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Ecotypic responses of switchgrass to altered precipitation

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Abstract. Anthropogenic climate change is projected to alter precipitation patterns, resulting in novel environments for plants. The responses of dominant plant species (e.g. *Panicum virgatum* L. (switchgrass)) to climate changes can drive broader ecosystem processes such as primary productivity. Using a rainfall mesocosm facility, three ecotypes of *P. virgatum* (collected from Kansas, Oklahoma and Texas, USA) were subjected to three precipitation regimes (average, –25%, +25%) to determine the physiological and growth responses to altered precipitation in a common garden setting. Results showed mean maximum photosynthetic rates, stomatal conductance, transpiration, midday water potential and dark-adapted chlorophyll fluorescence were lowest in the Kansas ecotypes. Increased precipitation treatments raised the mean midday water potentials and lowered water-use efficiency. Aboveground biomass responded positively to changes in precipitation, but flowering initiation was later and rates were lower for Texas ecotypes. In general, ecotype origin was a better predictor of differences in physiological responses and flowering, whereas the precipitation treatments had greater control over biomass production. Depending on the growth variable measured, these results show responses for *P. virgatum* are under varying ecotypic or environmental control with few interactions, suggesting that future predictions to climate change need not inherently consider localised adaptations in this economically important and widely distributed species.

Additional keywords: aboveground biomass, chlorophyll fluorescence, climate change, ecotype, gas exchange, *Panicum virgatum*.

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Introduction

Anthropogenic climate change is creating novel environments for plants in terrestrial ecosystems. Mean annual air temperatures for the central North American Great Plains have been projected to increase by 4°C by 2100 (Christensen *et al*. 2007), along with greater interannual and intra-annual variability in rainfall. Climate models for the Great Plains region predict shifts in precipitation from summer to winter months, resulting in an increased likelihood of growing season drought (Easterling *et al*. 2000; Meehl *et al*. 2005; Christensen *et al*. 2007). Longer drought periods are likely to result in highly variable soil moisture, especially in the upper soil layers (Knapp *et al*. 2002). Summer precipitation and soil water availability are key predictors of grassland annual net primary productivity (ANPP; Nippert *et al*. 2006); therefore, to understand the impacts of these forecasted changes on ecosystem processes, potential plant responses to experimental manipulations of climate conditions must be assessed.

Within ecosystems, dominant species often influence community structure, dynamics, invasibility and ecosystem function (Grime 1998; Smith and Knapp 2003; Emery and Gross 2007). Dominant species generally have larger population sizes and higher intraspecific genetic variation than species with smaller populations in the same communities (McNaughton and Wolf 1970). Because of this, they will contribute to and affect ecosystems more than rarer species (Hillebrand *et al*. 2008; Hughes *et al*. 2008). Populations of dominant species with significant intraspecific genetic variation enable a broad range of physiological and growth responses to environmental change, making these species more capable of responding to alterations in environmental conditions (Norberg *et al*. 2001; Jump and Peñuelas 2005). Thus, in order to accurately predict the responses of ecosystems to future climate change, multiple ecotypes of a dominant species within a resource gradient should be examined (Callaway *et al*. 2003). Responses to short-term disturbances are largely governed by the plasticity of the species to environmental conditions, but if the variation in these plastic responses provides any selective advantage, then the plasticity has evolutionary consequences. Examining ecotypic variation in response to environmental manipulation in a dominant species, such as *Panicum virgatum* L. (switchgrass), provides insight into the traits most likely to respond to natural selection as the climate changes, as well as the impact that these changes may have on ecosystem functioning (Ward and Kelly 2004). *P. virgatum* is a common perennial C_4 grass of the tallgrass prairie ecosystems of the Central Great Plains, with a broad range of adaptation to growing conditions across North America (Parrish and Fike 2005; Hartman *et al*. 2011). Across North America, *P. virgatum* possesses large genotypic and phenotypic variability (Casler *et al*. 2004; Das *et al*. 2004) that allows it to be broadly adapted to a wide range of environmental conditions (Parrish and Fike 2005). In the past, *P. virgatum* has been used as forage, and in the 1970s, agronomic work focussed on increasing its forage value and yield (Berg 1971). In the last 15 years, it has been identified and studied extensively as a biofuel crop species (McLaughlin and Kszos 2005).Variable precipitation significantly affects physiological processes in individual plants, with physiological responses that translate to ecosystem processes (Silletti and Knapp 2001; Knapp *et al*. 2002; Fay *et al*. 2008; Nippert *et al*. 2009; Fay *et al*. 2011). *P. virgatum* productivity is often co-limited by nitrogen and water availability (Heaton *et al*. 2004). Response to water availability varies across ecotypes, but in general, *P. virgatum* is less drought tolerant compared with other co-occurring C_4 grass species such as *Andropogon gerardii* Vitman, *Axonopus scoparius* (Flugge) Kuhlm, *Dactylis glomerata* (L.), *Sorghastrum nutans* (L.) Nash and *Schizachyrium scoparium* (Michx.) Nash (Knapp 1984; Knapp 1985; Stout 1992; Stout *et al*. 1988; Muir *et al*. 2001; Tucker *et al*. 2011). Water availability is the dominant environmental control over individual plant tiller growth, where individuals of *P. virgatum* under water stress have been shown to delay inflorescence development and decreased reproductive output (Sanderson and Reed 2000). Water stress has also been shown to reduce the biomass production of *P. virgatum* by up to 80% (Barney *et al*. 2009). Because soil water availability affects the rate of development of *P. virgatum* (Sanderson 1992), this species is a likely candidate to exhibit altered growth responses to a variable and probably drier future climate. For *P. virgatum*, previous studies have focussed on single genotypes or agronomic cultivars (Evers and Parsons 2003; Berdahl *et al*. 2005; Barney *et al*. 2009; Wang *et al*. 2010), with little understanding of the differences among natural populations to gradients in precipitation conditions.

Therefore, we conducted an experiment to characterise the physiological responses and growth of three naturally occurring ecotypes of *P. virgatum* to changes in precipitation amount. By using different ecotypes growing in a gradient of soil moisture conditions, our objective was to assess the physiological responses and differences in aboveground biomass among ecotypes across a precipitation gradient and determine the plasticity of responses. These objectives will address whether physiological and growth responses vary according to ecotype, precipitation treatment or ecotype × precipitation interactions.

