

THESIS

CLIMATE CHANGE CONSEQUENCES OF GEOGRAPHIC VARIATION IN GROWTH
AND PHENOLOGY OF TWO DOMINANT CENTRAL US GRASSES

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ABSTRACT

CLIMATE CHANGE CONSEQUENCES OF GEOGRAPHIC VARIATION IN GROWTH AND PHENOLOGY OF TWO DOMINANT CENTRAL US GRASSES

Species can exist in a given range of climatic conditions, and these ranges have shifted in response to geologic climate change. Plant species with slower migration rates, however, may not be able to keep up with the current predicted rate of climate change. Thus, populations located peripherally to a biome may play a more significant role in sourcing future generations than previously thought. As a result of many studies, we know a lot about populations that exist central to their range, or dominant populations (DPs), of two key C₄ grass species, *Bouteloua gracilis* and *Andropogon gerardii*, that account for much of the biomass of the shortgrass steppe and tallgrass prairie, respectively. However, we know little about their corresponding peripheral populations (PPs).

This study examines ecophysiological, morphological, and whole plant differences between DPs and PPs of *B. gracilis* and *A. gerardii* under well-watered and water-stressed conditions in a reciprocal common garden experiment. Traits that were measured included predawn and midday leaf water potential, total biomass, reproductive biomass percentage, and individual reproductive and vegetative tiller mass (*A. gerardii* only), specific leaf area, fluorometer, height, and reproductive tiller density.

We found that key traits differed between DPs and PPs in both species, but these key traits were unique to each species. For *B. gracilis* phenological traits of DPs and PPs were

primarily different, whereas productivity traits were significantly different between populations of *A. gerardii*.

If, in fact, PPs of these two C₄ grasses are the propagules of future generations, the differences observed in this study may have implications as we look ahead to predicted climate patterns. In *B. gracilis*, an understanding of the differences in phenological traits may be important when we account for future adaptation, whereas knowledge about productivity differences in *A. gerardii* may help us better predict effects on ecosystem function. In both cases, more research is necessary to further develop our understanding of PPs and the potentially significant role they will play in the future.

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Chapter 1: Introduction

Overview

Pleistocene glaciations represent global warming events 5-10 times the size of that observed in the twentieth-century, but the paleorecord indicates that species moved quickly enough to track climate change instead of going extinct or evolving at the species level (Huntley 1991, Coope and Wilkins 1994, Pitelka et al. 1997, Parmesan 2006). Shifted ranges have also been documented in response to more recent climate change (Parmesan & Yohe 2003, Root et al. 2003) and it is expected that these shifts will accelerate in the future (Morin et al. 2008). However, vegetation models have suggested that migration rates much faster than those observed during post-glacial times will be required to keep up with predicted climate change (Malcolm et al. 2002; Solomon & Kirilenko 1997).

In addition to fast migration rates, species will be presented with a new challenge because many natural landscapes have been fragmented by human development (Earn et al. 2000). This will be particularly difficult for species with limited dispersal abilities like grasses (Solomon & Kirilenko 1997).

As species are faced with these challenges, individuals located peripherally to biomes or in adjacent biomes may become a significant source of traits for future dominant populations. We are better able to predict how a species will respond to predicted climate changes when we understand the biogeography and physiology of the species (Lovejoy & Hannah 2006). This master's thesis compares traits (ecophysiological, morphological, and whole plant) of individuals from peripheral populations (PPs) to those of today's dominant populations (DPs) under well-watered and water-stressed conditions.

In this study we focused on dominant C₄ grass species in two different biomes: *Bouteloua gracilis* (common name: blue grama, Figure 1.1) of the shortgrass steppe biome and *Andropogon gerardii* (common name: big bluestem, Figure 1.2) of the tallgrass prairie biome.

Due to time and money constraints, PPs are often not studied as much as DPs despite their potentially critical role in the future. For both species, effects on DPs due to grazing (Towne et al. 2005, Reeder et al. 2004, Hart 2001), fire (Towne and Kemp 2003, Parmenter 2008) and rainfall (Swemmer et al. 2006, Joern and Mole 2005) have been documented, but it is currently unknown what fundamental differences there are between DPs and PPs, or if these populations differ in their responses to water stress. We address these questions in this study because once we have a better understanding of how a dominant species will respond to climate change, we can look at more complex interactions to better understand the mechanisms (Jensen 2003).

Objectives

My objectives for this study are the following:

1. How do ecophysiological, morphological, and whole plant traits compare between individuals collected from DPs vs. individuals from PPs for C₄ grasses that dominate the shortgrass steppe (*B. gracilis*) and tallgrass prairie biomes (*A. gerardii*)?
2. Do individuals of *B. gracilis* and *A. gerardii* from DPs respond differently to water stress than individuals from PPs?

DPs of *B. gracilis* were collected from the Shortgrass Steppe Long-Term Ecological Research (SGS) site in Colorado and PPs of *B. gracilis* were collected from the Konza Prairie Biological Station (KNZ) in Kansas. All individuals were transplanted into two common

gardens, one located at SGS (Figure 1.3) and the other at KNZ (Figure 1.4). We hypothesized that DPs and PPs would have significant differences, and that the dominant populations coming from Colorado, an environment with lower water resources, would be less sensitive to water stress due to local adaptation.

To check for consistency, we did the reciprocal experiment with *A. gerardii*. DPs were collected from KNZ where native grasslands are dominated by this species, and PPs were collected from the Front Range of northern Colorado. We again hypothesized that DPs and PPs would not exhibit identical traits, and that the PPs (from CO, the lower resource environment) would be less sensitive to water stress.



Figure 1.1: *Bouteloua gracilis* (common name: blue grama)



Figure 1.2: *Andropogon gerardii* (common name: big bluestem)



Figure 1.3: The Shortgrass Steppe (SGS) common garden site located at the Central Plains Experimental Range, is a semi-arid grassland located in northeastern Colorado ($40^{\circ}49'N$, $104^{\circ}46'W$). *B. gracilis* is located to the left; *A. gerardii* is located to the right. More detailed garden site descriptions are in Table 2.1.



Figure 1.4: The Konza Prairie Biological Station (KNZ) common garden site is a native tallgrass prairie located in the Flint Hills of northeastern Kansas ($39^{\circ}05'N$, $96^{\circ}35'W$). Half of the garden experienced water-stress conditions due to the construction of the rainout shelter seen above. More detailed garden site descriptions are in Table 2.1.

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Chapter 2: Climate change consequences of geographic variation in growth and phenology of two dominant central US grasses

Summary

1. The rate of climate change may exceed many plant species' migration rates, particularly for long-lived perennial species that dominate most ecosystems. If bioclimatic envelopes shift more rapidly than dominant species can migrate, individuals located peripheral to biomes or in adjacent biomes may become a significant source of traits for future dominant populations. Thus, traits of individuals from peripheral populations (PPs) may affect future ecosystem functioning more than those of today's dominant populations (DPs).
2. We assessed differences in key traits of individuals collected from populations that currently dominate two Central US grasslands, the shortgrass steppe (*Bouteloua gracilis*) and the tallgrass prairie (*Andropogon gerardi*), and compared them to individuals from PPs. DPs and PPs were subjected to high and reduced water availability in common gardens located in each biome. Traits measured included: individual plant biomass, reproductive allocation, specific leaf area and several physiological attributes. We focused on the climate-change relevant comparisons of traits in PPs vs. DPs under the climate of DPs.
3. PPs of *B. gracilis* differed from DPs primarily in phenological traits. Under a semi-arid shortgrass steppe climate, PPs initiated flowering later in the season, produced fewer reproductive tillers, and were more sensitive to water stress. Biomass differences between populations were minimal.

4. For *A. gerardii*, biomass in PPs was 50% lower than in DPs under the mesic tallgrass prairie climate and reproductive tillers were considerably smaller, despite higher specific leaf area (SLA) in PPs. Biomass of PPs was less sensitive to water stress, however.
5. From these results, we conclude that key traits of PPs differed from DPs in both grassland types, but potential effects on reproductive phenology were greater for the bioclimatic shift in which a mesic biome becomes arid, whereas ecosystem productivity may be affected more when a semi-arid biome becomes more mesic.

Introduction

Biomes are defined by a range of climatic parameters (principally temperature and precipitation) and a relatively few dominant (or foundation) plant species (Whittaker 1965, Grime 1998, Ellison et al. 2005). Such dominant species, though widely distributed can be relatively rare taxonomically. In grasslands for example, only ca. 5% of the approximate 11,000 species in the *Poaceae* are capable of functioning as dominant species (Edwards et al. 2010). Nonetheless, dominant species contribute most to the total plant biomass in an ecosystem and their traits are closely linked to ecosystem function (Huston 1997, Aarsen 1997, Grime 1998). Thus, dominant species will determine many community and ecosystem responses to environmental change (Smith and Knapp 2003).

