Timing of climate variability and grassland productivity

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Future climates are forecast to include greater precipitation variability and more frequent heat waves, but the degree to which the timing of climate variability impacts ecosystems is uncertain. In a temperate, humid grassland, we examined the seasonal impacts of climate variability on 27 y of grass productivity. Drought and high-intensity precipitation reduced grass productivity only during a 110-d period, whereas high temperatures reduced productivity only during 25 d in July. The effects of drought and heat waves declined over the season and had no detectable impact on grass productivity in August. If these patterns are general across ecosystems, predictions of ecosystem response to climate change will have to account not only for the magnitude of climate variability but also for its timing.

Konza | net primary production | streamflow | critical climate periods

Future climates are likely to include more frequent droughts, high-intensity precipitation patterns, and heat waves, (i.e., periods of elevated air temperatures) (1, 2). At their most severe, extreme climate events, such as the mid-American heat waves of 1980 and 2011 and the 2003 European heat wave, involve months of hot, dry weather (3, 4), increasing mortality in humans and wildlife (5, 6) while reducing agricultural and natural-systems productivity (7–10). An increase in climate extremes would have unambiguously negative effects on ecosystems. However, most climate variability would not be considered extreme and occurs on much shorter time scales throughout the growing season with temperature and precipitation frequently disassociated. The response of ecosystems to short-term climate variability at different times of year is thought to vary (11–16), but we know little about how the timing of short-duration climate variability impacts key ecosystem dynamics such as plant productivity.

To understand better how the timing of climate variability affects grassland productivity, we applied the critical climate period approach (17, 18) to long-term measurements of grass productivity in a humid, temperate grassland. Aboveground net primary productivity of grass ($ANPP_G$) was measured at the time of peak standing biomass from 1984–2010 in both shallow-soil upland and deep-soil lowland topographic positions in an annually burned, ungrazed watershed that is dominated by grasses with the C_4 photosynthetic pathway. In attempting to understand how the timing of climate variability affects grass productivity, we analyzed long-term records of precipitation, stream discharge, and air temperature to examine how variation in drought, precipitation intensity, and heat waves affect grass productivity at different times of the growing season.

Results and Discussion

Across 27 y, drought reduced grass productivity over a wide range of dates but had declining effects as the season progressed. $ANPP_G$ decreased with decreasing precipitation summed from April 15 to August 2 [day of year (DOY) 105–214] (Fig. 1). $ANPP_G$ declined 0.60 ± 0.12 g·m^{-2} for each millimeter decline in precipitation. With precipitation varying across years from 799–170 mm during this date range, precipitation variation caused $ANPP_G$ to vary by 377 g·m^{-2} among years. Seasonally, the response to drought during the growing season was greatest when soils typically were wettest, not driest. The sensitivity of $ANPP_G$ to drought declined as the season progressed (Fig. 2), e.g., from DOY 95–259 ($r^2 = 0.81$, $P < 0.001$) or DOY 105–214 ($r^2 = 0.62$, $P < 0.001$). Droughts in August did not impact productivity because there was no relationship between precipitation during any period in August and $ANPP_G$ ($P > 0.25$).

Precipitation pattern—the magnitude and distribution of precipitation events—can alter soil-water availability to plants beyond the total amount of precipitation (2). However, quantifying precipitation patterns in an ecologically meaningful manner has been difficult (19), and we know little about how these patterns affect productivity outside of experimental conditions (20). We used stream discharge data from a US Geological Survey gauging station on a Konza stream (21) as an index of precipitation pattern. High stream discharge for a given amount of precipitation can serve as an index of a precipitation pattern. When precipitation patterns are intense, a smaller fraction of the soil water is retained, and losses to streams increase (21, 22). With more water lost to streams, intense precipitation patterns also should lower terrestrial plant productivity. After controlling for interannual variation in total precipitation and air temperature during critical periods (Fig. S1), precipitation patterns that generated high stream discharge during the critical precipitation period (Discharge$_{105–214}$) also reduced $ANPP_G$, but, again, this effect was not seen in August (Fig. 1). Across years, 25.7×10^6 m^3 of stream discharge were unexplained by precipitation amounts and mean maximum temperature during critical periods. Each additional 10^6 m^3 of residual stream discharge was associated with a reduction in $ANPP_G$ of 7.1 ± 3.0 g·m^{-2}. Variation in precipitation pattern that impacted Discharge$_{105–214}$ therefore could cause a total reduction of $ANPP_G$ of 182 g·m^{-2}. In August, there was no relationship between precipitation and discharge ($P = 0.99$) and no relationship between discharge during this period and $ANPP_G$ ($P = 0.44$). The relationship between streamflow and ANPP was adjusted for the relationships with temperature and precipitation, so any reductions in ANPP ascribed to streamflow could not be the result of greater evapotranspiration caused by low precipitation or high temperatures.