Materials and methods

Study site and mesocosm facility

This research was conducted in the Rainfall Mesocosm Facility at the Konza Prairie Biological Station (KPBS). KPBS is a 3487 ha Long Term Ecological Research (LTER) site located in north-eastern Kansas, USA (39.1°N, 96.9°W), characterised by a mid-continental climate with cool, dry winters and warm, wet summers. Long-term annual precipitation is 860 mm (1891–2006) with 75% of the rainfall occurring during the growing season (April–September). The rainfall mesocosm facility contains 64 isolated $2.6\,m^3$ mesocosms. The mesocosms were constructed in 2003 using plastic-lined plywood sheets, and arranged in a pair of 2×16 m arrays underneath an 11×25 m rainout shelter (Rainbow Plus, Stuppy Greenhouse Manufacturing, North Kansas City, MO, USA). The shelter has open walls and ends, 2.4-m high eaves that maximise air movement and heat dissipation, and a roof of clear corrugated polycarbonate (DynaGlas Plus, SPS International, San Jose, CA, USA) that allows >90% light transmission. Each mesocosm 'cell' ($1.44\,m^2 \times 1.8$ m deep) contains a reconstructed soil profile from soil collected at KPBS. Previously, this facility was used for a precipitation variability experiment with native tallgrass prairie plant communities (Fay *et al*. 2008). During the summer (June to August) of 2008, all relic above- and belowground plant biomass was removed by hand and the top 30 cm of soil was homogenised. Subsequent volunteer plants that germinated were weeded by hand, without the application of herbicide.

Panicum virgatum L. rhizomes were randomly collected in the early summer of 2008, from three geographically distinct natural populations (hereafter, ecotypes) in native tallgrass prairie. These locations span a latitudinal gradient and include the Konza Prairie in north-east Kansas, the Tallgrass Prairie Preserve in north-east Oklahoma and native tallgrass prairie in east central Texas (United States Department of Agriculture – Agriculture Research Service landholdings near Temple, TX). These locations have similar mean annual precipitation amounts and similar environmental histories (Table 1). At each site, ~50 rhizomes of *P. virgatum* were collected from 10 distinct locations encompassing a range of site conditions (elevation, aspect, soil type, and burning and grazing histories when applicable). This method of collection provided the greatest amount of representative genetic variation within the range of site conditions across each of the three locations. The three ecotypes were randomly assigned to the mesocosm facility, with each mesocosm cell containing rhizomes collected from the 10 sample locations of a single geographic ecotype. Rhizomes were planted with 40 cm spacing, a distance that facilitates a high number of tillers per plant, but still allows competition with neighbouring individuals (Sanderson and Reed 2000). During 2008, all mesocosms were watered every 3–5 days to promote establishment and minimise water stress. During May and June of 2009, additional individuals of *P. virgatum* from Kansas and Oklahoma were planted to augment the number of cells with switchgrass ecotypes. The mesocosms were frequently weeded throughout the growing season to maintain *P. virgatum* species in each cell, and were watered as needed. Of the 64 cells, 21 contained individuals from Konza Prairie (Kansas), 16 from

Table 1. General information for the sites from which each ecotype was sampled

Konza Prairie precipitation and temperature averaged from 1891 to 2006, Temple from 1914 to 2010 and Tallgrass Prairie Preserve from 1895 to 2010

Site	MAP (mm)	Mean temperature range (°C)	Latitude and longitude	Area (ha)
Konza Prairie, Kansas	860	–1.8–26.5	39.1°N, 96.9°W	3487
Tallgrass Prairie Preserve, Oklahoma	877	1.2–27.8	36.50°N, 96.25°W	15 410
Temple, Texas	878	9.2–28.9	31.05°N, 97.34°W	178

Tallgrass Prairie Preserve (Oklahoma) and 16 from Temple (Texas).

Three precipitation treatments were implemented, reflecting climate change predictions for this region (Alley *et al*. 2007): contemporary average for the growing season (626.25 mm), a 25% increase and a 25% decrease. Hereafter, these treatments are referred to as average, increased, and decreased. For Kansas ecotypes, the three treatments had an equal number of cells each (7). For the Oklahoma and Texas ecotypes, there were five cells each allocated to the increased and average treatments, and six to the decreased treatment. The unbalanced treatment design resulted from the removal of a previously planted (and unsuccessfully grown) northern ecotype. The timing of rain events was not altered, and precipitation was applied every 6 days, which is the long-term average ambient rainfall interval. Rainfall was applied through a metered hand sprayer (model TM075; Great Plains Industries, Wichita, KS, USA), using water from an onsite well. This water was applied at the soil surface to minimise losses to canopy interception or runoff. Precipitation treatments were applied from late April to early October 2010.

Sampling procedure and variables measured

Sampling of the physiological variables was conducted on 10 dates over the course of the growing season and classified into three seasonal periods: early season, mid-season and late season. Data were collected on 28 May, 31 May and 9 June for the early season sampling period (Period 1); 30 June, 22 July, 23 July, 27 July and 30 July for the mid-season sampling period (Period 2) and 11 August and 26 August for the late season sampling period (Period 3). Sampling periods were chosen rather than monthly responses because previous work at Konza has shown the greatest increase in biomass in May–early June (Period 1), allocation to reproductive growth during late June–July (Period 2) and the lowest rates of growth in August–September (Period 3) (Knapp *et al*.1998).

For each sampling date, one individual was randomly selected from each mesocosm cell and gas exchange, dark-adapted chlorophyll fluorescence (F_v/F_m) and midday water potential (Ψ_{mid}) were measured. These physiological measurements were conducted on the newest, fully expanded mature leaf, on the widest portion of the grass blade. For each sampling period, individuals were tagged to ensure that all physiological measurements were conducted on the same individual leaf, to minimise within-plant variability. Because physiological measurements vary based on the time of day, measurement order for each population was randomised for each sampling period. Gas exchange measurements were conducted between 0900 hours and 1600 hours Central Standard Time when solar radiation was typically above 70% of full sun levels. Soil moisture (0–10 cm) data was collected concurrently with gas exchange and water potential measurements using a Hydra Probe II Soil Sensor (Stevens Water Monitoring Systems, Portland, OR, USA) in units of water fraction by volume (wfv).

