

Precipitation and environmental constraints on three aspects of flowering in three dominant tallgrass species

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Summary

1. Flower production can comprise up to 70% of above-ground primary production in grasslands. Yet we know relatively little about how the environment and timing of rainfall determine flower productivity. Evidence suggests that deficits or additions of rainfall during phenologically relevant periods (i.e. growth, storage, initiation of flowering and reproduction) can determine flower production in grasslands.

2. We used long-term data from the Konza Prairie LTER to test how fire, soil topography and precipitation amounts during four phenologically relevant periods of the growing season constrain three aspects of flowering in three dominant C4 grass species. Specifically, we examined the probability of flowering, flowering stalk density and individual flowering stalk biomass for *Andropogon gerardii*, *Schizachyrium scoparium* and *Sorghastrum nutans*.

3. We found that each of the three species responded to the amount of precipitation during phenologically relevant periods in unique ways. All aspects of *A. gerardii* flowering were sensitive to precipitation during the flowering stalk elongation period (20 June – 3 August). The probability of *S. nutans* flowering was partly determined by precipitation during the rapid growth phase (21 April – 4 June), whereas flowering stalk density of this species depended on rainfall during flowering stalk elongation (20 June – 3 August). In contrast, all aspects of flowering of *S. scoparium* were relatively independent of rainfall during any period.

4. Our results demonstrate that three functionally similar, co-dominant C4 grass species respond differently to phenologically relevant precipitation periods. As a result, drought during any phenological window during the growing season can adversely impact biomass and flowering production of grasslands via species-specific reductions in flowering stalk density and biomass.

Key-words: Bayesian hierarchical model, critical climate periods, drought, flowering, hurdle model, masting

Introduction

First European explorers of tallgrass prairies in the central US were struck by their height, with ‘... its tall grass, with seed stalks from six to ten feet high, like tall slender reeds waving in the gentle breeze’ (George Flower, 1817, *in* Price 2014). Historical first-hand accounts accurately, albeit unknowingly, linked the productivity of tallgrass prairies to the growth of tall flowering stalks, which can comprise >70% of above-ground net primary production (ANPP) in certain years and locations (Knapp & Hulbert 1986). As a result, interannual variability in ANPP partly reflects variability in flower production by the dominant

grass species (Craine, Towne & Nippert 2010; La Pierre *et al.* 2011). Flower production of these grasses is neither normally nor uniformly distributed across years. Instead, numerous low production years are punctuated by occasional years of high flowering stalk biomass, yielding strong positive-skew in reproductive effort (Craine, Towne & Nippert 2010; La Pierre *et al.* 2011). High flowering years were historically attributed to fire (Curtis & Partch 1950; Kucera & Ehrenreich 1962), with most extraordinary flowering events observed following fire in infrequently burned sites (Knapp & Hulbert 1986) as a result of pulsed availability of multiple resources (e.g. light, nitrogen; Knapp & Seastedt 1986). However, not all dominant tallgrasses display the same level of flowering with fire (La Pierre *et al.* 2011). For example the dominant C4

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grass *Andropogon gerardii* exhibits high flowering after infrequent fire, whereas two other dominant and functionally similar C4 grasses, *Sorghastrum nutans* and *Schizachyrium scoparium*, display different patterns. Instead, *S. nutans* and *S. scoparium* flower more frequently with annual burning but often in different years (Knapp & Hulbert 1986; La Pierre *et al.* 2011). Thus, fire alone does not explain variation in flowering among tallgrasses or across years and high flowering years likely derive from a combination of other climatic or topographic variables (Knapp & Seastedt 1986).

Timing of precipitation appears to partially mediate flower production in tallgrass prairies (Craine *et al.* 2012; Dietrich & Smith 2015). For example *A. gerardii* and *S. scoparium* produce more flowering stalk biomass in years of high rainfall during mid- to late-summer (Dietrich & Smith 2015), with flowering stalk biomass often higher in lowland sites that possess greater soil moisture than upland sites (Craine, Towne & Nippert 2010; La Pierre *et al.* 2011). Soil moisture deficits during mid-summer, reflecting the flowering stalk elongation period, reduce *A. gerardii* flower stalk biomass by up to 94% (Dietrich & Smith 2015). In contrast, flowering stalk biomass of *S. nutans* appears sensitive to variation in early to late spring precipitation (Craine, Towne & Nippert 2010). Given that climate change will result in more variable precipitation regimes, as well as more frequent and severe droughts (Dai 2013; Trenberth *et al.* 2014), it is increasingly important to identify how fire, topography and climate interactively regulate flowering of dominant C4 tallgrasses.

Previous research has documented the effects of climate, fire and topography on total flowering stalk biomass in tallgrass prairies (Knapp & Hulbert 1986; Craine, Towne & Nippert 2010; La Pierre *et al.* 2011). Although these studies advanced our understanding of climatic constraints and interactions among climate, fire and topography on flowering, they suffer from two important limitations. The first limitation is the ways in which plant phenology and physiology were incorporated into analyses of climatic constraints on flowering. Craine, Towne & Nippert (2010) used critical climate periods analysis, which searches thousands of date ranges of varying length to determine which date range correlates most strongly with flower production. This method is agnostic of plant phenology and physiology and suffers from the same drawbacks as multiple *post hoc* comparisons. La Pierre *et al.* (2011) used five climate periods in their analyses: dormancy (15 September – 14 March), emergence (15 March – 14 April), vegetative growth (15 April – 14 July), flowering stalk elongation (15 July – 14 August) and reproduction (15 August – 14 September). These periods incorporate phenology/physiology of dominant grasses but were of different lengths, with the period of vegetative growth the longest. As a consequence, this approach was unable to capture finer-scale variation in climate during the critical period of rapid vegetative growth and carbon assimilation. Indeed, Dietrich &

Smith (2015) showed that precipitation deficits at finer scales during this period can be an important determinant of flowering for *A. gerardii*.

