipitation, and native species richness, it is important to investigate the influence of environmental conditions on plant species richness in post-disturbed areas as well. If disturbance does alter the precipitation-richness correlation, we predict that there will be a greater disparity between native and disturbed sites in more moderate climates, which could impact how we focus on future management efforts in light of predicted regional climate change scenarios. With varying evidence on the influence on harsher, drier environments on invasion, it is clear that there is more need for exploration into the influence of environmental conditions in post-disturbance communities.

The primary objective of this study was to investigate plant community diversity, as determined by plant species richness, among intact remnant grasslands with high floristic quality, and grasslands dominated by non-native species across a west to east gradient with increasing precipitation, evapotranspiration, and decreasing average temperatures. Additionally, we assessed plant species richness in disturbed sites and undisturbed or native sites and investigated potential relationships between plant species richness and several environmental variables. Specifically, we hypothesized 1) grasslands experiencing greater average annual precipitation and cooler temperatures exhibit greater plant species richness, compared to grasslands receiving less annual precipitation and warmer temperatures, and that this greater richness will be driven by an increase in C_3 forbs (Jones et al., 2016) in combination with lower moisture availability; and 2) there are tighter correlations between environmental variables and plant species richness in native sites compared to disturbed sites; and 3) differences in richness and diversity between native and disturbed sites will be greatest in areas receiving greater precipitation because while native grasslands increase in species richness as precipitation increases, the same may not be true of disturbed areas facing invasion because the impacts of invasion might outweigh environmental influences.

METHODS

To evaluate plant species composition of native and disturbed grasslands along a longitudinal precipitation gradient we selected high-quality native and nearby disturbed grassland sites throughout Oklahoma, Kansas, Missouri, and Illinois (Table 1). Analyses were conducted in the summers of 2013 and 2015. The quality of the native and disturbed sites was determined through personal communication with local landowners or conservation officials. In the summer of 2013 the plant communities of four non-native disturbed sites were compared to three adjacent undisturbed remnant grassland sites. These field surveys were conducted in or near three military bases across the Midwestern United States: Chanute Air Force Base, IL; Fort Riley, KS; and Tinker Air Force Base, OK. In 2015, additional sites were added to the dataset to increase representation of the east-west precipitation gradient. There were a total of 19 native/remnant sites and 16 disturbed sites. Native and disturbed sites were paired logistically across the gradient (figure 1).

At each site we established replicate randomly located 1m^2 plots in native and adjacent disturbed areas (see Table 1). Plot replication varied among sites due to size of the site. Plant species composition was assessed for each replicate plot using the point-intercept sampling method (Middleton et al., 2010). Vegetation composition was assessed within each 1m^2 plot consisting of 60 intercepts arranged in a diagonal grid within the plot. Plant species occurrence and abundance at each intercept was sampled by dropping a 1m long metal stake. Each plant species' presence under the grid was recorded and each species that touched the stake was identified and the number of times that plant species touched the stake was recorded. In addition to the 1m^2 plots, 30m walking transects that were spaced at least 20 meters apart were performed. At each walking transect, species occurrence in a 0.25m radius was recorded. For each site mean annual precipitation (cm) [referred in tables as P]; maximum [MaT], mean [MeT], and minimum [MiT] temperatures (C°) were obtained the PRISM dataset (PRISM Climate Group). Annual estimates were based on 30-year normal from 1981-2010. Site evapotranspiration [ET] was calculated from PRISM variables with the equation described in Sanford and Selnick (2013).

Data Analysis

Unless otherwise indicated, all data analysis was performed in R v. 3.2.3 (R Core Team 2015). Data collected from walking transects were used to calculate plant species richness at each site. Data collected from the point intercept method were used to calculate plant species abundance (total number of touches of a species in each plot) and plant species richness. Plant species richness for each site was calculated using the VEGAN package in R software. Average richness was calculated by combining richness calculations for all plots within a site. Site plant species richness-environmental relationships were analyzed using a linear model for each environmental predictor. Linear relationships for native and disturbed sites were analyzed separately and together, with site history as an additional predictor.

In addition to linear models, we also used an information-theoretic approach (Anderson & Burnham, 2002) to determine the effects of each environmental variable on species richness. Models were generated separately for disturbed sites and native sites. For each group of data, we first fitted a global linear model using the GLM function in R. The global models included only environmental variables that were significantly correlated with species richness in the linear models. To generate a full set of models, we used the dredge function in the MuMIn package package (Barton, 2015). Each of the models generated were ranked using Akaike's Information Criterion corrected (AICc) for small sample size. Models with a ΔAICc less than 2 indicated near equivalent significance as $p < 0.05$ (Murtaugh, 2014) from the highest ranked model.

RESULTS

Linear Regression Analysis: Linear regressions of the average site plant species richness of all sites combined showed a strong correlation to site history (disturbed or native), which masked the effects of all environmental variables ($r^2 = .60$, $p<0.0001$).

Because of this, further linear model analysis was separated by site history. Linear regressions of average site plant species richness against each environmental variable showed that richness was most strongly positively correlated with average annual precipitation (see figure 2, $p < 0.001$) and weakly negatively correlated with annual maximum temperature (see figure 3, $p<0.05$). Linear regressions of disturbed site plant species richness against each environmental variable revealed a significantly negative correlation with maximum temperature (see figure 3, $p<0.05$).

To compare the influence of environmental variables in disturbed and native sites along the gradient we compared the r^2 of each linear regression. Greater dissimilarity of r^2 values indicate more influence of the environmental variable. For mean annual precipitation (cm) there was a significant correlation with average native site plant species richness, while disturbed site plant species richness was not significantly correlated. Both r^2 values are in the same direction and the s r^2 of the native site plant species richness was 0.34 greater than the r^2 for the disturbed sites (see figure 2). Both native and disturbed site plant species richness were significantly correlated with annual maximum temperature, but had nearly identical negative r^2 (figure 3). Annual mean temperature (figure 4), annual minimum temperature (figure 5), and annual evapotranspiration (figure 6) were not significantly correlated with average richness in either disturbed or native sites. However, for both temperature parameters the slope of the disturbed site plant species richness was slightly greater than the slope of the native site plant species richness and the slope of the native average richness was slightly greater than the essentially non-existent slope of the disturbed site plant species richness.

Model Generation: Annual maximum temperature and annual precipitation were the only environmental variables that showed a significant relationship with average richness, so only these were kept for model generation. Model generation resulted in only one top model for both native (table 2) and disturbed (table 3) site plant species richness. All other models were not within 2 ΔAICc of the top model, which conveys a likelihood similar to a p-value of <0.05 (Murtaugh, 2014) that the models within this range are as predictive as the top model. The top model for native sites included both maximum temperature and annual precipitation. The top model for the disturbed sites was annual maximum temperature, which confirmed our linear modeling results.

DISCUSSION

Linear modeling: Current predictions of climate change include extreme alterations in both precipitation and temperature (Pachauri et al., 2014), resulting in disruptions of current plant communities. For example, throughout the grasslands of North America, climate change is expected drive alterations in geographical distribution and composition of rangeland vegetation, including an increase in exotic species (Polley et al., 2013). The response of rangeland ANPP to climate change drivers, such as changes in precipitation and temperature, are directly influenced by feedbacks from changes in the plant community (Polley et al., 2014). Understanding how our current environmental gradients correspond with community traits such as plant species richness is essential in predicting the impacts of climate-driven changes on future plant community dynamics and our linear models suggest that native and disturbed site plant species richness are each influenced by different environmental gradients.

Mean annual precipitation was strongly positively correlated with average native site plant species richness (figure 2), but not richness in disturbed sites. The positive relationship between native site plant species richness and precipitation coincides with previous research showing increased C_3 forb presence with increased precipitation (Jones et al., 2016) and decreases in grassland plant diversity as a response to decreased annual precipitation (Harrison et al., 2015). Additionally, the difference in r^2 values between the two regression lines (figure 2) indicate that there was a greater difference in plant species richness between native and disturbed sites on the more mesic end of the precipitation gradient, compared to the dryer end. Stohlgren et al. (2005) suggests that native presence is a strong predictor of non-native plant presence, but also that biotic, rather than anthropogenic or environmental factors, have far greater influence on both native and non-native plant presence. We suspect that the differences observed in our data are the result the biotic influence of invasion in almost all disturbed sites, presumably due to a stronger influence on site plant species richness, compared to precipitation. In addition to precipitation, we predicted that additional environmental gradients (e.g. temperature and evapotranspiration) would be strong predictors of native site plant species richness. Despite the observation of a strong positive correlation between native site plant species richness and precipitation, our linear models did not indicate that any other environmental driver had a strong relationship to native site plant species richness. Annual maximum temperature was also a significant predictor of native site plant species richness, but only a weakly negative correlation was observed (figure 3).

