

Controls of Aboveground Net Primary Production in Mesic Savanna Grasslands: An Inter-Hemispheric Comparison

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ABSTRACT

Patterns and controls of annual aboveground net primary productivity (ANPP) are fundamental metrics of ecosystem functioning. It is generally assumed, but rarely tested, that determinants of ANPP in one region within a biome will operate similarly throughout that biome, as long as physiognomy and climate are broadly consistent. We tested this assumption by quantifying ANPP responses to fire, grazing history, and nitrogen (N) addition in North American (NA) and South African (SA) savanna grasslands. We found that total ANPP responded in generally consistent ways to fire, grazing history, and N addition on both continents. Annual fire in both NA and SA consistently stimulated total ANPP

(28–100%) relative to unburned treatments at sites with deep soils, and had no effect on ANPP in sites with shallow soils. Fire did not affect total ANPP in sites with a recent history of grazing, regardless of whether a single or a diverse suite of large herbivores was present. N addition interacted strongly and consistently with fire regime in both NA and SA. In annually burned sites that were not grazed, total ANPP was stimulated by N addition (29–39%), but there was no effect of N fertilization in the absence of fire. In contrast, responses in forb ANPP to fire and grazing were somewhat divergent across this biome. Annual fire in NA reduced forb ANPP, whereas grazing increased forb ANPP, but neither response was evident in SA. Thus, despite a consistent response in total ANPP, divergent responses in forb ANPP suggest that other aspects of community structure and ecosystem functioning differ in important ways between these mesic savanna grasslands.

Key words: ANPP; Fire; Grasslands; Grazing; Nitrogen; Savannas.

Received 21 February 2009; accepted 3 July 2009; published online 17 September 2009

Conceived of or designed study: AKK, MDS, GMB, SLC, JMB, NG, RWSF, CEB.

Performed research: GMB, RWSF, DEB, AJC, KPK, JMB.

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INTRODUCTION

Mesic sub-tropical savannas and temperate grasslands (annual precipitation >600 mm; hereafter referred to as savanna grasslands, *sensu* Scholes and Archer (1997)), share similar historical and present-day determinants of structure and function. These determinants include highly variable climatic regimes with strong seasonality, frequent fire, and grazing by large herbivores (Archer 1995; Scholes and Archer 1997; Knapp and others 1998a; Oesterheld and others 1999; Scholes and others 2003a, b). Each of these key drivers have undergone some degree of comparative analyses, but only the effects of climatic variability on annual aboveground net primary productivity (ANPP) have been explicitly and directly compared between these structurally similar, but geographically and historically different ecosystems. Results from these studies suggest that both inter- and intra-annual rainfall patterns affect annual ANPP and the growth dynamics of the dominant C₄ grasses in consistent ways in North America and southern Africa (Knapp and others 2002; Knapp and others 2006; Scholes and others 2003a, b; Nippert and others 2006; Swemmer and others 2007; Swemmer and Knapp 2008).

Although responses of sub-tropical and temperate savanna grasslands to climate appear convergent, many have argued (Scholes and others 2003a, b; Lusk and Bellingham 2004; Uys and others 2004; Coetsee and others 2008) that community and ecosystem responses to fire and grazing in North American temperate grasslands are not consistent with how fire and grazing affects ecosystem function and structure in South Africa savanna grasslands (Briggs and Knapp 1995; Collins and others 1998; Knapp and others 1999; Scholes and others 2003a, b; Fynn and others 2004; Uys and others 2004). This assertion has not been rigorously tested by direct comparative studies, but if true, it calls into question our ability to broadly apply generalizations of how fire and grazing underpin and create patterns (Lawton 1999) in these important grass-dominated ecosystems worldwide. Assessing the extent to which we can generalize about the determinants of ecological patterns and processes is necessary for forecasting responses of biomes to global change (Dynesius and others 2004). This is based on the premise that if the drivers responsible for the structure and dynamics of particular ecosystems have been correctly identified and are mechanistically understood, such knowledge should have predictive value in congruent ecosystems (Knapp and others 2004; Navarrete and others 2008). However, there are a number of

potential contingent factors that may alter the effects of fire and grazing on savanna grasslands in South Africa (SA) versus North America (NA). These include differences in the dormant season climate, the greater diversity of extant large herbivores in SA, potential differences in soil fertility in SA due to greater weathering of soils and parent material, and very different evolutionary histories in the two continents.

Our goal was to explicitly evaluate how three well-known determinants of pattern and process in grassland ecosystems (fire, grazing, and N availability) affect a key ecosystem function, ANPP, in sites in NA and SA (Knapp and others 2004, 2006). We compared ANPP responses to different fire frequencies (annually burned, fire at 3–4 years intervals and unburned) over multiple years within the context of three ongoing long-term experiments. Combined, these experiments permitted us to directly compare ANPP response to fire in: (1) sites with no recent (20–50 years) history of grazing, (2) sites grazed by either a diverse suite of herbivores or by single-species herds of grazers, and (3) historically ungrazed sites fertilized with nitrogen (N). On both continents, similar experimental designs and identical sampling protocols were used, with the exception that it was possible to compare ANPP responses under different levels of large herbivore diversity (diverse herbivores versus a single-species grazer) only in SA. We assessed the following responses, based primarily on studies from NA, for their consistency in both hemispheres: (1) fire increases total ANPP in the absence of any large ungulate grazing (Briggs and Knapp 1995), (2) total ANPP responses to fire frequency in sites with a history of grazing would be reduced (Johnson and Matchett 2001), regardless of herbivore diversity, (3) annually burned sites would respond strongly to N fertilization because annual fire reduces levels of available soil N, whereas sites subjected to low fire frequency would not respond to N (Seastedt and others 1991; Blair and others 1998), and (4) forb ANPP would decrease with annual fire, but grazing would offset this reduction (Briggs and Knapp 2001; Collins and others 1998).

METHODS

Study Sites

The Konza Prairie Biological Station (KPBS) is a 3,487 ha temperate savanna grassland located in northeastern Kansas, USA (39° 05' N, 96° 35' W). KPBS is dominated by native, perennial C₄ grasses such as *Andropogon gerardii* and *Sorghastrum nutans*

that account for the majority of herbaceous primary productivity (Knapp and others 1998b). In all but the most frequently burned sites, woody plants are common and may comprise as much as 25% of the total plant cover (Heisler and others 2003). Maximum mean monthly air temperature in July is 27°C and annual precipitation averages 835 mm/year, with more than 70% falling as rain during the April–September growing season (Figure 1A). Soils are fine textured, silty clay loams (Table 1; Ransom and others 1998).

