

Climate controls on grass culm production over a quarter century in a tallgrass prairie

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Abstract. The flowering of grasses is a process critical to plant population dynamics and genetics, herbivore performance, and human health. To better understand the climate factors governing grass flowering, we analyzed the patterns of culm production over 25 years for three perennial tallgrass prairie species at Konza Prairie in Kansas, USA. The three species (*Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium*) all utilize the C₄ photosynthetic pathway and were measured annually at the same locations for the past 25 years in an annually burned watershed. Culm production of all three species increased with higher growing-season soil moisture and precipitation but differed in their responses to water availability at different times during the growing season. Relative to *Andropogon*, *Sorghastrum* responded more to precipitation early in the growing season, and *Schizachyrium* responded more to precipitation late in the growing season. Flowering by each species also revealed a threshold relationship with late-season soil moisture at ~1 m depth, which likely is a proxy for season-long water balance. Although flowering can be influenced by conditions antecedent to the current growing season, neither soil moisture nor precipitation during the previous year influenced flowering over the 25-year period. Flowering culm production averaged 9% and 7% of total graminoid aboveground net primary production (ANPP) in the uplands and lowlands, respectively. Interannual variation in ANPP correlated only with *Sorghastrum* flowering, suggesting a predominant role of the species in ANPP responses to climate.

Key words: aboveground net primary production (ANPP); *Andropogon gerardii*; climate; flowering; Konza Prairie; *Schizachyrium scoparium*; soil moisture; *Sorghastrum nutans*; tallgrass prairie.

INTRODUCTION

Interannual variation in the flowering of grasses is a critical phenomenon in the ecology of grasslands. Beyond controlling variation in seed production and plant population dynamics, flowering affects a number of ecological processes. Variation in seed production influences populations of a number of seed predators such as insects and rodents (McKone et al. 1998, Lima et al. 2008). The production of low-protein, high-lignin culms that accompany flowering can reduce the performance of large grazers (Craine et al. 2009), decrease standing crop decomposition rates, and increase the likelihood of fire (Knapp 1998). Of more direct human impact, the production of pollen during flowering has significant health impacts (D'Amato et al. 2007), while culms are economic resources and have the potential to contribute to C sequestration and biofuel production (Lemus et al. 2002, Christian et al. 2008).

Despite the obvious importance of flowering as a central ecological process in grasslands, the proximal and distal mechanisms that determine interannual variation in flowering are understood poorly (Kelly

and Sork 2002). For example, it is unknown if flowering of perennial grasses in a native grassland responds to cues that are independent of resource availability, i.e., masting (McKone et al. 1998, Kelly and Sork 2002, Koenig and Knops 2005), or whether variation in grass flowering can largely be ascribed to plant resource accumulation and the factors that drive the accumulation (Hay et al. 2008). It is well known that the length of the prereproductive period and onset of first flowering in many perennials is related to the accumulation of a threshold amount of some limiting resource (Samson and Werk 1986, Weiner 1988), but the controls on subsequent interannual variation in flowering and reproductive effort are unknown. As flowering is resource intensive (Primack and Hall 1990), flowering might be a direct function of resource availability. As such, flowering would be expected to be greater in years with high resource availability. Without direct measurements of resource accumulation in plants, it is difficult to separate masting from resource accumulation, which would be associated with a positive relationship between resource accumulation and flowering.

Understanding climate controls on flowering is made more complex by the potential for the influence of antecedent conditions. Flowering in a given year has the potential to be influenced by the condition of the plants or the state of the ecosystem in the previous year. For example, flowering might be greater following a year

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that was favorable to growth, such as a year with high precipitation, which allowed for resources and/or meristems to accumulate. Flowering also has the potential to be greater following a year with low precipitation (Knapp and Hulbert 1986). For example, although growth and resource accumulation by plants is lower in a dry year, rewetting of a dry soil can lead to pulses of nutrient mineralization (Turner and Haygarth 2001, Fierer and Schimel 2002) that could stimulate flowering in the following year.

Although we know little about the responses of different species to climate variation, not all species are expected to respond similarly. Species can differ in their timing of resource uptake, degree to which they are limited by a given resource, allocation to vegetative and sexual reproduction, or phenology of flowering. Alternatively, co-dominant species might respond similarly to climate variation if they are ecologically separated by factors that are independent of climate, such as susceptibility to specific enemies (Janzen 1970), or if the climate affects the species' differences similarly (Houle 1999). These differences among species in their responses to climate variation are important not only for understanding community dynamics, but also corresponding ecosystem processes such as aboveground net primary productivity (ANPP). For example, it is uncertain what proportion of ANPP can be ascribed to culm production, no less which species might be driving interannual variation in ANPP through variation in flowering (Fay et al. 2003).

To better understand the patterns of flowering and climate control over flowering, we analyzed a 25-year record of flowering for three perennial C_4 grass species in two landscape positions from an annually burned watershed at Konza Prairie Biological Station. If water availability directly or indirectly limits production, then flowering should be greater in years with greater soil moisture and/or precipitation. If plants are dependent on resource accumulation during the previous year, then flowering should be greater after a wet year than a dry year. Alternatively, if flowering is limited by N and N supply is greater after a dry year, then plants should show greater flowering after a dry year.

