

Responses to fire differ between South African and North American grassland communities

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Abstract:

Question: Does fire frequency affect mesic grassland plant community structure and composition similarly in North America and South Africa? **Location:** Konza Prairie Biological Station (KNZ), Kansas, USA, and Ukulinga Research Farm (URF), KwaZulu-Natal, South Africa. **Methods:** Plant community structure and composition were compared among annually burned, unburned and intermediate treatments within two long-term fire frequency manipulation experiments in native grasslands in North America and South Africa using comparable methodology over a 5-yr period. Because fire may reduce soil nitrogen (N) availability and thus affect plant community structure, N additions were superimposed on the fire treatments as a means of assessing direct vs indirect mechanisms driving responses to fire. **Results:** The total number of species was higher at URF (183) than at KNZ (57). Overall divergence in plant community response to fire frequency occurred despite similar responses to nutrient additions. At KNZ, more frequent fire resulted in dominance by a few, tall, deep-rooted rhizomatous grasses (e.g. *Andropogon gerardii*). On unburned sites, shorter, more shade-tolerant species such as *Poa pratensis* increased in abundance, although *A. gerardii* remained dominant. Species richness increased with decreasing fire frequency at KNZ. At URF, frequent fire resulted in short, diverse grassland weakly dominated by a range of grass species, including *Themeda triandra*, *Tristachya leucothrix* and *Hyparrhenia hirta*. Decreasing fire frequency reduced species richness and resulted in dominance by a few, relatively tall caespitose grasses such as *Aristida junciformis*. There was a complete turnover of dominant species between annually burned and unburned treatments at URF, while at KNZ *A. gerardii* and *Sorghastrum nutans* occurred across the range of treatments. N addition reduced species richness in both sites. **Conclusions:** Different responses to fire frequency between KNZ and URF are likely linked to

the dominant species and their characteristic traits, including height and method of clonal reproduction, with the rhizomatous growth form of *A. gerardii* dominating the North American grassland. South Africa does not have an equivalent grass species; instead, a range of tufted, non-rhizomatous species dominate across the fire frequency treatments at URF. Reductions in soil N due to frequent fire did not appear to be a common mechanism driving responses in community composition in these two grasslands.

Keywords: Community ecology | Divergence | Fire frequency | Konza Prairie Biological Station | Mesic grassland | Nitrogen | Nutrient addition | Richness | Tallgrass prairie | Ukulinga Research Farm

Article:

Nomenclature

North America: Towne (2002)

South Africa: Germishuizen & Meyer (2003)

Introduction

Natural disturbances are important regulators of ecological diversity in systems ranging from rain forests to coral reefs (Connell 1978; Pickett & White 1985). Indeed, the intermediate disturbance hypothesis (IDH) is one of the most frequently applied general models in ecology, although its validity has been harshly challenged (Fox 2013). In fact, application of the IDH may be especially problematic in ecosystems that are affected by multiple interacting disturbances that vary in frequency, intensity and scale (Peters et al. 2011). Tanentzap et al. (2013), however, demonstrated both theoretically and empirically that demographic traits may indeed lead to positive and hump-shaped relationships between disturbance frequency and species diversity. Thus, a causal link between diversity and disturbance frequency may be found in at least some herbaceous plant communities.

Mesic grasslands are characterized by a complex disturbance regime, the components of which interact to affect community composition and diversity (Collins & Barber 1985; Gibson 2009). As a consequence, human alteration of disturbance regimes, along with altered resource availability and inter-annual climate variability, are likely to have significant impacts on the composition and structure of grassland ecosystems globally. Currently, grasslands cover ca. 40% of the Earth's surface, making them one of the most extensive biomes in the world (White et al. 2000). Although globally extensive, grasslands are also one of the most threatened biomes, due to multiple aspects of global change such as chronic nutrient additions from agriculture and atmospheric deposition, invasion by alien species and altered disturbance regimes (Gibson 2009).

Conservation of natural grasslands depends largely on response of grasslands to disturbance. Perceptions of grassland responses to disturbance, however, vary regionally and among continents (Morgan 1999; Morgan & Lunt 1999; Fuhlendorf & Engle 2001, 2004; Briske et al. 2008; Gibson 2009; O'Connor et al. 2010; Morris 2011), with little appropriate data available for rigorous comparisons. A few studies have found similarities in how mesic

grasslands respond to precipitation, fire frequency, nitrogen (N) addition or grazing by native herbivores. For example, North American and South African grasslands showed similar levels of productivity with similar rainfall amounts. In addition, annual burning increased productivity in ungrazed, but not in recently grazed sites, and N addition increased productivity in annually burned sites but had no effect in sites not burned for several decades (Knapp et al. 2006; Buis et al. 2009). However, comparative studies on responses of plant community composition and diversity to common drivers of grassland ecosystem dynamics are rare (Buis et al. 2009; Burns et al. 2009).

In grasslands, one of the most common and influential disturbances is fire. Mesic grasslands (>500 mm mean annual precipitation) are often considered to be fire-derived or fire-maintained, with fire affecting vegetation diversity, species richness and heterogeneity (Collins 1992; Collins et al. 1995; Bond & Keely 2005), in isolation and in combination with other factors such as grazing by large herbivores (Bond & Keely 2005; Koerner & Collins 2013) and rainfall (Sankaran et al. 2005). Today most humid grasslands are managed to some degree by manipulating fire frequency, seasonality and intensity.