Gas exchange measurements were conducted using a LI-COR 6400 IRGA with an artificial red–blue light-emitting diode light source (6400–02B, LI-COR, Lincoln, NE, USA). Plants were placed inside the leaf chamber and allowed to reach steady-state photosynthesis at mean ambient carbon (C_a) ($400\,\mu mol\,mol^{-1}$) and at a saturating light intensity ($2000\,\mu mol\,m^{-2}\,s^{-1}$). Leaf temperature was allowed to vary with ambient air temperature. Relative humidity in the cuvette was adjusted to reflect ambient environmental conditions (generally ranging from 30% to 50%). The variables measured included CO_2 assimilation at ambient C_a (A_{max}), stomatal conductance to water vapour (g_s), leaf-level transpiration (E), and instantaneous water use efficiency (WUE; $A_{max}\,E^{-1}$). Midday water potential (Ψ_{mid}) was measured concurrently with gas exchange, using a Scholander-type pressure bomb (PMS Instruments, Albany, OR, USA). Ψ_{mid} measurements were conducted on the same selected individual used for gas exchange measurements; however, a different leaf was used. Dark-adapted maximum photochemical efficiency (F_v/F_m) was assessed using a MINI-PAM photosynthesis yield analyser (Heinz Walz GmbH, Effeltrich, Germany). Measurements were conducted on the same individuals within the sampling date, using the same leaf that was used for gas exchange measurements. F_v/F_m measurements were recorded during the night. Individuals were allowed to adapt for a minimum of 1 h after complete darkness before measurement.

Aboveground biomass was harvested, dried at 65°C for at least 48 h, and weighed for each individual at the conclusion of the growing season (September–October). Individuals were monitored for flowering tillers starting in mid-July, and the total number of flowering tillers was counted on seven dates. As measures of fitness, the reproductive biomass and tiller numbers were measured. The flowering tillers from each plant were separated and weighed. The percent biomass allocated to reproduction was determined and used as a measure of fitness. Other characteristics such as flowering and non-flowering tiller height, and number of leaves per tiller were also measured.

Statistical analyses

Changes in *P. virgatum* physiological responses between ecotypes and precipitation treatments were analysed using a mixed effects model ANOVA (Proc Mixed, SAS ver. 9.2, SAS Institute, Cary, NC, USA) with the precipitation treatments, ecotypes and sampling period as fixed effects, and the specific mesocosm cell as a random effect. Multiple comparison tests between ecotypes, precipitation treatments and sampling period were performed using Tukey's Honestly Significant Difference test.

Non-linear regression analysis was conducted to assess the relationship of g_s to F_v/F_m among ecotypes. The relationship was fitted using a two parameter logarithmic equation ($y = y_0 + a \times \ln(\mathrm{abs}(x))$; Sigmaplot ver. 11.0, Systat Software, San Jose, CA, USA). Residual analysis was performed to determine if the model's fit produced statistically significant regression models. Fitted models were then tested with ANOVA to determine if significant differences existed among the model fits across ecotypes (Sokal and Rohlf 1995).

Results

The precipitation treatments successfully altered the soil moisture in this experiment. Mean soil moisture was significantly higher in the increased precipitation treatment (0.24 ± 0.006 wfv) compared with the average ($P = 0.0012$;

0.21 ± 0.006 wfv) and decreased treatments ($P < 0.0001$; 0.18 ± 0.006 wfv), and the average treatment was significantly greater than the decreased treatment ($P = 0.0358$). Mean soil moisture for all treatments at the beginning of the season ranged from 0.30 to 0.40 wfv; at the end of the season, the range was 0.10–0.15 wfv. The soil moisture for all treatments decreased over the course of the season as ambient temperature increased.

Physiology

Mean physiological responses varied according to ecotype (Table 2). Kansas ecotypes displayed significantly lower A_{max}, g_s, E, Ψ_{mid} and F_v/F_m (Fig. 1) compared with the Texas and Oklahoma ecotypes. To examine the potential for correlation between leaf-level gas exchange and leaf photochemistry as environmental conditions changed over the summer, F_v/F_m–g_s response curves were compared by ecotype (Fig. 2). Fitted models were significantly different from zero for Kansas ($P < 0.0001$), Oklahoma ($P = 0.0011$) and Texas ($P < 0.0001$) F_v/F_m–g_s response curves. Kansas ecotypes exhibited significantly lower ($P = 0.0402$) F_v/F_m values as g_s decreased compared with the Texas ecotype. Fitted models did not significantly differ between Kansas and Oklahoma ecotypes ($P = 0.1337$) or between Texas and Oklahoma ecotypes ($P = 0.5545$). At an F_v/F_m below 0.77, Texas and Oklahoma ecotypes had similar rates of g_s (near 0 mol m^{-2} s^{-1}), but as g_s increased, Texas ecotypes responded with higher F_v/F_m.

Among the physiological parameters, only WUE and Ψ_{mid} varied due to precipitation treatments (Fig. 1). Mean WUE in the increased treatment was only 80% of the WUE in the decreased treatment, and 72% of the WUE in the average precipitation treatment. Ψ_{mid} was closely associated with soil moisture, where the Ψ_{mid} levels of individuals in the decreased treatment were 15% lower than in the increased treatment and 5% lower than the average treatment. Mean Ψ_{mid} responses for the average precipitation treatment was 10% lower compared with the increased treatment.

All of the physiological parameters displayed significant decreases over the course of the growing season (Table 2). Photosynthetic rates declined by 86%, g_s by 87% and Ψ_{mid} by 82% over the course of the growing season. The effect of precipitation on A_{max}, g_s and E did depend on the sampling period (Table 2). Increased precipitation only increased A_{max}, g_s and E in the early season period (Fig. 3). In the mid-season and late season sampling periods, increased precipitation did not exhibit the same effect on gas exchange responses as it did in the early season, and only decreased WUE during the mid-season. Later in the season, high temperatures negated the potential positive physiological responses of increased water. Ecotype × precipitation interactions were not observed in any of the physiological responses (Table 2).