Among the three species whose flowering patterns we investigated (*Andropogon gerardii* Vitm., *Sorghastrum nutans* L., and *Schizachyrium scoparium* (Michx.) Nash), the caespitose *Schizachyrium* is more shallowly rooted and considered more drought tolerant than the other two species (Weaver and Clements 1938). As such, its flowering might be reduced less, if not increased, by lower precipitation or soil moisture compared to the other C_4 grasses. *Andropogon* and *Sorghastrum* are similar in their distributions along ecological gradients, although *Andropogon* is often considered more drought tolerant than *Sorghastrum* (Swemmer et al. 2007, Nippert et al. 2009). If so, flowering of *Sorghastrum* might be more sensitive to changes in precipitation than *Andropogon*. To better understand how much of the

variation in grass ANPP can be explained by flowering of each species, we also investigate the relationships between flowering and graminoid production across years.

METHODS

Site description

The research on flowering was conducted on Konza Prairie Biological Station, a 3487-ha native tallgrass prairie located in northeastern Kansas (latitude = 39°4'5" N, longitude = 96°33'36" W). To study how fire affects the structure and function of grassland vegetation, Konza watersheds are used as large experimental units subjected to different long-term fire and grazing regimes. For this study, flowering was measured on a 42-ha watershed (watershed 1D) that had been ungrazed and burned annually in the spring (mid- to late April) since the station was established in 1971. Topographically, the watershed consists of shallow xeric upland soils (cherty, silty clay loams overlying limestone and shale layers; Udic Argiustolls, Florence series), and mesic lowland soils (deeper colluvial and alluvial deposits; Pachic Argiustolls, Tully series). Vegetation on both topographic positions are dominated by perennial warm-season grasses, primarily *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium*, with a high diversity but low abundance of other graminoids and perennial forbs.

Climate for the area typically has hot summers, cold winters, and moderately strong surface winds. Mean annual temperature is 13°C, with mean minimum and maximum monthly temperatures ranging from -3°C in January to 27°C in July. Annual precipitation for Konza Prairie averaged 826 mm from 1983 to 2007, with ~75% falling in the April through September growing season. All climate data used in this study were collected from a weather station located at Konza Prairie headquarters, ~5 km away from the 1D watershed.

Field measurements

The flowering responses of the three grass species were measured at the end of the growing season (after late September) from 1984 to 2008 along four permanent transects on both the upland and lowland topographic positions. Along each transect, all flowering culms that occurred in six randomly spaced 0.25-m² quadrats were counted ($n = 24$ plots per topographic position). The flowering culms of each grass species in the plot were then harvested at ground level, dried at 60°C for 2–3 days, and weighed.

In addition to annual measurements of flowering, at two points in the lowlands of watershed 1D, soil moisture was measured at two-week intervals during the growing season. Soil moisture was measured with a neutron depth moisture gauge (Troloxer Electronic Incorporated, Research Triangle Park, North Carolina, USA) in thin-walled aluminum access tubes buried 2 m

deep. Readings were taken at 25-cm increments from 25 to 150 cm from 1984 to 2008.

Soil moisture data were expressed as an index of apparent field capacity (Briggs and Knapp 1995). To accomplish this, data for two points for each date were averaged. For each soil depth, maximum soil moisture was determined for dates before and after 1998. In 1998, a new probe head was employed, requiring that data be standardized for differences in maximum soil moisture before and after this date. Minimum soil moisture was determined among all soil depths. All data were decreased by this amount, and then data were divided by the maximum for each depth. This index standardizes soil moisture from 0, which is the lowest soil moisture observed among all depths, to 1, which is the maximum soil moisture read in each depth.

ANPP was measured at the end of the each growing season by clipping all vegetation in five randomly selected quadrats (20×50 cm) adjacent to the flowering transects ($n = 20$ quadrats in each landscape position each year). Biomass was clipped to ground level, separated into graminoid, forb, and woody components, and dried at 60°C before weighing. Graminoid ANPP included live biomass as well as the current year's dead biomass, which was measured separately from live biomass for 17 of the 25 years.

Data analysis

To determine the average mass of individual culms for each species at each landscape position, correlations between the number of culms and culm mass at the plot level were calculated. Log-transformed data were used to determine whether culm mass changes with increasing number of culms per unit area. Culm biomass data were then used exclusively in assessing relationships among species and soil types as well as the relationships between flowering and climate.