Accumulation of standing and fallen litter in the absence of fire or grazing results in reduction of available light energy and changes to the microclimate. It also alters the physiology of emerging shoots that reduces carbon dioxide uptake and the conversion of immediately usable inorganic N in rainwater to less readily available organic N in microbial biomass. Furthermore, litter accumulation causes the inhibition of N fixation by free-living microbes and blue-green algae, and reduction in soil temperatures, which reduces root productivity, invertebrate and microbial activity (Knapp & Seastedt 1986). Regular defoliation will reduce the amount of both standing and fallen litter accumulation, thus affecting the levels of available resources. Competition theory contributes explanations on how plants cope with these varying levels of resources under differing levels of disturbance and with differing productivity potential. For example, Grime (1988), in his tripartite model, proposed that competition for resources grows with increasing levels of productivity. Tilman (1987), with his resource ratio hypothesis, proposed that competition remains constant across productivity levels, but shifts from above-ground competition for light in nutrient-rich environments to below-ground competition for nutrients in nutrient-poor environments. Both models highlight competition for resources, but the tripartite model emphasizes tolerance of stress or disturbance. Implicit in these models, plant traits governing growth, reproduction and survival can affect the outcome of competition for resources and the co-existence of species (Grime 2007; Tilman 2007), and the relationships between traits are increasingly being highlighted in explaining the distribution and abundance of species (Suding et al. 2003).

The effect of fire on soil nutrient availability, particularly soil N, has been suggested to be one of the mechanisms through which fire influences grassland composition and structure (Seastedt et al. 1991). Soil nutrient status in grasslands influences overall vegetation productivity as well as species competitive interactions and composition (Wedin & Tilman 1993; Fynn & O'Connor 2005; Fynn et al. 2005b; Collins & Calabrese 2012). Grassland response to N additions can also be mediated through soil phosphorus (P) levels. In North American grasslands, which typically have high soil P, N additions lead to increased productivity, dominance by C₄ grasses and a decrease in species richness (Collins et al. 1998). South African

grasslands respond similarly to addition of N, but, because they typically have low levels of soil P, their responses are much stronger when P is also added. Here, N addition alone led to intermediate productivity gains and the dominance of tall, narrow-leaved species (Fynn & O'Connor 2005).

Conventional wisdom holds that South African and North American ecosystems differ in their responses to fire because of a longer history of disturbance, higher plant diversity and lower soil fertility in South Africa compared to North America (Scholes et al. 2003). However, two challenges that limit inter-site comparisons are the use of both different field methods and temporal extents of measurement. We used comparable methods in two long-term fire frequency manipulations, one in South Africa (since 1950) and one in North America (since 1977), coupled with short-term (5 yrs) N addition experiments, to more rigorously compare the individual and interactive effects of fire frequency and N availability on grassland community structure and composition on each continent. Based on past studies conducted with varying methods, we hypothesized that fire frequency treatments and soil nutrient status would affect plant community structure and composition differently in South African compared to North American grasslands, with reduction in fire frequency increasing species richness in North American grasslands and decreasing richness in South African grasslands (Knapp et al. 1998; Fynn et al. 2005a; Benson & Hartnett 2006). We also predicted that N addition would reduce richness and diversity, favouring dominance of a few species, but only under high fire frequency, in both North America and South Africa. Finally, because of the larger species pool and longer evolutionary history, we predicted that the combination of reduced fire with nutrient addition would result in more drastic and rapid changes in composition in South Africa compared to North America.

Methods

Study sites

This research occurred at two mesic grassland sites, Konza Prairie Biological Station (KNZ) in North America and the Ukulinga Research Farm (URF) in South Africa. These sites are both dominated by perennial C₄ grasses, with a diverse suite of forbs, and have similar growing season climates and general soil characteristics (Knapp et al. 2006; Buis et al. 2009). In addition, both sites are home to long-term (>25 yrs) fire manipulation experiments (Knapp et al. 1998; Morris & Tainton 2002), which we utilized for this study.

KNZ is a 3487-ha grassland in northeast Kansas, USA (39°05' N, 96°35' W) dominated by C₄ grasses such as *Andropogon gerardii* and *Sorghastrum nutans*, that account for the majority of above-ground net primary productivity (ANPP; Knapp et al. 1998). Scattered shrub and tree species include *Cornus drummondii*, *Gleditsia triacanthos* and *Prunus* spp. Numerous sub-dominant grasses and forbs contribute to the floristic diversity of the site (Towne 2002). Mean annual precipitation is 820 mm (43-yr mean), with 75% falling as rain during the April–October growing season. The climate is continental, with mean maximum temperature of 33.1 °C in July and a mean maximum temperature of 3.6 °C in January (29-yr mean). Soils are fine textured, silty clay loams derived from limestone and shales (Ransom et al. 1998). KNZ includes fully replicated watershed-level fire treatments, in place since 1977. Replicate watersheds (mean size

~60 ha) are burned at 1-, 2-, 4-, 10- and 20-yr intervals. The watersheds used in this study have not been grazed for more than 30 yrs.

URF of the University of KwaZulu-Natal is a 350-ha farm located close to Pietermaritzburg, KwaZulu-Natal ($29^{\circ}40' S$, $30^{\circ}24' E$). The vegetation is described as KwaZulu-Natal Hinterland Thornveld (Mucina & Rutherford 2006). The site is dominated by C₄ grasses, such as *Themeda triandra* and *Heteropogon contortus*, which account for much of the herbaceous ANPP (Fynn et al. 2005b). Scattered tree species include *Acacia sieberiana*, *A. nilotica* and *A. karroo*. Mean annual precipitation is 790 mm (32-yr mean), falling mostly as convective storms during summer (October–April). Summers are warm with a mean maximum of 26.4 °C in February. Winters are mild with a mean maximum 13.2 °C in July (43-yr mean), with occasional frost. Soils are fine-textured and derived from shales. Long-term experimental plots were established at URF in 1950. The experiment is a randomized block (three replicates), split-plot design with 11 subplot fire or mowing treatments (Morris & Fynn 2001). Subplot burning treatments include 1-, 2- and 3-yr burns, and unburned plots. Subplot sizes are 251 m². There has been no grazing on the experimental site for >60 yrs.