Kruger National Park (KNP) encompasses nearly 2 million ha of protected savanna grassland in northeastern South Africa (22° 25′–25° 32′ S, 30° 50′–32° 2′ E). The south-central region of KNP (near Satara), where we conducted our research, is co-dominated by a variety of C₄ grasses such as *Bothriochloa radicans*, *Panicum coloratum*, *Urochloa mozambicensis*, *Digitaria eriantha*, *Themeda triandra*, and C₃ woody species including *Acacia nigrescens* (Knob thorn) and *Sclerocarya birrea* (Marula trees). Maximum mean monthly air temperature occurs in January (29°C) with mean annual rainfall of 518 mm (Venter and others 2003) falling primarily during the months of September–March (Figure 1B). Although this site has precipitation inputs below 600 mm, almost 90% of total annual precipitation falls during the growing season, resulting in herbaceous ANPP and a general vegetation structure similar to KPBS and the other site sampled in South Africa (see below). The dormant season (April–September) is mild, dry, and frost free. The soils are fine textured clay and loam of basalt parent material (Table 1; Venter and others 2003). KNP supports many of the large herbivores such as African buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*), and Burchell's zebra (*Equus burchelli*), that evolved in the grasslands of southern Africa (du Toit and others 2003).

The Ukulinga Research Farm (URF) at the University of KwaZulu-Natal is located in southeastern South Africa near Pietermaritzburg (30° 24′ S, 29° 24′ E). Grasslands at URF are dominated by the C₄ grasses *T. triandra* and *Heteropogon contortus* in the frequently burned areas, with scattered C₃ trees in areas protected from fire (Morris and Tainton 2002). Summers are warm with a maximum mean monthly air temperature of 26.4°C occurring in February, and winters are mild with occasional frost. Mean annual precipitation is 838 mm, mostly from convective storms during summer (Figure 1C, Knapp and others 2006). Soils are derived from shales and are fine textured (Table 1; Fynn and others 2003).

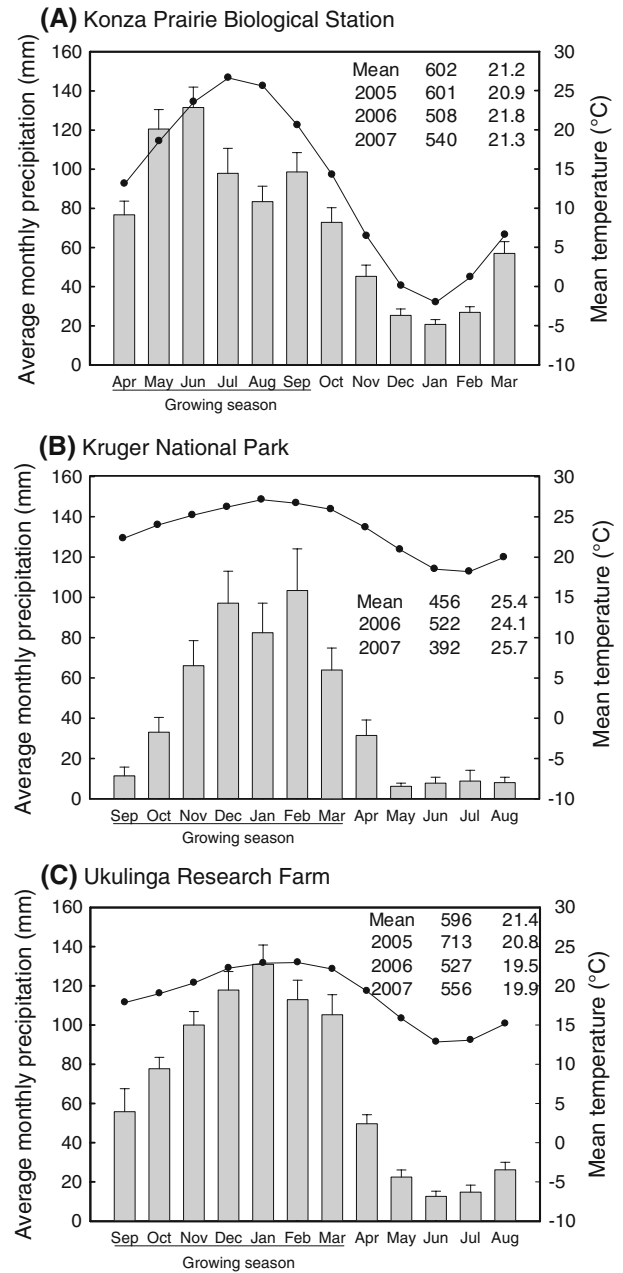


Figure 1. Growing season precipitation and temperature for North American and South African study sites. Shown are mean monthly precipitation (and standard error) as bars and temperature (line) for **A** Konza Prairie Biological Station near Manhattan, Kansas (NA; data from 1960–2002), **B** Kruger National Park near the Satara Camp (SA; 1984–2004), and **C** Ukulinga Research Farm near Pietermaritzburg (SA; 1960–2002). Lines under the x-axis denote the growing season. Inset values are means of growing season precipitation, and mean growing season temperature for each site and beneath these are values for the years of this study. Standard deviations for long-term means are: KPBS 176 mm and 4.9°C, KNP 176 mm and 0.1°C, and URF 109 mm and 2.1°C.

Table 1. General Soil Characteristics for the Three Savanna Grasslands Studied in North America and South Africa

Research site	KPBS	KNP	URF
Latitude	39° 05'N	22° 25'–25° 32'S	30°24'S
Longitude	96° 35'W	30° 50'–32° 2'E	29°24'E
A horizon depth (cm)	0–18	0–15	0–25
Chemical properties			
pH	5.9	6.4	5.1
CaCO ₃ (mg g ⁻¹)	0.1	0.2	0.0
Org C (mg g ⁻¹)	3.5	2.2	3.1
Total N (mg g ⁻¹)	0.4	0.1	0.3
Physical properties			
Sand–silt–clay (%)	10–60–30	30–40–30	23–50–27
Bulk density (g cm ⁻³)	1.3	1.2	1.2
Parent material	Chert/shale	Basalt	Shale
Soil classification	Udic argiustolls	Haplic luvisols	Chromic luvisols
Landform type	Alluvial terrace	Upland	Colluvium fan

Data are from Melzer (2009).

