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Forage Nutritive Quality in the Serengeti Ecosystem: The Roles of Fire and Herbivory

T. Michael Anderson,^{1,*} Mark E. Ritchie,^{2,†} Emilian Mayemba,^{3,‡} Stephanie Eby,^{2,§} James B. Grace,^{4,||} and Samuel J. McNaughton^{2,#}

1. Community and Conservation Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands;

2. Department of Biology, Syracuse University, Syracuse, New York 13244;

3. Serengeti Wildlife Research Center, P.O. Box 661, Arusha, Tanzania;

4. U.S. Geological Survey, National Wetlands Research Center, Lafayette, Louisiana 70506

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ABSTRACT: Fire and herbivory are important determinants of nutrient availability in savanna ecosystems. Fire and herbivory effects on the nutritive quality of savanna vegetation can occur directly, independent of changes in the plant community, or indirectly, via effects on the plant community. Indirect effects can be further subdivided into those occurring because of changes in plant species composition or plant abundance (i.e., quality versus quantity). We studied relationships between fire, herbivory, rainfall, soil fertility, and leaf nitrogen (N), phosphorus (P), and sodium (Na) at 30 sites inside and outside of Serengeti National Park. Using structural equation modeling, we asked whether fire and herbivory influences were largely direct or indirect and how their signs and strengths differed within the context of natural savanna processes. Herbivory was associated with enhanced leaf N and P through changes in plant biomass and community composition. Fire was associated with reduced leaf nutrient concentrations through changes in plant community composition. Additionally, fire had direct positive effects on Na and nonlinear direct effects on P that partially mitigated the indirect

negative effects. Key mechanisms by which fire reduced plant nutritive quality were through reductions of Na-rich grasses and increased abundance of *Themeda triandra*, which had below-average leaf nutrients.

Keywords: fire, herbivory, leaf nutrients, forage element concentration, plant community composition, structural equation modeling.

Fire and herbivory are fundamental ecological and evolutionary forces that have influenced the distribution, structure, composition, and functioning of earth's savanna-grassland ecosystems (Huntley and Walker 1982; Coughenour 1985; Skarpe 1992; Bond and van Wilgen 1996; Bond and Keeley 2005). By affecting the balance between woody plant invasion and herbaceous vegetation growth, fire and herbivory influence the stability of many savanna grasslands around the world (Scholes and Archer 1997; Higgins et al. 2000; Roques et al. 2001; House et al. 2003; van Langevelde et al. 2003; Sankaran et al. 2004). As a result of their effects on primary production and plant-soil nutrient pools, fire and herbivory exert control over terrestrial ecosystem energy flow (McNaughton 1976; Frost and Robertson 1987; Detling 1988; Holland et al. 1992; Frank et al. 1998; Oesterheld et al. 1999) and often work in tandem to influence the cycling and availability of nutrients (Hobbs et al. 1991; Hobbs 1996; Blair et al. 1998; Knapp et al. 1999).

From the standpoint of herbivores, nutrient availability is often experienced through the nutritive quality of plants. Plant nutritive quality is of fundamental importance across savanna-grassland ecosystems because of its role in the seasonal movements of migratory ungulates (Fryxell and Sinclair 1988; McNaughton 1988), the spatial distribution of resident herbivore population (McNaughton 1990; Ben-Shahar and Coe 1992), and key ecosystem properties such as decomposition and nutrient cycling (Hobbie 1992; Ritchie et al. 1998). In turn, ungulate migratory patterns and the location of resident herds are essential factors in the design of parks and reserves meant to protect endangered grazing ecosystems (Coughenour 1991; Wallis De Vries

* E-mail: t.m.anderson@rug.nl.

† E-mail: meritchi@syr.edu.

‡ E-mail: emilianmayemba@yahoo.com.

§ E-mail: sleby@syr.edu.

|| E-mail: jim_grace@usgs.gov.

E-mail: sjmnaug@syr.edu.

1995; Thirgood et al. 2004). Thus, it is important to understand how factors such as fire and herbivory, pervasive in savanna grassland and grazing ecosystems, influence forage nutritive quality and plant-derived animal nutrition.

Models of herbivore influences on plant nutritive quality generally emphasize herbivore selectivity and the ability of plants to recover after defoliation (Pastor and Naiman 1992; Jefferies et al. 1994; Hobbs 1996; Augustine and McNaughton 1998; Ritchie 2000). Selective herbivory can decelerate nutrient cycling by shifting plant species composition toward unpalatable, low-nutritive-quality species. In contrast, generalist herbivores can promote or maintain palatable, high-nutritive-quality plant species when nutrient inputs, temporal variability, or the timing of defoliation are sufficient to maintain such species (Hobbs 1996; Augustine and McNaughton 1998; Frank et al. 1998). Herbivory can have a wide range of direct effects on leaf-tissue chemistry that depend on soils, available water, and frequency and intensity of defoliation (Holland and Detling 1990; Pastor et al. 1993; de Mazancourt et al. 1998; Ritchie et al. 1998; Sirotiak and Huntly 2000). Commonly, it has been observed that nutrient concentration is increased in postdefoliation regrowth through the replacement of older, low-quality leaves by younger, high-quality tissue (Hamilton et al. 1998) or from physiological upregulation of enzymes stimulated by defoliation (Anderson et al. 2006).

In comparison with herbivory, fire is almost always a generalist consumer (*sensu* Bond and Keeley 2005) and thus can have homogenizing effects on nutrient cycling and availability (Hobbs et al. 1991; Hobbs 1996). Like herbivory, however, defoliation due to fire can have wide-ranging effects on nutrient concentrations in postfire regrowth (Knapp 1985; Ojima et al. 1994; Blair 1997; Turner et al. 1997; van de Vijver et al. 1999). Increased leaf nutrient concentrations after fire can occur because of rapid short-term increases in rates of nutrient mineralization and availability (Hobbs and Schimel 1984; Ojima et al. 1994), removal of older tissues (Knapp 1985), or increased leaf : stem ratios (van de Vijver et al. 1999). Decreased leaf nutrient concentrations are expected to be associated with decreased mineralization rates and accumulated N loss from repeated burning (Blair 1997). The direct effects of fire on tissue chemistry are typically short-lived, usually lasting only a few months (Hobbs et al. 1991; Ojima et al. 1994; van de Vijver et al. 1999). However, fire can also have indirect effects on the nutritive quality of a plant community by promoting the abundance of fire-tolerant species (Gibson and Hulbert 1987; Hartnett et al. 1996) and increasing germination rates of disturbance-adapted species (Tyler 1995; Benwell 1998; Jutila and Grace 2002).

The influences of fire and herbivory on plant nutritive quality discussed thus far can be generalized into rela-

tionships that (1) are independent of changes in the plant community or (2) occur because of changes in the plant community. Influences that occur because of changes in the plant community can also be further subdivided into those that depend on (i) plant abundance (i.e., quantity) or (ii) plant species composition (i.e., quality). There are many ways that fire and herbivory can influence plant nutritive quality independent of the plant community, including upregulating metabolism in defoliated plants (Karban and Myers 1989; Anderson et al. 2006), translocating nutrients from roots to shoots (Ourry et al. 1988), or affecting soil-available nutrients through various mechanisms (Huntly 1991; Sirotiak and Huntly 2000; Knops et al. 2002). Thus, a conceptual illustration of the influences of fire and herbivory on plant nutritive quality includes a system of possible direct and indirect paths with unique signs and strengths (fig. 1).

