

Explaining temporal variation in above-ground productivity in a mesic grassland: the role of climate and flowering

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Summary

1. Annual above-ground net primary productivity (ANPP) in mesic grasslands is known to be highly temporally variable. While yearly precipitation or average yearly temperature can explain some of this temporal variability, much of the variation in ANPP remains unexplained.

2. Here we address the heretofore unexplained variation in 25 years of productivity data from a mesic grassland at Konza Prairie (north-eastern Kansas) by examining the effects of precipitation and temperature during periods relevant to the phenology and growth cycle of the dominant C₄ grasses and the flowering stalk production of these species. We assessed both the direct effects and indirect effects via flowering of phenologically relevant climate periods on ANPP using structural equation modelling (SEM).

3. We found ANPP to be strongly positively influenced by flowering stalk production of the dominant C₄ grasses, precipitation during periods relevant to vegetative growth (15 April–14 July) and flowering stalk elongation (15 July–14 August) of the dominant grasses, and fire. In addition, flowering stalk production was negatively influenced by high temperatures during the flowering stalk elongation period, which therefore resulted in a negative indirect effect on ANPP. We found little evidence for the effects of the previous year's total annual precipitation or mean annual temperature on ANPP.

4. By including flowering stalk production and separating climate variables into phenologically relevant periods we were able to increase the percentage of observed variance in ANPP explained by six models, relating to different topographic positions and burn regimes, from an average of 22% to 48%, with the best model explaining 61% of variation in ANPP.

5. *Synthesis.* The link between climatic periods relevant to the phenology and growth of dominant C₄ grasses, flowering stalk production of these grasses and ANPP shown here improves our ability to predict productivity in mesic grasslands, an ecologically and economically important ecosystem.

Key-words: climate variability, dominant species, inflorescence, intra-annual variation, plant–climate interactions, precipitation, structural equation modelling, tallgrass prairie, temperature

Introduction

Above-ground net primary productivity (ANPP) in mesic grasslands is known to be highly temporally variable, as compared to other systems (Risser *et al.* 1981; Knapp *et al.* 1998; Knapp & Smith 2001). This temporal variability is thought to be driven primarily by climate (Briggs & Knapp 1995; Knapp *et al.* 1998; Knapp & Smith 2001; Fig. 1). Much of the previous work considering the effects of climate on ANPP has

focused on yearly or growing season precipitation and average yearly temperatures (Old 1969; Sala *et al.* 1988; Lauenroth & Sala 1992; Epstein, Lauenroth & Burke 1997; Knapp & Smith 2001; Hu *et al.* 2007). However, variation in precipitation or temperature during periods pertinent to the life history of species in the system may be more relevant drivers of temporal variation in ANPP. Moreover, because flowering in mesic grasslands can be highly temporally variable (Craine, Towne & Nippert 2010) and makes up a large proportion of productivity in any one year (Knapp & Hulbert 1986), species-specific flowering responses to temperature and rainfall may be an

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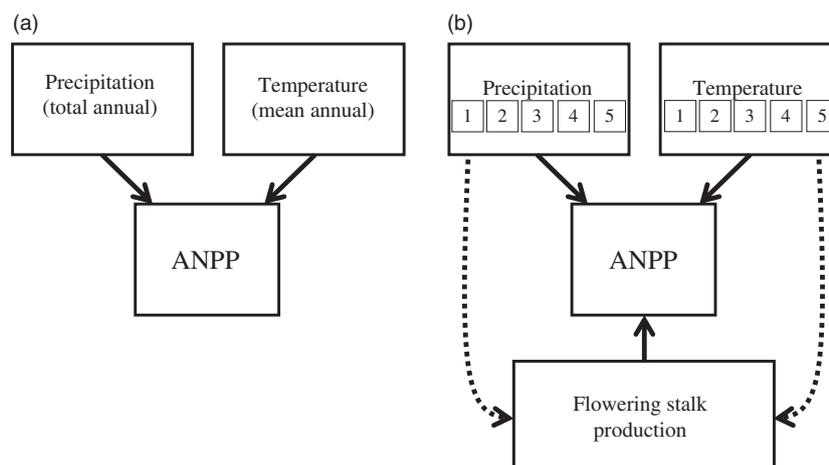


Fig. 1. (a) Annual precipitation and temperature are generally thought to be primary drivers of temporal variability in above-ground net primary production (ANPP) for ungrazed, mesic grasslands. (b) However, precipitation and temperature separated into periods relevant to the phenology and growth of the dominant grasses species in the system (1–5, see text for details) as well as flowering stalk production of the dominant grasses may have greater power to explain temporal variability in ANPP than yearly climate alone. Importantly, the effect of the climate periods could be indirect (dashed lines) via their effect on flowering stalk production.

important, yet unexplored, driver of interannual variation in ANPP. Thus, if we are to increase our understanding of how climate drives temporal variation in ANPP in mesic grasslands, it is clear that the incorporation of climate variables relevant to the growth and phenology of species in the system, as well as their flowering, is needed. Such understanding is critical for predicting how mesic grasslands may respond to forecasted climate change in the future.

The biomass of the dominant species largely drives ANPP in grasslands (Whittaker 1965; Smith & Knapp 2003), often with only a few dominant grasses contributing disproportionately to productivity (Whittaker 1965; Grime 1998; Smith & Knapp 2003). For example, in tallgrass prairie the dominant C_4 grass *Andropogon gerardii* can comprise more than 80% of above-ground biomass (Smith & Knapp 2003) and in shortgrass steppe the dominant C_4 grass *Bouteloua gracilis* can comprise more than 90% of above-ground biomass (Coffin & Lauenroth 1988). Therefore, separating annual precipitation and temperature variables into phenologically relevant periods may result in an improved ability to explain interannual variation in ANPP.

Interannual variation in ANPP in mesic grasslands may also be influenced by variation in flowering stalk production of the dominant grass species. Flowering stalks can comprise much of the above-ground biomass of individual grass tillers in any one year (Weaver & Fitzpatrick 1932; Weaver 1958; Knapp & Hulbert 1986) and the number of flowering stalks can vary substantially from year to year (Craine, Towne & Nippert 2010). Therefore variation in flowering stalk production can help to explain a portion of the heretofore unexplained variation in ANPP. If both flowering and ANPP are resource dependent, then a year with high resource levels would result in both high flowering stalk production and high ANPP (Kelly & Sork 2002). Therefore, it is important to understand what factors are driving the variation in flowering stalk production

in these systems and whether these factors correspond to those driving variation in ANPP.

It is currently unknown what factors determine whether a grass individual will flower during a given year. Reproductive effort is known to be controlled by nutrient resources (Curtis & Partch 1950; Snook, Camara-Cabrales & Kelty 2005; Hay, Kelly & Holdaway 2008; Way *et al.* 2010) and climatic factors (Montserrat-Marti *et al.* 2009; Souza *et al.* 2010) in some plant species. In addition, it has been suggested that carbon acquisition by an individual grass tiller may be the primary driver of flowering, where a threshold of carbon gained by the plant must be met to trigger flowering (Gifford & Evans 1981; Colvill & Marshall 1984; Bouwmeester, Smid & Loman 1995). As flowering is resource intensive, a perennial grass individual often does not flower annually, with only approximately a third of individuals flowering in any one year (Weaver 1954). Because flowering responses are binary (i.e. the individual will flower or not based on resources available), flowering stalk production is likely to be influenced by precipitation and temperature during specific periods of the growing season relevant to a species' timing of emergence and ability to gain sufficient carbon to trigger flowering stalk production. Moreover, the periods which are relevant in determining flowering stalk production may not correspond with periods of the growing season most relevant to vegetative growth or total ANPP.