Although precipitation was not a significant predictor of disturbed site plant species richness in our linear models, annual maximum temperature was a significant predictor of disturbed site plant species richness (figure 3). Previous studies have reported warming to have negative effects on aspect of plant community richness in the presence of invasion, but not in native communities lacking invasion (Gornish & Miller, 2015). In two studies of California grasslands (Pfeifer‐Meister et al., 2015; Sandel & Dangremond, 2012), increasing temperatures were found to be responsible for increased exotic richness and an increase in annual invasions. The lack of plant species richness in warmer disturbed sites seen in our results potentially indicates that invasion success was greater in these areas, compared to cooler disturbed areas, providing supporting evidence for the tie between increasing annual temperatures and increased invasion success.

There was a slightly negative association between native site plant species richness and annual maximum temperature, inferring that there is an interaction between the influence of regional native site plant species richness and annual maximum temperatures. Species rich areas tend to be more resistant to invasion (Tilman, 1997) and a lack of local species richness can accelerate invasion (Fridley et al., 2007) while the establishment and success of invaders is reduced with increases in local species diversity (Kennedy et al., 2002). It might be reasonable to assume that if the effects of plant species richness and annual maximum temperature are working concurrently to influence invasion, then plant communities in warmer climates could be more susceptible to post-disturbance invasion because of already lower plant species richness and the promotion of invasive plants by warmer temperatures.

Model Building: The impacts of climate change include simultaneous changes in multiple environmental variables (Pachauri et al., 2014). Therefore, it is important to look at these changes not only individually, but also to incorporate models that include multiple environmental drivers and the interactions between them. Because the relationships between environmental drivers and plant communities are not always predictable with a single predictor, there has been a greater recognition of the need to understand the interactive effects of many environmental drivers in plant community dynamics (Ehrlén et al., 2016). The results of our model testing using AICc (table 2) values produced a better fitting model than the linear modeling for native site plant species richness ($r^2 = 0.58$, $p < 0.001$) that included both precipitation and temperature, but only confirmed our results from the linear models for disturbed site plant species richness (see table 3 and figure 3). This suggests that the best fitting model for explaining native site plant species richness involves multiple predictors and does not hold true in disturbed areas.

Annual precipitation occurred as a parameter in the top model predicting native site plant species richness, but alone was not as significant (ΔAICc > 2) of a predictive model as the top model which indicates that the combination of temperature and precipitation drive plant community richness trends to a greater extent than precipitation alone. While there is sufficient evidence of the influence of precipitation alone on plant community composition (Hsu et al., 2012), there are knowledge gaps in our understanding of the interactive effects of multiple climate drivers (Polley et al., 2013). Our findings provide evidence that, while precipitation has an important impact on plant communities, the interactive effects of multiple climate factors have more of an influence on plant species richness then either climate driver alone. In the case of disturbed site plant species richness, where the results of model building confirmed our linear modeling results, these methods elucidated information that would not have been otherwise gleaned from linear modeling alone. We were able to observe that not only do disturbed areas respond to different climate drivers (temperature vs. precipitation) than native plant communities, but that the interactive effects of climate drivers do not have the same influence in these areas as they do in native areas. Interactions between invasion and warming can contribute to shifts in community composition in grasslands (Shi et al., 2015) and our results indicate that drivers related to temperature are primarily influencing disturbed site plant species richness.

Overall, the results from both the linear models and AICc weighted models indicate that richness of disturbed areas tend to have a direct response to temperature, while richness in native and remnant grasslands are the product of not just precipitation, but also the interaction of precipitation with temperature. The increase in the complexity of the top model explaining species richness from disturbed to remnant sites and the much higher AICc scores for the native site top model could be explained by considering the differing successional time scales associated with each plant community. Abiotic factors can be more important for species composition in early successional stages (Zhang et al., 2015), while in later successional stages biotic factors become more influential due to increasingly complex filter effects (Wiström & Nielsen, 2016). Since most of our remnant sites were at later successional stages, biotic factors are expected to be strongly linked to plant community richness in these sites, as microbial-mediated plant and soil feedbacks have been shown to be drivers of succession and community diversity (Bauer et al., 2015) and that these feedbacks contribute to large scale differences in community diversity observed along environmental gradients (Reynolds et al., 2003). The consideration of the interaction between these types of biotic drivers (e.g. microbial community composition and plant-soil feedback) and abiotic environmental drivers (e.g. temperature and precipitation) are essential in further development of more accurate predictive models of plant community composition under global climate change scenarios.

CONCLUSION

We have elucidated the importance of assessing environmental drivers both individually and together, but our selection of variables is by no means comprehensive. We suspect that the inclusion of local biotic (such as microbial community composition; plant phenology) and abiotic factors (i.e. nutrient availability), as well as the interactions between these biotic and abiotic factors with climatic drivers (i.e. annual precipitation and temperature) will serve to account for more of the variation present in our data. There are many forces acting concurrently to shape plant communities; therefore, it is essential to assess multiple drivers acting simultaneously to develop the most accurate model. Our research shows the importance of examining the predictive power of environmental variables both individually and interactively and how these influence both native areas and those that have experienced disturbance.

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APPENDICES

TABLES

CHAPTER II

Table 1. Site locations, sampling information, and site information. For disturbed sites site information includes dominant invasive plants (if applicable) and type of disturbance. For native sites, information includes type of remnant and any current management techniques (e.g. burning, grazing, or haying).

Marvin-Klemme Range Research Station Bessie, OK		Hays, KS	
2015	2015	2015	2015
8	8	8	8
Native	Disturbed	Native	Disturbed
Remnant, grazed	Invaded by *Bothriochloa spp.* and grazed	Remnant, burned and historically grazed	Invaded by *Bothriochloa spp.* and grazed
35° 25' 11.11" N	35° 23' 42.27" N	38° 51' 24.56" N	38° 51' 26.19" N
099° 03' 18.21" W	099° 03' 47.81" W	099° 22' 50.98" W	099° 23' 23.13" W

Ft. Riley, KS		Range Research Station, Stillwater, OK		Tinker AFB, Midwest City, OK	
2013	2013	2015	2015	2013	2013
12	12	8	8	12	12
Disturbed	Native	Native	Disturbed	Disturbed	Native
Tank training area, dominated by *B. inermis*	Remnant, burned	Remnant, burned and grazed	Invaded by *Bothriochloa spp*., currently grazed	Artificial pond fill, dominated by *Bothriochola spp*.	Remnant, burned
39° 08' 00.98" N	39° 07' 34.88" N	36° 03' 53.49" N	36° 03' 34.53" N	35° 25' 12.51" N	35° 25' 12.56" N
096° 34' 22.34" W	096° 36' 06.76" W	097° 14' 20.53" W	097° 14' 18.40" W	097° 23' 30.82" W	097° 23' 30.58" W

KU Field Station, Lawrence, KS	Rockefeller Native Prairie, Lawrence, KS	Welda, KS		Konza Prairie, Manhattan, KS		
2015	2015	2015	2015	2015	2015	2013
4	4	4	4	8	8	12
Disturbed	Native	Native	Disturbed	Native	Disturbed	Disturbed
Invaded by *B. inermis* and *F. arundinaceae*	Remnant, burned	Remnant, hayed	Old Field, *F. arundinaceae* dominated	Remnant, burned	Invaded by *Bothriochloa spp*.	Tank training area, dominated by *Bothriochloa spp*.
39° 03' 05.13" N	39° 02' 42.91" N	38° 10' 51.55" N	38° 10' 30.64" N	39° 04' 29.16" N	39° 06' 04.70" N	39° 09' 51.23" N
095° 11' 29.06" W	095° 12' 18.57" W	095° 15' 54.88" W	095° 16' 24.29" W	096° 34' 29.34" W	096° 36' 38.46" W	096° 31' 32.74" W

Morris Prairie, Sullivan Co., MO	Taberville Prairie, El Dorado, MO		Wah-Kon-Tah Prairie, El Dorado, MO		Osage Prairie, Nevada, MO	
2015	2015	2015	2015	2015	2015	2015
8	2	2	2	2	4	4
Disturbed	Native	Disturbed	Native	Disturbed	Native	Disturbed
Previously grazed, *F. arundinaceae* invaded	Remnant, burned and grazed	Post Tillage-Old Field, *F. arundinaceae* dominated	Remnant, burned	*F. arundinaceae* invaded	Remnant, historically grazed and hayed	Post Tillage-Old Field, *F. arundinaceae* dominated
40° 23' 00.99" N	38° 03' 23.78" N	38° 02' 15.03" N	37° 55' 05.00" N	37° 55' 07.50" N	37° 44' 33.63" N	37° 44' 33.63" N
092° 56' 20.13" W	093° 57' 59.04" W	093° 57' 59.59" W	094° 00' 23.41" W	094° 00' 27.48" W	094° 19' 49.76" W	094° 19' 49.76" W

