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Effect of genotypic richness, drought and mycorrhizal associations on productivity and functional traits of a dominant C_4 grass

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Abstract

While the relationship between genetic diversity and plant productivity has been established for many species, it is unclear whether environmental conditions and biotic associations alter the nature of the relationship. To address this, we investigated the interactive effects of genotypic diversity, drought and mycorrhizal association on plant productivity and plant traits. Our mesocosm study was set up at the Konza Prairie Biological Research Station, located in the south of Manhattan, Kansas. *Andropogon gerardii*, the focal species for our study, was planted in two levels of genotypic richness treatment: monoculture or three-genotype polyculture. A rainout shelter was constructed over half of the experimental area to impose a drought and Thiophanate-methyl fungicide was used to suppress arbuscular mycorrhizal fungi in selected pots within each genotypic richness and drought treatment. Genotypic richness and mycorrhizal association did not affect above-ground biomass of *A. gerardii*. Drought differentially affected the above-ground biomass, the number of flowers and bolts of *A. gerardii* genotypes, and the biomass and the functional traits also differed for monoculture versus polyculture. Our results suggest that drought and genotypic richness can have variable outcomes for different genotypes of a plant species.

Keywords tallgrass prairie, *Andropogon gerardii*, C_4 grass, genetic diversity, mutualism

基因型多样性、干旱、菌根对优势C_4植物生产力及功能性状的影响

摘要：虽然许多物种的遗传多样性和植物生产力之间的关系已经得到证实，但环境条件和生物群落是否会改变这种关系尚不清楚。针对这一问题，本文研究了基因型多样性、干旱和菌根对植物生产力和植物性状的交互作用。该研究建立在堪萨斯州曼哈顿南部的康扎草原生物研究站。本研究对焦点物种大须芒草(*Andropogon gerardii*)采用两种水平的基因型丰富度处理：单种栽培和3基因型混合栽培。在试验区的一半以上建立避雨棚进行抗旱处理，并在每个基因型丰富度和抗旱处理的选定盆栽中使用硫菌酯–甲基杀菌剂抑制丛枝菌根真菌的生长。结果表明，基因型丰富度和菌根对大须芒草的地上生物量无显著影响。干旱对大须芒草各基因型地上生物量、成花数和过早结实有不同的影响，而且生物量和功能性状在

单独栽培和混合栽培处理中有显著差异。这些研究结果说明，干旱和基因型丰富度对不同基因型的植物有不同的结果。

关键词：高草草原，大须芒草(*Andropogon gerardii*)，C_4植物，遗传多样性，互利共生

INTRODUCTION

Genetic diversity within a plant species has been found to positively affect ecological functions (Bailey *et al.* 2009; Govindaraj *et al.* 2015; Hughes *et al.* 2008;) such as arthropod diversity (Cook-Patton *et al.* 2011; Crutsinger *et al.* 2006; Johnson *et al.* 2006), pollination rates (Genung *et al.* 2010), resistance to herbivores (Hughes and Stachowicz 2004; McArt and Thaler 2013), resilience to climate extremes (Reusch *et al.* 2005) and productivity (Crutsinger *et al.* 2006; Di Falco and Chavas 2006; Prieto *et al.* 2015). The effects of genetic diversity on productivity, however, are not always positive, and some studies have found no direct relationship between genetic diversity and productivity (Avolio and Smith 2013a; Avolio *et al.* 2015; Chang and Smith 2014; Fridley and Grime 2010). While the importance of genetic diversity has been established by numerous studies, the role of genetic diversity on influencing various ecosystem functions such as productivity remains controversial and may depend on environmental conditions and biotic interactions.

The genetic diversity effect on several ecosystem functions may vary as environmental conditions change. For instance, the effect of planted genetic diversity of *Oenothera biennis* on plant productivity was enhanced by deer herbivory (Parker *et al.* 2010) but that of *Taraxacum officinale* was decreased by mowing (Drummond and Vellend 2012). Environmental variability might influence the expression of genetic variance (Charmantier and Garant 2005), thus influencing the effect of genetic diversity on ecosystem function. Different genotypes of natural and experimental populations of several plant species have shown variation in their phenotypic responses to environmental variability such as light, water and nutrients (Matesanz *et al.* 2010; Pigliucci *et al.* 1995; Westerman and Lawrence 1970). The genetic diversity effect on ecosystem functions under different environmental conditions needs to be further explored.

Drought is predicted to occur with an increasing evapotranspiration rate due to rising global temperature (Trenberth *et al.* 2014) and will affect all vegetation types (Farooq *et al.* 2009). Drought stress has been well documented in various plants and has been found to affect plant productivity (reviewed by Jaleel and Llorente 2009). Studies have found plant species diversity can buffer drought effects on plant survival (Nagase and Dunnett 2010), above-ground productivity (Craven *et al.* 2016; Tilman *et al.* 2012; Wagg *et al.* 2017) and below-ground productivity (Kahmen *et al.* 2005). Similarly, studies have found plant genetic diversity can buffer drought effects on productivity (Peleg *et al.* 2005) and community stability (Prieto *et al.* 2015). Theoretically, plant genetic diversity is essential for the adaptation of species to future environmental changes (Barrett and Schluter 2008; Raza *et al.* 2019) as higher genetic diversity can provide a larger trait variability and, thus, a greater chance of surviving unfavorable conditions (Westerband *et al.* 2021; Yachi and Loreau 1999). However, the experimental studies, exploring the role of plant genetic diversity under future global changes like drought, are underexplored.