Like drought and intense precipitation patterns, heat waves reduced grass productivity at Konza but over a shorter period than for precipitation. Across 27 y, high temperatures reduced grass productivity significantly only during a 25-d critical period (DOY 190–214; July 9–August 2) (Fig. 1). Over this 25-d period, years varied in mean daily maximum temperature by 6.2 °C (29.4–35.6 °C) (Fig. 2). Although important only during a short period, critically timed heat waves could cause large reductions in productivity. For every 1 °C increase in mean daily maximum temperature in the period DOY 190–214, productivity was
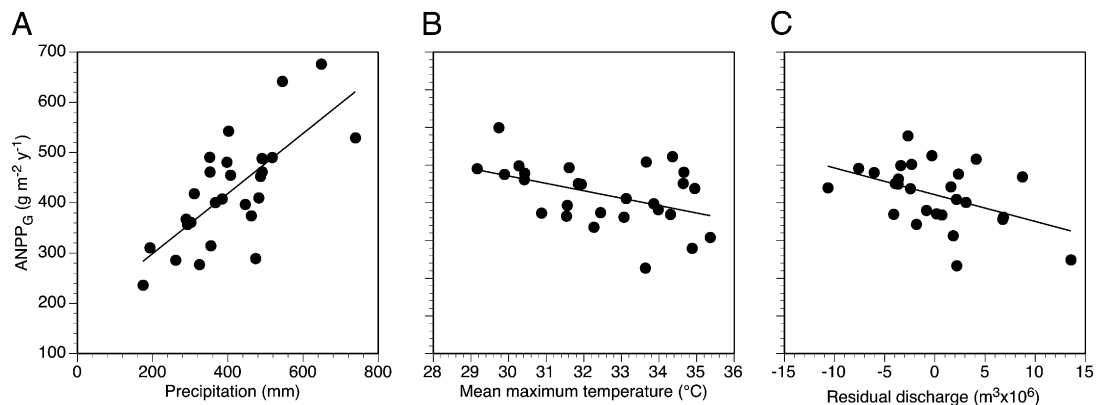
Fig. 1. Partial residual plots over 27 y of annual $ANPP_G$ averaged between two landscape positions and climate indices. (*A*) Precipitation from DOY 105–214 ($P < 0.001$). (*B*) Mean daily maximum air temperatures from DOY 190–214 ($P = 0.02$). (*C*) Residual discharge after accounting for total precipitation and air temperature during critical periods ($P = 0.02$). Model $r^2 = 0.72$.

reduced by 19.6 ± 8.3 g·m^{-2}. During the critical temperature period, there was just a trend for high temperatures to have less effect on $ANPP_G$ in wet years than in dry years ($P = 0.15$). Given the mean $ANPP_G$ in the two topographic positions and the range in variation observed in midseason mean maximum temperatures, $ANPP_G$ could vary by 121 g·m^{-2} as a result of differences in mean maximum temperature among years during this period.

Seasonal patterns of the effects of air temperatures on $ANPP_G$ at Konza paralleled the results of the critical maximum temperature period (Fig. 2). Maximum temperatures had little effect in June and strong effects in early July which declined progressively in magnitude until August, when they effectively were zero (Fig. 2). Before DOY 190, the effects of high temperatures on productivity were low and variable, and high temperatures were not a significant predictor of $ANPP_G$. For example, mean daily maximum temperature had no significant effect on $ANPP_G$ during the critical precipitation period before the critical temperature period (DOY 105–189, $P = 0.2$).