Paxton Railroad Prairie, Paxton, IL	Roadside near Paxton, IL	Chanute AFB, Rantoul, IL	Goose Lake Prairie Nature Preserve, Morris, IL	Weston Cemetery Prairie Nature Preserve, Chenoa, IL	
2013	2015	2013	2015	2015	2015
2	4	12	2	2	8
Native	Disturbed	Disturbed	Native	Native	Native
Abandoned railroad remnant, burned	Dominated by *B. inermis*, Roadside near agricultural field	Previous landfill, dominated by *F. arundinaceae*	Historically grazed remnant, burned	Historically grazed remnant, burned	Remnant, burned
40° 15' 42.53" N	40° 27' 43.07" N	40° 10' 15.59" N	41° 21' 48.18" N	40° 44' 47.67" N	40° 23' 00.09" N
088° 03' 49.44" W	088° 03' 31.01" W	088° 04' 45.80" W	088° 18' 37.32" W	088° 36' 53.86" W	092° 56' 26.92" W

Location	Sunbury Railroad Praire Nature Preserve, Ransom, IL	Pellsville Cemetery Prairie, Rankin, IL	Shortline Railroad Prairie, Gifford, IL	Loda Prairie, Loda IL
Year sampled	2015	2013	2013	2013
No. plots sampled	2	4	2	4
Invasion status	Native	Native	Native	Native
Land Use History	Abandoned railroad remnant, burned	Cemetery remnant, burned	Abandoned railroad remnant, burned	Remnant, burned
Latitude	41° 05' 05.70" N	40° 16' 35.58" N	40° 11' 00.47" N	40° 18' 58.58" N
Longitude	088° 36' 16.28" W	087° 33' 16.90" W	087° 35' 49.47" W	088° 02' 42.71" W

Table 2. Models predicting average site plant species richness for native sites. The best model and 2 candidates within 2 AICc units of the best model are presented. The Akaike weights (w_i) represent the relative likelihoods of each model being the best model.

Model Number	**Intercept**	**Temperature Coefficient**	**Precipitation Coefficient**	**AICc**	**ΔAICc**	**w_i**
1	12.088	-1.020	0.265	123.332	0	0.810
2	-8.469	-	0.283	126.278	2.946	0.186
3	41.298	-1.212	-	134.255	10.922	0.003

Table 3. Models predicting average site plant species richness for disturbed sites. All possible models are presented. The Akaike weights (w_i) represent the relative likelihoods of each model being the best model. Models over 2 AICc units from the top model were not significantly predictive

Model Number	**Intercept**	**Temperature Coefficient**	**Precipitation Coefficient**	**AICc**	**ΔAICc**	**w_i**
1	22.099	-0.770	-	89.972	0	0.492
2	15.479	-0.684	0.052	92.300	2.328	0.154
3	0.329	-	0.075	92.571	2.600	0.134

FIGURES

CHAPTER I

$$\boldsymbol{I_s = \left[G(A)_\alpha - G(A)_\beta - G(B)_\alpha + G(B)_\beta\right]}$$

Equation 1. Interactions coefficient equation used to quantify feedback interactions between native and non-native plants in both their own and the other's soil. This equation incorporates both plants in each condition where, I_s is the feedback coefficient, $G(A)_\alpha$ is growth of plant A in its own soil, $G(A)_\beta$ is growth of plant A in plant B's soil, $G(B)_\alpha$ is growth of plant B in plant A's soil and, $G(B)_\beta$ is growth of plant B in its own soil.

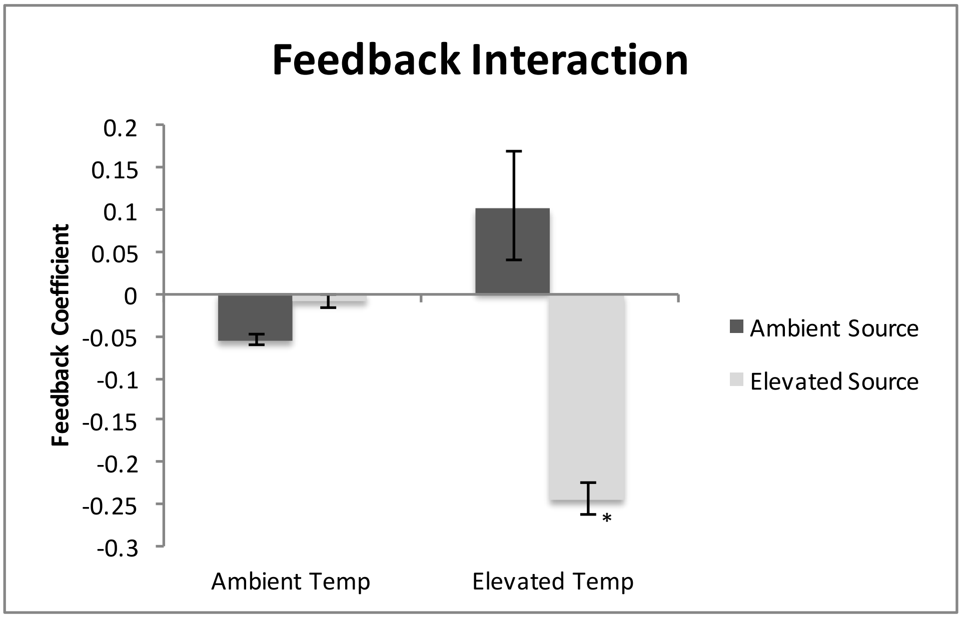

Figure 1. Interaction coefficient for PSF interaction in root biomass (g) between source temperature and experimental temperature. Dark grey bars indicate soil from ambient temperature and light grey bars indicate soil from elevated temperatures. Asterisk indicated that feedback coefficient was the result of a significant difference in conspecific growth.

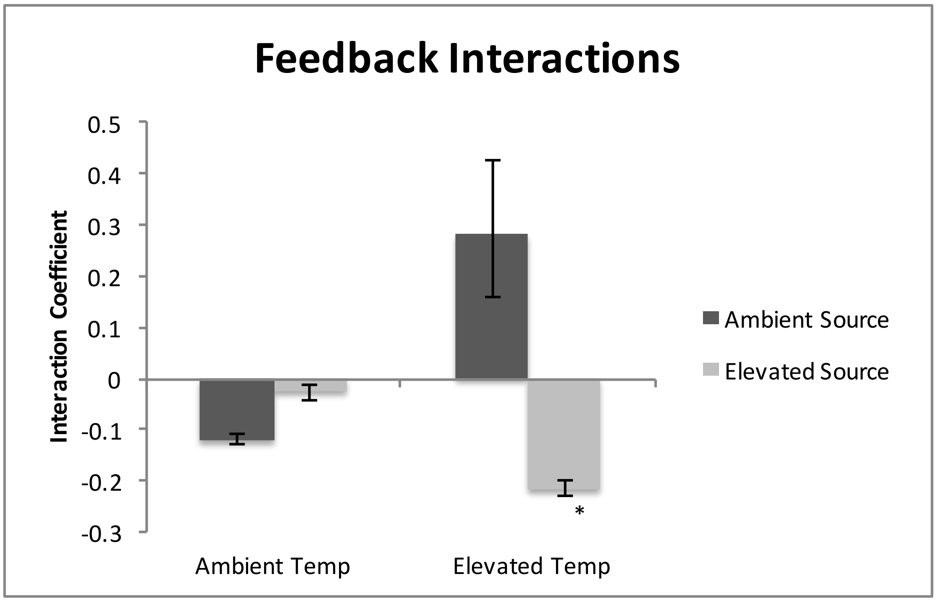

Figure 2. Interaction coefficient for PSF interaction in total biomass (g) between source temperature and experimental temperature. Dark grey bars indicate soil from ambient temperature and light grey bars indicate soil from elevated temperatures. Asterisk indicated that feedback coefficient was the result of a significant difference in conspecific growth.