Although relatively unexplored, genetic diversity effects could also be affected by symbiotic interactions (Aavik *et al.* 2021; Van Geel *et al.* 2021). Arbuscular mycorrhizal fungi (AMF) colonize most terrestrial plant species and provide host plants with increased water and nutrients acquisition along with drought tolerance (Augé 2001; Johnson *et al.* 2010) in exchange for host plant's photosynthates (Drigo *et al.* 2010). Also, environmental conditions can affect AMF abundance and biomass (Avolio *et al.* 2014; Williams and Rice 2007; Zeglin *et al.* 2013) and can have consequences for ecosystem function. It is well documented that AMF can enhance productivity as well as influence above-ground plant structure and diversity (Hartnett and Wilson 1999; Maherali and Klironomos 2007; van der Heijden *et al.* 2008). van der Heijden *et al.* (2006) have reported that under higher plant species diversity, the positive effect of AMF on productivity decreased as soil nutrients was more effectively utilized. However, the effect of AMF association on the productivity of a genetically diverse pool within a plant species has not been studied before.

Plant functional traits, defined as any morphological, physiological or phenological feature of a plant that affects its fitness (Pérez-Harguindeguy *et al.* 2016; Violle *et al.* 2007) are known to respond to environmental changes and affect ecosystem function (La Pierre and Smith 2015; Violle *et al.* 2007). These traits can vary among genotypes and impact population performance and community functioning (Ellers *et al.* 2011), and thus, can help understand the mechanism between plant genotypic diversity and productivity. Genotypic identity has also been reported to affect population productivity (Vellend *et al.* 2010) and thus, some genotypes of a plant species may perform better than others under future global change scenarios. Drought effects on plant functional traits on a variety of plant ecosystems including the forests and grasslands are well studied (Cenzano *et al.* 2013; Jaleel and Llorente 2009; O'Brien *et al.* 2017). However, interactive effect of drought, AMF associations and genotypic richness on plant functional traits is not well understood. Grasslands are important ecosystems to study the effect of drought and AMF associations as they are highly susceptible to drought (Lei *et al.* 2020), and most grassland species have a symbiotic relationship with AMF (Johnson *et al.* 2010). For our study, we chose *Andropogon gerardii* Vitman, one of the dominant C_4 grasses of the tallgrass prairie ecosystem, as the focal species. Contributing up to 80% of above-ground productivity (Smith and Knapp 2003), the fate of *A. gerardii* under changing biotic and abiotic conditions will have a significant effect on the community structure and prairie ecosystem (Chaves and Smith 2021; Gustafson *et al.* 2004). Here, we measured plant functional traits and above-ground plant productivity of *A. gerardii* at two levels of genotypic diversity (monoculture and a three-genotype polyculture) under different drought (droughted or ambient rainfall) and AMF association treatments (fungicide treated and an untreated control) to assess how genetic diversity, drought and mycorrhizal fungi interact to affect the plant functional traits and productivity of *A. gerardii*. We hypothesized that: (i) above-ground productivity of *A. gerardii* would be higher in polyculture compared with monoculture, and higher genetic diversity would offset the negative effect of drought and fungicide treatment on above-ground productivity, and (ii) above-ground biomass and functional traits of *A. gerardii* genotypes would be affected by the genetic diversity, drought and mycorrhizal association treatments.

MATERIALS AND METHODS

Site characteristics

This study was conducted from 2011 to 2015 at the Konza Prairie Biological Research Station, a Long-Term Ecological Research (LTER) site, located to the south of Manhattan, KS (39.1069° N, 96.6091° W). Historically, the name 'Konza' comes from the native Americans, Kansa or, Kaw Indians who inhabited the area before the colonization by European settlers. Konza LTER is a tallgrass prairie ecosystem, and its production is primarily driven by perennial C_4 grasses, including *A. gerardii* (Smith and Knapp 2003). In 2011, we established our study site in a watershed unit, AL, a lowland agricultural site that was annually burned and ungrazed prior to the study. The mean annual precipitation of the site is ~892 mm, of which 75% occurs during April–September and mean annual air temperature is 13 °C (Felton *et al.* 2020).

Focal species

Andropogon gerardii is a perennial, clonal grass that primarily reproduces through rhizomatous buds (Benson and Hartnett 2006) and is genetically diverse ranging from four to nine genotypes with an average of 5.2 (±0.73 standard error [SE]) in a 1 m^2 plot (Avolio *et al.* 2011). Also, genotypes of this grass are phenotypically diverse and have been well documented to demonstrate a wide range of traits plasticity to water and nutrient manipulation (Avolio *et al.* 2018; Avolio and Smith 2013b; Chang and Smith 2014).

Experimental design

The split-plot experimental design was completely randomized. We selected a total of five genotypes (Genotypes 2, 3, 4, 5 and 12) of *A. gerardii* for this mesocosm study representing the most common genotypes found in the headquarter regions of the natural tallgrass prairie ecosystem of the LTER site (Avolio and Smith 2013a). We used meristem tissue culturing to propagate *A. gerardii* genotypes for this experiment. Original genotypes for tissue culturing collected in 2009 from the Konza Prairie Biological Research Station. After harvesting, the plant rhizomes were stored for a month at 4 °C and then established in the Marsh Botanical Gardens greenhouse at Yale University, New Haven, CT. Germplasm tissue was harvested from three individual plants of each genotype and sent to SMK Plants LCC (Billings, MT) for meristem tissue culturing to remove maternal effects. Tissue culture plants were planted in the greenhouse in 2011 for hardening and root development for 3 weeks before transplanting to the field site at Konza Prairie Biological Research Station.

