

Intraspecific variation in precipitation responses of a widespread C₄ grass depends on site water limitation

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Abstract

Aims

Variation in precipitation strongly influences plant growth, species distributions and genetic diversity. Intraspecific variation in phenotypic plasticity, the ability of a genotype to alter its growth, morphology or physiology in response to the environment, could influence species responses to changing precipitation and climate change. Despite this, the patterns and mechanisms of intraspecific variation in plasticity to variable precipitation, and the degree to which genotype responses to precipitation are influenced by variation in edaphic conditions, remain poorly understood. Thus, we determined whether genotypes of a widespread C₄ grass (*Panicum virgatum* L., switchgrass) varied in aboveground productivity in response to changes in precipitation, and if site edaphic conditions modified genotype aboveground productivity responses to precipitation. We also determined if genotype productivity responses to precipitation are related to plasticity in underlying growth and phenological traits.

Methods

Nine *P. virgatum* genotypes originating from an aridity gradient were grown under four treatments spanning the 10th to the 90th percentiles of annual precipitation at two sites in central Texas: one site with deep, fine-textured soils and another site with shallow, coarse-textured soils. We measured volumetric soil water content (VWC), aboveground net primary productivity (ANPP), tiller production (tiller number), average tiller mass, canopy height, leaf area index (LAI) and flowering time on all plants at both sites and examined genotype responses to changes in precipitation.

Important Findings

Across precipitation treatments, VWC was 39% lower and more variable at the site with shallow, coarse-textured soils compared to the site with deep, fine-textured soils. ANPP averaged across genotypes and precipitation treatments was also 103% higher at the site with deep, fine-textured soils relative to the site with shallow, coarse-textured soils, indicating substantial differences in site water limitation. Where site water limitation was higher, ANPP of most genotypes increased with increasing precipitation. Where site water limitation was less, genotypes expressed variable plasticity in response to precipitation, from no change to almost a 5-fold increase in ANPP with increasing precipitation. Genotype ANPP increased with greater tiller mass, LAI and later flowering time at both sites, but not with tiller number at either site. Genotype ANPP plasticity increased with genotype tiller mass and LAI plasticity at the site with deep, fine-textured soils, and only with genotype tiller mass plasticity at the site with shallow, coarse-textured soils. Thus, variation in genotype ANPP plasticity was explained primarily by variation in tiller and leaf growth. Genotype ANPP plasticity was not associated with temperature or aridity at the genotype's origin. Edaphic factors such as soil depth and texture may alter genotype ANPP responses to precipitation, and the underlying growth traits contributing to the ANPP response. Thus, edaphic factors may contribute to spatial variation in genotype performance and success under altered precipitation.

Keywords: climate change, *Panicum virgatum*, phenology, phenotypic plasticity, precipitation

Received: 2 July 2015, Revised: 18 January 2016, Accepted: 23 April 2016

INTRODUCTION

Water availability is the single most important abiotic factor governing plant growth and function (Boyer 1982; Chaves *et al.* 2003; Nemani *et al.* 2003; Schulze 1986). Thus, anticipated changes in precipitation in future climate scenarios (Collins *et al.* 2013) are likely to have substantial impacts on plant growth and fitness (Allen *et al.* 2010; Fay *et al.* 2002, 2003; Heisler-White *et al.* 2009; Knapp *et al.* 2002, 2008; Weltzin *et al.* 2003). Ultimately, altered precipitation will impact the persistence, geographic distributions and genetic diversity of populations and species (Avolio *et al.* 2013; Parmesan and Yohe 2003).

Phenotypic plasticity, defined as the ability of a genotype to alter its phenotype in response to environmental change (Bradshaw 1965), will strongly influence how plants respond to altered precipitation and global change (Avolio and Smith 2013; Nicotra *et al.* 2010; Valladares *et al.* 2007). Phenological (e.g. flowering time) or growth (e.g. leaf area, biomass) plasticity, for example, may allow plants to maximize productivity and reproduction when conditions are optimal, and avoid stress when conditions are less favorable (Anderson *et al.* 2012; Bazzaz *et al.* 1987; Schlichting 1986; Sultan 2000). Alternatively, low plasticity in growth and function may result in greater tolerance or stability, and may help plants maintain fitness under more variable or stressful conditions (Baquedano *et al.* 2008; Grime 1977; Warren and Lake 2013).

Because of the potential adaptive importance of phenotypic plasticity, intraspecific (i.e. genotypic) variation in phenotypic plasticity has been recognized as a key determinant of species' ecological and evolutionary responses to climate change (Franks *et al.* 2013; Juenger 2013; Jump and Peñuelas 2005; Pfennig *et al.* 2010; Valladares *et al.* 2014). In the short term, plasticity could delay adaptive evolution by reducing selective pressures. However, plasticity could also help preserve genetic diversity in the face of stressful conditions brought about by climate change, resulting in evolutionary adaptation over longer time scales (Crispo 2008). Despite this, the factors influencing genotypic variation in phenotypic plasticity remain poorly understood, particularly in the context of altered precipitation and climate change (Aspinwall *et al.* 2015; Moran *et al.* 2015). For instance, we know little about the growth and phenological traits (e.g. leaf area, flowering time) that underlie variation in genotype aboveground net primary productivity (ANPP) under altered precipitation. In addition, few studies have examined how a genotype's response to altered precipitation may depend on edaphic conditions (e.g. soil properties) which modify the degree of water limitation. The overall scarcity of information regarding within-species patterns of variation in phenotypic plasticity limits our ability to predict populations and species responses to climate change across variable landscapes (Franks *et al.* 2013; Nicotra *et al.* 2010; Peñuelas *et al.* 2013; Valladares *et al.* 2014).

Panicum virgatum is a native perennial C₄ bunchgrass, broadly distributed throughout North American grasslands.