In Serengeti National Park (SNP), Tanzania, frequent fires and chronic herbivory are major ecological and evolutionary forces influencing the savanna-grassland plant communities (Sinclair and Norton-Griffiths 1979; McNaughton 1985). As one of the last fully functional grazing ecosystems and home to the largest aggregation of migratory ungulates on earth (Sinclair et al. 2007), the Serengeti provides a seminal example of how fire and herbivory can influence nutrient availability in a natural system. Although many studies have focused on N availability, research in SNP has demonstrated that the spatial and temporal distribution of at least seven elements is associated with resident herbivore densities (McNaughton 1988) and the timing of migratory herbivore movements (McNaughton 1990). In particular, phosphorus (P) and sodium (Na) in aboveground forage are particularly important to herbivores because they are required to sustain pregnancy and lactation (Murray 1993, 1995). Like all natural ecosystems, the influences of fire and herbivory on plant nutritive quality in SNP operate within a system of multiple influences that obscure the true relationships between these variables (Shiple 2000); the most prominent of these in SNP are strong gradients in climate and soil fertility (McNaughton et al. 1988; Sinclair and Arcese 1995; Anderson et al. 2007).

In this study, observations of forage nutritive quality were examined in relation to patterns of fire frequency and herbivore density in Serengeti savanna grasslands. To account for the influences of climate and soils, variation in rainfall and soil nutrient data were incorporated into the analysis as broadscale environmental influences. The primary goal of the study was to partition the influences of fire frequency and herbivore density on plant nutritive quality into those effects that occurred independently of changes in the plant community (i.e., direct effects) and those that occurred because of changes in the plant com-

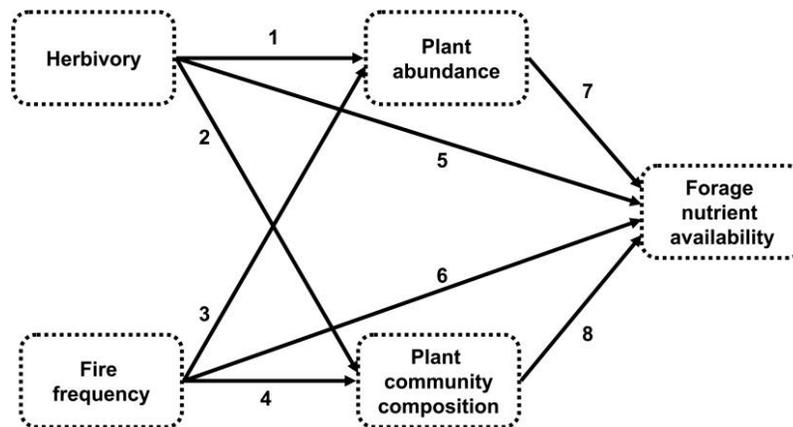


Figure 1: Conceptual diagram demonstrating some of the multivariate effects by which herbivory and fire frequency may influence the availability of nutrients in forage. Herbivore effects on leaf nutrient concentrations can be direct (5), and therefore independent of changes in the plant community, or they can be indirect, and occur because of changes in plant abundance (1 → 7) or plant community composition (2 → 8). Similarly, fire effects on leaf nutrient concentrations can be direct (6), and thus independent of changes in the plant community, or they can be indirect, occurring via effects brought about by changes in plant abundance (3 → 7) or changes in the composition of the plant community (4 → 8). See table 1 for a description of the processes linked to each path in the conceptual model.

munity (i.e., indirect effects; fig. 1). Structural equation modeling (SEM), a means of accomplishing such partitioning, was used to address the following questions. (1) What is the relationship between herbivore density, fire frequency, and vegetation community properties, specifically, plant abundance and species composition? (2) Are the relationships between herbivore density, fire frequency, and plant N, P, and Na predominantly independent of changes in the plant community, dependent on changes in the plant community, or both? Finally, (3) how do the relationships whereby fire frequency and resident herbivore density influence plant nutrients differ? While the specific effects of fire and herbivory in particular plant communities are generally known, an understanding of the network of connections relating fire and herbivory to forage nutritive quality is lacking. By incorporating variation in rainfall and soils into our analysis, we build on the current understanding of the complex contingencies that operate in African savanna grasslands (McNaughton 1983, 1985).

Methods

Site Selection and Compilation of Environmental Data Layers

The nature of our study questions required that we sample across sites that varied in fire frequency and herbivore use but that were not confounded by differences in soil fertility and rainfall. The network of game reserves and wildlife management areas on the western edge of SNP (fig. 2)

have created a gradient of herbivore use because hunting in the reserve areas reduces resident herbivore densities compared with inside the national park, where hunting has been banned since 1951 (Sinclair and Arcese 1995). The average rainfall in this region is high and, therefore, herbaceous fuel is abundant, whereas areas to the south and east have lower average rainfall and infrequent fires (Norton-Griffiths 1979). Fires set by park officials and people living near the park are common in the reserves and on the western edge of SNP (Norton-Griffiths 1979). The conditions created by the reserve areas allowed us to sample sites with contrasting herbivore densities and various fire frequencies while controlling for variation in soil fertility and rainfall.

Thirty study sites along the western edge of SNP were sampled from February 5 to March 15, 2005, corresponding to the plant growing season and the period when herds of migratory wildebeests and zebras were located in their wet-season calving grounds in the Serengeti Plains. The timing of the study ensured that the sites had not been influenced by the annual migration for several months, as migratory animals typically move into the Serengeti Plains in November (Murray 1995; Thirgood et al. 2004). Satellite data, collected by the Moderate-Resolution Imaging Spectroradiometer (MODIS) at a spatial resolution of 250 m² between 2000 and 2004, was used a priori to identify sites that varied in fire frequency (see app. A and table B1 in the online edition of the *American Naturalist*).

As a measure of long-term resident herbivore use at each of the 30 sites, we utilized resident herbivore counts obtained by aerial surveys conducted by the Frankfurt