Relationships between lowland soil moisture and flowering were determined for each species and landscape position by computing a piecewise regression with a nonlinear formula that parameterizes the intercept, the slope of the first segment, the inflection point that separates the two segments, and the slope of the second segment (Toms and Lesperance 2003). Piecewise regression was selected over other relationships such as a first- or second-order regression, as it would allow for an inflection point in relationships without forcing flowering to be less than zero or flowering to increase at low soil moisture. For each combination of species and landscape position, soil moisture data from eight 15-d date ranges (early June–late September) and six 25-cm soil depths (25–150 cm in 25-cm increments) were used to individually determine the ability of lowland soil moisture to predict flowering with the piecewise regression. The one soil moisture data subset of the 48 combinations of date ranges and soil depths that explained the highest proportion of variation in flowering was selected for each combination of species and landscape position. From each of these six relationships

(two landscape positions by three species), we calculated the residual variation in flowering that could not be explained by soil moisture for the most critical date range and depth. Soil moisture at different times and depths during the current year did not explain any of the residual variation in flowering. We then tested the role of soil moisture from June to November during the previous year (covering the period 1983–2007) in explaining residual variation in flowering using the exact approach as mentioned above but with soil moisture from the previous year.

In addition to assessing the role of soil moisture at different times of year in the interannual variation of flowering, we also calculated the critical climate periods (Craine et al. 2009) of precipitation and temperature for flowering. From the daily climate data, we calculated total precipitation and average temperature for 880 periods between day 60 (1 March) and day 275 (2 October). The number of periods corresponds to all possible periods between the two dates with a minimum length of 15 days where start and end dates are incremented in 5-day steps, e.g., day 60–75, 60–80, ..., 260–275. To determine the critical climate period for each species and soil type, a forward stepwise regression was initiated using the current year's precipitation data from all 880 periods. The climate period that explained the highest amount of variation in flowering was then selected as a predictor variable. In general, a number of climate periods significantly explained flowering. Most of the periods that explained the most variation differed by a few of the 5-day increments for the start or the end date.

For each of the six combinations of species and landscape positions, residual variation in flowering relative to the most important critical climate period also was calculated. Examining this residual variation relative to the critical climate periods for the current year with stepwise regression, neither precipitation nor temperature during different periods in the current year significantly explained any of the residual variation (data not shown). In general, temperature alone explained significant amounts of variation in flowering. Yet temperature explained consistently less variation than precipitation alone, and likely reflected the inverse correlations between precipitation and temperature among years (data not shown). After testing the roles of precipitation and temperature during the current year in explaining flowering, the same process of determining critical climate periods was used to test antecedent effects of precipitation and temperature in determining flowering. This involved another stepwise regression model with precipitation and temperature for 880 periods, but instead of the current year's climate, the periods used the previous year's climate. For critical climate periods, a more restrictive P value (0.01) was used as the threshold for acceptance, due to the large number of predictor variables in any one regression.

To determine the potential role of flowering of different species in contributing to variation in ANPP, we examined correlations between culm biomass and graminoid ANPP from 1984–2008 for each species and landscape position.

All statistics were computed in JMP 7.0.1 (SAS 2007).

RESULTS

Total culm mass was highly correlated with total number of culms within species and soil types from 1984 to 2008 ($r = 0.85\text{--}0.93$, $n = 576$ for each comparison. (Appendix A: Fig. A1, Table A1). Ratios between the culm number and mass indicate that each *Andropogon* culm averaged 1.59 g and 1.97 g in the upland and lowland soils, respectively; 1.74 g and 2.04 g for *Sorghastrum*, and 0.44 g and 0.41 g for *Schizachyrium*. Slopes of the standardized major axis regressions of the log-transformed data (excluding plots with no culms) were all consistently >1 (1.13–1.33), indicating that mass per culm increased with increasing numbers of culms (Appendix A: Table A1).

Over the 25 years, averaged across all plots in the two landscape positions, total culm mass ranged from 0 g/m² to 35.9 g/m² for *Andropogon*, 0.4 g/m² to 63.0 g/m² for *Sorghastrum*, and 0 g/m² to 30.1 g/m² for *Schizachyrium* (Fig. 1). There were no significant differences between soil types among years in average culm biomass for *Andropogon* or *Schizachyrium* ($P > 0.39$, $P > 0.14$, respectively, paired t test), but *Sorghastrum* culm production averaged 4.1 g/m² higher in lowlands than in uplands ($P = 0.02$). Culm production was positively correlated between landscape positions among years ($r = 0.58$, 0.88, 0.70 for *Andropogon*, *Sorghastrum*, and *Schizachyrium*, respectively; $P < 0.001$ for all comparisons). In general, culm production was positively correlated between species at a given landscape position, except for *Andropogon* and the other two species in the lowlands, for which there was no significant relationship among years (Fig. 2). There were no significant trends over time for culm production of any species ($P > 0.16$), nor was there any relationship between current and previous year's flowering ($P = 0.48$ for uplands and $P = 0.91$ for lowlands).