Aboveground biomass

Aboveground biomass responses varied by both ecotype and precipitation individually, with few interactions (Table 3). Total biomass, total tillers, flowering tiller biomass, flowering tiller height, leaves per flowering tiller and the percent biomass allocated to reproductive tillers all showed a significant

Table 2. Mixed-effects model ANOVA of precipitation treatments and ecotype (fixed, precipitation, ecotype, period, random, cell) on physiological variables

F- and *P*-values are provided with significant responses. *, $P < 0.05$; **, $P < 0.10$; A_{max}, CO_2 assimilation at ambient CO_2; g_s, stomatal conductance to water vapour; WUE, water-use efficiency; F_v/F_m, dark-adapted chlorophyll fluorescence; Ψ_{mid}, midday water potential

Response	Precipitation		Ecotype		Period		Precipitation × ecotype		Precipitation × period		Ecotype × period		Precipitation × ecotype × period	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
A_{max}	1.2	0.30	10.65*	0.0002*	73.71*	<0.0001*	1.5	0.19	2.85*	0.0001*	0.8	0.68	0.9	0.52
g_s	0.4	0.63	8.59*	0.0007*	63.64*	<0.0001*	0.8	0.48	2.43*	0.0013*	0.5	0.90	1.0	0.45
WUE (A_{max} E^{-1})	4.41*	0.0175*	1.8	0.16	9.75*	<0.0001*	1.6	0.16	1.56**	0.0704**	1.3	0.18	0.7	0.82
E	1.3	0.26	7.83*	0.0012*	45.85*	<0.0001*	1.1	0.35	2.01*	0.0099*	1.3	0.16	0.9	0.52
F_v/F_m	1.3	0.27	7.91*	0.0012*	30.22*	<0.0001*	0.1	0.95	0.8	0.55	1.4	0.16	0.4	0.98
Ψ_{mid}	10.1*	0.0003*	4.95*	0.0116*	234.44*	<0.0001*	1.8	0.14	1.0	0.42	1.56**	0.0788**	0.9	0.52

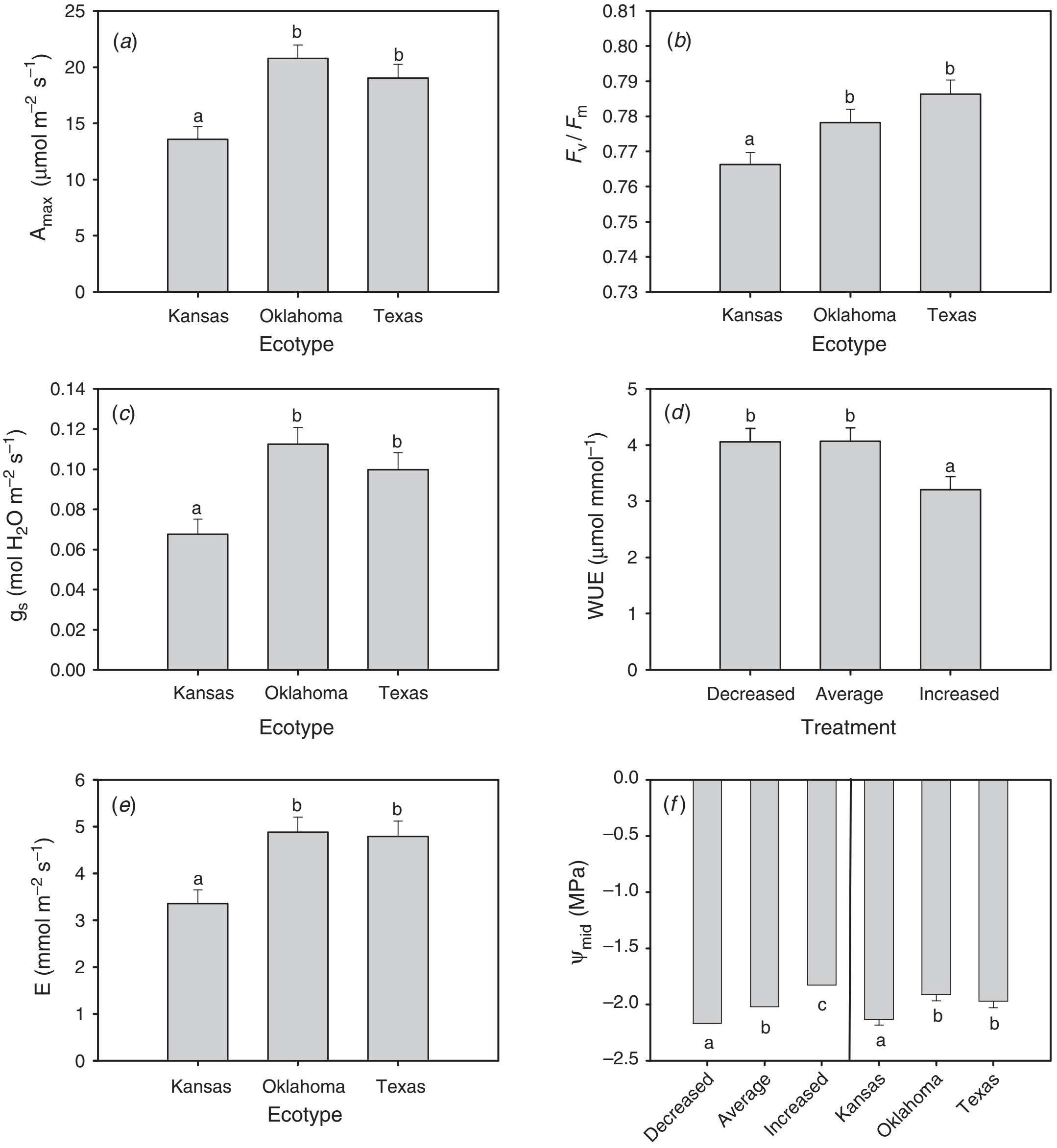

Fig. 1. Physiological responses for *Panicum virgatum* ecotypes across precipitation treatments. Each point is the overall mean response (±1 s.e.) of the ecotype within the precipitation treatment. (*a*) carbon assimilation at ambient CO_2; (*b*) dark-adapted chlorophyll fluorescence; (*c*) stomatal conductance; (*d*) water use efficiency (*e*) transpiration; (*f*) midday leaf-level water potential. In (*a*), (*b*), (*c*) and (*e*), statistically significant ($P < 0.05$) ecotype effects were present (varying letters among ecotypes denotes $P < 0.05$). Significant precipitation treatment effects are present in (*d*). In (*f*), statistically significant ecotype and treatment effects were present, and significant differences are denoted by varying letters within each section of the panel.

response to the precipitation treatments (Table 4). Individuals in the increased treatment had, on average, 15 more tillers, and double the total aboveground and flowering tiller biomass. Those individuals in the increased treatment also displayed a 22% and 28% increase in mean tiller height compared with the average and decreased treatments respectively. The increased treatment contained individuals with a greater number of leaves per tiller and that allocated over 94% of their biomass to reproductive tillers (Table 4).