The effects of drought and heat waves on productivity were not limited to the measured field sites on Konza but instead decreased productivity across the vast majority of grassland areas of Konza (Fig. 3). We analyzed the effects of precipitation, precipitation pattern as indexed by residual streamflow, and mean daily maximum temperatures on a remotely sensed index of productivity, the normalized difference vegetation index (NDVI) collected from 2000–2010 at 250-m resolution for the whole of Konza. At this scale, years with low precipitation from DOY 105–214, high residual streamflow over the same period, or high temperatures from DOY 190–214 consistently had lower late-August NDVI on Konza. NDVI for 98.4% of Konza was negatively impacted by early- to midseason drought, 78.1% of Konza was negatively impacted by high residual streamflow, and 79.5% of Konza was negatively impacted by late-July heat waves ($P < 0.001$ for all) (Fig. 3). In general, upland grasslands were most sensitive to climate variability, and gallery forests along streams and shrub-dominated areas were the least sensitive regions. The responsiveness of NDVI to drought, high residual streamflow, and high temperatures decreased with increasing woody cover ($P < 0.001$ for both drought and heat waves, $P = 0.01$ for streamflow) and was lower for low-elevation sites ($P < 0.001$ for all three).

Although drought and heat waves reduce grass productivity in general, whether a common mechanism underlies their effects is poorly understood. Just as drought reducing productivity can be explained by reduced water availability limiting photosynthesis (23), heat waves can lower productivity by lowering soil moisture through increased evapotranspiration (12, 24, 25). Focusing on the indirect effects of heat waves on water balance allows for a common mechanism that links the effects of heat waves with drought and precipitation pattern, but other mechanisms are possible. For example, the possibility that high temperatures associated with heat waves generated physiological stress directly cannot be ruled out (26). That said, peak temperatures from DOY 190–214 generally were below the optimum temperatures reported for photosynthesis for C_4 grasses (27, 28), and increases in peak air temperature that were well below optimum photosynthetic temperatures were associated with lower productivity (Fig. S2). The highest air temperature observed from DOY 190–214 was lower than 42 °C, and 70% of the years never had an air temperature above 40 °C during this time (although leaf temperatures often can be higher than air temperatures) (29, 30). Finally, high temperatures also could impact soil N mineralization negatively (31) and increase the feeding rate of grasshoppers (32, 33), thereby generating a lower apparent ANPP.

Acknowledging alternative contributing explanations, declines in productivity associated with increasing late-season temperature can be explained by the reduction in soil moisture that accompanies high temperatures. For each year from 2001–2010, we calculated the evapotranspiration of a hypothetical reference grass stand from DOY 190–214 ($ET_{190-214}$) and then scaled it to Konza lowland grassland using locally generated coefficients (34). Across the 10-y period, $ET_{190-214}$ varied by 43% (119.8–171.4 mm) and generally was greater in years with higher mean daily maximum temperatures during this period ($MaxTemp_{190-214}$): $ET_{190-214} = -114.2 + 7.8 * MaxTemp_{190-214}$; $r^2 = 0.80$, $P < 0.001$. Using the observed range in temperatures over the 27-y period and a typical water-use efficiency for C_4 grasses of 250 g of biomass per gram of water (35), 25 d of greater evapotranspiration could cause a reduction in net primary productivity (NPP) by 192 g·m^{-2} just through greater evapotranspiration. By comparison, across the 27-y period, variation in mean daily maximum temperature was associated with a 123 g·m^{-2} variation in $ANPP_G$, a reasonable fraction of NPP given the ratios of ANPP and belowground NPP for the predominant C_4 grasses at Konza (36). The greater reduction in soil moisture during times with high temperature is apparent in a long-term (1984–2010) biweekly record of soil moisture taken in the lowlands of watershed 1D at Konza (Fig. S3).