Thus, the three sites are broadly similar in growth form dominance and vegetative physiognomy, growing season climate, and general soil characteristics (Figure 1, Table 1). Further, they all share a long evolutionary history of grazing by large ungulates (Milchunas and Lauenroth 1993). However, they differ significantly in other aspects of their history, with the present-day NA Great Plains grassland ecosystems considered relatively young having been strongly influenced by Pleistocene glaciers (Axelrod 1985). In contrast, SA savanna grasslands are generally considered to be much older (Bond and others 2003), the region is tectonically quiescent with highly weathered soils (Hartshorn and others 2009) and these systems lack the historic and extreme large faunal extinctions that occurred in NA (Martin 1984).

Effects of Fire and Nutrient Availability on ANPP

To examine the effects of fire and N limitation on aboveground net primary production in the absence of herbivores, we sampled two additional experiments at KPBS and URF. In 1977, KPBS established fully replicated watershed-level fire experiments. Ungrazed, watersheds (mean size ~ 60 ha) are burned at 1-, 2-, 4-, 10- and 20-year intervals, mainly in the spring or late in the dormant season. The URF, established in 1950, was designed to test the combined effects of mowing and fire on grassland ecosystems. Within this large experiment are unmowed plots burned with varying fire return frequencies including annual, 3-year

burned and unburned plots. The experiment is fully replicated and blocked ($n = 3$) along a topography and soil depth gradient. No grazing has occurred at this site for more than 50 years facilitating comparisons of the long-term experimental plots at URF to the long-term ungrazed plots at KPBS.

Prior to the 2005 growing season we established plots (13.7 m × 18.3 m) in ungrazed areas burned annually, at 3–4-year intervals, and unburned ($n = 3$ per fire treatment) at both KPBS and URF. Areas with trees or large shrubs were avoided as our main goal was to evaluate responses in the herbaceous plant community. ANPP was estimated from end-of-season harvests in 2005–2007 (September for KPBS, April for URF). In 10, 0.1-m² (20 cm × 50 cm) quadrats randomly located in each plot ($n = 30$ /treatment/site; Briggs and Knapp 1995; Knapp and others 1998a), we harvested the vegetation at ground level and separated it into grass, forb, and previous year's dead biomass. Samples were dried at 60°C to a constant weight. For annually burned plots, total biomass harvested represents ANPP. For the intermediate and unburned sites, we calculated ANPP by summing all but the previous year's dead component.

To assess potential N limitation under different fire regimes, N was added to two 2 × 2 m² (+N) subplots within plots of each of the three fire regimes. In early spring of the 2006 and 2007 growing seasons, the +N subplots were amended with ammonium nitrate at a rate of 10.0 g N/m² (Seastedt and others 1991). To assess relative soil N availability, resin bags containing 10 g of a 1:1 mixture of cation and anion exchange resins

($n = 2$ /subplot) were installed to a depth of 5–10 cm at each site ($n = 12$ resin bags per fire regime; that is, 2 resin bags per subplot \times 2 +N/control subplots per plot \times 3 plots per fire regime). These were incubated in situ during the growing season in both +N and control plots to provide an integrated index of NO_3^- and NH_4^+ availability (Baer and others 2003). At the end of each growing season, we sampled ANPP within three 0.1 m² quadrats within each of the +N subplots as described above ($n = 18$ quadrats per fire regime; that is, 3 quadrats per subplot \times 2 +N subplots per plot \times 3 plots per fire regime). We compared ANPP from the +N plots to the ten control quadrats harvested for estimating ANPP.

We analyzed data from each year and site separately with fire treatment and year as main effects in an ANOVA design to assess the impact of fire regime on ANPP and soil N availability. We did not treat samples as a repeated measure across years because plots were large enough to sample different locations and there was no indication of a statistical or spatial relationship between years. When the year effect was not significant, we also combined across years and re-analyzed with fire treatment as the main effect. Plots used for the study of fire effects at KPBS were located on relatively shallow-soil upland sites, where fire may not consistently affect ANPP (Knapp and others 1998b), whereas sites at URF were arrayed across a significant topographic and soil depth gradient. Thus, we also analyzed the URF data by the two extremes in soil depth (deep versus shallow). We compared these results, with long-term data at KPBS that had been collected across topographic and soil depth gradients as part of the Long-Term Ecological Research (LTER) Program. We focused on the extremes in fire frequency (unburned versus annual fire) because this is where the largest differences have been observed in past studies from KPBS (Briggs and Knapp 2001).

The impacts of N addition on ANPP and resin bag data were analyzed as a split plot design, with fire as the whole plot treatment and N addition as the subplot treatment. ANPP data were averaged and analyzed at the plot level (that is, $n = 3$ N control/treatment/site, $n = 3$ +N/treatment/site). The resin bag data were square root transformed prior to analysis. All analyses were performed in SAS 9.1 (SAS Institute 2003), and the level of significance for all tests was $P \leq 0.05$ unless otherwise noted.

Effects of Fire and Grazing on ANPP

To assess the impacts of fire on ANPP in grazed areas, we established herbivore exclusion treat-

ments in KBPS in North America and KNP in South Africa. At KBPS, bison (*Bos bison*) were reintroduced to KPBS in 1988 in a 1,000 ha portion of the preserve that includes replicate watersheds burned at 1-, 2-, 4- and 20-year intervals. Current herd size is approximately 260 individuals and densities are based on a target of average consumption of 25% of ANPP with the overall grazing intensity being considered moderate (Milchunas and Lauenroth 1993; Knapp and others 1999). In 1954, KNP established the Experimental Burn Plots (EBPs) to examine the effects of fire frequency (including fire exclusion, 1,3-y burn intervals) and season on plant and animal communities (Biggs and others 2003). Each burn plot measures approximately 180 m by 370 m (~7 ha). These plots are open to all herbivores such as elephant (*Loxodonta Africana*), rhinoceros (*Cerathotherium simum*), Burchell's zebra (*E. burchelli*), blue wildebeest (*C. taurinus*), warthogs (*Phacochoerus aethiopicus*), and impala (*Aepyceros melampus*). Impala, Burchell's zebra, and blue wildebeest were most commonly observed during this study (C. Burns, unpublished data). Grazing intensity in the Satara region (south-central) of the park is very heterogeneous spatially and temporally, but at the landscape scale it is considered moderate (W. Trollope, personal communication).