Ecotype was a significant predictor of some aboveground biomass responses (Table 3), with differences in the total number of tillers, biomass per non-flowering tiller, non-flowering tiller biomass, leaves per non-flowering tiller and percent biomass allocated to reproduction (Table 4). Texas ecotypes had a mean of less than 50 tillers per individual and over double the non-flowering tiller biomass and biomass per non-flowering tiller compared with Kansas and Oklahoma ecotypes. Texas ecotypes also displayed significantly less biomass allocation to reproductive tillers (75%) compared with Kansas (87%) and Oklahoma ecotypes (94%).

There were few ecotype × precipitation interactions (Table 3), but the total biomass per tiller, biomass per

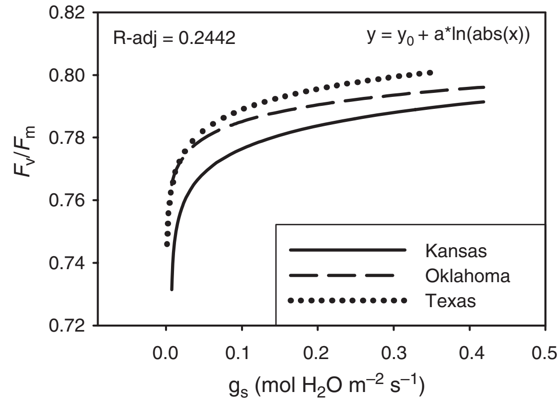

Fig. 2. Representative F_v/F_m–g_s curves for all ecotypes. Curves were fit for all data points for each ecotype. The R-adjusted value is for the overall fit of all ecotype data points.

flowering tiller and the number of non-flowering tillers showed interactions among ecotypes and precipitation treatments (Table 5). Texas ecotypes had significantly greater biomass per tiller in the increased treatments, with the same results for biomass per flowering tiller. Kansas and Texas ecotypes decreased the amount of non-flowering tillers as the soil moisture increased; Oklahoma ecotypes displayed the opposite trend. Oklahoma ecotypes had significantly fewer non-flowering tillers in the decreased treatment compared with the other two ecotypes (Table 5).

Flowering

Flowering phenology was affected by both ecotype and precipitation individually (Table 3). Texas ecotypes had half the number of flowering tillers at the end of season compared with Kansas and Oklahoma ecotypes (Table 4, Fig. 4). Texas ecotypes also initiated flowering a month later than the other ecotypes and flowered at a slower rate (Fig. 4). Flowering phenology varied significantly with precipitation treatments. Individuals in the increased treatment had 40% and 38% more flowering tillers at the end of the season compared with the average and decreased treatments respectively (Table 4, Fig. 4). Precipitation treatments affected flowering rates, with the increased treatment flowering at a greater rate compared with the average and decreased treatment (Fig. 4).

Discussion

The primary objective of this study was to characterise the ecotype-specific physiological responses and growth of *P. virgatum* to changes in forecasted precipitation amount for the Central Plains region of the United States by the year 2100. Our results show that the precipitation treatments significantly affected soil moisture and the corresponding responses of plant growth and physiology. Significant effects of ecotype

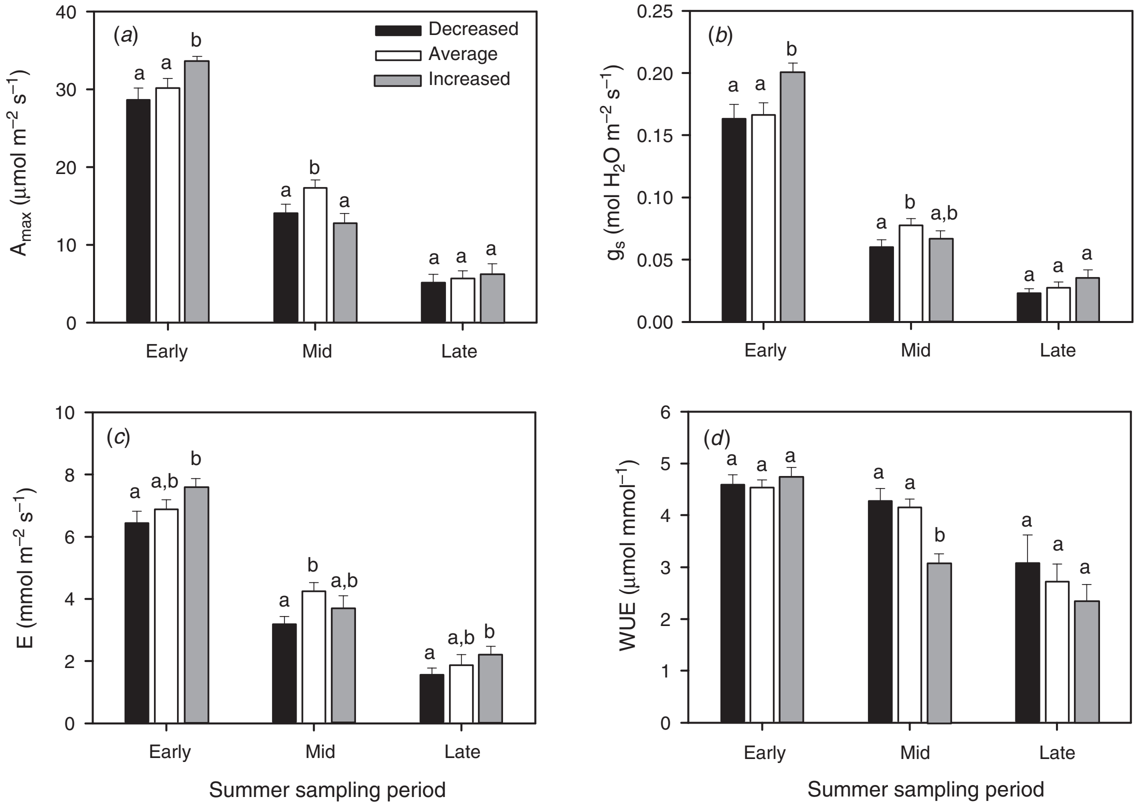

Fig. 3. Gas exchange responses by treatment during the early, mid-season and late periods of the growing season. (*a*) Carbon assimilation at ambient CO_2; (*b*) stomatal conductance; (*c*) transpiration; (*d*) water use efficiency (A_{max} E^{-1}). Bars are means (±1 s.e.) and significant differences are indicated by letters within each sampling period.