Although it is clear that grass productivity responds differently to climate variability at different times of year, the reasons for this difference are unclear. For example, the low average soil moisture in early August and the reduction in soil moisture during hot, dry weather does not explain why years with environmentally favorable Augusts are not associated with greater productivity.
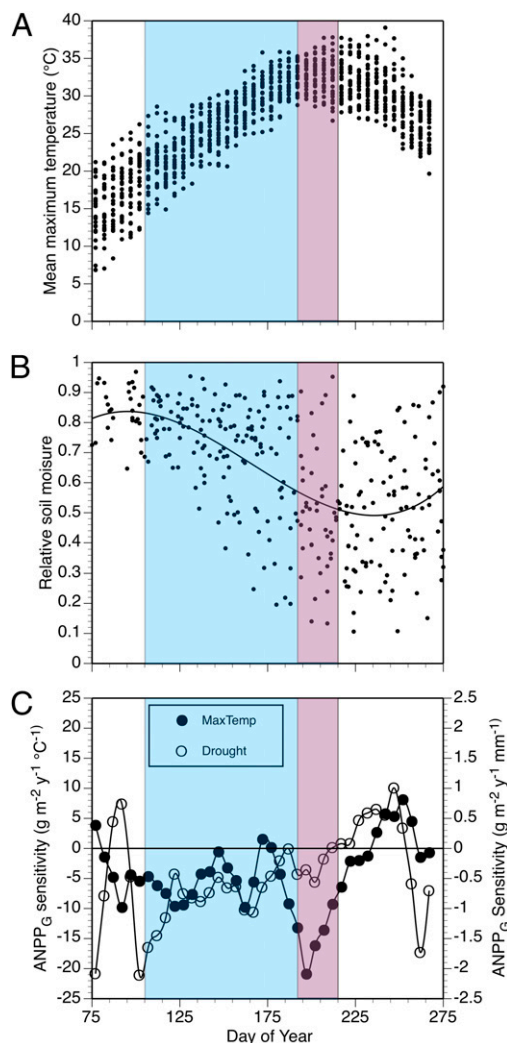
Fig. 2. Temperature, soil moisture, and productivity sensitivity over the growing season. Distribution from 1984–2010 of (*A*) mean daily maximum temperatures averaged over 15-d intervals and (*B*) soil moisture at 25 cm taken approximately every 15 d. (*C*) Sensitivity of0(ANPP$_G$ to variation in drought and heat waves assessed every 15 d in 5-d increments. The critical climate period for drought (DOY 105–214) is shown in blue, and the critical climate period for heat waves (DOY 190–214) is shown in red. Overlapping regions are shown in purple.

The lack of response of ANPP$_G$ to August climate variability is not because grass ceases to grow in August. Biweekly harvests of standing grass biomass were conducted from 1984–1999 in the lowlands of a different annually burned watershed at Konza (watershed 1A) (37), which had patterns of ANPP$_G$ across years similar to those of watershed 1D during this period ($r = 0.79$, $P < 0.001$). During these years, 10% of the standing grass biomass present at the end of August was produced during that month (55 of 485 g·m^{-2}; Fig. S4) compared with 23% in July. Still, August ANPP$_G$ could be as high as 132 g·m^{-2}. Using the critical climate period approach, 77% of the variation in August ANPP$_G$ is explained by late-July precipitation (DOY 190–214; Jul 9–Aug 2) with precipitation or maximum temperatures during August having no effect on August ANPP$_G$ ($P > 0.3$ for both). In contrast, July ANPP$_G$ is best explained by precipitation before and also during July (critical precipitation period = DOY 120–214; April 30–Aug 2; $r^2 = 0.80$). The available eddy covariance observations from the site (2006–2010) generally support the hypothesis that the critical climate periods that control August ANPP also underlie interannual

variation in August ecosystem carbon exchange (Fig. S5). Based on the lack of response in biweekly ANPP and net ecosystem exchange in August to climate variability, the greater effect of early-season precipitation than late-season precipitation does not appear to be caused by a compounding effect of increases in growth early season that is not realized later in the season. Neither is the lack of responsiveness of August ANPP to August climate the result of early senescence of the C$_4$ grasses.