Herbivore exclosures in grazed areas in KPBS and KNP were erected prior to the 2006 growing season. These exclosures kept large herbivores from removing biomass during the period when ANPP was estimated, but allowed plant species composition and soil nutrient status to reflect past herbivore impacts. The exclosures were 7 m in diameter, 2 m tall, and constructed of diamond mesh (5-cm diameter). Seven exclosures were established in each of three blocks of the three fire treatments—annually burned, intermediate burn (3-years for KNP or 4-years for KPBS), and unburned ($n = 21$ exclosures/treatment/site). As our focus was on ANPP responses of the herbaceous layer, exclosures were not located beneath trees or where dense shrub patches were present.

Additionally, in the Satara region of KNP is a 900-ha permanent enclosure containing 80–90 adult African buffalo (*S. caffer*). This enclosure was erected in 2000 and was divided into six areas (100–200 ha each), with these burned on a rotational basis including plots burned annually and plots that were unburned. The African buffalo is a grazer considered functionally similar to bison (the primary grazer at KBPS) in terms of diet and body size (du Toit 2003). We used the unburned and annually burned areas in the buffalo enclosure to provide a direct comparison for determining the

effects of a single-species large grazer in KNP and KPBS, and to assess the effects of large herbivore diversity at adjacent sites in KNP. Similar exclosures were built in the African buffalo enclosure at KNP. We placed 7 exclosures in the three blocks of each fire treatment (annually burned and unburned) resulting in 21 exclosures/treatment.

We sampled ANPP by harvesting plant biomass from three 0.1 m² quadrats per herbivore exclosure at the end of the growing season in 2006–2007. To assess impacts of fire in grazed savannas, we analyzed ANPP data using ANOVA models as described for ungrazed areas. ANPP data were analyzed at the exclosure level ($n = 21$ /treatment/site). Forb ANPP data were analyzed with the same statistical models as total ANPP; however, due to the frequent absence of forbs from the KNP grazed sites, model assumptions regarding normality were difficult to achieve even after data transformation.

RESULTS

Total ANPP Response to Fire

Responses of total ANPP to the range of fire frequencies imposed were broadly similar in NA and SA (Figure 2). On both continents, there was no effect of fire frequency on ANPP in 2 of 3 years. However, in year 3, when fire effects were evident, ANPP was increased by 52–179% in burned sites (including the infrequently burned treatment in SA). When results were combined over all 3 years, both sites responded similarly with no significant fire effects detected (Figure 2 inset). However, as noted earlier, these results were obtained in relatively shallow-soil upland sites at KPBS, where fire may not consistently affect ANPP due to other resource limitations (Knapp and others 1998b), whereas the experimental design at URF is arrayed across a topographic and soil depth gradient. Thus, we parsed the long-term data at KPBS and the URF data by topography and soil depth (lowland deeper versus upland shallower soils) to test the hypothesis that topography/soil depth would affect ANPP responses to fire similarly at both sites. We found that ANPP in the annually burned treatments at both sites was significantly higher than in the unburned treatment in lowlands with deeper soils (KPBS $P < 0.0001$; URF $P = 0.0209$), whereas there was no significant fire effect on ANPP at the upland shallower soil sites (Figure 3). Thus, despite the much shorter period of data collection at URF relative to KPBS (3 versus 22 years) as well as only modest differences in soil depth at URF, this comparison suggests that topography and soil depth

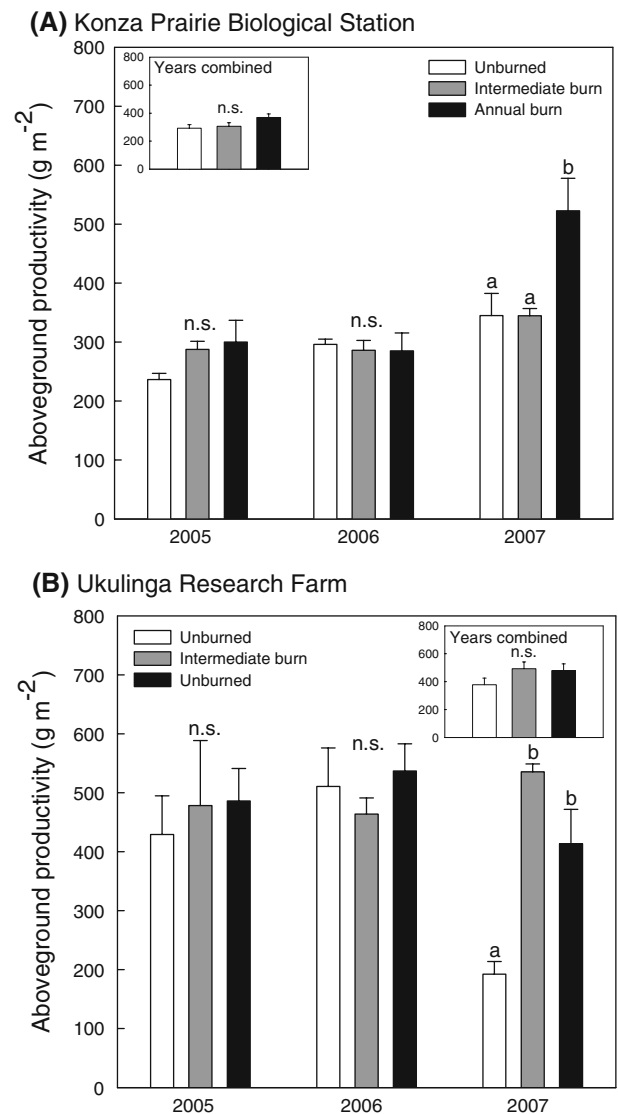


Figure 2. Patterns of annual aboveground net primary productivity (ANPP) for ungrazed sites in response to three fire treatments (unburned, intermediate (3–4-year intervals) and annual fire) at **A** Konza Prairie Biological Station (KPBS) and **B** Ukulinga Research Farm (URF). Different letters above the bars indicate significant differences among burn treatments. Error bars indicate ± 1 SE calculated by plot ($n = 3$ /treatment/year). *Inset*: ANPP for ungrazed fire treatments with years combined and replicates treated independently rather than as repeated measures. Error bars indicate \pm SE with pooled variance.

have similar effects on ANPP responses to fire at both sites.