Table 3. Mixed-effects model ANOVA of precipitation treatments and ecotype (fixed, precipitation, ecotype; random, cell) effects on aboveground biomass variables

F- and *P*-values are provided with significant responses. *, $P < 0.05$; **, $P < 0.10$

Response	Precipitation		Ecotype		Ecotype × precipitation	
	F	*P*	*F*	*P*	*F*	*P*
Tillers (per individual)	3.71*	0.0326*	3.38*	0.0429*	1.1	0.35
Biomass (g per individual)	9.48*	0.0004*	2.1	0.12	1.5	0.21
Biomass per tiller (g per individual)	4.49*	0.0168*	11.09*	0.0001*	4.31*	0.0050*
% allocated to reproduction (per individual)	4.83*	0.0127*	5.99*	0.0050*	1.91	0.12
Flowering tillers (per individual)	7.54*	0.0015*	8.48*	0.0008*	0.5	0.68
Flowering tiller biomass (g per individual)	11.46*	<0.0001*	0.8	0.44	1.5	0.19
Biomass per flowering tiller (g per individual)	2.86**	0.0681**	13.33*	<0.0001*	3.51*	0.0142*
Flowering tiller height (cm per individual)	5.12*	0.0100*	1.8	0.16	1.6	0.17
Leaves per flowering tiller (per individual)	5.47*	0.0075*	2.2	0.11	1.1	0.35
Non-flowering tillers (per individual)	3.25*	0.0481*	2.91**	0.0651**	2.87*	0.0337*
Non-flowering tiller biomass (g per individual)	1.1	0.32	4.84*	0.0126*	0.5	0.67
Biomass per non-flowering tiller (g per individual)	0.07	0.93	15.85*	<0.0001*	1.7	0.15
Non-flowering tiller height (cm per individual)	0.9	0.38	3.05**	0.0576**	1.1	0.36
Leaves per non-flowering tiller (per individual)	0.2	0.80	6.70*	0.0029*	1.8	0.13

Table 4. Mean responses (±1 s.e.) of various aboveground biomass measurements for ecotype and precipitation treatment effects

Within the ecotype or treatment category, bolded numbers show significance at the $P \leq 0.05$ level and italicised numbers show marginal significance at the $P \leq 0.10$ level. Superscripts display significant differences between precipitation treatments or ecotypes within a category. NS signifies no significance between the ecotypes or the precipitation treatments

Variables	Precipitation			Ecotype		
	Decreased	Average	Increased	Kansas	Oklahoma	Texas
Tillers (per individual)	**56 ± 5^{a,b}**	**47 ± 6^{b}**	**71 ± 6^{a}**	**69 ± 5^{a}**	**58 ± 6^{a,b}**	**48 ± 6^{b}**
Biomass (g per individual)	**202 ± 28^{b}**	**181 ± 30^{b}**	**352 ± 30^{a}**	NS	NS	NS
Biomass per tiller (g per individual)	**3.6 ± 0.3^{b}**	**4.0 ± 0.3^{a,b}**	**5.0 ± 0.3^{a}**	**3.0 ± 0.3^{b}**	**4.4 ± 0.3^{a}**	**5.2 ± 0.3^{a}**
Flowering tillers (per individual)	**35 ± 4^{b}**	**36 ± 4^{b}**	**58 ± 4^{a}**	**53 ± 4^{a}**	**48 ± 5^{a}**	**27 ± 5^{b}**
Flowering tiller biomass (g per individual)	**157 ± 27^{b}**	**157 ± 28^{b}**	**325 ± 28^{a}**	NS	NS	NS
Biomass per flowering tiller (g per individual)	*4.1 ± 0.4^{b}*	*4.9 ± 0.7^{a,b}*	*5.6 ± 0.4^{a}*	**3.2 ± 0.4^{b}**	**5.0 ± 0.4^{a}**	**6.4 ± 0.4^{a}**
Flowering tiller height (cm per individual)	**94 ± 7^{b}**	**101 ± 8^{b}**	**129 ± 8^{a}**	NS	NS	NS
Leaves per flowering tiller (per individual)	**4.7 ± 0.1^{b}**	**5.1 ± 0.2^{a,b}**	**5.6 ± 0.2^{a}**	NS	NS	NS
Non-flowering tillers (per individual)	**21 ± 2^{a}**	**11 ± 3^{b}**	**12 ± 3^{a,b}**	*15 ± 2^{a,b}*	*9 ± 3^{b}*	*20 ± 3^{a}*
Non-flowering tiller biomass (g per individual)	NS	NS	NS	**20 ± 9^{b}**	**14 ± 11^{b}**	**59 ± 11^{a}**
Biomass per non-flowering tiller (g per individual)	NS	NS	NS	**0.7 ± 0.1^{b}**	**0.8 ± 0.1^{b}**	**2.0 ± 0.1^{a}**
Non-flowering tiller height (cm per individual)	NS	NS	NS	*27 ± 3^{a,b}*	*24 ± 4^{b}*	*38 ± 4^{a}*
Leaves per non-flowering tiller (per individual)	NS	NS	NS	**3.2 ± 0.2^{b}**	**3.0 ± 0.3^{b}**	**4.4 ± 0.3^{a}**
% allocated to reproduction (per individual)	**77 ± 3^{b}**	**85 ± 3^{a,b}**	**94 ± 3^{a}**	**87 ± 3^{a}**	**94 ± 4^{a}**	**75 ± 4^{b}**

and precipitation were present, but there were few ecotype × precipitation interactions. In general, physiological differences reflected ecotype origin, whereas differences in aboveground biomass largely reflected differences in soil water availability from the precipitation treatments.

Ecotype effects

Differences among means in the physiological variables measured largely reflected differences by ecotype and corresponding adaptation to the local environment of origin. Within each ecotype, similar changes in $A_{\max}$, g_s and E reflect the coupled gas exchange relationships documented previously for other dominant prairie grasses (Polley *et al*. 1992). It has also been shown that carbon assimilation in switchgrass is controlled mostly by population responses to local environmental conditions (Wullschleger *et al*. 1996). In this study, the Kansas ecotypes had the lowest carbon assimilation rates, providing support for the local environmental condition response (Wullschleger *et al*. 1996).

