

Local versus landscape-scale effects of savanna trees on grasses

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Summary

1. Savanna ecosystems – defined by the coexistence of trees and grasses – cover more than one-fifth the world's land surface and harbour most of the world's rangelands, livestock and large mammal diversity. Savanna trees can have a variety of effects on grasses, with consequences for the wild and domestic herbivores that depend on them.

2. Studies of these effects have focused on two different spatial scales. At the scale of individual trees, many studies have shown net positive effects of trees on sub-canopy grass nutrient concentrations and biomass. At the landscape scale, other studies have shown negative effects of high tree densities on grass productivity. These disparate results have led to different conclusions about the effects of trees on forage quality and ungulate nutrition in savannas.

3. We integrate these approaches by examining the effects of trees on grasses at both spatial scales and across a range of landscape-scale tree densities. We quantified grass biomass, species composition and nutrient concentrations in these different contexts in an *Acacia drepanolobium* savanna in Laikipia, Kenya.

4. Individual trees had positive effects on grass biomass, most likely because trees enrich soil nitrogen. Grass leaf phosphorus in sub-canopy areas, however, was depressed. The effects of individual trees could explain the effects of increasing landscape-scale tree cover for the biomass of only two of the four dominant grass species.

5. The negative effects of trees on grass and soil phosphorus, combined with depressed grass productivity in areas of high tree cover, suggest that ungulate nutrition may be compromised in areas with many trees.

6. *Synthesis.* We conclude that few, isolated trees may have positive local effects on savanna grasses and forage, but in areas of high tree density the negative landscape-scale effects of trees are likely to outweigh these positive effects. In savannas and other patchy landscapes, attempts to predict the consequences of changes in patch abundances for ecosystem services (e.g. rangeland productivity and carbon sequestration) will depend on our understanding of the extent to which local, patch-scale dynamics do or do not predict landscape-scale dynamics.

Key-words: *Acacia drepanolobium*, forage quality, Laikipia, nitrogen, phosphorus, rangeland, scaling up, tree–grass interactions

Introduction

A fundamental question in ecology is the extent to which local species interactions predict the abundance of species in the

landscape (Wiens 1989; Levin 1992; Hewitt *et al.* 2007). Despite widespread recognition that local interactions do not necessarily predict landscape-scale patterns, relatively few studies explicitly compare interspecific dynamics at these two scales (Hewitt *et al.* 2007). Savanna ecosystems are defined by the coexistence of two plant guilds – trees and grasses – which are known to have strong interactions (for recent reviews, see Scholes & Archer 1997; House *et al.* 2003; Sankaran,

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Ratnam & Hanan 2004). Studies of the effects of trees and shrubs on the herbaceous community, however, have generally focused on one of two different scales of inquiry (Scholes & Archer 1997; Sankaran, Ratnam & Hanan 2004). While individual tree-scale studies have often shown positive effects of trees on grass nutrients and productivity, landscape-scale studies have shown negative effects of 'woody encroachment' (increases in tree or shrub abundance) on grass productivity (Scholes & Archer 1997). These two approaches have led to different conclusions about the effects of trees on the nutrition and population dynamics of grazing ungulates. Surprisingly, few studies have attempted to integrate these disparate approaches (Breshears 2006).

An understanding of the effects of savanna trees on grasses at both scales and across a range of tree densities is central to the management of these biologically and socio-economically important ecosystems. Savannas cover one-fifth of the world's land surface and are home to much of the world's rangelands, livestock and wild ungulate herbivores (Scholes & Archer 1997; Sankaran *et al.* 2005). Many savanna systems across the globe have undergone, or are currently undergoing, dramatic changes in tree abundance (Bond 2008). In most cases tree and shrub densities are increasing, due to a combination of CO₂ fertilization, fire suppression and overgrazing (see Bond 2008 for a recent review). In parts of sub-Saharan Africa, however, tree densities are declining due to heavy browsing (primarily by elephants) inside parks and protected areas (Birkett 2002; Augustine & McNaughton 2004; Western & Maitumo 2004) and harvesting of trees for charcoal production outside of protected areas. An understanding of the consequences of changes in tree density for grasses and the herbivores that eat them is therefore critical to management decisions that aim to slow or reverse these changes (Smit 2004).

At the individual-tree scale, savanna trees have been shown to have both positive and negative effects on the grasses growing immediately below their canopies ('sub-canopy grasses') relative to the grasses growing in inter-canopy areas. These effects include: enriched soil and grass leaf nutrients (Ludwig *et al.* 2001, 2004b; Treydte *et al.* 2007; Ludwig, de Kroon & Prins 2008), reduced evapotranspiration (Belsky *et al.* 1993; Breshears *et al.* 1997; Ludwig *et al.* 2001), increased soil water availability due to hydraulic lift (Ludwig *et al.* 2003), decreased soil water availability due to competition (Ludwig *et al.* 2004a,b) and increased overall grass productivity (Belsky *et al.* 1993). Herbaceous species composition under trees can also be different from species composition between trees (Scholes & Archer 1997). Often, the net effects of trees on sub-canopy grass nutrients and biomass are positive. This has led to the conclusion that reductions in landscape-scale tree abundances (e.g. due to high elephant densities) will have negative effects on ungulate nutrition and population dynamics (Treydte *et al.* 2007; Ludwig, de Kroon & Prins 2008).