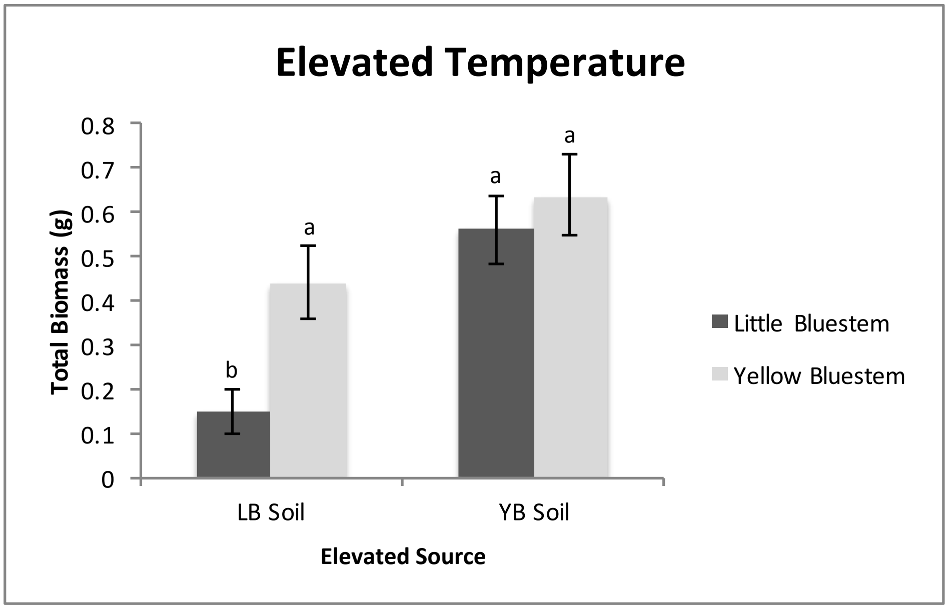

Figure 3. Total biomass production of native (*Schizachyrium scoparium*; dark gray bar) and invasive (*Bothriochloa ischaemum*; light grey bar) warm-season grasses grown in native soil (LB Soil) and invasive soil (YB Soil) which contribute to the fourth bar of figure 2. Plants were maintained at elevated (29 °C) temperatures and were from elevated source soil (29 °C). Bars with different letters differ significantly from each other ($p < 0.05$).

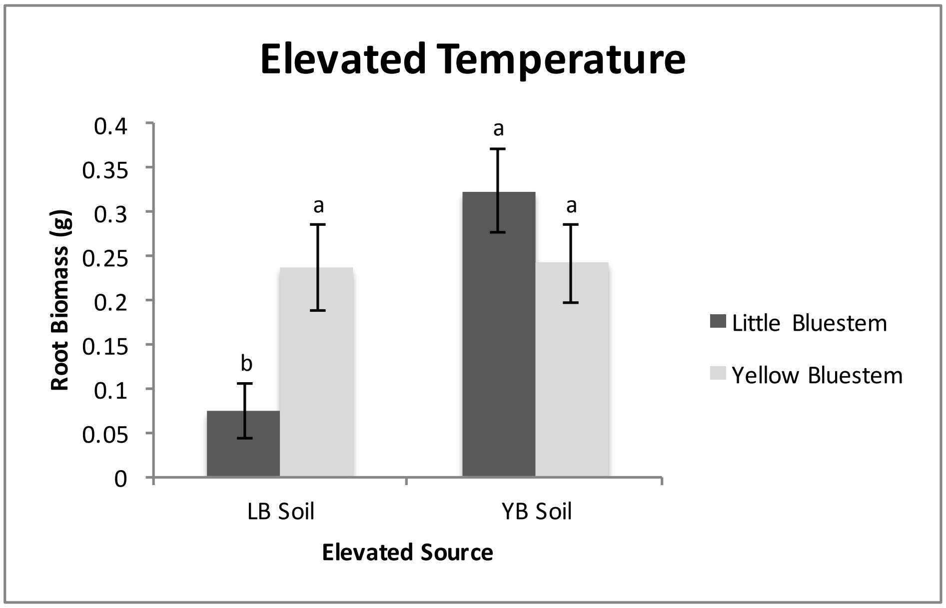

Figure 4. Total biomass production of native (*Schizachyrium scoparium*; dark gray bar) and invasive (*Bothriochloa ischaemum*; light grey bar) warm-season grasses grown in native soil (LB Soil) and invasive soil (YB Soil) which contribute to the fourth bar of figure 2. Plants were maintained at elevated (29 °C) temperatures and were from elevated source soil (29 °C). Bars with different letters differ significantly from each other ($p < 0.05$).

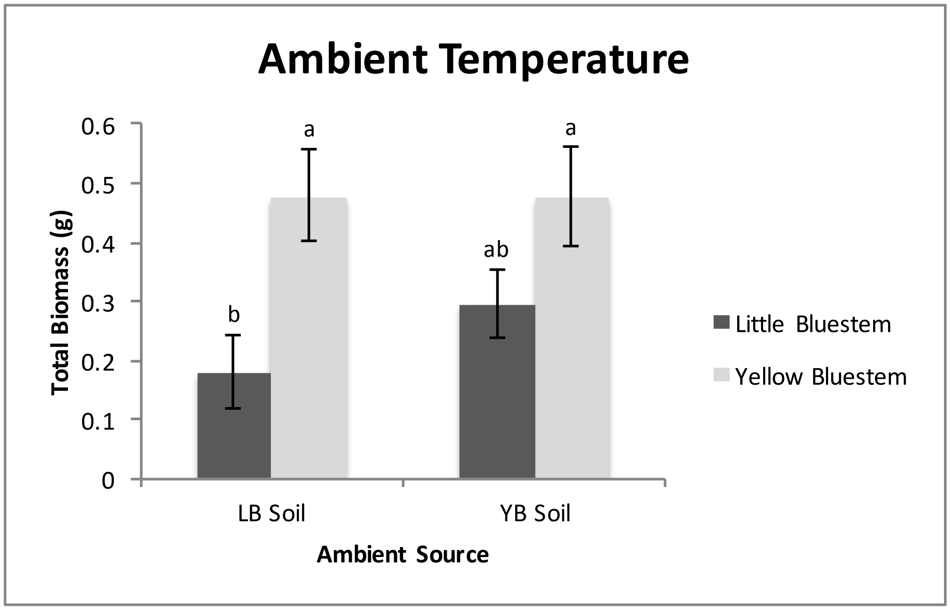

Figure 5. Total biomass production of native (*Schizachyrium scoparium*; dark gray bar) and invasive (Bothrio*chloa ischaemum*; light grey bar) warm-season grasses grown in native soil (LB Soil) and invasive soil (YB Soil) which contribute to the first bar of figure 2. Plants were maintained at ambient (24 °C) temperatures and were from ambient source soil (24 °C). Bars with different letters differ significantly from each other ($p < 0.05$).

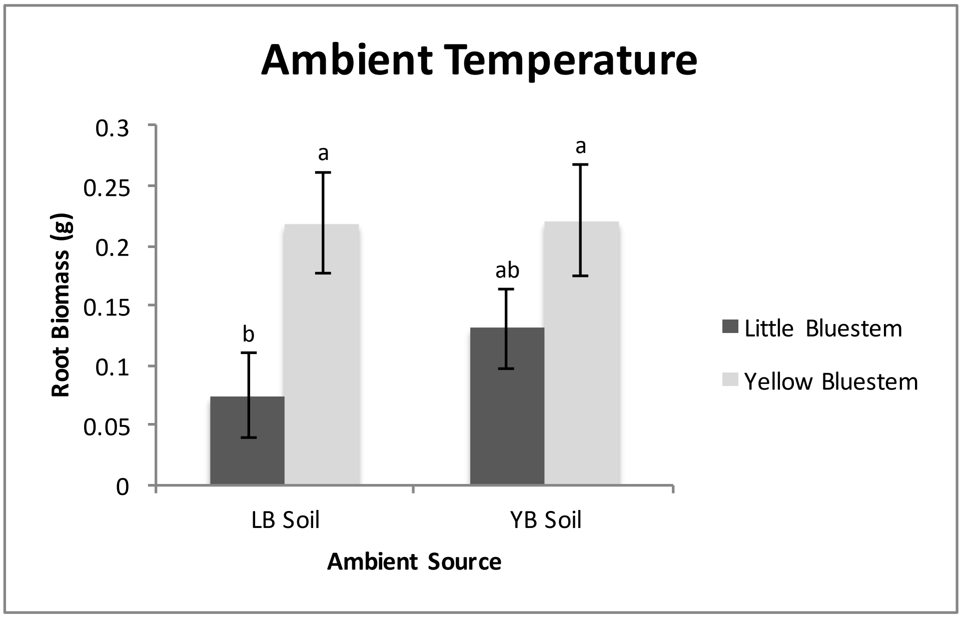

Figure 6. Root biomass production of native (*Schizachyrium scoparium*; dark gray bar) and invasive (*Bothriochloa ischaemum*; light grey bar) warm-season grasses grown in native soil (LB Soil) and invasive soil (YB Soil) which contribute to the first bar of figure 1. Plants were maintained at ambient (24 °C) temperatures and were from ambient source soil (24 °C). Bars with different letters differ significantly from each other ($p < 0.05$).

