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ORIGINAL ARTICLE

Revisiting Patterns and Controls of Productivity in a Mesic Grassland 30 Years Later: Do We Know Now What We Knew Then?

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ABSTRACT

Given the rapid pace of global change, determining if our past understanding of the controls of ecosystem structure and function remains robust today is essential for managing and conserving ecosystems. Here, we revisit a foundational study that evaluated patterns and controls of aboveground net primary productivity (ANPP) across topographic gradients and in response to fire frequency treatments from 1975 to 1993 in tallgrass prairie (Konza Prairie). We replicated this 30-year-old study for a contemporary period (2005–2023) and found that overall patterns of ANPP across fire treatments and topographic gradients remained consistent. However, the magnitude of ANPP responses to fire increased substantially ($>$ twofold) in lowlands, resulting in greater landscape-scale divergence in ANPP. Differences in temporal variability among topographic positions and fire regimes also increased ($\sim$ fourfold). Annual precipitation remained a primary determinant of ANPP, but atmospheric vapor pressure deficit (VPD) has emerged as a new driver in contemporary times. Furthermore, air temperature and deep soil moisture have now become significant controls of ANPP in unburned grassland. We conclude that despite myriad global changes, the primary controls of ANPP have not changed dramatically over three decades, but additional drivers have emerged (notably VPD), and the magnitude of responses to fire have been altered. Increased spatial variation in ANPP as well as interannual variability in ANPP differing more strongly among sites will be particularly challenging for managing this rare grassland. As temperatures and VPD continue to increase, additional revision to our understanding of the functioning of this and other ecosystems will likely be necessary.

Key words: ANPP; Climate; Grassland; Net primary production; Precipitation; Tallgrass prairie; Vapor pressure deficit.

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INTRODUCTION

The value of long-term observations and experiments in the ecological sciences is well documented (that is, Franklin and others 1990; Likens and others 1996; Lindenmayer and others 2010; Knapp and others 2012). While such studies can be quite impactful (Hughes and others 2017), they are challenging by their very nature to replicate. But replication, in all its forms (Filazzola and Cahill 2021) can help establish the reliability and generalizability of past research. Conceptual replications, which repeat tests of hypotheses, or replicate experiments under different background conditions often with alternative methods (Schmidt 2009; Lynch and others 2015; Hudson 2023), are common in ecology as a means of evaluating the generality of ecological principles. Less common, but especially relevant in this era of rapid global change, is the conceptual replication of studies conducted in the same location but during a much later time period. Such studies have revealed both expected and unexpected impacts of changing climate and disturbance regimes on the structure and function of a wide array of ecosystems (Damschen and others 2010; Jules and others 2022; Cipa and others 2024; Stevens 2024). Similarly, temporal changes in ecological processes have been documented by assessing long-term trends (for example, Ponce-Campos and others 2013; Jiao and others 2021; Denissen and others 2022). But the conceptual replication of studies that comprehensively assess both patterns and controls of ecosystem processes over many years is less common. Doing so can be valuable, however, for determining if our understanding of the controls of ecosystem functioning based on the past remains robust in today's rapidly changing world (Schmidt 2009; Lynch and others 2015; Guttinger 2020).

Thirty years ago, Briggs and Knapp (1995, hereafter referred to as *BK95*) evaluated how aboveground net primary production (ANPP), an important integrative variable of ecosystem function and a key component of the global carbon cycle (Abrams 1993; Fahey and Knapp 2007), varied in a native tallgrass prairie. The *BK95* analyses focused on the influence of climate and topography on ANPP along with fire, an important historic driver and contemporary management tool in these productive mesic grasslands (Hulbert 1969). This paper, based on 19 years of data collected as part of the Konza Prairie LTER program (Knapp and others 1998), represented one of the more comprehensive analyses of the patterns and controls of productivity for a grassland type that has largely disappeared (Samson and Knopf 1994). Based on almost two decades of annual measurements of ANPP from upland and lowland sites in watersheds that were subjected to either annual fire or protected from fire (unburned), *BK95* provided a broad summary of the spatial and temporal dynamics of ANPP for this now rare grassland type (Table 1). This analysis expanded significantly on what could be inferred from past, mostly short-term studies of ANPP in this grassland type (for example, Ehrenreich 1959; Kucera and Ehrenreich 1962; Hadley and Kieckhefer 1963; Hulbert 1969; Old 1969). Moreover, while the Konza Prairie lies as the western, drier edge of the original extent of the tallgrass prairie (Knapp and others 2001), the inclusion of sites with deep, lowland soils, more typical of the historic grasslands further east (Ransom and others 1998) provided insight into the controls of productivity for the wetter (now agricultural) regions of this once vast grassland. A biome that extended from Texas to Canada and from eastern Kansas through Illinois and further east as the prairie peninsula (as described by Transeau 1935).

More than 30 years have passed since 1993—the final year included in the *BK95* analysis, providing us with an opportunity to revisit this assessment of the dynamics of ANPP, and if necessary, revise our understanding of the key aspects of grassland functioning. Here, we replicate (to the extent pos-

Table 1. Key Results from *BK95*

- In this mesic grassland, the most productive sites were annually burned lowlands, with ANPP ~ 33% greater than in annually burned uplands or unburned sites
- During the 19-year period, ANPP varied dramatically – as much as 4-fold across all sites
- Coefficients of variation for ANPP across years were similar among sites, varying from 23.2–28.6%
- Precipitation, pan water evaporation (a surrogate for atmospheric demand or vapor pressure deficit, VPD) and soil moisture were related to interannual variability in ANPP, but only in annually burned sites
- When graminoid ANPP was assessed separately, climatic controls remained the same as total ANPP, whereas the dynamics of forb ANPP were unrelated to any climatic variable regardless of fire regime
- A negative correlation between grass and forb ANPP was reported across all site

sible) the *BK95* study to reassess the patterns and controls of ANPP today. Because the Konza Prairie is an LTER site with a core mandate to provide consistent long-term data on patterns and controls of primary production (Callahan 1984), we were able to conduct this study with ANPP data estimated with the same methods, and from the same sites, included in *BK95*. Importantly, our goal was not to provide an extension of past analyses, but to conduct a true conceptual replication based on non-overlapping data (1975–1993 *vs*. 2005–2023), allowing us to independently evaluate how our past understanding of ANPP dynamics in this once extensive grassland ecosystem has changed.