Total ANPP Response to Fire and Grazing

At the three recently grazed sites, ANPP was unaffected by different fire frequencies (Figure 4). This result was the same regardless of whether

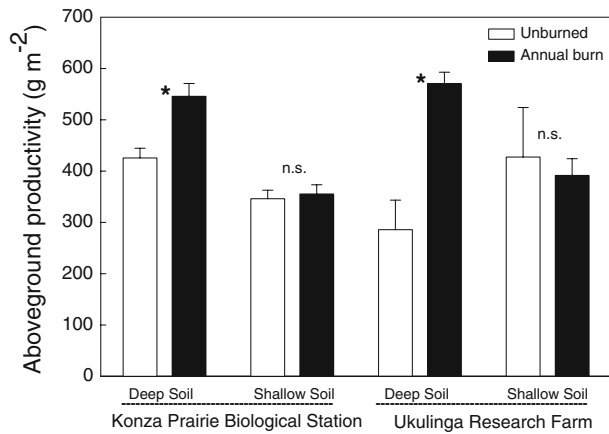


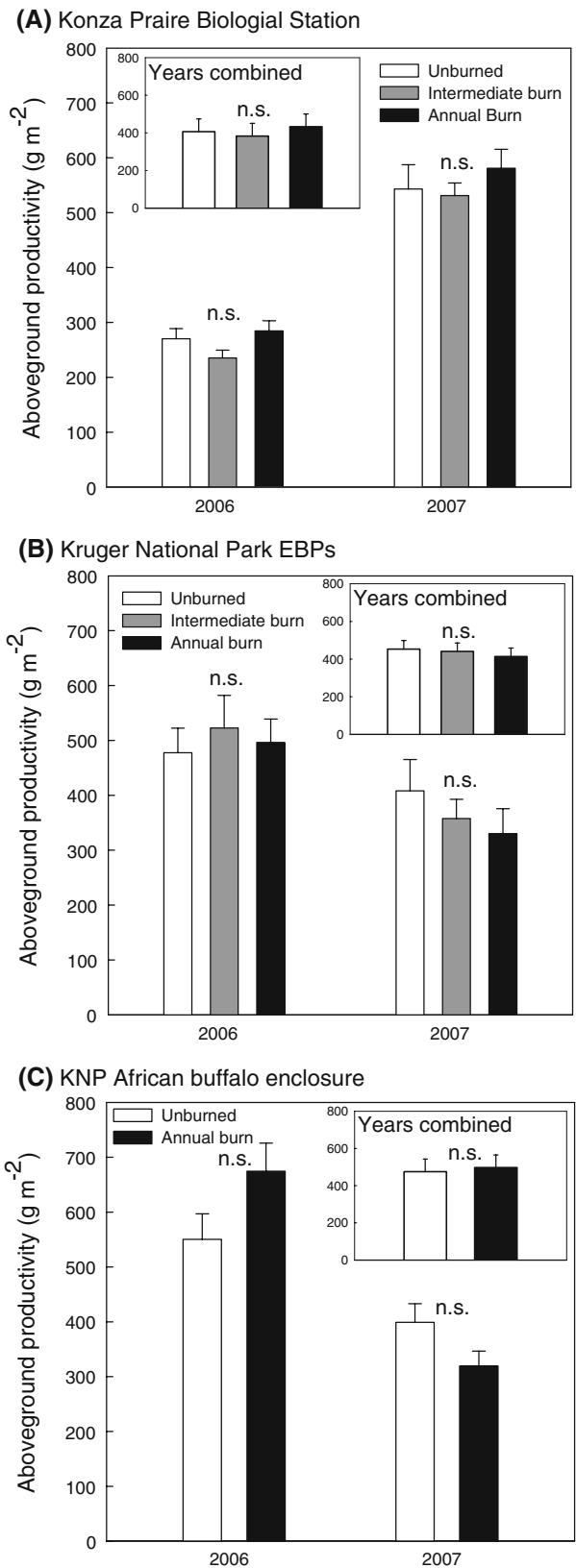
Figure 3. Effect of fire (unburned versus annual) on annual aboveground net primary productivity depending on soil depth in ungrazed treatments at KPBS (long-term data from <http://www.konza.ksu.edu/>—data set pab01 comparing soils greater than 1.0 m versus less than 30.0 cm) and URF (treatment plots were compared that ranged in soil depth from a mean of 36.7 cm to 20.0 cm). Values are means with error bars indicating the standard error by year (KPBS $n = 17$ /treatment/soil type, URF $n = 3$ /treatment/soil type). Mean ANPP values at KPBS encompass sampling from 1984 to 2005 and 3 years of data (2005–2007) at URF. Asterisk indicates significant differences at $P \leq 0.05$.

individual years or the 2 years combined were compared (Figure 4 inset). Furthermore, there was no evidence that a diverse suite of large herbivores in SA had any impact different from a single-species herd of grazers on ANPP responses to annually burned versus unburned fire treatments (Figure 4B versus C).

Total ANPP Response to Nitrogen Addition

Results from resin bag estimates of relative soil N availability (NO_3^- and NH_4^+ combined) were

Figure 4. Patterns of annual aboveground net primary productivity (ANPP) for grazed sites in response to fire treatments (unburned, intermediate and annual) at **A** Konza Prairie Biological Station (KPBS) and **B** Kruger National Park Experimental Burn Plots (KNP EBPs) and **C** KNP African buffalo enclosure. Quadrats were averaged and analyses were conducted at the enclosure level ($n = 21$ /treatment/year). No significant differences were detected among fire treatments. Error bars indicate ± 1 SE calculated by quadrat ($n = 63$ /treatment/year). Intermediate burn interval is 4 years at KPBS and 3 years at KNP sites. Inset: ANPP for treatments with years combined and replicates treated independently rather than as repeated measures. Error bars indicate \pm SE with pooled variance ($n = 63$ /treatment).



consistent across all 3 years and across both continents, with N availability in unburned sites always much higher than in sites burned annually or at

