

ELEVATED TEMPERATURES AND DROUGHT
FAVOR INVASIVE GRASSES OVER NATIVE
SPECIES

By

ERIC BENJAMIN DUELL

Bachelor Science in Natural Resource Ecology and

Management

Oklahoma State University

Stillwater, Oklahoma

2012

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
May, 2015

ELEVATED TEMPERATURES AND DROUGHT
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SPECIES

Thesis Approved:

Dr. Gail Wilson

Thesis Adviser
Dr. Karen Hickman

Dr. Tyson Ochsner

ACKNOWLEDGEMENTS

I would like to first thank my thesis advisor Dr. Gail Wilson for all she has taught me over the years. Her guidance has helped me to establish myself as a scientist, and has given me a passion and drive for research. Her constant encouragement has given me the confidence to continue my education and pursue a career in the field of ecology, and has helped me build a strong foundation upon which to shape my future career.

I would also like to thank Dr. Karen Hickman for her assistance and guidance along the way. Her expertise in invasive species ecology was invaluable for my research. I would also like to thank her for her constant encouragement, as well as challenges, throughout this process, making me a better person and researcher in the end.

I would like to express my gratitude to Dr. Tyson Oschner for the use of his lab facilities when calculating soil moisture levels. I also thank him for his critiques on my thesis and his many words of encouragement and advice.

Many thanks to Dr. Mitch Greer for his constant advice, support, and encouragement throughout the years. While serving as my mentor, he gave me much invaluable advice that was instrumental in the early development of my scientific career.

Last, but certainly not least, I am especially grateful for my family: Mom and Dad, Jennifer, Jason, and Annie. I would not be where I am today, were it not for their constant support and encouragement throughout my time as a Master's student. Since childhood, through my undergraduate career, and now through my Master's studies, they have been the one constant in my life, through thick and thin, and will always be there for me.

Name: ERIC B. DUELL

Date of Degree: MAY, 2015

Title of Study: ELEVATED TEMPERATURES AND DROUGHT FAVOR INVASIVE GRASSES OVER NATIVE SPECIES

Major Field: NATURAL RESOURCE ECOLOGY AND MANAGEMENT

Abstract: Projected global-scale anthropogenic alterations to native ecosystems include intense and prolonged droughts, increases in atmospheric temperatures, and invasion by non-native species. Understanding how native and non-native grasses tolerate drought and elevated temperatures is essential for projecting native species competitive success. We assessed the effects of elevated temperature and drought on the performance of different growth stages (seed, seedling, and mature plant) of invasive grasses, relative to native species. Further, we determined responses of warm- and cool-season functional groups. The invasive warm-season cespitose grass, *Bothriochloa ischaemum* was paired with functionally similar native *Schizachyrium scoparium*. The invasive cool-season grass, *Bromus inermis*, was paired with functionally similar native *Pascopyrum smithii*. We assessed each growth stage at ambient [warm-season (24° C); cool-season (17° C)] and elevated [warm-season (29° C); cool-season (22° C)] temperatures. Seeds were maintained under three water-availability treatments (100%; 83.5%; or 65% field capacity). Seedlings of each species were maintained under for 14 weeks at well-watered (100% field capacity) and extreme drought (65% field capacity). Mature individuals of each species were maintained for 14 weeks at well-watered (100% field capacity) and extreme drought (65% field capacity), as well as two intermediate soil moisture levels (85% and 75% field capacity). Generally, invasive species from each functional group surpassed the corresponding native in germination, biomass production, and re-growth at all climatic conditions. Because associations with AM and saprophytic fungi may aid in host water acquisition and thermal tolerance, we hypothesized these fungal groups would be relatively more abundant when plants were exposed to adverse conditions. However, few differences were apparent between soil microbial communities (i.e. total microbial biomass, or relative abundance of AM or saprophytic fungi) of either native or invasive grass species in response to adverse environmental conditions. Our results indicate invasive perennial grasses are competitively superior to functionally similar native species at all life stages, under ambient and extreme temperature and drought. As more intense and frequent droughts, coupled with elevated temperatures, are projected for grasslands worldwide, our data suggest invasive grasses will out-compete native species at potentially greater magnitudes than currently observed.

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CHAPTER I

EFFECTS OF ELEVATED TEMPERATURE AND DROUGHT ON GERMINATION AND SEEDLING SUCCESS OF INVASIVE AND NATIVE PRAIRIE GRASSES

ABSTRACT

Global-scale anthropogenic alterations include intense and prolonged droughts, increases in atmospheric temperatures, and invasion of native ecosystems by non-native species. Understanding how native and non-native species tolerate drought and elevated temperatures is essential for projecting native species competitive success. To determine the effects of altered climate on the performance of early growth stages of invasive grasses, relative to native, functionally similar species, we assessed germination and seedling growth of an invasive warm-season grass (*Bothriochloa ischaemum*), compared with a functionally similar native (*Schizachyrium scoparium*), and an invasive cool-season grass (*Bromus inermis*), compared to functionally similar native (*Pascopyrum smithii*). We assessed germination of warm-season grass seeds maintained under ambient (24° C) or elevated (29° C) temperatures. Because cool-season grasses are adapted to cool environments, we selected cooler ambient (17° C) and elevated (22° C) temperatures

for this functional group. Seeds were maintained under three water-availability treatments (100%; 83.5%; or 65% field capacity). Seedlings of each species were maintained under ambient and elevated temperatures for 14 weeks at well-watered (100% field capacity) and extreme drought (65% field capacity). Our data indicate increased germination, production, and biomass production may be primary mechanisms of successful invasibility for non-native perennial grasses and that elevated temperatures and intense drought may further exacerbate successful invasion of non-native grasses. Because associations with arbuscular mycorrhizal and saprophytic fungi may aid in host water acquisition and thermal tolerance, we hypothesized these fungal groups would be relatively more abundant when plants were exposed to adverse conditions. However, few differences were observed in soil microbial communities, including total biomass, or relative abundance of AM or saprophytic fungi, of either native or invasive species in response to adverse environmental conditions. Our results indicate invasive perennial grasses may be more successful (greater germination and biomass production) than native species at early life stages (i.e. germination and seedling growth), under ambient and extreme temperature and drought. As more intense and frequent droughts, coupled with elevated temperatures, are projected for grasslands worldwide, our data suggest invasive grasses will out-compete native species at potentially greater magnitudes than currently observed.

INTRODUCTION

Within ecosystems, successful germination and subsequent seedling recruitment are vital to the persistence of native plant communities, although the level of importance depends on the system (Gibson 2009) and level of ecosystem disturbance. Seedling

establishment can be particularly important in regions where large-scale disturbances such as drought or intensive grazing occur (Glenn-Lewin and van der Maarel 1992), leaving openings for seedlings to establish. For example, the Great Drought of 1934 in the central United States led to the loss of many native prairie dominants, leaving bare ground that was quickly colonized by drought-resistant seedlings (Weaver and Albertson 1936). Similarly, perennial grasslands in sub-Saharan Africa are characterized by seedling survival that is greatest on bare ground, and greatly reduced by the presence of established grasses (Zimmerman et al. 2008). Ecosystem disturbance has also been documented to decrease resilience stability and resistance to invasive non-native species in grassland plant communities (Schoolmaster and Snyder 2007). Invasion by non-native invasive species is currently a major threat to native plant communities (Vitousek 1994). In native grasslands worldwide, successful seedling recruitment requires a variety of environmental factors concurrently occurring at appropriate levels (O'Connor 1996; Zimmerman et al. 2008). Of all environmental abiotic factors, water is considered the single most limiting resource in terms of germination and seedling survival and regeneration (Qi and Redmann 1993; Cornaglia et al. 2005). Low water availability has been shown to reduce total germination and slow the rate of successful germination (Young et al. 1983), as well as inhibit subsequent seedling growth and development (Abbott and Roundy 2003; Fay and Schultz 2009). However, dependency on soil moisture may be species-specific (Frasier et al. 1984, 1987; Frasier 1989). In addition to moisture, temperature is also considered to be a predominant limiting factor for plant growth and establishment, as well as plant community assemblages and biodiversity metrics (Bond and Richardson 1990; Jonas et al. *in press*), possibly through negative effects on

germination and seedling establishment of native species. Temperature has been shown to be especially critical when in combination with soil moisture stress, especially in terms of early plant life stages (Laude and Chaugule 1953; Tadmor et al. 1969; Qi and Redmann 1993). Therefore, as future global-scale climate scenarios suggest the central and southern regions of the Great Plains will experience more intense and prolonged droughts (Solomon 2007; Jung et al. 2010; Mishra and Singh 2010; Min et al. 2011; Rummukainen 2013), occurring in tandem and exacerbated by increases in atmospheric temperatures (Solomon 2007), understanding how native and non-native seeds and seedlings differentially tolerate drought and elevated temperatures is essential for projecting native species competitive success.

While several previous studies have examined climatic alterations on mature individuals, populations, or community-level assemblages, little research has assessed climatic tolerances of invasive or native plant species at the seed germination or seedling establishment stage. The ability of non-native species to establish and spread is, in part, due to their ability to competitively suppress their native counterparts, often through greater phenotypic plasticity compared to their native counterparts (Levine et al. 2003; Funk 2008). This plasticity provides a competitive advantage over native species through an increased ability to tolerate a wider array of climatic conditions (Walther et al. 2009), allowing further range expansion as native plant species frequently exhibit decreases in production when subjected to elevated temperature or reduced soil moisture (Weltzin et al. 2003; Godoy et al. 2009; Weißhuhn et al. 2011).