In mid-June 2011, the young plants were transferred to the field and planted within in 30 cm diameter collars that were buried 30 cm in the intact soil. The collars (hereafter pots) limited horizontal root spread but not vertical. Each pot was assigned a genotypic richness treatment, either monoculture (individual plants of the same genotypes) or three-genotype polyculture. For three-genotype polyculture, genotypes were selected from a pool of five genotypes such that there was an equal distribution of the five genotypes in ten different combinations of polyculture. In total, 140 pots were used which had nine individual plants each and two levels of genotypic richness—the nine individuals were planted in a rectangular array with 9 cm between plants. There were 60 pots with plants in monoculture and 80 for polyculture. The experiment area was divided into two main plots for manipulating the amount of water received by the *A. gerardii* plants. A rainout shelter using clear, 6 mil, UV-transparent polyethylene greenhouse film was constructed on one of the two main plots to exclude rainfall by 100% such that two levels of drought treatment were (i) ambient (that received ambient rainfall) and (ii) droughted (Fig. 1). Fay *et al.* (2000) have reported a decrease in light reduction by about 21% in similar rainout shelter. Both plots, ambient and droughted, had equal numbers of monoculture and polyculture pots in a completely randomized design. Each main plot was then randomly assigned levels of mycorrhizal treatment within monocultures and polycultures. The two levels of mycorrhizal treatment were (i) untreated (only received water) and (ii) fungicide treated. Thiophanate-methyl fungicide (70% solution by weight) was used for fungicide-treated plots (Wilson and Williamson 2008). 500 mL of fungicide or water was applied every 2 weeks over the course of the growing season for the duration of the 5-year experiment. Plants under droughted treatment only received the 500 mL of fungicide or water whereas plants under ambient treatment received ambient rainfall in addition to the 500 mL of fungicide or water.

Environmental conditions measurements

In 2011, ambient temperature and humidity above the soil surface were measured daily to understand the effect of the rainout shelter on local climate using ibuttons (Model DS 1923, Maxim Integrated, San Jose, CA, USA). There was no difference in air temperature ([mean ± standard deviation] out in the open 26 ± 8 °C compared with under the rainout shelter 22 ± 6 °C) or relative humidity (64% ± 25%

Figure 1: Research site showing the mesocosm study to assess the effect of genotypic richness, drought and mycorrhizal association in *Andropogon gerardii*. Our study area was divided into two main plots. The rainout shelter on the right were used to exclude 100% of ambient rainfall and simulate drought on one of the two main plots. Each main plot had two levels of genotypic richness: monoculture (nine individuals of the same genotype) and polyculture (nine individuals of three different genotypes). Thiophanate-methyl fungicide was used to suppress AMF in half of the pots of each genotypic richness level in each main plot. Pots that received fungicide were marked with pink flags, and other pots received water.

ambient, rainout shelter 62% ± 20%) based on a *t*-test (Supplementary Fig. S1). In 2012, we measured volumetric water content weekly from selected five pots under both drought and ambient treatments using probes from EC-20 ECH$_2$O soil moisture probes (Decagon Devices, Inc., Pullman, WA, USA) at 10 cm to see if there is a difference between the treatments. The shelter reduced soil moisture in average by 60% compared with ambient (Supplementary Fig. S2) (ambient 15% ± 7%, rainout shelter 6% ± 3%). Please note that 2012 was a drought year, and soil moisture was also low in the ambient plots.

During mid-August 2012, we collected soil from selected pots (0–10 cm) using a hand probe (2.5 cm diameter) from drought and mycorrhizal treatment and tested for phosphorus (P) and nitrogen (N) content of soil. Plant available P concentration obtained from Mehlich 3 test (Ziadi and Sen Tran 2008) was different for ambient and droughted treatments (Supplementary Fig. S4) with a mean of 68 ± 16 ppm for ambient treatment and 56 ± 9 ppm for droughted treatment. Phosphorus concentration did not differ for mycorrhizal treatment. Our field site being a former agricultural land had history of added soil nutrients. Ammonium N and nitrate N were extracted for 24 h in a 2 mol/L KCl solution, filtered and then analyzed colorimetrically with Alpkem autoanalyzer (Alpkem Cororation, College Station, TX). Both the extractable ammonium and nitrate N did not significantly differ between ambient and droughted treatments and between fungicide and control treatments. Our experiment site had a mean of 7.7 and 6.5 ppm of ammonium N and nitrate N, respectively.

Soil microbial community measurements

From the soil collected from selected pots during mid-August 2012, we did phospholipid-derived fatty acids (PLFA) analysis to determine the effectiveness of fungicide treatment and to see if microbial biomass differed between treatments. We assessed the biomass of gram-positive and gram-negative bacteria, AMF and saprophytic fungi. This work was done in the lab of Gail T. Wilson, Oklahoma State University, Stillwater, Oklahoma. Qualitative and quantitative PLFA analyses were done using Bligh and Dyer method (Frostegård *et al.* 1991) using an Agilent 6890 gas chromatograph (Agilent Technologies, Palo Alto, CA, USA) and Sherlock software (MIDI, Newark, NJ, USA). The fatty acids used as indicators were: 16:1ω5c for AMF; 18:2ω6,9 for other fungal PLFAs (Schnoor *et al.* 2011); and 15:0, a17:0, i15:0, i16:0, i17:0, 16:1ω7, 17:0, cy17:0 and cy19:0 for bacteria (Moore-Kucera and Dick 2008).

A. gerardii biomass and functional traits measurements

For each year of the experiment, 2011–2015, aboveground biomass was clipped 2.5 cm from the ground at the end of the growing season (September–October), leaving the plant rhizome and all belowground structures intact for next year's growth. 2011 was an establishment year, and due to the small stature of the plants, these data were not included in analyses. In 2012, several functional traits that are indicators of plant growth strategies of individual plants were measured. Maximum height of each individual plant (height of the tallest tiller), number of flowers and number of bolts were measured at the end of the growing season. Plant height is associated with growth form and competitive vigor (Pérez-Harguindeguy *et al.* 2016), number of flowers and bolts are reproductive traits that are directly linked to plant fitness (Aguilar *et al.* 2008; Weltzin *et al.* 2003). Additionally, the weight of each individual plant was recorded at the end of the growing season and linked to planted genotype. For years 3–5 (2013–2015), only the biomass of the whole pots were recorded.