The second limitation of previous studies is that analysing total flowering stalk biomass combines two potentially independent reproductive processes: (i) the probability of flowering and (ii) reproductive effort during flowering years. Partitioning flowering into these two processes can provide several novel insights because both processes need not experience the same constraints. A plant species might produce flowers every year but vary the number of flowers depending on climatic conditions, topography or fire. Alternatively, climatic variables might determine when a species flowers, but the number of flowers might depend upon local environmental conditions, herbivory or other life-history trade-offs (Obeso 2002; Strauss *et al.* 2002). Furthermore, no study has yet determined whether climatic conditions, topography or fire similarly affect the abundance of flowering stalks and the size of individual stalks (i.e. few, large stalks vs. many, small stalks). Climate conditions and resource availability can alter trade-offs in reproductive effort (Hovenden *et al.* 2008; Liu *et al.* 2012), and it is important to identify how these factors affect reproductive effort both across all individuals (i.e. total flowering stalk biomass of all plants) and within individuals (i.e. average mass per stalk of a single plant).

Our objective was to identify how climate, topography and fire interactively affect flowering (probability of flowering, total number of flowering stalks and individual stalk weight) of three dominant C4 grass species in tallgrass prairies: *A. gerardii*, *S. nutans* and *S. scoparium*. Specifically, we analysed the effects of precipitation during four specific phenological periods [rapid growth, carbon accumulation, flowering stalk elongation and reproductively active) during the growing season (cf. Dietrich & Smith (2015)]. Precipitation deficits during these periods were previously shown to be important for determining *A. gerardii* flowering stalk numbers and biomass (Dietrich & Smith 2015). We focused on precipitation, rather than both precipitation and temperature, since precipitation is typically a more important predictor of flowering stalk biomass than temperature (La Pierre *et al.* 2011). Based on previous studies, we expected that fire (whether a site had been burned that year or not) would be the most important predictor of probability of flowering, but the effects of fire would vary between the three grasses (Knapp & Hulbert 1986; La Pierre *et al.* 2011). Conversely, we expected precipitation, particularly during periods of carbon accumulation and flowering stalk elongation, to be an important predictor of flowering stalk number and individual stalk weight and that the effects would be consistent across all three tallgrass species. We expected, however, that precipitation effects would be mediated by fire and topography, with the highest number of stalks and weight of stalks occurring in lowland, frequently burned sites.

Materials and methods

STUDY SITE

We used data from the Konza Prairie Biological Station (KPBS), a National Science Foundation Long-term Ecological Research (LTER) site encompassing 3487 ha of unplowed, native tallgrass prairie in northeastern KS (39°5'N, 96°25'W). Native C4 grasses, particularly *A. gerardii*, *S. scoparium* and *S. nutans*, comprise most of ANPP at KPBS. The station is divided into ~60 watershed units with long-term fire frequency treatments (i.e. burned every 1, 2, 4 or 20 years) applied at the watershed level. The 18 ungrazed watersheds included in our analysis were burned in the spring (early to late April), a typical time of burning for much of the region. Each watershed encompasses a range of topography from relatively flat upland sites to lowland areas (~100 m elevation change). Upland sites consist of shallow, Florence cherty clay loam soil, whereas lowlands are considerably deeper Tully silty clay loam soil (Briggs & Knapp 1995). Lowland soils are more fertile and productive than upland soils by virtue of higher soil moisture and nitrogen availability (Knapp *et al.* 1993; Blair 1997). We downloaded annual flowering data ranging from 1984 to 2014 (Konza dataset PRE022). We did not include seasonal burn treatments in our analysis, focusing only on watersheds burned in the spring. All data are publicly available on the Konza Prairie LTER website.

FLOWERING DATA

Detailed methods on flower data collection have been described previously (Craine, Towne & Nippert 2010; La Pierre *et al.* 2011). Briefly, flower production for the C4 rhizomatous grasses, *A. gerardii* and *S. nutans*, and the C4 caespitose (bunchgrass) grass, *S. scoparium*, has been monitored every year since 1984 along eight permanently located 50 m transects in each watershed ($n = 4$ transects per upland and lowland topographic position). Along each transect, six evenly spaced 0.5×0.5 m quadrats were sampled in October of each year. Each quadrat can include multiple tillers of *A. gerardii* and *S. nutans* and often only a single individual (bunch) of *S. scoparium*. Quadrats were relocated each year to prevent resampling. All flowering stems of the three target grasses within each quadrat were counted and harvested for biomass. Flowering data from 1993 were removed from the dataset due to collection errors. For our analysis, the total weight of flowering stalks was divided by the number of stalks in each quadrat to estimate the mean individual stalk mass per quadrat. We then averaged both the total number of flowering stalks and individual stalk mass over the entire transect. These two response variables comprised one multivariate observation per transect.