Flowering stalk production and ANPP may also be influenced by the previous year's precipitation or temperature (lag effects). If the previous year had conditions conducive to high flowering rates, then many of the individuals who flowered the previous year may not have the resources necessary to flower in the current year regardless of environmental conditions. Evidence for lagged effects of precipitation on ANPP has been found in other systems (Cable 1975; Oesterheld *et al.* 2001; Wiegand *et al.* 2004; Posse, Oesterheld & Di Bella 2005). Additionally, Knapp & Hulbert (1986) showed that flowering

increased by several orders of magnitude in annually burned tallgrass prairie in a year with average growing season precipitation following a year with an extreme drought. However, recent work by Craine, Towne & Nippert (2010) in the same annually burned tallgrass prairie system showed that lag effects do not appear to play a role in determining flowering stalk production over a long time scale.

Here, we address the relative effects of climate periods relevant to the phenology and growth cycle of the dominant grasses and flowering stalk production on interannual variation in ANPP in order to determine whether a greater portion of the temporal variation in ANPP can be explained for an economically important mesic grassland, the tallgrass prairie (Fig. 1). Further, we aim to determine what climatic factors significantly influence flowering stalk production of the dominant grass species in tallgrass prairie and how these relationships may indirectly influence variation in ANPP. We hypothesize that precipitation and temperature at specific periods relevant to the phenology and growth of the dominant C_4 grasses will play an important role in determining ANPP. Specifically, we predict that increased precipitation during the middle of the growing season when leaf tissue is rapidly growing (15 April–14 July) will have a direct positive influence on ANPP by allowing increased vegetative growth. We also predict that increased precipitation and temperature at the beginning of the growing season, when plants are emerging (15 March–14 April), will have a positive effect on flowering stalk production of the dominant grasses, likely due to its positive effect on growing season length, thereby permitting greater seasonal carbon gain. We do not expect to see a significant effect of previous year's climate variables on flowering stalk production. Additionally, we predict that flowering stalk production will be a significant predictor of ANPP. Climatic factors influencing flowering stalk production in dominant grasses may differ from those driving variation in ANPP, therefore we expect different climatic factors have the potential to influence ANPP, either directly or indirectly, through flowering. To address these predictions, we used a combination of multiple regression analysis and structural equation modelling (SEM) to analyse 25 years of ANPP and flowering data from a tallgrass prairie in north-eastern Kansas subjected to a range of fire frequencies (every 1, 4 and 20 years) and located in two topographic positions (upland and lowland) known to significantly affect both ANPP and flowering stalk production in tallgrass prairies (Hulbert and Wilson 1983; Knapp & Hulbert 1986; Briggs & Knapp 1995; Knapp *et al.* 1998).

Materials and methods

SITE DESCRIPTION

This study was conducted at the Konza Prairie Biological Station, located in the Flint Hills region of north-eastern Kansas. Konza Prairie is a 3487-ha tract of native tallgrass prairie (39°5' N, 96°35' W). The area is dominated by warm-season C_4 grasses, particularly *A. gerardii* (Vitman), *Sorghastrum nutans* (L.) Nash and *Schizachyri-*

um scoparium (Michx.) Nash. We utilized data collected from three watersheds (c. 60 ha each) burned in the spring at either 1- (1D), 4- (4B), or 20-year (20B) intervals (since 1973 for the 4- and 20-year burns and 1978 for the annual burn). These watersheds were selected because they have the most long-term and complete records for both above-ground productivity and flowering stalk production at the site. Within each watershed, we focused on two topographic positions: (i) upland, characterized by shallow, Florence cherty silt loam soils (Typic Natrustolls) and (ii) lowland, characterized by deep, Tully silty clay loam soils (Pachic Argiustolls).

ANPP AND FLOWERING STALK PRODUCTION DATA

Above-ground biomass was collected from twenty 0.1-m² quadrats located within each topographic position and watershed from 1984 to 2008 (LTER data set PAB011). Quadrats were placed every 10 m in a different location each year (to avoid reharvesting the same quadrat) along four permanent transects (50 m in length) with five quadrats per transect. Above-ground biomass was harvested by clipping all biomass at ground level within each 0.1-m² quadrat. Harvests occurred at peak biomass each year (August–September). Collected biomass was dried at 60 °C for 48 h, sorted by grass, forb and woody biomass as well as previous year's dead biomass, and weighed. One quadrat with woody biomass greater than two standard deviations from the mean woody biomass per plot was excluded from the analysis as that level of biomass was deemed to be unrepresentative of grass-dominated sites. Total above-ground biomass was calculated as the sum of current year's grass, forb and woody biomass per quadrat. Because decomposition and herbivory are low in these ungrazed watersheds, above-ground biomass is considered to be a close proxy to ANPP (Briggs & Knapp 1991) and hereafter will be referred to as ANPP.

Flowering stalk production was determined annually for *A. gerardii*, *S. nutans* and *S. scoparium* from 1984 to 2008 (LTER data set PRE022). Flowering stalks were collected from twenty-four 0.25-m² quadrats within each topographic position and burn treatment. Flowering stalk production was sampled simultaneously with ANPP and plots were located along the same four permanent transects used for ANPP ($n = 6$). However, flowering stalk production was sampled from plots distinct from those used to sample ANPP and therefore are independent samples. As with ANPP, quadrats were relocated each year to prevent harvesting from the same area twice. Within each quadrat, flowering stalks were harvested by clipping at ground level. Collected flowering stalks were separated by species, dried at 60 °C for 48 h, and weighed. Flowering stalk production from the 20-year burn regime in 1984 and from all three burn regimes in 1993 were excluded from the analysis due to collection errors.

CLIMATE DATA

Average temperature (°C) and total precipitation (mm) were collected daily from a micrologger located at the Konza Prairie headquarters (HQ) area from 1984 to 2008 (LTER data set AWE012). Precipitation (P) and temperature (T) data were aggregated into five climate periods following Moore *et al.* (1991) and were intended to capture specific phenology and growth periods of the dominant C_4 grasses (dates generalized from Weaver 1954 and personal observation):

- P1, T1 – 15 September – 14 March, dormant period
- P2, T2 – 15 March – 14 April, emergence
- P3, T3 – 15 April – 14 July, vegetative growth
- P4, T4 – 15 July – 14 August, flowering stalk elongation

P5, T5 – 15 August – 14 September, reproduction (including anthesis and seed production).

Average temperature and total precipitation were calculated for each climate period within each year. Because yearly phenological data are not available for these species for the duration of this study, the same climate periods were used for all species, watersheds and years. In addition, current year's total annual precipitation and average annual temperature were calculated for the period beginning at the end of the previous growing season and ending at the end of the current growing season (sum P1 through P5; average T1 through T5). Finally, the previous year's total annual precipitation and average annual temperature were calculated to examine their potential lag effects on ANPP.