Further, the role of altered biotic interactions in mediating vegetation responses to climate change remains poorly-understood, but elucidating effects of invasive species on

soil biota will be essential to understanding consequences of climate change for grassland structure and function. In the grasslands of central North America, most native species, particularly perennial grasses, are highly dependent on the presence of arbuscular mycorrhizal fungi (AMF) to complete their life cycle. These fungi associate with the roots of the host plant, increasing absorptive surface area, allowing for enhanced uptake of essential nutrients and increase water-availability and drought tolerance (Augé 2001, 2004; Allen 2011). Recent evidence suggest that non-native grasses invading into native grasslands of the Great Plains are altering these soil microbial communities, creating a feedback that increases invasibility of native grasslands (Wilson et al. 2012). Roots also host other fungi that together comprise the root mycobiome. Previous studies are limited, but it has been suggested these non-AM fungi may also participate in host water and nutrient acquisition (Barrow 2003; Herrera et al. 2011; Newsham 2011), and in thermal tolerance (McLellan et al. 2007; Song et al. 2012). Therefore, understanding plant traits and biotic associations that influence water acquisition and tolerance to drought of native and non-native invasive species will become increasingly important in predicting grassland responses to environmental change. To assess drought and temperature tolerances of early developmental stages of dominant native and non-native invasive grass species, we conducted a climatic perturbation experiment examining germination and seedling growth of two native and two non-native invasive grass species of warm- and cool-season functional groups. *Bothriochloa ischaemum*, a devastating invasive warm-season grass species of the central and southern Great Plains was paired with the most dominant, functionally similar species of native tallgrass prairie ecosystems (*Schizachyrium scoparium*). *Bothriochloa ischaemum* was introduced from Eurasia in

the early 1920's as means of erosion control and fast-growing forage (Celarier and Harlan 1955). *Bromus inermis*, a cool-season bunchgrass, highly invasive in the northern and central Great Plains of North America was paired with functionally similar *Pascopyrum smithii*, a dominant species in the northern Great Plains and a sub-dominant in many areas through the central and southern Great Plains. *Bromus inermis* was purposely introduced into the Great Plains in the late 1880's for soil stabilization and forage. Specifically, we addressed the following questions: (1) What roles do decreased soil moisture and elevated temperatures play in the germination success of invasive grasses, compared to that of functionally similar, dominant native species? (2) How do these experimental climatic conditions affect seedling growth of invasive grasses and non-native species? We hypothesized that increased temperature and decreased soil moisture would result in a greater reduction in germination success, and lower seedling biomass production of native grasses, as compared to the invasive species. Further, we predicted that mycorrhizal and saprophytic fungi would increase in importance under adverse growing conditions at the seedling stage, and this would be reflected by increases in fungal abundance with increases in temperature and decreased soil moisture.

MATERIALS AND METHODS

Germination Study

Soil collection and preparation: A growth chamber experiment was conducted to assess the germination success of native and invasive grass seeds when exposed to variable moisture and temperature treatments. This experiment was conducted at the Oklahoma State University Mycorrhizal Ecology laboratory, in Stillwater, Oklahoma,

USA. Soil was collected from Konza Prairie Biological Station, Manhattan, Kansas, in an area dominated by warm-season grasses such as *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Bouteloua spp.* The plant community also consisted of important sub-dominant cool-season grasses, including *Pascopyrum smithii* and *Dichanthelium oligosanthes*.

Study species: Invasive species *Bothriochloa ischaemum* was paired with *S. scoparium*, a functionally similar native warm-season grass species and invasive species *Bromus inermis* was paired with the native, functionally similar bunchgrass, *P. smithii*.

Experimental design: Freshly collected soil was sieved through a 10 mm sieve to remove any coarse plant material or rocks. Forty grams of the sieved soil were then placed into each petri dish (90mm x 15mm). Seeds were surface-sterilized by soaking in 7% sodium hypochlorite solution for ten minutes and then rinsing thoroughly with distilled water (Ruiz et al. 2003), after which 50 seeds of the designated species were placed on the soil contained in the petri dishes. The complete experimental design for the warm-season grass seeds consisted of 12 treatment combinations: 2 plant species (native and invasive) x 2 warming treatments x 3 moisture treatments, arranged in a complete randomized block design with 6 replications for a total of for a total of 72 petri dishes. Experiments were conducted in Controlled Environmental Chambers, (Convicon-PGW 36, interior dimension: 98”Wx54”Dx93”H, growth area: 36ft², and growth capacity: 240 ft²) under a photoperiod of 14 hours, located on the campus of Oklahoma State University in Stillwater, OK. Ambient temperature was maintained at 24° C, elevated temperature was maintained at 29° C. This 5° increase is the projected temperature change for the central and southern Great Plains within the next century (Solomon 2007).

Soil was maintained at one of three soil moisture levels: 100% field capacity (FC), 83% FC, or 65% FC. Soil moisture treatments were based on permanent wilt point of grasses in grassland soils, determined by the pressure-plate apparatus method, in which 1.5 MPa of pressure was exerted onto the soil sample until equilibrium is reached (Richards and Weaver 1943).

As cool-season grasses are adapted to cooler environments than warm-season grasses, ambient temperature was maintained at 17° C, and elevated temperature at 22° C. Therefore, the complete experimental design for the cool-season grass seeds consisted of 12 treatment combinations: 2 plant species (native and invasive) x 2 warming treatments x 3 moisture treatments (100% FC, 83% FC, or 65% FC), arranged in a complete randomized block design with 6 replications for a total of for a total of 72 petri dishes. Seeds were monitored daily for 21 days. Germination was considered successful and recorded once the radicle had reached 2 mm in length. Once a seed had germinated, the individual was recorded, then removed from the petri dish and discarded.

Seedling Study

Soil collection and preparation: A greenhouse experiment was conducted to assess the responses of native and invasive prairie grasses to projected climatic conditions. This experiment was conducted at Oklahoma State University, in Stillwater, Oklahoma, USA. Soil was collected from Konza Prairie Biological Station, Manhattan, Kansas. Four liter pots were filled with 9 kg of homogenized native prairie soil. Seedlings were germinated in vermiculite flats and a single individual at the second leaf stage was transplanted into one four liter pot. The four species used in the previously described

germination experiment were selected to evaluate early life cycle responses of dominant native and invasive warm- and cool-season prairie grasses maintained at various levels of temperature and water-availability.

Experimental design: Two temperatures [ambient (24° C) and elevated (29° C)] and two soil moisture treatments (field capacity and drought [35% less than field capacity]) were initiated after seedling transplant. The complete experimental design consisted of 16 treatment combinations: 4 plant species (native and invasive warm-season; native and invasive cool-season) x 2 warming treatments x 2 water-availability treatments, arranged in a complete block design with 6 replications for a total of for a total of 96 pots. As cool-season species are adapted to cooler temperatures than warm-season grasses, greenhouse temperatures were maintained at an ambient temperature of 17° C and an elevated temperature of 22° C.

Harvest: Plants were maintained for 24 weeks at which time plants were harvested, and roots and shoots were weighed. Aboveground biomass was separated into reproductive and vegetative biomass. A sub-section of roots were selected for assessment of AM fungal root colonization. Soil was collected to assess relative abundance of selected functional groups of soil microbial communities, including AMF.

Assessment of Intra-Radical Mycorrhizal Colonization: Intra-radical AM fungal colonization was assessed microscopically. A small (> .5 g) subsample of roots were oven-dried for 48 hours at 60° C, stained with Trypan blue were scored using the magnified gridline intersect method (McGonigle et al. 1990).

Quantification of Soil Microbial Communities: Soil subsamples of 5g were collected at harvest from each experimental pot to assess soil microbial communities. Phospholipid fatty acid (PLFA) and neutral lipid fatty acid (NLFA) biomarkers were used to determine total microbial biomass, as well as abundances of selected microbial functional groups, such as gram+ and gram- bacteria, AM fungi, and saprophytic fungi. PLFAs are constituents of biological membranes that can be used to estimate the biomass of fungi, because biovolume and cell surface area are well correlated (Tunlid and White 1992). The NLFAs are the basic storage product of many fungi and serve as the primary energy reserve in fungi (Larsen and Bødker 2001). Therefore, NLFA data were used to assess AMF and saprophytic fungal biomass. PLFA and NLFA 16:1 ω 5c, 20:1 ω 9 and 22:1 ω 13 were used to quantify AM fungal biomass (Olsson 1999). 18:2 ω 9, 12, and 18:1 ω 9c were used quantitatively for saprophytic fungi. Biomarkers selected to determine biomass for the gram positive bacteria functional group included i-15:0, a-15:0, i-17:0, and i-16:0. For gram negative bacteria, biomarkers included 16:1 ω 7, cy19:0, and 2-OH 16:0. Microbial biomass was assessed as total microbial biomass (gram+, gram-, AM fungi, saprophytic fungi, and non-specific fungi and bacteria). PLFA and NLFA were extracted from the soil using a modification of the Bligh and Dyer (1959) extraction (Allison and Miller 2005). Total lipid extracts were separated into PLFA's and NLFA's using silicic acid chromatography; the fatty acids cleaved from the glycerol backbone using KOH saponification; and the harvested fatty acids methylated to form fatty acid methyl esters (FAME) (Allison and Miller 2005). The FAME's were then analyzed by gas chromatography and mass selection detection using a GCMS unit (Agilent MS 5975C/GC 7890A).

Statistical Analysis

Data were analyzed using SigmaPlot 12.5 (SigmaStat). Percent germination, biomass production, mycorrhizal root colonization, and relative abundance of soil microbial functional groups (PLFA and NLFA) were analyzed using a three-way Analysis of Variance (ANOVA) with a Tukey's test for multiple comparisons. Factors in the analysis were species, soil moisture, and temperature. Total germination was calculated after the 21 day germination period. Because we saw similar trends for below- and aboveground biomass production, data from our seedling performance experiments are presented as total biomass.

RESULTS

Germination Study

Warm-Season Grass Germination: Germination of warm-season grasses was inhibited by reduced water-availability and increased temperature. However, these reductions in germination varied across species (Figure 1). When maintained under ambient temperature and 100% field capacity (FC), germination of native *S. scoparium* was significantly lower compared to invasive *B. ischaemum* ($p < 0.05$). When maintained at ambient temperature, each level of reduction in water availability significantly reduced germination of both native and invasive seeds. However, percent germination of the invasive seed remained greater than that of the native species at each level of water availability (Figure 1).

When maintained at elevated temperature and well-watered conditions (100% FC), germination of both species was significantly reduced compared to ambient

temperatures; however, germination of *S. scoparium* was significantly lower ($p < 0.001$) than *B. ischaemum* (Figure 1). When maintained at elevated temperature and drought conditions (83% FC or 65% FC), germination of both species was negligible or no germination was observed (Figure 1).

Cool-Season Grass Germination: At ambient temperatures, germination of cool-season grasses was inhibited to a lesser extent than that which we observed in the two warm-season species and only at the lowest water-availability (65% FC) was there a significant reduction in germination of either cool-season grass (Figure 2). However, there were noticeable differences between the native and invasive species. When seeds were germinated under ambient temperature and 100% or 83% FC, native *P. smithii* germination was significantly less than that of invasive *B. inermis* ($p < 0.001$). When soil moisture was reduced to 65% FC, germination of both native and invasive species was reduced significantly ($p < 0.05$), although the invasive species remained significantly greater in germination compared to the native under these drought conditions (Figure 2).

When temperatures were increased by 5° C, germination of native grass *P. smithii* was reduced by 54.3%, with only 13.7% of native seeds successfully germinating, even when maintained under well-watered conditions (100% FC) (Figure 2). Under these same environmental conditions, germination of invasive *B. inermis* was substantially and significantly greater (54.0%), compared to *P. smithii* (13.7%). When soil moisture was reduced to 83% FC, germination of *P. smithii*, already quite low, dropped slightly. However, germination of *B. inermis* was reduced significantly under drought conditions ($p < 0.001$), and germination of the invasive and native species were not significantly different from each other under these adverse environmental conditions (Figure 2).