Experimental design

We used comparable experimental treatments and sampling procedures at URF and KNZ (Fig. 1) to assess the interactive effects of fire frequency and N limitation on plant community composition, structure and dynamics. At both sites we used three fire frequencies from the long-term experiments: every year (annual), 3- (URF) or 4-yr (KNZ) fire return interval (intermediate), and unburned control (unburned), with all burns taking place in spring. All burn treatments were replicated three times ($n = 3$ plots/fire frequency/site). In 2005 we established four 2 × 2-m subplots in each replicate of the annual, intermediate and unburned plots at both sites ($n = 12$ subplots/fire frequency/site). We then randomly selected two subplots per plot for the fertilization treatment, leaving the other two subplots as unfertilized controls (Fig. 1). From 2006 at KNZ and 2007 at URF, we added 10 g·N·m⁻² in the form of NH₄⁺NO₃⁻ at the start of each growing season.

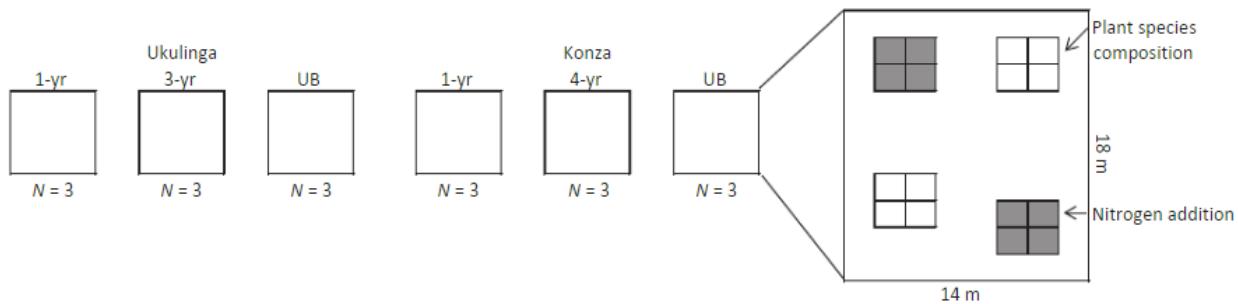


Figure 1. Experimental design for comparative analysis of plant community response to fire frequency and nitrogen addition at the Konza Prairie Biological Station, Kansas, USA, and the Ukulinga Research Farm, South Africa (UB = unburned).

Each of the 2 × 2-m subplots was divided into four 1 × 1-m quadrats (Fig. 1). From 2005 through 2010, canopy cover (to nearest%) of each species rooted in each quadrat was visually estimated twice during the growing season to sample early- and late-season species following a modified

procedure outlined in Daubenmire (1959). Highest cover values for each species during each season were then averaged across the four quadrats, and relativized maximum cover values of each species in fertilized and control treatments were used to calculate annual plot-scale averages of total abundance. We also calculated aggregated abundance of grasses and forbs, changes in composition over time and average species richness per 1 m² as well as cumulative yearly species richness at the 4-m² subplot scale. For the purpose of this study, the term ‘forbs’ included ferns, sedges and tree seedlings, i.e. all non-grasses. Subplots were located to avoid trees.

Statistical analyses

Data from URF and KNZ were analysed separately. For each site, canonical correspondence analyses (CCA; ter Braak 1987) of the entire data set were conducted to detect patterns of change in composition. Species occurring in fewer than eight samples over the 6 yrs were removed from the data set prior to CCA analyses.

Treatment effects were analysed with PERMANOVA, a multivariate analysis of variance technique suitable for use with abundance data, in which statistical significance is based on permutation of the dissimilarity matrix. First, we ran PERMANOVA using a Bray–Curtis dissimilarity matrix (Clark & Warwick 2001) to determine overall main and interactive effects of fire frequency and N addition over the 6 yrs of the experiment. The distance matrix was permuted 999 times, and type III sums of squares were used to test for significance of the factors. We then ran a two-way analysis of similarity (ANOSIM), which determines differences in community similarity among treatment groups using permutation procedures, to determine if fire, N and the fire × N interaction had significant effects on species composition in treatment compared to control plots. The resultant R statistic (scale –1 to +1) indicates no differences between communities when zero, and indicates increasing differences up to a value of ±1. Next, we used SIMPER as a *post hoc* analysis to determine which species contributed the largest amount to the differences in composition between treatments. Finally, we conducted the same suite of analyses (PERMANOVA on Bray–Curtis dissimilarity, CCA, ANOSIM and SIMPER) on community data for each year individually at KNZ and URF. All analyses were conducted with PRIMER-e 6.2 (PRIMER-E Ltd, Plymouth, UK), except the CCAs, which were conducted with CANOCO v. 4.5 (Biometrics – Plant Research International, Wageningen, NL).

Statistical analyses of community structure were conducted using linear mixed models procedures in SAS 9.1 (SAS Institute, Cary, NC, US) to determine the individual and interactive effects of fire and N addition on mean species richness, grass richness, forb richness, total cover, grass cover, forb cover and on cumulative richness at the 2 × 2-m subplot scale. We used a repeated measures model on data from all 6 yrs (using the MIXED procedure, which is a repeated measure analysis based on restricted maximum likelihood to estimate all unknown variance-covariance parameters). Fire frequency (annual, intermediate and unburned) was treated as a whole plot fixed effect. Nitrogen treatment (fertilized, control) was treated as a subplot fixed effect within fire frequency. Year was treated as a repeated effect. Type III sums of squares were used to orthogonally compare the effect of fire frequency and N addition over time. Means separations were performed using *post hoc* t-tests of least squares means produced by the MIXED procedure.

Results

Community responses to fire frequency and N addition

A total of 57 and 183 species occurred across all plots at KNZ and URF, respectively. Many of these species were rare, occurring in <10% of samples across plots over time. At KNZ, none of fire frequency, N addition or year independently altered community composition (PERMANOVA pseudo $F = 5.15, 1.27, 0.87, P = 0.16, 0.31, 0.65$, respectively). At URF, fire frequency significantly altered community composition (PERMANOVA pseudo $F = 26.89, P < 0.001$) whereas N addition and year were not significant ($F = 1.53, 0.35, P = 0.16, 1.0$, respectively). At each site there was separation of annual, intermediate and unburned plots along the first CCA axis in order of increasing burn frequency, with the treatments at URF showing a higher spread in relation to species composition (Fig. 2). Species composition did not vary considerably over time, with the centroids of the years clustered around the centre of the ordination plot (Fig. 2).