DATA ANALYSIS

Repeated-measures ANOVAS

Because fire regimes were not replicated, we could not directly assess the effects of fire on ANPP and flowering stalk production. Instead, we conducted repeated-measures (RM) ANOVAS for each watershed, representing the different burn regimes separately, with topographic position and year as fixed factors and year as a repeated factor to determine the effects of topographic position and time on ANPP and flowering stalk production of the three dominant grasses. For data from the 4-year-burn watershed, an additional RM ANOVA with topographic position, years since burning, and species as fixed factors and year as a repeated factor was performed to determine the effects of topographic position, fire and species on flowering stalk productivity of the three dominant grasses, *A. gerardii*, *S. nutans* and *S. scoparium*. For the RM ANOVAS, ANPP and flowering stalk production were averaged by transect and transects were considered independent measures, as they are spatially dispersed across each topographic position within the watersheds. RM ANOVAS were performed in SAS version 9.2 (SAS Institute Inc., Cary, NC, USA).

Multiple regression analyses.

We used four stepwise multiple regression models (Table 1) to determine the amount of variation in ANPP explained by yearly climate variables (current year's total annual precipitation and mean annual temperature; Model 1), climate variables partitioned into periods relevant to the growth and phenology of the dominant grasses (Model 3), and each of these in combination with flowering by the three domi-

nant C_4 grasses (Models 2 and 4). We recognize that ANPP includes flowering stalk production and therefore including separate variables of flowering stalk production and ANPP in the same model may be considered a confounding factor in our analyses. However, we believe our analyses were appropriate given our goal of determining which variables explain the greatest amount of variation in ANPP for several reasons. First, there is strong evidence to suggest that flowering stalk production and ANPP are both resource intensive (Kelly & Sork 2002) and therefore the two are likely responding to variation in climate (i.e. resources) in similar ways, rather than flowering having a negative effect on ANPP. In addition, the measures of ANPP and flowering stalk production included in our models were collected independently. Finally, we also used SEM to assess both the direct and indirect relationships between climate variables partitioned into periods relevant to the growth and phenology of the dominant grasses, flowering stalk production of the three dominant grasses and ANPP (Model 5). If ANPP and flowering stalk production were confounded, we would expect to observe a strong direct effect of flowering on productivity and/or strong indirect effects of climate variables on ANPP via flowering, neither of which were observed (see below).

Models 1–4 were analysed separately for each burn regime by topographic position ($n = 6$). For the 4-year burn regime only, fire was included as a binary variable in all four models, indicating the occurrence or lack of occurrence of fire during a given year. In addition, all four models were including previous year's total annual precipitation and mean annual temperature to determine whether lag effects of these climatic variables influence ANPP. Prior to the analysis, bivariate plots were visually inspected for nonlinearity for all combinations of variables, and in all cases relationships were determined to be linear. The criteria for inclusion of a variable in each model was $P < 0.05$. For each model, an adjusted R^2 and AIC value was calculated to account for the number of variables included in the model. For each watershed and topographic position, models were evaluated by comparing AIC values. The model with the lowest AIC value was considered the best at explaining the data. All multiple regressions were performed in SAS version 9.2 (SAS Institute Inc.).

Structural equation modelling

While multiple regression analysis is a powerful way to assess the effects of multiple independent and uncorrelated variables on a dependent variable, SEM has the added power of being able to assess both direct and indirect effects of multiple independent variables (regardless of correlation) on a dependent variable (Grace 2006).

Table 1. Multiple regression models used to examine the effects of climate and flowering on variation in ANPP in tallgrass prairie. Each model was analysed with and without the inclusion of lag effects of total precipitation and temperature from the previous year (Plag and Tlag). Fire was included for all models for the 4-year burn regime, but for clarity is not shown below

No.	Model	Description
1	$ANPP = Pann + Tann (+ Plag + Tlag)$	Total annual precipitation (Pann; mm) and mean annual temperature (Tann; °C)
2	$ANPP = Pann + Tann + ANGE + SONU + SCSC (+ Plag + Tlag)$	Total annual precipitation (mm), mean annual temperature (°C), and flowering stalk biomass of <i>Andropogon gerardii</i> (ANGE), <i>Sorghastrum nutans</i> (SONU) and <i>Schizachyrium scoparium</i> (SCSC)
3	$ANPP = P1 + P2 + P3 + P4 + P5 + T1 + T2 + T3 + T4 + T5 (+ Plag + Tlag)$	Precipitation and temperature by seasonal climatic period
4	$ANPP = P1 + P2 + P3 + P4 + P5 + T1 + T2 + T3 + T4 + T5 + ANGE + SONU + SCSC (+ Plag + Tlag)$	Precipitation and temperature broken down by climatic period and flowering stalk biomass of <i>A. gerardii</i> (ANGE), <i>S. nutans</i> (SONU) and <i>S. scoparium</i> (SCSC)

Therefore, we used SEM to examine both the direct effects of precipitation and temperature divided into periods relevant to the phenology and growth cycle of the dominant grasses on ANPP and flowering stalk production of the three dominant grasses, as well as their indirect effects on ANPP as mediated by flowering stalk production of the dominant grasses (Model 5, Fig. 1). Separate models were assessed for each topographic position and burn regime for a total of six SEM models. Again, fire was included for the 4-year burn regime analysis as a binary variable indicating whether the watershed was burned. A maximum-likelihood approach was used in AMOS version 17.0.2 (Amos Development Corporation, Chicago, IL, USA) to parameterize the model. To develop the most parsimonious models possible, paths with the highest *P*-values (least significant) were removed from the models in a step-wise fashion until the chi-squared value increased by a significant amount (3.84 for 1 d.f.) (Grace 2006). At this point, the model in the previous step was considered to be the most parsimonious model. When a variable no longer had any paths leading from it, it was removed from the model completely. These models were analysed with and without the inclusion of the previous

year's total annual precipitation and mean annual temperature to determine whether the addition of these lag effects improved model fit. Models with lag effects added were compared to those without lag effects using AIC.

Results

TEMPORAL DYNAMICS OF ANPP AND FLOWERING IN RESPONSE TO FIRE AND TOPOGRAPHIC POSITION

For all three burn regimes, ANPP differed significantly between topographic position, with greater ANPP in lowlands versus uplands, and over time (Fig. 2, Table 2). For the 1- and 4-year burn regimes only, we also observed a significant topographic position \times year interaction on ANPP in which the magnitude of the difference in ANPP between the upland and lowland topographic position varied over time (Table 2).