Seedling Study

Warm-Season Seedling Performance: Growth of invasive *B. ischaemum* seedlings were not reduced when grown under elevated temperatures, compared to growth under ambient temperatures at either 100% or 65% water-availability (Figure 3). However, growth at elevated temperature in combination with drought (65% FC) was significantly reduced, compared to plants receiving sufficient water under either ambient or elevated temperatures (Figure 3).

Biomass production of native *S. scoparium* was strikingly and significantly reduced as compared to invasive *B. ischaemum*. In fact, the native plants were more than 300% smaller than corresponding invasive plants when grown under ambient temperature and sufficient water-availability and continued to produce considerably less biomass when grown at either temperature or drought treatment (Figure 3). Native *S. scoparium* produced significantly greater biomass when grown under ambient temperature and maintained near 100% FC, compared to growth under elevated temperatures or drought (Figure 3).

Cool-Season Seedling Performance: Production of neither native nor invasive cool-season species was affected by temperature. As observed for warm-season native species, the native cool-season grass produced significantly less biomass, compared to the invasive, when grown under well-watered conditions (Figure 4). However, growth of each species was significantly reduced when grown under drought conditions (65% FC), and invasive *B. inermis* produced equivalent biomass as native *P. smithii* under these conditions (Figure 4).

Microbial Communities

Soil Microbial Communities of Warm-Season Grasses: Root colonization by AM fungi was not affected by temperature or soil moisture for either warm- or cool season grass species (Figure 5). To evaluate relative abundance of selected functional groups of soil microbial communities associated with native and invasive warm- and cool-season grasses grown under varying climatic conditions, we performed phospholipid fatty acid (PLFA) and neutral lipid fatty acid (NLFA) analyses. Generally, there were no significant interactions between the two warm-season species for total microbial biomass, regardless of experimental climatic perturbation (Figure 6). However, under elevated temperature and drought, microbial biomass associated with the invasive was significantly greater, compared to all other treatment combinations (Figure 6).

Neutral lipid fatty acid analyses indicated AM fungal biomass was significantly different between native and invasive species when grown under ambient temperatures ($p = <0.001$). Invasive *B. ischaemum* was associated with greater AMF biomass, compared to native *S. scoparium* at both water-availability treatments (Figure 7). A significant reduction in AM fungal biomass associated with *B. ischaemum* was observed between ambient and elevated temperature ($p = < 0.001$), while no differences were found in *S. scoparium* between temperature regimes (Figure 7). When grown at ambient temperatures, *B. ischaemum* soils were characterized by significantly greater AM fungal biomass, as compared to *S. scoparium* ($p = < 0.001$), while no differences were found between the two species at elevated temperatures (Figure 7).

Saprophytic fungal biomass production, as assessed through NLFA analyses, was greater under elevated temperatures and drought conditions, as compared to growth under ambient temperatures receiving reduced water-availability (Figure 8). No other clear patterns were observed between treatments or between native and invasive species.

Soil Microbial Communities of Cool-Season Grasses: Mycorrhizal colonization was not significantly different between native *P. smithii* and invasive *B. inermis* cool-season grasses (Figure 9). However, when grown under ambient temperatures, reduced water-availability significantly decreased AMF colonization in *B. inermis* roots, as compared to well-watered plants (Figure 9). As determined through PLFA analyses, total microbial biomass associated with native *P. smithii* was consistently greater than biomass associated with invasive *B. inermis*, regardless of temperature or water-availability (Figure 10). However, within species, we found no significant interactions between soil moisture or temperature treatments (Figure 10).

Mycorrhizal fungal biomass extracted from soils associated with *B. inermis* was significantly reduced when plants were grown under drought conditions and under ambient temperature, as compared to *P. smithii*, and compared to AM fungal biomass associated with well-watered *B. inermis* plants grown under either temperature (Figure 11). Mycorrhizal biomass associated with the native cool-season species, *P. smithii*, did not differ between temperature or water-availability treatments (Figure 11). Saprophytic fungal biomass associated with *P. smithii* was greater, as compared to biomass production associated with *B. inermis*, when plants were grown under drought conditions at either temperature (Figure 12). In fact, saprophytic fungal biomass associated with *B.*

inermis at the high temperature and drought was significantly reduced compared to all other *B. inermis* or *P. smithii* treatments (Figure 12).

DISCUSSION

Invasion by non-native species and climate change are among the two most important anthropogenic drivers altering native biodiversity (Vitousek 1994; Hellmann et al. 2008; Bradley et al. 2010; Verlinden and Nijs 2010). Our study indicates increases in atmospheric temperature and drought may further exacerbate successful invasion of non-native grasses. Germination of both warm- and cool-season invasive grasses substantially and significantly exceeded germination of native, functionally similar species. This was apparent not only at current climatic conditions (ambient temperature and well-watered soil), but also under elevated temperature, reduced water-availability, and the combination of these climatic stressors. Having superior germinability, relative to native species, gives the invasive species a tremendous advantage in population persistence, especially as climate change scenarios project more intense and frequent droughts. Furthermore, invasive species have been reported to have higher fecundity, compared to native species (Bennett et al. 2011). Earlier germination capabilities may provide invasive grasses yet another competitive advantage over native grasses. Seeds of invasive grasses have been observed to begin germination as much as five days earlier than native species (Callaway and Josselyn 1992; Lenz and Facelli 2005; Serpe et al. 2006; Cervera and Parra-Tabla 2009; Chrobock et al. 2011; Wainwright et al. 2012) or begin germination in autumn, out-competing spring-germinating native grasses (Ray-Mukherjee et al. 2011). Indeed, phenological adaptations may play an important role in successful invasibility; a wider niche breadth and the ability to adapt to a broader range

of climatic conditions have been suggested as key mechanisms for invasive plant success under environmentally-stressed conditions (Dukes and Mooney 1999; Diez et al. 2012). Successful invaders often occupy a phenological niche not occupied by native species (Wolkovich and Cleland 2010). In addition to timing of germination, these phenological niches may include flowering and other reproductive activities (Godoy et al. 2009; Wainwright and Cleland 2013), allowing competitive advantages through uptake of available resources that are temporally distinct from the activity of native species. Extensive seed production combined with phenological separation and greater germination success, even under adverse environmental conditions, may play a critical role in the continued success of non-native species invasibility.

It has been argued that seed production and germination success of grasslands dominated by rhizomatous grass species, such as those of the southern and central Great Plains in North America has minimal importance to plant population persistence and productivity as belowground vegetative meristems have been shown to be the primary source of plant re-growth (Benson et al. 2004; Benson and Hartnett 2006; Ott and Hartnett 2012). An important consequence is that grassland communities with high belowground meristem densities have the potential to regulate exotic species invasions. However, disturbances may reduce meristem densities (Burke and Grime 1996; Smith and Knapp 2001) with important consequences in grassland stability. West (2012) reported that decreases in belowground meristems of rhizomatous grass species following disturbance led to substantial increases in seed germination, with resultant increases in successful establishment by non-native invasive grasses. Further, seedling recruitment

may be the primary source for plant recruitment for many caespitose, or bunchgrass, grassland species (Bertiller and Coronato 1994).

Following germination, continuation of the life cycle depends on successful seedling growth and establishment. In our current study, both invasive grasses produced greater biomass than did their native, functionally similar counterpart, when not exposed to drought, at both ambient and elevated temperatures. This is not unexpected, as common traits often accompanying invasive species include increased biomass production (Pyšek and Richardson 2007; van Kleunen et al. 2010; Dickson et al. 2012; Wilson et al. 2012). Indeed, both *B. ischaemum* and *B. inermis* were introduced because of greater biomass production, to serve as both a forage and facilitator of soil stabilization (Celarier and Harlan 1955; Eck and Sims 1984).

In our study, reductions in germination of the invasive grasses under drought were less substantial compared to the reduction in biomass production under similar water stress. Previous studies have found soil moisture appropriate for seed germination may not be adequate for seedling growth and development (Qi and Redmann 1993; Llorens et al. 2004). Due to soft, palatable tissues and small size, the seedling establishment stage of the plant's life cycle is the most sensitive to damage or death as a result of environmental stressors such as extreme temperatures and drought (Grubb 1977; Qi and Redmann 1993; Abbott and Roundy 2003; Cipriotti et al. 2008). We observed greater percent reductions in biomass production between well-watered and drought conditions for invasive species of both functional groups, compared to native counterparts. This may suggest native seedlings have greater physiological adaptations to warmer, drier conditions. However, the considerable increase in biomass production of the invasive species, of each

functional group, as evidenced by increased germination, growth rate, and biomass production may be the primary mechanism of successful invasibility for invasive perennial grasses. That the warm-season native species produced negligible biomass under elevated temperature or drought, while the corresponding invasive species successfully established may become a particularly important mechanism of invasibility during periods of intense drought and elevated temperatures.

Most research on factors influencing exotic plant invasions has focused on propagule availability or aboveground plant traits of the invading species (e.g. Tilman 1988), and indeed multiple aboveground characteristics have been shown to be potentially important factors increasing invasibility. Traits often accompanying invasive species include broad range and rapid dispersal (Dukes and Mooney 1999), greater phenotypic plasticity (Droste et al. 2009; Davidson et al. 2011), enhanced abilities to withstand disturbances (Willis et al. 2010; Jiménez et al. 2011; Wolkovich et al. 2013), increased biomass production (Wilson et al. 2012), higher fecundity (Bennett et al. 2011), and production of allelopathic chemicals (Greer et al. 2014). However, above- and belowground communities are inextricably linked, and it is well documented that soil organisms play important roles in regulating ecosystem-level processes in native systems. Additionally, plants can alter soil microbial communities in ways that feed back to affect the performance of that species or other plant species (Bever et al. 1997). These soil feedbacks can alter the success of invasive species, with individual studies showing both positive and negative feedbacks during invasion (Reinhart et al. 2003; Bever et al. 2010). Recent studies have indicated AM fungi play an important role in plant invasions, determining patterns of abundance and invasiveness of non-native species (Pringle et al.

2009; Johnson et al. 2013). Non-native invasive plant species have been shown to alter the density and/or composition of the AM fungal communities, which may feedback on the subsequent spread of the introduced plant species (Bever 2002, 2003; Reinhart and Callaway 2006). One mechanism of invasion success may be that native soil microbial communities, including AM fungi, facilitate the success of non-native plant species (Reinhart and Callaway 2006) or that a non-native plant species directly degrade beneficial microbial communities (Cipollini et al. 2012).