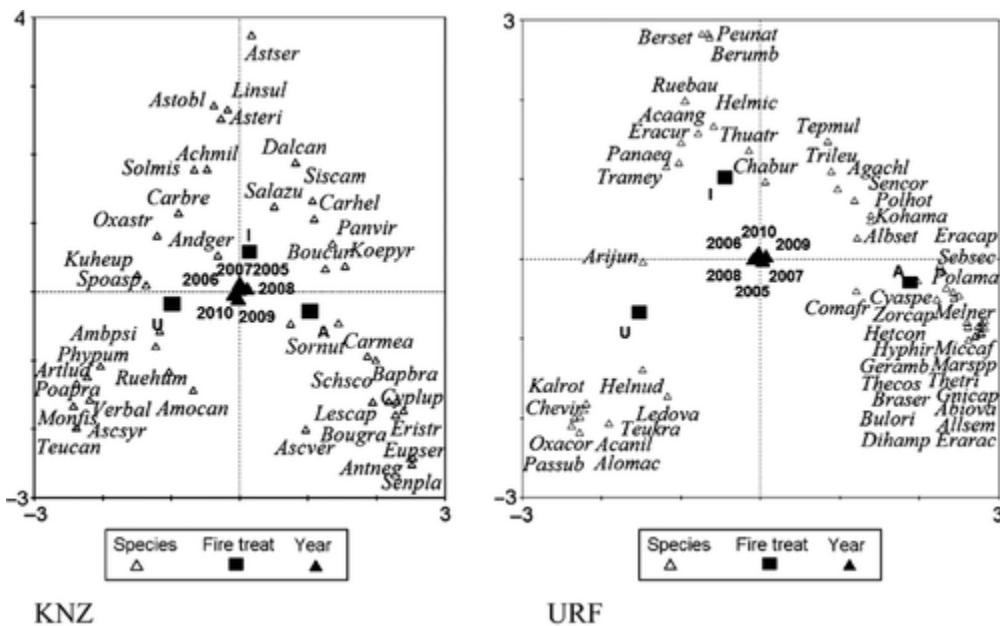


Figure 2. Canonical correspondence analysis ordinations of plant community composition from 2005 through 2010 for Konza Prairie Biological Station (KNZ), Kansas, USA, and Ukulinga Research Farm (URF), South Africa, for three fire treatments: 1-yr (A), 3–4-yr (I) and unburned (U). Species with an occurrence of <10% and <20% for KNZ and URF, respectively, were omitted from the ordination diagrams to reduce clutter. For KNZ, the first two axes accounted for 40.3% and 13.2% of the variance in species data, and 68.8% and 22.3% of the variance in species and environment relations, respectively. For URF, the first two axes accounted for 27.4% and 14.1%, respectively, of the variance in species data, and 61.8% and 31.9%, respectively, of the variance in species and environment relations. The figure shows separation in species composition among the three treatments at both sites. Full species names are shown in Appendix 1.

At KNZ there was a significant year \times fire frequency interaction (PERMANOVA pseudo $F = 3.46, P = 0.009$) and the fertilization \times fire frequency interaction was nearly significant

(PERMANOVA pseudo $F = 1.94$, $P = 0.062$), with the fertilizer–control comparison (across all burn treatments) not significant, but there were significant differences between annually burned and unburned communities at KNZ (R statistic = 0.161, $P = 0.02$). The differences between annually burned and intermediate burn, and intermediate burn and unburned communities were not as strong (R statistic = 0.135, $P = 0.08$; R statistic = 0.133, $P = 0.13$). Four abundant grasses were identified by similarity percentage (SIMPER) analysis to be driving the differences between the fire treatments (Fig. 3). In general, *A. gerardii*, *Schizachyrium scoparium* and *S. nutans* were significantly more abundant on the annually burned sites, whereas *Poa pratensis* increased in abundance on the unburned sites, although *A. gerardii* co-dominated (Fig. 4).