A separate body of literature has focused on the widespread phenomenon of woody encroachment. Increases in tree or shrub abundances are thought to result from heavy or prolonged grazing, fire suppression and CO₂ fertilization (van Vegten 1984; Archer, Schimel & Holland 1995; Scholes &

Archer 1997; van Auken 2000; Roques, O' Connor & Watkinson 2001; Morgan *et al.* 2007). Woody encroachment has occurred in savannas all over the world and can have profound negative consequences for the economic viability of affected rangelands (Scholes & Archer 1997; Tobler, Cochard & Edwards 2003). Several studies have shown that soil moisture and grass productivity are suppressed at the landscape scale in areas with high densities of trees (but not necessarily closed canopies) relative to areas with a low densities of trees (Scholes & Archer 1997; Smit & Rethman 2000; Smit 2005). This has led to the conclusion that increases in landscape-scale tree abundance will have negative consequences for grazing ungulates (Scholes & Archer 1997). Whether and how landscape-scale tree abundances affect other attributes of the grass community – such as nutrient concentrations and species composition – have rarely been studied.

These two disparate approaches have reached different conclusions about the effects of trees on grasses in part because they have focused on different scales of inquiry, in savannas with different abundances of trees and on different outcomes (e.g. grass nutrients versus productivity). A key question, therefore, is to what extent the effects of individual trees scale up in the landscape. Do the effects of individual trees on sub-canopy grasses predict the effects of increasing abundances of trees in the landscape? And do these individual-tree effects themselves vary depending on the density of surrounding trees in the landscape?

There are a variety of mechanisms by which the effects of individual trees may or may not scale up. For example, if the trees themselves are driving the characteristics of the grasses growing beneath their canopies, landscape-scale tree cover may be directly related to landscape-scale grass distributions and abundances. Alternatively, the effects of trees on grasses could change as tree cover increases for at least three reasons. First, landscape-wide grass distributions and abundances may be driven by other factors that co-vary with tree density or cover. These might include precipitation or soil characteristics, both of which are known to be important determinants of savanna tree cover (Sankaran *et al.* 2005). Second, the effects of individual trees may be overridden or enhanced by the collective, overlapping influences of neighbouring trees as tree density increases (Breshears 2006). For example, in areas where trees are widely spaced, many inter-canopy areas will be entirely unshaded by trees, whereas at high tree densities the shadows cast by individual trees may overlap – even if tree cover is considerably < 100% – so that grass in most of the inter-canopy zone is shaded (Breshears 2006). Similarly, grass may be affected by tree roots that extend beyond the canopy radius and deplete water or nutrients in the inter-canopy zone (Scholes & Archer 1997). Such an effect could become increasingly important at high tree densities. Third, landscape-wide grass distributions and abundances may be driven by factors that are driven by landscape-wide tree cover, rather than by individual trees. For example, many herbivores appear to spend more time in areas with few trees, which may have a number of repercussions for the grass community in those areas (Riginos & Grace 2008).

Here, we examine relationships among individual trees, tree densities, soil nutrients, grass nutrients and understorey grass communities to determine whether the local effects of trees on grasses could be used to predict stand- or landscape-wide grass patterns. We quantified grass biomass and species composition in sub-canopy and inter-canopy habitats over a range of tree densities and cover values in an *Acacia drepanolobium* savanna in Kenya. This approach allowed us to separate ‘tree effects’ (local effects of individual trees) from ‘stand effects’ (effects of factors operating stand-wide) (Fig. 1a). We then used sub-canopy and inter-canopy grass patterns from the sites with the lowest tree covers to predict the relationships between tree canopy cover and stand-wide grass patterns. By comparing these predicted relationships with observed relationships (Fig. 1b), we illustrate how local tree effects may or may not scale up in the landscape. We also quantified sub-canopy and inter-canopy grass nutrient concentrations and soil characteristics. Specifically, we set out to address the following questions: (i) what are the relationships between trees and grasses at local and landscape scales across a range of tree densities? and (ii) what mechanisms could explain these relationships?