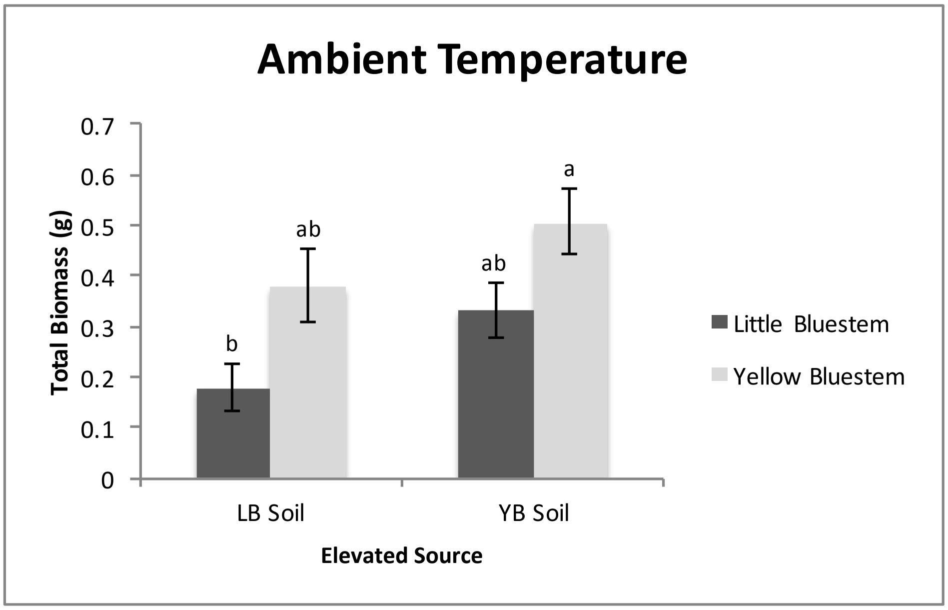

Figure 7. Total biomass production of native (*Schizachyrium scoparium*; dark gray bar) and invasive (*Bothriochloa ischaemum*; light grey bar) warm-season grasses grown in native soil (LB Soil) and invasive soil (YB Soil) which contribute to the second bar of figure 2. Plants were maintained at ambient (24 °C) temperatures and were from elevated source soil (29 °C). Bars with different letters differ significantly from each other ($p < 0.05$).

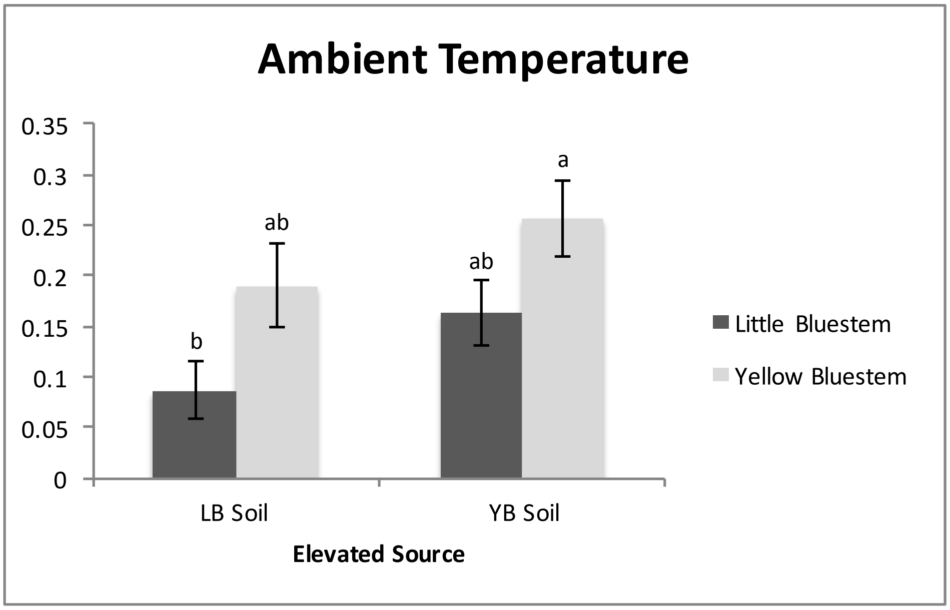

Figure 8. Root biomass production of native (*Schizachyrium scoparium*; dark gray bar) and invasive (*Bothriochloa ischaemum*; light grey bar) warm-season grasses grown in native soil (LB Soil) and invasive soil (YB Soil) which contribute to the second bar of figure 1. Plants were maintained at ambient (24 °C) temperatures and were from elevated source soil (29 °C). Bars with different letters differ significantly from each other ($p < 0.05$).

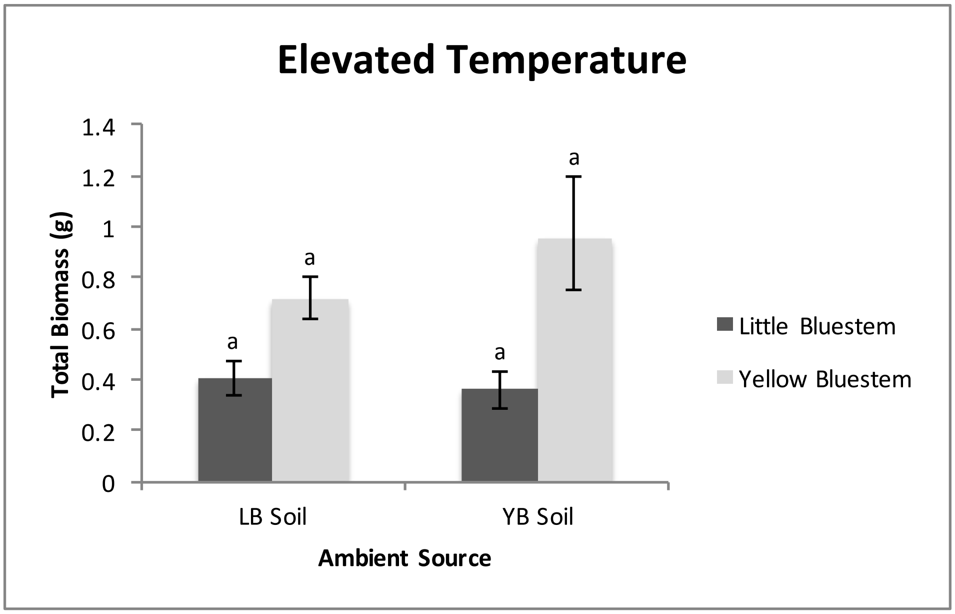

Figure 9. Total biomass production of native (*Schizachyrium scoparium*; dark gray bar) and invasive (*Bothriochloa ischaemum*; light grey bar) warm-season grasses grown in native soil (LB Soil) and invasive soil (YB Soil) which contribute to the third bar of figure 2. Plants were maintained at elevated (29 °C) temperatures and were from ambient source soil (24 °C). Bars with different letters differ significantly from each other ($p < 0.05$).