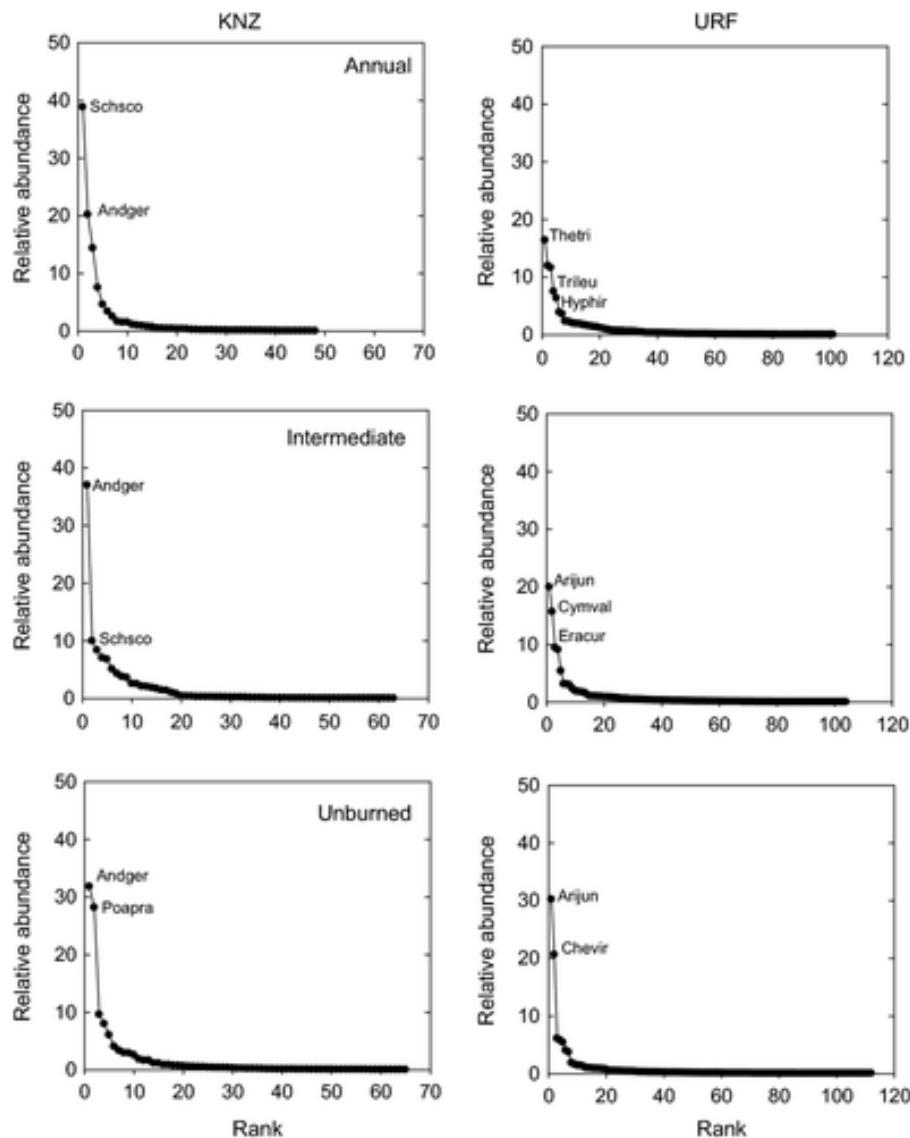


Figure 3. Species rank abundance curves for the annual, intermediate and unburned treatments at Konza Prairie Biological Station (KNZ) and Ukulinga Research Farm (URF).

Schsco = *Schizachyrium scoparium*, Andger = *Andropogon gerardii*, Poapra = *Poa pratensis*, Thetri – *Themeda triandra*, Trileu = *Tristachya leucothrix*, Hyphir = *Hyparrhenia hirta*, Arijun = *Aristida junciformis*, Cymval = *Cymbopogon validus*, Eracur = *Eragrostis curvula*, Chevir = *Cheilanthes viridis*.

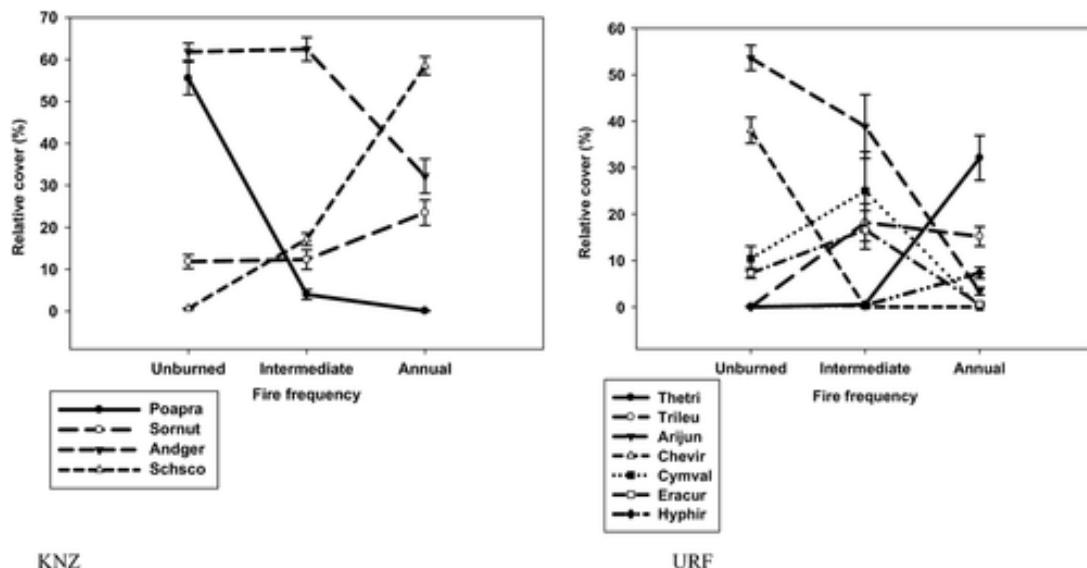


Figure 4. Patterns of mean relative cover (\pm SE) for the most dominant species on unburned, intermediate and annually burned treatments (2005–2010) at Konza Prairie Biological Station (KNZ) and Ukulinga Research Farm (URF). Full species names appear in Appendix 1.

At URF there were no significant interactions, although similar to KNZ, the fertilization \times burn frequency interaction was nearly significant (PERMANOVA pseudo $F = 1.80$, $P = 0.064$). These patterns were confirmed by ANOSIM. Similar to KNZ, the fertilizer-control comparison (across all burn treatments) was not significant at URF, supporting the PERMANOVA analysis. However, there were significant differences between the plant communities of the annually burned and unburned treatments at URF (R statistic = 1.0, $P = 0.01$), and between annually burned and intermediate burns, and intermediate burns and unburned communities (R statistic = 0.75 and 0.59, respectively, $P = 0.01$ for both). SIMPER analysis identified six grass and one forb species that contributed the most to differences among burning treatments (Fig. 3). *Aristida junciformis* and *Cheilanthes viridis* were more abundant on the unburned treatments, whereas *Eragrostis curvula* and *Cymbopogon validus* were more abundant in the intermediate burn treatment, and *T. triandra* and *Tristachya leucothrix* were more abundant in the annually burned treatments (Fig. 4). There was a higher turnover of species dominance across treatments at URF compared to KNZ (Fig. 4).

Species richness in response to fire frequency and N addition

Species richness varied significantly over time at both sites for all burn treatments (Table 1, Fig. 5). For KNZ, species richness tended to be higher in the intermediate burn treatment, whereas it was highest in the annually burned treatment, intermediate with the intermediate burn treatment and lowest in the unburned treatment at URF (Figs 5, 6). The decline in richness with decreasing fire frequency at URF was driven primarily by a reduction in grass species richness (Fig. 6). For both URF and KNZ, nutrient addition resulted in a drop in richness (Fig. 6). The decline in richness at KNZ appeared to be driven by a decline in forb richness, while at URF both forb and grass richness declined.