CLIMATE DATA

We obtained daily precipitation records at Konza for the years 1984–2014 from the ClimDB database maintained by LTER and

the US Forest Service. We identified four precipitation periods during the growing season (mid-April–early September) relevant to plant physiology and life history: rapid growth, carbon capture, flowering stalk initiation and flowering stalk elongation [Table 1, Dietrich & Smith (2015)]. During the rapid growth phase, these species increase their height by 300% until entering the carbon capture phase, wherein growth ceases but photosynthetic rates increase (Dietrich & Smith 2015). In mid-summer, flowering stalks begin to appear, followed by rapid flowering stalk growth during the late summer months (Dietrich & Smith 2015). Daily precipitation values were summed within each precipitation period to yield an aggregate estimate of rainfall for each life-history stage.

STATISTICAL ANALYSES

We implemented a Bayesian multivariate, hierarchical hurdle model to assess the effects of fire, topography (soil type) and the four phenological precipitation periods on the probability of flowering, total number of flowering stalks and individual stalk biomass for *A. gerardii*, *S. scoparium* and *S. nutans*. Here, the probability of flowering represents the probability that an individual plant flowers in a given year. Since the number and size of flowering stalks were averaged over a transect to yield per-plant averages, a value of 0 represents the scenario in which no plant in the transect produced flowers.

The observed data Y_s is an $n \times j$ matrix containing all n observations of both j response variables for the s th species. Thus, total number of flowering stalks and individual stalk biomass were nested within each of the three grass species. The likelihood of each observation i was given by:

$$L(Y_{ij,s}) = \begin{cases} 1 - \theta_{ij,s} & \text{if } Y_{ij,s} = 0 \\ \theta_{ij,s} \times \text{Gamma}(\alpha_{ij,s}, \beta_{j,s}) & \text{if } Y_{ij,s} > 0 \end{cases} \quad \text{eqn 1}$$

where $\theta_{ij,s}$ is the probability of flowering and $\alpha_{ij,s}$ and $\beta_{j,s}$ are the shape and rate parameters of the gamma distribution respectively. The shape parameter for each observation was calculated from the mean response $y_{ij,s}$ as $\alpha_{ij,s} = y_{ij,s} \beta_{j,s}$, where each response j for each species s had unique rate parameters. This conversion allowed variance to increase proportionally to the mean and for the proportionality constant (i.e. $1/\beta_{j,s}$) to differ among responses and species.

Both the probability of flowering $\theta_{ij,s}$ and the mean of each response $y_{ij,s}$ were linear functions of the predictor matrix X and parameters B or G :

$$\text{logit}(\theta_{ij,s}) = X_i G_{j,s} \quad \text{eqn 2}$$

$$\log(y_{ij,s}) = X_i B_{j,s} \quad \text{eqn 3}$$

where $G_{j,s}$ and $B_{j,s}$ contains the parameters for the j th response variable of the s th species. The design matrix X contained the four phenological precipitation periods (P1P, P2P, P3P, P4P), a dummy variable for whether the watershed had been burned that year, and a dummy variable for soil type (i.e. upland or lowland). We also included two-way interactions between burning and each

Table 1. We defined four precipitation periods relevant to plant physiology and phenology based on Dietrich & Smith (2015)

Name	Abbreviation	Date range	Plant life-history stage
Period 1 precipitation	P1P	Day 111–Day 155	Rapid growth
Period 2 precipitation	P2P	Day 141–Day 185	Carbon accumulation
Period 3 precipitation	P3P	Day 171–Day 215	Flower stalk elongation
Period 4 precipitation	P4P	Day 201–Day 245	Active reproduction

phenological precipitation period as well as soil and each phenological precipitation period. We included all three-way interactions between burning, soil type and each phenological precipitation period. Burning and soil type represent resource availability because burning increases light and nitrogen availability and soil type is a proxy for soil moisture content. The four phenological precipitation variables depict various climatic constraints on flowering.

Species were treated as fixed effects rather than random effects, omitting hyper-parameters (e.g. overall effects), because we had only three species. Such a low number of species causes inaccurate estimates of among-species variance. In addition, multivariate gamma distributions were not available in our software, so we did not model the correlation between total number of flowering stalks and individual stalk biomass; both responses were treated as independent. Since both total number of flowering stalks and individual stalk biomass must be present at the same time (i.e. there must be at least one stalk to have individual stalk biomass), estimates for probability of flowering, $G_{j,s}$, were identical for both responses. Here, we present G for total number of stalks.

Precipitation variables were standardized prior to analysis. Linear predictors $G_{j,s}$ and $B_{j,s}$ were given $N(0, 1)$ priors and rates $\beta_{j,s}$ were given $\text{Gamma}(7.1, 1)$ priors, which concentrates the prior probability between 0 and 10 (Lemoine *et al.* 2016). The model was run for 5000 burn-in iterations, followed by 5000 sampling iterations. We ran four chains simultaneously, resulting in 20 000 posterior samples for each parameter. Convergence was assessed using traceplots and density plots of posterior samples of each parameter. The model was run in STAN accessed via PySTAN in the Python programming language (Stan Development Team 2016). Consistent with Bayesian statistics, we report results in the probability that a coefficient is greater or less than zero, $Pr(>0)$ or $Pr(<0)$, where high values indicate high probabilities that the effect is significant (e.g. Lemoine & Shantz 2016). We define statistically significant coefficients as those where $Pr \geq 0.95$ and marginally significant coefficients as those where $Pr \geq 0.9$.