METHODS

Study Site

Konza Prairie Biological Station (KPBS) is a 3487-ha native tallgrass prairie located in the Flint Hills of Northeast Kansas, USA (Knapp and others 1998). KPBS has a temperate mid-continental climate with an average annual precipitation of 876 mm over the past five decades. Most precipitation (~ 75%) occurs during the growing season (April–September). The topography of KPBS is typical of the Flint Hills, featuring rolling hills with shallow-soiled uplands (Florence series soils) and deep-soiled lowlands (Tully series soils) that are separated by steep slopes (Ransom and others 1998). Fire is a key component shaping plant communities in the tallgrass prairie (Collins and Wallace 1990) and has been estimated to have had a 2–4-year return interval in the Flint Hills region over the past three centuries (Allen and Palmer 2011). When fire is frequent, tallgrass prairie plant communities are dominated by perennial C_4 grass species (*Andropogon gerardii, Sorghastrum nutans, Panicum virgatum, and Schizachyrium scoparium*) that co-occur with sub-dominant C_3 grasses and forbs. However, in the absence of fire, woody plants rapidly expand into this relatively mesic grassland, becoming a locally dominant form of vegetation (Briggs and others 2005; Ratajczak and others 2014a). KPBS is divided into experimental watersheds, each assigned a prescribed (spring) fire treatment (including 1-y and 20-y fire return intervals, with the latter often referred to as ''unburned''). Some watersheds on KPBS have been subject to the annual and unburned fire treatments since 1975. Grazing treatments (native bison, cattle, or no grazing) exist as well but were not included in the *BK95* analyses.

Climate Data

Annual and growing season (April–September) climate data were evaluated during two non-overlapping 19-year periods: a historical period (1975–1993), evaluated previously by *BK95*, and a contemporary period (2005–2023) that we assessed. We used the same data sets and sources that *BK95* used as much as possible. Thus, following *BK95*, precipitation data used for analysis were from Manhattan, KS (~ 10 km north of KPBS). In addition to precipitation, *BK95* evaluated pan water evaporation—a surrogate for atmospheric demand. Unfortunately, pan water evaporation data were not available for the contemporary period, so average daytime vapor pressure deficit (VPD) and temperature measured for the growing season at KPBS headquarters were used as proxy variables for both time periods (dataset: AWE012; Nippert 2024). Average values for VPD and temperature were calculated from hourly measurements between the times of 8:00 am and 7:00 pm, which correspond to ~ 1.5 h after the average time of sunrise and before the average time of sunset for the growing season. To reduce bias introduced by missing data, only days with at least 8 of the 12 h of measurements were included in analysis (16 days removed), and gap filling was completed for all days with missing and erroneous data using the average value from the prior and subsequent 3 days of data.

Soil Moisture Data

Soil moisture measurements have been made in the lowlands of annually burned and unburned watersheds since 1983 at a biweekly frequency during the growing season and at a monthly frequency during the rest of the year (dataset: ASM01; Nippert 2023). Measurements were made using a neutron probe (Troxler Electronic Inc., Research Triangle Park, NC; InstroTek Inc., Research Triangle Park, NC) at two locations in each watershed recorded at 25 cm increments to a depth of 150 cm. Over the duration of the study, the neutron probe was replaced on two occasions with newer models that resulted in measurement variation. To account for differences in probe sensitivity, soil moisture was expressed as an index of field capacity, similar to the approach used by BK95 and Craine and Nippert (2014) (See supporting information for additional details). Soil moisture values were averaged by month, and monthly values were averaged for the growing season (April–September).

Productivity Data

Aboveground net primary productivity (ANPP) was evaluated for grasses (graminoids including sedges), forbs, and total herbaceous plants using long-term ANPP data from KPBS (dataset: PAB011; Blair and Nippert 2024). We used the same data analyzed in *BK95* (from uplands and lowlands of annually burned or unburned ungrazed watersheds). Because there were some minor treatment changes over the years at KPBS, we also repeated the *BK95* analysis for just those sites that were also measured during the contemporary period. Eliminating these few sites from the *BK95* analysis had minimal impact on the results reported (Table S1), and thus, we were able to use LTER data collected from the same watersheds for both historical and contemporary periods. In all cases, ANPP was measured at the end of the growing season (late August–September) by harvesting all vegetation in five 50 cm × 20 cm quadrats that are evenly spaced along a permanent sampling transect. Each watershed contains four transects in the lowlands and four transects in the uplands (20 quadrats per topographic position). Biomass was harvested at ground level and sorted into living, current year's dead, and previous years dead. Living biomass was further sorted by functional group: grasses, forbs, and woody plants. Following the methods of *BK95,* total herbaceous ANPP was calculated as the sum of the grass, forb, and current year dead biomass. In some quadrats, significant woody plant biomass occurred in the lowlands of the unburned treatment but usually not present before 2005 and to be consistent with *BK95* and to avoid biasing contemporary ANPP estimates with biomass from woody plant parts that contained multiple years of growth. Prior to 1983, biomass was not sorted by functional group, and thus, only total biomass was evaluated for the entire historical period (Briggs and Knapp 1995). Comparisons between historical and contemporary periods for functional group ANPP were made using a condensed historical timeframe (1983–1993). Following the methods of *BK95*, the ANPP of all plots and transects were averaged to provide a single estimate per topographic position per watershed.

Statistical Analysis

Statistical analysis was performed in R version 4.3.2 (R Core Team 2023). As in *BK95*, temporal trends in ANPP, climate, and soil moisture; and the relationship for ANPP with climate, and soil moisture were evaluated using linear regression analysis. Separate analyses were completed for each combination of topographical position (upland and lowland) and fire return interval (annual vs unburned) for each period. Changes in the relationship of ANPP with climate and soil moisture between periods were evaluated using multiple regression. ANCOVA was used to evaluate differences in resource-use efficiency for ANPP between periods (Ex. changes in precipitation-use efficiency). Changes in the patterns of total and functional group ANPP across topographical positions, fire regimes, and periods were evaluated using ANOVA, and a Tukey's HSD test was used for pairwise comparisons (Emmeans package; Lenth 2021). The coefficient of variation for ANPP was also calculated for each site during each period following *BK95*. In addition to the abiotic drivers of ANPP, we evaluated grass ANPP as a biotic control of forb ANPP across topography and fire regimes. Linear regression models were used to evaluate the relationship between grass and forb ANPP and the relationship between annual changes in grass and forb ANPP.