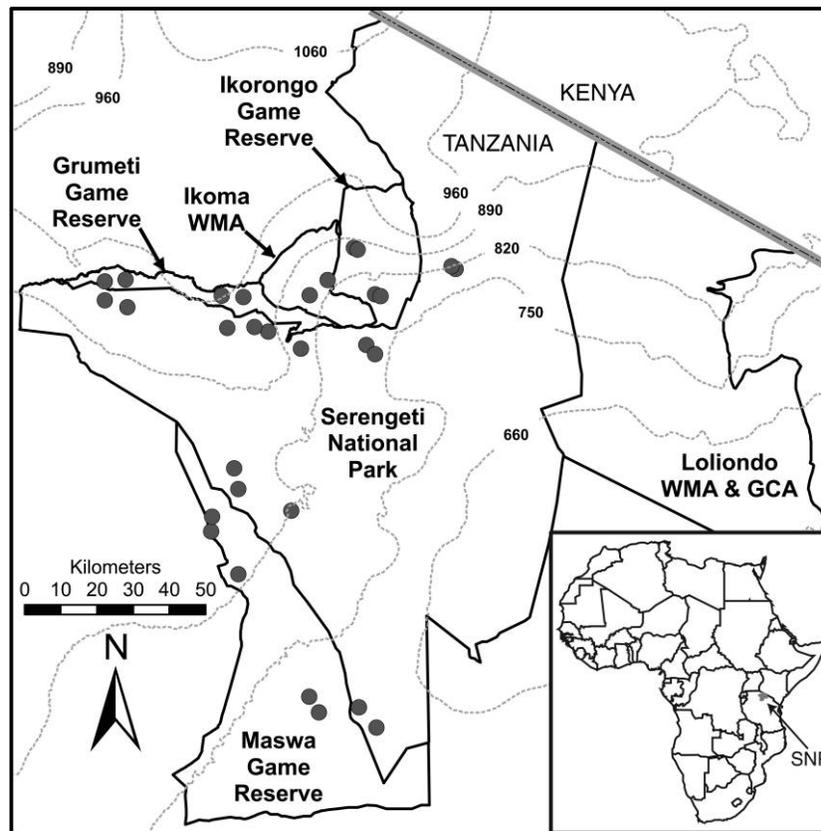


Figure 2: Diagram showing the location of 30 study sites (dots) in the western part of the Serengeti ecosystem. The Serengeti ecosystem is composed of a network of game reserves, wildlife management areas (WMA), and game control areas (GCA) in which human activities, such as hunting, reduce herbivore densities compared with the core protected area of Serengeti National Park (in which such activities are prohibited). Isoleths (dotted lines) show average annual rainfall values (in mm), interpolated from data collected over the last 40 years (see “Methods”). Inset in the bottom-right corner shows the location of the Serengeti ecosystem within the country of Tanzania on the continent of Africa.

Zoological Society in 1988, 1991, 1996, 2001, and 2003. The available data included counts of four ungulate species: giraffe (*Giraffa camelopardalis*), Coke’s hartebeest (*Alcelaphus buselaphus*), topi (*Damaliscus korrigum*), and impala (*Aepyceros melampus*). The methods used to count herbivores and estimate herbivore densities in SNP are described by Campbell and Borner (1995). For each species, ArcGIS version 9.1 (ESRI, Redlands, CA) was used to produce map layers that consisted of 5-km² grid cells of herbivore densities averaged across the five surveys. Densities of the four species were then combined to produce a final map layer from which the average ungulate density was extracted using the Universal Transverse Mercator (UTM) coordinates of the sites (app. A).

As a measure of climate effects on leaf nutrients at each of the sites, monthly precipitation data from over 30 years and 58 rain-gauge locations across SNP were obtained from the Serengeti Environmental Monitoring Program. Data at each rain gauge were averaged annually, but only

those years with data from each of the 12 calendar months were included in the calculations. The values for mean annual rainfall at each rain gauge were then interpolated using inverse-distance weighting to create a geographic information system (GIS) layer of mean annual precipitation across SNP. The UTM coordinates of each site were then used to extract mean annual precipitation at each of the sites using ArcMap (ESRI; <http://www.esri.com>).

Data Collection at Each Site

Each site consisted of a 1,000-m² (50 × 20 m) plot in which plant species composition, standing plant biomass, and soil and leaf-tissue nutrient concentrations were collected within five nested 1-m² subplots. Plant species abundance was measured by visually estimating percent cover of each species within subplots (app. A). Standing plant biomass was collected by clipping all aboveground vegetation from a 0.5-m² area within each subplot and weigh-

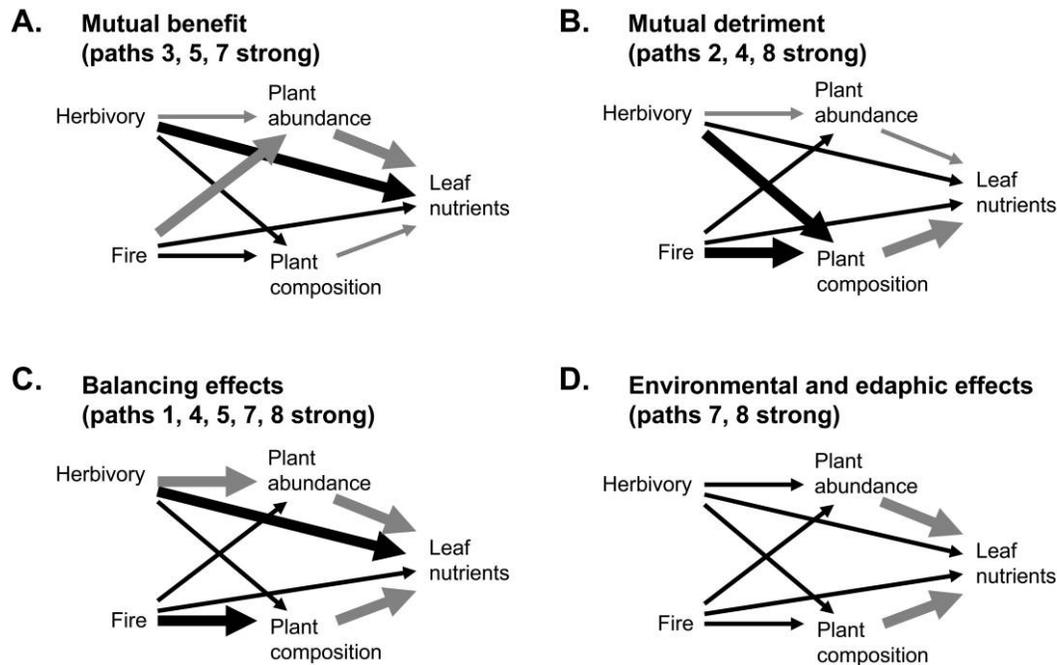


Figure 3: Path diagrams representing four specific hypotheses addressed within the framework of the conceptual model (fig. 1). The effect of fire and herbivory on leaf nutrients can have mutual benefit (A), mutual detriment (B), or balancing effects (C) on leaf nutrient availability. In contrast, variation in leaf nutrients can be independent of fire and grazing and instead related to environmental and edaphic effects (D). Widths of the arrows are proportional to the strength of the proposed effect; gray arrows represent negative effects, black arrows represent positive effects; path numbers refer to those in the construct model (fig. 1). See text for more detailed explanation of the hypotheses.

ing the samples after they were oven-dried. Subsequent to weighing, all plant biomass samples were ground and analyzed for N, P, and Na using standard methods (app. A). In order to understand how leaf nutrient concentrations of dominant species influenced the community sample, five replicate individuals of the grass *Themeda triandra* were randomly collected in each plot and measured for N, P, and Na using the same methods. *Themeda triandra* is among the most commonly occurring herbaceous species in the Serengeti and often the most locally abundant (Anderson et al. 2006). Soil samples were collected within each subplot and analyzed for 21 soil elements and soil organic matter with standard methods (app. A). Soil organic matter was highly correlated with the abundance of soil elements and is therefore used as a surrogate measure of soil fertility for the remainder of this article (app. A). Site averages, calculated from replicate soil, leaf tissue, and standing crop biomass within plots, were used in all subsequent analyses.