Relative yield calculation

To understand the effect of growing and competing with individuals of the same and different genetic backgrounds, we calculated relative yield as:

(yield in polyculture − yield in monoculture)/yield in monoculture

We calculated relative yield only for 2012 data where we had individual plant weight. A positive value would mean higher yield of a genotype in polyculture compared with its yield in monoculture. Similarly, a negative value would mean a higher yield of a genotype in monoculture.

We also looked for the mechanism explaining the difference in yield of *A. gerardii* between monoculture and polyculture. We used the equation by Loreau and Hector (2001) to calculate the complementarity and selection effects:

$$\Delta Y = N\overline{\Delta RY_1}\ \bar{M} + N\,\mathrm{cov}(\Delta RY_i,\ M_i)$$

where ΔY is the difference in yield between polyculture and monoculture, $\Delta RY_i = \frac{O_i}{M_i} - RY_E$ is the relative yield difference (observed − expected) of genotype i where O_i is the yield of genotype i in polyculture, M_i is the yield of genotype i in monoculture and RY_E is the expected relative yield of each genotype in polyculture ($1/N$, where N is the number of genotypes in the polyculture). The term $N\overline{\Delta RY_1}\,\bar{M}$ represents the complementarity effect and $N\,\mathrm{cov}(\Delta RY_i,\ M_i)$ is used to determine the selection effect. A positive complimentary effect would mean a higher yield of a genotype in polyculture compared with monoculture due to resource partitioning, and a positive selection effect would mean a higher yield of a genotype in polyculture compared with monoculture due to one or, more high yielding genotypes. We assessed differences in relative yield, and selection and complementarity effects of *A. gerardii* genotypes under different experimental conditions.

Statistical analysis

A linear mixed model for a split-plot design was used to analyze the effect of genotypic richness, drought treatment and mycorrhizal treatment on the biomass of *A. gerardii* over the years of 2012–2015 using 'nlme' package in R version 3.6.4 (Pinheiro *et al.* 2013). We used year, genotypic richness, drought treatment and mycorrhizal treatment as our main effects, and pot number and polyculture combinations as our random effects. Using the 2012 plant data, the only year we had functional trait measurements of each genotype, we did additional analyses of height, number of flowers and number of bolts for individual plant from each pot. We again used a linear mixed model with genotype, genotypic richness, drought treatment and mycorrhizal treatment as our main effects, and pot number and polyculture combinations as random effects. We used pot number that was assigned to each pot during establishment as a random effect to account for spatial variation, and the polyculture combination as our random effect on biomass, number of flowers and number of bolts to account for different polyculture types. Predictor variables were checked for multicollinearity using VIF > 4.0 before fitting them into our models and normality and homoscedasticity assumptions of the model were checked and verified using diagnostic residual versus fitted and *Q*–*Q* plots.

We conducted a nonmetric multidimensional scaling (NMDS) to see the difference in microbial community (gram-negative bacteria, gram-positive bacteria, AMF and saprophytic fungi) under drought and mycorrhizal treatment under *A. gerardii* genotypes from soils collected from selected pots in 2012, based on Bray–Curtis dissimilarity using the vegan package (Oksanen *et al.* 2005).

RESULTS

Soil microbial community

Fungicide treatment had no effect on the biomass of arbuscular mycorrhizal or saprotrophic fungi, but fungal biomass of both AM and saprotrophic fungi was lower in droughted pots compared with pots that received ambient rainfall in 2012 (Supplementary Fig. S3a and b). In addition, the biomass of gram-positive and gram-negative bacteria were not significantly affected by the fungicide treatment, but gram-positive bacteria biomass was slightly higher under ambient treatment than under droughted treatment (Supplementary Fig. S3c and d). Similarly, overall microbial biomass was higher under ambient conditions compared with the droughted treatment but did not differ under mycorrhizal treatment. Overall, microbial communities' biomass significantly differed between ambient and droughted treatments but there was no significant difference between control and fungicide-treated plants (Fig. 2) or among plant genotypes.

Effect of genotypic richness, drought and fungicide treatment on the overall above-ground biomass of *A. gerardii*

Our model explained about 49% of the variation in the overall above-ground biomass of *A. gerardii* over the years of 2012–2015. Year × drought treatments interaction significantly affected the above-ground biomass of *A. gerardii* (Table 1; Fig. 3). The above-ground biomass of *A. gerardii* was significantly higher under ambient than droughted treatment in 2012, 2013 and 2014. However, in 2015, the biomass did not differ significantly between drought treatments. By contrast, genotypic richness and fungicide treatment had no significant effect on the above-ground biomass of *A. gerardii* (Table 1).

Effect of genotypes, genotypic richness, soil moisture and mycorrhizal treatment on functional traits of *A. gerardii* in 2012

Above-ground biomass

In 2012, the interaction between genotype and drought treatment had a significant effect on the above-ground biomass of individual *A. gerardii* plants (Table 2; Fig. 4). Only genotypes G2 and G3 had significantly higher above-ground biomass under ambient treatment than the droughted treatment (Fig. 4). Genotypic richness had no significant main effect on the above-ground biomass of *A. gerardii*, although the

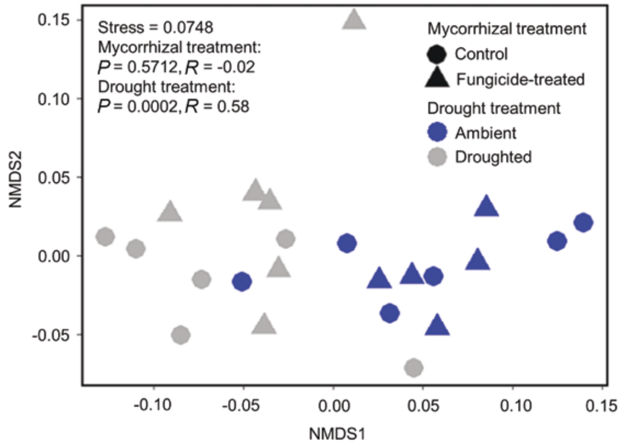

Figure 2: Ordination of microbial communities using NMDS generated from abundances of AMF, saprotrophic fungi, gram-positive and gram-negative bacteria. The data were obtained from PLFA tests of soil samples (n = 22) collected mid-August 2012 from selected pots of the experiment.