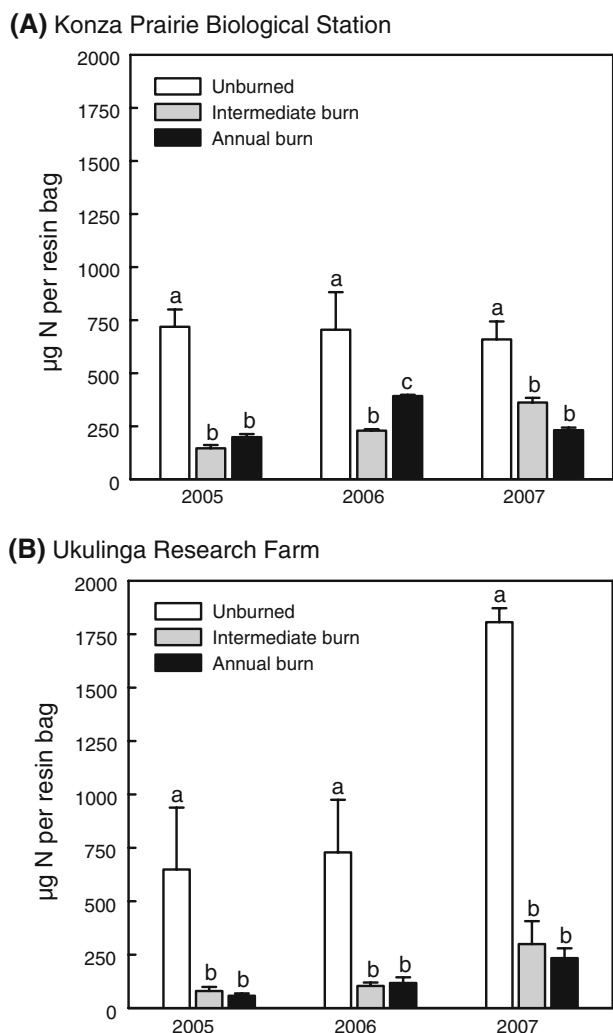


Figure 5. Effect of fire (unburned, intermediate and annual) on total inorganic nitrogen in unfertilized, ungrazed sites at **A** Konza Prairie Biological Station and **B** Ukulinga Research Farm. Patterns in NO_3^- and NH_4^+ were similar to those of total inorganic nitrogen. Data were square root transformed for analysis ($n = 12/\text{treatment}/\text{year}$). Different letters indicate significant difference of transformed data at $P < 0.05$. Error bars depict ± 1 SE among the three replicates of each treatment, each year.

3–4-year intervals (typically 8–10-fold higher, Figure 5). As expected, in the 2 years of N fertilization, resin bags located in subplots with added N averaged a 15-fold increase in available N (430 versus 6,667 $\mu\text{g N}$ per resin bag). The responsiveness of total ANPP to N addition reflected these fire-induced differences in soil N availability. In both NA and SA, ANPP in annually burned plots responded positively and significantly to N addition, whereas ANPP in unburned plots was not responsive to N addition (Figure 6). Thus, both soil N estimates and N-fertilization responses were consistent with the

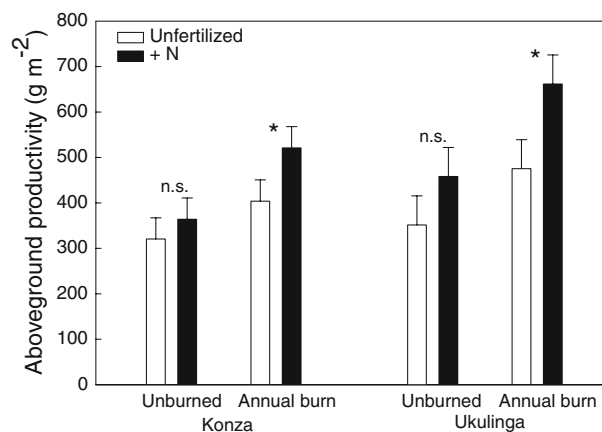


Figure 6. Effect of nitrogen addition on annual aboveground net primary productivity (ANPP) in two fire treatments (unburned and annual) at KPBS and URF. Quadrats were averaged and analyses were conducted at the plot level ($n = 6/\text{treatment} \times \text{N treatment}$). Error bars depict standard error using pooled variance by site ($n = 36/\text{site}$). Asterisk indicates significant difference at $P \leq 0.05$. Data include 2 years of treatments. We included only the fire frequency extremes (annually burned and unburned) because historically, this is where the greatest difference in productivity is found.

generalization that annual fire leads to greater N limitation of ANPP in mesic savanna grasslands in the absence of large grazers.

Forb ANPP Responses

In the long-term ungrazed sites at URF and KPBS, responses in forb ANPP to fire differed across continents. Annual fire resulted in a four-fold reduction in forb ANPP at KPBS, whereas there was no significant effect of fire on forb ANPP at URF (Figure 7). Similar to results for total ANPP, no significant effects of fire were detected for forb ANPP in sites that were recently grazed (Figure 7). Estimates of forb ANPP from the SA sites were difficult to evaluate, however, due to the frequent absence of forbs from the quadrats harvested. However, this absence of forbs from most quadrats does suggest that grazing was not having a large positive effect on forb ANPP in SA, a response opposite from that in NA where forb ANPP was 10-fold higher in recently grazed versus ungrazed annually burned plots (Figure 7). Finally, there was no significant response of forb ANPP to N additions over 2 years at either site in any of the three fire treatments.

DISCUSSION

Ecosystems dominated or co-dominated by graminoids cover vast areas of all continents, but

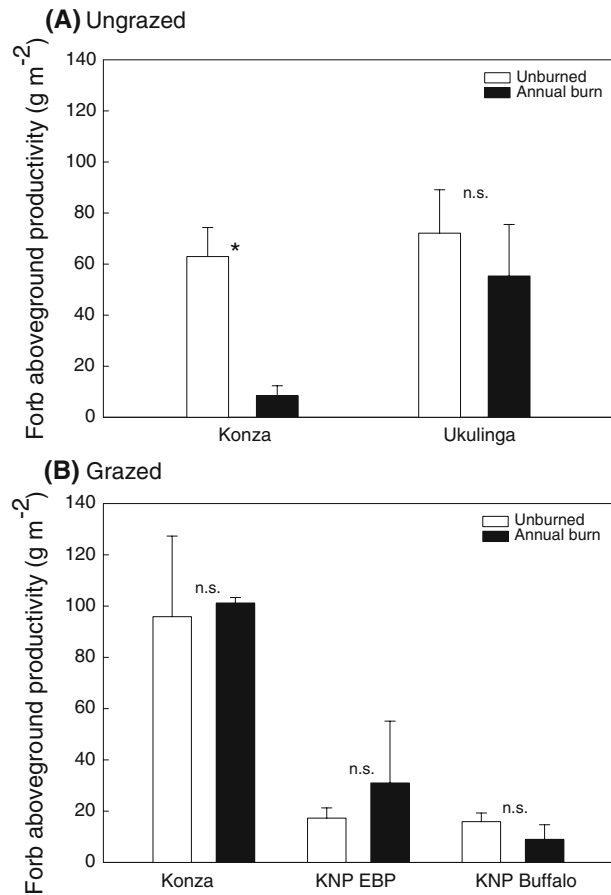


Figure 7. Effect of fire (unburned versus annual) on forb aboveground net primary productivity (ANPP) in **A** ungrazed treatments at KPBS and URF and **B** grazed treatments at KPBS, the KNP EBP, and the KNP African buffalo enclosure. We focused on responses to extremes in fire frequency (annual fire versus unburned) because this is where the largest differences have been observed in past studies from KPBS (Briggs and Knapp 2001). The vertical bars denote the means of 3 years of data for (A) and 2 years of data for (B). Quadrats were averaged (A) $n = 30/\text{treatment}/\text{year}$, (B) $n = 63/\text{treatment}/\text{year}$, and analyses were performed at the plot level (A) $n = 9/\text{treatment}$, (B) $n = 42/\text{treatment}$. Error bars depict standard error by year. Asterisk indicates significant difference at $P \leq 0.05$.