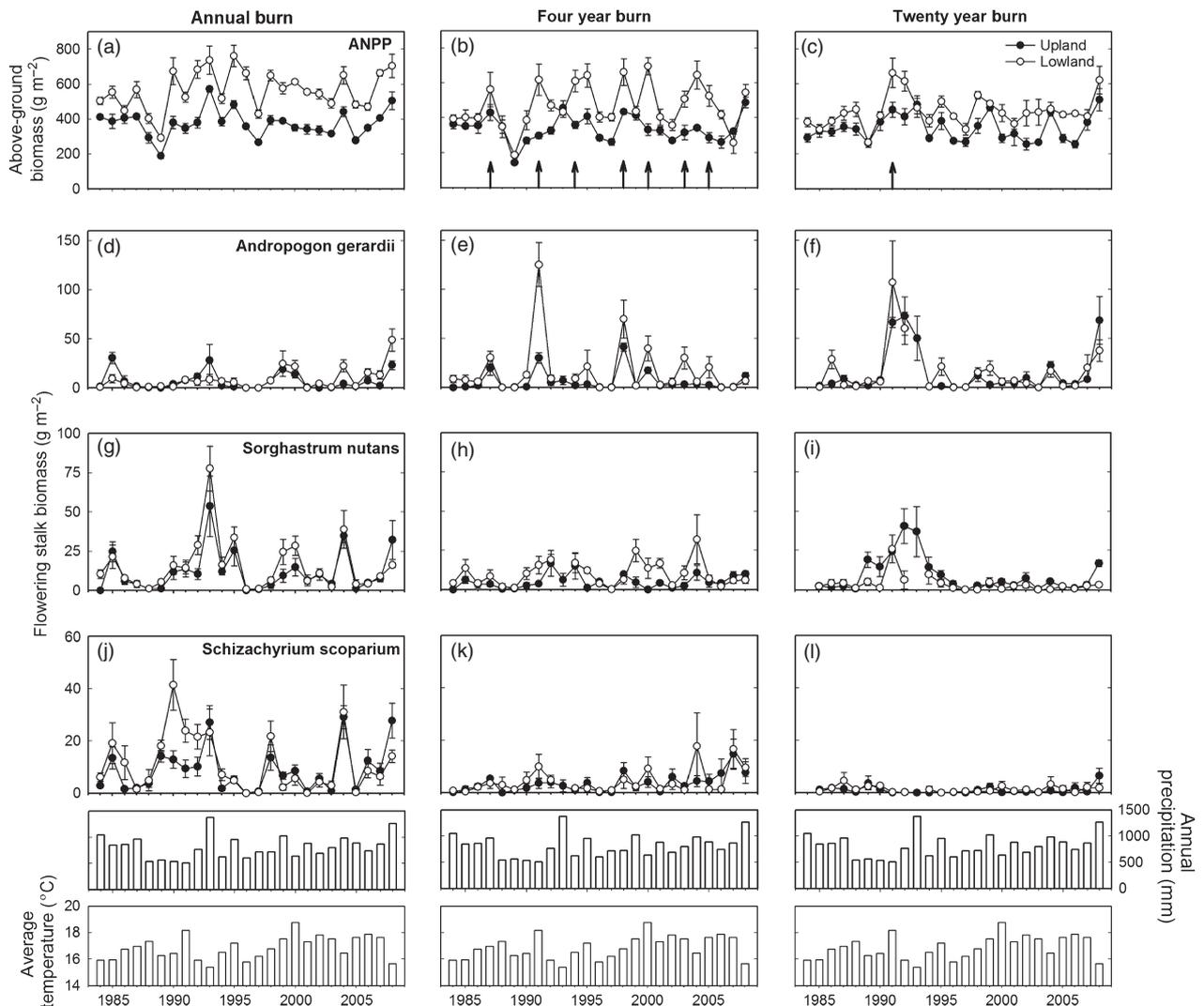


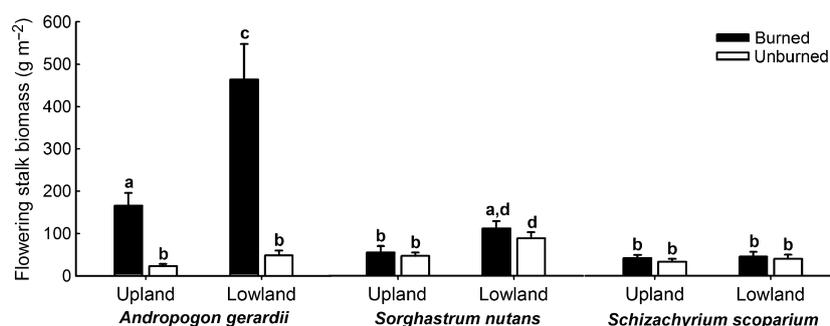
Fig. 2. Productivity (a–c) and flowering stalk biomass of *Andropogon gerardii* (d–f), *Sorghastrum nutans* (g–i) and *Schizachyrium scoparium* (j–l) within annual (left), 4-year (middle) and 20-year (right) burn regimes. Arrows indicate years with fire in 4-year and 20-year burn regimes. Note the difference in scales between the panels. Also shown are annual precipitation and average annual temperature (repeated in each column for ease of comparison with production measures). Flowering data from the annually burned watershed (d, g, j) are also presented in Craine, Towne & Nippert (2010).

Table 2. ANOVA results showing the effects of topographic position and year on above-ground net primary production and flowering stalk weight of the three dominant species, *Andropogon gerardii*, *Sorghastrum nutans* and *Schizachyrium scoparium*

	Annual burn regime			Four-year burn regime			Twenty-year burn regime		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
ANPP									
Topographic position	59.77	1,6	0.0002	16.04	1,6.01	0.0071	29.30	1,6	0.0016
Year	20.34	24,144	<0.0001	12.06	24,141	<0.0001	7.83	24,144	<0.0001
Interaction	3.00	24,144	<0.0001	4.65	24,141	<0.0001	1.48	24,144	0.0831
<i>A. gerardii</i> flowering									
Topographic position	0.49	1,6	0.5086	14.26	1,6	0.0092	0.02	1,5.95	0.9055
Year		24,144	<0.0001	18.77	24,144	<0.0001	10.28	24,142	<0.0001
Interaction	2.62	24,144	0.0002	5.56	24,144	<0.0001	1.50	24,142	0.0758
<i>S. nutans</i> flowering									
Topographic position	3.49	1,6	0.1110	8.74	1,6.04	0.0034	23.02	1,5.73	0.0034
Year	14.29	24,144	<0.0001	3.89	24,143	<0.0001	6.61	24,143	<0.0001
Interaction	1.05	24,144	0.4029	1.71	24,143	0.0284	3.60	24,143	<0.0001
<i>S. scoparium</i> flowering									
Topographic position	0.56	1,6.01	0.4815	0.16	1,6.01	0.7066	0.21	1,6.02	0.6655
Year	15.70	24,144	<0.0001	3.33	24,143	<0.0001	2.03	24,143	0.0059
Interaction	3.05	24,144	<0.0001	0.87	24,143	0.6471	1.12	24,143	0.3320

Flowering stalk production was also highly variable over time and with respect to topographic position. Flowering stalk production of *A. gerardii* varied significantly over time in all three burn regimes, however, the effect of topographic position was only significant in the 4-year burn regime, with higher flowering stalk production in the lowlands than the uplands (Fig. 2, Table 2). In addition, we found a significant interactive effect between topographic position and year on *A. gerardii* for the 1- and 4-year burn regimes. *Sorghastrum nutans* flowering stalk biomass was also significantly affected by year across all three burn regimes, but only differed by topographic position in the 4- and 20-year burn regimes (Fig. 2, Table 2). In addition, there was a significant interactive effect of topographic position and year on *S. nutans* flowering stalk biomass in the 4- and 20-year burn regimes. Finally, *S. scoparium* flowering stalk biomass was significantly influenced by year across all burn regimes, but was not influenced by topographic position. There was a significant topographic position \times year interaction in the annual burn regime, but not in the 4- and 20-year burn regimes (Fig. 2, Table 2).