RESULTS

Changes in Climate

Mean climate conditions at KPBS differed modestly between historical and contemporary periods. There were no significant long-term trends in annual and growing season precipitation measured from 1975 to 2023, and growing season VPD measured from 1982 to 2023 during the study period (Figure 1). Nor did the mean values of these climate variables differ between historical and contemporary periods. In contrast, growing season temperatures at KPBS increased from 1982 to 2023 (Figure 1; $P = 0.008$), leading to higher growing season temperatures during the contemporary period (+ 0.9 °C; $P < 0.001$). However, this trend was not evident regionally as growing season temperature and VPD measured at two nearby weather stations did not increase significantly from 1975 to 2023 (Figure S1; Manhattan Regional Airport and Fort Riley Marshall Army Airfield). Finally, atmospheric CO_2, although not a climatic variable nor measured locally at KPBS, increased from a mean of 349 ppm for the years in the *BK95* analysis versus 404 for the contemporary period (Figure S2; $P < 0.001$).

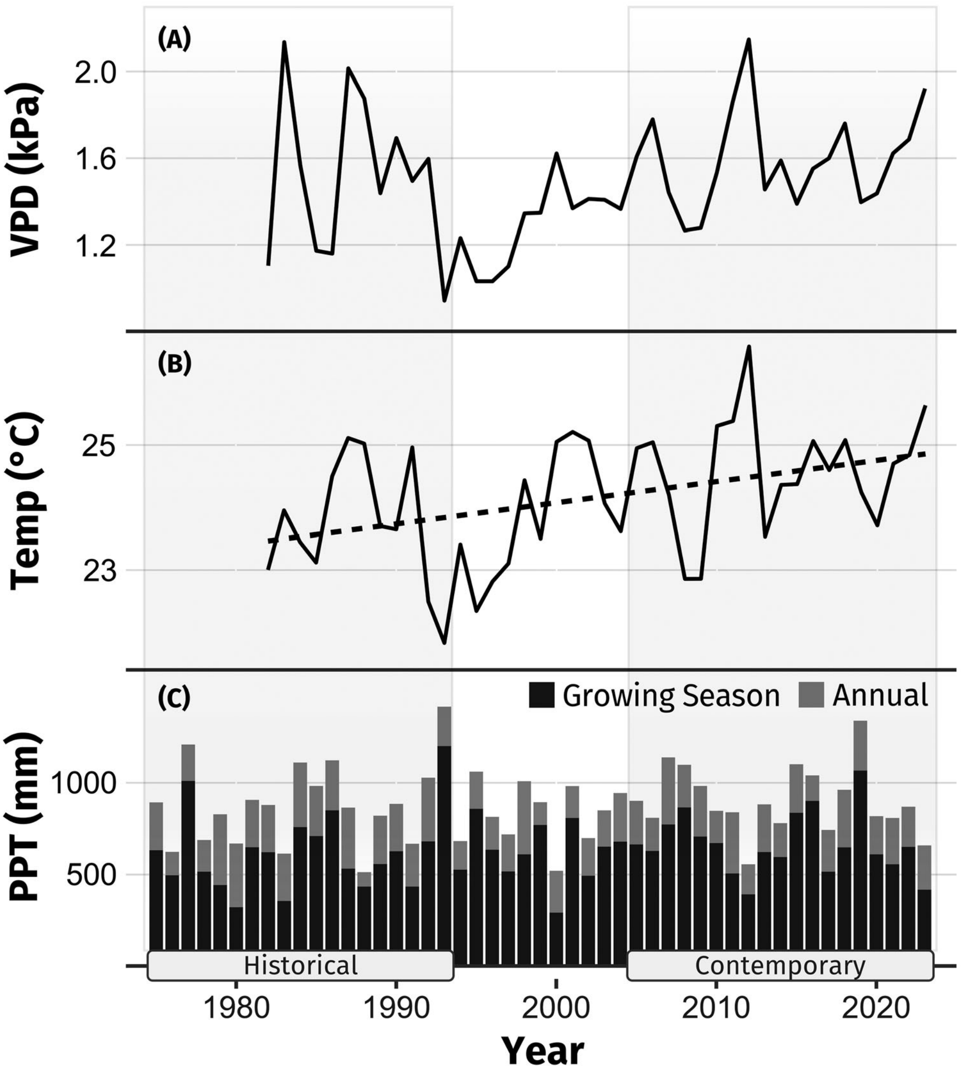


Figure 1. Long-term trends in (top) growing season vapor pressure deficit (VPD), (middle) growing season temperature, and (bottom) annual and growing season precipitation. Statistically significant monotonic trends ($P < 0.05$) are indicated by a dotted black line. Mean annual precipitation and its interannual CV were 880 ± 229 and 26.0 during the historical period and 904 ± 184 and 20.3 during the contemporary period

Patterns and Climate Controls of Total Productivity

Few changes occurred in the overall patterns of total herbaceous productivity between historic and contemporary periods. Changes in ANPP, however, tended to amplify patterns reported in *BK95* (Table 1; Figure 2a). Historically, ANPP was higher in annually burned lowland prairie (by ~ 33%), and no differences occurred among the other three treatments (annually burned uplands, unburned uplands, or unburned lowlands, Figure 2a). Over time, ANPP of lowlands has increased with annual burning ($P < 0.001$), but decreased in the absence of fire ($P < 0.001$; Figure 2b, Figure S3) while remaining unchanged in uplands. These changes have led to a greater magnitude of difference among treatments in the contemporary period (ANPP is now > twofold higher in annually burned vs. unburned lowlands today). However, the only notable change in ANPP pattern is that ANPP is now lower in unburned lowlands compared to annually burned uplands in the contemporary analysis ($P < 0.001$), whereas these treatments were historically similar ($P = 0.69$; Figure 2a).