Culm production was generally greater for all three species in years with greater soil moisture deep in the soil profile (Fig. 3 and Appendix B: Table B1). Each species showed threshold responses in their relationships with soil moisture. *Andropogon* and *Sorghastrum* culm production in both uplands and lowlands was best related to early August soil moisture in the lowlands at 100 or 125 cm depth, but only after deep soil moisture exceeded a threshold that ranged from 74% to 87% of maximum soil moisture. Below this threshold, culm production was relatively low and invariant with soil moisture. In contrast, upland *Schizachyrium* culm production was more dependent on deep lowland soil moisture in early September. *Schizachyrium* culm production changed little over a range of low to

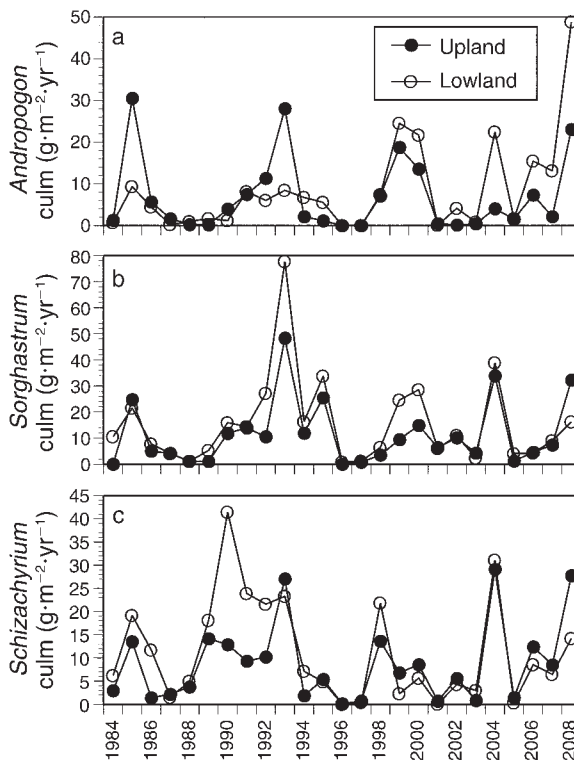


FIG. 1. Flowering culm biomass (g/m²) over time for *Andropogon*, *Sorghastrum*, and *Schizachyrium* in upland and lowland soils.

intermediate soil moistures, but increased markedly when lowland soil moisture in early September at 125 cm depth was above 85% maximum soil moisture for upland sites and 81% for lowland sites. For none of the three species, in either soil, did soil moisture at any depth during the previous year explain any of the variation in the current year's culm production that was explained by current year's soil moisture (data not shown).

Culm production increased with increasing precipitation, although each species responded differently to precipitation at different times in the growing season (Table 1, Fig. 4). *Andropogon* culm production in uplands was best explained by precipitation from 25 May to 8 August ($r^2 = 0.40$, $P < 0.001$), with culm mass (measured as grams per square meter per millimeter of precipitation) increasing at a rate of 0.052 g·m⁻²·mm⁻¹. In lowlands, *Andropogon* culm production was best explained by precipitation over a similar but more restrictive time period as uplands, (20 May–14 July; $r^2 = 0.30$, $P = 0.004$), although it was less responsive to late July precipitation. With increases in precipitation, culm production increased at a greater rate in the lowlands (0.072 g·m⁻²·mm⁻¹) than in uplands (0.052 g·m⁻²·mm⁻¹), likely due to the narrower critical climate period during which less precipitation falls.