Examining the 4-year burn regime more closely, we found that flowering stalk production was significantly influenced by all three factors in the model: topographic position, whether or not the area had been burned that year, and species ($F_{1,586} = 38.85$, $P < 0.0001$; $F_{1,586} = 74.64$, $P < 0.0001$; and $F_{2,586} = 48.44$, $P < 0.0001$, respectively; Fig. 3). Additionally, we found a significant topographic position \times burn, topographic position \times species, and burn \times species interactions ($F_{1,586} = 16.49$, $P < 0.0001$; $F_{2,586} = 16.05$, $P < 0.0001$; $F_{2,586} = 59.55$, $P < 0.0001$, respectively; Fig. 3). Finally, we found a significant three-way interaction between topographic position, burn and species ($F_{2,586} = 14.91$, $P < 0.0001$; Fig. 3). Overall, flowering stalk productivity was higher in the lowlands than in the uplands and increased in years when the grassland was burned. The response to burning was greater in the lowlands than in the uplands. *Andropogon gerardii* flowering stalk productivity was greater than that of *S. nutans* and *S. scoparium* overall, and increased in years when the watershed was burned. This response of *A. gerardii* flowering stalk production to burning

**Fig. 3.** Effects of fire on flowering productivity of the dominant C₄ grass species, *Andropogon gerardii*, *Sorghastrum nutans* and *Schizachyrium scoparium*, within the 4-year burn regime. Burned (closed bars) indicates years in which the watersheds were burned, while unburned (open bars) indicates years in which the watersheds were not burned. Letters indicate significant differences between soil type, burn and species effects.

was greater in the lowlands than in the uplands. Flowering stalk production of *S. nutans* and *S. scoparium*, on the other hand, did not differ between burned and unburned years.

EFFECTS OF ANNUAL CLIMATE VERSUS CLIMATE PERIODS AND FLOWERING STALK PRODUCTIVITY ON ANPP: MULTIPLE REGRESSION MODEL COMPARISONS

In Model 1, the current year's annual climate variables were able to explain 13.4–41.7% of the variation in ANPP for the different topographic position by burn regime combinations (Table 3). For all regressions, the current year's mean annual temperature had no significant effect on variation in ANPP (see Table S1 in Supporting Information for all final multiple regression models). For the 4-year burn regime, fire was also a significant predictor of ANPP (Table 4).

Stepwise multiple regressions including the current year's annual climate variables and flowering stalk production as explanatory variables (Model 2) were a better fit than model 1, explaining 27.1–51.0% of variation in ANPP (Table 3). Within model 2, flowering stalk production of at least one of the dominant species explained a significant portion of the variation in ANPP in all regressions (Table 4). Model 3, stepwise multiple regressions including seasonal climate periods as explanatory variables, was a better fit than Model 1, explaining 12.0–60.9% of variation in ANPP (Table 3). Overall, for the annual and 4-year burn regimes, seasonal precipitation and temperature periods explained more variation in ANPP than Model 2. In contrast, for the 20-year burn regime, Model 2 explained more variation in ANPP than Model 3.

Models including both flowering stalk production and climate variables segregated into phenologically relevant periods (Model 4) fit better than models including only the current year's annual climate variables (Model 1) in all topographic positions and burn regimes, explaining 35.2–62.1% of variation in ANPP (Table 3). In addition, in all topographic positions and burn regimes, inclusion of both flowering and seasonal climate variables improved model fit over Model 2, which included only flowering stalk production. Model 4 was significantly better than the model including only seasonal climate variables (Model 3) in annually burned lowlands, both uplands and lowlands burned every 4 years, and both uplands and lowlands burned every 20 years. Models 3 and 4 were equivalent predictors of ANPP in annually burned uplands.

To determine whether lag effects can explain additional variation in ANPP, we also included the previous year's total annual precipitation and mean annual temperature in Models 1–4. In most cases (15 of 24) lag effects were not included in the final model after stepwise selection. In the nine cases where either the previous year's total annual precipitation or mean annual temperature was included in the final model, the adjusted R^2 of the models only increased by an average of 2.91% (Table S3). The effect of the previous year's climate variables on ANPP varied widely across models, topographic positions and burn regimes, with almost equal numbers of models having either a positive or negative effect of the previous year's total annual precipitation (two positive and three

Table 3. Adjusted R^2 and AIC values from stepwise multiple regressions examining temporal variation in total above-ground biomass in watersheds burned every 1, 4 and 20 years in upland and lowland topographic positions. Models shown are: (1) with total annual precipitation and mean annual temperature only, (2) with total annual precipitation and mean annual temperature and flowering stalk production of the three dominant grass species only (3) with climate variables broken down by period only and (4) with flowering stalk production of the three dominant grass species and climate variables broken down by period included in the variables. Improvement measures indicate differences in adjusted R^2 and AIC between the models indicated. AIC values are shown in parentheses. n.s. indicates the model was not significant at the 0.05 level

	Model 1	Model 2	Model 3	Model 4	Improvement with addition of flowering stalk production (Model 1 to 2)	Improvement with addition of climate variables by period (Model 1 to 3)	Improvement with addition of both flowering stalk production and climate variables by period (Model 1 to 4)
1 year, upland	0.4112 (844.89)	0.5104 (828.38)	0.6090 (805.88)	0.6090 (805.88)	0.0992 (16.51)	0.1978 (39.01)	0.1978 (39.01)
1 year, lowland	0.1137 (964.58)	0.2710 (948.30)	0.5191 (908.62)	0.5696 (898.46)	0.1373 (16.28)	0.3854 (55.96)	0.4359 (66.12)
4 year, upland	0.3786 (844.18)	0.4240 (836.66)	0.5549 (814.93)	0.5625 (813.23)	0.0454 (7.52)	0.1763 (29.25)	0.1839 (30.95)
4 year, lowland	0.2958 (956.89)	0.3325 (943.56)	0.4558 (933.55)	0.4645 (923.14)	0.0367 (13.33)	0.1600 (23.34)	0.1687 (33.75)
20 year, upland	0.1566 (904.27)	0.3120 (871.18)	0.2446 (894.22)	0.3520 (866.22)	0.1554 (33.09)	0.0880 (10.05)	0.1954 (38.05)
20 year, lowland	n.s. (953.89)	0.3021 (909.16)	0.1197 (943.10)	0.3389 (904.77)	0.3021 (44.73)	0.1197 (10.79)	0.3389 (49.12)

Table 4. Partial R^2 values from stepwise multiple regressions for models of above-ground net primary production in annual, 4-year and 20-year burn regimes in upland (up) and lowland (low) topographic positions. Models shown are: (1) with total annual precipitation (Pann) and mean annual temperature (Tann) only, (2) with total annual precipitation, mean annual temperature and flowering stalk weight of the three dominant grass species only, (3) with climate variables broken down by period only and (4) with flowering stalk weight of the three dominant grass species and climate variables broken down by period included in the variables. '.' indicates the variable was not included in the final model. Blank cells indicate the variable was not included in the analysis (ANGE, *Andropogon gerardii*; SONU, *Sorghastrum nutans*; SCSC, *Schizachyrium scoparium*)