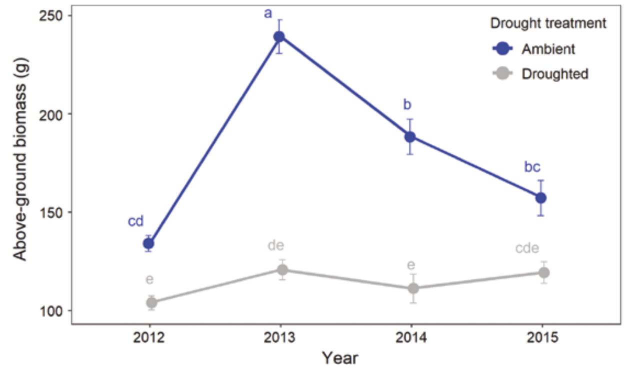

Figure 3: There was a significant interaction between year and drought treatment on the above-ground biomass of *Andropogon gerardii* from years 2012 to 2015. Letters show pairwise significant differences obtained by Tukey-HSD such that two points sharing no letters are significantly different to each other (P < 0.05). Each point represents the treatment mean and is shown with SE bars.

Table 1: ANOVA table showing results of linear mixed model for assessing the effect of drought treatment, genotypic richness and mycorrhizal association on biomass of *Andropogon gerardii* from 2012 to 2015

Variables	numDF	denDF	*F*	*P*
(Intercept)	1	289	80 434.43	<0.0001*
Year	3	36	18.57	<0.0001*
Drought	1	49	167.00	<0.0001*
Genetic richness	1	13	3.08	0.1029
Mycorrhizae	1	98	0.35	0.5531
Year: drought	3	49	10.84	<0.0001*
Year: genetic richness	3	36	0.45	0.7219
Drought: genetic richness	1	49	2.16	0.1481
Year: mycorrhizal treatment	3	98	0.32	0.8087
Drought treatment: mycorrhizal treatment	1	98	2.28	0.1340
Genotypic richness: mycorrhizal treatment	1	98	3.47	0.0655
Year: drought treatment: genotypic richness	3	49	0.21	0.8865
Year: drought treatment: mycorrhizal treatment	3	98	1.00	0.3940
Year: genotypic richness: mycorrhizal treatment	3	98	0.45	0.7204
Drought treatment: genetic richness: mycorrhizal treatment	1	98	0.00	0.9847
Year: drought treatment: genetic richness: mycorrhizal treatment	3	98	0.60	0.6161

denDF = denominator degrees of freedom, numDF = numerator degrees of freedom. *Significant at P < 0.05.

biomass was significantly affected by the interaction between genotypic richness and genotype (Table 2; Fig. 4). Genotype G2 had higher above-ground biomass within monoculture than polyculture while genotypic richness had no significant effect on the above-ground biomass of the other genotypes.

Table 2: ANOVA table showing results of linear mixed model for assessing the effect genotype, genotypic richness, soil moisture and mycorrhizal association on biomass of *Andropogon gerardii* in 2012

Variables	numDF	denDF	*F*	*P*
(Intercept)	1	1069	1978.1020	<0.0001*
Drought treatment	1	63	27.7140	<0.0001*
Genotypic richness	1	63	0.2900	0.5921
Mycorrhizal treatment	1	63	0.2852	0.5952
Genotype	4	1069	14.7147	<0.0001*
Drought treatment: genotypic richness	1	63	1.8403	0.1798
Drought treatment: mycorrhizal treatment	1	63	0.0810	0.7769
Genotypic richness: mycorrhizal treatment	1	63	1.1304	0.2918
Drought treatment: genotype	4	1069	3.4722	0.0079*
Genotypic richness: genotype	4	1069	6.1948	0.0001*
Mycorrhizal treatment: genotype	4	1069	1.2737	0.2785
Drought treatment: genotypic richness: mycorrhizal treatment	1	63	0.5898	0.4454
Drought treatment: genotypic richness: genotype	4	1069	1.1696	0.3226
Drought treatment: mycorrhizal treatment: genotype	4	1069	1.0764	0.3668
Genotypic richness: mycorrhizal treatment: genotype	4	1069	0.9372	0.4415
Drought treatment: genotypic richness: mycorrhizal treatment: genotype	4	1069	0.3047	0.8749

denDF = denominator degrees of freedom, numDF = numerator degrees of freedom. *Significant at $P < 0.05$.