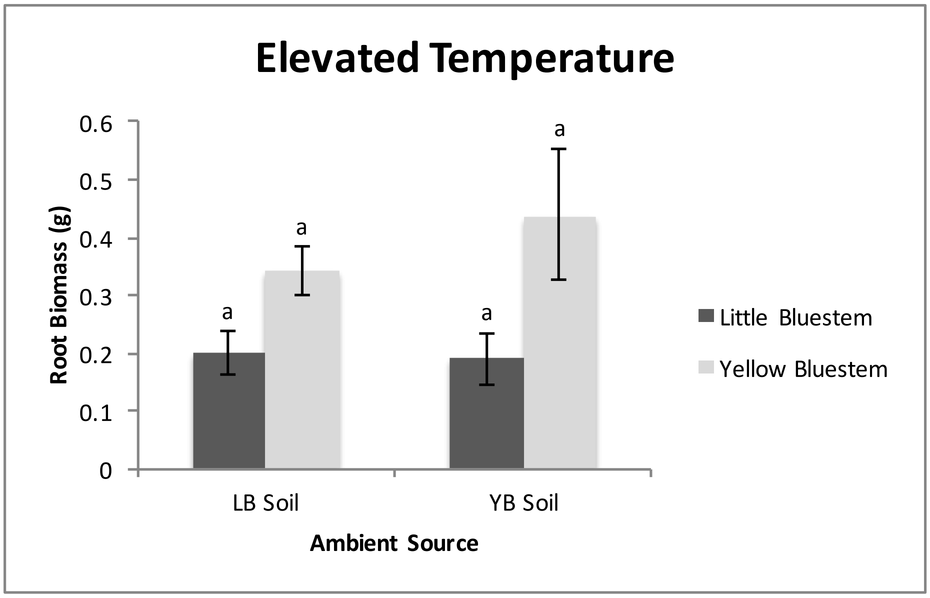

Figure 10. Root biomass production of native (*Schizachyrium scoparium*; dark gray bar) and invasive (*Bothriochloa ischaemum*; light grey bar) warm-season grasses grown in native soil (LB Soil) and invasive soil (YB Soil) which contribute to the third bar of figure 1. Plants were maintained at elevated (29 °C) temperatures and were from ambient source soil (24 °C). Bars with different letters differ significantly from each other ($p < 0.05$).

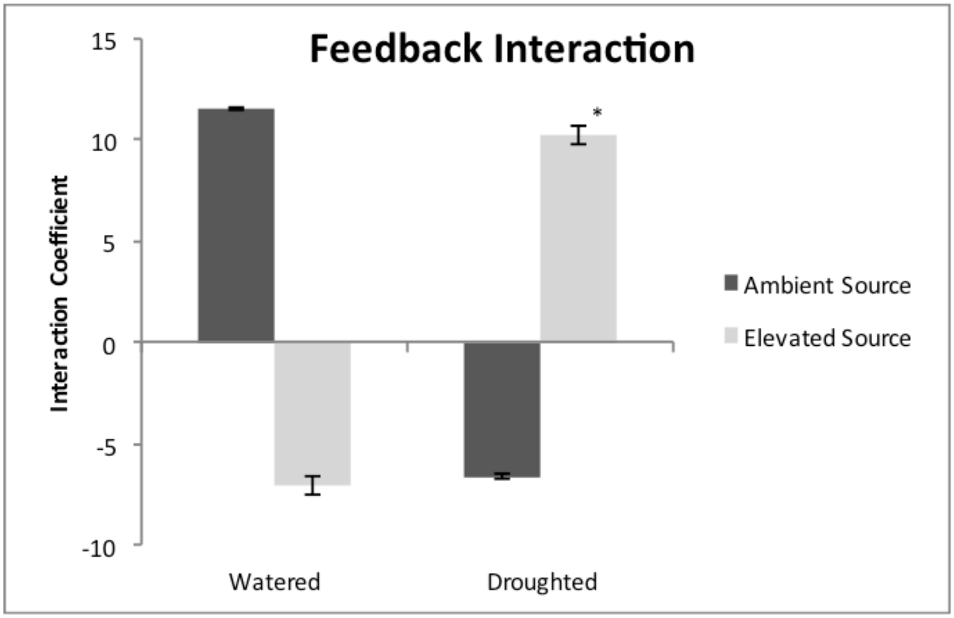

Figure 11. Interaction coefficient for PSF interaction in percent mycorrhizal fungal colonization between source temperature and experimental watering treatment. Dark grey bars indicate soil from ambient temperature and light grey bars indicate soil from elevated temperatures. Asterisk indicated that feedback coefficient was the result of a significant difference in congener growth.

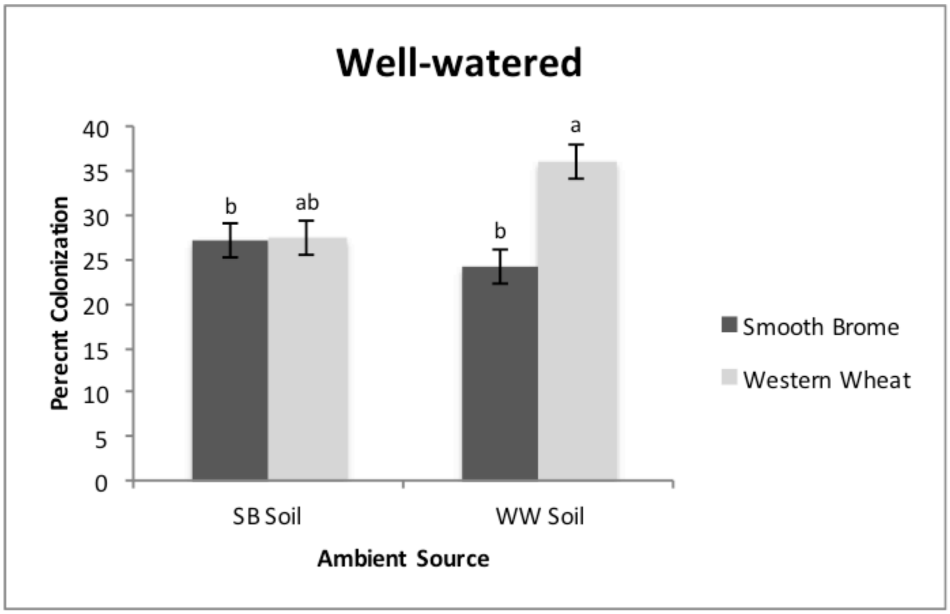

Figure 12. Mycorrhizal fungal colonization of native (*Pascopyrum smithii*; light gray bar) and invasive (*Bromus inermis*; dark grey bar) cool-season grasses grown in native soil (WW Soil) and invasive soil (SB Soil) which contribute to the first bar of figure 11. Plants were maintained at well-watered (100 % field capacity) conditions and were from ambient source soil (17 ºC). Bars with different letters differ significantly from each other ($p < 0.05$).

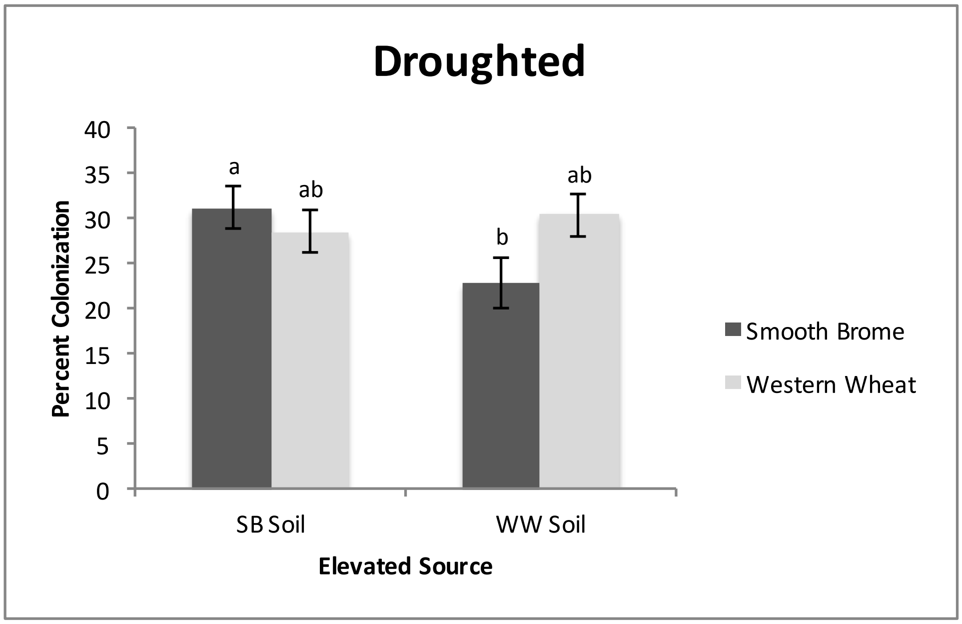

Figure 13. Mycorrhizal fungal colonization of native (*Pascopyrum smithii*; light gray bar) and invasive (*Bromus inermis*; dark grey bar) cool-season grasses grown in native soil (WW Soil) and invasive soil (SB Soil) which contribute to the third bar of figure 11. Plants were maintained at drought (65% field capacity) conditions and were from elevated source soil (22 ºC). Bars with different letters differ significantly from each other ($p < 0.05$).