Specific Hypotheses, Statistical Analyses, and Structural Equation Modeling

Statistical modeling was guided by the creation of an a priori conceptual model, also known as a construct model

(Grace 2006). In this model, we hypothesized that fire frequency and history of herbivory are associated with forage nutrient availability through changes in the plant community or through associations that do not depend on changes in the plant community. The construct model provided a framework for the specific analyses of data using structural equation modeling and the evaluation of four a priori hypotheses (fig. 3; table 1), which were tested against the observed data. The four specific hypotheses follow logically from what is known of the effects of fire and herbivory in savanna ecosystems. The first (fig. 3A) is that fire and herbivory have mutual benefits for plant nutritional quality: fire by reducing plant biomass (i.e., van de Vijver et al. 1999) and herbivory by enhancing nutrient cycling (i.e., McNaughton et al. 1997). The second (fig. 3B) is that both factors act as mutual detriments for plant nutritional quality by selecting for nutrient-poor unpalatable and/or fire-resistant species (i.e., Ritchie et al. 1998). Third (fig. 3C) is that fire and herbivory may have balancing effects on leaf nutritional quality because their relative effects oppose and offset one another. Our hypothetical diagram shows the negative effects of fire on plant community composition being offset by the stimulatory effects of herbivory, although several other bal-

Table 1: Descriptions of the processes that contribute to the effects of herbivory and fire frequency on forage nutrient availability in herbaceous plants

Path	Description	Potential mechanism
1	Herbivore effects on plant abundance	Reduction of plant abundance through consumption or stimulation of plant abundance through herbivore optimization. On an aerial basis, herbivores can also influence plant abundance by modifying plant density.
2	Herbivore effects on plant community composition	Changes in plant community composition through the addition, deletion, or replacement of plant species. Mechanisms include elimination of palatable species, promotion of herbivore-tolerant species, or altering abiotic conditions and the plant microclimate.
3	Fire effects on plant abundance	Fire can reduce biomass by negatively affecting growth or increase abundance by stimulating growth, removing dead/old tissue, and increasing light interception.
4	Fire effects on plant community composition	Changes in plant community composition through the elimination of fire-intolerant species and promotion of fire-tolerant species by improving survival, growth, and reproduction. Also, fire may alter abiotic conditions or the microclimate in a way that promotes coexistence or favors particular species over others.
5	Herbivore effects on leaf nutrient concentrations	Herbivory reduces the prevalence of older, lignified tissues and stimulates the growth of younger, less lignified leaves. Repeated defoliation may induce changes in leaf-tissue chemistry or alter the stoichiometry of regrowing tissue. Herbivory can also increase plant-available nutrients by increasing rates of nutrient cycling.
6	Fire effects on leaf nutrient concentrations	Fire can increase leaf nutrients by replacing senesced tissue with younger leaves, increasing leaf : stem ratios, or increasing soil nutrient availability via effects on the microbial community or in concentrated ash deposits. Fire can reduce leaf nutrient content through negative impacts on the microbial community, nutrient volatilization, destruction of soil organic matter, creation of soil crusts, or reductions in soil moisture.
7	Effects of plant abundance on leaf nutrient concentrations	Plant abundance influences leaf nutrients because plant size is related negatively to nutrient-use efficiency and positively to respiration rate. Thus, leaf nutrients are diluted relative to carbon in aboveground components as plants become larger.
8	Effects of plant composition on leaf nutrient concentrations	Compositional changes influence forage nutrient quality because species have different life-history strategies, nutrient-uptake capabilities, nutrient-use efficiencies, and carbon-allocation strategies that translate into different average leaf nutrient contents.

Note: The numbers in the column labeled "Path" match the numbers associated with the arrows in figure 1. In the conceptual schematic, the effects of herbivory and fire can influence leaf nutrients in ways that do not depend on changes in plant community properties (direct) or in ways that depend on changes in properties of the plant community (indirect).

ancing effects are possible (i.e., Sirotnak and Huntly 2000). Finally, variation in plant nutritional quality may be largely controlled by environmental and edaphic effects (fig. 3D). In this scenario, environmental factors, such as rainfall, and edaphic factors, such as soil fertility, impose a strong bottom-up effect on plant nutritional quality that is independent of the effects of fire and herbivory.

In developing the structural equation (SE) model, the general concept of plant abundance (i.e., quantity) in the construct model was represented in our data with estimates of standing plant biomass. Two types of specific data were used to represent plant species composition (i.e., quality). First was an ordination on the relative abundances of plant species (percent cover) using nonmetric multidimensional scaling (NMDS) in PC-ORD version 4 (McCune and Medford 1999). Species' abundances in the five subplots were summed within each whole plot before calculating species relative abundance. The first ordination axis of the NMDS

was used as an index of plant community composition across sites. Because individual plant species in SNP can vary drastically in the average Na concentration of leaves (Hamilton et al. 2001), a single species can exert a disproportionately large influence on Na availability to herbivores. Thus, the second measure of community composition used was the abundance of those species in SNP known to have a high leaf-tissue Na concentration (app. A; table B2). Finally, the general concept of history of herbivory was represented specifically in our data by density estimates of the four resident herbivore species, as described above. Estimates of resident herbivore densities do not capture the effects imposed by herds of migratory ungulates that graze in the western regions of SNP as they move toward dry season foraging grounds in Kenya. However, because the effects of migrants are ephemeral and more spatially uniform compared with long-term effects of resident herbivores, we argue that resident densities

provide an appropriate measure of herbivore effects. Finally, to account for some of the other major systemwide influences on plant nutritive quality (i.e., the “environmental and edaphic effects” hypothesis), average annual rainfall (as a measure of climate effects) and soil organic matter (as a measure of soil fertility) were controlled for as background variables in the SEM.

The estimation of the SE model was based on maximum likelihood solution procedures using version 4 of the software package Mplus (Muthén and Muthén 1998). Robust estimation techniques were used, including bootstrapping of the model parameter estimates. Model fit was assessed using the χ^2 statistic and its associated P value. The significance of individual path coefficients was evaluated using z -tests (standardized equivalent of t -tests) and by observing the effect on model fit when individual paths were omitted from the model. Model fit was judged adequate when the expected and observed covariances did not differ based on a critical P value of $\alpha > 0.05$. In the case where nonlinear paths existed between variables that could not be made linear through transformations (app. A), nonlinear modeling methods involving the construction of composite variables were used (Grace and Bollen 2007).

Univariate statistics were conducted to evaluate net effects. Mean differences between the paired study sites inside and outside the national park boundary were compared with nonparametric Wilcoxon matched pairs test statistics when discrete count data were analyzed (i.e., fire frequency); otherwise, paired t -tests were performed. Bivariate regressions were conducted to analyze the linear relationships between variables. Data were transformed when frequency distributions were significantly nonnormal. A multiple regression with rainfall, soil organic matter, herbivore density, and fire frequency as predictors was used to identify associations between these factors and *T. triandra* abundance. All statistics outside of the SEM analysis were performed in SAS version 8 (SAS Institute, Cary, NC).