The species is planted for forage, soil conservation and as a biofuel feedstock (Parrish and Fike 2005; Wright 2007). *P. virgatum* provides a valuable model system for examining local adaptation and genetic variation in phenotypic plasticity (Lowry *et al.* 2014). Genotypic variation in *P. virgatum* growth and phenology in part reflects climatic adaptation across latitudinal gradients. On average, southern warm-origin genotypes often show earlier growth, later flowering and higher productivity than northern cool-origin genotypes (Aspinwall *et al.* 2013; Casler *et al.* 2004; McMillan 1965). Southern genotypes are also adapted to more arid growing seasons and invest more heavily in leaf structure (thickness) and use water more conservatively than northern genotypes adapted to relatively cool, moist conditions (Aspinwall *et al.* 2013). These contrasting functional strategies may influence patterns of genotype growth plasticity (Chapin *et al.* 1993; Quiroga *et al.* 2013; Reich *et al.* 2003), where southern genotypes may be less responsive to precipitation than northern genotypes.

In this study, we examined genotypic variation in *P. virgatum* growth and phenological plasticity in response to four experimental precipitation treatments applied at two sites in central Texas, USA. We asked (i) Do genotypes originating from a temperature and aridity gradient vary in ANPP in response to changing amounts of precipitation? (ii) Do site differences in soil properties influence the degree of water limitation on *P. virgatum* productivity, and modify genotype productivity, growth and phenological responses (i.e. plasticity) to changing precipitation amounts? and (iii) Is genotypic variation in ANPP plasticity related to plasticity in underlying growth and phenological traits, including tiller production, tiller mass, canopy height, leaf area and flowering time?

MATERIALS AND METHODS

Experimental sites and facilities

This study was conducted near Temple, TX (31°3'25.7"N, 97°20'50.9"W) and Austin, TX (30°11'0.4"N, 97°52'35.2"W). The two sites differed in soil texture and depth. Temple soils are fine textured (Austin silty clay, fine silty, carbonatic, Udorthentic Haplustol) and moderately deep (50–100 cm) with medium to rapid runoff and moderate to low permeability. Austin soils are coarse textured (Speck clay loam, clayey, thermic Lithic Argiustolls) and are shallow (35–50 cm deep) with low runoff and slow permeability. The two sites are ~110 km apart and differ little in climate. The Temple site is 199 m above sea level. Mean maximum temperature (July–August) is ~35.0°C, mean minimum temperature (December) is ~3.0°C and mean annual precipitation (MAP) is 910 mm. The Austin site is 246 m above sea level. Mean maximum temperature is ~35.0°C, mean minimum temperature is ~5.6°C and MAP is 870 mm.

At each site, an 18.3×73.0 m rainout shelter was constructed (Windjammer Cold Frame, International Greenhouse Company, Danville, IL, USA). Details of the shelter design are provided in Aspinwall *et al.* (2013) (supplementary Fig. S1).

Beneath each shelter, sixteen 5 × 5 m plots were arranged in four blocks. Plots within blocks were spaced 0.25 m apart, and blocks were spaced 2.76 m apart. Below the soil surface, a 1.84-mm thick vertical barrier of pond liner (Firestone Specialty Products, Indianapolis, IN, USA) surrounds each plot. The barrier was buried 120 cm and 20 cm below the soil surface at Temple and Austin, respectively, due to differences in soil depth. The barrier limits subsoil water movement and root penetration from outside the plot, and extends 10 cm above the soil surface to eliminate overland flow into the plots.

Genotypes

Nine *P. virgatum* genotypes originating from 27°N to 41°N latitude in the Central USA were included in this study (Table 1; Aspinwall et al. 2013). Temperature and mean summer precipitation decreases and increases, respectively, with latitude such that southern genotypes originate from warm, arid conditions and northern genotypes originate from relatively cool, moist conditions. All genotypes were clonally propagated via repeated division of individual parent plants. Five genotypes (ENC, WWF, WBC, WIL and NOC) were clones of individual plants collected from natural populations, and four genotypes (NAS, VS16, KAN and AP13) were clones of individual plants originating from previously identified populations or cultivars. Genotype NAS originated from a northern Texas population used for land reclamation in the dry west, and genotypes VS16, KAN and AP13 were derived from the cultivars Summer, Kanlow and Alamo, respectively. Genotype, NOC, originated from the northern Great Plains and its exact collection location is unknown. Genotypes derived from cultivars have undergone minimal selection, and are genetically similar to their original prairie remnant populations (Casler et al. 2007). We prioritized sampling single genotypes (i.e. clones) from a number of populations across the climatic range of the species rather than sampling many genotypes

from within a few populations because we had limited space under each shelter, and because our primary objective was to determine how genotypes from a broad climatic gradient respond to variable precipitation. This approach does not allow us to explore within-population genetic variation, but it did allow us to meet the experimental objectives of exploring how genotypes from a broad climatic gradient respond to variable precipitation.

The genotypes in this study varied in ploidy level (see Table 1; Aspinwall et al. 2013), and ploidy level is strongly confounded with ecotype (Brunken and Estes 1975; Grabowski et al. 2014; Lu et al. 2013; Porter 1966). Four of the five tetraploid genotypes in the experiment (AP13, KAN, WBC, WIL) have the ‘lowland’ ecotype morphology (see Brunken and Estes 1975; Porter 1966), tall, thick tillers and large leaves. The fifth tetraploid (VS16) genotype has the ‘upland’ morphology, short, thin tillers and small leaves. Three of the four octoploid (ENC, NAS, NOC) genotypes are derived from dry upland habitats and possess the upland morphology. The fourth octoploid genotype (WWF) is intermediate in all traits and is morphologically distinct from either the upland or lowland ecotype. Because of the strong confounding of ploidy and ecotype, we focused on variation in phenotypic plasticity among genotypes.

Two replicates of each genotype were planted at 1 × 1 m spacing within each plot in spring 2011. Genotypes were assigned positions in a stratified random manner with replicates split between the east and west halves of the plots, with replicates never adjacent to each other. During 2011, all plots were well watered to facilitate plant establishment and received equal irrigation amounts.