The *BK95* analysis noted only modest differences among treatments in the coefficient of variation (CV) of ANPP over the 19-year study period (varying from ~ 23 to 28%; Table 2). In the con-

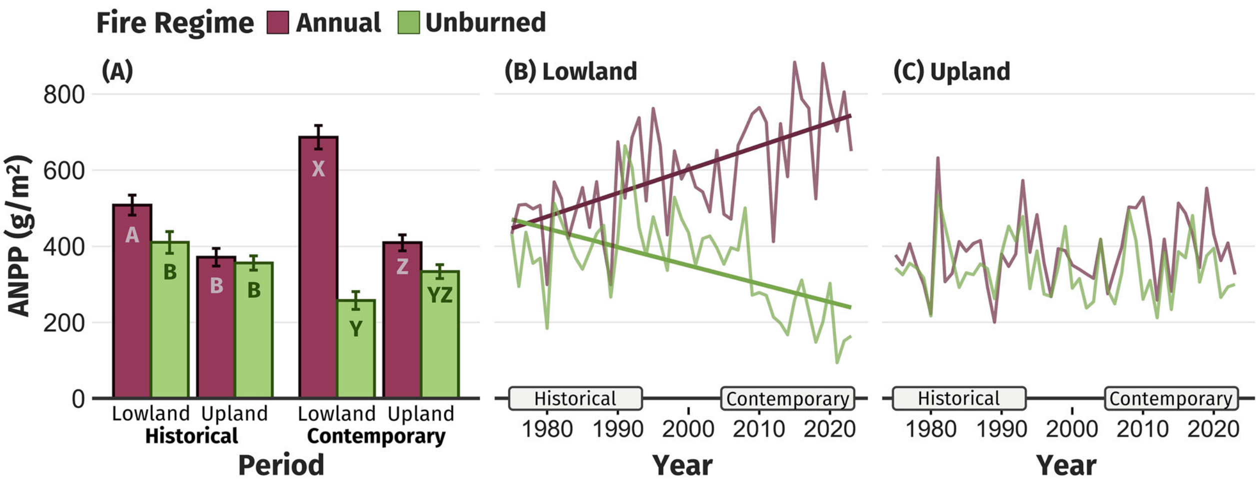


Figure 2. **A** Mean herbaceous ANPP (± 1SE) in upland and lowland prairies with different fire return intervals (annually burned = purple and unburned = green) during historical (1975–1993) and contemporary periods (2005–2023). Comparisons of mean ANPP between periods are not shown here but are provided in Figure S3. **B** and **C** Annual and long-term trends in herbaceous ANPP from 1975 to 2023 for lowlands (**B**) and uplands (**C**) of annually burned and unburned prairies. Regression lines indicate statistically significant long-term monotonic trends ($P < 0.05$)

Table 2. Changes in the Coefficient of Variation (CV) of Total ANPP in Upland and Lowland Prairies with Annual Burning or No Burning Between Historical (1975–1993) and Contemporary Periods (2005–2023)

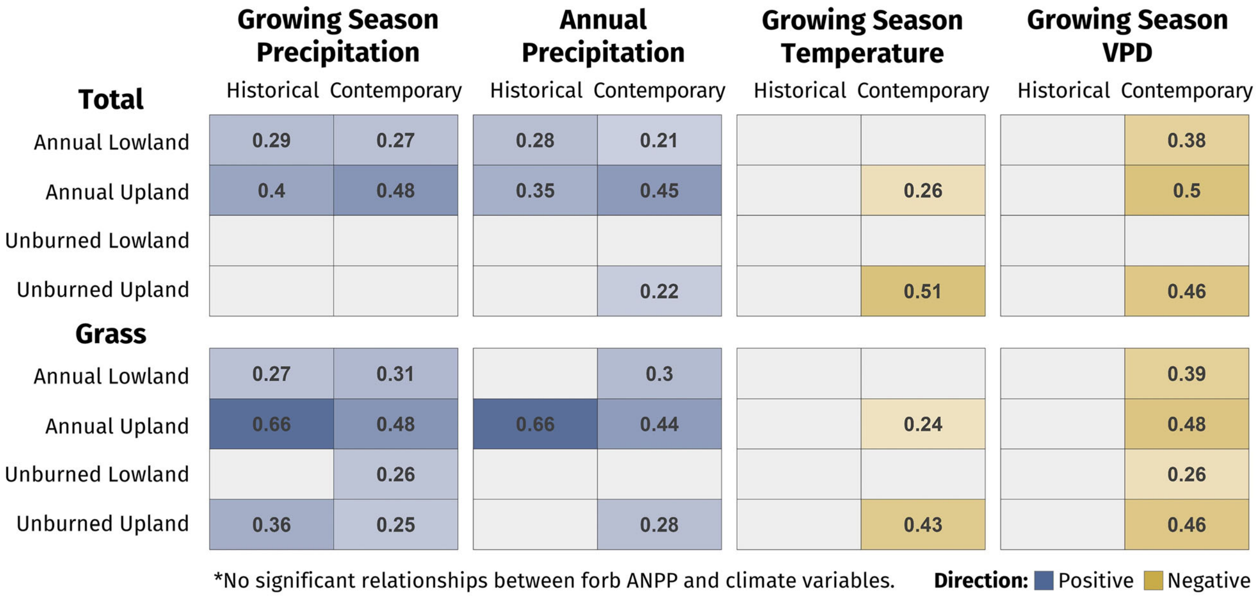
Fire Regime	Topography	CV	
		Historical	Contemporary
Annual Burn	Uplands	27.3	21.9
	Lowlands	22.6	19.7
Unburned	Uplands	21.8	23.8
	Lowlands	28.3	39.6

See Figure 1 for corresponding CVs for precipitation

temporary period, CV decreased in annually burned treatments and increased in unburned treatments, leading to a much larger range of CV across sites in contemporary times (CV = 19.7–39.6%; Table 2). Indeed, while BK95 noted that ANPP varied fourfold across all years and sites (Table 1), this range has now doubled to > eightfold in contemporary times (Figure 2).

During the historical period, annual and growing season precipitation were the primary determinants of interannual variability in ANPP in annually burned treatments, with stronger relationships in uplands (with shallow soils) than lowlands (Figure 3). While the strength and sensitivity of the relationships between total ANPP and precipitation remained similar in the contemporary period (Figures 3, 4; See Figure S4 for additional regression models), precipitation-use efficiency increased markedly in lowland sites because higher ANPP occurred across a wide range of precipitation inputs (ANCOVA $P < 0.001$; Figure 4a). In addition to this change, VPD and temperature measured at KPBS emerged as strong controls of ANPP in annually burned grassland during the contemporary period (Figure 3). To confirm that these emergent climatic controls were not a product of the shorter time period that climate data were available from KPBS, we compiled VPD and temperature data from two nearby weather stations (Manhattan Regional Airport and Fort Riley Marshall Army Airfield), which spanned the entire historical period (1975–2023). These data also showed no relationships between VPD, temperature, and ANPP historically (Figure S5).