Table 1. Results of repeated measures ANOVA ($P < 0.05$ in bold) for species richness at two scales (1 m^2 , 4 m^2), and grass and forb cover in response to fire frequency (fire), nitrogen addition (N) and time (year) at Konza Prairie Biological Station, Kansas, USA

Richness 4 m^2					Richness 1 m^2				
Effect	Num df	Den df	F value	Pr > F	Effect	Num df	Den df	F value	Pr > F
Year	4	24	8.78	0.0002	Year	4	24	9.86	< 0.0001
Fire	2	5.46	2.91	0.1378	Fire	2	6.42	1.56	0.2806
Year × Fire	8	24	2.34	0.0512	Year × Fire	8	24	2.38	0.0477
N	1	8.76	37.72	0.0002	N	1	8.69	56.27	< 0.0001
Year × N	4	23.6	2.27	0.0917	Year × N	4	23.6	1.22	0.3306
Fire × N	2	8.76	0.41	0.6734	Fire × N	2	8.69	0.87	0.4530
Year × Fire × N	8	23.6	2.43	0.0449	Year × Fire × N	8	23.6	1.11	0.3890
Relative cover of grasses					Relative cover of forbs				
Effect	Num df	Den df	F value	Pr > F	Effect	Num df	Den df	F value	Pr > F
Year	4	24	2.61	0.0605	Year	4	23.7	2.14	0.1072
Fire	2	1	17.01	0.1690	Fire	2	2.27	16.19	0.0452
Year × Fire	8	24	3.49	0.0083	Year × Fire	8	23.7	3.41	0.0095
N	1	8.13	1.7	0.2283	N	1	7.31	0.46	0.5193
Year × N	4	20.6	3.38	0.0280	Year × N	4	22.8	4.67	0.0067
Fire × N	2	8.13	0.13	0.8759	Fire × N	2	7.31	0.10	0.9036
Year × Fire × N	8	20.6	3.06	0.0194	Year × Fire × N	8	22.8	3.21	0.0136

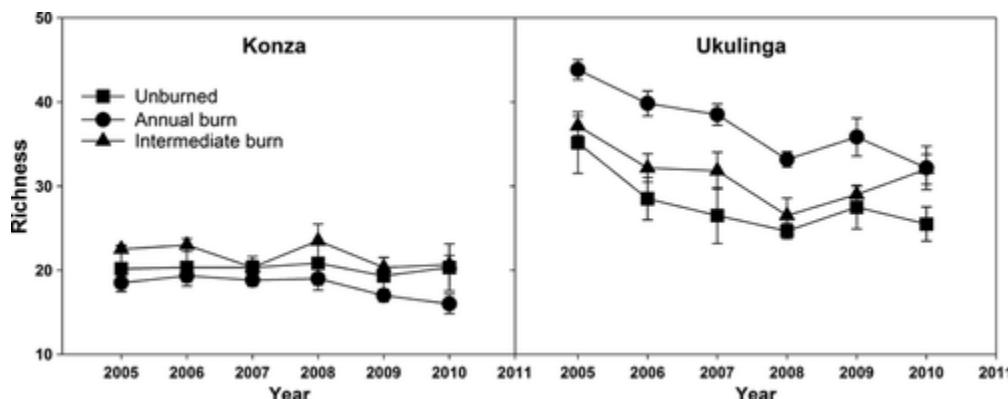


Figure 5. Temporal variability in mean species richness at Konza Prairie Biological Station, USA (left), and Ukulinga Research Farm, South Africa (right), at the 4-m^2 scale, in response to fire frequency.

For relative abundance of grasses, none of the main effects were significant at KNZ, but all interactions with year were significant (Table 1). The effect of fire varied depending on whether nutrients were added, in a way that differed from year to year. The strongest pattern of differences in cover occurred in the intermediate burn treatment, where grass cover increased significantly in the last 2 yrs of sampling, which was opposite to what was observed in the annual burn treatment at KNZ and to the intermediate burn at URF. Response patterns of forbs were quite similar to those of grasses (Table 1).

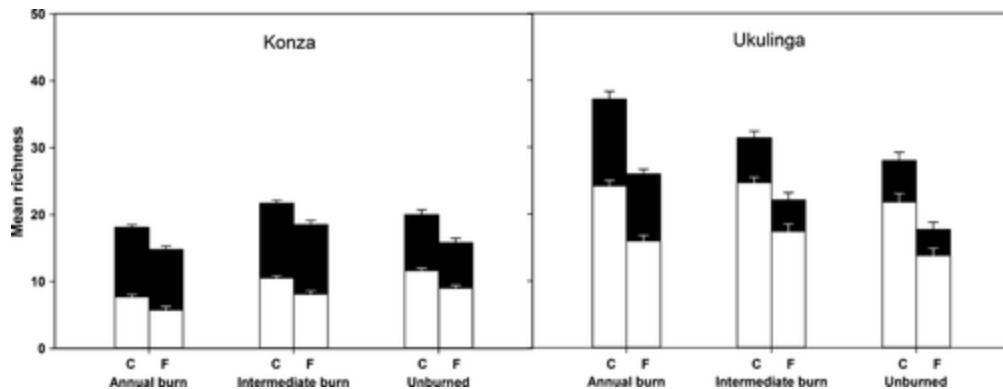


Figure 6. Mean species richness for Konza Prairie Biological Station (left) and Ukulinga Research Farm (right) burn treatments for the unfertilized control plots (C) 2005–2010 and the fertilized plots (F) (2006/7–2010) at the 4-m² scale. White fill represents forbs and black fill represents grasses.

At URF there was a significant fire by time interaction for both grass and forb cover (Table 2). As at KNZ, these differences among treatments existed from the first year of sampling, and the significant effect of year reflects changes in richness over time.