Results

PROBABILITY OF FLOWERING

Andropogon gerardii flowered in 88% of transects across all years, although the probability of flowering varied with fire, topography and precipitation period (Fig. S1, Supporting Information). Burning generally increased the probability of flowering for *A. gerardii* by $8.8 \pm 0.3\%$

(mean ± 1 SE, $Pr(>0) = 0.999$, Fig. S1). However, these effects varied with precipitation. Rainfall during the flowering stalk elongation period (P3P) was the strongest climatic determinant of flowering ($Pr(>0) = 1.0$, Fig. S1) and mediated the response of *A. gerardii* to burning. During years of abnormally low P3P, *A. gerardii* only flowered $32.9 \pm 13.0\%$ of the time in unburned watersheds, and burning increased the probability of flowering by $34.7 \pm 10.7\%$ (Fig. 1). In contrast, *A. gerardii* flowered every year of above-average P3P regardless of burning (Fig. 1). Precipitation during the P4P ($Pr(>0) = 0.985$) and P1P ($Pr(>0) = 0.944$) period also influenced the likelihood of *A. gerardii* flowering, but to a lesser degree than P3P (Figs S1 and S2). Topography alone had little effect on *A. gerardii* flowering; however, when combined with burning and lower precipitation during the P1P periods, the probability of flowering was reduced in lowland soils ($Pr(<0) = 0.944$).

In contrast to *A. gerardii*, both *S. scoparium* and *S. nutans* flowered consistently, producing flower stalks in 91.5 and 95.7% of transects. As a result, effects of fire and phenological precipitation periods on flowering were stronger for *A. gerardii* than either of these two species (Fig. S1). *Schizachyrium scoparium* flowered $6.4 \pm 2.6\%$ more frequently in burned years ($Pr(>0) = 0.998$), whereas fire increased the likelihood of *S. nutans* flowering by only $3.6 \pm 1.8\%$ ($Pr(>0) = 0.993$, Fig. 1). Interestingly, both species responded to different phenological precipitation periods. P4P most strongly influenced the probability of flowering for *S. scoparium* ($Pr(>0) = 0.960$), whereas *S. nutans* flowering probability was most sensitive to changes in P1P ($Pr(>0) = 0.996$, Figs 1 and S1). However, precipitation effects were weaker than those of *A. gerardii* for both *S. scoparium* and *S. nutans* (Fig. 1).

TOTAL NUMBER OF FLOWERING STALKS

Across all transects in all years, *A. gerardii* produced an average of 1.75 flowering stalks per 0.25 m². However, flower stalk numbers varied considerably, ranging from

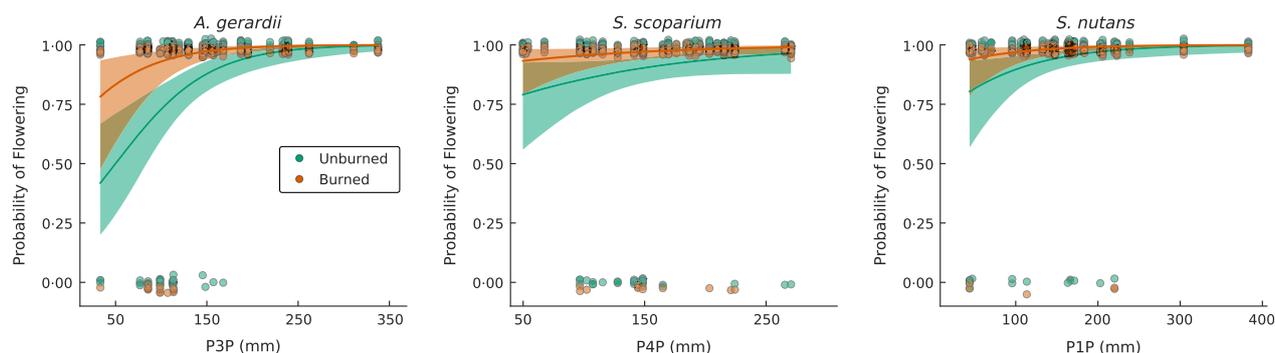


Fig. 1. Relationship between the probability of flowering, burning, the phenologically relevant periods of growing season precipitation for *Andropogon gerardii* (vs. P3P), *Schizachyrium scoparium* (vs. P4P) and *Sorghastrum nutans* (vs. P1P). For all panels, points have been jittered on the y-axis to prevent overlap. Regression lines represent the best fit line to the data and the shaded region denotes the 95% credible interval around the regression line (P1P = rapid growth period; P3P = flowering stalk elongation period; P4P = active reproduction, see Table 1).

0.04 to 19.75 flowers per m^2 . This variability was best explained by burning, topography and precipitation during P3P (Fig. S3). In years of average P3P, fire increased flowering stalks of *A. gerardii* by $86.8 \pm 22.3\%$ ($Pr(>0) = 1.0$); and plants in lowland sites produced $23.9 \pm 16.6\%$ more flowering stalks per m^2 than those in upland sites ($Pr(>0) = 0.938$, Fig. 2). P3P exerted much stronger control of *A. gerardii* flowering than topography; flower densities increased by $74.0 \pm 16.0\%$ in wet compared to dry years (Fig. 2).

Schizachyrium scoparium produced more flowering stalks than did *A. gerardii*, but flowering stalk numbers were similarly variable. Stalk densities averaged 3.28 stalks per m^2 but ranged from 0.04 to 28.71 flowering stalks per m^2 . Unlike *A. gerardii*, burning and topography interactively determined densities of *S. scoparium* flowering stalks. In lowlands, burning increased flowering stalk densities by $41.5 \pm 17.2\%$. The relative effect of burning was stronger

in uplands, where exposure to fire increased flowering stalk densities by $97.1 \pm 21.8\%$.