	Pann	Tann	ANGE	SONU	SCSC	P1	P2	P3	P4	P5	T1	T2	T3	T4	T5	Fire
Model 1																
1 year, up	0.4171
1 year, low	0.1425
4 year, up	0.3377	0.0536
4 year, low	0.2607	0.0496
20 year, up	0.1651
20 year, low
Model 2																
1 year, up	0.4171	.	0.0304	0.0777
1 year, low	0.0565	.	.	.	0.0365
4 year, up	0.3377	.	0.0981
4 year, low	0.0570	.	0.0377	0.2587
20 year, up	0.2103	.	0.1158
20 year, low	.	.	0.3092
Model 3																
1 year, up	0.4531	0.1508	0.0170
1 year, low	0.2592	0.1617	0.0297
4 year, up	0.3057	.	0.0917	0.0357	0.0608	0.0508	.	.	.	0.0879	0.0374
4 year, low	0.0383	0.1295	.	0.0497	0.2607
20 year, up	0.1899	0.0700
20 year, low	0.0561	.	0.0813
Model 4																
1 year, up	0.4531	0.1508	0.0170
1 year, low	.	.	.	0.0431	.	.	.	0.2592	0.1617	0.0394	0.0879	.
4 year, up	.	0.0958	.	0.0331	0.3057	.	.	0.0917	.	0.0305	0.0325
4 year, low	0.0386	.	0.1414	.	0.0482	0.2587
20 year, up	.	0.1270	0.2090	0.0359
20 year, low	.	0.3092	0.0432

negative) or mean annual temperature (two positive and two negative; Table S3).

DIRECT AND INDIRECT EFFECTS OF FLOWERING STALK PRODUCTION AND SEASONAL CLIMATE PERIODS ON ANPP: STRUCTURAL EQUATION MODELLING

Using SEM (Model 5), we were able to explain 40.1–65.2% of variation in ANPP. The addition of lag effects decreased model fit for all topographic positions and burn regimes (Table S6), therefore results presented hereafter are for models with only current year's climate effects. Precipitation in P3 (15 April–14 July) and P4 (15 July–14 August) directly positively affected ANPP across most topographic positions and burn regimes (Table 5, Fig. 4). In addition, fire was consistently important in explaining variation in ANPP in the 4-year burn regime. In the annual and 4-year burn regimes, ANPP was negatively influenced by precipitation in P5 (15 August–14 September), however precipitation during P5 had no effect on ANPP in the 20-year burn regime. The direct effect of temperature on ANPP varied by topographic position and burn

regime, with no temperature period having a consistent effect on ANPP across all topographic position and burn regime combinations. The effect of flowering stalk productivity on ANPP was consistent across all topographic positions and burn regimes, however, the species whose flowering stalk production explained most variation in ANPP varied across these treatments (Table 5). Only in the lowlands burned every 4 years did flowering stalk production not have an effect on ANPP.

The effects of climate variables on flowering stalk productivity were consistent across topographic position, burn regime and species. Flowering stalk production of all species was positively influenced by precipitation in P3 and P4 (Table S4). These direct effects of precipitation in P3 and P4 translated into indirect effects on ANPP (Table S5). However, the direct effects of P3 and P4 on ANPP were much stronger than these indirect effects and therefore overpowered the influence of indirect effects through flowering for these variables (Fig. 4). Temperature in T4 had a consistent negative effect on flowering stalk production across all species, topographic positions and burn regimes (Table S4). This resulted in an indirect negative effect of temperature in T4 on ANPP (Table S5).

Table 5. Standardized total effect sizes for structural equation models within annual, 4- and 20-year burn regimes in upland and lowland topographic position. Bold text indicates that the path was significant at the $P < 0.05$ level. Negative effect sizes indicate a negative relationship between variables. '.' indicates that the variable was not included in the final model. Blank cells indicate that the variable was not included in the analysis (ANGE, *Andropogon gerardii*; SONU, *Sorghastrum nutans*; SCSC, *Schizachyrium scoparium*)

	ANGE	SONU	SCSC	P1	P2	P3	P4	P5	T1	T2	T3	T4	T5	Fire
1 year, upland														
ANPP	0.127	0.171	.	0.042	0.096	0.576	0.362	-0.144	.	.	.	-0.045	.	.
ANGE	.	.	.	0.329	.	.	0.245	-0.158	.	.
SONU	-0.160	0.568	0.237	-0.145	.	.
SCSC
1 year, lowland														
ANPP	.	-0.162	0.305	-0.206	.	0.610	0.287	-0.318	0.081	-0.216	.	-0.102	0.023	.
ANGE
SONU	0.577	0.288	.	0.205	.	.	-0.308	0.135	.
SCSC	0.261	-0.497	0.147	.
4 year, upland														
ANPP	.	0.139	0.203	0.333	0.096	0.332	0.127	-0.278	-0.221	0.044	.	-0.029	-0.036	0.199
ANGE
SONU	.	.	.	-0.222	.	0.201	0.237	-0.210	-0.261	0.222
SCSC	.	.	.	-0.388	0.471	.	0.462	.	0.168	0.216
4 year, lowland														
ANPP	.	.	0.120	0.189	-0.279	0.381	.	-0.192	0.029	.	0.037	-0.036	.	0.544
ANGE
SONU
SCSC	0.285	.	.	0.237	.	0.310	-0.301	.	.
20 year, upland														
ANPP	0.277	.	.	.	0.206	0.370	0.299	.	0.047	.	.	-0.233	.	.
ANGE	0.207	0.349	.	0.169	.	.	-0.189	.	.
SONU
SCSC	-0.326	.
20 year, lowland														
ANPP	0.532	.	-0.162	.	.	0.134	0.208	-0.110	0.147	0.158	-0.040	.	.	.
ANGE	-0.208	.	0.298
SONU
SCSC	0.245	.	.	.

Discussion

Overall, we found that models accounting for precipitation and temperature variables segregated into periods relevant to the growth cycle and phenology of the dominant grass species increased our ability to explain variation in ANPP over a 25-year period, as compared to models including only annual precipitation and mean annual temperature, particularly in more frequently burned watersheds (1- and 4-year). As predicted, we found that models including flowering stalk production were able to explain a greater amount of variation in ANPP, however, this increase was weak for frequently burned grasslands. Moreover, including both the effects of flowering stalk production and seasonal climate variables on ANPP further increased our ability to explain variation in ANPP across all topographic positions and burn regimes studied. The results from our multiple regression analysis and the structural equation models were similar, however, SEM presents the opportunity to address indirect, as well as direct, effects of variables on ANPP. Our structural equation models showed that in addition to direct effects, climate variables, such as increased temperature during flowering stalk elongation, can have an indirect effect

on ANPP through their effects on flowering stalk production. However, these indirect effects were relatively minor with respect to the direct effects of climate.