Precipitation treatments

Plots were assigned to four precipitation treatments in a randomized complete block design. The treatments represented the 10 driest years (low), the 10 years nearest to the 25th

Table 1: ploidy (octoploid (8×), tetraploid (4×)), geographic origin and historical climate data for the nine *Panicum virgatum* genotypes included in this study

Variable ^a	VS16	NOC	KAN	NAS	WBC	WIL	AP13	WWF	ENC
Ploidy	4×	8×	4×	8×	4×	4×	4×	8×	8×
Lat. (°N)	40.7	—	35.1	33.1	30.1	29.1	28.3	28.1	26.9
Long. (°W)	95.9	—	95.4	96.1	98.0	98.2	98.1	97.4	98.1
MAP (mm)	857	—	1030	1110	856	727	713	932	625
MSP (mm)	516	—	505	462	407	347	370	505	376
MAT (°C)	10.8	—	15.5	17.2	20.3	20.6	21.2	21.2	22.3
MTCM (°C)	−4.9	—	2.5	5.4	10.1	10.3	12.1	12.3	13.2
MTWM (°C)	24.8	—	27.4	28.2	29.0	29.2	28.8	28.6	29.5
SHM (°C m ^{−1})	48.0	—	54.4	61.0	71.3	84.1	64.1	56.9	78.5
AHM (°C m ^{−1})	12.5	—	14.8	15.5	23.7	29.4	24.9	23.5	34.5

Climate data (1971–2000) is from the National Oceanic and Atmospheric Administration (NOAA) weather station closest to the genotype’s geographic origin. MSP, mean summer precipitation (May–September); MAT, mean annual temperature; MTCM, mean temperature of the coldest month; MTWM, mean temperature of the warmest month; SHM, summer heat: moisture index (MTWM:MSP); AHM, annual heat: moisture index (MAT:MAP). Higher SHM and AHM indices indicate greater evaporative demand (i.e. aridity).

percentile, the 10 years nearest to 75th percentile, and the 10 wettest years (high) at each site (Table 2). The sequence of experimental rainfall events for each treatment was produced using a stochastic weather generator, LARS-WG 5.5 (Semenov *et al.* 1998), which was calibrated using an 87-year precipitation record at each site. The rainfall sequences approximated the historic mean amount, seasonality, size distribution and spacing of rainfall events. The treatment amounts were generally 5% higher at Temple, consistent with the long-term difference in MAP between the two sites. By defining the treatments using percentiles, the range of treatments spans comparable extremes at each site (Knapp *et al.* 2015). The treatments also encompass the full range of precipitation amounts likely for these sites under future climate scenarios (Mearns *et al.* 2009).

Target annual amounts for the precipitation treatment percentiles at Temple ranged from 390 to 1352 mm (Table 2), and amounts applied between treatment initiation (19 March 2012) and the final harvest (26 October 2012) ranged from 226 to 883 mm. Target annual amounts for the treatment percentiles at Austin ranged from 345 to 1308 mm. Nominal precipitation amounts applied between treatment initiation and the final harvest ranged from 249 to 910 mm.

Treatments were applied using 90° sprinklers (Hunter HP2000, Hunter Industries Inc., San Marcos, CA, USA) attached to 1 m risers on the corners of each plot. The sprinklers were operated by a programmable controller (LEIT XRC Series Ambient Powered Irrigation Controller, DIG Corporation, Vista, CA, USA).

Microenvironmental data

Light, temperature and relative humidity conditions under each shelter were continuously monitored. Daily-integrated (total) photosynthetic photon flux density (PPFD) was measured with a quantum sensor (LI-190SL; LI-COR Inc., Lincoln, NE, USA). Air temperature (T_a) and relative humidity (RH) were measured hourly using a T_a – RH sensor (CS215, Campbell Scientific Inc., Logan, UT, USA). Air temperature and RH were used to calculate vapor pressure deficit (D , kPa). Conditions under each shelter were similar; mean and maximum daily T_a at Temple and Austin was $\sim 25^\circ\text{C}$ and $\sim 34^\circ\text{C}$, respectively. Similarly, mean and maximum daily D at Temple

and Austin was 1.3 and 3.5 kPa, respectively (supplementary Fig. S2).

Volumetric soil water content (VWC, $\text{m}^3 \text{m}^{-3}$) was measured in each plot by one soil moisture sensor (Decagon Devices 10HS, Decagon Devices Inc., Pullman, WA, USA) inserted to a depth of 20 cm. VWC was measured hourly and averaged for each day. All data were recorded using a datalogger (CR1000, Campbell Scientific Inc., Logan, UT, USA).

Flowering time, growth and aboveground productivity

Flowering time and a series of aboveground growth measures were recorded for each plant in all treatments at both sites (2 sites \times 9 genotypes \times 4 blocks \times 4 treatments \times 2 biological replicates = 576 plants). Flowering time was visually indexed as the day of year when 50% of plant tillers had reached full anthesis (F_{50}). Leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$) was estimated from ceptometer (AccuPAR model LP-80, Decagon Devices, Inc., Pullman, WA, USA) measurements at 10 cm height, taken in two perpendicular directions through the center of each plant. LAI and canopy height (cm) were measured during the middle of the growing season, at peak growth (18 May). On 20 October, tillers were counted and each plant was cut 10 cm above the soil surface, dried at 65°C to a constant mass, and weighed to determine aboveground net primary productivity (ANPP, g m^{-2}). Average tiller mass per plant ($\text{g dry mass tiller}^{-1}$) was calculated as ANPP divided by tiller number.