Virtually all perennial plants in natural grasslands form AM symbioses, but the degree to which they depend on the relationship varies among plant taxa, fertilization, season, or climatic conditions. A previous greenhouse study found AM colonization of a native warm-season grass did not differ from *Bothriochloa bladhii* (Wilson et al. 2012), while an earlier study that examined a wide array of grassland grasses found roots of *B. bladhii* were associated with significantly greater levels AM colonization (Wilson and Hartnett 1998). In our study, AM colonization within roots of either warm- or cool-season grasses did not differ between native or invasive species. However, AM fungal hyphae extracted from soil associated with the warm-season invasive grass were significantly more abundant, compared to the native counterpart when plants were grown under ambient temperatures, regardless of water-availability. It has been proposed that cool-season prairie grasses are relatively less dependent on the AM symbiosis for nutrient uptake, compared to warm-season grasses, and thus typically contain less AM fungal structures with their roots (Wilson and Hartnett 1998). We observed invasive and native species from both warm- and cool-season functional groups associated with AM fungi, as evidenced by considerable hyphal abundance, both in plant roots and soils.

Because associations with AM fungi, as well as non-AM fungi, may participate in host water acquisition (Augě et al. 2001; Barrow 2003; Kannadan and Rudgers 2008; Rudgers and Swafford 2009; Herrera et al. 2011) and in thermal tolerance (McLellan et al. 2007, Song et al. 2012), we hypothesized each of these fungal functional groups would be relatively more abundant when plants were exposed to environmental stress (temperature or water-availability). However, this was not supported by our data, as few differences were observed in total microbial biomass, including AM or saprophytic fungi, of either native or invasive species in response to adverse environmental conditions.

Our results indicate invasive perennial grasses are generally competitively superior to functionally similar native species at early life stages (i.e. germination and seedling growth), across all experimental temperature and drought combinations. As more intense and frequent droughts, coupled with elevated temperatures, are projected for North American Great Plains (Easterling et al. 2000; Solomon et al. 2007), our data suggest invasive grasses will continue to invade into native grasslands, out-competing native at potentially greater magnitudes than currently observed. We propose these highly invasive warm- and cool-season invasive perennial grasses are well adapted to low soil moistures and elevated temperatures, posing a serious threat to native grasslands of the Great Plains.

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FIGURES

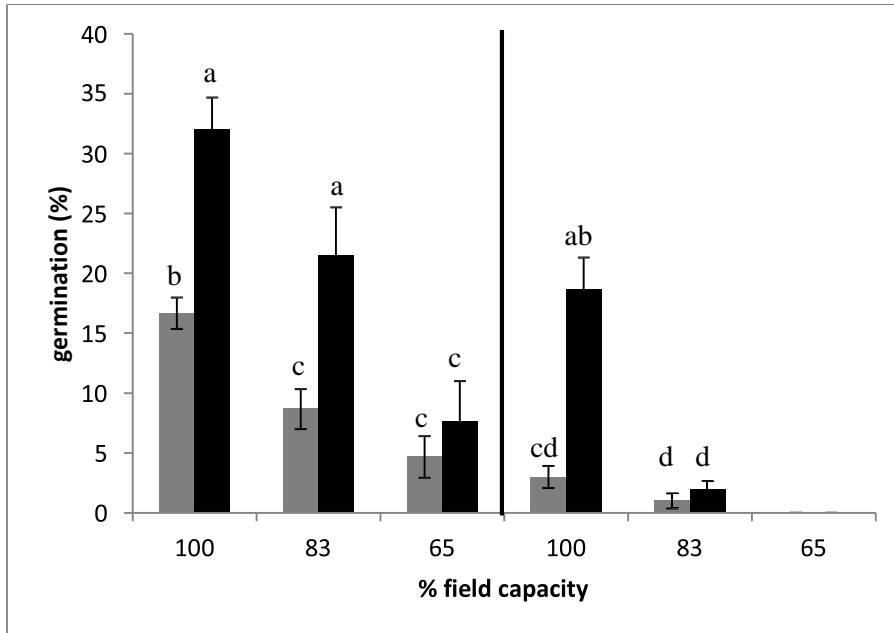


Figure 1. Germination of native (*Schizachyrium scoparium*; gray bar) and invasive (*Bothriochloa ischaemum*; black bar) warm-season grass seeds germinated under ambient (left panel: 24 °C) or elevated (right panel: 29 °C) temperatures maintained under well-watered, moderate, or drought conditions. Bars with different letters differ significantly from each other ($p < 0.05$).

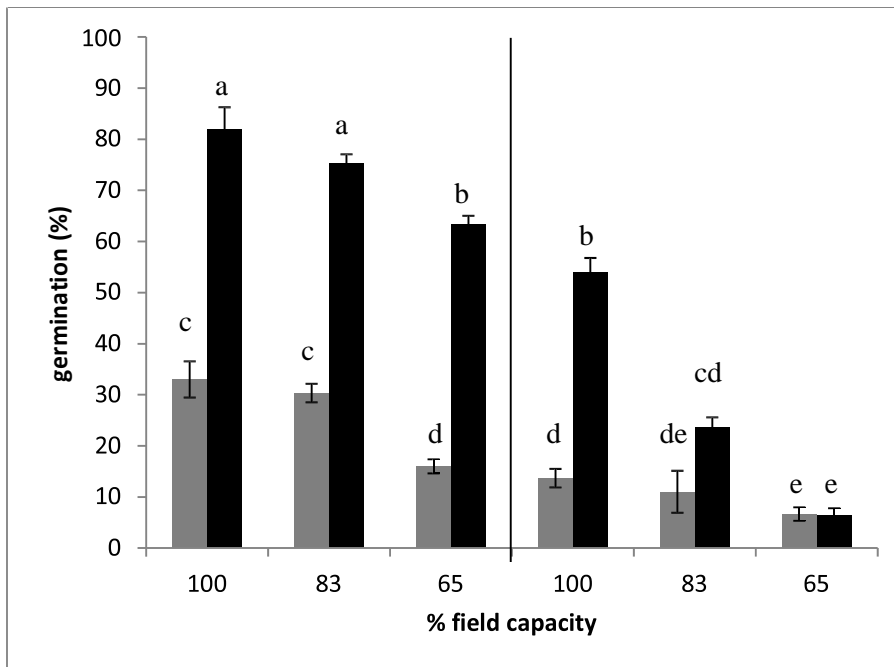


Figure 2. Germination of native (*Pascopyrum smithii*; gray bar) and invasive (*Bromus inermis*; black bar) cool-season grass seeds germinated under (left panel: 17°C) or elevated (right panel: 22 °C) maintained under well-watered, moderate, or drought conditions. Bars with different letters differ significantly from each other ($p < 0.05$).

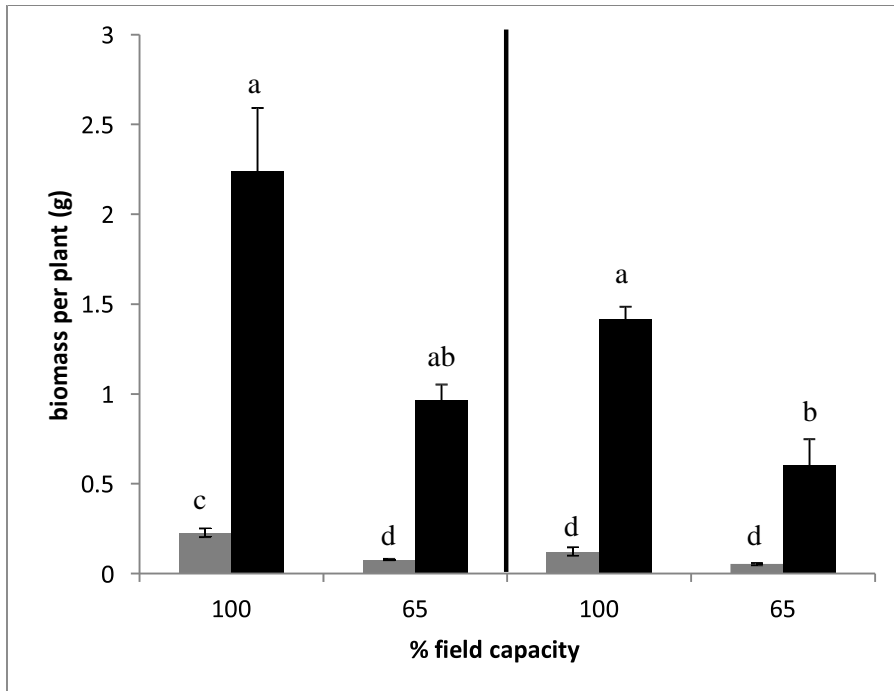


Figure 3. Biomass production of native (*Schizachyrium scoparium*; gray bar) and invasive (*Bothriochloa ischaemum*; black bar) warm-season grasses grown at ambient (left panel: 24 °C) or elevated (right panel: 29 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Bars with different letters differ significantly from each other ($p < 0.05$).

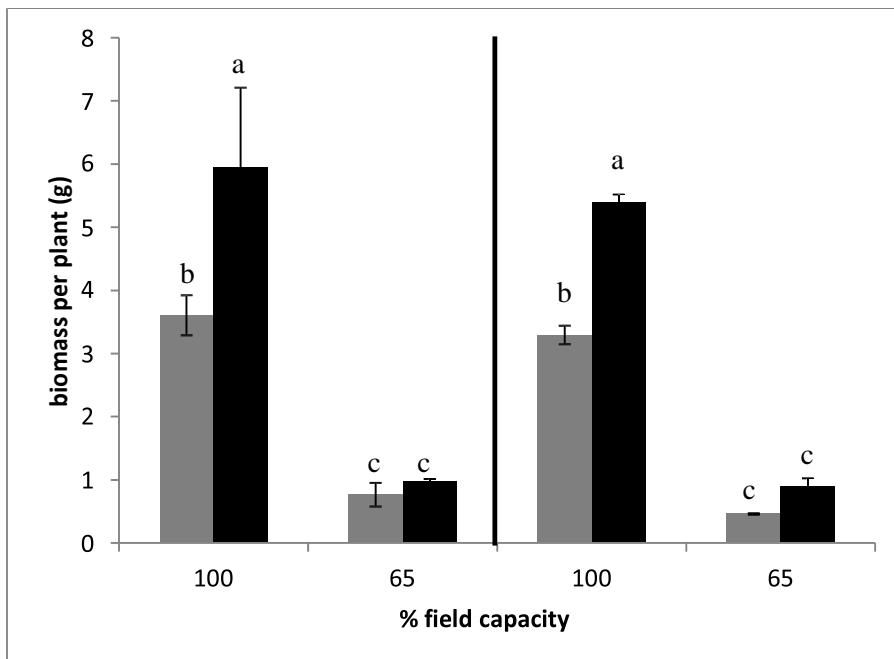


Figure 4. Biomass production of native (*Pascopyrum smithii*; gray bar) and invasive (*Bromus inermis*; black bar) cool-season grasses grown at ambient (left panel: 17°C) or elevated (right panel: 22 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Bars with different letters differ significantly from each other ($p < 0.05$).