Table 2. Results of repeated measures ANOVA ($P < 0.05$ in bold) for species richness at two scales (1 m², 4 m²), and grass and forb cover in response to fire frequency (fire), nitrogen addition N and time (year) at Ukulinga Research Farm, South Africa

Richness 4 m ²					Richness 1 m ²				
Effect	Num df	Den df	F value	Pr > F	Effect	Num df	Den df	F value	Pr > F
Year	3	36	9.44	<0.0001	Year	3	36	9.33	0.0001
Fire	2	12	12.27	0.0013	Fire	2	12	24.09	<0.0001
Year × Fire	6	36	1.89	0.1087	Year × Fire	6	36	4.45	0.0018
N	1	12	34.76	<0.0001	N	1	12	62.85	<0.0001
Year × N	3	36	0.22	0.8795	Year × N	3	36	0.67	0.5759
Fire × N	2	12	0.67	0.5310	Fire × N	2	12	0.49	0.6218
Year × Fire × N	6	36	0.27	0.9452	Year × Fire × N	6	36	0.49	0.8135
Relative cover of grasses					Relative cover of forbs				
Effect	Num df	Den df	F value	Pr > F	Effect	Num df	Den df	F value	Pr > F
Year	3	18	3.30	0.0442	Year	3	17.9	3.84	0.0277
Fire	2	11.8	7.92	0.0066	Fire	2	11.8	10.66	0.0023
Year × Fire	6	34.1	6.90	<0.0001	Year × Fire	6	32.4	5.86	0.0003
N	1	11.5	0.55	0.4739	N	1	11.5	0.67	0.4293
Year × N	3	18	1.74	0.1949	Year × N	3	18.1	0.97	0.4297
Fire × N	2	12.2	0.51	0.6109	Fire × N	2	12.1	0.62	0.5528
Year × Fire × N	6	24.2	0.18	0.9792	Year × Fire × N	6	25.5	0.08	0.9980

Discussion and conclusions

Over the 5-yr study period, the North American and South African grassland plant community responded differently to fire frequency but similarly to nutrient additions. As predicted, plant species richness at both sites decreased due to N additions. Although fire treatments resulted in different responses in species richness, fire frequency at both sites was the primary driver of

community composition, with the long-term application of fire treatments resulting in striking compositional differences among the fire treatments at both sites (Knapp et al. 1998; Fynn et al. 2005a).

The abundant grasses in the annually burned plots at KNZ, namely *A. gerardii*, *S. scoparium* and *S. nutans* are relatively tall species (Gibson & Hulbert 1987; Collins & Calabrese 2012) that appear to exclude shorter grasses and forbs by competing strongly for light (Turner & Knapp 1996). In contrast to URF, species dominant in annually burned treatments are still common and dominant in the intermediate and unburned treatments. At URF, the grasses dominant in the annually burned plots, *T. triandra*, *H. contortus*, *D. amplexens* and *T. leucothrix*, are relatively short (Gibbs-Russell et al. 1990; van Oudsthoorn 2002), which likely allows co-existence of a variety of other grasses and forbs in spaces between tufts (Fynn et al. 2005b, 2009, 2011). Thus grassland structural responses to annual burning appear to be different between the North American and South African sites. This is not simply the result of grasses being generally shorter at the South African site, as the less frequently burned plots at URF are also dominated by taller grasses. These responses may be region specific, however, a consequence of the traits of local ecotypes and different species assemblages. For example, *T. triandra* has been reported to be tall and dominant in Australia, and thus more likely to reduce species richness (Morgan & Lunt 1999).

In the unburned plots at KNZ, *P. pratensis* increased in dominance. This species is a relatively short, slow growing shade-tolerant species adapted to unburned grassland (McDougall & Turkington 2004) where litter inhibits light penetration and growth of high light tolerant, fast growing species (Knapp & Seastedt 1986). Similarly, at URF, the corresponding dominant grasses in the unburned plots are *A. junciformis* and *C. validus*, which though medium to tall, are also slow growing perennial species that are able to survive and dominate under conditions of shading and high litter levels (Fynn et al. 2011). In this regard, there was evidence of similar grass traits (slow growing, shade tolerant) in unburned grassland between the North American and South African sites, although *P. pratensis* at KNZ is short and *A. junciformis* and *C. validus* at URF are relatively tall.

While N addition had little effect on community composition and structure over the time period under study, N additions decreased richness in both grasslands, even in unburned treatments. This decline in richness is likely due to shading induced by increased productivity of dominant species, coupled with an intolerance of high N levels of some species. *T. triandra*, for example, has been reported to be intolerant to high N levels. Because annual fire affected communities differently, this suggests that indirect effects of fire, which can increase soil N limitation at both sites (Blair 1997), are not driving community responses. The lack of strong temporal responses to N addition could be a consequence of the perennial nature of the herbaceous communities at KNZ (Benson & Hartnett 2006) and in the humid grasslands of KwaZulu-Natal (Everson et al. 2009), which is likely to result in a slow turnover of species. Previous studies have demonstrated that the addition of N over longer periods of time will strongly impact community composition and structure. At URF, long-term addition (>50 yrs) of nutrients resulted in permanent changes in species composition and a decrease in richness (Fynn & O'Connor 2005; Tsvuura & Kirkman 2013), with similar responses at KNZ (Collins et al. 1998), as observed in the Park Grass Experiment (Crawley et al. 2005).