Results

As was intended by our sampling design, paired study sites occurring inside and outside the national park border transected an herbivore density gradient; sites inside had higher average herbivore density than plots outside SNP (in = 3.95 animals km⁻², out = 2.44 animals km⁻²; $t = 2.13$, $df = 14$, $P = .05$) but did not differ significantly with respect to the frequency of fires in the last 5 years (in = 2.13, out = 2.6; $z = 1.09$, $df = 14$, $P = .27$) or soil organic matter (in = 8.1%, out = 7.6%; $t = 0.63$, $df = 14$, $P = .54$). Because of the northwest to southeast orientation of the rainfall gradient and the fact that sites outside the park tended to be located northwest of the sites inside the

park (fig. 2), there was a tendency for sites outside to have higher rainfall than paired sites inside the park (in = 838.0 mm year⁻¹, out = 856.3 mm year⁻¹; $t = 2.39$, $df = 14$, $P = .032$). However, the difference between paired sites was much smaller than the range of rainfall captured across the gradient (min = 700 mm year⁻¹, max = 969 mm year⁻¹). The NMDS ordination scores of plant communities inside and outside of the national park boundaries varied consistently between paired sites (in = -0.21, out = 0.21; $t = 7.9$, $df = 14$, $P < .0001$), as did standing plant biomass (in = 452.8 g m⁻², out = 593.6 g m⁻²; $t = 2.79$, $df = 14$, $P = .015$). Finally, average leaf-tissue concentrations also differed inside and outside of the national park for leaf N (in = 1.14%, out = 0.90%; $t = 4.41$, $df = 14$, $P = .0003$) and leaf P (in = 2,362.1 mg kg⁻¹, out = 1,666.1 mg kg⁻¹; $t = 3.35$, $df = 14$, $P = .002$), but not for Na (in = 2,646.6 mg kg⁻¹, out = 1,719.8 mg kg⁻¹; $t = 1.76$, $df = 14$, $P = .12$).

Bivariate plots displaying the relationship between the explanatory variables—fire frequency, herbivore density, soil organic matter, and rainfall—and the response variables—leaf N, P, and Na—revealed nonsignificant statistical relationships in all but one case (fig. B1); leaf P displayed a significant unimodal relationship with fire frequency (leaf P = 1,062.5 + 823.3 × fire frequency - 139.1 × fire frequency; $F = 3.66$, $df = 2, 27$, $P = .04$, $R^2 = 0.21$). Bivariate relationships between plant community properties—such as standing plant biomass, ordination scores, and the abundance of Na-rich grasses—and the response variables—leaf N, P, and Na—exhibited four out of eight statistically significant relationships (fig. B2). Leaf N was negatively related to both plant biomass (leaf N = -0.0017 × biomass + 1.46; $F = 15.25$, $df = 1, 28$, $P = .0005$, $R^2 = 0.35$) and plant community composition, as indicated by the NMDS ordination score (leaf N = -0.30 × NMDS + 1.02; $F = 9.37$, $df = 1, 28$, $P = .005$, $R^2 = 0.25$). In this case, positive ordination scores were associated with a greater abundance of the grasses *Themeda triandra*, *Eragrostis heteromera*, *Sporobolus pyramidalis*, and *Microchloa kunthii*, while negative scores were associated with the grasses *Pennisetum mezzianum*, *Cynadon dactylon*, *Digitaria macroblephara*, and the greater abundance of sedges. Leaf P was also negatively related to plant biomass (leaf P = -4.13 × biomass + 3,094.56; $F = 12.55$, $df = 1, 28$, $P = .001$, $R^2 = 0.31$). Finally, leaf Na was positively associated with the relative abundance of Na-rich grasses (leaf Na = 4,619.93 × Na-rich grasses - 227.24; $F = 36.34$, $df = 1, 28$, $P < .0001$, $R^2 = 0.56$).

SEM Results

The SE model that was accepted and used for interpretation demonstrated a close fit of data to model as judged

by the χ^2 goodness-of-fit statistic ($\chi^2 = 24.95$, $df = 30$, $P = .73$). Note that the large P value associated with the χ^2 value in this instance indicates that the covariance structure of the data did not differ significantly from that expected, based on the model. The amount of variance in leaf nutrient concentrations explained by the final SEM was relatively high, ranging from 44% in leaf N to 78% for leaf Na (fig. 4). Statistically significant correlations existed between several of the explanatory variables, such as between precipitation and soil organic matter and between fire frequency and soil organic matter (table B3).

Within the context of the SEM results, larger resident herbivore densities had negative paths to standing plant biomass and plant community ordination scores, both of which had negative paths to leaf tissue N and leaf P. Direct paths from herbivore density to leaf nutrients were not detectable, and there was no evidence that herbivore density was associated with leaf Na through any indirect path. The total effect of herbivore density on both leaf N and P was 0.30. Herbivore density was the single variable explaining variation in plant biomass, and much of the observed variation in biomass remained unexplained (fig. 4).

In contrast to herbivore density, the relationship of fire frequency to other variables in the final SE model was

relatively complex, including associations with all three leaf tissue nutrients through either direct or indirect paths. With respect to leaf N, fire frequency had a net negative association mediated through changes in plant community composition and a total effect of -0.19 . In contrast, fire frequency had both direct and indirect paths to leaf P and Na. Like leaf N, a negative association between fire frequency and leaf P was mediated through changes in plant community composition. However, the model also revealed a large nonlinear, unimodal path between fire frequency and leaf P (fig. 4); as indicated by the bivariate relationship (fig. B1), leaf P increases with fire frequency up to approximately 3 years, after which it declines with greater fire frequency. The total effect of fire frequency on leaf P was 0.30; however, because of the nonlinear direct path, only the magnitude of the total effect (not its sign) is relevant, which in this case is similar to that of herbivore density on leaf N and P. With respect to leaf Na, the results revealed a modest, positive, direct path from fire frequency to leaf Na and an indirect path mediated through changes in the abundance of Na-rich grasses. The negative association of the indirect path offset the direct path such that the total effect of fire frequency on leaf Na was -0.20 .

The SEM results showed strong direct paths between

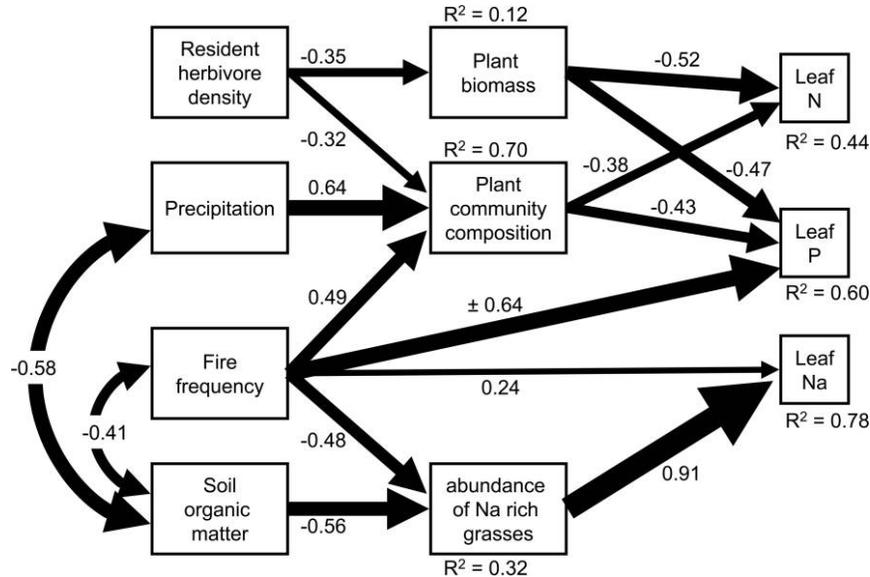


Figure 4: Final model results ($\chi^2 = 24.95$, $df = 30$, $P = .73$), in which variation in herbivore density, fire frequency, precipitation, and soil organic matter were used to explain variation in concentrations of leaf N, P, and Na, either directly or because of changes in plant composition and abundance. By convention, curved, double-headed arrows represent significant ($\alpha = 0.05$) correlations between variables, while straight, single-headed arrows represent significant directed effects of one variable on another. Values associated with the arrows are raw Pearson correlation coefficients (curved arrows) or standardized path coefficients (directed paths) and are proportional to arrow thickness. In the case of the directed path from fire frequency to leaf P, the \pm symbol indicates that the relationship was unimodal and that a negative second-order polynomial term was included. The R^2 values associated with response variables indicate the proportion of their variance explained by relationships with other variables. See figure 1 and table 1 for hypothetical processes that may contribute to direct and indirect paths among variables.