The linkages between August productivity and July climate likely are caused by ecophysiological changes in the grasses in response to water stress. During drought, the dominant C$_4$ grasses resorb nitrogen from their leaves, decreasing the grasses' ability to gain carbon once water stress is removed (38, 39). However, even in years with favorable climates during July, August productivity was not responsive to climatic conditions. The lack of responsiveness to August climate is unlikely to be due to the result of changes in growing season length, because in almost all years there was still production and green leaf area throughout August. One distal explanation of why favorable August climates are not associated with greater productivity could be phenological (40). Similar to long-lived temperate trees senescing in conjunction with photoperiod cues to minimize damage from low temperatures (41), there might be an evolutionary response of the predominant long-lived C$_4$ grasses (42) to minimize the risks associated with the extreme environmental conditions observed in August by adjusting their timing of reproduction and senescence (17, 43). August has the most variable temperature and soil moisture at Konza, and although August is cooler on average than July, August has had the most extreme heat waves (Fig. 2). The majority of the grass biomass in watershed 1D at Konza is produced by a few C$_4$ grass species (44); future research would need to compare the physiology of a range of grass species with different evolutionary histories to test this possibility. Likewise, although other studies have quantified the seasonal sensitivity of aspects of plant productivity to precipitation (14, 15, 45), more research in other sites will be necessary to understand the geographic patterns of seasonal sensitivity to climate.

Another question raised by these results is why the window for heat waves affecting ANPP$_G$ is narrower than the window for drought if both affect ANPP$_G$ through the same mechanism. Most likely, higher temperatures early in the growing season do not have a large net negative effect on ANPP$_G$ early in the growing season because the reduction in growth associated with a decline in soil moisture at that time is offset in part by the positive effects of high temperatures. For example, high temperatures early in the growing season might promote growth directly by raising leaf temperatures closer to the optimum temperature for C$_4$ photosynthesis (27, 28) or indirectly by increasing N mineralization (46).

Although severe climate events will have unambiguously negative effects on ecosystems, future climates are likely to include more subtle shifts in climate variability. Across a quarter-century record of grass productivity, climate, and soil moisture, it is clear that drought and heat waves may share a common mechanism in reducing productivity, but they can be effectively decoupled from one another at different times of year. In addition, for modeling productivity in grasslands, it is apparent that the impacts of climate variability differ throughout the growing season, and climate variability can have minimal impact later in the growing season. Modeling plant productivity also must account for site hydrology as well as plant phenology. As such, accurately forecasting future ecosystem function will require identifying the drivers of seasonal patterns of climate variability and also the seasonal sensitivity of key ecosystem processes to climate variability for a range of ecosystems.