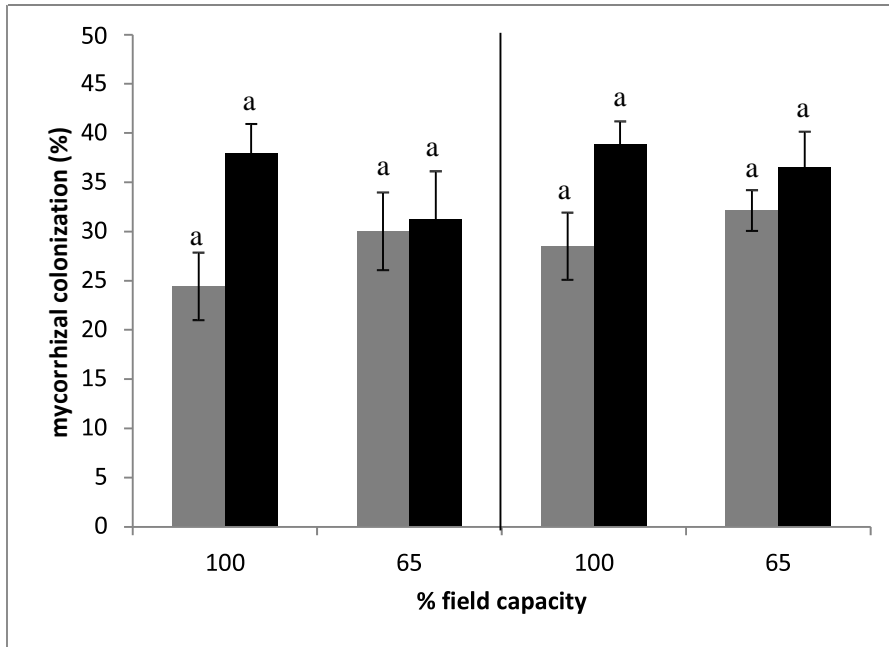


Figure 5. Mycorrhizal fungal colonization of native (*Schizachyrium scoparium*; gray bar) and invasive (*Bothriochloa ischaemum*; black bar) warm-season grasses grown at ambient (left panel: 24 °C) or elevated (right panel: 29 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Bars with different letters differ significantly from each other ($p < 0.05$).

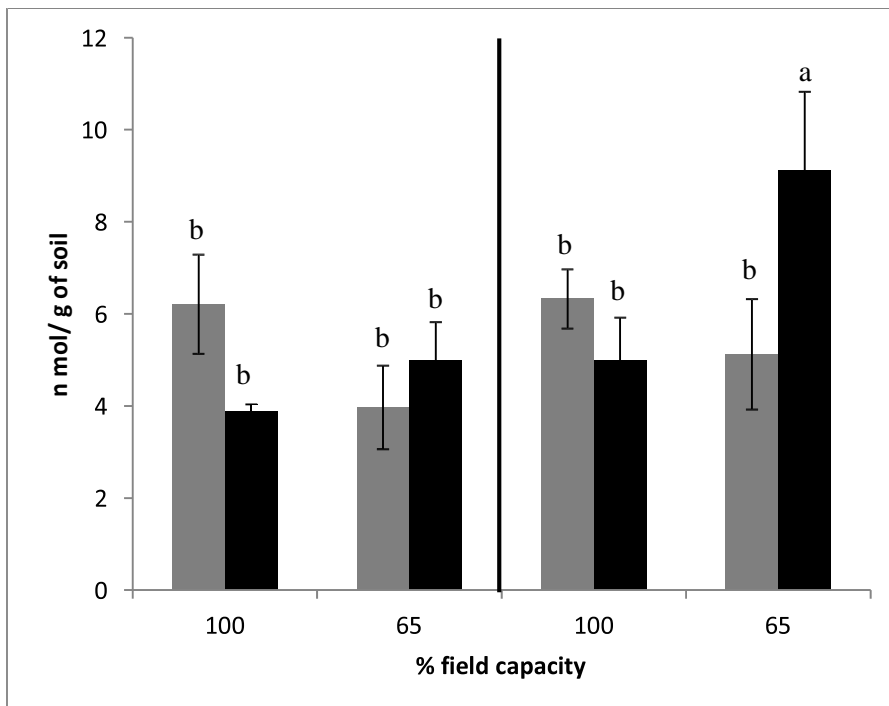


Figure 6. Total microbial biomass of native (*Schizachyrium scoparium*; gray bar) and invasive (*Bothriochloa ischaemum*; black bar) warm-season grasses grown at ambient (left panel: 24 °C) or elevated (right panel: 29 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Microbial biomass was determined by phospholipid fatty acid analyses. Bars with different letters differ significantly from each other ($p < 0.05$).

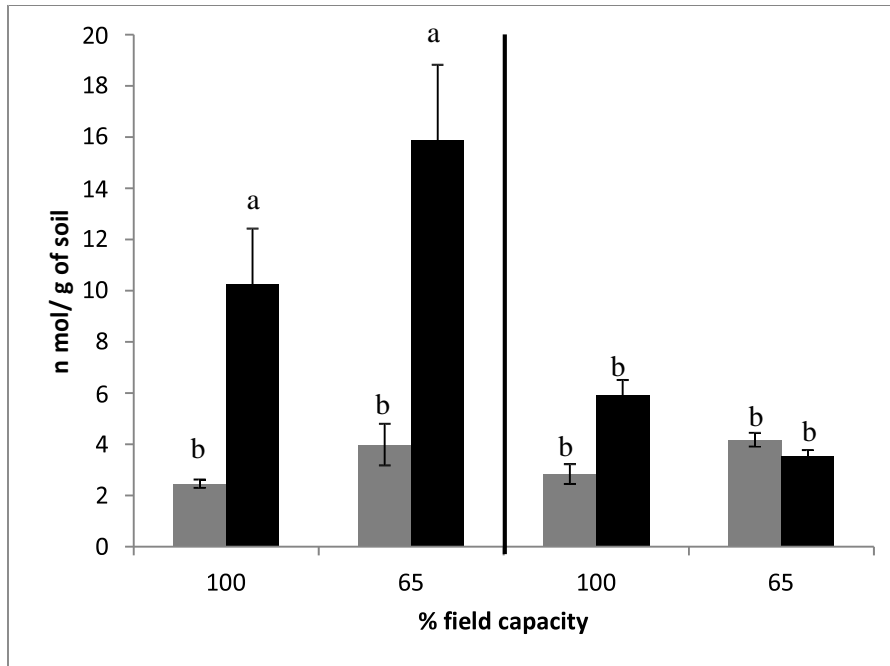


Figure 7. Mycorrhizal fungal biomass of native (*Schizachyrium scoparium*; gray bar) and invasive (*Bothriochloa ischaemum*; black bar) warm-season grasses grown at ambient (left panel: 24 °C) or elevated (right panel: 29 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Microbial biomass was determined by neutral lipid fatty acid analyses. Bars with different letters differ significantly from each other ($p < 0.05$).

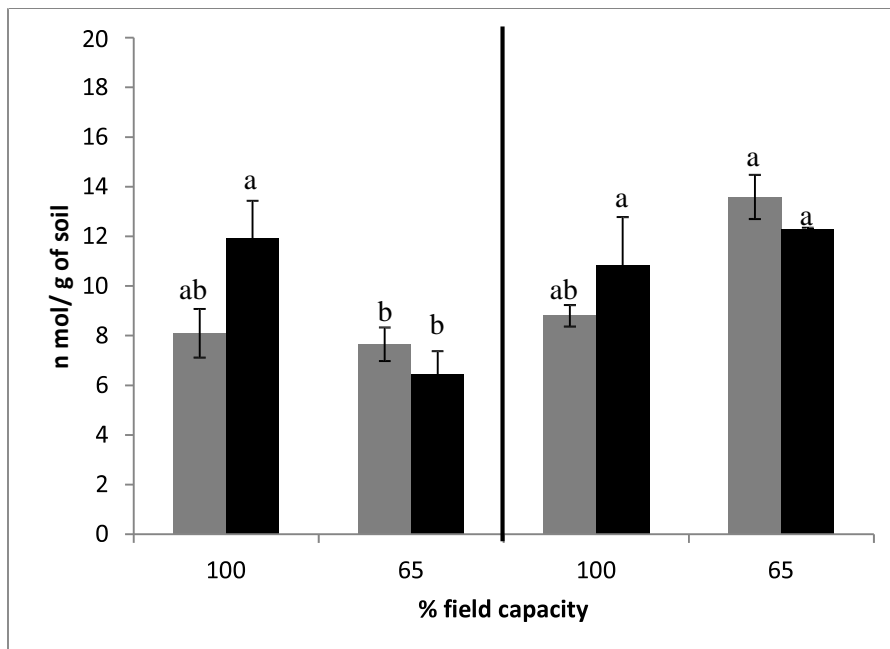


Figure 8. Saprophytic fungi biomass of native (*Schizachyrium scoparium*; gray bar) and invasive (*Bothriochloa ischaemum*; black bar) warm-season grasses exposed to ambient (left panel: 24 °C) or elevated (right panel: 29 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Microbial biomass was determined by neutral lipid fatty acid analyses. Bars with different letters differ significantly from each other ($p < 0.05$).

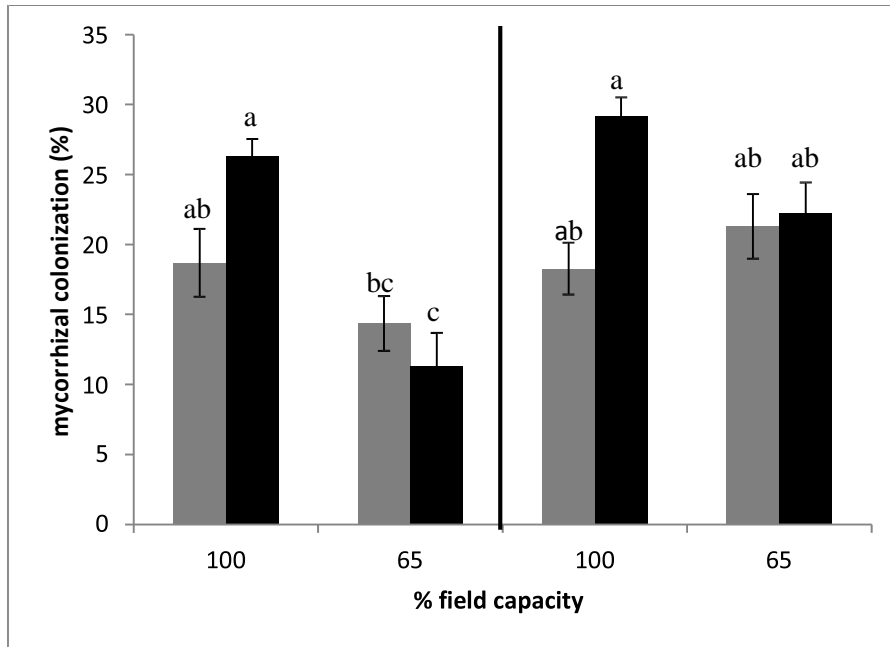


Figure 9. Mycorrhizal fungal colonization of native (*Pascopyrum smithii*; gray bar) and invasive (*Bromus inermis*; black bar) cool-season grasses exposed to ambient (left panel: 17°C) or elevated (right panel: 22 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Bars with different letters differ significantly from each other ($p < 0.05$).