Although dominant species are expected to be abundant throughout their biomes, their physiographic ranges almost always extend far beyond where they function ecologically as dominant species. For example, *Andropogon gerardii* is a dominant grass throughout much of the tallgrass prairie grasslands in the central US, but this species can be found 800 km west of the tallgrass prairie and throughout much of the eastern two-thirds of the US (<http://plants.usda.gov>). Thus, it may be useful to distinguish between populations found in areas where they function as the dominant species (dominant populations = DPs) from those populations where they are simply components of the flora (peripheral populations = PPs). Not surprisingly, PPs are less often studied than DPs because they are minor components of the community or are only locally abundant.

Latitudinal and altitudinal range shifts have been documented for numerous species as a result of climate change (Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003), with these predicted to be more prevalent in the future (Morin et al. 2008). Although dynamic global

vegetation models have been limited in their ability to accurately assess plant migration and local vegetation change (Neilson et al. 2005, Thuiller et al. 2008), most studies suggest that plant migration rates faster than those observed during post-glacial times will be required to keep pace with the projected rate of global warming (Solomon & Kirilenko 1997; Malcolm et al. 2002), particularly in biomes with little topographic relief (Loarie et al. 2009, Jump et al. 2009). If present-day populations of dominant species cannot keep pace with shifting climatic envelopes, those populations that dominate future (geographically shifted) biomes are more likely to reflect traits of individuals from PPs already present rather than those from the DPs left behind – in other words, traits from PP individuals may be more important than those of DPs for predicting ecosystem function as biomes expand into new areas (Figure 2.1).

With forecasts of continued warming and altered precipitation amounts and regimes in the Great Plains (IPCC 2007, Giorgi & Diffenbaugh 2008), the bioclimatic envelope that defines the current distribution of the shortgrass steppe ecosystem (dominated by *Bouteloua gracilis*, blue grama) may extend eastward leaving behind migration-limited DP individuals. Thus, those PP individuals that already occur farther east would serve as the founder population for future shortgrass steppe ecosystems dominated by *B. gracilis*. If individuals from DPs and PPs are functionally similar, then there may be little alteration in ecosystem function as biome distributions shift. But if they are functionally distinct, then the new dominant populations (derived from former PP individuals) may drive important changes in ecosystem function and behavior, at least until local adaptation occurs (Jump and Penuelas 2005).

In this study, we compared traits from geographically distinct DP and PP individuals for two dominant C₄ Great Plains grasses, *B. gracilis* and *Andropogon gerardii* (big bluestem). We used a reciprocal transplant common garden approach to address this issue (Turesson 1922; Clausen et

al. 1940) and focused on a few key ecophysiological, morphological, and whole plant traits. We collected individuals from populations of *B. gracilis* and *A. gerardii* that currently dominate their respective grassland types or are found in peripheral ecosystems, set up common gardens for both species, and subjected all populations to two levels of water availability at each garden. This design allowed us to assess differences between individuals collected from DPs and PPs and their responses to water stress under common environmental conditions. Although reciprocal transplant experiments represent a well-established approach for assessing adaptation and responses to local environmental conditions (e.g., Bradshaw 1984, Linhart & Grant 1996), in this garden approach our focus was on climate change relevant comparisons of traits of individuals from present-day PPs *vs.* those from DPs, when grown together in an environment appropriate for that species to dominate. Moreover, although drying in general is forecast for much of this region of the world, some areas are predicted to become wetter (Chou et al. 2009). Thus, this reciprocal design allowed us to focus on scenarios of both mesic PPs influencing future xeric grasslands as well as xeric PPs impacting future mesic grasslands.

Methods

Population and Garden Site Descriptions

Individuals from DPs and PPs of *A. gerardii* and *B. gracilis* were collected from an array of undisturbed sites in Colorado and Kansas, USA (Table 2.1). A total of 12 populations were sampled, 6 for each species (3 DP, 3 PP). Populations were collected from a range of sites to capture natural variability within the populations. For *B. gracilis*, DPs were collected from different sites that varied in grazing intensity at the Shortgrass Steppe Long Term Ecological

Research site in Weld County, CO (SGS, see description below). The PPs for this species came from the Konza Prairie Biological Station Long Term Ecological Research site in Geary County, KS (KNZ, description below); to increase variability in traits, each population was collected from a different KNZ watershed that varied in grazing regime and long-term fire history. For *A. gerardii*, the DPs were located at KNZ (also in different watersheds with different grazing and burning histories), and the PPs of this species were located along the Front Range of CO, two from Boulder County and one from Larimer County. These populations were found within 70 km of each other.

Transplants along with some residual soil to include mycorrhizae and other important soil biota were moved to two common gardens at the start of the 2008 growing season. The SGS common garden, located at the Central Plains Experimental Range, is a semi-arid grassland located in northeastern Colorado ($40^{\circ}49'N$, $104^{\circ}46'W$). SGS is primarily dominated by the C₄ grass *B. gracilis*, with other major species including *Buchloe dactyloides* (buffalo grass), *Artemisia frigida* (fringed sagewort), *Sphaeralcea coccinea* (scarlet globemallow) and *Opuntia polyacantha* (plains prickly pear) (Lauenroth & Burke 2008). SGS has a mean annual precipitation of 321 mm (Lauenroth & Sala 1992) and a mean annual temperature of 8.6°C (Milchunas & Lauenroth 1995). Average aboveground net primary productivity (ANPP) is estimated at ca. 100 g m⁻² (Lauenroth & Sala 1992), with *B. gracilis* comprising up to 90% of the total biomass (Lauenroth et al. 1978). The garden was established near the site headquarters on a soil with clay loam texture (top 20 cm), which is typical of SGS (Lauenroth & Burke 2008).

The KNZ common garden was established at the headquarters area of the site, which is a native tallgrass prairie located in the Flint Hills of northeastern Kansas ($39^{\circ}05'N$, $96^{\circ}35'W$). KNZ encompasses 3487 hectares of native tallgrass prairie, and is dominated by C₄ grasses,

primarily *A. gerardii* Vitman and *Sorghastrum nutans* (L.) Nash (Freeman 1998). Average ANPP at KNZ is ca. 420 g m^{-2} (Knapp et al. 1998), with *A. gerardii* comprising up to 80% of the total (Smith & Knapp 2003). The climate consists of cold, dry winters and warm, wet summers (Hayden 1998). Mean annual precipitation is 835 mm, and mean annual temperature is 13°C . The garden was established on soil with a silt loam texture (top 20 cm), which is typical of KNZ (Knapp et al. 1998).

Population Collection and Common Garden Establishment

From each population, 30 individuals were collected, 15 for each garden. We defined an individual in these strongly clonal species as all tillers found within a 20-30 cm diameter circle where the target species was as isolated from other species as possible. We collected all roots and rhizomes to 15-20 cm soil depth as well as all aboveground tissue. Despite the strongly clonal habit of these species, it is possible that more than one genotype was included in each individual sample (Avolio et al. 2011). Samples were stored in a cool, moist environment until they were transplanted (within two weeks of collection). Transplant survival success was >95%.

To establish the common gardens, a 10 m x 10 m area was tilled to 25 cm and the perimeter was fenced to exclude grazers. Plastic lawn edging was formed into 39 cm diameter circles and inserted 10 cm into the ground to isolate and contain the individuals. We transplanted 144 individuals into these circular plots in each garden; 12 individuals of *B. gracilis* and *A. gerardii* from each of the 12 populations. Transplants were arrayed in a 6 x 6 Latin square design repeated once for each species – this allowed us to subject half the transplants to a water availability treatment in the second year. Intact rhizomes and tillers were separated from other vegetation initially to establish mono-specific stands in each plot, and we removed other species

throughout both growing seasons via weeding by hand. Three extra individuals from each population were placed around the perimeter of the gardens to provide replacements in the case of transplant mortality. The 2008 growing season was dedicated to the establishment, growth and acclimation of the populations, thus all plants were watered frequently to facilitate survival and growth.

Watering treatments began in the second year (2009) with half of each garden exposed to a different level of water availability. Four soil moisture probes were placed in each half of each garden to monitor treatments. At SGS, ambient conditions constituted the dry side of the garden. We irrigated the other half of the garden to reduce water stress; each individual received water twice daily via drip irrigation. The amount of water added varied depending on rainfall and the water status of the plants (see below). Conversely at KNZ, ambient conditions constituted the wet side of the garden, and a rain exclusion shelter was erected over half the garden to reduce soil moisture (Figure 1.4). The shelter consisted of clear polyethylene greenhouse material stretched across a wooden frame approximately 2 m above the plants (similar to the design described in Fay et al. 2000). The roof deflected most rainfall off the plot and could be removed if the plots became too dry. However, due to the winter recharge of moisture in the deep soils at this site, the roof remained intact over half the garden for most of the growing season. The shelter was designed with open sides so that alterations to air movement, temperature, and relative humidity were minimized. The roof was slanted to facilitate water run-off and the plastic sheeting reduced the transmission of light by 19%.