The $F_v/F_m - g_s$ relationship developed (Fig. 2) shows a statistical relationship between responses of leaf photochemistry to changes in stomatal conductance that varies by ecotype. Reduced F_v/F_m values indicate a decreased efficiency of non-photochemical quenching, and are reflective of the functioning of the light reactions of photosynthesis (Maxwell and Johnson 2000). Changes in F_v/F_m can be especially useful in studies where physiological performance is strongly decreased from long periods of drought (Resco *et al*. 2008). These data show that nearly one-quarter of the variation the maximum efficiency of PSII can be statistically attributed to changes in stomatal conductance (Fig. 2). From first principles, one would assume that a reduction in stomatal water loss would result in increased

Table 5. Mean responses (±1 s.e.) of various aboveground biomass measurements for interactions between ecotypes and precipitation treatments
Bolded numbers show significance at the $P \leq 0.05$ level. Superscripts display significant differences between ecotype × precipitation combinations; NS signifies no significant difference between the means

Variables	Ecotype × precipitation								
	Decreased			Average			Increased		
	Kansas	Oklahoma	Texas	Kansas	Oklahoma	Texas	Kansas	Oklahoma	Texas
Tillers (per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Biomass (g per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Biomass per tiller (g per individual)	**$2.8 \pm 0.5^{\mathrm{b}}$**	**$4.2 \pm 0.5^{\mathrm{b}}$**	**$3.8 \pm 0.5^{\mathrm{b}}$**	**$2.9 \pm 0.5^{\mathrm{b}}$**	**$5.0 \pm 0.6^{\mathrm{a,b}}$**	**$4.2 \pm 0.6^{\mathrm{b}}$**	**$3.4 \pm 0.5^{\mathrm{b}}$**	**$3.9 \pm 0.6^{\mathrm{b}}$**	**$7.6 \pm 0.6^{\mathrm{a}}$**
Flowering tillers (per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Flowering tiller biomass (g per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Biomass per flowering tiller (g per individual)	**$2.8 \pm 0.7^{\mathrm{b,c}}$**	**$4.4 \pm 0.7^{\mathrm{b,c}}$**	**$5.1 \pm 0.7^{\mathrm{b,c}}$**	**$3.1 \pm 0.7^{\mathrm{b,c}}$**	**$6.5 \pm 0.8^{\mathrm{a,b}}$**	**$5.2 \pm 0.8^{\mathrm{a,b,c}}$**	**$3.6 \pm 0.7^{\mathrm{b,c}}$**	**$4.2 \pm 0.8^{\mathrm{b,c}}$**	**$9.0 \pm 0.8^{\mathrm{a}}$**
Flowering tiller height (cm per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Leaves per flowering tiller (per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Non-flowering tillers (per individual)	**$31 \pm 4^{\mathrm{a}}$**	**$5 \pm 5^{\mathrm{b}}$**	**$28 \pm 5^{\mathrm{a,b}}$**	**$8 \pm 4^{\mathrm{b}}$**	**$7 \pm 5^{\mathrm{a,b}}$**	**$18 \pm 5^{\mathrm{a,b}}$**	**$7 \pm 4^{\mathrm{b}}$**	**$15 \pm 5^{\mathrm{a,b}}$**	**$15 \pm 5^{\mathrm{a,b}}$**
Non-flowering tiller biomass (g per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Biomass per non-flowering tiller (g per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Non-flowering tiller height (cm per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Leaves per non-flowering tiller (per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS
% allocated to reproduction (per individual)	NS	NS	NS	NS	NS	NS	NS	NS	NS

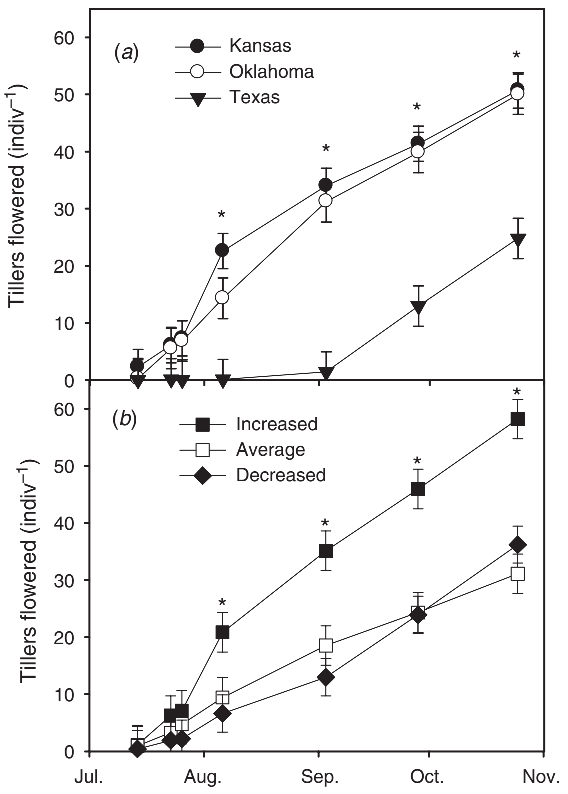

Fig. 4. Total tillers flowered per individual over the course of the growing season. (*a*) Flowering tillers by ecotype; (*b*) flowering tillers by precipitation treatment. Data points are means ± 1s.e. Asterisks indicate statistical significance ($P < 0.05$) between groups, within each sampling date.

leaf temperature, with the potential for corresponding decreased photochemistry during hot or dry summer conditions. For all ecotypes, F_v/F_m decreased nonlinearly with stomatal closure, but there were clear differences in this relationship between ecotypes, with a general trend of increasing F_v/F_m values for a given rate of stomatal conductance from Kansas to Oklahoma to Texas ecotypes. Texas ecotypes had higher maximum F_v/F_m values compared with Kansas ecotypes, with values near the accepted maximal value of 0.83 (Krause and Weis 1991). As g_s values decreased, Texas and Oklahoma ecotypes were able to maintain higher F_v/F_m values compared with the Kansas ecotypes, indicating a greater decrease in the photochemical efficiency of PSII in Kansas ecotypes. Interpretation of the relationship between F_v/F_m and g_s requires further investigation, but these data show promise for linking changes in stomatal conductance with the maintenance of leaf photochemistry, as the ability to cool the leaf through latent heat exchange becomes very limited with low g_s (Nippert *et al.* 2009) and photochemistry is subsequently reduced by increased leaf temperatures (Albert *et al.* 2011). Based on these F_v/F_m–g_s response curves (Fig. 2), Oklahoma and Texas ecotypes are potentially more tolerant of higher leaf temperature, with higher F_v/F_m at low rates of gas exchange compared with Kansas ecotypes.