Data analysis

All statistical analyses were conducted in SAS v9.3 (SAS Institute Inc. 2011). Data were analyzed using linear mixed effect models (PROC MIXED). The effects of site, precipitation, and genotype, and their interactions were considered fixed effects and were tested using the model:

$$Y_{ijk} = \mu + S_i + P_j + S_i P_j + G_k + S_i G_k + P_j G_k + S_i P_j G_k + \epsilon_{ijk} \quad (1)$$

where Y_{ijk} represents the response variable (e.g. ANPP, canopy height, LAI, etc.), μ represents the grand mean, S_i represents the i th site, P_j represents the j th precipitation treatment and G_k represents the k th genotype. All other terms represent interactions and ϵ_{ijk} represents the residual. The block within site

Table 2: summary of microclimate data, precipitation amounts applied to each treatment, daily mean (\pm standard deviation) volumetric water content (VWC) and the coefficient of variation (CV) of daily VWC at Austin (shallow, coarse-textured soil) and Temple (deep, fine-textured soil), TX, USA

Precipitation treatment	Target annual precip (mm)		Precip applied ^a (mm)		Mean VWC ($\text{m}^3 \text{m}^{-3}$)		CV of daily VWC (%)	
	Austin	Temple	Austin	Temple	Austin	Temple	Austin	Temple
Low	345	390	249	226	0.13 (0.09)	0.23 (0.10)	65.2	42.7
25 th	650	665	438	412	0.18 (0.08)	0.20 (0.09)	34.3	59.4
75 th	994	964	698	599	0.19 (0.12)	0.27 (0.10)	62.3	35.5
High	1308	1352	910	883	0.24 (0.14)	0.30 (0.09)	49.2	23.9
Overall mean					0.18 (0.12)	0.25 (0.11)	66.5	46.3

^acumulative precipitation applied between treatment initiation (19 March 2012) and the final harvest date (26 October 2012).

effect and interactions with block within site were included as random effects.

Response ratios were calculated to quantify genotype growth and flowering time plasticity in response to precipitation at both sites. The ratios were calculated by dividing genotype mean trait (e.g. ANPP) values under high precipitation by genotype mean trait values under low precipitation. The response ratios describe both the direction and magnitude of genotype plasticity in response to changes in precipitation. A response ratio of 1 indicates no response and response ratios greater than and less than 1 indicate positive and negative responses to precipitation, respectively. Associations between genotype growth traits (tiller mass, tiller number, height, LAI), flowering time (F_{50}), ANPP and their respective plasticity values were tested using linear regression (PROC REG).

RESULTS

Site differences in soil moisture, productivity and phenology

Averaged across precipitation treatments, soil VWC was 39% lower and more variable at the site with shallow, coarse-textured soils (Austin) than at the site with deep, fine-textured soils (Temple; Table 2; supplementary Fig. S3). Site differences in soil moisture were associated with substantial differences in mean productivity averaged across genotypes and precipitation treatments (Tables 3 and 4). Mean ANPP was 103% higher; mean LAI, tiller number and tiller mass averaged 42% to 53% higher;

and flowering time was 10 days earlier at the site with deep, fine-textured soils compared to the site with shallow, coarse-textured soils (Table 4). Canopy height did not vary between sites (Table 4). Thus, for these genotypes, water limitation of ANPP was greater at the site with shallow, coarse-textured soils.

Certain genotypes exhibited notable differences in mean trait values between sites (site \times genotype; Table 3). All genotypes produced more tillers on the deep, fine-textured soil relative to the shallow, coarse-textured soil, but some genotypes increased tiller production much more than others; WWF doubled mean tiller production, while VS16 only increased mean tiller production by 10% (supplementary Fig. S4a). Genotypes also varied in flowering time between sites. Later flowering genotypes (WBC, WIL, WWF, ENC) consistently showed earlier flowering (15–40 days) on the deep, fine-textured soil. Earlier flowering genotypes showed more variability in flowering time between sites; VS16, KAN and NAS flowered later, AP13 flowered earlier, and NOC flowering time did not change on the deep, fine-textured soil, relative to the shallow, coarse-textured soil (supplementary Fig. S4b). Genotypes showed consistent differences in canopy height across sites and precipitation treatments. Mean canopy height of KAN, WBC and AP13 was roughly double the mean canopy height of VS16, NOC and NAS (supplementary Fig. S4c).

Genotype aboveground responses to precipitation

Genotypes showed considerable variation in ANPP in response to precipitation, but the magnitude (i.e. plasticity) of their

Table 3: analysis of variance of site, precipitation, and genotype effects on aboveground net primary productivity (ANPP) tiller mass, end of season tiller number, leaf area index (LAI) canopy height, and flowering time (F_{50}), at two sites in central Texas

Effect	ANPP		Tiller mass		Tiller number		LAI		Canopy height		F_{50}	
	df	F	df	F	df	F	df	F	df	F	df	F
Site (S)	1,6	58.4**	1,6	20.7*	1,6	74.2**	1,6	21.1**	1,6	0.1	1,6	31.8**
Precipitation (P)	3,18	13.1***	3,18	17.5***	3,18	4.4*	3,18	4.5*	3,18	7.4**	3,18	6.9**
S \times P	3,18	0.3	3,18	2.7*	3,18	0.2	3,18	0.9	3,18	1.5**	3,18	6.1**
Genotype (G)	8,411	52.3***	8,410	119.1***	8,463	94.3***	8,480	94.4***	8,480	99.0***	8,371	741.0***
S \times G	8,411	7.1***	8,410	9.8***	8,463	16.1***	8,480	6.3***	8,480	1.4	24,371	16.7***
P \times G	24,411	3.4***	24,410	3.1***	24,463	1.1	24,480	1.8*	24,480	1.1	24,371	1.1
S \times P \times G	24,411	1.8*	24,410	1.8*	24,463	0.9	24,480	1.3	24,480	0.9	24,371	1.0

F-values with **, ***, and **** are significant at $P < 0.05$, $P < 0.01$ and $P < 0.0001$, respectively.

Table 4: least-squared mean values (\pm standard error) for *Panicum virgatum* aboveground net primary productivity (ANPP) tiller mass, tiller number, leaf area index (LAI) canopy height, and flowering date (F_{50}) for two sites in central Texas, averaged across precipitation treatments and genotypes

Variable	Site = Austin (shallow, coarse-textured soil)	Site = Temple (deep, fine-textured soil)
ANPP (g m ⁻²)	622 \pm 58	1261 \pm 61
Tiller mass (g dry mass tiller ⁻¹)	3.85 \pm 0.2	5.47 \pm 0.3
Tiller number (count)	139 \pm 6.0	212 \pm 5.9
LAI (m ² m ⁻²)	2.23 \pm 0.2	3.39 \pm 0.2
Height (cm)	100.0 \pm 5.3	102.9 \pm 5.3
F_{50} (day of year)	209 \pm 1.5	199 \pm 1.2

response to precipitation changed between sites (i.e. site \times precipitation \times genotype interaction, $P < 0.01$; Table 3). On the deep, fine-textured soils, the two smallest genotypes, NOC and VS16, increased ANPP 200–400% with increased precipitation, while the two largest genotypes, WBC and WIL, increased ANPP 137–200% (Figs 1b and 2a). The remaining genotypes, KAN, NAS, AP13, WWF and ENC, showed little change in ANPP with increased precipitation (Figs 1b and 2a). On the shallow,

coarse-textured soils, all genotypes except VS16 increased ANPP with increasing precipitation (65–245%), with genotype NOC increasing ANPP over 500% (Figs 1a and 2a). Thus, the majority of genotypes showed consistent and larger increases in ANPP with increasing precipitation at the site with shallow, coarse-textured soil, where water limitation was greater.