Flowering stalk densities of *S. nutans* were similar to those of *A. gerardii*, averaging 2.08 flowering stalks per m^2 and ranging from 0.04 to 18.17 stalks per m^2 . Likewise, *S. nutans* flowering stalk densities were only affected by burning, topography and precipitation during P3P, although unlike *A. gerardii* there was a significant interaction between burning and topography ($Pr(>0) = 0.999$, Figs 2 and S3). The benefit of burning was strongest in lowland sites, where fire increased flowering stalk densities by $140.1 \pm 24.7\%$. In upland sites, the benefit of burning was less than half as strong, as fire increased flowering stalk densities by $58.1 \pm 15.9\%$ (Fig. 2). Precipitation amount also affected flower production of *S. nutans*; during high P3P years, *S. nutans* produced $60.1 \pm 18.2\%$ more flowers than in years of low P3P ($Pr(>0) = 0.990$, Fig. 2).

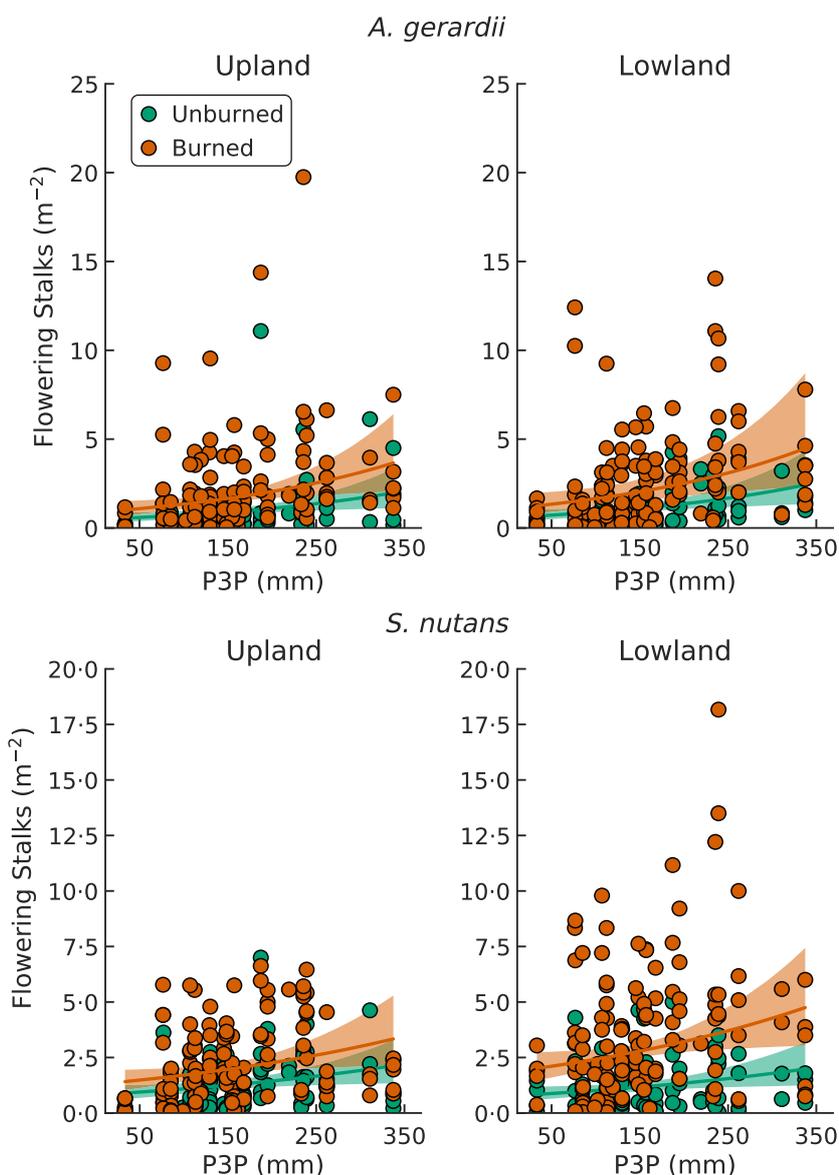


Fig. 2. Relationship between flowering stalk density, topography, fire and precipitation during the flowering stalk elongation period (P3P; see Table 1) for *Andropogon gerardii* and *Sorghastrum nutans*. Regression lines represent the best fit line to the data and the shaded region denotes the 95% credible interval around the regression line.

INDIVIDUAL STALK BIOMASS

Individual stalk mass of *A. gerardii* depended on a combination of burning, topography and precipitation during P3P and, to a lesser extent, P2P (Fig. S4). Burning reduced individual stalk biomass, as flowering stalks in burned areas weighed $13.2 \pm 4.9\%$ less than in unburned areas ($Pr(<0) = 0.993$, Fig. 3). Alternatively, plants in lowland areas produced flowering stalks $51.7 \pm 8.6\%$ larger than plants in upland areas ($Pr(>0) = 1.0$, Fig. 3). P3P had the strongest influence of stalk mass of any precipitation periods; during high P3P stalks weighed $51.8 \pm 12.7\%$ more than in years of abnormally low P3P ($Pr(>0) = 0.998$, Fig. 3). Although stalk mass of *A. gerardii* was also positively correlated with P2P, the effect was much weaker than that of P3P, with an increase of only $34.1 \pm 14.9\%$ in wet years compared to dry years ($Pr(>0) = 0.974$).