Materials and methods

STUDY SITE

This study was conducted at the Mpala Research Centre (36°52' E, 0°17' N) and the adjacent Jessel Ranch in Laikipia, Kenya. Mean annual rainfall at this site is *c.* 500 mm. The study area is underlain by poorly drained, clay-rich ‘black cotton’ soil. Five species of perennial bunchgrasses make up 90% of the herbaceous cover: *Brachiaria lachnantha*, *Pennisetum stramineum* (Maasai grass), *Pennisetum mezianum* (bamboo grass), *Themeda triandra* (red oat grass) and *Lintonia nutans*

(Young *et al.* 1998). Only 2% of the herbaceous layer is composed of dicots (forbs). The woody vegetation is dominated by the whistling thorn acacia (*A. drepanolobium*), which makes up 98% of the woody cover. *Acacia drepanolobium* is one of the most abundant and wide-spread tree species in eastern Africa – typically found on black cotton soils where it forms nearly monospecific stands over hundreds of square kilometres and can be a serious rangeland invader (Pratt & Gwynne 1977). At this site, trees are single stemmed and almost all (95%) < 4 m tall (Young, Stubblefield & Isbell 1997).

The Mpala Research Centre (MRC) and Jessel Ranch are managed for both domestic cattle production and wildlife conservation. Wildlife biomass density on these ranches is *c.* 1.7 t km⁻² and livestock biomass density is *c.* 2.7 t km⁻² (Georgiadis *et al.* 2007). Common wild herbivores include: grazers, mostly plains zebras (*Equus burchelli*), hartebeest (*Alcelaphus buselaphus*) and oryx (*Oryx gazella*); browsers, mostly giraffes (*Giraffa camelopardalis*) and steinbuck (*Raphicerus campestris*); and mixed feeders, mostly Grant’s gazelles (*Gazella granti*), elephants (*Loxodonta africana*) and eland (*Taurotragus oryx*). Cattle at this study site are primarily grazers; grass makes up 96–98% of their diet (Odadi, Young & Okeyo-Owuor 2007).

A previous study examined the relationships among *A. drepanolobium* stand density, stand-wide grass species composition and ungulate habitat preferences (Riginos & Grace 2008). Here, we use a subset of the same sites to compare the local and stand-wide associations between trees and the grass community.

DATA COLLECTION

Ten 0.25-ha sites varying from 69 to 518 trees and from 9% to 43% canopy cover were located as described in Riginos & Grace (2008). Canopy cover was estimated from a high-resolution (60 cm) satellite image as described in Okello *et al.* (2008) and correlates strongly with tree density ($r^2 = 0.80$, $n = 34$, $P < 0.001$). In February 2007, we quantified grass biomass and species composition at 24 sample points throughout each site using a 10-point pin frame. Total number of pin

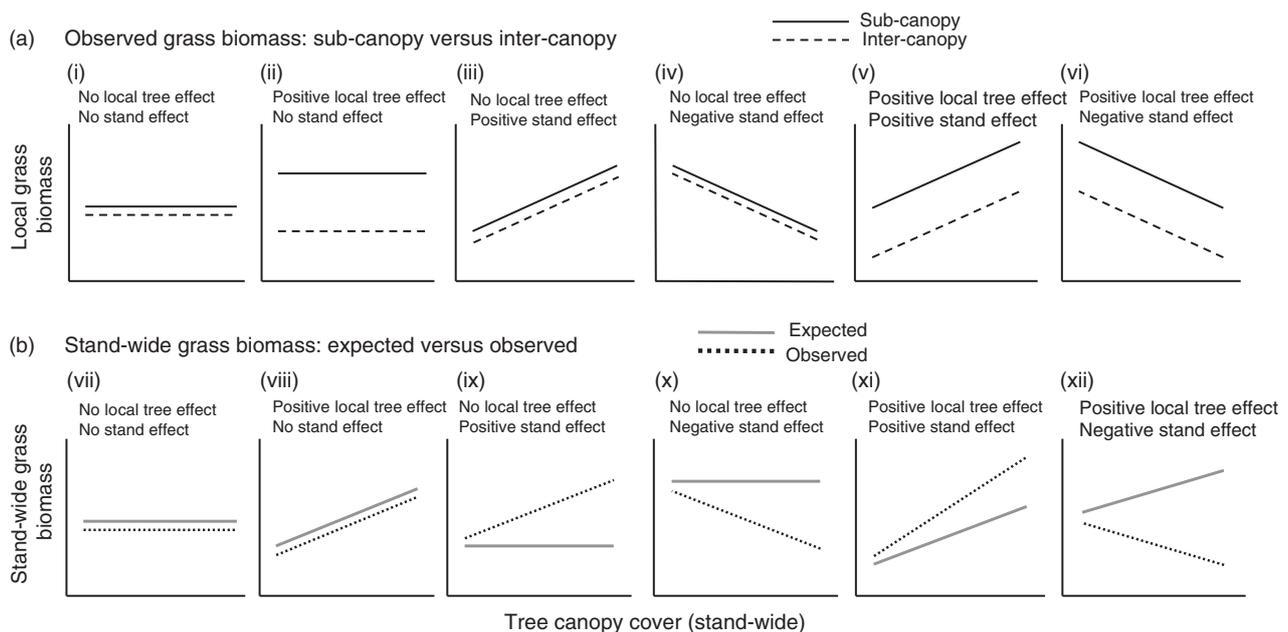


Fig. 1. Schematic diagrams illustrating hypothetical effects of micro-habitat (sub-canopy versus inter-canopy) on grass biomass over a range of stand-wide tree covers (a) and how these effects can lead to differences in expected and observed stand-wide patterns of grass biomass as tree cover increases (b).