environmental variables and plant community composition. Specifically, there was a strong positive path from precipitation to the plant community ordination score and a strong negative path from soil organic matter to the abundance of Na-rich grasses. Within the model, precipitation had an indirect association with leaf N and P, in which the total effects were -0.24 and -0.28 , respectively. Similarly, the negative path from soil organic matter to abundance of Na-rich grasses led to an indirect negative association with leaf Na with a total effect of -0.51 . None of the direct paths from environmental variables to leaf nutrients were retained in the final SEM.

Assessing the Specific Hypotheses

The results of the SEM analysis demonstrated that fire frequency and herbivory commonly have offsetting effects on leaf nutrient concentrations, which occur via changes in plant community composition and abundance. Although this result is conceptually similar to the hypothesis of “balancing effects,” the effects of fire and herbivory were not equally offsetting for any of the three nutrients (fig. 5). For leaf N (fig. 5A), the positive effects of herbivore density (0.30) mediated through changes in plant biomass and community composition outweighed the negative effects of fire (-0.19) that occurred because of changes in the plant community. Similarly, for leaf P (fig. 5B), the indirect positive effects of higher herbivore density (0.30) outweighed the negative effects of fire (-0.21). However, as already discussed, this interpretation is complicated somewhat by the fact that there exists a direct nonlinear effect of fire on leaf P. For Na (fig. 5C), an offsetting pattern was observed within the effects of fire frequency itself, although the indirect negative effects (-0.51) that occurred via changes in the abundance of Na-rich grasses strongly outweighed the direct positive effects (0.24).

Specific Patterns for a Dominant Grass: *Themeda triandra*

The abundance of *Themeda triandra* varied from being absent at one site to composing 78.5% of the community at another (mean \pm SE = $26.8\% \pm 3.4\%$). *Themeda triandra* abundance exhibited a strong positive association with the NMDS ordination scores ($r = 0.59$, $P = .0006$). A stepwise multiple regression demonstrated that fire frequency was the only explanatory variable required to explain *T. triandra* abundance (fig. 6A; percent *T. triandra* = $0.094 \times$ fire frequency + 0.047 ; $F = 20.18$, $df = 1, 28$, $R^2 = 0.42$, $P = .0001$). Across sites, average nutrient concentrations were lower in the aboveground tissues of *T. triandra* than in randomly collected plant community samples (fig. 6B). The ratio of the average plant community sample to that of *T. triandra* was

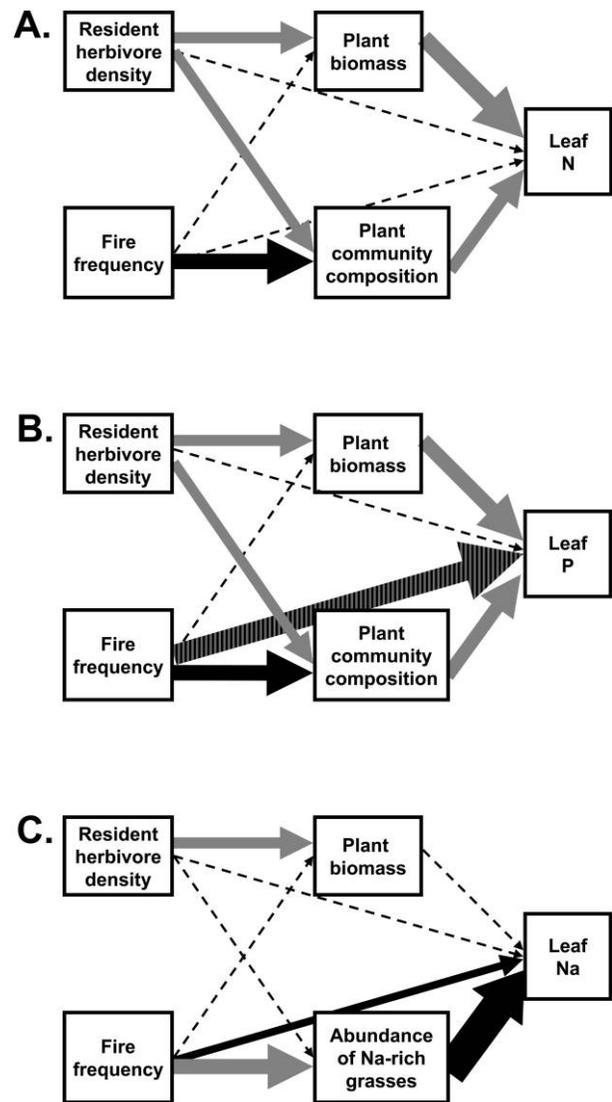


Figure 5: Schematics showing the submodel results that evaluate the specific hypotheses (fig. 3) for leaf N (A), P (B), and Na (C), separately. Widths of the arrows are proportional to the strength of the observed effect; gray arrows represent negative effects; black arrows represent positive effects; dashed arrows represent paths found to be insignificant in the final model result. The black and gray striped line in B represents the direct nonlinear effect of fire on leaf P. The results show that herbivore density was associated with indirect paths enhancing leaf nutrients, fire was associated with indirect paths reducing leaf nutrients and direct paths enhancing nutrients, and offsetting effects between fire and herbivory were common.

approximately 1.4 for both N (*T. triandra* = 0.72%, community = 1.02%; $t = -7.01$, $df = 29$, $P < .0001$) and P (*T. triandra* = $1,379.49 \text{ mg kg}^{-1}$, community = $2,014.09 \text{ mg kg}^{-1}$; $t = -7.08$, $df = 29$, $P < .0001$), whereas in the case of leaf Na, the ratio was approximately 4.6