Antarctica. In such widespread and extensive ecosystems, there is a pressing need to identify convergence in ecological processes and general patterns of response to key drivers, particularly those being altered in this era of rapid global change (Knapp and others 2004). One approach for elucidating convergence is to conduct global syntheses and meta-analyses of the results of numerous individual studies. This has been especially valuable for generalizing relationships between precipitation and ANPP (Rutherford 1980; Sala and

others 1988; Huxman and others 2004; Knapp and others 2006; Yang and others 2008). Similarly, our understanding of the effects of fire and grazing in savanna grasslands has also been advanced through reviews and analyses of past studies (Hobbs and others 1991; Ojima and others 1994; Scholes and Walker 1993; Knapp and others 1998b; Frank and others 1998; Milchunas and others 1988; McNaughton 1983, 1985; Oesterheld and others 1999; du Toit and others 2003; Diaz and others 2007; Harris and others 2007). Although drawing generalities from largely independent studies can be difficult due to the differing methods and approaches employed (see Knapp and others 2004 for a review of the trade-offs between *post hoc* synthesis and a direct comparative approach), several important patterns relevant to our research have emerged. These include generalizations that: (1) grazing tends to have a negative effect on ANPP in productive grasslands (Milchunas and Lauenroth 1993), (2) growth form responses to grazing can be quite variable unless climate and herbivore history are controlled for (Diaz and others 2007), and (3) fire effects on ANPP will only be positive in more mesic systems (Oesterheld and others 1999).

In this study, we employed an approach complementary to meta-analyses of independent studies by using identical sampling methods within the framework of similar long-term experiments to directly compare the effects of fire, grazing and N amendments on a key aspect of ecosystem function (ANPP) in savanna grasslands in different hemispheres. Despite large geographical distance between our study sites, we predicted convergence in ecosystem function because both systems: (1) are dominated by C₄ grasses coexisting with C₃ woody plants, (2) have similar growing season patterns and amounts of precipitation (Figure 1), (3) have similar growing season temperatures (Figure 1), and (4) share fire, grazing by large ungulates, and extreme climatic variability as key drivers of ecosystem function and structure (Scholes 1993; Knapp and others 1998b; Knapp and others 2004; Frank and others 1998; Scholes and others 2003a, b; Bond and others 2003). Conversely, differences in the cause of the dormant season (low temperature in NA versus drought in SA), evolutionary history, the diversity and identity of large herbivores, and purported differences in soil fertility might result in fire and grazing having very different effects on savanna grasslands in SA than NA, as posited by Scholes and others (2003a, b).

Our results provide evidence of substantial functional convergence in the controls of ANPP in both hemispheres, particularly by fire in the

absence of grazing and by N (Figures 2, 3, 4, 5, 6). With respect to fire, both short- and long-term studies of burning in mesic NA grasslands have demonstrated that when large grazers are absent, fire enhances the early season energy environment (light and temperature) through the removal of accumulated litter, but can reduce soil water availability (Knapp and Seastedt 1986). As a result, stimulation of ANPP by fire is reliably seen only in lowland, deep soil sites with high levels of soil moisture and occurs less frequently in uplands with shallow soils where soil moisture is more likely limiting (Briggs and Knapp 1995). In these latter cases, stimulation of ANPP by spring fire may still occur but less consistently so (Knapp and others 1998a). Fire regimes can affect ANPP not only through short-term changes in the energy environment, but also through long-term changes in community composition. This is particularly striking at URF, where the unburned plots are dominated by slow growing species such as *Aristida junceiformis* (Fynn and others 2005a). Finally, long-term annual burning can lead to significant reductions in soil N and strong N limitation to ANPP relative to unburned sites in mesic NA grasslands (Seastedt and others 1991; Ojima and others 1994; Blair 1997).

Across both continents we found consistent patterns of: (1) intermittent stimulation of ANPP by fire (Figure 2), (2) a strong soil depth effect on post-fire ANPP responses (Figure 3), (3) strong effects of fire on soil N availability (Figure 5), and (4) ANPP responses to N addition (Figure 6). The soil depth effect at URF, where differences in soil depth were much more modest than at KPBS suggests that lowland topographic positions with the potential for subsidized water inputs from the surrounding landscape may also play a role. Thus, minimal soil water limitation, regardless of the mechanism, appears as key for a positive post-fire response in ANPP. We expected a muted ANPP response to N addition in burned sites in SA as other nutrients, such as P, potentially would limit responses in the older and more weathered SA soils (Fynn and others 2005b; Craine and others 2008; Hartshorn and others 2009), particularly because P limitation has not been observed at KPBS (J. Blair, unpublished data). However, N limitation in annually burned sites as inferred from resin bag collection of soil solution inorganic N or from ANPP responses to N fertilization, was similar in SA and NA. This is not consistent with greater soil P limitation in SA, at least in these annually burned savanna grasslands, but is consistent with recent evidence that the pyromineralization of soil P may

play a critical biogeochemical role in the supply of labile P to plants. Moreover, in a fertilization study in KNP in sites burned infrequently and not grazed (Craine and others 2008), no evidence for N limitation was found, similar to our results for the unburned treatments at URF. Craine and others (2008) argued for widespread N and P co-limitation of ANPP in these systems. Finally, Coetsee and others (2008) recently concluded that annual burning did not lead to N limitation in savanna grasslands in KNP, but they suggested that these results could be attributed to the presence of large ungulate grazing. Grazing is well known to alter (usually increasing) N cycling and availability in grasslands (see below) and one of the strengths of our study is that we can compare fire and grazing as independent treatments.