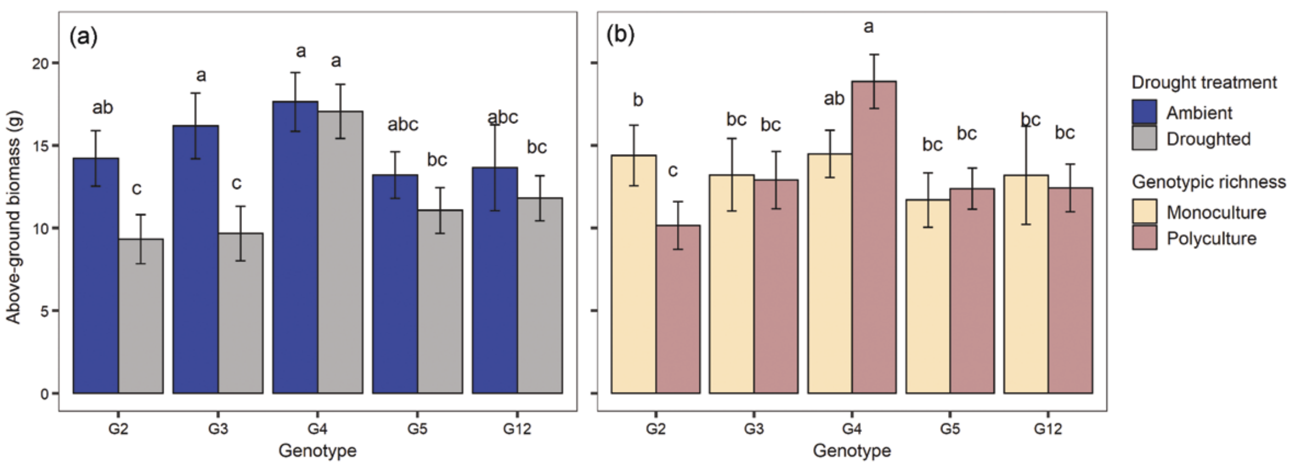

Figure 4: There were significant interactions between genotype and drought treatment (**a**), and between genotype and genotypic richness (**b**) on the above-ground biomass of *Andropogon gerardii* in 2012. Letters show pairwise significant differences obtained by Tukey-HSD such that two points sharing no letters in a graph are significantly different to each other ($P < 0.05$). Each bar represents the mean and is shown with SE bars.

Height, flower and bolt number

Drought treatment and genotype had a significant effect on the height of *A. gerardii* plants (drought treatment P = <0.0001, genotype P = 0.0041). *Andropogon gerardii* plants were shorter when grown in the droughted treatment (63.34 ± 1.05 cm) compared

Table 3: Mean values of measured plant functional traits of five genotypes of *Andropogon gerardii* in 2012 across all treatments

Genotypes	Mean trait values (±SE)		
	Plant height (cm)	Number of flowers	Number of bolts
G2	72.69 ± 1.07	0.839 ± 0.15	0.687 ± 0.02
G3	68.3 ± 1.50	0.004 ± 0.06	0.483 ± 0.10
G4	66.39 ± 0.63	0.246 ± 0.08	0.702 ± 0.02
G5	68.06 ± 0.97	0.099 ± 0.01	0.390 ± 0.07
G12	69.3 ± 1.09	0.039 ± 0.09	0.570 ± 0.10

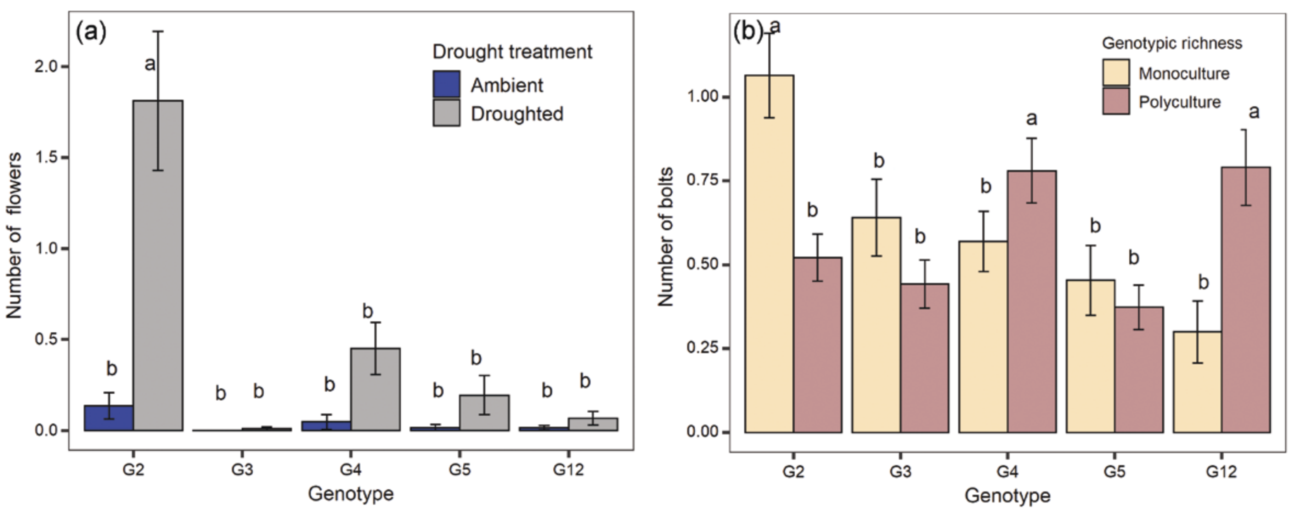

Figure 5: There was a significant interaction between genotype and drought treatment on the number of flowers (**a**), and between genotype and genotypic richness on the number of bolts of *Andropogon gerardii* (**b**) in 2012. Letters show pairwise significant differences obtained by Tukey-HSD such that two points sharing no letters in a graph are significantly different to each other ($P < 0.05$). Each bar represents the mean and is shown with SE bars.

with the ambient treatment (74.46 ± 1.09 cm). Genotype G2 was significantly taller than genotypes G4 and G5 (Table 3). Genotypes G3 and G12 did not significantly differ in height with either G2 or G4 and G5 (Table 3).

There was a significant genotype × drought treatment interaction on the number of flowers of *A. gerardii* in 2012 (Fig. 5) where only genotype G2 had significantly more flowers under droughted treatment than under ambient treatment (Fig. 5). There was also an interactive effect of genotype and genotypic richness on the number of bolts of *A. gerardii* (Fig. 5). Genotype G2 had more bolts under monoculture than polyculture while genotype G12 had more bolts in polyculture than in monoculture (Fig. 5). Drought treatment also significantly affected the number of bolts of *A. gerardii* such that the plants under droughted treatment had higher number of bolts than under ambient treatment.