CLIMATE AND ANPP

As predicted, variation in ANPP was positively and consistently affected by precipitation during vegetative growth (P3) and flowering stalk elongation (P4) and negatively affected by precipitation during reproduction (P5) across all topographic positions and burn regimes. The bulk of the precipitation (% of total) that falls during the year generally occurs during the periods of vegetative growth and flowering stalk elongation, and the positive relationship between ANPP and precipitation from 15 April to 14 July and 15 July to 15 August is likely a direct result of increased growth with increased precipitation within this time frame. The negative effect of precipitation from 15 August to 14 September on the other hand, may result from an increased incidence of a competitor, herbivore, disease or decomposer stimulated by late-season precipitation. Alternatively, increased precipitation during this period may reflect a seasonal shift in precipitation, with less rainfall

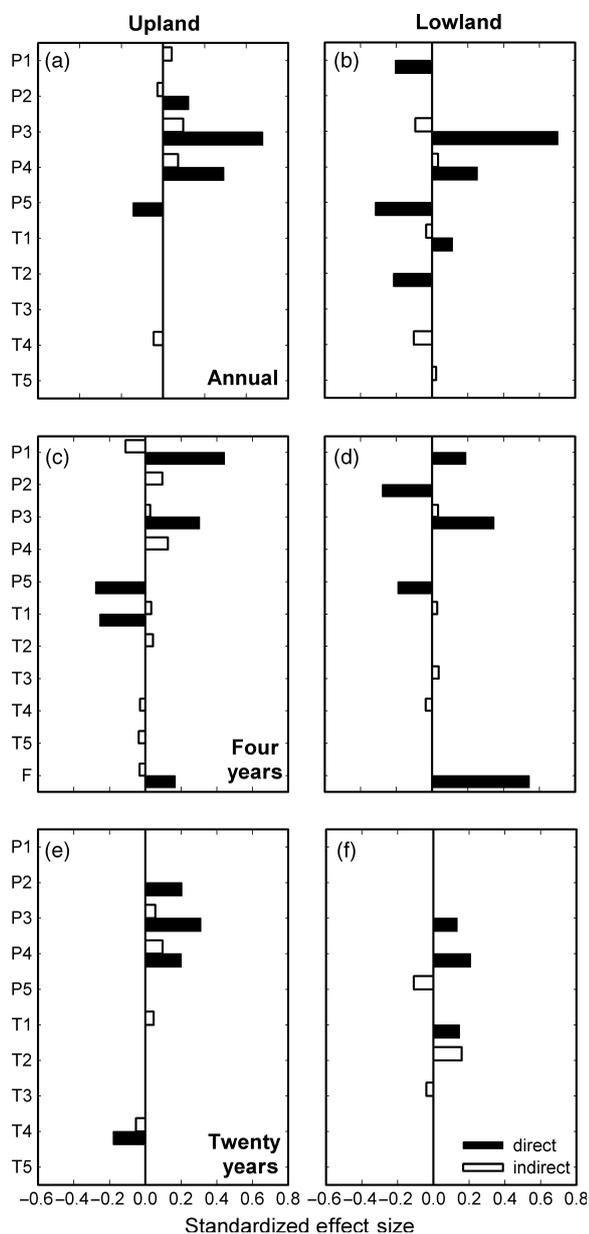


Fig. 4. Standardized direct (closed bars) versus indirect (open bars) effect sizes of precipitation (P1–5), temperature (T1–5) and fire (F) on above-ground net primary production (ANPP) within annual (a, b), 4-year (c, d) and 20-year (e, f) burn regimes and upland (a, c, e) and lowland (b, d, f) topographic positions. Indirect effects are those mediated by flowering productivity of three dominant C_4 grasses. Positive and negative effect sizes indicate a positive or negative relationship, respectively, between a variable and ANPP.

during the first portion of the growing season, thus resulting in decreased growth. Interestingly, the response to seasonal precipitation was strongest in the frequently burned areas (annual burn regime) and weaker in the infrequently burned areas (20-year burn regime). Frequently burned tallgrass prairie has been shown to have greater densities of rhizome meristems (Benson, Hartnett & Mann 2004), which may allow for a greater ability of the vegetation to respond to variation in precipitation (Knapp & Smith 2001). Temperature appears to

play a weaker role in directly influencing ANPP, with its effects varying by topographic position and burn regime. Fire is a strong predictor of ANPP in the 4-year burn regime, consistent with the well-documented response of grassland productivity to fire (Hulbert 1969; Abrams, Knapp & Hulbert 1986; Wilson & Shay 1990; Buis *et al.* 2009; Augustine, Derner & Milchunas 2010; Romero-Ruiz *et al.* 2010).

The previous year's climate has been shown to play a role in determining ANPP in other systems (Cable 1975; Oosterheld *et al.* 2001; Wiegand *et al.* 2004; Posse, Oosterheld & Di Bella 2005); however, we did not find evidence for a consistent effect of the previous year's precipitation or temperature across all topographic positions and burn regimes. Most of our climate and flowering models were not improved by the addition of lag effects, and those which did include lag effects did not explain substantially more variation in ANPP than models without lag effects. Additionally, the inclusion of lag effects to our structural equation models decreased the explanatory power of all models in describing ANPP. These results indicate that the previous year's climate has a limited effect on ANPP in tallgrass prairie. However, where the effect of the previous year's climate on ANPP does occur, the effect may be mediated by flowering stalk production, as models which improved with the addition of lag effects generally also included flowering stalk production (Table S2). Because flowering is a binary and resource-intensive process, an individual grass will likely not flower two years in a row. An increase in flowering in 1 year likely leads to a decrease in flowering the next and, conversely, low levels of flowering in one year likely lead to an increase in flowering the next. Because flowering can influence productivity, climatic variables which have a large influence on flowering in a given year may result in altered productivity in the following year.

Water is not generally thought to be the primary limiting resource in mesic grasslands (Seastedt & Knapp 1993; Briggs & Knapp 1995; Knapp *et al.* 1998), however precipitation clearly has an influence in determining ANPP. This may be the result of precipitation occurring in a period when the availability of the primary limiting resource is high (Seastedt & Knapp 1993). The resource which primarily limits this grassland may vary throughout the season and across burn regimes and topographic positions. For example, light availability is thought to limit primary production in infrequently burned prairie due to high levels of detritus (Knapp & Seastedt 1986), therefore increased water availability in the early portions of the growing season when light is less limiting may play a stronger role in determining ANPP. However, the availability of only one of these resources may result in decreased levels of ANPP as light is the primary limiting resource but direct sunlight increases water stress (Brown & Trlica 1977). In this way, precipitation during different periods of the growing season may be interacting with primary limiting resources to result in increased ANPP in this non-equilibrium system (Seastedt & Knapp 1993). Further examination of the co-occurrence of precipitation and limitation by other resources demands further study.

FLOWERING STALK PRODUCTIVITY AND ANPP

As predicted, our models showed that flowering stalk production does contribute to variation in ANPP, particularly in less frequently burned areas. In contrast to Craine, Towne & Nippert (2010), we found that while flowering stalk production of *S. nutans* was a strong predictor of ANPP in annually burned uplands, *S. scoparium* flowering stalk production was the strongest predictor of ANPP in annually burned lowlands. *Schizachyrium scoparium* flowering stalk production was also a strong predictor of ANPP in uplands burned every 4 years, and lowlands burned every 20 years, *S. nutans* flowering stalk production was a strong predictor of ANPP in uplands burned every 4 years, and *A. gerardii* flowering stalk production was a strong predictor of ANPP only in the 20-year burn regime.