Similar to *A. gerardii*, individual stalk mass of *S. scoparium* varied depending on the combination of burning, topography and P3P precipitation, as evidenced by the significant three-way interaction between these variables (Pr

$(<0) = 0.032$). However, the effects of all three variables on individual stalk mass were relatively weak, suggesting that *S. scoparium* stalk mass is largely independent of resource or climatic constraints (Fig. 3). For example P3P in upland sites had little effect on individual stalk mass of *S. scoparium* (Fig. 3). Likewise, *S. scoparium* individual stalk mass was independent of P3P in lowland, unburned areas. Only lowland burned areas demonstrated a weak, positive relationship between P3P and *S. scoparium* individual stalk mass (Fig. 3).

Individual stalk mass of *S. nutans* also responded to burning, topography and precipitation amount during the P2P and P3P periods (Fig. S4). Burning decreased individual stalk biomass by only $7.4 \pm 3.7\%$ ($Pr(<0) = 0.973$), whereas plants grown in lowland sites produced stalks that were $24.2 \pm 5.1\%$ heavier ($Pr(>0) = 1.0$, Fig. 3). P4P had a strong and surprisingly negative effect on stalk mass; stalks were $49.2 \pm 25.1\%$ heavier in years of low P4P than in years of high P4P ($Pr(<0) = 0.988$, Fig. 3). Comparatively, individual stalks were only $25 \pm 12.4\%$ heavier during years of high P2P and P3P.

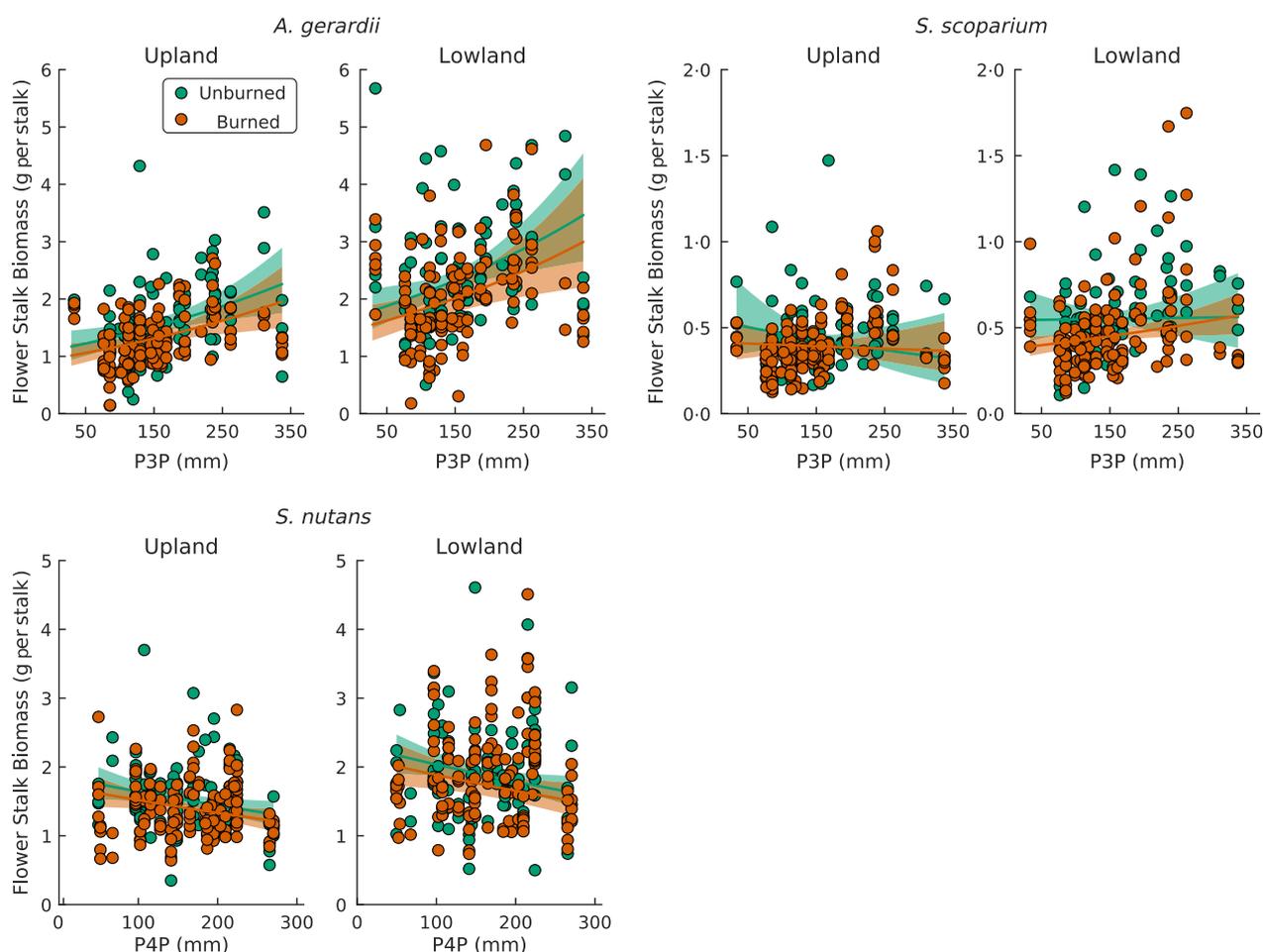


Fig. 3. Relationship between individual stalk biomass, topography, fire and the phenologically relevant periods of growing season precipitation (P3P = flowering stalk elongation period; P4P = active reproduction period; see Table 1) for *Andropogon gerardii*, *Schizachyrium scoparium* and *Sorghastrum nutans*. Regression lines represent the best fit line to the data and the shaded region denotes the 95% credible interval around the regression line.