Data Collection

For all sites (the 2 gardens and the collection sites for the 12 populations) soil texture and pH were determined from composite samples of three 10 cm depth soil cores (Colorado State University Soil, Water and Plant Testing Laboratory). In both gardens in 2009, soil moisture (volumetric water content in the top 20 cm) was estimated at approximately weekly intervals with ECH₂O soil moisture sensors (Decagon, Pullman, WA, USA). Eight probes were placed in eight plots (four each in the dry and wet portions) arrayed in two transects through each garden (NE to SW and NW to SE).

Leaf water potential (LWP) was measured for each species at three-week intervals throughout the growing season (PMS 1000 pressure chamber). For both pre-dawn and midday estimates, single leaves were measured (n=3 from each population for each treatment) from both wet and dry portions of the garden. In addition, as a measure of photosynthetic capacity dark-adapted chlorophyll fluorescence (the Fv/Fm ratio, Zunzunegui et al. 2011) was measured (OS1-FL Modulated Chlorophyll Fluorometer, Opti-Sciences) at three-week intervals on mature upper canopy leaves of each population (n=3).

At the end of the season, biomass was measured by harvesting all individuals in 10 cm x 10 cm quadrats, drying the biomass at 60°C for at least three days to ensure all water was removed, and weighing to the nearest 0.01 grams. To determine reproductive allocation, reproductive biomass was separated and divided by total biomass to calculate the proportional allocation. Additionally for *A. gerardii*, 10 individual tillers (both reproductive and vegetative) were randomly selected in each plot, harvested, dried, and weighed.

The total number of flowering tillers in each plot was censused every two to three weeks throughout the growing season for both species. Additionally, six stages of reproductive phenology were monitored in each plot every two to three weeks for *A. gerardii* only (emergent reproductive tiller, covered flower, flower 3 cm exposed, fully exposed flower, anthesis, post-anthesis). Each stage was scored 1-6, respectively, and an average phenological stage was computed for both DPs and PPs under wet and dry treatments.

Specific leaf area (SLA), the ratio of leaf area to dry weight was measured on fully expanded green leaves for each population ($n=3$) at three-week intervals during the growing season. This trait was chosen because SLA is often positively correlated with plant growth (Garnier et al. 2001, Shipley 2002) and may be indicative of the trade-off between rapid biomass production (high SLA) and efficient conservation of nutrients (low SLA, Poorter and de Jong, 1999).

Statistical Analysis

A two-way mixed model analysis of variance (ANOVA, SAS 9.2, SAS Institute 2005) was performed for biomass, reproductive allocation, individual reproductive tiller mass, and individual vegetative tiller mass for each species at each garden. A two-way mixed model repeated measures ANOVA was performed for phenology, Fv/Fm, predawn and midday leaf water potential, and SLA. Fixed effects were water treatment (wet/dry) and population (DP/PP). Random effects were row (water), column (water), pop (individual population), water*pop. A Latin Square analysis was initially performed for each response variable to assess row, column, or individual population effects. None of these effects were significant, thus the six individual populations were combined into two geographic locations (DP and PP). When necessary, log (y+c) transformations were used to satisfy homogeneity assumptions for the ANOVA model (*B.*

gracilis: biomass, reproductive allocation of biomass, predawn, phenology; *A. gerardii*: biomass, individual tiller mass, predawn). The constant “c” varied depending on the variable and was chosen (reflecting the lower values in the data) so that zeroes did not dominate the analyses. Based on the Akaike Information Criterion (AIC) goodness of fit test, an autoregressive parameter was included for several analyses at both gardens (*B. gracilis*: phenology, Fv/Fm, SLA (SGS only); *A. gerardii*: phenology, Fv/Fm (SGS only), SLA).

Results

Soils – Soils in each garden ranged in pH from 6.2 – 6.9 and most of the population collection sites fell within this range, with soil texture varying from loam to sandy loam. There were no consistent patterns noted among the 12 collection sites or the two gardens.

Water availability treatments – In order to create a wet vs. dry treatment at each site, we excluded precipitation to half of the KNZ garden and irrigated half of the SGS garden in 2009. In general, differences in soil moisture between wet vs. dry treatments increased over the growing season and were greater at SGS than the KNZ garden, likely because the deep soils at KNZ were nearly saturated prior to erecting the rain exclusion shelter. Average growing season soil moisture was $28.2\% \pm 0.5$ in the wet vs. $17.6\% \pm 0.9$ in the dry treatment at SGS ($p<0.05$) and $29.0\% \pm 0.4$ in the wet vs. $24.7\% \pm 0.7$ in the dry treatment at KNZ ($p<0.05$). The seasonal maximum treatment differences observed at each garden were 23.2% at SGS and 9.3% at KNZ. Leaf water potential measurements (predawn and midday) confirmed that these two grasses experienced different levels of water availability in both gardens (Table 2.2) with the more shallow rooted *B. gracilis* generally responding more strongly to the water treatments than the deeper rooted *A. gerardii*.

B. gracilis – Our focus for comparing traits from PPs and DPs for *B. gracilis* was in the SGS garden since this represents the climate where this species is dominant. Thus, individuals from PPs from a higher resource environment (greater precipitation) were compared to DP individuals from a low resource environment (PP vs. DP in Figure 2.1). In the SGS garden, we detected no difference between these two populations in total end-of-season biomass (Figure 2.2, top), but PPs allocated less biomass to reproduction than DPs (Figure 2.2, bottom) and were significantly shorter at the end of the season (DP average maximum height = 39.8 ± 1.9 cm vs. 16.6 ± 2.1 cm for PP). PPs also initiated flowering later and had lower reproductive tiller density throughout the growing season compared to DPs (Figure 2.3, top). When water availability was reduced, biomass as well as reproductive tiller density was also reduced in both population types (Figure 2.2, top; Figure 2.3, top), but only the PPs experienced a decrease in reproductive allocation (Figure 2.2, bottom). There was no measurable population or water stress effect on SLA (Figure 2.4), but water stress did reduce Fv/Fm significantly in DPs at the end of the growing season (data not shown). There were no significant differences in predawn or midday LWP between PPs and DPs under wet or dry conditions (Table 2.2).

Although trait responses for *B. gracilis* in the reciprocal mesic environment garden (KNZ) were not the focus of this study, individuals from PPs produced significantly more biomass growing in Kansas than those from the more arid DPs (Figure 2.2, top), the dry treatment reduced SLA for PPs (Figure 2.4), and in contrast to responses in the SGS environment, reproductive allocation in DPs was negatively effected by a reduction in water availability (Figure 2.2, bottom). Patterns in reproductive phenology were similar for both gardens, with the exception that PPs surpassed DPs in reproductive tiller density by the end of the season at KNZ (Figure 2.3, bottom).

A. gerardii – For *A. gerardii* we focus on traits of individuals from PPs vs. DPs growing in the tallgrass prairie climate (KNZ garden). Under wet conditions at KNZ, PPs produced only half as much biomass as DPs (Figure 2.5, top) and although the populations did not show significant differences in reproductive allocation, (Figure 2.5, middle), individual reproductive tiller size was reduced by ca. 60% in individuals from PPs compared to DPs (Figure 2.5, bottom). Vegetative tiller size was similarly reduced (data not shown). Despite their small individual size, PPs increased their reproductive tiller density more rapidly and had a much higher density at KNZ throughout the season (Figure 2.6, top). PPs were again more phenologically advanced than DPs (data not shown), and SLA was greater in PPs at KNZ (Figure 2.7, left), and at the end of the growing season, Fv/Fm of PPs were significantly lower than DPs (data not shown). Individuals from PPs were less affected by reduced water availability in biomass, reproductive allocation and individual reproductive tiller size than those from DPs (Figure 2.5, left). As with *B. gracilis*, there were no differences in LWP between populations under wet or dry conditions (Table 2.2).

In the reciprocal garden (at SGS), no population or treatment effects were observed in total biomass (Figure 2.5, top). However, contrary to the KNZ garden, individuals from PPs allocated significantly more biomass to reproduction (Figure 2.5, middle). The density of reproductive tillers at the end of the season was significantly greater in PPs (Figure 2.6) and the individual reproductive tillers of PPs were again reduced in size (Figure 2.5, bottom). Differences in SLA between populations at SGS were similar to patterns at KNZ (Figure 2.7, right) but contrary to KNZ, when there were significant differences in Fv/Fm, this measure of photosynthetic capacity was higher in PPs than in DPs at SGS (data not shown).

Discussion

There has been much recent interest in the attributes and traits of organisms found in the core vs. edge of a species range (Jarema et al. 2009, Munwes et al. 2010, Villellas et al. 2012, Dudaniec et al. 2012), the strength of local adaptation in core populations which may limit their ability to respond to climate change (Hereford 2009, Bennington et al. 2012) and potential climate change barriers to migration (Jalili et al. 2010, Chen et al. 2011). We have argued that if the rate of climate change is greater than the rate of migration for species that dominate biomes, individuals from populations peripheral to biomes today may play a significant role in determining initial ecosystem structure and function in these future geographically shifted biomes (Figure 2.1). This is because it is the dominant species that largely determine ecosystem structure and function (Whittaker 1965, Grime 1998, Ellison et al. 2005). Thus, the goal of this study was to better understand the potential consequences of ecosystems being dominated by individuals with traits of formerly PPs.