In all, merely documenting an increase in the likelihood for future droughts or heat waves is insufficient for predictions of future ecosystem productivity. In understanding plant productivity, it is possible that the timing of climate variability is just as important—if not more—than its magnitude.
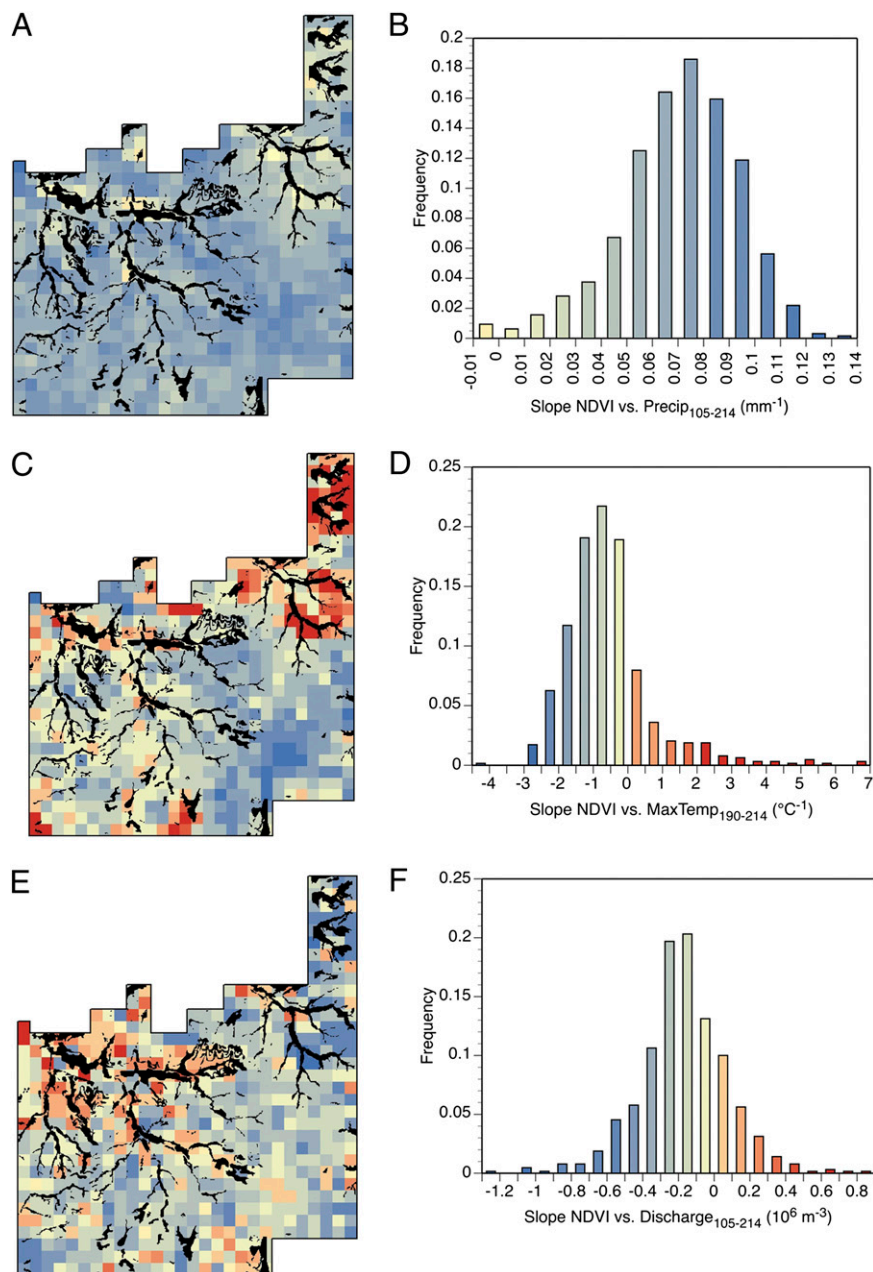
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Fig. 3. Maps of Konza showing the slopes of the relationships between NDVI and climate indices. Shown are (*A*) precipitation from DOY 105–214, (*C*) stream discharge over the same period, and (*E*) mean daily maximum temperatures from DOY 190–214. Also shown are the univariate distributions of these slopes (*B*, *D*, and *F*). Colors of slopes on maps correspond to colors in histograms.

Materials and Methods

Long-term ecological research (LTER) datasets ASD01, PAB01, and AWE012 are archived in the on-line Konza LTER database (www.konza.ksu.edu).

Graminoid ANPP was measured at the end of each growing season from 1984–2010 by clipping all vegetation in five quadrats (20 × 50 cm) in four transects in each of two landscape positions in an annually burned, ungrazed watershed (watershed 1D). Clipping dates ranged from August 31 to October 14 among years, but there was no relationship between the date of clipping and ANPP (*P* = 0.73). Each year, biomass was separated into graminoid, forb, and woody components. All biomass was oven-dried before weighing. Graminoid biomass, which is almost all grasses, composes 96% of the herbaceous biomass in the watershed and is examined exclusively here. Biweekly clipping of biomass from May to September was conducted in one transect of 20 plots in the lowlands of an adjacent annually burned, ungrazed watershed (watershed 1A) from 1984–1999 using the same methodologies as the end-of-year sampling in watershed 1D. For seasonal