Discussion

Flowering stalk production by dominant tallgrass species can comprise up to 70% of ANPP during years of extraordinary flowering (Knapp & Hulbert 1986; La Pierre *et al.* 2011). Production of flowering stalks depends on fire, topography and precipitation during critical climate periods (Knapp & Seastedt 1986; Craine, Towne & Nippert 2010; Pérez-Ramos *et al.* 2010; La Pierre *et al.* 2011). These critical precipitation windows differ among species, but previous estimates encompassed most of the growing season, pertained to multiple periods of grass phenology, or only reflected total flowering stalk biomass (Craine, Towne & Nippert 2010; La Pierre *et al.* 2011). Here, we analysed how phenologically relevant precipitation, fire and topography affect three potentially independent aspects of flowering at the site level (based on average values of stalk density or individual stalk biomass for transects located within different watersheds and topographic positions): (i) the probability of flowering, (ii) flowering stalk density and (iii) individual stalk biomass for three dominant tallgrass species. These three aspects of flowering need not respond to the same environmental drivers (e.g. Boulangeat, Gravel & Thuiller 2012; Lemoine *et al.* 2015). Indeed, our results suggest that climatic drivers differ in their impacts both among species and among aspects of flowering within species. Thus, the processes governing flower production are complex and climate change will alter flowering patterns in unique ways among species.

Of the three species considered here, *A. gerardii* exhibited the most annual variation in flower production but was also by contrast the most consistent in terms of climatic and environmental constraints on flowering. All aspects of flowering were sensitive to precipitation occurring during flowering stalk elongation (June 20 – August 3), matching previous observations and experiments (La Pierre *et al.* 2011; Dietrich & Smith 2015). This time period has the highest water deficit during the growing season at KPBS (Knapp *et al.* 1993), such that increased precipitation during this time period has a greater positive effect on soil moisture availability than precipitation during any other phenological period during the growing season. Furthermore, densities and biomass of flowering *A. gerardii* flowering stalks were highest in lowland sites, which have greater soil moisture content compared to their upland counterparts (Briggs & Knapp 1995). Taken together, these results suggest that *A. gerardii* experiences strong water limitation, consistent with earlier work showing that *A. gerardii* is the least drought tolerant of the three species examined here (Weaver & Fitzpatrick 1932; Heckathorn & Delucia 1994). In contrast, *S. scoparium* is considered the most xeric-adapted and drought tolerant of the three species (Weaver & Fitzpatrick 1932; Heckathorn & DeLucia 1996). Appropriately, *S. scoparium* flowering stalk production was relatively insensitive to changes in precipitation during the four phenological windows. Instead, flowering of this species may depend on longer term (inter-annual) variation in

growing season precipitation (Craine, Towne & Nippert 2010). *Sorghastrum nutans*, on the other hand, is similar to *A. gerardii* in terms of water requirements (Weaver & Fitzpatrick 1932; Heckathorn & Delucia 1994) and was somewhat sensitive to within-season precipitation variability. Severe water deficits during the rapid growth phase (April 21–June 4) decreased the probability of *S. nutans* flowering, but neither the number of flowering stalks nor individual stalk mass were strongly correlated with precipitation during other phenological windows.

Of the environmental drivers considered here, only fire exhibited consistent effects on flowering across all species, increasing both the probability of flowering and the number of flowering stalks but decreasing individual stalk mass. Higher likelihoods of flowering and stalk numbers following burning can be partially attributed to the combined increased in inorganic soil nitrogen concentrations and light availability largely attributed to increased light availability following the removal of litter (Curtis & Partch 1950; Knapp & Seastedt 1986). Litter removal increases light availability, which stimulates flowering and increases culm densities of *A. gerardii* (Curtis & Partch 1950; Knapp & Seastedt 1986; Hulbert 1988), *S. nutans* (Hulbert 1988) and *S. scoparium* (Roos & Quinn 1977). In addition, fire often increases soil N availability (Knapp & Seastedt 1986). Increased nutrient concentrations can also stimulate flower production because seed production is a costly investment that requires plentiful nutrients (Loehle 1987; Grainger & Turkington 2013). However, N-enrichment following burning exerts a significantly weaker impact on flower production than does alleviation of light limitation (Curtis & Partch 1950; Hulbert 1988). Greater light and nitrogen availability following fire might enable plants to surpass the critical size threshold required for flowering stalk production (Sharman 1947; Ott & Hartnett 2011), thereby increasing flowering stalk densities of all species.

Despite increasing flower stalk densities, burning reduced individual stalk biomass in both *A. gerardii* and *S. nutans*, indicative of a trade-off between number of flowering stalks and individual stalk mass. Negative correlations between total abundance and mass of flowers are common both among and within species, a result of adaptive evolution on reproduction arising from a limited resource pool available for sexual reproduction (Sato & Yahara 1999; Sargent *et al.* 2007). However, trade-offs between flower number and size were not apparent for *S. scoparium*, and the lack of negative correlations could occur for a number of reasons. First, *S. scoparium* may trade-off the number of seeds versus the size of individual seeds within an inflorescence, as is common for grassland species (Jakobsson & Ericksson 2000). Second, *S. scoparium* may be trading off resource investment in flower size and flower number, but the conversion of resource (i.e. energy/carbon) into the actual trait (i.e. flowers) can obscure this trade-off (de Jong 1993). Regardless, annual burning consistently yields more flowering stalks across all species, indicative of the dominant role that fire plays in grassland ecosystems.