Historically, *BK95* reported that total ANPP was not related to any climatological variables in the unburned watersheds at KPBS (Figure 3). This remained true in unburned lowlands in the con-



	Growing Season Precipitation		Annual Precipitation		Growing Season Temperature		Growing Season VPD	
Total	Historical	Contemporary	Historical	Contemporary	Historical	Contemporary	Historical	Contemporary
Annual Lowland	0.29	0.27	0.28	0.21				0.38
Annual Upland	0.4	0.48	0.35	0.45		0.26		0.5
Unburned Lowland								
Unburned Upland				0.22		0.51		0.46
Grass								
Annual Lowland	0.27	0.31		0.3				0.39
Annual Upland	0.66	0.48	0.66	0.44		0.24		0.48
Unburned Lowland		0.26						0.26
Unburned Upland	0.36	0.25		0.28		0.43		0.46

*No significant relationships between forb ANPP and climate variables. **Direction:** ▨ Positive ▨ Negative

Figure 3. The coefficient of determination (R^2) for statistically significant relationships between climate variables and total ANPP (top) and grass ANPP (bottom) across topographic positions and fire return intervals. Shading indicates the direction of the relationship (positive = blue and negative = yellow). Light gray blank cells indicate no significant relationship between climate and ANPP. Forb ANPP is not shown since no significant relationships with climate variables were detected

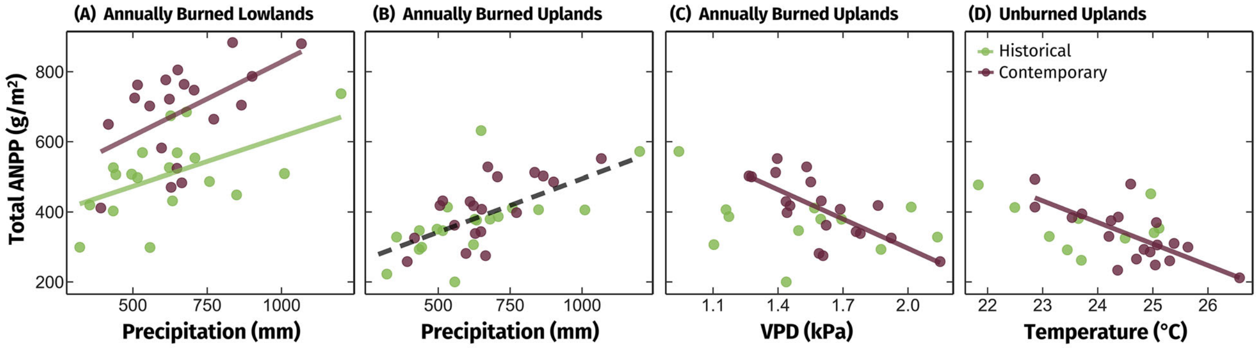


Figure 4. Relationships between total ANPP and growing season climate variables: **A** precipitation in annually burned lowland prairie, **B** precipitation in annually burned upland prairie, **C** vapor pressure deficit in annually burned upland prairie, and **D** temperature in unburned upland prairie. Colors indicate historical (green) and contemporary (purple) periods. Solid-colored regression lines represent significant relationship for a given period, dotted black regression lines represent significant relationships for both periods with no significant difference between periods, and the absence of a regression line indicates no significant relationship ($P > 0.05$). All other plotted regressions between climate and ANPP are shown in Figure S4

temporary period, but in the unburned uplands, new climate variables became important controls of ANPP (Figure 3). Strong negative relationships between ANPP and both air temperature and VPD emerged in unburned uplands during the contemporary period ($R^2 = 0.51$ and 0.46; Figures 3 and 4d), as well as a positive relationship between ANPP and annual precipitation ($R^2 = 0.22$; Figure 3).

Patterns and Climate Controls of Grass and Forb ANPP

During both time periods, a majority of the total herbaceous ANPP across all sites was comprised of grasses (Figure S6). Grass ANPP was also the primary driver of changes in total ANPP over time and in response to climatological variables (Figure S6). As with total ANPP, grass ANPP was greatest in lowland prairie with annual burning, and it increased over time leading to greater grass ANPP in the contemporary period ($P =\ < 0.001$; Figure S6). In the absence of burning, grass ANPP decreased long-term in lowland prairie leading to reduced productivity in the contemporary period ($P = 0.012$; Figure S6). Overall, grass ANPP exhibited slightly stronger relationships with climate during both periods compared to total ANPP (Figure 3).

Responses of forbs are of particular interest because this growth form is responsible for most of the diversity of plant species in tallgrass prairie communities (Collins and Calabrese 2012; Towne 2002). Overall, the ANPP of forbs remained similar between historical and contemporary periods across most sites, with changes in forb ANPP evident only in unburned lowlands (Figure S6; $P = 0.0047$). Historically, unburned lowland sites had higher forb ANPP relative to other sites and forbs contributed nearly 33% of the total ANPP (Figure S6). But decreasing ANPP of forbs in unburned lowlands diminished differences between unburned uplands and lowlands ($P = 1.00$, Figure S6). Decreased ANPP of forbs in unburned lowland prairie was not related to changes in soil moisture or climate variables (Figure 3, Figure S6). During both periods, forb ANPP was significantly greater in unburned relative to annually burned treatments (Figure S6; $P < 0.001$).

Consistent with the results of *BK95*, a significant negative correlation between grass and forb ANPP was evident in the contemporary analysis when data from all fire treatments and topographic locations were combined ($P < 0.001$; $R^2 = 0.14$). However, when topography and fire frequency were included in this analysis, no significant relationships occurred between the two growth forms in annually burned treatments or in unburned uplands (Figure 5). The only significant relationship between forb and grass ANPP was found in unburned lowlands where grass ANPP was positively related to forb ANPP ($P = 0.012$; $R^2 = 0.23$). Relationships between grass and forb ANPP did not change between historical and contemporary periods.