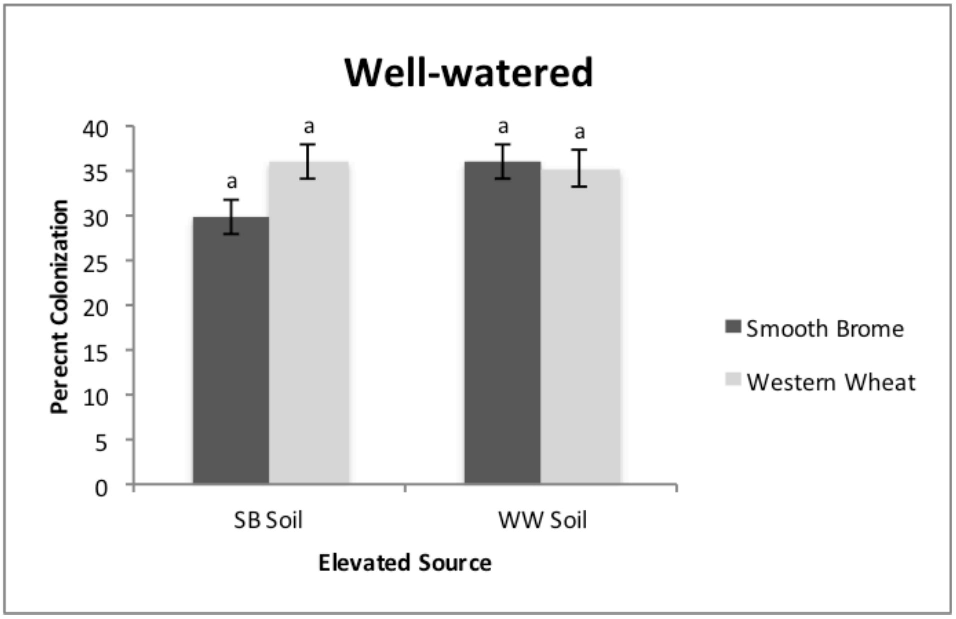

Figure 14. Mycorrhizal fungal colonization of native (*Pascopyrum smithii*; light gray bar) and invasive (*Bromus inermis*; dark grey bar) cool-season grasses grown in native soil (WW Soil) and invasive soil (SB Soil) which contribute to the second bar of figure 11. Plants were maintained at well-watered (100 % field capacity) conditions and were from elevated source soil (22 ºC). Bars with different letters differ significantly from each other ($p < 0.05$).

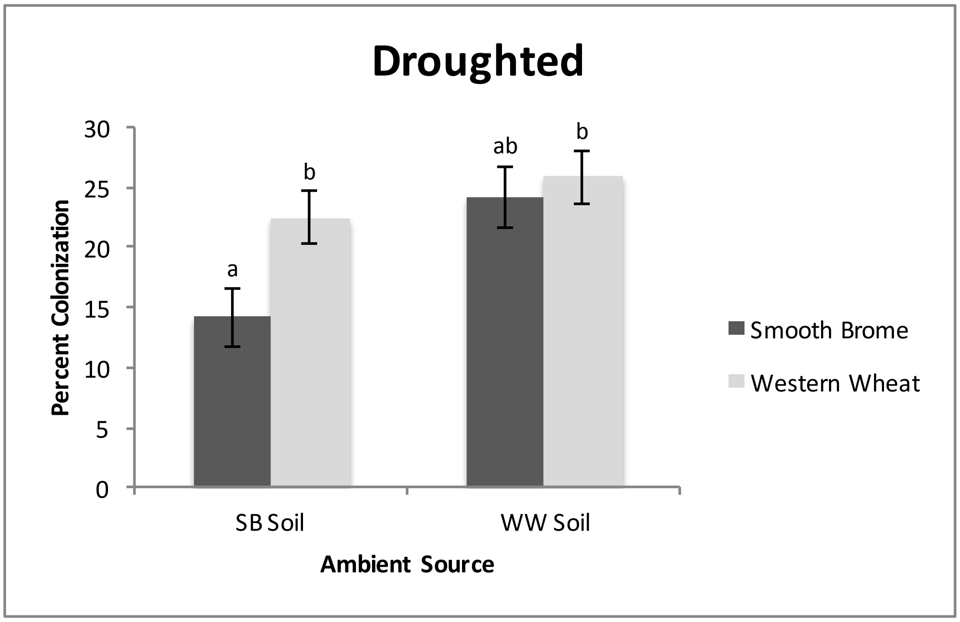

Figure 15. Mycorrhizal fungal colonization of native (*Pascopyrum smithii*; light gray bar) and invasive (*Bromus inermis*; dark grey bar) cool-season grasses grown in native soil (WW Soil) and invasive soil (SB Soil) which contribute to the third bar of figure 11. Plants were maintained at drought (65% field capacity) conditions and were from ambient source soil (17 ºC). Bars with different letters differ significantly from each other ($p < 0.05$).

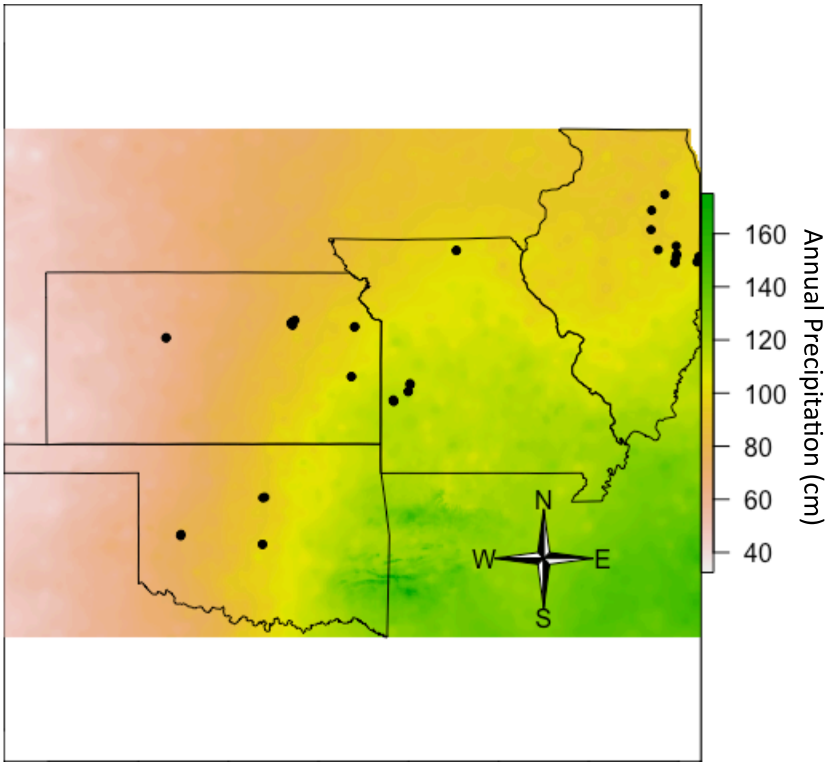

Figure 1. Map of site locations overlayed on map of annual precipitation (cm). Copyright © 2016, PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu Map created March 2016.

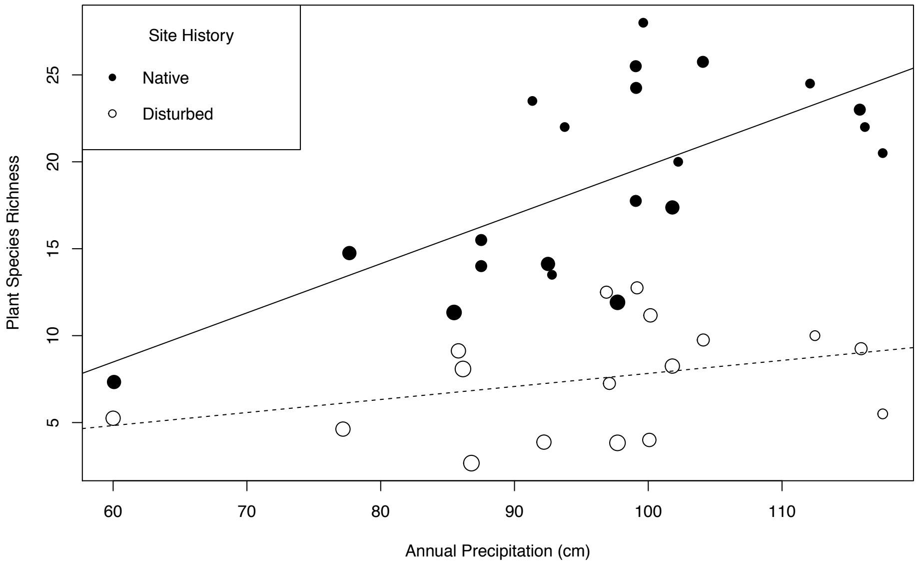

Figure 2. Average site plant species richness as a function of mean annual precipitation (cm). Filled circle indicate native sites and open circle indicate disturbed sites. Solid line represents the fit for native site ($r^2 = 0.4503$, $p < 0.001$) and dashed line indicates the fit for disturbed sites ($r^2 = 0.111$, $p = 0.1912$). Circle size represents relative amount of replication at each site.