The effects of fire and precipitation on flowering, however, were mediated by grassland topography. In many cases, lowland individuals responded more strongly to burning and inter-annual variation in growing season precipitation than their upland counterparts (La Pierre *et al.* 2011). This pattern probably emerges because lowland sites support higher plant biomass and, as a result, burning provides a greater release from light limitation in lowlands (Turner & Knapp 1996). Since lowland sites also possess greater soil moisture and nitrogen content (Briggs & Knapp 1995; Blair 1997), plants are able to more effectively capitalize on reduced light limitation in these environments.

Overall, differential responses to fire and phenological precipitation ultimately stem from the contrasting life-history strategies of these species. Both *A. gerardii* and *S. nutans* are rhizomatous grasses that reproduce vegetatively via tillering from horizontally spreading rhizomes (McKendrick, Owensby & Hyde 1975), whereas *S. scoparium* is a longer lived bunchgrass (McMillan 1956). Rhizomatous species might be more responsive to fire due to their lower carbohydrate reserves and shorter life spans, however, *S. nutans* and *A. gerardii* exhibited weak and strong sensitivity to burning respectively. Differences between these two species arise because, although rhizomatous, *S. nutans* has biennial rhizomes with indeterminate growth, whereas *A. gerardii* has annual, determinate rhizomes (McKendrick, Owensby & Hyde 1975). Determinate rhizomes in grasses tend to require high light to form new shoots, potentially explaining why *A. gerardii* is more responsive to fire than either *S. nutans* or *S. scoparium*. Moreover, these life-history differences also help explain the differential responses to phenologically relevant precipitation periods. The third precipitation period had the greatest effect on flowering in *A. gerardii* and *S. scoparium*, due to the potential effect that increased precipitation had on the ability of tillers to reach the critical size threshold for flowering (Sharman 1947). In contrast, flowering of *S. nutans* responded most to the first precipitation period. Increased precipitation during this period would favour growth of overwintering tillers, allowing them to meet a critical size threshold for flowering, whereas increased precipitation later in the growing season (period 4) would favour growth of new tillers ensuring their survival in the following growing season.

In summary, water stress can have severe consequences on individual performance and biomass production in grasslands (Knapp 1984; Briggs & Knapp 1995; Knapp *et al.* 2002). Since global change is expected to increase both the intensity and severity of drought (Dai 2013; Trenberth *et al.* 2014), it is imperative to understand how precipitation variability will affect grassland ecosystem function. Yet we know relatively little about the effects of rainfall deficits on flowering production and sexual reproduction. Here, we demonstrate that flowering of three dominant tallgrass species exhibits considerable interspecific variability in sensitivity to rainfall variation during phenologically relevant periods during the growing season.

Although all three grasses exhibit very low natural seedling recruitment rates (Benson & Hartnett 2006), such low recruitment rates are sufficient to maintain genetic diversity within clonal plant populations (Watkinson & Powell 1993). Reduced prevalence of sexual reproduction and seedling recruitment during drought periods might negatively affect genetic diversity, which in turn weakens ecosystem resilience (Avolio & Smith 2013). Our results therefore suggest that precipitation deficits during critical growth periods may impact ecosystem function beyond reduced biomass, including the potential for genetically homogenizing populations of dominant grass species.

Authors' contributions

M.D.S. formulated the hypothesis, J.D.D. obtained and cleaned the data with help from N.P.L., N.P.L. analysed the data and wrote the manuscript with help from J.D.D. and M.D.S.

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Data accessibility

Data from the Konza Prairie Biological Station were collected as part of the Konza Prairie LTER program (NSF grants DEB-8012166 and BSR-8514327, BSR-9011662), Division of Biology, Kansas State University, Manhattan, KS. Data and supporting documentation are stored (Dataset Code = PVC02) in the Konza Prairie Biological Station LTER Data Bank (<http://lter.konza.ksu.edu/content/pvc02-plant-species-composition-selected-watersheds-konza-prairie>). Climate data are from the ClimDB database maintained by LTER and the US Forest Service (<https://climhy.lternet.edu>). A snapshot of the data as used in this paper is in the Dryad Digital Repository <https://doi.org/10.5061/dryad.69gt3> (Lemoine, Dietrich & Smith 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Coefficient estimates for the probability of flowering for each of the three species. Black dots indicate ‘statistically significant’ coefficients where $Pr(>0)$ or $Pr(<0)$ is ≥ 0.95 . Grey dots indicate ‘marginally significant’ coefficients where $Pr(>0)$ or $Pr(<0)$ = 0.90.

Fig. S2. Probability of flowering for *Andropogon gerardii* in unburned and burned transects in both upland and lowland soils.

Fig. S3. Coefficient estimates for the number of flowering stalks produced by each of the three species. Black dots indicate ‘statistically significant’ coefficients where $Pr(>0)$ or $Pr(<0)$ is ≥ 0.95 . Grey dots indicate ‘marginally significant’ coefficients where $Pr(>0)$ or $Pr(<0)$ = 0.90.

Fig. S4. Coefficient estimates for individual stalk biomass produced by each of the three species. Black dots indicate ‘statistically significant’ coefficients where $Pr(>0)$ or $Pr(<0)$ is ≥ 0.95 . Grey dots indicate ‘marginally significant’ coefficients where $Pr(>0)$ or $Pr(<0)$ = 0.90.