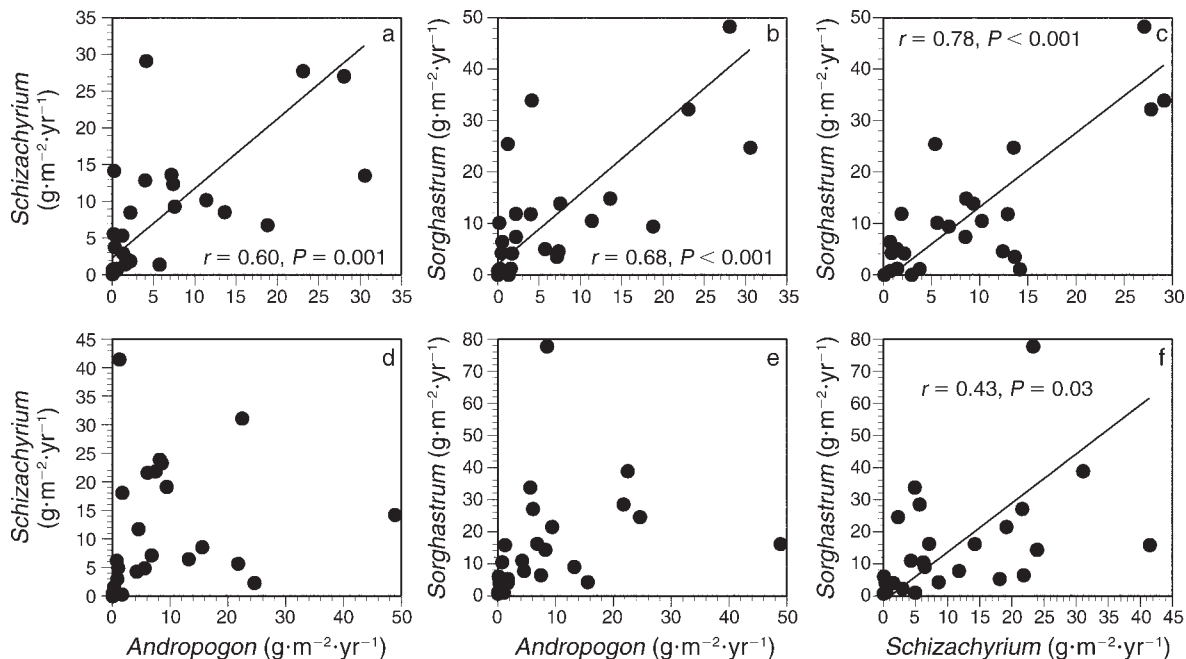


FIG. 2. Relationships over 25 years in flowering culm biomass between grass species for (a–c) upland and (d–f) lowland soils. Standard major axis regression lines are shown where significant ($P < 0.05$).

In contrast to *Andropogon*, *Sorghastrum* culm production was more responsive to early-season precipitation, and exhibited higher precipitation use efficiencies (Table 1, Fig. 4). Upland *Sorghastrum* culm production

was best explained by precipitation from 15 April to 24 July ($r^2 = 0.57, P < 0.001$), with culm mass increasing at a rate of $0.068 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$. In lowlands, *Sorghastrum* culm production was best explained by precipitation

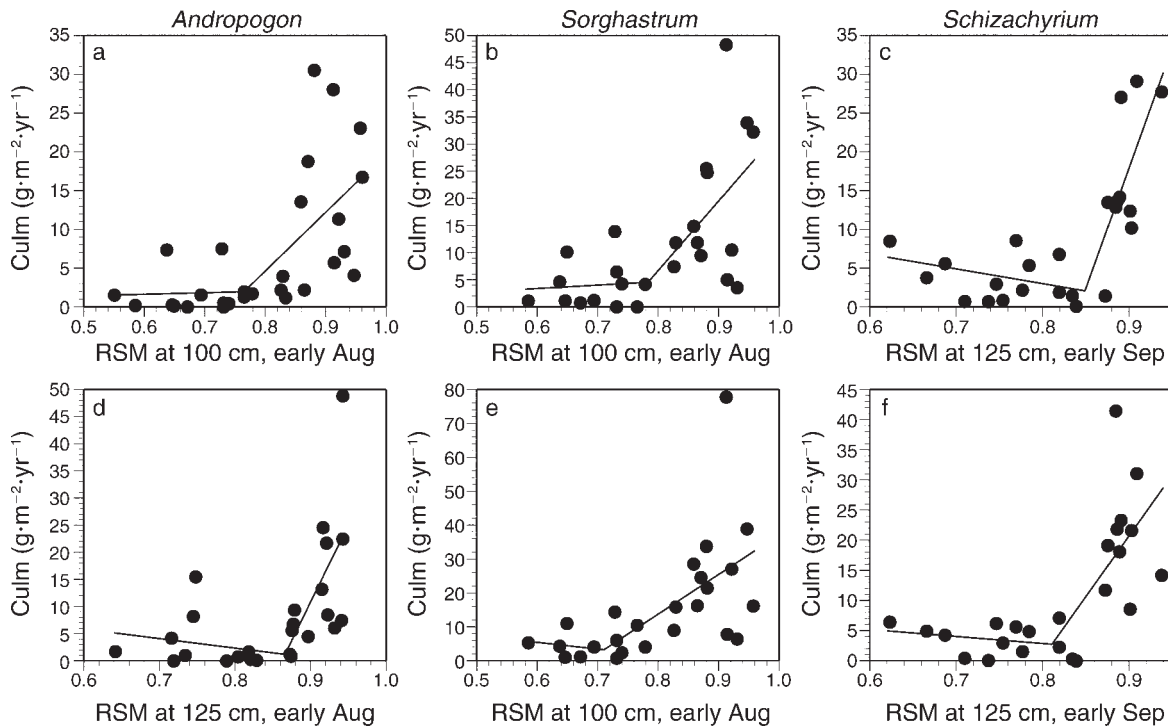


FIG. 3. Relationships between relative soil moisture (RSM; soil moisture relative to maximum) and flowering culm biomass ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) from 1984 to 2008 for (a–c) uplands and (d–f) lowlands: (a, d) *Andropogon*; (b, e) *Sorghastrum*, and (c, f) *Schizachyrium*. Lines represent piecewise regressions. See Appendix B: Table B1 for details on relationships.

TABLE 1. Relationships between precipitation and flowering for three species at two landscape positions.