contacts with the grass canopy is strongly correlated with grass biomass in this system (Augustine 2003). Sample points were arranged in a 40 × 50 m grid, with 10 m between each grid point. Each sample point was categorized as either 'sub-canopy' (directly under a tree canopy; within 1 m of the tree trunk, for trees with canopy radius > 1 m) or 'intercanopy' (not under any tree canopy). This approach was designed to allow us to assess grass community characteristics in both of these micro-habitats as well as 'stand-wide' (averaging across all sample points, regardless of proximity to trees). To boost the number of sample points for the sub-canopy habitat, we quantified grass cover and composition under 30 additional, randomly selected trees per 0.25 ha site. Trees were stratified into three size classes (10 trees per size class: < 1, 1–2.5 and > 2.5 m tall) to assess the effect of tree size on grass community characteristics. As no significant effects of tree size were detected, however, we averaged results for all sub-canopy sample locations. Similarly, we averaged results for all inter-canopy sample locations. Thus, for each site we obtained one averaged estimate of biomass for each grass species under tree canopies, between tree canopies and across the whole site.

Soil characteristics (texture, total C, total N, total P and extractable P) were quantified from samples collected in October 2006. Five inter-canopy subsamples were collected from random locations (but avoiding termite mounds) at each of the 34 sites described in Riginos & Grace (2008). For comparison, we also collected five subsamples from sub-canopy areas in each of the 10 focal sites. Here, we present inter-canopy results from the larger pool of 34 sites and use the 10 focal sites to further explore differences between inter-canopy and sub-canopy areas in terms of soils. Sub-canopy samples were taken from beneath trees > 2.5 m in height. Inter-canopy samples were taken halfway between each sub-canopy sample tree and an adjacent neighbour, at least 1 m from the edge of each tree's canopy. At each subsample location, a soil core was extracted at 5–30 cm depth. All five subsamples from each micro-habitat type within each site were thoroughly mixed to create one bulked sample. Soil particle size was analysed using the hydrometer method. Soil carbon and nitrogen were quantified using an automated C/N combustion analyser. Total phosphorus was quantified using the Kjeldahl acid digestion method (Taylor 2000), and extractable phosphorus was quantified using the Olsen extractant method (Olsen & Sommers 1982).

Similarly, we collected grass leaf samples from three random sub-canopy and three adjacent inter-canopy subsample locations in each of the 10 focal sites. These subsamples were bulked to create one sample from each micro-habitat type from each site. Only green leaves from at least three individuals of *Brachiaria lachmantha* (the most abundant and widely distributed species in both micro-habitats and a preferred forage species (Odadi, Young & Okeyo-Owuor 2007)) were collected so as to control for species effects. Leaves were collected in October 2007 and dried in a 70 °C oven for 48 h. Grass leaf nitrogen, phosphorus and potassium were analysed using the Kjeldahl acid digestion method (Thomas, Sheard & Moyer 1967). All soil and plant tissue analyses were carried out by the International Centre for Research in Agroforestry Soil and Plant Laboratory in Nairobi, Kenya.

GRASS BIOMASS PREDICTIONS

For each site, we calculated expected values of stand-wide grass biomass under the assumption that local-scale patterns scale up linearly. Our objective was to facilitate comparison between expected and observed biomass values and to explore possible mechanisms underlying grass responses to increasing tree cover. In calculating expected biomass values, we assumed that sub-canopy and inter-canopy

micro-habitats would be most distinct at the two sites with the lowest tree cover (9% cover in both cases). That is, we assumed that the average sub-canopy grass biomass at these sites most closely represented the effects of individual trees, while average inter-canopy grass biomass most closely represented grass in isolation from all trees. We used mean sub-canopy and inter-canopy biomass values from these two sites to calculate the expected grass biomass for the four most common grass species and for all grasses combined at all 10 sites as follows:

$$\begin{aligned} \text{Expected grass biomass} = & (\text{mean sub-canopy grass biomass} \\ & \times \text{stand-wide tree canopy cover}) \\ & + (\text{mean inter-canopy grass biomass} \\ & \times (1 - \text{stand-wide tree canopy cover})) \end{aligned}$$