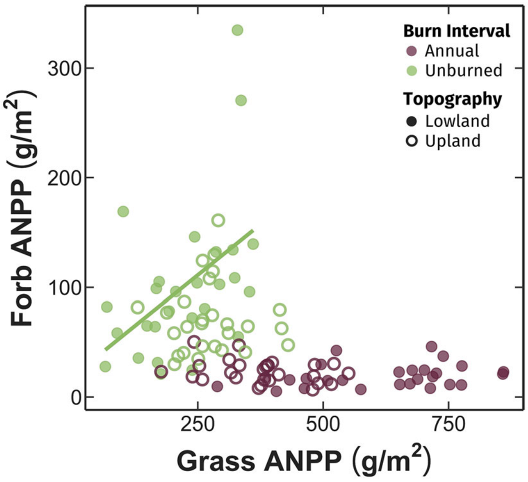


Figure 5. Relationship between forb and grass ANPP across topographic positions and fire return intervals from 1984 to 2023. The solid green regression line indicates a statistically significant relationship between grass and forb ANPP in unburned lowland prairie ($R^2 = 0.23$)

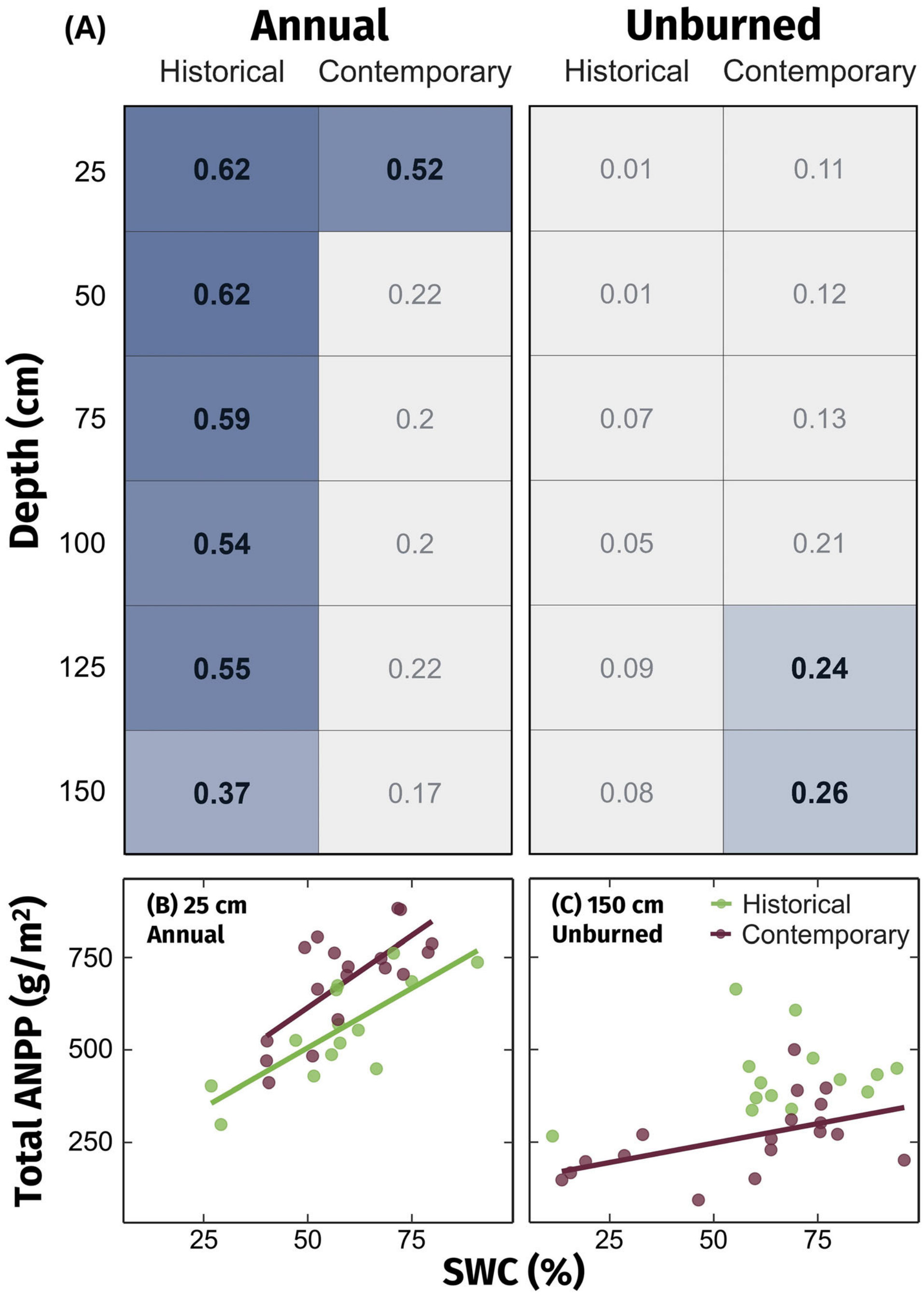
Soil Moisture Control of ANPP

The effect of soil moisture during the growing season on ANPP could only be evaluated in annually burned and unburned lowlands. For both time periods, soil moisture was related to ANPP more strongly with annual burning (Figure 6a). In unburned prairie, soil moisture was not related to total ANPP historically at any soil depth (Figure 6a). This remained true for shallow depths during the contemporary period, but at deeper depths, soil moisture has become weakly related to total ANPP, with the strongest relationship occurring at a depth of 150 cm (Figure 6c, $R^2 = 0.26$, $P = 0.02$). This contrasts with annually burned lowlands where soil moisture was most strongly related to total ANPP at shallow soil depths—the strongest relationship was at 25 cm depth (Figure 6b). In the annually burned lowlands, the relationship between soil moisture and ANPP was weakened at all depths in the contemporary period, with a significant relationship only occurring at the 25 cm depth ($P < 0.001$; $R^2 = 0.52$; Figure 6a). Finally, at 25 cm depth, ANPP of annually burned lowlands was greater in the contemporary period compared to the historical period across a wide range of soil moisture values (Figure 6b; ANCOVA $P = 0.003$).

Relationships between grass ANPP and soil moisture were very similar to total ANPP as detailed above (Figure S7). Forb ANPP was not related to soil moisture at any depth during either period (Figure S7).