Species	Position	Equation	Date range	r^2	P
<i>Andropogon</i>	upland	$-7.96 + 0.052x$	25 May–8 August	0.40	<0.001
	lowland	$-7.23 + 0.072x$	20 May–14 July	0.30	0.004
<i>Sorghastrum</i>	upland	$-12.8 + 0.068x$	15 April–24 July	0.57	<0.001
	lowland	$-21.4 + 0.096x$	20 April–3 August	0.61	<0.001
<i>Schizachyrium</i>	upland	$-9.54 + 0.053x$	4 June–7 September	0.55	<0.001
	lowland	$-3.21 + 0.052x$	4 June–18 August	0.30	0.005

Notes: The range of dates define the critical climate period for each combination of species and landscape position. Precipitation was measured in millimeters, and flowering as mass in grams per square meter.

from 20 April to 3 August ($r^2 = 0.61$, $P < 0.001$), with culm mass increasing at a rate that was 41% greater than uplands ($0.096 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$). Including early-season precipitation for *Sorghastrum* increased the coefficient of determination by 0.12 and 0.14 for uplands and lowlands, respectively, relative to the critical climate periods of *Andropogon*.

Compared with the other two grasses, *Schizachyrium* culm production was more responsive to precipitation later in the growing season. *Schizachyrium* culm production was less responsive to precipitation in April and May and more responsive in late August, congruent with its dependence on late August soil moisture. The best predictor of upland *Schizachyrium* culm production

was precipitation from 4 June to 17 September ($r^2 = 0.55$, $P < 0.001$), with culm mass increasing with increasing precipitation at a rate similar to upland *Andropogon* ($0.053 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$). In lowlands, *Schizachyrium* culm production was less sensitive to precipitation in late August and early September than upland *Schizachyrium* (4 June–18 August), but had similar precipitation use efficiencies ($0.52 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$). Like *Andropogon*, precipitation during this period explained less of the interannual variation in culm production ($r^2 = 0.30$) than in the uplands. Previous year’s precipitation explained none of the variation in culm production that was not explained by current year’s precipitation.

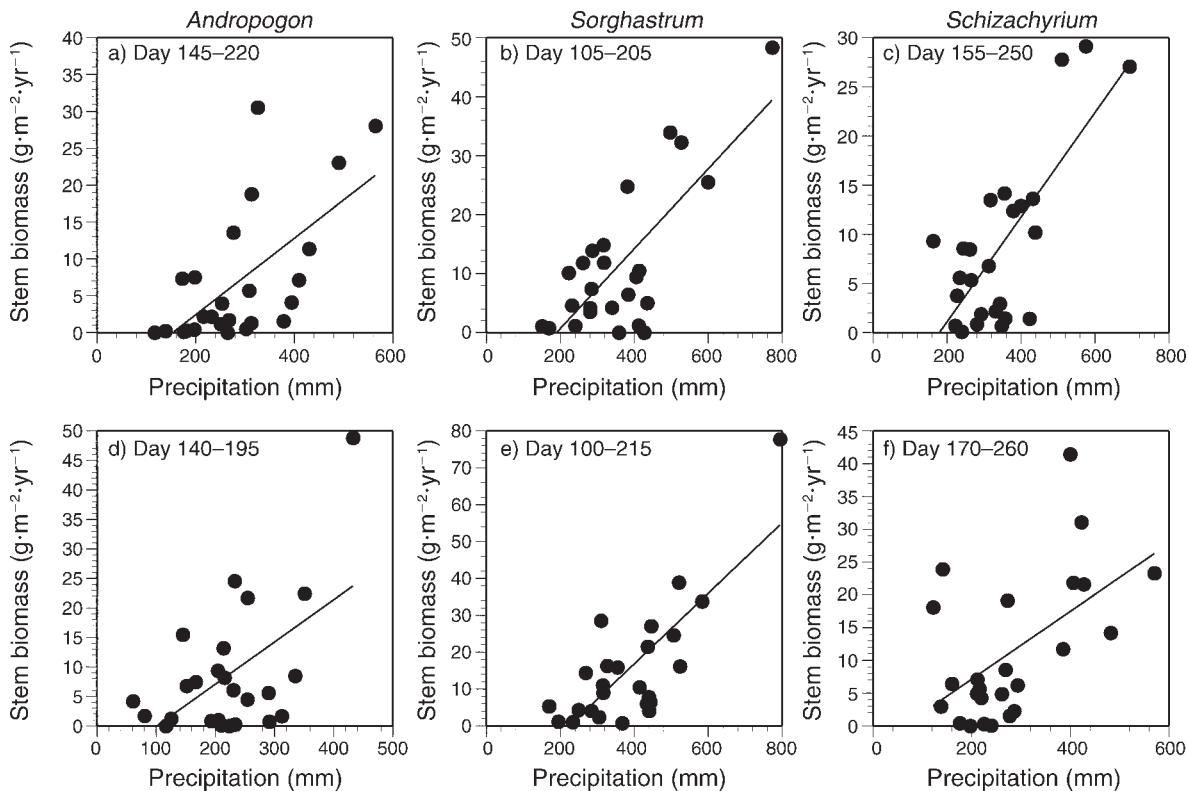


FIG. 4. Relationships between precipitation during critical climate periods (“Day” is day of year) and flowering culm biomass for (a–c) uplands and (d–f) lowlands: (a, d) *Andropogon gerardii*; (b, e) *Sorghastrum nutans*; and (c, f) *Schizachyrium scoparium*. See Table 1 for details on regressions.