STATISTICAL ANALYSES

We used both *t*-tests and linear regressions to test the effects of micro-habitat (sub-canopy versus inter-canopy) and variation in stand-wide tree canopy cover on grass biomass and grass leaf nutrients. All analyses were carried out in JMP version 7.0 (SAS Institute, Inc., Cary, NC, USA). Hypothetical outcomes of these analyses are given in Fig. 1a. We used paired *t*-tests (paired by site) to test the overall effects of micro-habitat on these variables, with significant effects representing a 'tree effect' (Fig. 1a). We used linear regressions to examine the effects of stand-wide tree canopy cover on these variables, with separate regressions fitted for each micro-habitat, since sub-canopy and inter-canopy data from the same site could not be treated independently. A significant effect of canopy cover within either or both micro-habitats indicates a 'stand effect' in this analysis (Fig. 1a). Finally, we examined whether the effects of micro-habitat differed across sites varying in canopy cover. To do this, we regressed the difference between average sub- and inter-canopy values at each site against tree canopy cover. A significant effect in this analysis indicates an interaction between the effects of micro-habitat and canopy cover.

We used a similar approach to examine differences between the expected and observed grass biomass responses to increasing tree canopy cover. Hypothetical outcomes of these analyses are given in Fig. 1b. Here, we used paired *t*-tests to examine overall differences between expected and observed grass biomass across all sites. We also used linear regression to examine the effects of tree canopy cover on observed grass biomass and on the difference between observed and expected biomass (note, the relationship between tree canopy cover and expected biomass is perfectly linear, by definition). Here, a significant effect of canopy cover on the difference between observed and expected biomass indicates that the local effects of trees on grasses do not scale up linearly in the landscape.

In examining the effects of micro-habitat on soil characteristics, we also used paired *t*-tests to compare sub-canopy and inter-canopy soils within each of the 10 focal sites. Only one parameter (soil N) exhibited a micro-habitat effect, and there was no evidence that this parameter was related to stand-wide tree cover. We then used inter-canopy soil data from the larger set of 34 sites to examine the relationships between tree cover and soil characteristics. Results from the 10 focal sites and the larger set of 34 sites were qualitatively consistent, but the latter afforded greater power to detect any trends.

Results

Grass community characteristics varied substantially depending on micro-habitat and stand-wide tree cover. At the local