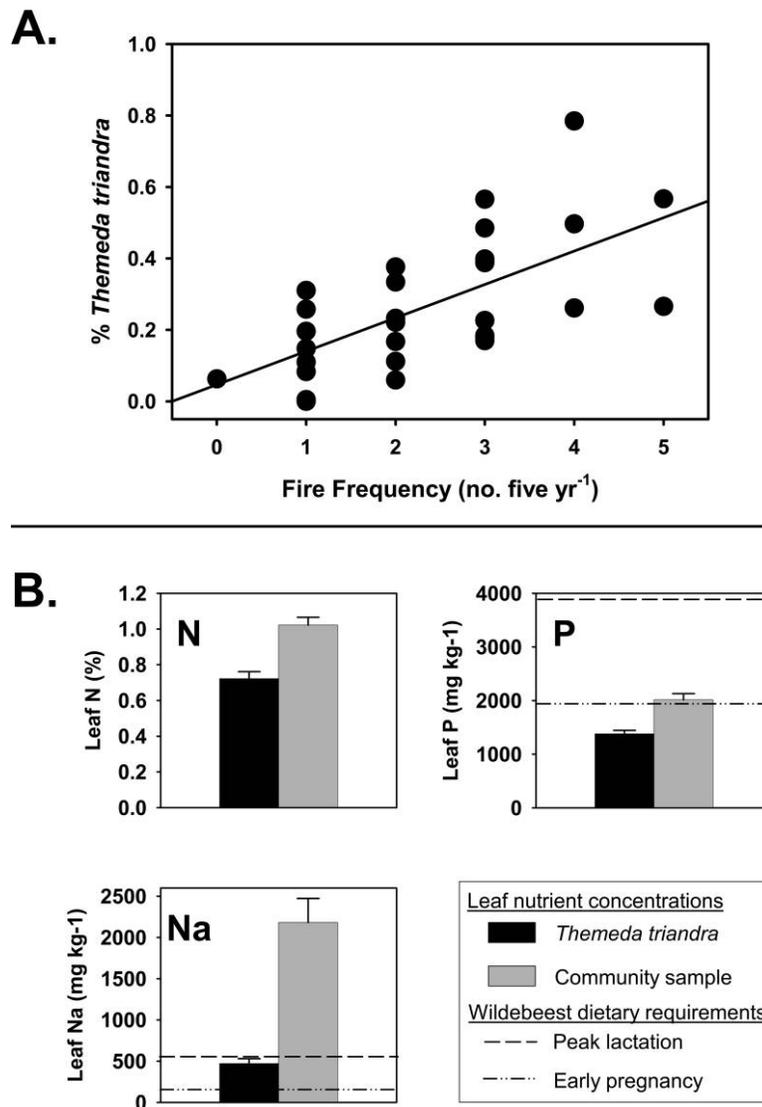


Figure 6: A, Relationship between fire frequency and the abundance of the dominant Serengeti grass *Themeda triandra* across 30 study sites. B, Comparison of mean leaf N, P, and Na concentrations in a sample of *T. triandra* (black bars) and a randomly collected plant community sample (gray bars) across 30 study sites. The lines shown on the graphs of leaf P and Na represent the nutrient concentrations required to sustain an adult female wildebeest at a weight of 143 kg during early pregnancy (dotted-dashed line) or during peak lactation (dashed line) as calculated by Murray (1995).

(*T. triandra* = 470.91 mg kg⁻¹, community = 2,183.20 mg kg⁻¹; $t = -6.64$, $df = 29$, $P < .0001$).

Discussion

In a classic conceptual diagram summarizing his work, McNaughton (1983, fig. 25, p. 314) outlined how interactions within a system of “composite environmental factors” may influence plant composition in African savanna grasslands. Composite environmental factors, such as her-

bivory, fire, soils, and rainfall, were defined as the broad conceptual features of a system whose effects are actually composed of constellations of weak forces that are probabilistic, intermittent, and contingent on other properties of the system. Furthermore, McNaughton (1983) suggested that “attempting an empirical evaluation of the importance of each of the many factors that ultimately affect community composition is presently technically impossible.” Now, more than 20 years later, with recent advances in structural equation modeling (Shipley 2000; Kline 2005;

Grace 2006), analytical tools are available that allow researchers to characterize some of the inherent complexities in natural systems, such as those described by McNaughton (1983) for the Serengeti. These methodological advances extend SEM beyond the traditional methods of path analysis and include advanced model solution procedures, hypothesis testing, and nonlinear modeling procedures involving composite variables (Grace 2006; Grace and Bollen 2007).

Analysis of our data by standard univariate statistical methods revealed consistent differences in herbivore densities, rainfall, standing plant biomass, and plant community composition between SNP and adjacent wildlife management areas. Differences in the plant community and exogenous factors were paralleled by differences in plant tissue N and P between paired sites inside and outside SNP. Moreover, bivariate scatter plots highlighted some important linear and unimodal relationships between variables, especially between fire frequency and leaf P (fig. B1) and between leaf nutrients and plant community properties (fig. B2). Based on the univariate results and knowledge of savanna-grassland plant communities (Sarmiento 1984; Tohill and Mott 1985; Walker 1987; Sinclair and Arcese 1995; Solbrig et al. 1996; du Toit et al. 2003), the most plausible conclusion is that greater plant N and P inside SNP is linked to higher resident herbivore densities, lower average rainfall and plant biomass, and shifts in community composition toward species with leaves of higher nutritive quality. While these conclusions are consistent with those of the SEM analyses, failure to explore the data past the univariate results leads to oversimplifying the relationships between variables, missing interesting results regarding Na, and neglecting important contingencies that characterize the Serengeti (McNaughton 1983).

For example, returning to the questions posed in the introduction, the analytical approach using SEM revealed that fire frequency and resident herbivore densities have opposing relationships with plant community composition and that this contributes to opposite associations with leaf N and P. In addition, the relationships between fire frequency and nutritive quality and between herbivore density and nutritive quality manifest themselves differently. Resident herbivore density was related to leaf N and P only indirectly, whereas fire frequency had direct effects on leaf P and Na in addition to indirect influences on leaf N, P, and Na. Whether offsetting effects of fire and herbivory on forage nutrient availability are a common property of savanna ecosystems is not known. Fire and bison grazing have contrasting effects on root production and root C : N ratios in temperate tallgrass prairies in Kansas (United States), thus creating offsetting effects on N cycling (Johnson and Matchett 2001). Either way, the answer

should be one of considerable interest for the future conservation of endangered grazing ecosystems (Frank et al. 1998).

Additional insight was gained through the SEM analysis because the standardized path coefficients allow a comparison of the relative strengths of associations between fire frequency and leaf nutrient concentrations and between herbivore density and leaf nutrient concentrations. Within the context of the SEM results, the sum of the total effects of fire (0.68) was slightly greater than that of herbivore density (0.61), whereas the total effects of precipitation (0.52) and soil organic matter (0.51) were similar. In terms of individual path strengths, environmental variables had comparatively large effects; the strongest individual paths were from rainfall to plant community composition and from soil organic matter to Na-rich grass abundance. The negative indirect path from soil organic matter to Na-rich grass abundance implies that fertile soils (i.e., high soil organic matter) have lower available forage Na because they contain a lower abundance of species with Na-rich leaves.

Perhaps the most intriguing results from the SEM analysis were the direct paths from fire frequency to leaf Na and P. Such results may arise from increased green : dead leaf ratios, greater leaf : stem ratios, and equivalent total nutrient allocation distributed in proportionally less aboveground biomass (Hobbs et al. 1991; van de Vijver et al. 1999). Although the effects of a single fire on plant nutrients can last up to 1 year (Jensen et al. 2001), often the effects are short-lived, lasting just a few months (Hobbs et al. 1991; van de Vijver et al. 1999). Of the 14 sites in our study that were burned in the fire season just before sampling, eight burned in June, four in July, one in August, and one in September. Therefore, it is unlikely our results are linked to the initial nutrient-rich flush of regrowth that follows fire. Instead, it is more likely that these direct paths result from longer-lasting mechanisms, such as fire effects on green : dead leaf ratio, litter inputs, soil nutrient pools, microbial dynamics, or alteration of the plant microclimatic environment (Singh et al. 1991*a*, 1991*b*; Bond and van Wilgen 1996; DeBano et al. 1998).