In general, air temperature did not affect culm production, beyond what could be explained by precipitation. If precipitation was not included in the regression model, critical climate periods for air temperature explained less variation in culm production than precipitation, with cooler years, which generally have more precipitation, having greater culm production (data not shown). Critical climate periods for air temperature did not explain any additional variation in culm production beyond precipitation.

In testing the dependence of graminoid ANPP on culm production, upland graminoid ANPP from 1984 to 2008 varied by 424 g/m^2 , ranging from 126 g/m^2 to 551 g/m^2 . Lowland graminoid ANPP varied by 564 g/m^2 (185 g/m^2 to 749 g/m^2) during this period. In comparison, total culm production varied by 103.3 g/m^2 (range = 0.1 g/m^2 to 103.4 g/m^2) in the uplands and 108.7 g/m^2 (range = 0.8 g/m^2 to 109.5 g/m^2) in the lowlands. Mean culm mass was 8.2% and 6.9% of graminoid ANPP in uplands and lowlands, respectively, with ranges from 0% to 21.5% and 0% to 15.3% among years. The percentage of aboveground biomass that was culms, an index of relative allocation to flowering, increased with increasing growing season precipitation in uplands and lowlands. For uplands, this percentage increased by 3.3% for every 100 mm of additional precipitation within the critical climate period of 9 June to 27 September ($\%ANPP_c = -0.046 + 0.00033 \times \text{Precip}$; $r^2 = 0.39$, $P = 0.001$). For lowlands, this percentage increased by 2.8% for every additional 100 mm of precipitation within the critical climate period of 9 June–7 September ($\%ANPP_c = -0.024 + 0.00028 \times \text{Precip}$; $r^2 = 0.44$, $P < 0.001$). $ANPP_c$ represents the percentage of aboveground net primary production that is derived from culms.

Examining the species-specific relationships between culm production and graminoid ANPP, *Sorghastrum* culm production was more strongly correlated with graminoid ANPP than were the other two species. *Sorghastrum* culm biomass (B_c) was positively correlated with graminoid ANPP for both uplands ($ANPP_g = 222.1 + 8.03 \times B_c$; $CI = 5.21\text{--}12.39$; $r = 0.74$, $P < 0.001$) and lowlands ($ANPP_g = 352.5 + 9.34 \times B_c$; $CI = 4.54\text{--}19.18$; $r = 0.58$, $P = 0.003$). Neither *Andropogon* nor *Schizachyrium* culm production related to graminoid ANPP, except for upland *Andropogon* culm production ($r = 0.52$, $P = 0.01$). The significance of this relationship was due to the correlation in culm production between the two species in the uplands rather than a direct effect of *Andropogon* culm production on graminoid ANPP (partial $r = 0.04$ in a multivariate correlation that also included *Sorghastrum* culm biomass).

DISCUSSION

For all three species at both landscape positions, years with greater flowering coincided with greater precipitation and soil water availability during the current growing season. Although precipitation and soil water

availability could be a cue to flowering, due to water's pivotal role in carbon gain and nutrient availability, more than likely the greater flowering can be tied directly to greater resource accumulation caused by higher water availability. It is unlikely that soil water at depths of $\sim 1 \text{ m}$ late in the growing season is directly responsible for the resource accumulation, but instead likely serves as an integrator of soil moisture availability to plants throughout the growing season. For example, in years with high precipitation, soil water is more available at shallow depths throughout the growing season and deep water is less depleted later in the growing season (Nippert and Knapp 2007). Although measuring soil moisture in the uplands would have likely shed more light on how soil moisture more specifically affects flowering, the close correspondence between upland and lowland flowering among years as well as the relationships between lowland soil moisture and upland flowering suggests that late season lowland soil moisture serves as a good indicator of season-long water availability for upland plants, too.

The relationships between precipitation and flowering largely corresponded to the relationships between soil moisture and flowering. One difference was the nonlinear relationship with soil moisture that was not observed with precipitation. Flowering might be responding linearly to cumulative soil moisture availability, but soil moisture at depths of $\sim 1 \text{ m}$ can vary greatly in years with little rain, thereby creating a nonlinear relationship between soil moisture and flowering. Alternatively, the presence of an inflection point in the relationship between soil moisture and flowering might indicate that there is a threshold resource accumulation that is required for flowering. With uncertainties in interpreting the presence of an inflection point in the relationships between soil moisture and flowering, it is difficult to interpret differences in the value of the inflection point among species or sites. For example, *Schizachyrium* having an inflection point at a lower soil moisture than *Sorghastrum* (Fig. 3) might indicate a better ability to flower in dry years.