Genotypes showed significant variation in tiller mass in response to precipitation, but the magnitude of their responses

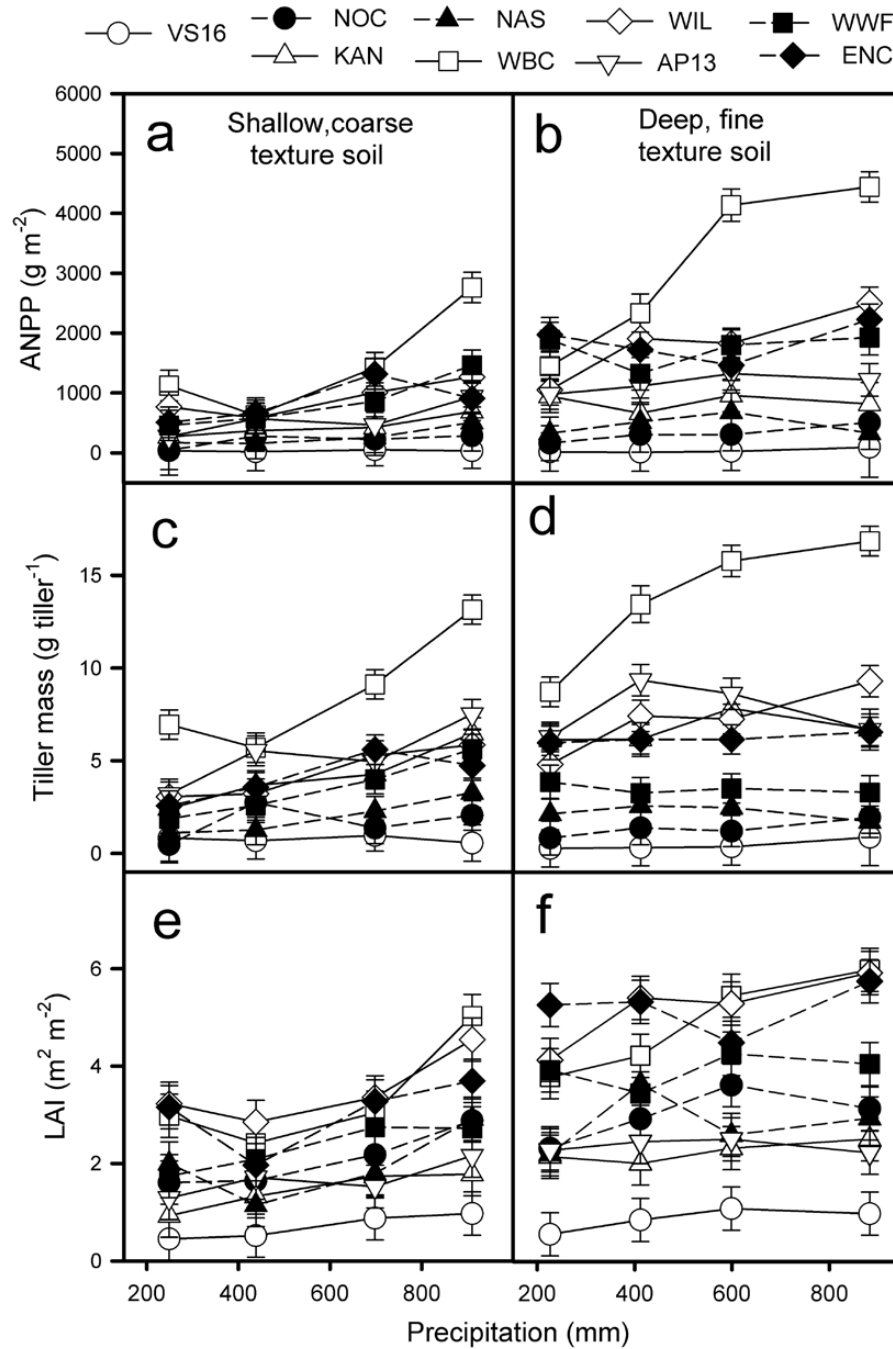


Figure 1: least-squared mean (\pm standard error) values for aboveground net primary productivity (ANPP) (a,b), average tiller mass (c,d) and leaf area index (LAI) (e,f) of *Panicum virgatum* genotypes growing under experimental precipitation treatments at two sites in central Texas varying in soil depth and texture. Genotypes with filled symbols and dashed lines are octoploid, and genotypes with open symbols and solid lines are tetraploid genotypes.