DISCUSSION

Ecologists have been diligent in documenting the wide range of impacts that global change has had on organisms and ecosystems (for example, Parmesan and Yohe 2003; Song and others 2019). However, determining the degree to which global



Depth (cm)	Annual Historical	Annual Contemporary	Unburned Historical	Unburned Contemporary
25	**0.62**	**0.52**	0.01	0.11
50	**0.62**	0.22	0.01	0.12
75	**0.59**	0.2	0.07	0.13
100	**0.54**	0.2	0.05	0.21
125	**0.55**	0.22	0.09	**0.24**
150	**0.37**	0.17	0.08	**0.26**

Figure 6. A Coefficient of determination (R^2) for relationships between total ANPP and soil moisture by soil depth in lowlands of annually burned and unburned prairies during historical and contemporary periods. Blue-filled cells indicate statistically significant positive relationships ($P < 0.05$), and gray cells indicate non-significant relationships. **B** Linear regression of ANPP and soil moisture at 25 cm depth in annually burned prairie. **C** Linear regression of ANPP and soil moisture at 150 cm depth in unburned prairie

change has altered our understanding of the patterns and controls of ecosystem functioning remains a challenge. Replicating historical research (as closely as possible) focused on ecosystem processes, patterns, and their controls offers opportunities to determine if the past knowledge requires revision. As envisioned by Callahan (1984), long-term ecological research (LTER) sites have documented many of the key variables controlling the structure and functioning of ecosystems across

North America (Knapp and others 1998; Priscu 1998; Bowman and Seastedt 2001; Havstad and others 2006; Chapin and others 2006; Magnuson and others 2006; Lauenroth and Burke 2008; Brokaw and others 2012; Hobbie and Kling 2014; Childers and others 2019). Today, LTER sites have continued to collect many core datasets, making them uniquely valuable for revisiting and potentially revising our past understanding of the ecology of key ecosystems and biomes. In this specific study, we re-assessed the major findings of a past analysis of patterns and controls of ANPP at the Konza Prairie, a mesic grassland LTER site. Our approach was to repeat this analysis 30 years later to determine if our understanding of the patterns and controls of productivity, as influenced by fire frequency and topographic position, has been altered over time.

Changes in the Patterns of Productivity

Our results revealed that changes in ANPP between the two time periods varied by topographic position and fire regime. Lowland sites exhibited significant changes in ANPP, with fire regime determining the direction of change, while upland topographic positions remained relatively unchanged from the *BK95* analysis. While these changes led to few differences in the overall patterns of ANPP across topographic positions and fire regimes, greater divergence among sites and treatments were evident as a doubling of the range of ANPP among sites (from fourfold historically to eightfold) and a fourfold increase in the range in interannual variability in ANPP among sites.

ANPP increased by 35% in annually burned lowlands from the period assessed in *BK95*, leading to greater divergence from the annually burned uplands, where ANPP remained unchanged. This change was not directly related to changes in climate variables or soil moisture. Although the mechanism for this divergence between the wetter lowlands and the drier uplands with annual burning is unclear, it is somewhat consistent with changes in productivity that have occurred worldwide where arid grasslands have become less productive on average and wetter grassland sites have become more productive on average (MacDougall and others 2024). These changes are often attributed to concurrent changes in precipitation (Feng and Zhang 2015), but this cannot explain such divergent patterns at a single site. One potential mechanism for increasing divergence between the uplands and lowlands of annually burned grassland is that increased temperatures may extend the growing season length and increase N-cycling in the wetter lowlands leading to increased ANPP (Wang and others 2006; Dong and others 2024). In contrast, increased temperatures may exacerbate water stress in the drier uplands, negating the positive effects of other factors such as growing season length on ANPP. Increased CO_2 concentrations may also differentially affect ANPP in the wetter lowlands than the drier uplands, although the previous research suggests that drier sites may benefit more, driven by CO_2-induced reductions in stomatal conductance (Morgan and others 2004; Ainsworth and Long 2005). Changes in ANPP of annually burned prairies could also be due to differences in the cumulative number of fires that have occurred between the two periods. Annual burning had occurred for 1–19 years during the historical period, but for 31–49 years in the contemporary period. While early research suggested that long-term annual burning might decrease N-availability over time, lowering ANPP (Ojima and others 1994), there is little evidence that N-limitation of ANPP progressively increases with long-term annual fire in this grassland (Turner and others 1997; Wilcox and others 2016). Indeed, our results show increasing ANPP with time in the lowlands of annually burned prairies. Finally, shifts in community structure, resulting from long-term changes in any of the above factors, can alter ecosystem functioning (Field and others 2007; Smith and others 2009). While the previous research indicates that the community composition has remained relatively similar between periods in annually burned prairie (Collins and others 2012; Bookout and others 2025), sites without frequent fire have shown a dramatic increase in woody plant abundance (mostly shrubs; Briggs and others 2005; Ratajczak and others 2014a). Such a shift in the abundance of this growth form can lead to a concurrent shift in ecosystem functioning (Lett and Knapp 2005; Knapp and others 2008).

In contrast with the increased ANPP in the annually burned lowlands, ANPP in unburned lowlands was reduced by 37%. This change is consistent with the previous research at this site (Ratajczak and others 2014a; Ratajczak and others 2014b) and has been linked to the increase in taller shrubs in more recent times given that the dominant C_4 grass species are relatively shade intolerant (Knapp 1985a, b; Schimel and others 1991; Turner and Knapp 1996; Ratajczak and others 2014a, Ratajczak and others 2014b). The previous research has shown that woody plant encroachment is extensive in the lowlands of KPBS, where water availability is high, but it has had less impact in the drier uplands (Ratajczak and others 2011). This difference could explain why herbaceous ANPP has decreased in the lowlands but not uplands of unburned prairie.

Changes in the Climatic Controls of Productivity

Historically, annual and growing season precipitation were the primary controls of ANPP with annual burning, and uplands were more strongly related to precipitation than lowlands. In contrast, neither variable was related to ANPP in unburned prairie. In the contemporary period, the strength and sensitivity of the relationship between ANPP and precipitation did not change. However, the amount of herbaceous ANPP per unit precipitation was increased in annually burned lowland prairie, so much so that the average ANPP produced on the driest 20% of years was roughly equal to the wettest 20% of years historically. Trends of increasing precipitation-use efficiency have been seen in other ecosystems, and they are often attributed to elevated atmospheric CO_2, which can enhance plant water-use efficiency (Keenan and others 2013; Liu and others 2020; Liu and others 2022).