We assessed key traits in individuals from PPs and DPs of *B. gracilis* and *A. gerardii* in a reciprocal transplant common garden experiment with two levels of water treatments, as appropriate for a largely water-limited grassland region (Huxman et al. 2004). Our focus was on how PPs and DPs compared when grown in environments where the species currently dominates. We were particularly interested in two scenarios – (1) a mesic grassland (tallgrass prairie in Kansas) drying to the extent that it becomes semi-arid and thus *B. gracilis* might be expected to dominate (with traits from PPs currently in Kansas). And (2) a semi-arid grassland (shortgrass steppe in Colorado) becoming more mesic and thus *A. gerardii* (with traits from PPs currently in Colorado) would be expected to dominate. Although the former is more likely to occur than the latter in this particular region, there are areas of the world that are forecast to become wetter with

climate change (IPCC 2007, Chou et al. 2009) providing relevance for the latter scenario.

For the first scenario, although there were no significant differences between DPs and PPs in total biomass of *B. gracilis* in the shortgrass prairie environment (a climate similar to what PPs will experience in the future), differences were noted in reproductive allocation, reproductive tiller density, flower initiation, average maximum end-of-season height, and sensitivity to water stress (Figures 2.2-2.4).

For the second scenario, *A. gerardii* biomass and growth traits differed significantly between DPs and PPs. Individuals from PPs had much reduced biomass under well-watered conditions compared to DPs (despite greater SLA), as well as significantly smaller reproductive tillers (although at a higher density). Biomass of individuals from PPs was less sensitive to water stress however. Thus in both scenarios, under common garden conditions the traits of individuals from PPs differed in a number of ecologically meaningful ways from individuals collected from today's DPs. Although production responses might be expected to have the greatest array of ecosystem consequences, alterations in reproductive phenology could be very important for the capability of these dominant species to locally adapt to new climatic conditions (Jump and Penuelas 2005).

While it would be unwise to generalize from these two specific scenarios, our results lead to two important conclusions. First, a relatively broad range of traits differed between PPs and DPs - from phenological, to those related to growth, and to sensitivity to resource limitation (water stress). Second, these trait differences between populations were distinctive – they were largely related to reproduction for the first scenario vs. growth in the second. Both of these support the contention that present day ecosystem functioning, as determined by traits of the dominant species, may be altered significantly as a function of these population-level trait differences. This

intraspecific geographic variation in the traits of dominant species adds another, more subtle layer of uncertainty to our ability to predict future ecosystem function based on our extant knowledge. Previous studies have already identified no-analog environmental conditions and novel community composition as mechanisms driving changes in future ecosystem structure and function (Nippert et al. 2006, Williams and Jackson 2007, Seastedt et al. 2008, Veloz et al 2012). The results of this research suggest that even without these two mechanisms, forecasting the future of ecosystems and the services they provide will require knowledge, currently lacking, on the migration rates (and barriers to migration) of key species. If today's populations of dominant plant species cannot keep pace with climate change, then greater understanding of genetic and phenotypic variation throughout a species range, and the rates of adaptation for these dominant species must be investigated, particularly under conditions where there are realistic interspecific interactions (Lesica and Allendorf 1995, Eckert et al. 2008, Hoffman and Blows 1994, Moser et al. 2011).

Table 2.1: General description of the collection sites for the dominant and peripheral populations of the semi-arid grassland dominant *B. gracilis* and the tallgrass prairie dominant *A. gerardii*. Mean growing season precipitation (ppt) and temperatures (temp) are 30-year averages (1971-2000) for the months of May through September. 2009 data are shown as context for the common garden results.

	Dominant Populations	Peripheral Populations
<i>B. gracilis</i>	(from Colorado)	(from Kansas)
Latitude	40°48'43" - 40°48'44" N	39°04'28" - 39°04'40" N
Longitude	105°12'55" - 104°38'51" W	96°34'57" - 96°33'37" W
2009 growing season ppt	254 mm	528 mm
Mean growing season temp	18.6°C	23.0°C
2009 growing season temp	17.2°C	21.2°C
<i>A. gerardii</i>	(from Kansas)	(from Colorado)
Latitude	39°04'25" - 39°04'54" N	39°58'24" - 40°31'59" N
Longitude	96°33'51" - 96°33'41" W	105°12'55" - 105°8'12" W
2009 growing season ppt	528 mm	218.3 mm*
Mean growing season temp	23.0°C	18.5°C
2009 growing season temp	21.2°C	18.9°C

*averaged between Fort Collins, CO and Boulder, CO (where populations were collected)

Table 2.2: Seasonal minima leaf water potential (LWP) when differences between watering treatments were generally greatest. Water potentials were averaged across populations to determine if watering treatments were effective.

	SGS Garden		KNZ Garden	
	<i>B. gracilis</i>	<i>A. gerardii</i>	<i>B. gracilis</i>	<i>A. gerardii</i>
Predawn wet (MPa)	-0.87 ± 0.20	-0.24 ± 0.06	-1.03 ± 0.16	-0.17 ± 0.08
dry (MPa)	-0.71 ± 0.20	-0.43 ± 0.06	-1.94 ± 0.18	-0.47 ± 0.08
Midday wet (MPa)	-2.40 ± 0.23	-1.42 ± 0.15	-2.31 ± 0.30	-1.45 ± 0.11
dry (MPa)	-2.99 ± 0.24	-1.95 ± 0.15	-3.78 ± 0.31	-1.68 ± 0.11

*statistical significance between watering treatments at p=0.05 level

Table 2.3: Results from ANOVAs for the main effects of water treatment (wet vs. dry) and population (DP vs. PP) at both gardens (SGS, KNZ). End-of-season data used unless otherwise noted. NA indicates that data were not collected.

	<i>B. gracilis</i>				<i>A. gerardii</i>			
	water treatment		population		water treatment		population	
	SGS	KNZ	SGS	KNZ	SGS	KNZ	SGS	KNZ
Soil Moisture ^a	<0.0001*	<0.0001*	NA	NA	<0.0001*	<0.0001*	NA	NA
Predawn ^b	0.5019	0.0074*	NA	NA	0.0344*	0.0320*	NA	NA
Midday ^b	0.0416*	0.0072*	NA	NA	0.0278*	0.1747	NA	NA
ANPP	<0.0001*	0.0120*	0.8404	0.0005*	0.0726	0.1537	0.9128	0.1273
Rep. tiller mass	NA	NA	NA	NA	0.3102	0.3306	0.0287*	0.0072*
Veg. tiller mass	NA	NA	NA	NA	0.0498*	0.6969	0.0006*	0.0329*
Rep. percentage	0.0121*	0.0246*	0.0492*	0.0033*	0.0744	0.0208*	0.0102*	0.1700
Rep. tiller density	<0.0001*	0.0026*	0.0009*	0.0504*	0.0032*	0.0226*	<0.0001*	0.0012*
SLA	0.0334*	0.0004*	0.0637	0.1906	0.0076*	0.5225	0.0115*	<0.0001*
Height	<0.0001*	0.0024*	0.0021*	0.0761	0.1717	0.0751	0.7802	0.0571
Fluorometer ^a	0.0527	0.0395*	0.0592	0.3156	0.0035*	0.7034	0.0029*	0.1550

*statistical significance at p=0.05 level

^a measured through season; in the case of soil moisture an average was used

^b measured when differences between watering treatments were generally greatest

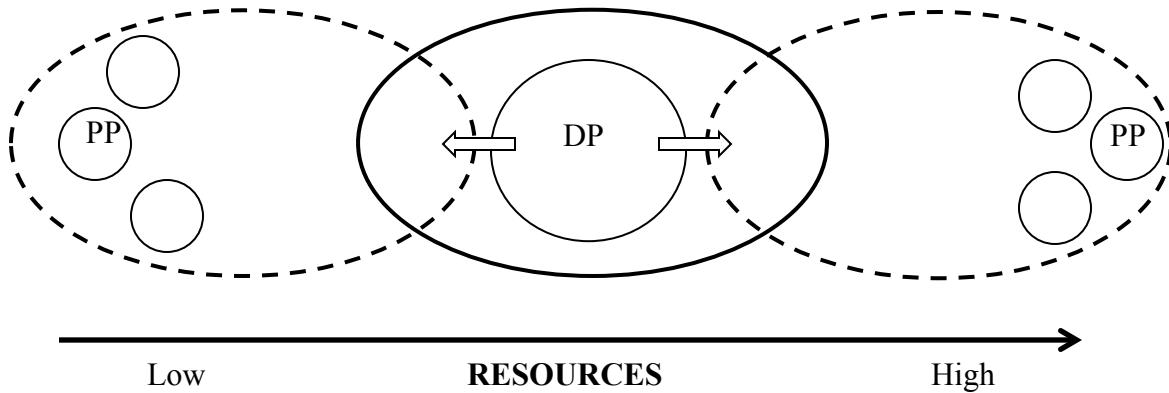


Figure 2.1: Idealized depiction of how a directional shift in climate can result in a shift in traits for the species that currently dominates a biome. In the diagram above, contemporary boundaries are indicated by the solid lines and potential future biome boundaries by the dashed lines. Biomes are characterized by a range of climatic conditions (often temperature and moisture) and the presence of one to a few dominant species (represented by the dominant populations – DP – above). However, the distribution of these dominant species is not limited to the biome; individuals are much more widespread and thus peripheral populations (PP) typically occur well outside the biome boundary. In this simplified example, the extant biome is characterized by a certain range of water (resource) availability, but populations of the dominant species occur where this resource is both more abundant (higher resources) than in the biome as well as where water is more limiting (lower resources). Climate change may shift future biome boundaries (dashed lines) to regions that historically had either higher or lower resource levels and do so more rapidly than individuals of the DP can migrate. Thus individuals from PPs (which are likely to have different traits) may contribute strongly to future ecosystem structure and function in geographically shifted biomes.