Competitive outcomes of genotypes under drought treatment in 2012

Post hoc comparisons using the Tukey-HSD test indicated that the mean relative yield of the genotype G4 was significantly higher than the genotypes G2 and G3, meaning it grew more in polyculture versus monoculture, but not significantly different from G12 under ambient treatment (Fig. 6a). Similarly, genotype G4 had significantly higher relative yield than other genotypes under droughted treatment (Fig. 6a). Genotype G5 had positive relative yield under ambient treatment but had negative relative yield under the droughted treatment. Overall, under ambient treatment, there was a positive

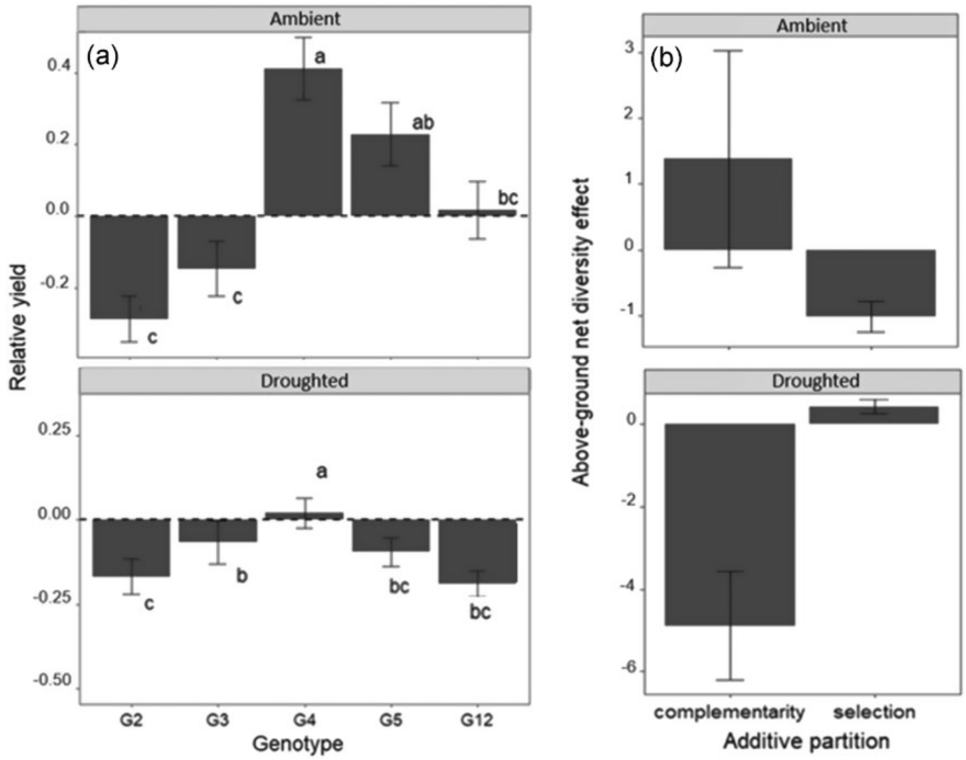

Figure 6: Competitive outcomes of the genotypes. (**a**) Mean relative yield biomass (±1 SE) of genotypes under ambient and droughted treatment in 2012. Values above zero mean higher yield in polyculture than monoculture and values below zero mean lower yield in polyculture than monoculture. (**b**) Mean complementarity and selection effects (±1 SD) on the above-ground biomass of *A. gerardii* under ambient and droughted treatment. Letters in the plots show pairwise significant differences obtained by Tukey-HSD such that two points sharing no letters are significantly different from each other ($P < 0.05$).

complementarity effect but a large variation in the effect while there was a negative complementarity effect under droughted treatment (Fig. 6b). The selection effect was negative under ambient treatment but approximately zero under droughted treatment (Fig. 6b).

DISCUSSION

Abiotic and biotic factors like drought and mycorrhizal association have the potential to affect plant productivity and plant functional traits which can have implications for plant structure, composition and survival in the changing climate (Koerner *et al.* 2014; McCain *et al.* 2011). We assessed the effect of planted genetic diversity on the productivity a C_4 grass, *A. gerardii*, under droughted and ambient water conditions, and under fungicide treated and control mycorrhizal treatments in a multiyear mesocosm study. In addition to productivity, we also assessed trait variation among *A. gerardii* genotypes to look at possible mechanism of the relationship between genetic diversity and productivity. Overall, genotypic richness and mycorrhizal association did not affect above-ground biomass of *A. gerardii* over the 4 years of our experiment. However, drought treatment significantly decreased the above-ground biomass of *A. gerardii* in all the years of the experiment. Interestingly, drought differentially affected the traits of *A. gerardii* genotypes, and the traits of genotypes also differed for monoculture versus polyculture.

Surprisingly, as evident form the PLFA tests, the biomass of AMF and saprophytic fungi in the soil collected from selected pots in 2012 did not differ for fungicide treated and control pots. Usually, fungicide Thiophanate-methyl is used to suppress root colonization of AMF with host plants (Hartnett and Wilson 1999). Because this was a multiyear study, we did not collect the root samples for determining root colonization by AMF. However, the high phosphorus content in our soils might have suppressed the AMF abundance and colonization in the first place as has been found in several studies (Avolio *et al.* 2014; Balzergue *et al.* 2011; Breuillin *et al.* 2010; Carbonnel and Gutjahr 2014). Generally, the phosphorus content characteristic to the Konza Prairie Biological Station ranges from 4 to 26 ppm (Myster 2011; Rothrock and Squiers 2003) but our research site had exceptionally high amount of phosphorus content in the soil (up to 79 ppm). High phosphorus content in the soil is thought to make AMF colonization less important for plants (Avolio *et al.* 2014; Chen *et al.* 2019). Our field site being a former agricultural land had high phosphorus and thus, about twenty times lower AMF fungi biomass than is characteristic of the site which has been reported up to 60 nmol/g soil (Manoharan *et al.* 2017). Had our experiment been on a field site with lower soil P content, we could have seen negative effects of fungicide on biomass and functional traits of *A. gerardii*, however, the mycorrhizal treatment had no significant effect on the above-ground biomass and functional traits of *A. gerardii*. McCain *et al.* (2011) reported a decrease in plant productivity of dominant grasses after 4 years of AMF suppression in restored tallgrass prairie.