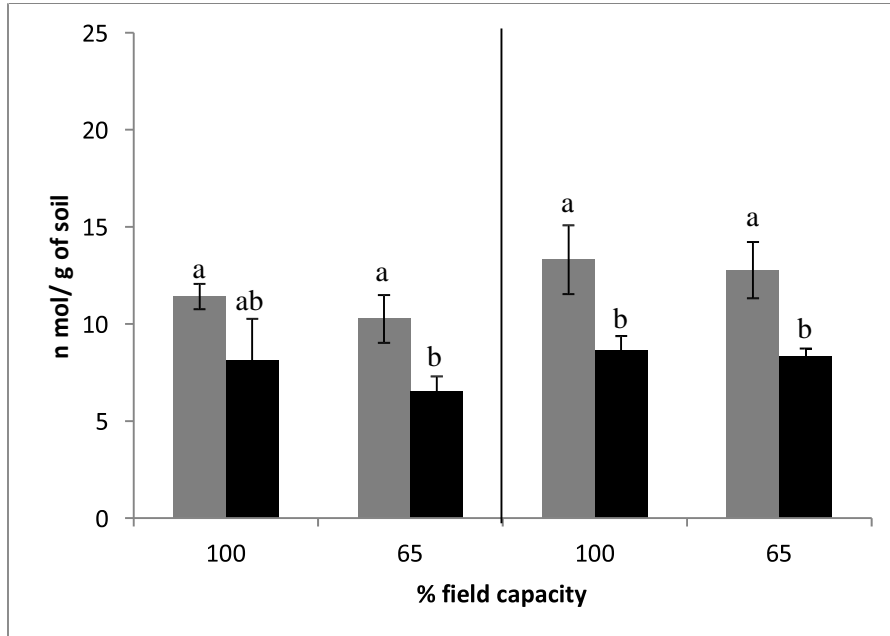


Figure 10. Total microbial biomass of native (*Pascopyrum smithii*; gray bar) and invasive (*Bromus inermis*; black bar) cool-season grasses exposed to ambient (left panel: 17°C) or elevated (right panel: 22 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Microbial biomass was determined by phospholipid fatty acid analyses. Bars with different letters differ significantly from each other ($p < 0.05$).

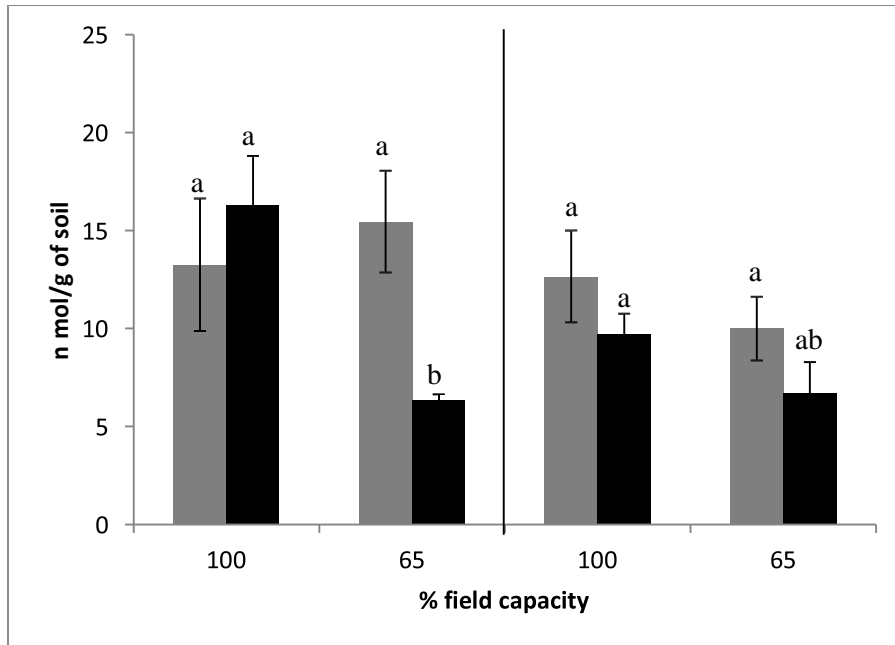


Figure 11. Mycorrhizal fungal biomass of native (*Pascopyrum smithii*; gray bar) and invasive (*Bromus inermis*; black bar) cool-season grasses exposed to ambient (left panel: 17°C) or elevated (right panel: 22 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Microbial biomass was determined by neutral lipid fatty acid analyses. Bars with different letters differ significantly from each other ($p < 0.05$).

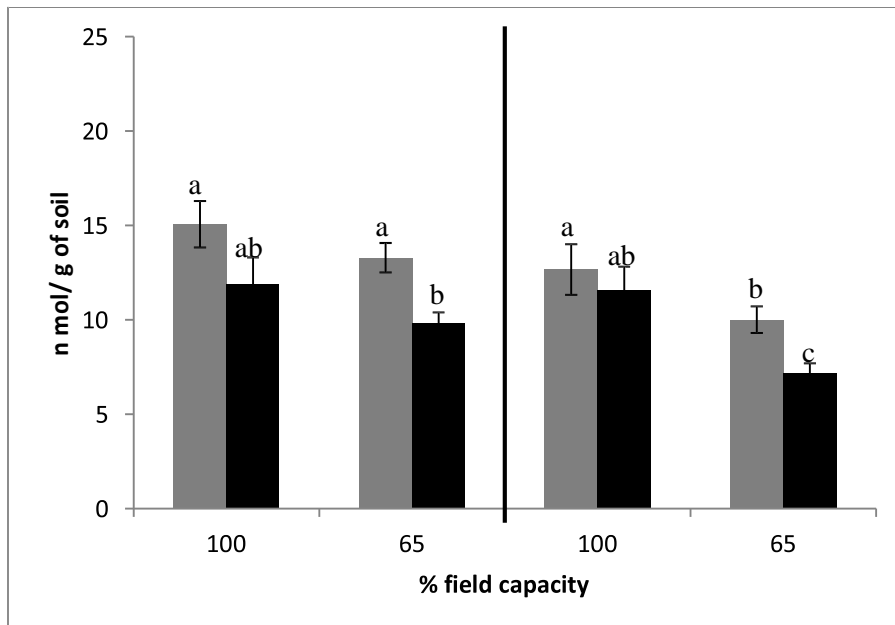


Figure 12. Saprophytic fungal biomass of native (*Pascopyrum smithii*; gray bar) and invasive (*Bromus inermis*; black bar) cool-season grasses exposed to ambient (left panel: 17°C) or elevated (right panel: 22 °C) temperatures. Seedlings were maintained at well-watered (100 % field capacity) or drought (65% field capacity) conditions. Microbial biomass was determined by neutral lipid fatty acid analyses. Bars with different letters differ significantly from each other ($p < 0.05$).

CHAPTER II

INVASIVE PRAIRIES GRASSES OUT-PERFORM NATIVE GRASSES AT ELEVATED TEMPERATURE AND DROUGHT

ABSTRACT

Biological invasion by non-native plants is a major cause of native ecosystem loss. It has been suggested that climate change will increase the success of biological invaders, yet studies that combine these global changes are limited. Climate change may directly increase success of non-natives as these species often possess traits that are favored by increasing temperatures, or indirectly through negative impacts on native vegetation or alterations in native soil communities, including symbiotic arbuscular mycorrhizal (AM) fungi. In our study, we assessed native and invasive grasses maintained under elevated temperature and drought. Our experiment, a full-factorial design, examined two caespitose warm-season grasses (native [*Schizachyrium scoparium*] and invasive [*Bothriochloa ischaemum*]) and two cool-season grasses (native counterpart [*Pascopyrum smithii*] and invasive [*Bromus inermis*]). Each species was grown at two temperatures (ambient; ambient+5C) and four soil water treatments (100% field capacity [FC]; 85% FC; 75% FC; 65% FC). Plant vegetative and reproductive

biomass and percent root colonization by AM fungi was assessed at senescence. Our data indicated invasive warm-season grasses produced as much as 500% greater vegetative and reproductive biomass across all treatments, compared to their paired native counterparts. Furthermore, increased temperature and soil moisture treatments showed no effect on reproductive biomass of invasive grasses, compared to ambient treatments, while drought treatments reduced reproductive biomass in native species. Mycorrhizal root colonization was significantly greater in the invasive grass, *B. ischaemum*, as compared to the native grass, *S. scoparium*. Biomass production was similar between native and invasive cool-season grasses when receiving sufficient water. However, drought resulted in a significantly greater reduction in biomass production of native *P. smithii*, compared to invasive *B. inermis*. Understanding how belowground associations are influenced by plant invasions, with subsequent plant-soil feedbacks, could provide critical links to the conservation and restoration of native systems. Our results suggest invasive grasses may increase as a major threat to native grasslands as global temperature and regional drought increase.

INTRODUCTION

One of the most imminent ecosystem-level threats to native biodiversity is the invasion of non-native species (Vitousek et al. 1997; Clavero and García-Berthou 2005), which has been linked to more species extinctions than any other aspect of global change (D'Antonio and Vitousek 1992). Invasive plant species threaten native biodiversity by outcompeting native species for nutrient or water acquisition, altering nutrient cycling, or shifting disturbances such as fire frequency (D'Antonio and Vitousek 1992; Dukes and Mooney 1999; Brooks et al. 2004; Dilleuth et al. 2008; Corbin and D'Antonio 2010).

Some of the characteristics of invasive plants that facilitate invasibility include plant anatomical traits such as production of taller biomass or longer and wider leaves or greater root: shoot ratio, or physiological traits such as improved seed production, as compared to native species (Sandel and Dangremond 2012). Invasive plants may also alter biotic interactions, such as soil biota. And plant-soil-microbial interactions.

Non-native invasive plants are a major factor in the reduction and fragmentation of native ecosystems altering landscape and habitat dynamics, with corresponding losses in biodiversity, habitat quality, and alterations in ecosystem functions. In the central Great Plains of North America, non-native plants frequently dominate following soil disturbances, such as tilling, and become persistent problems for land managers (D'Antonio and Vitousek 1992; Thuiller 2007), decrease native biodiversity, with resultant community- and ecosystem-level effects. For example, community level alterations of the Great Plains have been documented for *Bromus inermis* (Baum et al. 2004; Dilleuth et al. 2008; Grant *et al.* 2009) and *Bothriochloa ischaemum* (Hickman et al. 2006), with reductions in abundance and diversity of grassland arthropod communities following establishment of these non-natives into native grasslands. These community-level alterations may lead to ecosystem-level disruptions, such as grassland songbird populations (Hickman et al. 2006) or small mammal populations (Greer 2013).