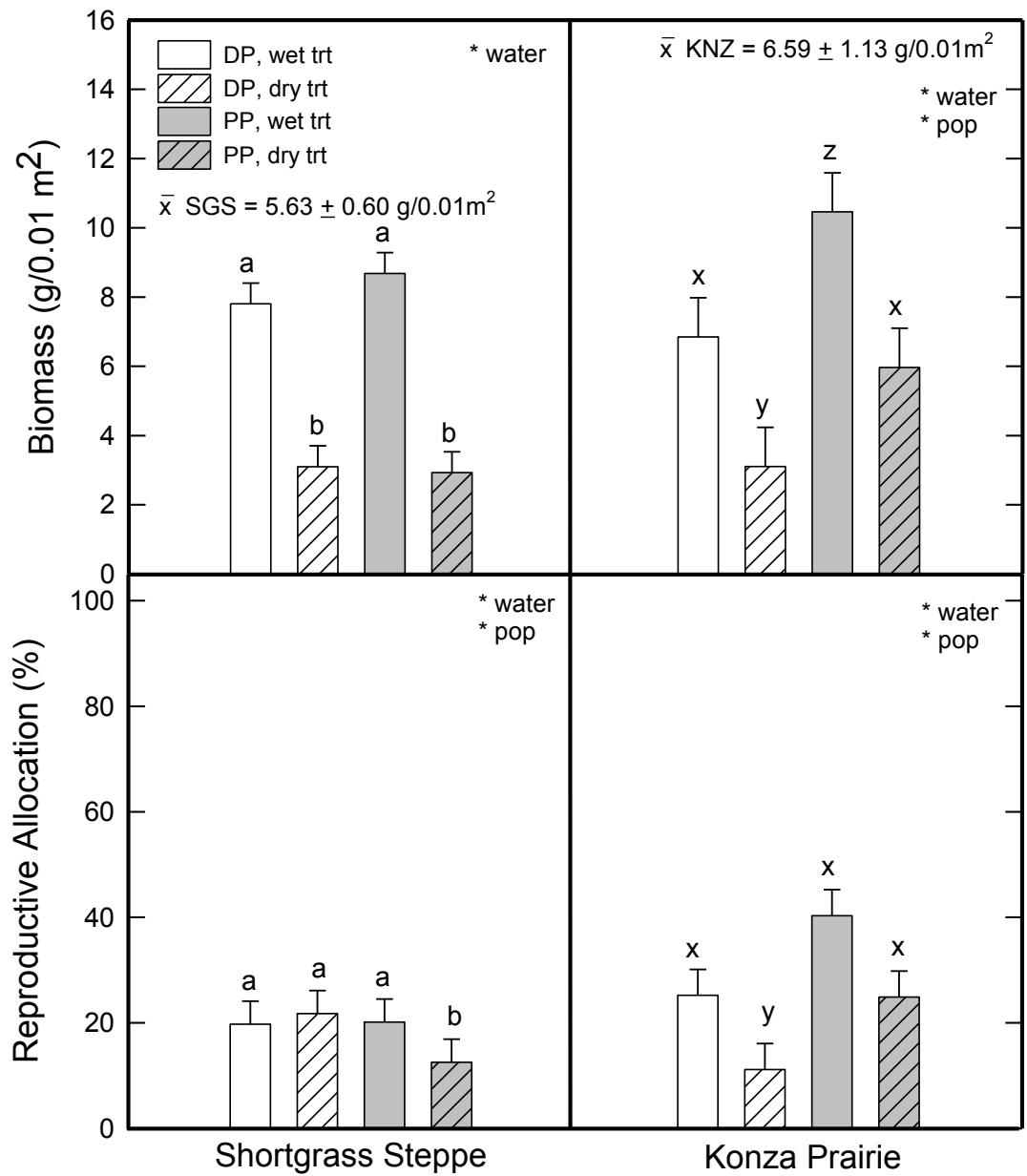


Figure 2.2: *B. gracilis* biomass (top panel) and reproductive allocation (bottom panel) at Shortgrass Steppe (left) and Konza Prairie (right) garden sites. There was a significant difference between the total biomass at each garden (top panel). Significant main effects (*) and pairwise comparisons (different letters) are noted in each panel ($P = 0.05$). Main effect *p*-values can be found in Table 2.3; no significant interactions were detected. Mean values + 1 SE are shown.

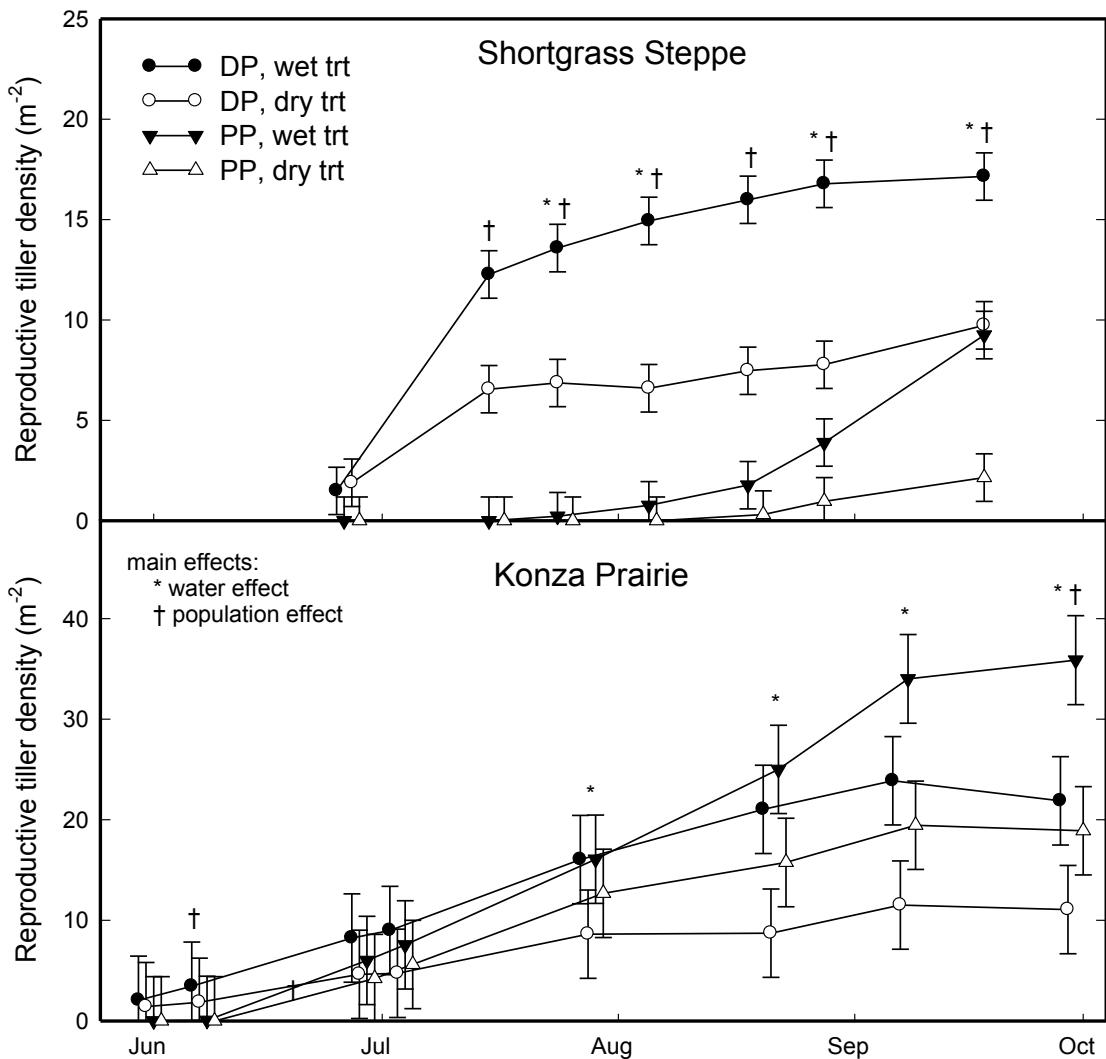


Figure 2.3: *B. gracilis* reproductive tiller density (m^{-2}) at Shortgrass Steppe (top panel) and Konza Prairie (bottom panel) garden sites. Significant main effects are indicated by * (water effect) and/or † (population effect) directly above the date where significance occurred ($P = 0.05$). Main effect p -values can be found in Table 2.3. Some points were offset slightly so error bars can be seen clearly. Note the change in scale between panels; KNZ was much more productive than SGS despite the similar trends at both sites. Mean values ± 1 SE are included.