biomass patterns, a spline (λ = 10⁴) was fit for the relationship between grass biomass and DOY for each year, allowing calculation of biomass at specific dates. Daily climate data were collected from a weather station located at Konza Prairie headquarters, ~5 km away from watershed 1D. Growing season soil moisture at 25 cm was assessed biweekly from two points in the lowlands of watershed 1D from 1984–2010. Soil moisture was measured with a neutron depth moisture gauge (Troxler Electronics, Inc.) in thin-walled aluminum access tubes buried 2 m deep. Soil-moisture data were expressed as an index of apparent field capacity (17). Daily stream discharge data (1984–2010) were taken from a US Geological Survey hydrologic station (06879650) on King's Creek, which drains a 1,060-ha watershed.

For the critical climate period analysis, precipitation was summed, and daily maximum air temperature was averaged for 861 periods between DOY 60 (March 1) and DOY 274 (October 1). The number of periods corresponds to all possible periods between the two dates with a minimum length of 15 d where start and end dates are incremented in 5-d steps (e.g., day 60–74,

60–79. . .260–274). A forward stepwise regression was initiated using precipitation data and mean daily maximum temperatures from all 861 periods to explain variation in response to variables such as $ANPP_G$. Although we refer to "heat waves" categorically, our analyses treat temperature continuously, using the continuous relationship between temperature and $ANPP_G$ as a surrogate for a categorical representation of elevated air temperatures. Then the critical precipitation or temperature period that explained the highest amount of variation in flowering was selected as a predictor variable, and the process was repeated for the next most significant climate period. Critical climate periods of the same climate variable that overlapped in time were not allowed in the final model. With no significant interactions between landscape position and critical climate periods (Fig. S6), $ANPP_G$ values for the two landscape positions were averaged for each site for all analyses.

To determine the effects of seasonal patterns of drought on $ANPP_G$, we first determined the residual variation in $ANPP_G$ after accounting for $MaxTemp_{190-214}$ and stream discharge. We then determined bivariate relationships between residual $ANPP_G$ and each 15-d sum of precipitation from DOY 60–274. The same process was used for 15-d averages of mean daily maximum temperatures, except that residuals were calculated against daily precipitation from DOY 190–214 ($Precip_{105-214}$) and $Discharge_{105-214}$. From 1984–2010, there was no relationship between $Precip_{105-214}$ and $MaxTemp_{190-214}$ ($P = 0.11$). Daily evapotranspiration of a reference grass stand was calculated with local climate data using the modified Penman–Monteith equation (47) and scaled to a Konza lowland grass stand using a crop coefficient of 0.97 (34).

The moderate-resolution imaging spectrometer (MODIS) collects daily observations of the Earth's surface at a grain size of 250 m. From these data NDVI is calculated for the MODIS Vegetation Indices product (MOD13Q1; http://modis.gsfc.nasa.gov/), which incorporates the highest NDVI value in each 16-d period. We extracted these NDVI data for the 16-d period starting August 29 of each year from 2000–2010. The resulting data set included 640 pixels over the study region, each with 11 NDVI observations. For each pixel, we ran a bivariate regression with $Precip_{105-214}$, $Discharge_{105-214}$, and $MaxTemp_{190-214}$ as model effects ($n = 11$). There was no relationship between the two climate parameters from 2000–2010 ($P = 0.23$), so the regressions were run independently. The resulting slope of the NDVI–climate relationship was recorded for each pixel. A spatial pattern in this quantity was evident whereby the NDVI–climate relationship was stronger (increased slope) at higher elevations. Elevation data (30-m resolution) were acquired from the US National Hydrography Dataset and aggregated up to 250 m to match the resolution of MODIS. For each pixel, we calculated the fraction of the area that was woody vegetation with a supervised classification using a 2010 US Department of Agriculture National Agriculture Imagery Program (http://www.fsa.usda.gov/Internet/FSA_File/naip_2009_info_final.pdf) projection (1-m resolution).

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