Because flowering stalk production makes up a portion of ANPP, it is clear that factors influencing variation in flowering stalk production of the dominant species in a system can indirectly influence ANPP, even if these factors do not have a direct effect on vegetative growth. Flowering has been shown several different systems to correlate with annual variation in precipitation (Kelly & Sork 2002) and particularly with precipitation during specific periods of the growing season (Fay *et al.* 2000; Jentsch *et al.* 2009; Perez-Ramos *et al.* 2010).

In this study, we found that flowering stalk production of *S. scoparium* was strongly influenced by precipitation during emergence (P2), vegetative growth and flowering stalk elongation and early season temperature (T1, T2). The positive effect of early season temperature and precipitation on *S. scoparium* flowering stalk production is consistent with the idea that an early start to the growing season, leading to a longer growing season, can result in increased flowering by allowing more time for vegetative growth, photosynthesis and carbon gain. However, this mechanism was not directly tested here. *Schizachyrium scoparium* was also shown to be negatively influenced by high temperature late in the growing season (T4). *Schizachyrium scoparium* has been shown to delay time of flowering, thus shortening its reproductive period, with experimental warming (Sherry *et al.* 2007). This suggests that late-season warming may result in a delay or suspension of the development of flowering stalks, thereby decreasing flowering stalk productivity. In addition, productivity of *S. scoparium* has been shown to respond positively to mean annual precipitation (Epstein *et al.* 1996). Our results suggest that this relationship may be driven by the positive relationship between precipitation during emergence or flowering stalk elongation and *S. scoparium* flowering stalk biomass.

Based on our structural equation models, *S. nutans* flowering stalk productivity was positively influenced by precipitation during vegetative growth and flowering stalk elongation and by early season temperature (T1). *Sorghastrum nutans* was negatively influenced by precipitation during the dormant period (P1) and temperature during flowering stalk elongation. Again, this is consistent with the idea that increased vegetative growth due to a longer growing season can lead to an increase in photosynthesis and carbon gain, thereby promoting increased flowering stalk production.

The results of our RM ANOVA show that flowering stalk production of *A. gerardii* is strongly controlled by burning, while the results of our structural equation models suggest that precipitation during vegetative growth and flowering stalk elongation and temperature during emergence also influence flowering stalk production. Past work has shown that *A. gerardii* reduces flowering in dry or drought conditions (Swemmer, Knapp & Smith 2006) and that *A. gerardii* biomass is positively correlated with mean annual precipitation (Epstein *et al.* 1996). This is consistent with our findings that *A. gerardii* flowering stalk production is positively correlated with precipitation during vegetative growth and flowering stalk elongation. Like *S. scoparium*, *A. gerardii* flowering has been shown to be delayed with experimental warming (Sherry *et al.* 2007). However, unlike *S. scoparium*, *A. gerardii* does not shorten its reproductive period with warming, but rather lengthens it (Sherry *et al.* 2007). In addition, Nippert *et al.* (2009) have shown that physiological responses of *A. gerardii* are more sensitive to warming than precipitation. While our results showed that temperature during flowering stalk elongation negatively influences flowering stalk production in *A. gerardii*, we did find that temperature during emergence positively influences *A. gerardii* flowering stalk production. This again suggests that early season temperature may influence the amount of carbon gained by *A. gerardii* by lengthening the growing season and that this effect may lead to an increase in flowering stalk production.

Conclusions

By temporally separating our climate variables into periods relevant to the phenology and growth cycle of the dominant species, we were able to explain more of the temporal variation in ANPP (over 35% more in annually burned prairie) than by using only the current year's annual climate variables, particularly in frequently burned systems. This is consistent with studies in other systems, which have found rainfall or temperature during specific periods of the growing season to be a strong determinant of ANPP (Milchunas, Forwood & Lauenroth 1994; Jobbagy & Sala 2000; Nippert, Knapp & Briggs 2006; Suttle, Thomsen & Power 2007; Chou *et al.* 2008). Our models suggest that the drivers of ANPP are context dependent, with drivers varying within topographic positions and burn regimes within the tallgrass prairie system. However, some generalities can be drawn: precipitation during vegetative growth (15 April–14 July), flowering stalk elongation (15 July–14 August) and reproduction (15 August–14 September) consistently influence ANPP.

The inclusion of flowering stalk production as a variable to explain temporal variation in ANPP increased the explanatory power of our models, a pattern that few studies have examined (but see Craine, Towne & Nippert (2010) for an examination of flowering stalk production in an annually burned system). Because flowering stalk production increased the explanatory power of our models most significantly in the infrequently burned areas, but had a limited effect in frequently burned areas, our study

demonstrates the importance of examining patterns driving ANPP across different community types within the same ecosystem. Although the direct effect of temperature on ANPP was weak, the indirect effect of temperature on ANPP through its effect on flowering was consistent across all burn regimes and topographic positions. By examining the effect of climatic variables during biologically relevant time periods on flower stalk production, we were able to explain more variation than by using total yearly climate variables. This relationship between climate, flowering stalk production and ANPP clearly warrants further study.

Climate change models predict increased maximum temperatures, more frequent droughts and more extreme precipitation events (Easterling *et al.* 2000; IPCC 2007). These changes could result in shifts in productivity patterns in tallgrass prairie. Depending on the timing of these projected changes in climate, effects of climate change on ANPP may vary. Above-ground net primary production might be expected to decrease with increased incidence of high temperatures and drought during the periods relevant to the vegetative growth (April–July) and flowering stalk elongation (July–August) of the dominant C₄ grasses, while alterations in climate during the dormant period might have a relatively limited affect on ANPP. In addition, our results suggest that changes in flowering stalk production may occur with future climate change, with subsequent consequences for ANPP. Our results suggest that responses to predicted climate changes are likely to be inconsistent from species to species and even between sites within the same ecosystem. As climate patterns continue to change world-wide, we may begin to see unpredicted alterations to productivity and community dynamics in many different ecosystems. By examining the effects of seasonal climatic periods and flowering stalk production on productivity in many systems around the world, we may be able to better understand and predict the changes to primary production and plant community dynamics in the face of future climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Final multiple regression models examining the effects of climate and flowering on variation in above-ground net primary production in tallgrass prairie (ANGE, *Andropogon gerardii*; SONU, *Sorghastrum nutans*; SCSC, *Schizachyrium scoparium*; n.s. indicates the model was not significant at the 0.05 level; see text for description of precipitation (P) and temperature (T) periods).

Table S2. Adjusted R^2 and AIC values from stepwise multiple regressions examining temporal variation in total aboveground biomass in watersheds burned every 1, 4, and 20 years in upland and lowland topographic positions.

Table S3. Final multiple regression models examining the effects of climate and flowering on variation in above-ground net primary production in tallgrass prairie including lag effects of previous year's precipitation and temperature (ANGE, *Andropogon gerardii*; SONU, *Sorghastrum nutans*; SCSC, *Schizachyrium scoparium*; n.s. indicates the model was not significant at the 0.05 level; see text for description of precipitation (P) and temperature (T) periods).

Table S4. Standardized direct effect sizes for structural equation models within annual, 4-, and 20-year burn regimes in upland and lowland topographic position.

Table S5. Standardized indirect effect sizes for structural equation models within annual, 4-, and 20-year burn regimes in upland and lowland topographic position.

Table S6. AIC values comparing structural equation models with and without lag effects from previous year's total annual precipitation and mean annual temperature within annual, 4-, and 20-year burn regimes in upland and lowland topographic position.

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