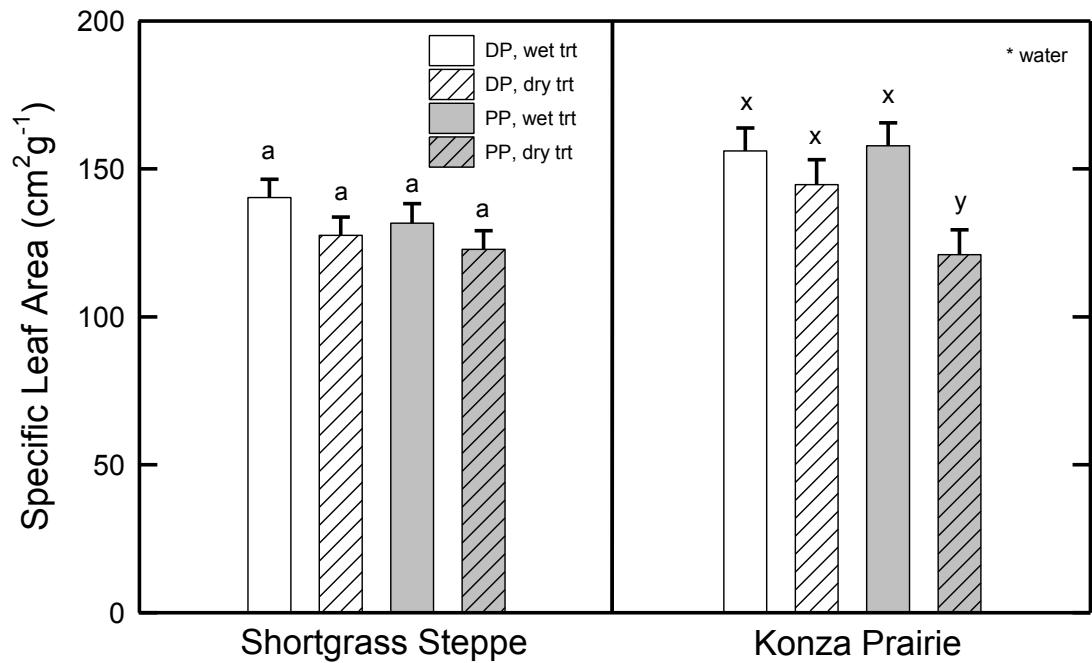


Figure 2.4: *B. gracilis* specific leaf area (SLA) at Shortgrass Steppe (left) and Konza Prairie (right) garden sites. Significant main effects (*) and pairwise comparisons (different letters) are noted ($P = 0.05$). Main effect p -values can be found in Table 2.3; no significant interactions were detected. Mean values + 1 SE are included.

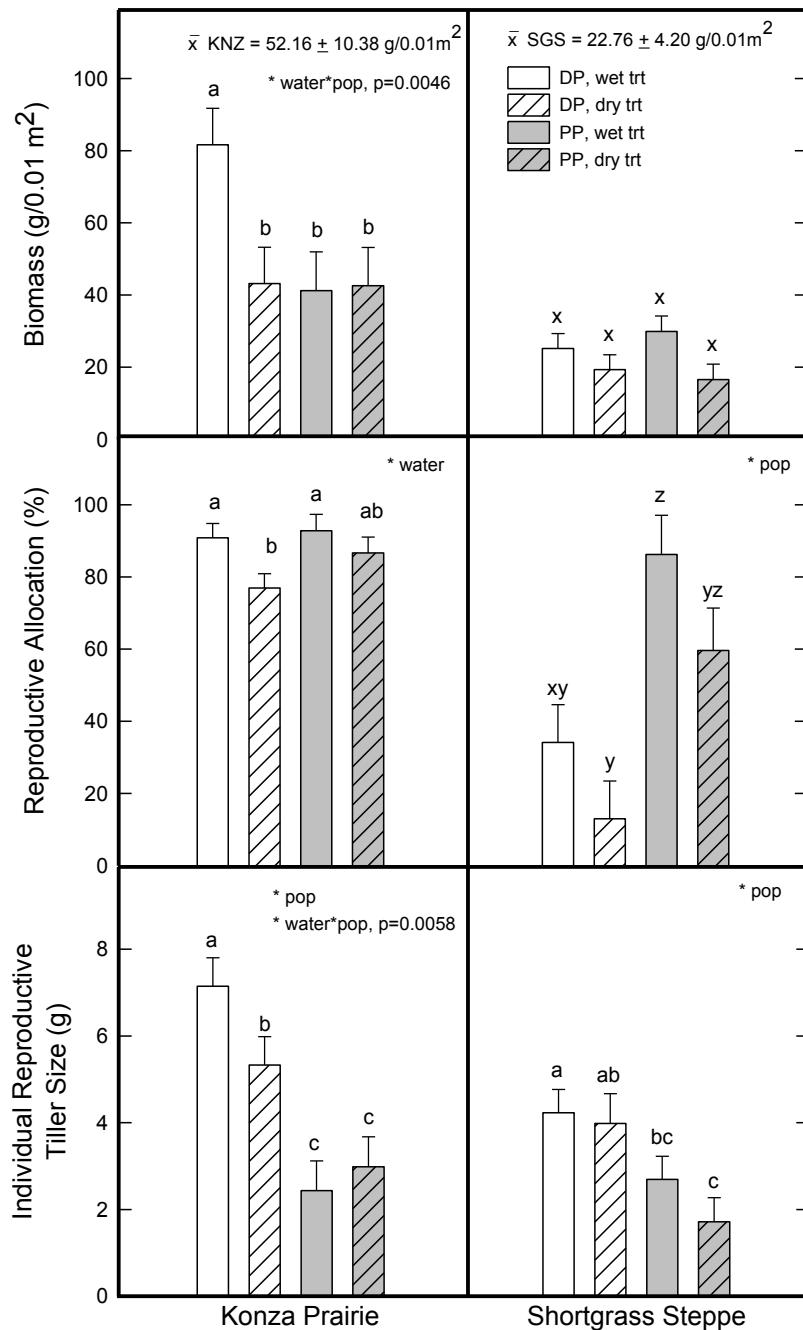


Figure 2.5: *A. gerardii* biomass (top panel), reproductive allocation (middle panel), and individual reproductive tiller size (bottom panel) at Shortgrass Steppe (left) and Konza Prairie (right) garden sites. There was a significant difference between the total biomass at each garden (top panel). Significant main effects and interactions (*) and pairwise comparisons (different letters) are noted in each panel ($P = 0.05$). Main effect p -values can be found in Table 2.3; significant interaction p -values are indicated by appropriate asterisks. Mean values + 1 SE are included.