In unburned sites, the previous research indicated that the accumulation of detritus was a critical factor limiting ANPP by reducing light availability and temperature, as well as altering nitrogen cycling (Knapp and Seastedt 1986; Blair 1997). Fire in annually burned prairies removes this litter and mitigates these effects. Previously, *BK95* proposed that detritus accumulation in the absence of fire may be more critical in limiting ANPP than climate and soil moisture, leading to the lack of climate relationships in unburned grassland. In the contemporary period, relationships between ANPP and precipitation remained weak or absent in the unburned lowlands, while ANPP decreased. As noted above, increased woody plant abundance may contribute to the continued lack of relationships and decreased ANPP by further altering many of the same factors as detritus, such as further reducing light availability and soil temperature and altering nutrient cycling (Lett and Knapp 2005; McCulley and Jackson 2012). Greater woody plant abundance can also alter hydrologic cycles (Huxman and others 2005). Research at KPBS indicates that woody plants have increased preferential flow through soil macropores, leading to greater infiltration of precipitation to deeper soil layers (Keen and others 2024; Jarecke and others 2025). This may lead to greater dynamics in deep soil water and explain the emergence of a weak relationship between ANPP and deep soil moisture in unburned lowlands during the contemporary period.

While precipitation not temperature is the limiting factor in many grasslands (Mowll and others 2015), mounting evidence suggests that rising VPD resulting from increased temperatures will become an increasingly important factor regulating water availability and carbon uptake in many ecosystems (Novick and others 2016; Yuan and others 2019; Grossiord and others 2020; Green 2024). However, the extent of VPD's control on productivity across sites of varying water availability, soil properties, and plant community composition is not well understood (Knapp and others 2024; Green 2024). While VPD was not historically a control of ANPP in this mesic grassland, it has emerged as a strong control of ANPP across most sites in the contemporary period. Interestingly, data from KPBS indicated that air temperatures have increased during the contemporary period, but it did not result in significantly greater VPD due to high interannual variability in relative humidity. However, annual productivity may be influenced by changes in VPD at several temporal scales (for example, from seasonal to diurnal; Noguera and others 2023) and differentially between wet and dry years. Our results further highlight this complexity, showing that responses to rising VPD can vary by topographic position and fire regime within a single ecosystem. These site-level differences may result from variability in other resources and their interactions with VPD. Moreover, differences in VPD and temperature between topographic positions and fire regimes may also contribute to differences in their control over ANPP but were not measured at this scale in the study (Knapp 1985a, b). In this grassland, VPD has emerged as a control of ANPP in uplands, where water is more limited; and in annually burned sites, where soil moisture and precipitation were the primary controls of ANPP; but not in unburned lowlands, where other factors such as light availability were more limiting. Increased control of VPD in annually burned lowlands was also associated with weakened control of ANPP by soil moisture (across all soil depths). Indeed, increasing VPD has been predicted to reduce soil moisture control on ANPP in many ecosystems including grasslands (Novick and others 2016; Konings and others 2017). While soil moisture was not measured in the more arid upland sites, the emergence of VPD as a control of ANPP was associated with annual precipitation emerging as a control of ANPP in unburned uplands and increased control by precipitation in annually burned uplands. Combined, these changes suggest greater overall hydrological limitation of ANPP in contemporary times.

Patterns and Controls of Grass and Forb ANPP

At KPBS, the dominant grasses primarily determine ecosystem functioning, while forbs contribute substantially to overall biodiversity (Collins and others 1998; Smith and Knapp 2003). Historically, *BK95* found that grass biomass tended to strengthen relationships between ANPP with soil moisture and precipitation. Whereas forb ANPP was unrelated to climatic variables regardless of topographic position and fire regime. This trend persisted during the contemporary period and also occurred for VPD and temperature, with neither variable related to forb ANPP. Contemporary changes in the patterns of mean grass ANPP followed the same patterns as total ANPP across all topographical positions and fire regimes. Whereas forb ANPP decreased in the unburned lowlands but did not change at any other site. Decreased forb ANPP in the unburned lowlands is likely due to increased woody plant abundance in unburned lowland prairie. The previous research has shown lower forb ANPP associated with woody canopies compared to open unburned grassland (Lett and Knapp 2005).

BK95 reported a negative correlation between grass and forb ANPP, which was interpreted as forb productivity being limited primarily by competitive interactions with grasses. However, our contemporary analysis suggests that fire is the primary factor limiting forb ANPP. In unburned prairie, forb ANPP did not decrease with increasing ANPP, but instead, forb ANPP varied widely, reaching high values across the entire range of grass ANPP values ($\sim$ 50–400 g/m^2). Forb ANPP even showed a weak positive trend with grass ANPP in unburned lowland prairie, perhaps due to co-occurring long-term declines in both grass and forb ANPP from woody plant encroachment (Ratajczak and others 2014a; Wieczorkowski and Lehmann 2022).

CONCLUSION

Assessing the degree to which global changes are impacting the structure and functioning of key ecosystems is essential from both basic and applied perspectives. By replicating an historical analysis of the patterns and controls of ANPP in mesic grassland for an equivalent contemporary period (30 years later), we show that ANPP in this once widespread grassland ecosystem has become much more variable in response to fire frequency and across topographic gradients. Given that ANPP (as forage for livestock) is perhaps the ecosystem service of most value in this, and most grasslands, increased divergence in productivity across time, fire regimes, and topographic gradients has clear management implications. Additionally, while the primary controls of ANPP (precipitation and soil moisture) have not changed dramatically over the past three decades, VPD has emerged as a new determinant, reflecting a shift toward greater complexity in the hydrological control of ecosystem functioning in the future. Finally, given the rapid pace of global change, we would urge others to replicate historic analyses where possible (for example, LTER and other research sites with long-term data). Of particular value would be revisiting those studies that have formed the basis for our understanding of ecological patterns, processes, and their controls across a range of ecosystems. Doing so will allow us to determine if our past understanding of ecosystems is still robust today and help to identify the mechanisms underlying any changes.

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DATA AVAILABILITY

Data are publicly available at the Konza Prairie LTER data repository (http://lter.konza.ksu.edu/data) or from online sources as indicated in the text.

Declarations

Conflict of interest The author does not have any conflict of interest to declare.

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