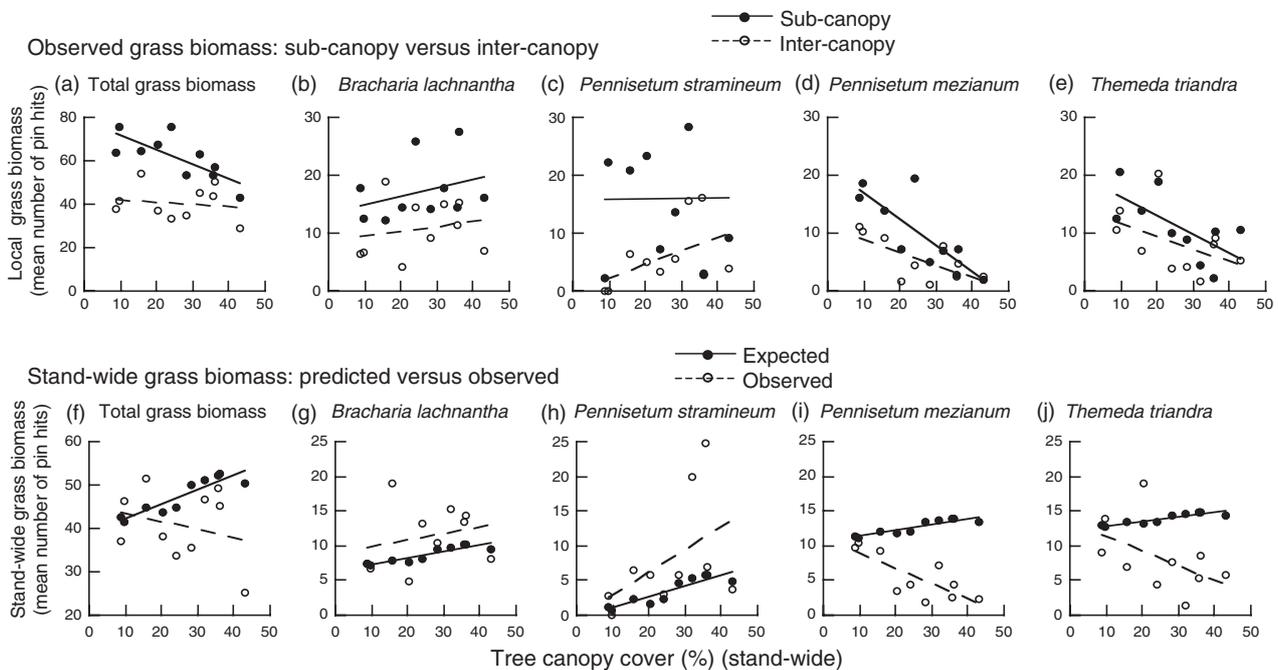


Fig. 2. Panels a–e show observed effects of micro-habitat (sub-canopy versus inter-canopy) and stand-wide tree cover on grass biomass for total grass (a) and the four dominant grass species (b–e). Panels f–j show the differences between expected and observed stand-wide patterns of grass biomass for total grass (f) and for the four dominant grass species (g–j) as stand-wide tree cover increases. Grass biomass is measured as the mean number of pin hits on a 10-point pin frame at each sample location. Grasses make up 98% of the herbaceous biomass at this site.

(tree) scale, grass biomass was generally higher in sub-canopy areas than in inter-canopy areas (Fig. 2a–f; Table 1). This was the case for total grass biomass and for three of the four dominant grass species; only *T. triandra* did not have significantly higher biomass under individual tree canopies. *Pennisetum mezianum*, *T. triandra* and total grass biomass all exhibited a negative ‘stand effect’ in the sub-canopy habitat – that is, sub-canopy grass biomass was negatively related to tree cover (Table 2). Further, for both *P. mezianum* and total grass, there was a significant negative effect of canopy cover on the difference between sub- and inter-canopy biomass. This indicates that the positive ‘tree effect’ was stronger at sites with low tree cover (Fig. 2a,d). In contrast, for *P. stramineum*, inter-canopy grass biomass (but not sub-canopy grass biomass) was positively related to canopy cover.

Table 1. Results of paired *t*-tests on the difference between average sub-canopy and inter-canopy grass biomass within each site. Significant results indicate that biomass is, on average, higher in the sub-canopy habitat than in the inter-canopy habitat (see Fig. 2a–e). Results are presented for total biomass and for biomass of the four most common grass species (average percent of total biomass given in parentheses for each species). $N = 10$ in all cases

	d.f.	<i>t</i>	<i>P</i>
Total grass biomass	9	5.65	<0.001
<i>Bracharia lachnantha</i> (28%)	9	3.48	<0.01
<i>Pennisetum stramineum</i> (20%)	9	4.34	<0.01
<i>Pennisetum mezianum</i> (15%)	9	2.89	0.02
<i>Themeda triandra</i> (19%)	9	2.19	0.06

Expected grass biomass for *B. lachnantha* and *P. stramineum* did not differ significantly from observed biomass (Table 3). Both expected and observed biomass of these species exhibited positive relationships with tree cover (Fig. 2g,h), suggesting that the local positive effects of trees did scale up. In contrast, for *P. mezianum*, *T. triandra* and total grass, expected biomass was, on average, significantly higher than the observed biomass (Table 3, Fig. 2f,i,j). For *P. mezianum* and *T. triandra*, there was a significant positive relationship between canopy cover and the difference between expected and observed biomass (Table 4). This indicates that the discrepancy between expected and observed biomass was greater in areas of high tree cover. Thus, these species appear to have exhibited negative stand effects with increasing tree cover – despite a positive local tree effect in the case of *P. mezianum*.

Grass leaf tissue characteristics also varied with both micro-habitat and stand-wide tree cover. Leaf phosphorus was significantly higher in inter-canopy areas than in sub-canopy areas (sub-canopy: $0.135 \pm 0.004\%$; inter-canopy: $0.150 \pm 0.004\%$; $t = -4.62$, $n = 10$, d.f. = 9, $P = 0.017$). Consequently, leaf N : P ratios were higher under trees (sub-canopy: 12.86 ± 0.39 ; inter-canopy: 11.12 ± 0.39 ; $t = 3.41$, $n = 9$, d.f. = 8, $P = 0.009$). In general, leaf phosphorus (ranging from 0.12% to 0.17%) declined and leaf nitrogen content (ranging from 1.4% to 2.1%) increased with increasing stand-wide tree cover. Although neither of these trends was statistically significant by itself, grass leaf N : P ratios (ranging from 9.5 to 14) were significantly positively related to tree cover in the inter-canopy habitat ($r^2 = 0.58$, slope = 0.06, $n = 9$, $P = 0.018$), with a strong but non-significant trend in the same direction for the

Table 2. Linear regression results for the relationships between stand-wide tree canopy cover and grass biomass for each micro-habitat (sub-canopy and inter-canopy) and for the difference in biomass between these two habitats. Results presented for total grass biomass and biomass of the four most common grass species. $N = 10$ for all models