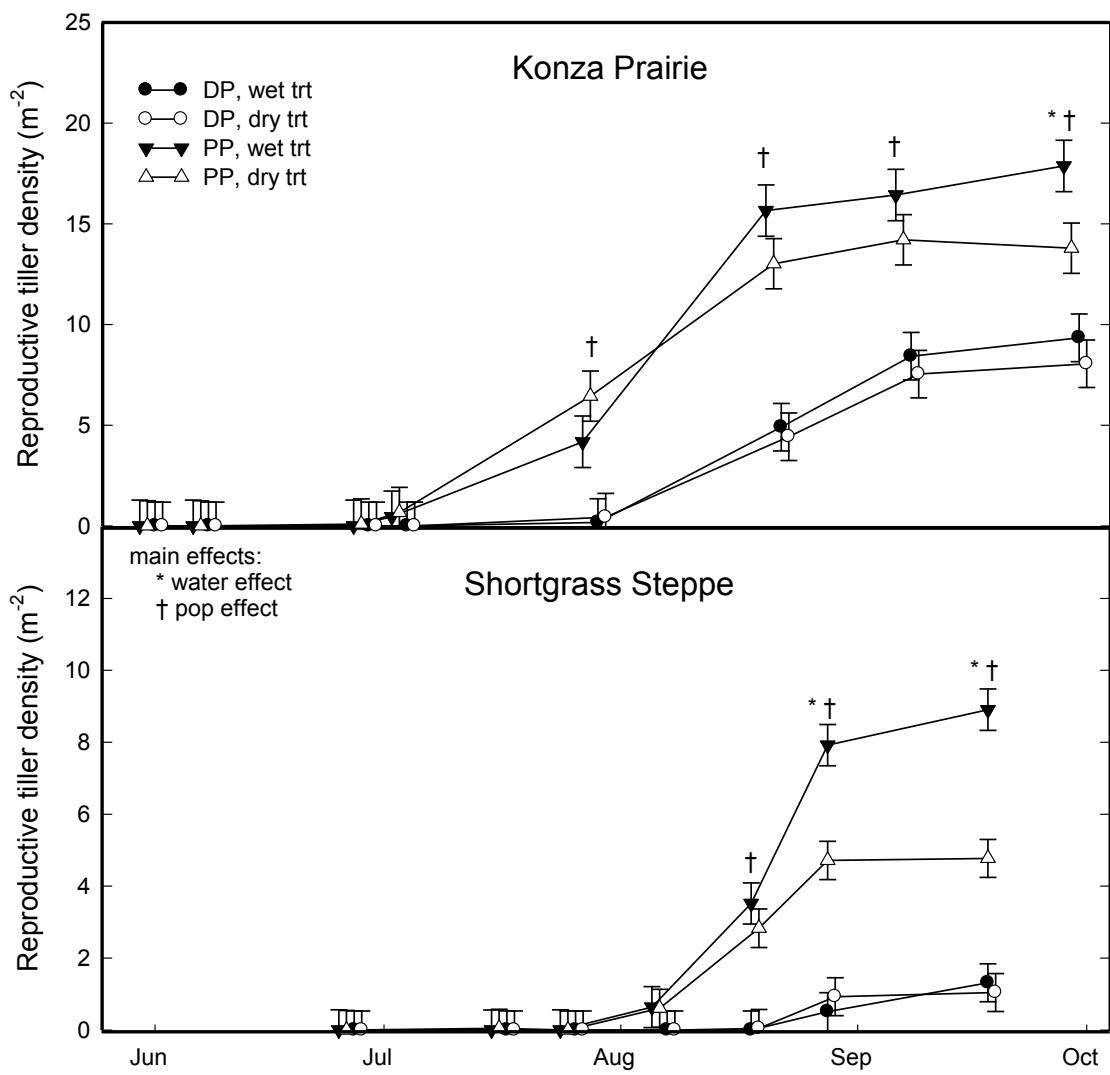


Figure 2.6: *A. gerardii* reproductive tiller density (m^{-2}) at Konza Prairie (top) and Shortgrass Steppe (bottom) garden sites. Significant main effects are indicated by * (water effect) and/or † (population effect) directly above the date where significance was found ($P = 0.05$). Main effect p -values can be found in Table 2.3. Some points were offset slightly so error bars can be seen clearly. Note the change in scale between panels. While similar trends were seen between sites, KNZ was much more productive than SGS. Mean values ± 1 SE are included.

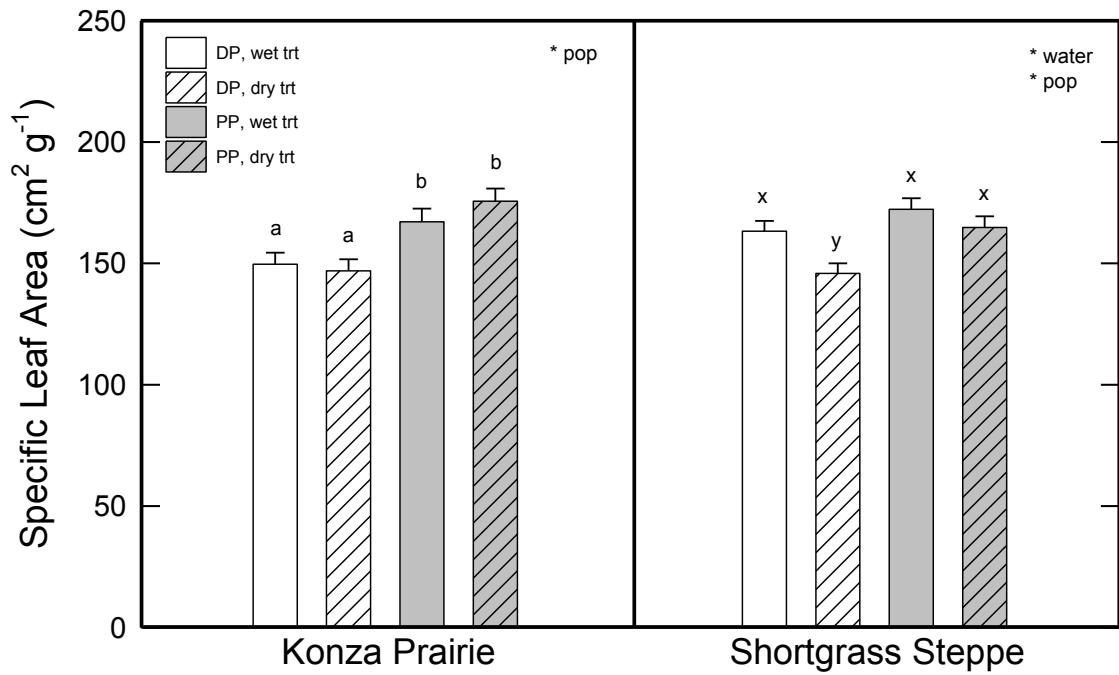


Figure 2.7: *A. gerardii* specific leaf area (SLA) at Konza Prairie (left) and Shortgrass Steppe (right) sites. Significant main effects (*) and pairwise comparisons (different letters) are noted ($P = 0.05$). Main effect p -values can be found in Table 2.3; no significant interaction p -values were observed. Mean values + 1 SE are included.

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Chapter 3: Summary and directions for future research

Summary

Compared with the slow rate that many plant species migrate, in some places the predicted rate of climate change is spectacular (Malcolm et al. 2002; Solomon & Kirilenko 1997). If dominant populations of C₄ grasses are unable to migrate quickly enough, ecosystem structure and function in tallgrass prairie and shortgrass steppe grassland types may suffer consequences. Plant species exist across a range; because climate change may outpace plant species migration, it is here speculated that populations on the periphery of the range may be responsible for sourcing future generations. Thus, the goal of this thesis research was to determine how dominant populations (DPs) and peripheral populations (PPs) of two dominant C₄ grasses prevalent on the shortgrass and tallgrass prairies, *Bouteloua gracilis* and *Andropogon gerardii*, respectively, differ from one another. In addition, we compared how DPs and PPs respond to water stress.

To address these goals, we measured key ecophysiological, morphological, and whole plant attributes of DPs and PPs under well-watered and water-stressed conditions in a reciprocal common garden experiment. The following traits were measured for both species: predawn and midday leaf water potential, total biomass, reproductive biomass percentage, and individual reproductive and vegetative tiller mass (*A. gerardii* only), specific leaf area, fluorometer, height, and reproductive tiller density.

We found that while both species had traits that differed between DPs and PPs, the majority of the traits were unique to the species. Specifics for each species are described here.

B. gracilis – Individuals of *B. gracilis* from more mesic PPs grown in a shortgrass steppe climate showed phenological differences when compared to DP individuals. PPs initiated flowering later in the season, produced fewer reproductive tillers by the end of the season, and also had greater sensitivity to water stress. Biomass differences between populations were minimal in this species.

A. gerardii – Contrary to *B. gracilis*, biomass differences for *A. gerardii* were significant. Under the well-watered treatment, individual plant biomass of PPs was 50% lower when compared to DPs grown in the tallgrass prairie climate. Total biomass of PPs also showed reduced sensitivity to water stress. Despite no differences between end-of-season reproductive allocation of biomass, individual PP tillers were considerably smaller in size and SLA was greater in PP.

If PPs are responsible for sourcing future generations, we found that effects on reproductive phenology were more sensitive to shifts from mesic to arid biomes (*B. gracilis*), whereas effects on productivity were greater for bioclimatic shifts in which arid biomes become more mesic (*A. gerardii*). Given the potential severity of the forecasted changes in climate, reproductive phenology may play a significant role when accounting for adaptation. However, since these species are long-lived perennials that can vegetatively reproduce, perhaps productivity differences will have a greater impact because of the potential effects on ecosystem function. For both species, more research is necessary to better understand PPs.

Directions for Future Research

Ecosystem processes will be impacted by forecasted changes in precipitation and temperature (Sala et al. 1988). In a model presented by Williams and Jackson (2007), climatic changes may result in shifts in species distributions, community disaggregation, formation of new communities, and extinction of species because species are being forced out of their climatic envelopes. Changes in species density, range, timing of events, and morphology have already been observed as a result of climate change (Parmesan & Yohe 2003, Root et al. 2003), and future research could explore limits to speed and distance of migration of *B. gracilis* and *A. gerardii* so models could predict future scenarios with more accuracy. Additionally, since the species studied in this experiment do not exist in isolation, research on their abilities to compete with other species would be valuable, particularly in areas of their range in which they are not dominant (Moser et al. 2011).