Most previous research assessing non-native plant invasions has focused on propagule availability or aboveground plant traits of the invading species (Bever et al. 2010; Elgersma and Ehrenfield 2011; Rout and Callaway 2012). As a result, we know considerably less about invasibility as an emergent property of the comprehensive plant-soil interactions or influencing factors (Levine et al. 2004). However, above- and

belowground communities are inextricably linked (Wilson et al. 2012), and it is well documented that soil organisms play important roles in regulating ecosystem-level processes in native systems (Vogelsang and Bever 2009; Bever et al. 2010). Additionally, plants can alter soil characteristics that feed back to affect the performance of that species or other plant species (Bever et al. 1997). For example, the alteration of arbuscular mycorrhizal (AM) fungi can be a focal point shaping the invasion and survival of non-native species (Herre et al. 1999; Hawkes et al. 2006; Van der Putten et al. 2007; Jordan et al. 2012; Johnson et al. 2013). Alternatively, non-native invasive grasses such as *Cynodon dactylon* and *Bothriochloa ischaemum* have been shown to directly inhibit establishment and growth of native grasses through exudation of allelopathic phytotoxic chemicals (Mahmoodzadeh 2010; Greer et al. 2014).

Climate change scenarios indicate possible increases in atmospheric temperatures of 5° C within the next century, exacerbated by more intense and prolonged droughts (Easterling et al. 2000; Solomon 2007; Pyke et al. 2008; Mishra and Singh 2010). At global, regional, and local scales, temperature and precipitation are the major limitations to plant distributions (Bond and Richardson 1990; Guisan and Zimmermann 2000; Knapp and Smith 2001, Walther et al. 2002; Thuiller et al. 2005). The net effect of climatic alterations on ecosystem invasibility is likely to depend on community-level composition of non-native and native species that are more competitive under the new climate (Bradley et al. 2010), and the net effects these environmental changes have on native species of the region (Byers 2002). For example, with rising temperatures, novel competitive interactions between cool-season and warm-season grasses are likely to occur (Alward et al. 1999; Dukes and Mooney 1999).

It has been suggested that increases in temperature and drought will (Dukes and Mooney 1999; Hellmann et al. 2008; Verlinden et al. 2013) favor species with traits often possessed by invasive species, such as broad environmental tolerance and rapid growth rates (Sexton et al. 2002). Furthermore, these alterations in climate will likely result in reductions of resiliency of native ecosystems with concomitant decrease in dominance of natives (Niu and Wan 2008), providing windows of opportunity for successful establishment of non-native species (Gritti et al. 2006).

In the central Great Plains of North America, problematic invasive plant species have been seeded extensively for decades for erosion control and fast-growing forages for livestock (Celarier and Harlan 1955), resulting in vast areas of non-native species that are potentially highly adaptable and able to tolerate a wide variety of climatic conditions (Sexton et al. 2002). However, little empirical data exists that comparatively assess growth of non-native and native plant species under projected climate change. Our study assesses biomass production of a warm- and a cool-season non-native grassland grass species compared with a functionally similar native species grown under ambient and elevated temperatures superimposed with a wide continuum of drought conditions.

MATERIALS AND METHODS

Soil collection: Soil was collected from Konza Prairie Biological Station, Kansas, USA and transported to Oklahoma State University Greenhouse facilities. Konza Prairie Biological Station is a native tallgrass prairie research site, and soil was collected from areas dominated by native warm-season grasses that include *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium*, and sub-dominants including warm-

season species such as *Bouteloua curtipendula*, and *B. hirsuta*, as well as cool-season grasses such as *Pascopyrum smithii*, and *Koeleria macrantha*.

Study species: Invasive species *Bothriochloa ischaemum* was paired with *S. scoparium*, a functionally similar native warm-season grass species and invasive species *Bromus inermis* was paired with the native, functionally similar caespitose grass, *P. smithii*.

Rhizome collection: Plant communities consisting of monoculture stands of invasive and native warm- and cool-season grasses were located in upland prairie locations. Invasive and corresponding native species were collected from adjacent sites. Plant samples were excavated using a 10.8 cm diameter core to a 10 cm depth and all above- and belowground structures (rhizomes, roots, stems) and associated soil were collected in a plastic bag, stored in a cooler for transport to a greenhouse facility at Oklahoma State University, Stillwater, OK. The soil cores were closely examined to determine there were no rhizomes of non-target species within the sample. Aboveground biomass was clipped to a height of 5 cm prior to transplanting rhizomes. Soil cores containing plant samples were transplanted into four liter pots and pots were filled with 3 kg of native prairie soil collected in areas from which the soil cores were collected.

Experimental design: The complete experimental design consisted of 32 treatment combinations: 4 plant species (2 warm-season and 2 cool-season) x 2 temperatures x 4 drought treatments, arranged in a complete randomized block design with 6 replications for a total of for a total of 192 pots. The warm-season plants were held at an ambient temperature of 24° C with an elevated temperature of 29° C. The cool-season plants were

maintained an ambient temperature of 17° C, with the elevated temperature of 22° C. This 5 degree increase is based on the projected temperature change of central and southern Great Plains within the next century (Solomon 2007). Soil moisture treatments were based on permanent wilt point of grasses in grassland soils, determined by the pressure-plate apparatus method, in which 1.5 MPa of pressure is exerted onto the soil sample until equilibrium (Richards and Weaver 1943). Soil moisture was maintained at 90-100% field capacity (FC) (i.e. well-watered), 85% (moderate), 75% (drought), and 65% FC (i.e. near permanent wilt point, extreme drought). Soil moisture and air temperature were monitored daily throughout the study.

Harvest: Plants were maintained for 24 weeks, at which time plants were harvested, roots and shoots were separated, dried at 60° C for 48 hours, and weighed. Aboveground biomass was separated into reproductive and vegetative biomass. We also assessed intra-radical arbuscular mycorrhizal fungal (AMF) colonization.

Quantification of intra-radical mycorrhizal colonization: Three subsamples of dried roots from each individual plant was stained with Trypan blue to determine percent mycorrhizal root colonization. AM fungal root colonization was scored by using the magnified gridline intersect method (McGonigle *et al.* 1990), using a compound microscope (200-400x) to measure the percentage of root colonized by total (hyphae + vesicles + arbuscules) AM root colonization.

Statistical Analyses

To assess temperature and water-availability on biomass production or AM fungal root colonization of native and invasive prairie grasses, a three-way analysis of variance

for species (native, invasive) x temperature (ambient, elevated) x soil moisture (100, 85, 75, and 65% field capacity) was conducted for each parameter. To distinguish production within a single species, a two-way analysis of variance was conducted for temperature x soil moisture. Tukey's Honest Significant Difference (HSD) test was performed to determine significant differences. All statistical analyses for these experiments were performed by using SigmaStat statistical package (version 12.5, Systat Software, San Jose, CA). Statistical significance level used in all the analyses was $P \leq 0.05$.

RESULTS

Warm-season grasses: Bothriochloa ischaemum biomass production exceeded that of native *S. scoparium* by nearly 500% (Table 1), regardless of temperature or water-availability. Temperature and water-availability did not affect reproductive success of the invasive *B. ischaemum*, as there were no significant differences in reproductive biomass production between temperature or water-availability combinations (Table 2). However, reproductive capability of *S. scoparium* decreased in response to reduced water-availability (Table 2).

When grown under ambient temperature, *B. ischaemum* roots were associated with significantly greater AM root colonization at 100% , 75%, and 65 % FC, as compared to the native grass, *S. scoparium* (Table 3). When subjected to elevated temperatures, *B. ischaemum* had greater percent root colonization, compared to native *S. scoparium* at all soil moisture levels (Table 3).

Cool-season grasses: We assessed plant growth and intra-radical mycorrhizal colonization of an invasive (*B. inermis*) and native (*P. smithii*) cool-season caespitose

grass. Both species are commonly found in the central and northern Great Plains. Biomass production by *B. inermis* was significantly less at 65% and 75% FC, compared to 100% and 85% FC, when grown under ambient temperatures (Table 4). However, there were significant decreases in biomass production by the native grass, *P. smithii*, as water-availability decreased (Table 4). At ambient temperatures, *P. smithii* produced significantly greater biomass at 100% and 85% FC than at 65% FC (Table 4). However, at elevated temperatures, *P. smithii* exhibited a significant decrease in biomass production from 100% FC to 85% FC, as well as 75% FC to 65% FC (Table 4), suggesting the effects of drought are exacerbated under elevated temperatures. Under ambient temperatures, native *P. smithii* produced greater total biomass at 100% and 85% FC when compared to the invasive *B. inermis*, but produced noticeably less at 75% FC and significantly less at 65% FC (Table 4). Regarding reproductive biomass production, *B. inermis* successfully reproduced in all four moisture treatments when exposed to ambient temperatures (Table 5), whereas *P. smithii* only did so at 100% and 85% FC (Table 5). At elevated temperatures, *B. inermis* showed signs of reproductive capabilities at 100% and 85% FC (Table 5), while *P. smithii* failed to show any evidence of reproductive efforts (Table 5). In all combinations of moisture and temperature treatments, *B. inermis* displayed greater colonization by symbiotic AM fungi (Table 6).

DISCUSSION

It has been suggested that invasive grasses are able to tolerate wider climatic conditions, as compared to native species (Bradley et al. 2010; Verlinden and Nijs 2010; Diez et al. 2012). In our study, total biomass production by *B. ischaemum* was not affected by either drought or temperature. Total biomass production by *S. scoparium* was

not significantly affected by climate; however, little biomass was produced by this species under any of the temperature or drought conditions. Further, there was a decrease in reproductive effort as drought intensity increased when *S. scoparium* was maintained at both the ambient and elevated temperature. In fact, *B. ischaemum* produced nearly 500% greater biomass than *S. scoparium* across all treatments. This tremendous increase in production by the invasive species, compared to the native species suggests that *B. ischaemum* may not require adaptations to elevated temperatures or drought stress, but will continue to persist under projected climatic scenarios due to its ability to consistently produce greater biomass than functionally similar native species, regardless of climate. *Pascopyrum smithii* produced greater biomass when plants received adequate water (100 and 85% FC) under ambient temperature. This was surprising, as we hypothesized *B. inermis* would out-perform native *P. smithii* regardless of moisture conditions or temperature, as this is a frequent competitive trait of many invasive grass species. However, when plants were stressed, by reducing water-availability (75% or 65% FC) or elevating temperature, the invasive grass out-performed the corresponding native species. This suggests that if temperatures do not increase above current average (ambient) temperature and water-availability remains close to field capacity, *P. smithii* may be able to successfully compete with *B. inermis* for resources. However, when plants were subjected to drought conditions, *B. inermis* exerted a competitive advantage over *P. smithii* by producing significantly greater biomass, suggesting physiological capabilities allowing *B. inermis* to better utilize available moisture than the native *P. smithii*. These data agree with previous research suggesting invasive plant species possess a wider breadth of climatic tolerances (Bradley et al. 2010; Diez et al. 2012; Verlinden et al.