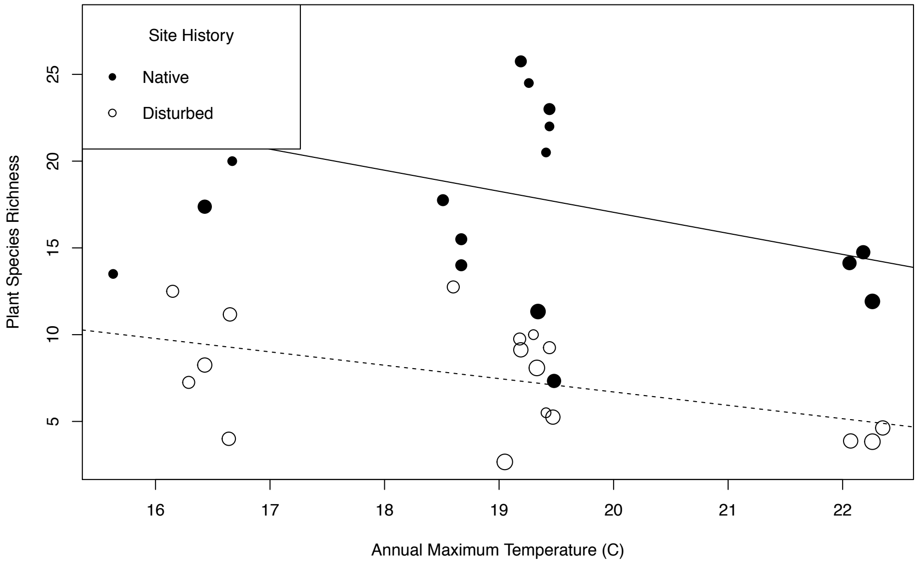

Figure 3. Average site plant species richness as a function of maximum temperature (C). Filled circle indicate native sites and open circle indicate disturbed sites. Solid line represents the fit for native site ($r^2 = 0.1963$, $p = 0.04429$) and dashed line indicates the fit for disturbed sites ($r^2 = 0.2371$, $p = 0.04746$). Circle size represents relative amount of replication at each site.

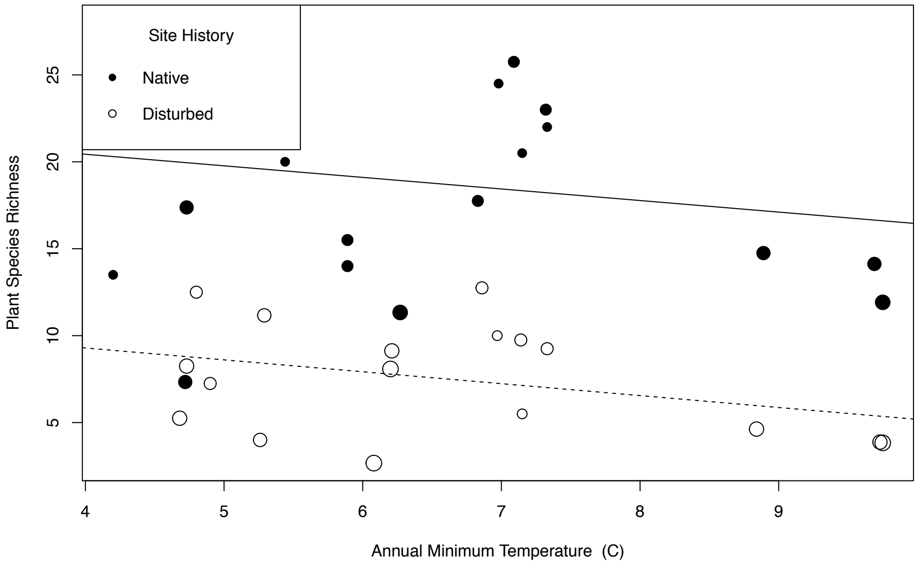

Figure 4. Average site plant species richness as a function of minimum temperature (C). Filled circle indicate native sites and open circle indicate disturbed sites. Solid line represents the fit for native site ($r^2 = 0.03734$, p=0.4013) and dashed line indicates the fit for disturbed sites ($r^2=0.1246$, p=0.1644). Circle size represents relative amount of replication at each site.

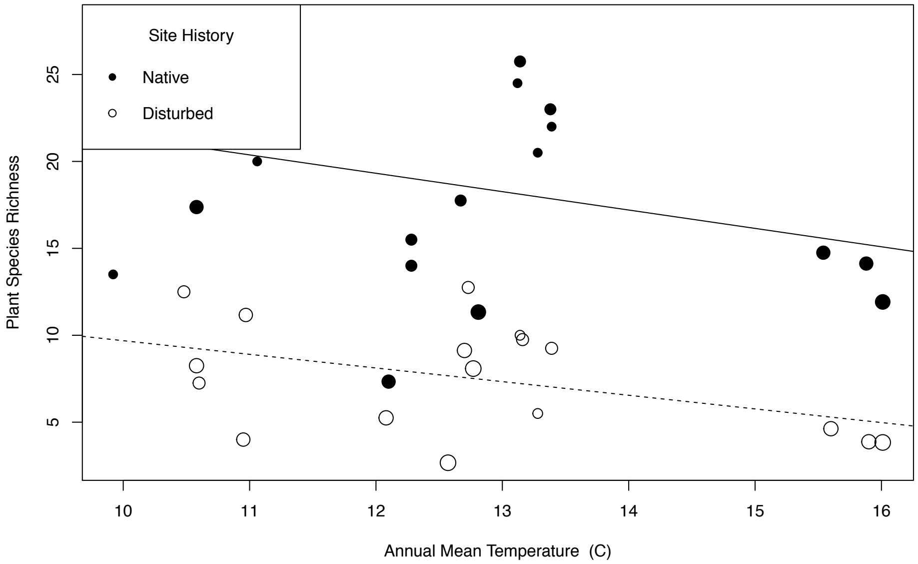

Figure 5. Average site plant species richness as a function of mean temperature (C). Filled circle indicate native sites and open circle indicate disturbed sites. Solid line represents the fit for native site ($r^2 = 0.1153$, p=0.132) and dashed line indicates the fit for disturbed sites ($r^2=0.1924$, p=0.0782). Circle size represents relative amount of replication at each site.

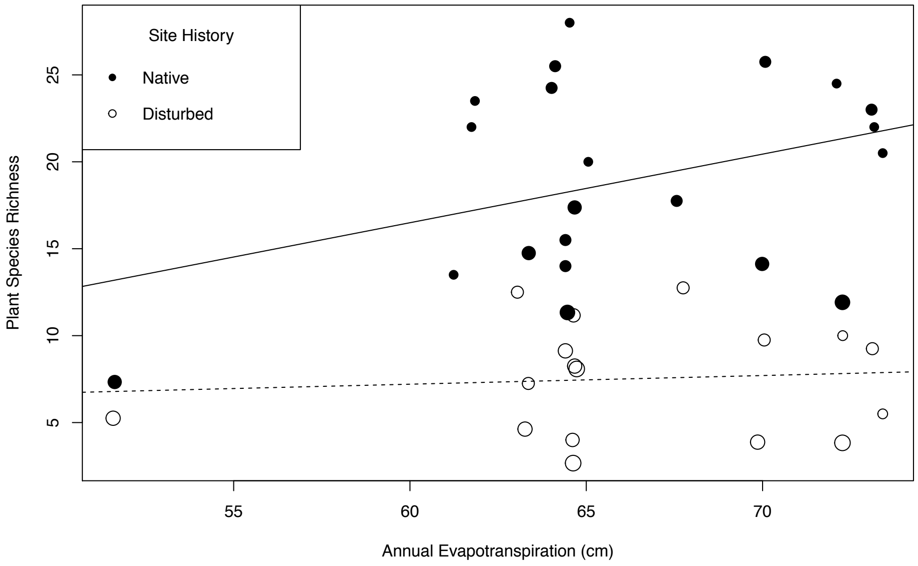

Figure 6. Average site plant species richness as a function of annual evapotranspiration (cm). Filled circle indicate native sites and open circle indicate disturbed sites. Solid line represents the fit for native site (r^2 =0.1355, p=0.1007) and dashed line indicates the fit for disturbed sites (r^2=0.007, p=0.7498). Circle size represents relative amount of replication at each site.

VITA

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