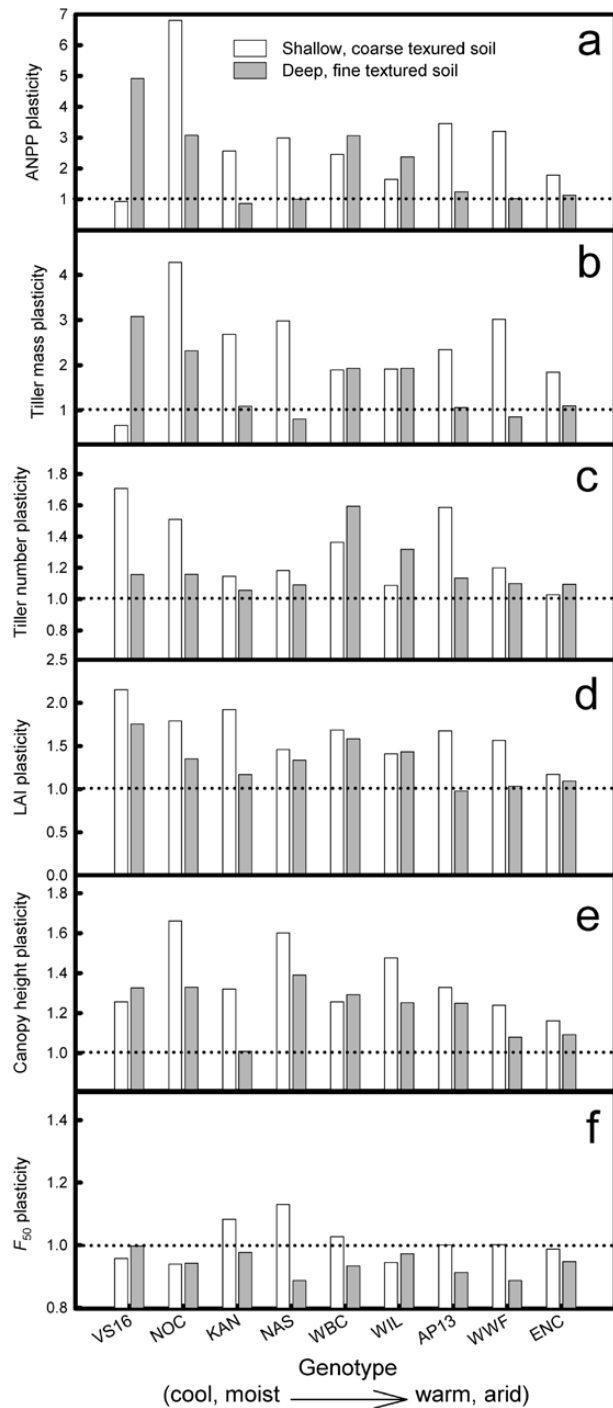


Figure 2: (a) aboveground net primary production (ANPP), (b) tiller mass, (c) tiller number, (d) leaf area index (LAI), (e) canopy height, and (f) flowering time plasticity (genotype mean under high precipitation/genotype mean under low precipitation) of *Panicum virgatum* genotypes exposed to experimental precipitation treatments at two sites in central Texas varying in soil depth and texture. Genotypes are arranged based on their climate of origin (see Table 1). A plasticity value of '1' (dotted line) indicates no response.

also changed between sites (i.e. site \times precipitation \times genotype interaction; $P < 0.05$; Table 3). Similar to their ANPP responses

to precipitation, genotypes KAN, NAS, AP13, WWF and ENC showed a limited response to precipitation at the site with deep, fine-textured soil, but all five genotypes showed relatively large increases in tiller mass with increasing precipitation (84–198%) at the site with shallow, coarse-textured soil (Figs 1c, d and 2b). In comparison, tiller mass of VS16 and NOC increased 131–208% with increasing precipitation on the deep, fine-textured soils, but only NOC increased tiller mass on the shallow, coarse-textured soils (328%; Figs 1c, d and 2b). WBC and WIL showed similar increases in tiller mass in response to increasing precipitation at both sites (89–93%; Figs 1c, d and 2b).

Genotypes varied in LAI in response to precipitation, but this variation was consistent across sites (i.e. precipitation \times genotype interaction; $P < 0.01$; Table 3). Averaged across sites, genotypes AP13, WWF and ENC showed moderate increases (12–23%) in LAI with increasing precipitation, while genotypes NOC, KAN, NAS, WBC and WIL showed larger increases (39–63%) in LAI with increasing precipitation (Figs 1e, f and 2c). The smallest genotype, VS16, showed the largest increase in LAI with increasing precipitation (~93%; Figs 1e, f and 2c).

Genotype plasticity in growth, ANPP and flowering time

Genotype mean ANPP, averaged across precipitation treatments, strongly increased with genotype mean tiller mass, LAI and F_{50} at both sites, and with canopy height on the site with shallow, coarse-textured soils (Fig. 3). Yet, genotype mean ANPP was unrelated to genotype mean tiller number at either site (Fig. 3). Although several traits predicted ANPP, genotype ANPP plasticity was only correlated with plasticity in tiller mass and LAI. Genotype ANPP plasticity increased strongly with genotype tiller mass plasticity at both sites and also with LAI plasticity at the site with deep, fine-textured soils (Fig. 4a and b). Plasticity in flowering time or other growth metrics were unrelated to genotype ANPP plasticity ($P > 0.05$). At the site with shallow, coarse-textured soils, a significant negative correlation ($r = -0.79$ to -0.86 , $P < 0.05$) was found between genotype LAI plasticity and temperature and aridity parameters at the genotypes origin (supplementary Table S1). Thus, genotypes from warmer, more arid climates showed smaller changes in LAI with varying precipitation, but only at this site. No other significant correlations were observed between genotype growth and phenological plasticity, and climatic variables at the genotype's origin (supplementary Table S1).

DISCUSSION

These *P. virgatum* genotypes demonstrated substantial plasticity in ANPP in response to changing precipitation. Under a higher degree of water limitation at the site with shallow, coarse-textured soils, nearly all genotypes showed large increases in ANPP with increased precipitation. In contrast, water limitation was comparatively lower at the site with deep, fine-textured soils, and fewer genotypes responded to increased precipitation indicating that the expression of ANPP