In a global meta-analysis of grazing effects on ANPP, Milchunas and Lauenroth (1993) concluded that most effects were negative, particularly in grasslands with high ANPP. Comparison of ANPP in grazed and ungrazed sites on KPBS and KNP versus URF (Figures 2, 4) suggests a neutral response. Less is known of the legacy effect of grazers on ANPP responses to different fire frequencies, although grazing during the growing season can either stimulate or reduce ANPP (Chapin 1989; McNaughton and others 1989; Oesterheld and others 1999; Georgiadis 1989), increase N cycling and soil N availability (Frank and Evans 1997; Johnson and Matchett 2001; Holland and Detling 1990), and lead to substantial alterations in plant community structure due to large ungulate activities (Knapp and others 1999; Hobbs and others 1991; du Toit 2003). In sites that were recently grazed, we found little evidence for any response in total ANPP to the different long-term fire frequencies imposed in both NA and SA (Figure 4). It is important to note that the exclosed plots sampled were not grazed in the actual years of ANPP measurement. Instead, we assessed the legacy of past grazing activities, which are known to significantly alter plant community composition (Collins and others 1998) and soil nutrients (Johnson and Matchett 2001).

The lack of response to fire in these recently grazed sites could be due to any number of factors interacting with plant community changes. Large ungulate grazing activities open the plant canopy and reduce detritus accumulation (Johnson and Matchett 2001), which enhances light penetration (one mechanism by which fire stimulates ANPP in ungrazed grasslands; Knapp and Seastedt 1986). High densities of large ungulates are usually associated with burned areas (Coppock and Detling 1986; Vinton and others 1993; Archibald and Bond

2004) and their activities increase spatial heterogeneity of resources and canopy structure (Knapp and others 1998a; McNaughton 1984) and alter N cycling and plant community composition more in annually burned sites than those exposed to lower fire frequencies (Collins and others 1998). The net effect appears to be that fire neither stimulated nor reduced total ANPP in these recently grazed sites (Figure 4). Moreover, the diversity of large grazers had no measurable impact on total ANPP in SA, although the African buffalo enclosure was only in place for 6–7 years and we cannot rule out that ecosystem and plant community changes are still occurring.

Linking ANPP to Community Structure

We analyzed forb ANPP separately because of the important role this life history group plays in plant community structure and overall floristic diversity in mesic savanna grasslands (Turner and Knapp 1996; Collins and Steinauer 1998; Uys and others 2004). Further, as a group the forbs respond strongly to fire and grazing at KPBS—decreasing in production, cover, and richness with annual fire and responding positively in cover and richness with grazing (Briggs and Knapp 2001; Collins and others 1998). A positive response of forb abundance to grazing was not consistently noted in an extensive meta-analysis of studies of grazing effects on growth forms by Diaz and others (2007), however, they noted that growth form responses were more consistent if results were compared from regions with similar climate and grazing history—as is the case in our study.

The general convergence in total ANPP responses to fire, grazing history, and N addition between NA and SA was not as evident in forb ANPP. As expected in long-term ungrazed plots, annual spring fire strongly reduced forb ANPP in NA, but a similar response was not evident in SA (Figure 7). In NA, the mechanism for reduced forb ANPP and cover in frequently burned grasslands has been posited to be the increased competitive abilities of the dominant C_4 grasses in such sites (Briggs and Knapp 2001), and not a consequence of any direct fire-related mortality of the forbs (Collins and Steinauer 1998). The mechanisms by which forbs remain similarly productive in burned and unburned environments in SA are unknown, but plant community diversity has also been reported to be unaffected by fire frequency in SA (Uys and others 2004; Fynn and others 2004) in contrast to NA where plant diversity typically decreases with frequent fire.

Forb ANPP responses to N addition (data not shown) and grazing history (Figure 7B) were consistent among sites in that forb productivity did not differ among treatments in these comparisons. Craine and others (2008) found forbs to be similarly unresponsive to N addition in KNP. Perhaps most surprising was the difference in forb ANPP in recently grazed versus ungrazed annually burned plots (Figure 7B versus A). In NA, the presumed strong competitive dominance of the C_4 grasses in ungrazed, annually burned sites is reduced with grazing because bison graze primarily on the C_4 grasses (Vinton and others 1993; Hartnett and others 1996). As a result, in this study and many others (Fahnestock and Knapp 1993; Collins and others 1998; Knapp and others 1999; Hartnett and others 1996), forb abundance and forb ANPP increased dramatically in annually burned treatments when large ungulates were present (almost 10-fold relative to ungrazed plots, Figure 7). This was not evident in SA, and there was no evidence that the diverse suite of herbivores in the EBPs affected forb ANPP differently from the grazing activities of African buffalo (Figure 7)—although conclusions for SA based on comparisons between grazed plots in KNP and ungrazed plots in URF must be tempered by the distance between the sites and their moderate climatic differences (Figure 1).

In summary, the primary determinants of total ANPP in savanna grasslands appeared to function broadly consistently in this inter-hemispheric comparison. This is an important finding for forecasting the future states of these ecosystems worldwide. Savanna grasslands sequester huge amounts of soil C, are economically important as grazing lands, and house much of the world's remaining great megafauna (Walker 1985; Owen-Smith 1988; Schimel and others 1994; Allen-Diaz 1996; Fuhlendorf and Engle 2001). As humans have and will continue to directly alter fire and grazing regimes in this biome and anthropogenic N inputs are increasing globally, a broader understanding of how these changes will affect ecosystem function is important. In particular, recognition that responses can be generalized throughout the more mesic portions of this biome has important implications for global forecasts. Our results do highlight one caution to such generalizations. Differences in forb responses to fire and grazing between SA and NA suggest that the relationship between ecosystem function and community structure (strongly influenced by forbs) may differ more strongly within this biome, consistent with the analyses of Diaz and others (2007). If true, these results suggest that convergence in ecosystem

function is not inconsistent with divergence in community structure in response to the major determinants of pattern and process in these globally important ecosystems.

ACKNOWLEDGEMENTS

We thank the staff of Kruger National Park for creating and maintaining the Experimental Burn Plots and Buffalo Enclosure, and for their efforts in supporting and encouraging our work. In particular, we thank Justice Sibuyi, Wisane Sibuyi, and Thembe Mabasa for field assistance. We would also like to thank UKZN for their support of our study at URF. Research at KPBS was supported by the KPBS staff and Konza Prairie LTER program. Special thanks to Jobie Carlisle, Patrick O'Neal, Jerry Naitken, and Freedom Linda for logistical support. Gene Kelly and Suellen Melzer provided soils information and data. This research was supported by the National Science Foundation (DEB 0516145 to MDS, and DEB 0516094 to AKK). GMB was supported by the National Science Foundation's GK12 program at Colorado State University. Long-term ANPP data set pab01 was supported by the NSF Long-Term Ecological Research Program at Konza Prairie Biological Station. Three anonymous reviewers improved this manuscript substantially.

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