The hypothesized mechanism underlying the positive relationship between genetic diversity and productivity has been attributed to complementarity effects, where each individual genotype grows better in polyculture versus monoculture, and selection effect, where the presence of a productive genotype accounts for the higher production (Loreau and Hector 2001). Complementarity effect results from niche partitioning between diverse genotypes so that resources like water and nutrients can be optimally utilized by the population. We found a small positive complementarity effect under ambient condition, but a negative complementarity effect in the drought treatment. This means that genotypes had higher above-ground biomass in polyculture compared with monoculture under ambient rainfall condition but had lower above-ground biomass in polyculture compared with monoculture in the drought treatment. Genotypes in the drought treatment seem to be competing with other genotypes for the scare resource, water. When water was not scare, the competition among the genotypes seems to be relaxed and slightly facilitative. Similarly, the selection effect was negative in the ambient treatment which suggests that some of the genotypes we selected for the experiment had overlapping niches for resources. Our findings add further support that environmental conditions affect the nature of the relationship between genetic diversity and productivity.

Although there was a small positive complementarity effect under ambient rainfall, the results of the study could not support our hypothesis regarding the positive relationship between genotypic diversity and productivity of *A. gerardii*. The above-ground biomass of *A. gerardii* from 2012 to 2015 did not significantly differ between monoculture and polyculture. This result is similar to the findings of Avolio *et al.* (2015) and Chang and Smith (2014). In contrast, Morris *et al.* (2016) used different cultivars of *A. gerardii* most of which are composites of various germplasms and found positive effect of genotypic diversity on productivity of *A. gerardii*. Our study used naturally co-occurring genotypes at Konza Prairie Biological Station to create genotypic diversity as done by Avolio *et al.* (2015) and Chang and Smith (2014), and found similar results, and thus our findings may be more realistic of what occurs in intact *A. gerardii* populations. Level of genotypic richness and the identities of the genotypes in the polyculture can affect the relationship between genotypic diversity and productivity of a plant species. We had three genotypes randomly selected from a pool of five genotypes in our polyculture. Genotypes G4 and G5 had higher above-ground biomass compared with G2 and G3 in polyculture than in monoculture under ambient rainfall. The positive and negative relative yield of the genotypes seems to have canceled each other out and resulted in overall no significant relationship between genotypic richness and productivity of *A. gerardii*. Genotype G2 has been previously reported to have lower above-ground biomass in polyculture compared with monoculture (Avolio *et al.* 2015). Phenotypic differences under different genetic diversity can have important implications for understanding genetic diversity–productivity relationship (Schöb *et al.* 2015). Consequently, studies that use different genotypic richness and different identities of genotypes might yield different results (Vellend *et al.* 2010).

As expected, drought negatively impacted the above-ground biomass of *A. gerardii*. The difference in above-ground biomass of droughted and ambient treatments fluctuated each year which might be due to yearly variability in ambient soil moisture and plants root age. Decreasing growth during abiotic stress such as drought is a coping mechanism (Kim *et al.* 2010). Many plant functional traits such as leaf traits and phenology are constitutive of plant strategies to drought adaptation (Chaves *et al.* 2003) and thus, are critical to study to understand plant growth under drought. We found that along with the above-ground biomass, drought treatment had a significant effect on the height, and number of flowers and bolts of

A. gerardii. *Andropogon gerardii* plants under drought were smaller in height and had more bolts. Decrease in height and higher bolting under abiotic stress has been attributed to plants strategy to shorten their vegetative phase and shift the resources to the reproductive parts (Heschel and Riginos 2005; Wolfe and Tonsor 2014). For instance, genotype G2 had lower above-ground biomass but higher number of flowers and bolts in the drought treatment, and thus it is likely that genotype G2 is shifting its resources to its reproductive parts to escape drought. Genotype G2 is more responsive to water treatment and more plastic for number of buds than other *A. gerardii* genotypes (Avolio and Smith 2013b), which might have helped genotype G2 to shift its resources to reproductive phase better than other genotypes when droughted. Additionally, consistent with our results, genotype G2 has been found to grow faster and taller while genotype G4 has been found to have shorter height with a slower growth rate (Avolio *et al.* 2011; Avolio and Smith 2013b). Since G2 grew taller but had lower above-ground biomass than genotype G4, genotype G4 might have produced more tillers than G2. Understanding how different genotypes of the same plant species can respond differentially under various biotic and abiotic factors can inform about their fate under the global change.

In our study, although there was no positive relationship between genotypic richness and above-ground productivity, we found evidence of differential trait and productivity response of naturally occurring genotypes of *A. gerardii* under different environmental conditions. The results further exemplify how environmental conditions can have variable outcomes for different genotypes in different competitive environments. Understanding the competitive outcomes of genotypic diversity under various environmental conditions of a dominant grass can help with grassland restoration decisions to better cope with the present and future climate change.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Mean monthly temperature (temp) and mean monthly relative humidity (RH) during the 2011 growing season of *Andropogon gerardii*.

Figure S2: Weekly volumetric water content across drought treatments during the 2012 growing season of *Andropogon gerardii*.

Figure S3: Mean biomass (±1 SE) of (a) saprophytic fungi (b) arbuscular mycorrhizal fungi (c) gram-positive bacteria and (d) gram-negative bacteria.

Figure S4: Mean phosphorus (P) concentration (±1 SD) of soil samples (n = 22) collected during mid-August 2012 from selected pots of the experiment using Mehlich test.

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