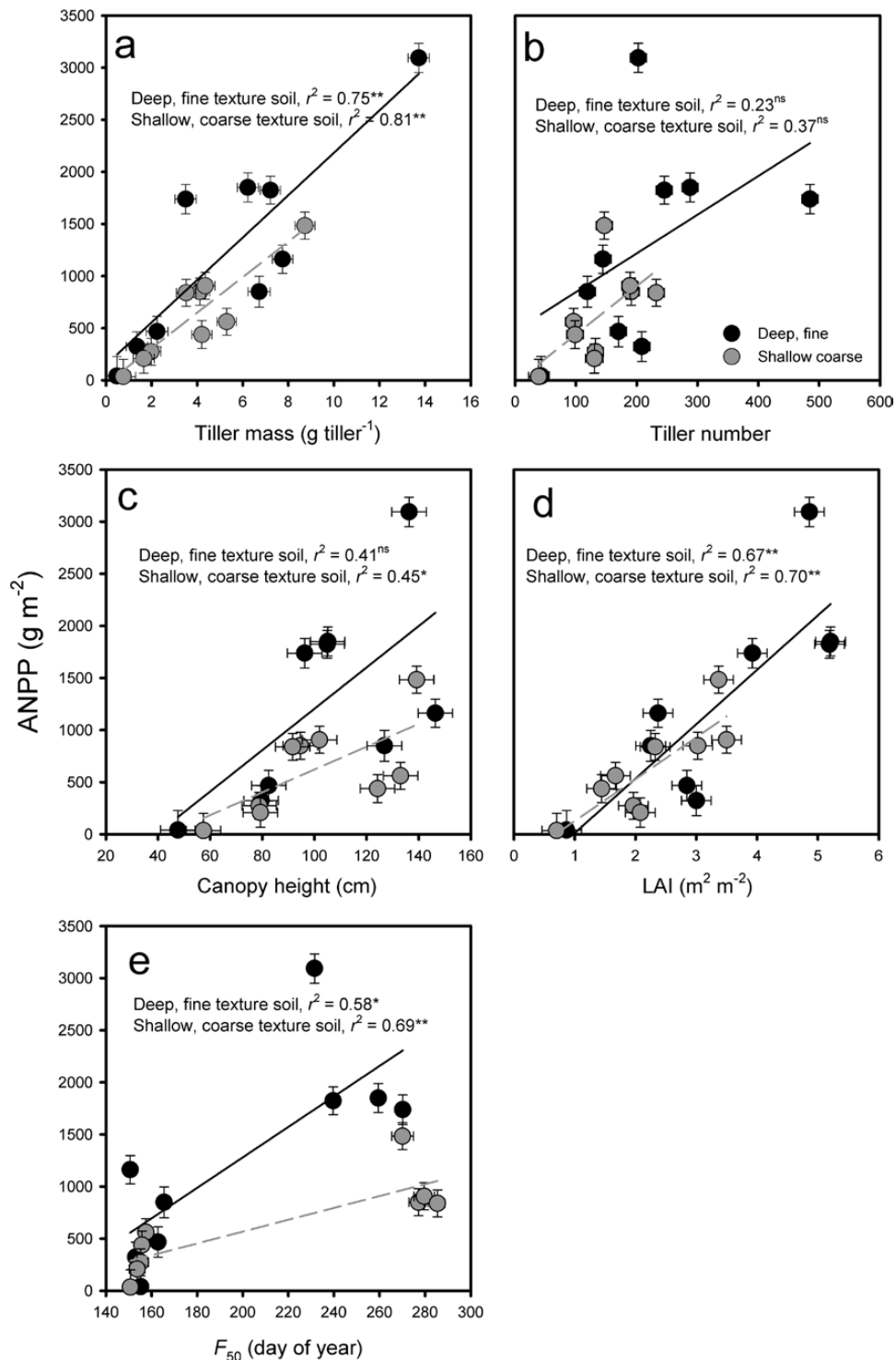


Figure 3: associations between *Panicum virgatum* genotype least-squared mean ANPP, averaged across precipitation treatments, and genotype mean growth and flowering time variables ((a) tiller mass, (b) tiller number, (c) canopy height, (d) leaf area index (LAI), (e) flowering time)) at two sites in central Texas varying in soil depth and texture. Black symbols indicate the site with deep, fine-textured soils. Gray symbols indicate the site with shallow, coarse-textured soils.

plasticity differed with the edaphic properties of these sites. Genotype ANPP plasticity was predicted by tiller mass plasticity at both sites, and by LAI plasticity at the less water-limited

site, suggesting that mediation of water limitation by site edaphic factors determines which traits contribute to genotype productivity responses to altered precipitation.

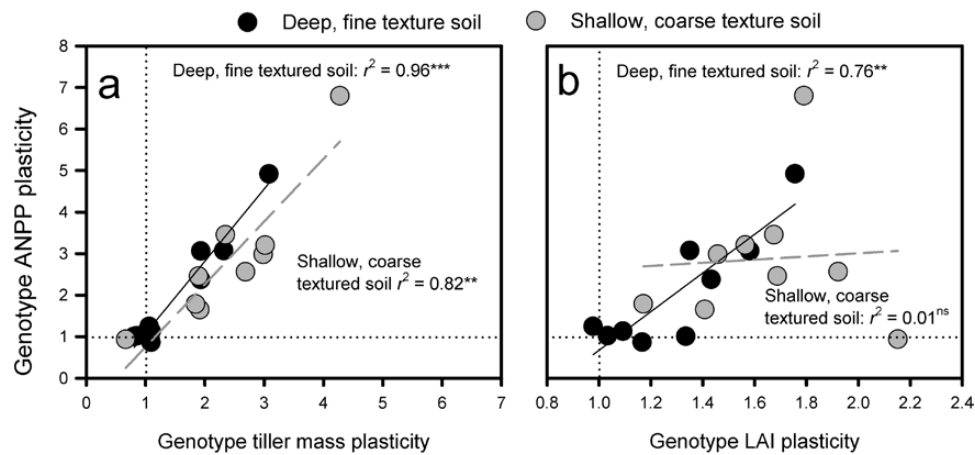


Figure 4: associations between *Panicum virgatum* genotype aboveground net primary productivity (ANPP) plasticity (genotype ANPP under high precipitation/genotype ANPP under low precipitation) and (a) genotype tiller mass plasticity and (b) leaf area index (LAI) plasticity in response to precipitation at two sites in central Texas varying in soil depth and texture. Plasticity values of '1' indicate no response.