	R^2	Slope	P
Total grass biomass			
Sub-canopy	0.54	-0.53	0.02
Inter-canopy	0.01	0.06	0.76
Difference	0.52	-0.59	0.02
<i>Brachiaria lachnantha</i>			
Sub-canopy	0.08	0.10	0.43
Inter-canopy	0.12	0.12	0.33
Difference	0.00	-0.01	0.93
<i>Pennisetum stramineum</i>			
Sub-canopy	0.01	0.07	0.81
Inter-canopy	0.39	0.25	0.05
Difference	0.12	-0.18	0.32
<i>Pennisetum mezianum</i>			
Sub-canopy	0.64	-0.37	< 0.01
Inter-canopy	0.30	-0.14	0.10
Difference	0.44	-0.22	0.04
<i>Themeda triandra</i>			
Sub-canopy	0.66	-0.32	< 0.01
Inter-canopy	0.29	-0.21	0.11
Difference	0.15	-0.11	0.26

Table 3. Results of paired t -tests on the difference between expected and observed grass biomass within each site. Positive effects indicate that expected biomass is, on average, higher than observed biomass, whereas negative effects indicate that observed biomass is greater than expected (see Fig. 2f-j). Results are presented for total biomass and for biomass of the four most common grass species. $N = 10$ in all cases

	d.f.	t	P
Total grass biomass	9	2.25	0.05
<i>Brachiaria lachnantha</i>	9	-1.98	0.08
<i>Pennisetum stramineum</i>	9	-2.06	0.07
<i>Pennisetum mezianum</i>	9	5.51	< 0.001
<i>Themeda triandra</i>	9	3.22	0.01

sub-canopy habitat ($r^2=0.30$, slope = 0.05, $n = 10$, $P = 0.10$). Given the magnitude of these effects, we hypothesize that the lack of statistical significance reflects low power rather than an absence of any trend. Taken together, these results suggest that increasing tree cover was associated with enhanced grass leaf N and depleted grass leaf P concentrations.

No significant relationships between stand-wide tree cover and soil nitrogen, carbon or total phosphorus were detected. Extractable phosphorus, however, exhibited a significant negative relationship with tree density ($r^2=0.17$, slope = -0.009, $n = 31$, $P = 0.021$). Soil nitrogen was also significantly higher in sub-canopy areas than in inter-canopy areas (sub-canopy: $0.114 \pm 0.005\%$; inter-canopy: $0.102 \pm 0.002\%$; $t = 2.57$, $n = 10$, d.f. = 9, $P = 0.030$). Soil texture variables were significantly related to tree cover but not micro-habitat. Tree cover

Table 4. Linear regression results for the relationships between stand-wide tree canopy cover and (i) observed stand-wide grass biomass and (ii) the difference between expected and observed stand-wide grass biomass. In all cases, expected stand-wide grass biomass (which is linear by definition) had slope < 0.01 (see Fig. 2f-j for a graphical representation of these results). Results presented for total grass biomass and biomass of the four most common grass species. $N = 10$ for all models

	R^2	Slope	P
Total grass biomass			
Observed	0.00	0.02	0.93
Difference	0.19	0.28	0.20
<i>Brachiaria lachnantha</i>			
Observed	0.18	0.13	0.22
Difference	0.03	-0.05	0.64
<i>Pennisetum stramineum</i>			
Observed	0.43	0.37	0.04
Difference	0.22	-0.22	0.17
<i>Pennisetum mezianum</i>			
Observed	0.43	-0.15	0.04
Difference	0.63	0.23	< 0.01
<i>Themeda triandra</i>			
Observed	0.33	-0.20	0.08
Difference	0.45	0.26	0.03

was negatively correlated with soil clay content ($r^2=0.21$, slope = -0.13, $n = 34$, $P = 0.007$) and positively correlated with soil silt content ($r^2=0.24$, slope = 0.09, $n = 34$, $P = 0.004$).

Discussion

Individual savanna trees are known to have a variety of effects on the grasses with which they coexist. Yet, little is known about how variation in tree cover at large spatial scales affects these grasses (Scholes & Archer 1997; Breshears 2006). We measured patterns of grass species composition, biomass and nutrient content across a range of tree covers. Our findings suggest that factors operating at the landscape scale can mitigate or even reverse the local effects of individual trees on grass community characteristics. These landscape-scale effects can have important implications, both positive and negative, for the herbivores that depend on grass forage resources.