For leaf Na, the strongest path from fire frequency was via a negative relationship with Na-rich grasses, but after controlling for this relationship, there remained a direct positive path to leaf Na. Along with other heavy elements, Na is not volatilized during fire, and it may become concentrated in ash deposits (Kellman et al. 1985; DeBano et al. 1998; Mills and Fey 2004). Evidence exists for slight but significant increases in plant Na absorption following fire (Kellman 2002), which may occur passively through increased uptake rates in plants that have no metabolic demand for Na or actively for C₄ or halophytic species (Brownell 1979; Marschner 1995; McNaughton et al.

1997). Similarly, increased inorganic P availability in ash deposits, coupled with the replacement of older leaf tissues, likely explains increased leaf P with fire frequency in our study (Jensen et al. 2001). However, the unimodal response of leaf P to fire frequency suggests that an additional mechanism must account for the decreased leaf P with higher fire frequency. Recent experiments on plant-mycorrhizae associations from South African savannas may provide an answer. Experiments demonstrated a strong negative relationship between fire frequency and the colonization of perennial grass roots by mycorrhizae (Hartnett et al. 2004). The authors suggested that the effects of increased fire frequency, such as intensified soil crusting, greater water runoff, and decreased soil moisture (Mills and Fey 2004), may have limited the colonization of roots by mycorrhizae (Hartnett et al. 2004). Alternatively, Hartnett et al. (2004) suggested that fire may have indirectly decreased mycorrhizae colonization rates by increasing soil-available P; with increased soil P, plants rely less on mycorrhizal associations and may reduce their investment in the mutualism. Our unimodal response of leaf P to fire frequency suggests that both may be occurring: fire may have increased plant-available P up to a point after which increased fire frequency damages associations between roots and mycorrhizae, thus reducing plant access to soil P. Root-fungal associations in SNP are an important component of nutrient-poor soils (McNaughton and Oesterheld 1990), although the importance of these associations for nutrient uptake is yet to be fully explored.

Placing the SEM Findings in a Broader Context

Conspicuously absent from our final SEM results were direct paths from herbivore density to leaf N and Na. Experiments in SNP, in which ungulate herbivores were uncoupled from grassland forages through fencing, suggest that herbivores have direct effects on the biogeochemical cycling, mineralization, and soil availability of N and Na (McNaughton et al. 1997). There may be several reasons why such direct paths did not emerge in the results of this study. First, the aforementioned studies compared hotspots, areas of high resident herbivore densities, with adjacent areas of low herbivore use (McNaughton et al. 1997). In our selection of study sites, no hotspots were sampled. Although hotspots play an important ecological role in SNP, the high herbivore densities and heavily utilized grasslands swards are not representative of our study sites. Second, our results indicate, at least for the western margins of the SNP ecosystem, that the compositional changes induced by long-term, pervasive herbivory may preclude direct effects that have been observed elsewhere under experimental conditions.

Also conspicuously absent from our SEM results was a

significant relationship between rainfall and plant biomass (fig. 4). A likely explanation is the relatively narrow range of rainfall captured by our study sites (700–969 mm year⁻¹; table B1). Rainfall varies from <400 to >1,100 mm year⁻¹ across the ecosystem, a gradient that has important implications for herbivore effects on plant communities (Anderson et al. 2007). However, despite the relatively narrow breadth of precipitation across sites, rainfall still had significant influence on forage nutritive quality. We can only speculate that such effects would increase across the larger SNP rainfall gradient.

Although not shown in our conceptual model, there are several different feedback pathways by which plant communities and forage nutrient availability can modify grazer preference and herbivore density. In addition to affecting nutrient distribution in forage, herbivores also respond to forage nutritive quality across a range of spatial scales, from the landscape to the individual plant (Senft et al. 1987; Huntly 1991; Skarpe 1992). Additionally, herbivory and fire frequency often interact in savannas; herbivores can modify fire frequency by removing aboveground biomass, while fire modifies herbivore density by altering plant chemistry in a way that attracts herbivores (Coppock and Detling 1986; Wilsey 1996) and by removing biomass that could otherwise be consumed by herbivores (Archibald et al. 2005; Bond and Keeley 2005). Although our study was not designed to address these issues, they are clearly important mechanisms in SNP. For example, hotspots in SNP rarely, if ever, burn because they cannot sustain fire (S. J. McNaughton, personal observation), and recently burned swards are more heavily utilized by small-bodied ungulates than by larger-bodied ungulates (Wilsey 1996).

Response of the Dominant Grass: Themeda triandra

An important distinction between fire and herbivory in terms of plant community associations was the way in which the factors correlated with the abundance of the dominant grass *Themeda triandra*. High rainfall and infrequent grazing are known to promote *T. triandra*, while frequent or severe defoliation decreases the abundance of *T. triandra* (Coughenour et al. 1985; Edroma 1985; Hodgkinson et al. 1989; O'Connor 1994; Fynn and O'Connor 2000). This is in part because *T. triandra* is not able to efficiently utilize reserved carbon stores under repeated defoliation (Danckwerts 1993). In contrast, *T. triandra* is particularly tolerant of fire, and continuous burning regimes maintain *T. triandra* grasslands throughout much of South Africa (Tainton and Mentis 1984). In turn, *T. triandra* promotes the spread of fire because its canopy is highly flammable. Despite this, the specific effects of fire on *T. triandra* abundance in SNP have been somewhat

inconsistent (e.g., McNaughton 1983; Belsky 1992). Our results demonstrate a strong correlation between fire frequency and *T. triandra* abundance across sites in SNP. This is consistent with previous studies of the effects of defoliation by fire and herbivory on *T. triandra*: few grasslands in SNP burn more than once a year, while heavily grazed areas are often subjected to repeated, if not persistent, defoliation. (Sinclair and Arcese 1995).

Calculations by Murray (1995) suggest that animals, especially residents, may have trouble meeting dietary requirements in the grasslands of the western corridor. This is especially true for *T. triandra*-dominated stands, as average leaf P and Na do not meet the dietary requirements of lactating female wildebeests, and leaf P does not meet requirements for pregnant female wildebeests (fig. 6). Resident animals have adapted to forage of poor nutritive quality by migrating along catena gradients throughout the year, selecting dry hilltops during the wet season and wetter bottom hillslopes during the dry season (Bell 1971; Seagle and McNaughton 1992). However, in addition to residents, grasslands in the western corridor provide important dry-season transitional zones for migrating zebras and wildebeests; animals typically enter these habitats during periods of tenuous body condition and vulnerability to senescence (Murray 1995; Sinclair and Arcese 1995). The results of our SEM analysis suggest that frequent fire may contribute to the loss of key elements, such as Na and P, from these important transitional zones and may promote low-nutritive-quality forage in the form of *T. triandra* dominated savannas.

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