Although several traits correlated with ANPP, genotype ANPP responses to precipitation were largely explained by plasticity in tiller mass. The absence of a contribution of tiller number was unexpected (Lauenroth *et al.* 1994; Reichmann and Sala 2014). Among several C_4 grasses examined in an intact native grassland, VanderWeide *et al.* (2014) found that ANPP increased with shoot density (i.e. tiller number), and plots with higher shoot density showed larger proportional reductions in ANPP with reduced precipitation. Thus, this study suggested that increased ANPP plasticity under drought was associated with higher shoot density. In our study, the primary importance of tiller mass plasticity for ANPP plasticity may be explained by the $>12\times$ range of tiller masses among the genotypes, compared to a $\sim 4\times$ range of tiller numbers. Tiller numbers in part reflect the population of rhizome buds (Benson *et al.* 2004), which were set the previous year when all plots received the same precipitation inputs. Changes in tiller numbers may contribute to ANPP plasticity after additional years of precipitation treatment, when belowground bud populations may be altered.

We also found that genotype ANPP plasticity was associated with genotype LAI plasticity at the site with less water limitation. Higher soil moisture at this site likely resulted in greater canopy development, light interception and carbon gain (Borrell *et al.* 2000; Clifton-Brown *et al.* 2002; Muller *et al.* 2011). As a result, LAI plasticity combined with tiller mass plasticity yielded greater responses in ANPP at the less water-limited site. However, where water limitation is greater, physiological stresses (e.g. low leaf water potential) may have reduced cell division and growth, resulting in reduced leaf area production and lower productivity (Tardieu *et al.* 2000; Westgate and Boyer 1985). Thus, differences in site water limitation originating from edaphic differences can decouple the relationship between leaf area and productivity responses to precipitation.

Variability in genotype productivity responses to precipitation across sites could also be influenced by interactions between soil depth or texture and genotype size. For instance,

genotypes with more aboveground biomass (i.e. large genotypes) could have larger or deeper root systems with improved access to water, greater resistance against dehydration or greater tissue capacitance (O'Toole and Bland 1987; Pinheiro *et al.* 2005; Wasson *et al.* 2014; Zwicke *et al.* 2015). In comparison, genotypes with less aboveground biomass could have smaller or shallower root systems and lower tissue capacitance, making them less drought tolerant. However, shallow soils may diminish the benefits of greater rooting depth in some genotypes more than in others, causing nearly all genotypes to increase ANPP with increasing precipitation. Even so, the spatial distribution of roots may be more important than rooting depth (Nippert and Holdo 2015).

Our finding of little to no correlation between the genotype's climate of origin and their trait plasticities contrasts with previous work showing how climatic adaptation influences genotype or population responses to climate change in other species (Drake *et al.* 2014; McLean *et al.* 2014; Pratt and Mooney 2013). Previous studies in *P. virgatum* have also demonstrated strong climatic adaptation among populations and genotypes that could influence patterns of responsiveness to precipitation (Aspinwall *et al.* 2013; Casler *et al.* 2004; Hartman *et al.* 2012; Lowry *et al.* 2014; McMillan 1965). The general lack of a relationship between genotype plasticity and climate in our study could be related to the lack of within-population replication. We sampled one genotype per population instead of several genotypes per population, and the individual genotypes we sampled may not be entirely representative of their source population. These genotypes also originate from a gradient that is stronger in temperature than precipitation (see Aspinwall *et al.* 2013), and thus they may express greater variation in their plasticity to temperature. Nonetheless, the significant negative relationship between genotype source climate aridity and LAI plasticity at the site with shallow, coarse-textured soils could indicate that genotypes from warmer, more arid climates may indeed be less

responsive in leaf production to precipitation than genotypes from less arid environments, particularly under conditions of intense water limitation.

Alternatively, other differences, such as ploidy level or ecotype may explain edaphic effects on genotypic variation in ANPP and trait plasticity. In *P. virgatum*, 'lowland' ecotypes adapted to riparian areas and flood plains are primarily tetraploid, and might be expected to exhibit greater trait plasticity under altered precipitation on deep-soiled or wetter sites. Conversely, 'upland' ecotypes from drier habitats occur primarily as octoploids in the central latitudes of the USA, and as both octoploids and tetraploids at higher latitudes (Brunken and Estes 1975; Costich *et al.* 2010; Lu *et al.* 2013; Porter 1966), and may have lower trait plasticity under altered precipitation. Results from other studies in *P. virgatum* are inconsistent: Cassida *et al.* (2005) found that lowland ecotypes were more sensitive to changes in soil moisture than upland ecotypes, but many other studies have found no strong or consistent relationship between genome size or ecotype variation and plant growth responses to variable soil moisture (Barney *et al.* 2009; Hartman *et al.* 2012; O'Keefe *et al.* 2013; Wullschleger *et al.* 2010). In our study, tetraploid genotypes, on average, appeared to show larger increases in ANPP with increasing precipitation than octoploid genotypes at the site with deep, fine-textured soils, but not at the site with shallow, coarse-textured soils. Alternatively, our results suggest that morphological traits, such as tiller mass or leaf area, may be stronger predictors of ANPP plasticity than genome size or ecotype classification.

We conclude that site edaphic factors that affect the degree of water limitation of plant growth, such as soil depth and texture, can alter genotype productivity responses to changing precipitation, and change how plasticity in underlying traits contributes to plasticity in genotype aboveground productivity. Thus, edaphic factors may contribute to spatial variation in the mechanisms contributing to genotype performance and success under altered precipitation. Understanding these mechanisms will improve predictions of plant population and species responses to climate change. Further work linking molecular, physiological and whole-plant responses may provide additional insight into the mechanisms of genotype productivity in responses to precipitation.

SUPPLEMENTARY MATERIAL

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

ACKNOWLEDGEMENTS

We thank K. Tiner, A. Naranjo and A. Gibson for technical support; several anonymous reviewers for their helpful comments; and K. Behrman for assistance with precipitation projections. USDA is an equal opportunity provider and employer. D.B.L. acknowledges support from USDA-NIFA postdoctoral fellowship (2011-67012-30696). P.A.F. acknowledges support from USDA-NIFA (2010-65615-20632).

Funding. the National Science Foundation Plant Genome Research Program (IOS-0922457) to T.E.J., C.V.H. and P.A.F.

Conflict of interest statement. None declared.

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