2013). This also suggests a different strategy between invasive species utilizing different photosynthetic pathways.

In our study, plants were allowed to grow for 14 weeks, at which time all but two *B. ischaemum* individuals produced inflorescences. However, nearly half (46%) of all *S. scoparium* individuals exhibited no evidence of inflorescence initiation at the time of harvest. Our study is in agreement with previous studies (Harmony and Hickman 2004; Wilson et al. 2012) that indicate *B. ischaemum* possesses traits often linked to superior competitive abilities, including rapid growth and earlier maturation. Our study furthers these findings to include superior performance of *B. ischaemum* when grown under extreme climatic conditions. Similarly, the invasive species *Bromus inermis* produced inflorescences at all moisture levels under ambient temperatures, whereas the corresponding native, *P. smithii*, failed to produce inflorescences when water-availability was reduced below 85% field capacity and no inflorescences were produced by the native species when maintained under elevated temperatures, while *B. inermis* was able to produce inflorescences at the well-watered treatments (100 and 85% FC). These data suggest *B. inermis* may continue to produce seed under warmer, drier conditions, allowing the species to persist, while reproduction of *P. smithii* could fail under climate scenarios projected for the Great Plains, negatively affecting future recruitment of the native species. Successful associations with AM fungi may play an increasingly important role in invasive species.

The association of arbuscular mycorrhizal (AM) fungi with a plant species can be a central force shaping in determining patterns of abundance and invasiveness of non-

native species (Bever et al. 2010). Non-native invasive species have been shown to disrupt closely interlinked relationships between plants and symbionts, many of which have co-evolved within native systems (Inderjit and van der Putten 2010). The potential disruption of this association may be particularly important for warm-season grasses, which dominate the vegetation of the Great Plains and are highly dependent on the symbiosis for nutrient and water uptake in these characteristically low nutrient soils (Wilson and Hartnett 1998; Antoninka *et al.* 2009; Hartnett and Wilson 2002). In our study, mycorrhizal colonization was greater within *B. ischaemum* roots (45-52%), compared to *S. scoparium* (25-40%), regardless of temperature or water-availability. The rapid growth and development of *B. ischaemum* could serve as a function of preempting more desirable AM fungal communities for its own growth and the detriment of the native species, as suggested by Wilson et al. (2012) in the congeneric *B. bladhii*. This microbially mediated outcome, as evidenced by greater AM colonization of the roots of *B. ischaemum*, is described as an ‘enhanced mutualism response’, in which native mutualisms facilitate the success of invasive plant species (Johnson et al. 2013). Cool-season grasses are typically less dependent on AM fungi than warm-season grass species (Wilson and Hartnett 1998), although these symbionts perform the same functions as with warm-season grasses, enhancing nutrient and moisture uptake. A similar ‘enhanced mutualism response’ was observed by the cool-season grasses of our study. Roots of invasive *B. inermis* were associated with greater levels of mycorrhizal colonization than *P. smithii*, possibly allowing this invasive species to commandeer the native fungi, facilitating successful invasibility. In our study, root colonization by AM fungi remained greater in both invasive grasses, as compared to native counterparts even under elevated

temperature and severe drought. Because associations with AM fungi may participate in host water acquisition (Augě et al. 2001) and in thermal tolerance (McLellan et al. 2007; Song et al. 2012) ‘winning the battle’ for selection of native fungi may play an increasingly important role as climate change incurs higher temperatures and more frequent and more severe droughts.

Our results indicate invasive forage grasses are competitively superior to functionally similar dominant native species under variable climatic conditions, including high levels of moisture stress and elevated temperatures. As more intense and frequent droughts, coupled with elevated temperatures, are projected for much of the Great Plains (Easterling et al. 2000; Solomon 2007), our data suggest invasive grasses will continue to out-compete native species. While our native warm-season grass exhibited drought tolerance, the considerable biomass production of the corresponding non-native invasive, coupled with superior reproductive capabilities, is expected to lead to further competitive exclusions by the invasive under projected climatic conditions. While the cool-season native species was generally more sensitive to moisture stress and elevated temperatures compared to the native warm-season grass; the non-native invasive cool-season exhibited capabilities of drought tolerance that far exceeded that of the native species, producing greater biomass and inflorescences when subjected to elevated temperatures in combination with extreme moisture stress. We propose these warm- and cool-season invasive perennial species are better adapted to low soil moistures and elevated temperatures, posing a serious threat to native grasslands of the Great Plains.

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TABLES

Table 1. Aboveground biomass (g/ per plant) of native (*Schizachyrium scoparium*) and invasive (*Bothriochloa ischaemum*) warm-season grasses exposed to ambient (24° C) and elevated (29° C) temperature and varying soil moistures (100%, 85%, 75%, and 65% FC). Different letters indicate significant differences within columns, asterisks indicate significant differences within rows ($p \leq 0.05$).

	100 %	85 %	75 %	65 %
<i>S. scoparium</i> (24°)	2.405 ^b	1.892 ^b	1.487 ^b	1.469 ^b
<i>S. scoparium</i> (29°)	3.272 ^b	2.677 ^b	2.586 ^b	2.038 ^b
<i>B. ischaemum</i> (24°)	11.145 ^a	7.117 ^a	6.151 ^{*a}	7.187 ^a
<i>B. ischaemum</i> (29°)	9.802 ^a	9.032 ^a	8.402 ^a	7.031 ^{*a}

Table 2. Reproductive biomass (g/ per plant) of native (*Schizachyrium scoparium*) and invasive (*Bothriochloa ischaemum*) warm-season prairie grasses exposed to varying soil moistures (100, 85, 75, and 65% field capacities) and ambient (24° C) and elevated (29° C) temperatures.

	100%	85%	75%	65%
<i>S. scoparium</i> (24° C)	0.28	0.003	0.11	0.09
<i>S. scoparium</i> (29° C)	0.26	0.15	0.10	0.13
<i>B. ischaemum</i> (24° C)	0.67	0.58	0.59	0.85
<i>B. ischaemum</i> (29° C)	1.05	0.62	0.95	0.84

Table 3. Mycorrhizal fungal colonization of native (*Schizachyrium scoparium*) and invasive (*Bothriochloa ischaemum*) warm-season grasses exposed to ambient (24° C) and elevated (29° C) temperatures and across soil moisture gradient (100%, 85%, 75%, and 65% FC). Different letters indicate significant differences within columns, asterisks indicate significant differences within rows ($p \leq 0.05$).

	100 %	85 %	75 %	65 %
<i>S. scoparium</i> (24°)	33.855 ^{*b}	41.967 ^a	45.161 ^b	35.859 ^{*b}
<i>S. scoparium</i> (29°)	36.167 ^b	25.183 ^{*b}	39.417 ^b	39.299 ^b
<i>B. ischaemum</i> (24°)	46.651 ^a	42.801 ^a	51.297 ^a	53.975 ^a
<i>B. ischaemum</i> (29°)	51.053 ^a	44.452 ^{*a}	55.679 ^a	44.067 ^{*a}

Table 4. Aboveground biomass (g/ per plant) of native (*Pascopyrum smithii*) and invasive (*Bromus inermis*) cool-season grasses exposed to ambient (17° C) and elevated (22° C) temperatures and varying soil moistures (100%, 85%, 75%, and 65% FC). Different letters indicate significant differences within columns, asterisks indicate significant differences within rows ($p \leq 0.05$).

	100 %	85 %	75 %	65 %
<i>P. smithii</i> (17°)	16.565 ^a	16.332 ^a	11.693 ^{*b}	8.583 ^{*b}
<i>P. smithii</i> (22°)	13.192 ^a	7.328 ^{*c}	6.221 ^{*c}	5.236 ^{*b}
<i>B. inermis</i> (17°)	15.094 ^a	14.372 ^a	13.251 ^a	11.388 ^{*a}
<i>B. inermis</i> (22°)	14.355 ^a	10.508 ^{*b}	11.197 ^{*b}	4.495 ^{*b}

Table 5. Reproductive biomass (g/ per plant) of native (*Pascopyrum smithii*) and invasive (*Bromus inermis*) cool-season prairie grasses exposed to varying soil moistures (100, 85, 75, and 65% field capacities) and ambient (17° C) and elevated (22° C) temperatures.

	100%	85%	75%	65%
<i>S. scoparium</i> (24° C)	0.21	0.57	0	0
<i>S. scoparium</i> (29° C)	0	0	0	0
<i>B. ischaemum</i> (24° C)	0.73	0.84	0.33	0.01
<i>B. ischaemum</i> (29° C)	0.22	0.18	0	0

Table 6. Mycorrhizal fungal colonization of native (*Pascopyrum smithii*) and invasive (*Bromus inermis*) cool-season grasses exposed to ambient (17° C) and elevated (22° C) temperatures and across soil moisture gradient (100%, 85%, 75%, and 65% FC). Different letters indicate significant differences within columns, asterisks indicate significant differences within rows ($p \leq 0.05$).

	100 %	85 %	75 %	65 %
<i>P. smithii</i> (17°)	4.325 ^{*a}	17.433 ^b	21.621 ^a	18.001 ^b
<i>P. smithii</i> (22°)	8.783 ^a	9.398 ^c	14.183 ^b	12.833 ^b
<i>B. inermis</i> (17°)	20.667 ^b	26.683 ^a	22.601 ^a	31.398 ^{*a}
<i>B. inermis</i> (22°)	13.267 ^b	17.633 ^b	23.842 ^{*a}	14.433 ^b

VITA

Eric Benjamin Duell

Candidate for the Degree of

Master of Science

Thesis: ELEVATED TEMPERATURE AND DROUGHT FAVOR INVASIVE GRASSES OVER NATIVE SPECIES

Major Field: Natural Resource Ecology and Management

Biographical:

Education:

Completed the requirements for the Master of Science in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, Oklahoma in May, 2015.

Completed the requirements for the Bachelor of Science in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, OK, USA in 2012.

Experience:

- Spring 2015, NREM 4464 Ornithology: teaching assistant and lab instructor, Oklahoma State University
- Spring 2013-May 2015, Graduate Research Assistant, Natural Resource Ecology and Management, Oklahoma State University
- Summer 2012-Fall 2012, Research Assistant, Natural Resource Ecology and Management, Oklahoma State University
- Summer 2011-Fall 2012, Wildlife Technician, Natural Resource Ecology and Management, Oklahoma State University
- Fall 2010-Spring 2012, Research Technician, Natural Resource Ecology and Management, Oklahoma State University

Professional Memberships:

- Ecological Society of America
- Oklahoma Society of Range Management
- Soil Ecological Society
- Oklahoma Invasive Plant Council