P. virgatum is a highly photoperiod sensitive species (Benedict 1940), and differences in flowering dates have been documented for various ecotype and cultivars (McMillan 1965; Van Esbroeck *et al.* 2003; Casler *et al.* 2004). Sanderson and Wolf (1995) recorded similar flowering dates for Alamo and Cave-in-Rock cultivars, compared with the ecotypes in this study. Alamo cultivars flowered around the end of September and Cave-in-Rock cultivars flowered around the first week of July. The flowering time and rates seen in this study correspond with known ecotype responses to changes in latitude.

Many of the aboveground biomass responses with significant ecotypic differences were a result of the Texas ecotypes producing fewer tillers, but with an increased biomass per tiller and number of leaves per tiller, while the Oklahoma and Kansas ecotypes had higher tiller density (Table 4). Typically, the best estimates to predict changes in biomass yield for this species are increased biomass per tiller and number of leaves per tiller (seen in Texas ecotypes) or higher tiller density (noted in the

Oklahoma and Kansas ecotypes; Boe and Beck 2008). Although total biomass was not significantly different among ecotypes, the Texas ecotypes contain components (higher biomass and leaves per tiller) that, if heritable, may lead to greater biomass in multiple generation studies.

Precipitation effects

The altered environmental conditions resulting from the precipitation treatments significantly altered responses in aboveground biomass measurements, with statistically significant responses in the physiological variables largely reflecting changes across the sampling periods (Fig. 3). Flowering tiller heights were greatest in the increased precipitation treatments, reaching mean heights of 1.29 m. These heights are reflective of those observed in prairie remnant populations although they are lower than those found in *P. virgatum* cultivars (Das *et al*. 2004; Casler 2005; Alexopoulou *et al*. 2008), but it should be noted that plant heights are variable from year to year (Alexopoulou *et al*. 2008). The average number of leaves per flowering tiller was lower than those found in agronomic *P. virgatum* cultivars (Van Esbroeck *et al*. 1997); however, these cultivars have been bred to optimise yield. These data illustrate individual biomass responses to precipitation of a dominant species in the tallgrass prairie ecosystem, further supporting the conclusions of others that future changes in precipitation are likely to significantly alter ecosystem productivity (Knapp 1984; Fay *et al*. 2003; Fay *et al*. 2008; Zhou *et al*. 2009).

Previous attempts to link leaf-level to whole-plant responses for grassland species have shown positive relationships between photosynthesis and plant success (McAllister *et al*. 1998), but leaf-level to whole-plant relationships in grasslands are commonly weak (Nippert *et al*. 2007). In this study, no clear relationships between leaf-level photosynthetic responses and total aboveground biomass were present for these ecotypes. Although the increases in leaf-level photosynthesis did not correspond to total biomass increases, other measurements of biomass increased from the increased precipitation, partially supporting the positive relationship between higher rates of gas exchange and plant success previously noted by McAllister *et al*. (1998).

The only physiological responses affected by precipitation treatments were Ψ_{mid} and WUE, with WUE being lowest in the increased treatments and Ψ_{mid} highest in increased treatments. Although ANOVA results showed significant precipitation × sample period interactions (Table 2), many of the effects were only seen in the early season period (Fig. 3). Later in the season, increasing summer temperatures negated the positive impacts of the added water. Decreased WUE across the growing season corresponding to higher air temperatures has been previously noted for C_4 species, where WUE can be reduced by 40% in drought conditions (Taylor *et al*. 2011). As water availability decreased, Ψ_{mid} decreased to a mean of –2.2 MPa. The decreased precipitation treatment did not lower soil water availability to the point where the critical water potential (leaf pressure potential when stomatal closure is less than 5% of the maximum) was reached for switchgrass ($\Psi_{\mathrm{crit}} = -3.2$ MPa; Tucker *et al*. 2011). Indeed, previous studies have shown that switchgrass can maintain growth and functioning at lower water potentials than those recorded here (Knapp 1984; Stroup *et al*. 2003). With more severe decreases in water availability, Ψ_{mid}, A_{max}, g_s, E and WUE should continue to decline, with the potential for increased cuticular conductance when drought-stressed (Manzoni *et al*. 2011).

Ecotype × precipitation interactions

Surprisingly, few ecotype × precipitation interactions were present for the variables measured in this study (Tables 2, 3), with the primary exception being greater biomass per tiller in the increased treatment for Texas ecotypes. These differences largely reflect the southern Texas ecotype being adapted to a longer growing season (Newell 1968). Growth of the Texas ecotype in a location with a shorter growing season delayed reproductive maturity, and although the overall biomass yield was not significantly greater for Texas ecotypes compared with Oklahoma and Kansas, under greater precipitation differences, the trends observed in the current study may become statistically significant. Because Texas ecotypes had a longer period in which they grew vegetatively, they were better able to take advantage of the increased precipitation treatment to produce higher biomass per tiller, greater biomass per flowering tiller and high non-flowering tiller counts in all precipitation treatments. These results from a southern Texas ecotype growing in a more northern location are similar to other studies that show increases in biomass, longer photosynthetic activity and delayed flowering for southern ecotypes grown in more northern latitudes (Quinn 1969; Lemus *et al*. 2002; Casler *et al*. 2004; Berdahl *et al*. 2005; Casler *et al*. 2007).

Conclusion

The physiological responses of A_{max}, g_s, E, F_v/F_m and Ψ_{mid} in *P. virgatum* were explained by ecotype differences; however robust responses to altered precipitation were seen in *WUE*, Ψ_{mid}, flowering times and many aboveground biomass variables. Ecotype differences were also seen in several aboveground biomass variables, and most strikingly in flowering initiation and rates. In this study, there were few interactions between ecotype and precipitation amount, suggesting that although precipitation is a strong driver of biomass production, local adaptations in the ecotypes used in the current study have less impact on these responses than initially expected. It was expected that the environmental differences among the origins of the ecotypes, mainly the effects of higher temperature coupled with similar mean annual precipitation (860–878 mm), would lead to significant ecotype × precipitation interactions in the parameters measured, with the Texas ecotypes being the most tolerant of the changes. The lack of interactions between genetic background and precipitation also has broader evolutionary implications; gene × environment interactions are a primary indicator of the potential for natural selection in a given trait (Schlichting 1989). The broader implications of the few ecotype × precipitation interactions for this widely-distributed species suggest that it is not likely to undergo selection in response to changes in precipitation. As many have correctly suggested, it is necessary to examine the role of genetic variation in the response of plant species to future changes in climate

(Callaway *et al*. 2003; Ward and Kelly 2004); however, as indicated by this study, it may not always be necessary to consider localised adaptation when working to project the impacts of climate change on the performance of a species like switchgrass across its geographical distribution.

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