Using comparable methods, we studied the interactive impacts of fire frequency and N availability on community structure in North American and South African mesic grasslands. We found similarities in response to nutrient addition, but strong differences in compositional responses to fire frequency on the two sites. Over the range of disturbance levels investigated, the data do not support the IDH. Indeed, the different compositional responses to fire frequency on the two sites do not support any particular unified theory of community structure and composition, although elements of different theories may be supported. For example, tolerance of limiting resources (such as light) in the unburned treatments at both sites, *sensu* Grime (1977), or the trade-offs among species' abilities to compete for resources, *sensu* Tilman (1987), may be supported with the data from South African grasslands (Fynn et al. 2005b, 2011). Examination of the individual species' traits governing growth, reproduction and survival at URF and KNZ may account for the divergent responses. Logan et al. (2009) showed that fire had positive effects on seed reproduction in *A. gerardii*, although vegetative reproduction far outweighs the role of seed in grass reproduction in tallgrass prairie (Benson & Hartnett 2006) and in South African humid grasslands (Everson et al. 2009). Rhizomatous spread may be a factor facilitating dominance of *A. gerardii* (Gough et al. 2012) and exclusion of other species, particularly forbs. At URF, none of the grass species are rhizomatous. Ghebrehiwot et al. (2012) and Kulkarni et al. (2012) showed differential responses of grass seedling growth to smoke and heat in South African grasslands, with *T. triandra* responding positively. This may contribute to its dominance in annually burned treatments. This is in line with conclusions reached by Suding et al. (2003), Grime (2007) and Tilman (2007) that plant traits of the dominant species affect species interactions and influence patterns of community structure.

Overall, our results show that similar net primary production (Knapp et al. 2006; Buis et al. 2009) does not translate into parallel responses of plant community structure to fire frequency in North American and South African mesic grasslands. The results indicate a need to focus on species traits and how these influence co-existence of species under varying conditions as a means of generalizing grassland responses to disturbances.

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Appendix

Abbreviations and full names for plant species found at Ukulinga Research Farm, South Africa, and Konza Prairie Biological Station, USA, that were used in the figures.

Ukulinga		Konza	
Abiova	<i>Abildgaardia ovata</i>	Achmil	<i>Achillea millefolium</i>
Acaang	<i>Acalypha angustata</i>	Ambpsi	<i>Ambrosia psilostachya</i>
Agachl	<i>Agathisanthemum chlorophyllum</i>	Amocan	<i>Amorpha canescens</i>
Albset	<i>Albuca setosa</i>	Andger	<i>Andropogon gerardii</i>
Allsem	<i>Alloteropsis semialata</i>	Antneg	<i>Antennaria neglecta</i>
Alomac	<i>Aloe maculata</i>	Artlud	<i>Artemisia ludoviciana</i>
Arijun	<i>Aristida junciformis</i>	Ascsyr	<i>Asclepias syriaca</i>
Berset	<i>Berkheya setifera</i>	Ascver	<i>Asclepias verticillata</i>
Berumb	<i>Berkheya umbellata</i>	Astobl	<i>Aster oblongifolius</i>
Braser	<i>Brachiaria serrata</i>	Astser	<i>Aster sericeus</i>
Bulori	<i>Bulbostylis oritrephe</i> s	Bapbra	<i>Baptisia bracteata</i>
Chabur	<i>Chaetacanthus burchellii</i>	Boucur	<i>Bouteloua curtipendula</i>
Chevir	<i>Cheilanthes viridis</i>	Carbre	<i>Carex brevior</i>
Comafr	<i>Commelina africana</i>	Carhel	<i>Carex heliophila</i>
Cyaspe	<i>Cyanotis speciosa</i>	Carmeia	<i>Carex meadii</i>
Cymval	<i>Cymbopogon validus</i>	Cyplup	<i>Cyperus lupulinus</i>
Dihamp	<i>Diheteropogon amplectens</i>	Dalcan	<i>Dalea candida</i>
Eracap	<i>Eragrostis capensis</i>	Eistr	<i>Erigeron strigosus</i>

Eracur	<i>Eragrostis curvula</i>	Eupser	<i>Euphorbia serpens</i>
Erarac	<i>Eragrostis racemosa</i>	Koepyr	<i>Koeleria pyramidata</i>
Geramb	<i>Gerbera ambigua</i>	Kuheup	<i>Kuhnia eupatorioides</i>
Gnicap	<i>Gnidia capitata</i>	Lescap	<i>Lespedeza capitata</i>
Helmic	<i>Helichrysum miconiifolium</i>	Linsul	<i>Linum sulcatum</i>
Helnud	<i>Helichrysum nudifolium</i>	Monfis	<i>Monarda fistulosa</i>
Hetcon	<i>Heteropogon contortus</i>	Oxastr	<i>Oxalis stricta</i>
Hyphir	<i>Hyparrhenia hirta</i>	Panvir	<i>Panicum virgatum</i>
Kalrot	<i>Kalanchoe rotundifolia</i>	Phypum	<i>Physalis pumila</i>
Kohama	<i>Kohautia amatymbica</i>	Poapra	<i>Poa pratensis</i>
Ledova	<i>Ledebouria ovatifolia</i>	Ruehum	<i>Ruellia humilis</i>
Marspp	<i>Mariscus species</i>	Schasco	<i>Schizachyrium scoparium</i>
Melner	<i>Melinis nerviglumis</i>	Senpla	<i>Senecio plattensis</i>
Miccaf	<i>Microchloa caffra</i>	Siscam	<i>Sisyrinchium campestre</i>
Oxacor	<i>Oxalis corniculata</i>	Solmis	<i>Solidago missouriensis</i>
Panaeq	<i>Panicum aequinerve</i>	Sornut	<i>Sorghastrum nutans</i>
Passub	<i>Passiflora suberosa</i>	Spoasp	<i>Sporobolus asper</i>
Peunat	<i>Peucedanum natalense</i>	Teucan	<i>Teucrium canadense</i>
Polama	<i>Polygala amatymbica</i>	Verbal	<i>Vernonia baldwinii</i>
Polhot	<i>Polygala hottentotta</i>		
Ruebau	<i>Ruellia baurii</i>		
Sebsed	<i>Sebaea sedoides</i>		
Sencor	<i>Senecio coronatus</i>		
Teukra	<i>Teucrium kraussii</i>		
Thecos	<i>Thesium costatum</i>		
Thetri	<i>Themeda triandra</i>		
Thuatr	<i>Thunbergia atriplicifolia</i>		
Tramey	<i>Tragia meyeriana</i>		
Trileu	<i>Tristachya leucothrix</i>		
Zorcap	<i>Zornia capensis</i>		