Adaptability may play a critical role under future climate predictions. Hence, another avenue of exploration would be studying how quickly it takes a species to shift its traits to become more compatible with its new climate. In addition, research could focus on developing an understanding of which life stages of *B. gracilis* and *A. gerardii* may be more susceptible to future climate change (Russell et al. 2012) or on examining storage capabilities of these species should lengthy periods of drought increase.

Local adaptation can also be explored in this reciprocal common garden experiment. Regional differentiation was first noted in plant species in the early 1920s and 1940s (Turesson 1922, Clausen et al. 1941). It has been well documented since then (Joshi et al. 2001, Nagy & Rice 1997, Levin 1993, Travis & Futuyma 1993), though others have found local adaptation to be less widespread in plant populations than commonly believed (Leimu & Fischer 2008).

Though this study did not focus on local adaptation, we did observe it retrospectively in *B. gracilis*; both DPs and PPs produced more biomass in their home gardens, and PPs had a higher density of reproductive tillers in their home garden. Local adaptation was not as readily observed with *A. gerardii*; both DPs and PPs produced more biomass at KNZ and both populations had significantly lower reproductive tiller densities at SGS. With this, it is possible that the driving factor for *A. gerardii* is climate, as KNZ receives twice as much precipitation as SGS. A more detailed study could focus on key characteristics associated with local adaptation and/or resource (water) level in a species' home garden.

Finally, this study compared the DPs of each species with just one PP. Many PPs of each species exist across the ranges of both grass species, and our findings may not be relevant to other parts of the species' ranges. Because we cannot be sure which PPs will contribute to future DPs, a more thorough investigation would include reciprocal common gardens for each existing PP.

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Appendix

In support of data presented in Chapter #2, additional response variables were measured for both species (fluorometer and height) while individual vegetative tiller mass was measured for *A. gerardii* only.

Fluorometer

Unusual changes in the overall bioenergetic status of a plant can be detected by a change in chlorophyll fluorescence. The Fv/Fm (dark-adapted) tests were performed with the OS1-FL Modulated Chlorophyll Fluorometer (Opti-Sciences) in the morning before the sun came up. This test gives information about the effectiveness of energy capture in the light harvesting complexes (LHCs). Environmental stresses can affect LHC efficiency, resulting in a lower Fv/Fm value.

For each plant, a dark-adapting clip was placed on a leaf. After 30 minutes, the sliding shutter was opened and the base level Fo (minimal fluorescence) was measured when all antenna sites were assumed to be open. A bright pulse of light was applied close to the reaction centers and the subsequent backup of energy led to the increase in fluorescence. Fm (maximal fluorescence) was measured at this point when all antenna sites were assumed to be closed. Fv/Fm ratio is the ratio of variable fluorescence to maximal fluorescence ($Fv/Fm = [Fm - Fo]/Fm$), with variable fluorescence (Fv) equal to the change in fluorescence due to initial electron backup in the antenna complex. To test for statistical significance, a two-way mixed model repeated measures ANOVA was performed with fixed effects of water (wet/dry) and population (dominant/peripheral) and random effects of row (water), column (water), pop (individual population), and water*pop. Results from these tests can be seen in Table 3.1. For the

A. gerardii KNZ data, there was evidence of lack of homogeneity of variance. However, we ran the ANOVA without transformation and since the time*treatment interaction variability was dramatically different at different dates, we separated out the time points individually and did an ANOVA for each date (no pooled variances).

For *B. gracilis*, fluorometer data did not show any significant differences for either of the main effects (watering treatment, population) at SGS, but when compared over time we noticed the patterns observed for wet and dry treatments to be significantly different. In a pairwise comparison, DP showed the effects of water stress at the end of the growing season with the non-stressed plants attaining higher Fv/Fm values. At KNZ, there was a significant effect of water stress on *B. gracilis* with the non-stressed plants again attaining higher Fv/Fm values throughout the season.

For *A. gerardii*, significant differences were not noted at KNZ for water stress, but towards the end of the season we did see DP attain significantly higher Fv/Fm values, indicating they were less stressed at their home garden. At SGS, both main effects were significant independently and over time. Significance was first noted between DP and PP at the end of the growing season. This data suggests that PPs were less stressed in their home environment.

These data indicate the watering treatments were successful for *B. gracilis* at KNZ and *A. gerardii* at SGS. Though stress was not observed at this scale for both species at both gardens, other data (soil moisture and leaf water potential – see Figure 2.2) supports the implementation of the water treatment. Also, despite the fact that significance was not noted for *B. gracilis* at SGS, p-values were close to significant at the end of the season (water stress: p=0.053, population: p=0.059). These data also suggest that DPs and PPs of *A. gerardii* are better adapted to their native environments.

Height

Maximum height was measured at the end of the growing season. In each plot, the three tallest flowering stalks were measured from ground to tip and an average was determined. A two-way mixed model analysis of variance (ANOVA) was performed for each species at each garden. The fixed effects were water (wet/dry) and population (dominant/peripheral). The random effects were row (water), column (water), pop (individual population), water*pop. Average height data and results from statistical tests are shown in Table 3.2.

For *B. gracilis*, in both gardens the plants receiving more water were significantly taller, as expected. We observed a marginally significant effect of population at KNZ ($P=0.08$), and very significant effect at SGS ($P<0.05$). Interestingly, both populations were taller in their home gardens.

For *A. gerardii*, we did not see a significant effect of water, perhaps due to the deep roots that can tap into lower resources *A. gerardii* is known to have. However, we did observe marginal population significance at KNZ ($P=0.0571$), again with the KS population taller in its home garden.

Individual Vegetative Tiller Mass

When clipping ANPP for *A. gerardii*, 10 individual tillers were randomly selected (some reproductive, some vegetative), clipped, dried at 60°C for at least three days, and weighed to the nearest 0.1 grams. The reproductive data is reported in Chapter 2 and the vegetative data is reported in Table 3.3.

We observed a significant effect of water stress at SGS only, but a population effect at both gardens. DPs produced significantly more massive vegetative tillers than the PPs. These trends are similar to what was observed with reproductive tiller mass.

Table 3.1. Fluorometer data (top panel: *B. gracilis*; bottom panel: *A. gerardii*)

<i>B. gracilis</i>	SGS p-values		KNZ p-values	
water		p=0.9497	water	p<0.0001*
pop		p=0.2691	pop	p=0.7287
water*time:		p=0.0072*	water*time:	p=0.6211
pop*time:		p=0.1864	pop*time:	p=0.4230

<i>A. gerardii</i>	SGS p-values		KNZ p-values	
water		p=0.0035*	water	p=0.7034
pop		p=0.0029*	pop	p=0.1550
water*time:		p<0.0001*	water*time:	p=0.1388
pop*time:		p=0.0359*	pop*time:	p=0.0005*

*statistical significance at p=0.05 level

Table 3.2. Average height data (top panel: *B. gracilis*; bottom panel: *A. gerardii*)

<i>B. gracilis</i>	SGS garden height (cm)	SGS p values	KNZ garden height (cm)	KNZ p values
DP, wet	40.4 ± 1.5	water: p<0.0001* pop: p=0.0021* water*pop: p=0.0052*	39.4 ± 3.7	water: p=0.0024* pop: p=0.0761 water*pop: p=0.6781
DP, dry	33.7 ± 1.5		26.0 ± 4.1	
PP, wet	32.0 ± 1.5		50.7 ± 3.7	
PP, dry	18.4 ± 1.6		34.6 ± 4.1	

<i>A. gerardii</i>	SGS garden height (cm)	SGS p values	KNZ garden height (cm)	KNZ p values
DP, wet	108.1 ± 9.4	water: p=0.1717 pop: p=0.7802 water*pop: p=0.2534	187.3 ± 9.5	water: p=0.0751 pop: p=0.0571 water*pop: p=0.0046*
DP, dry	115.5 ± 9.5		159.6 ± 9.5	
PP, wet	100.1 ± 12.1		137.3 ± 9.8	
PP, dry	88.1 ± 9.7		140.3 ± 9.9	

*statistical significance at p=0.05 level

Table 3.3. *A. gerardii* vegetative tiller mass data

	SGS tiller mass (g)	SGS p values		KNZ tiller mass (g)	KNZ p values
DP, wet	1.17 ± 0.14	water: p=0.0498*		1.09 ± 0.17	water: p=0.6969
DP, dry	0.79 ± 0.14	pop: p=0.0006*		0.93 ± 0.17	pop: p=0.0329*
PP, wet	0.53 ± 0.16	water*pop: p=0.8072		0.38 ± 0.19	water*pop: p=0.0229*
PP, dry	0.31 ± 0.15			0.58 ± 0.18	

*statistical significance at p=0.05 level