Although there was no relationship between climate in the previous year and current year's flowering over the 25 years we examined, intense droughts in the preceding year have the potential to increase current year's flowering. In another study at Konza (Knapp and Hulbert 1986), flowering was measured in the same watershed as studied here from 1981–1984, which preceded climate being measured on Konza. In 1981, lowland culm biomass was 282 g/m^2 (119 g/m^2 , 53 g/m^2 , and 110 g/m^2 for *Andropogon*, *Sorghastrum*, and *Schizachyrium*, respectively), which was 2.7 times greater than the most culm biomass recorded from 1984 to 2008. Flowering in upland soils in 1981 was even greater; 636 g/m^2 (237 g/m^2 , 119 g/m^2 , and 281 g/m^2 for *Andropogon*, *Sorghastrum*, and *Schizachyrium*, respectively), 5.8 times greater than any year from 1984 to 2008. Growing season precipitation from 1981 as measured at a weather

station 20 km from Konza (558 mm from 1 May 1 to 1 August) was similar to the mean over the same period from 1984 to 2008 measured at Konza. In contrast, precipitation in 1980 from 1 May to 1 August was just 222 mm. From 1984 to 2008, 1991 had the driest growing season precipitation, with 284 mm. As such, drying of the soils likely enhances mineralization and flowering in the following year, but the soil drying appears to have to be so severe that it rarely occurs at Konza.

Although upland sites have shallower soils and less soil resources available to plants, flowering was on average just as great in the uplands as lowlands. The lower soil resources in the uplands than lowlands should constrain flowering. Yet only a small fraction of tillers flower in a given year. Under those conditions, if tiller density was greater in the lowlands, the greater number of tillers would lead to similar resources available per tiller in the uplands and lowlands, which might equalize culm production on a per tiller basis. Although there are no data on plant size or densities along topographic gradients at Konza, patterns of tissue N concentrations suggest similar amounts of resources available at the plant level between uplands and lowlands. Schimel et al. (1991) showed similar foliar N concentrations for grasses on uplands as on lowlands in an annually burned watershed at Konza, while root N concentrations were even greater in the uplands.

The differences among species in their response to precipitation at different times of year largely reflects interspecific phenological differences, even though all three species are C₄ NADP-ME. *Schizachyrium* does not begin culm production until mid-August at Konza (J. B. Nippert, unpublished manuscript), which corresponds to the species response to precipitation in August. In contrast, *Sorghastrum* generally begins culm production after *Andropogon* (J. B. Nippert, unpublished manuscript), yet was more responsive to precipitation earlier in the growing season. This small paradox highlights our general ignorance of the phenology of resource uptake and development for these species. Swemmer et al. (2006) stated that reduction in flowering might contribute to the greater drought tolerance of *Andropogon* compared to *Sorghastrum*. Yet here, flowering in the two species seemed to be similarly sensitive to soil moisture and precipitation with neither species flowering much when soils are very dry, although the lower soil moisture inflection point in the lowlands could suggest that *Andropogon* flowering is more sensitive to dry soils or other environmental factors that are correlated with low soil moisture, such as high air temperatures (Fig. 3).

Flowering has the potential to be a large component of ANPP (Knapp and Hulbert 1986), yet culm production accounted for <10% of ANPP on average, and never exceeded 22%. As such, most of the variation observed among years in ANPP can be ascribed to leaf, not culm, production for the grasses at Konza. That said, in 1981, culm production was 73% of ANPP in the

lowlands (Knapp and Hulbert 1986), leaving the possibility of culm production dominating ANPP responses in an exceptional year. The correlations between culm production and ANPP suggested that *Sorghastrum* leaf production might be responsible for a large proportion of ANPP responses among years.

The controls over flowering observed here have ramifications for everything from population dynamics to ecosystem services to human health. From a global change perspective, the differences among species in responses to soil moisture at different times of year provide more evidence that changes in the timing of precipitation can be just as important as changes in the amount of precipitation (Craine et al. 2009). Here, shifts in precipitation within the growing season could alter dominance and relative abundance within the grassland community, depending on how climate also affects vegetative reproduction. For example, shifts in precipitation from July to August would likely favor *Schizachyrium* over the other two species, while shifts in precipitation from May to April would favor *Sorghastrum* over *Andropogon*. The grasses observed here have received considerable attention as potential biofuels, and analyses of components of ANPP are an important part of evaluating biofuel potential (Cassida et al. 2005, Samson et al. 2005, Schmer et al. 2008). There is little evidence that culm production in most years would be a significant component of biofuel production for these species. Instead, the majority of ANPP is derived from leaves, and it should be their production and turnover that should warrant the greatest attention in evaluating their biofuel dynamics. Lastly, the flowering of grasses also generates large amounts of pollen, which can cause allergic reactions in people. In Europe, grass pollen production has been linked to antecedent climate (Subiza et al. 1992, Stach et al. 2008), but no comparable research has been undertaken in the United States. If links between pollen abundance and climate can be quantified in North America, the linkages between climate and grass flowering could be a robust mechanism in better predicting human allergies to grass pollen.

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APPENDIX A

SMA relationships between number of culms and biomass of culms with data both untransformed and log-transformed (*Ecological Archives* E091-148-A1).

APPENDIX B

Relationships between soil moisture and culm production for each of three species and two landscape positions (*Ecological Archives* E091-148-A2).