GRASS BIOMASS AND COMPOSITION

Three of the four most common grass species had higher biomass in sub-canopy areas than in inter-canopy areas, and the fourth species (*T. triandra*) exhibited a non-significant trend in the same direction. As a result, total grass biomass was higher under trees than between trees, ranging from 25% higher in areas of high stand-wide tree cover to 67% higher in areas of low tree cover. These local positive effects of individual trees on grasses could be caused by a number of factors. Trees, especially *Acacias*, have been shown to increase nutrient levels in the soil beneath their canopies, leading to increased grass productivity (Belsky *et al.* 1993; Ludwig *et al.* 2001, 2004b). Here,

we found enriched soil nitrogen content under *A. drepanolobium*, which may have been a key factor contributing to increased grass biomass under trees in stands with low tree density. Trees can also facilitate grasses by reducing sub-canopy evapotranspiration (Belsky *et al.* 1993; Breshears *et al.* 1997; Ludwig *et al.* 2001) and by protecting them from herbivory. In this ecosystem, grasses under smaller trees with many low, thorny branches appear to be protected from grazing (C. Riginos, personal observation). Any or all of these mechanisms may underlie the high grass biomass we observed under trees. It is also possible that different mechanisms predominate for different sized trees. For example, larger trees may enrich sub-canopy soil nitrogen more than smaller trees (Ludwig *et al.* 2004b), whereas smaller trees may protect sub-canopy grasses from herbivory more than larger trees. This may explain why grass biomass in this study was elevated under all trees, regardless of their size.

Local, positive effects of trees on grasses have the potential to influence landscape-level patterns. Under a scenario of perfect up-scaling, one would expect grass biomass to vary in direct proportion to tree cover. There are a number of reasons, however, why this may not be the case. At our study site, biomass patterns for two of the common grass species did appear to scale up with tree cover; for the remaining two species, observed biomass at the stand scale was significantly lower than expected. Results from a companion study, in which we used structural equation modelling (SEM) to examine relationships among stand-wide grass biomass, tree density, soil characteristics and herbivore use (Riginos & Grace 2008), suggest some mechanisms that may underlie these patterns.

Pennisetum stramineum is the only species whose stand-wide grass biomass appears to have been directly influenced by trees. Tree cover was the primary determinant of *P. stramineum* biomass in structural equation (SE) models, consistent with the present finding that biomass of this grass is elevated both under trees and in areas with high tree cover. A plausible mechanistic explanation is that *P. stramineum* might be facilitated by the nitrogen-fertilizing effects of trees. This species also dominates nitrogen-rich termite mounds and glades in this landscape (Palmer 2003; Veblen 2008), suggesting that it gains a competitive advantage over other species where soil nitrogen is enriched. It is also possible that other effects of trees, such as shade provision, positively affect this species. For any of these factors, the zone of tree influence may extend beyond the canopy of the tree. For example, tree roots may be abundant in inter-canopy areas, enriching soil nitrogen in those areas if the trees are capable of nitrogen fixation (see below). This could explain why biomass of *P. stramineum* was most influenced by increasing tree density in the inter-canopy habitat.

Biomass patterns for *B. lachnantha* were similar to those for *P. stramineum*; biomass was elevated under individual trees, and biomass increased linearly with tree cover. The simplest explanation is that trees have a direct, positive influence on *B. lachnantha* and that this influence scales up in the landscape. SEM results, however, suggest that stand-scale biomass for this preferred forage species (Odadi, Young & Okeyo-Owuor 2007) is largely determined by herbivores (Riginos & Grace

2008). Wild herbivore use of low tree density areas is three times greater than their use of high tree density areas (Riginos & Grace 2008). Thus, *B. lachnantha* may have high biomass in high tree density areas simply because it is grazed less in those areas. Whether trees, herbivores or both contribute to the positive relationship between *B. lachnantha* biomass and tree density remains unclear. The case of this species, however, illustrates the potential for factors that co-vary with stand-scale tree density to affect its relationship with understory grasses.

For the remaining two grass species, *P. mezianum* and *T. triandra*, it is even more clear that factors other than tree density determine stand-scale biomass. Stand-wide biomass for these species exhibited strong negative relationships with tree cover – despite positive local effects of trees on *P. mezianum* and a trend in the same direction for *T. triandra*. For *P. mezianum*, it appears that herbivores are, again, an important determinant of stand-wide biomass patterns (Riginos & Grace 2008). This species is the least palatable of the common grasses in this system (Odadi, Young & Okeyo-Owuor 2007). As a result, it may gain a competitive advantage in the more heavily grazed, low tree density areas. For *T. triandra*, SEM results suggested that the negative relationship between stand-wide tree density and grass biomass is due to a different factor operating at the landscape scale: soil texture. Soil clay and silt appear to be important drivers of variation in both tree density and *T. triandra* biomass in this system (Riginos & Grace 2008).

These results suggest some of the local and landscape-scale mechanisms by which savanna trees affect grass biomass and species composition. Any number of other factors may also influence these relationships. Tree architecture, foliar density, size and age structure and rooting architecture, for example, may all affect tree–grass relationships. These factors may themselves vary with tree density or canopy cover. What seems clear is that the complex suite of potentially interacting variables that can determine grass biomass and composition renders it difficult to predict landscape-scale patterns from the patterns observed under isolated trees.

GRASS AND SOIL NUTRIENTS

Our results suggest that *A. drepanolobium* trees both elevate soil and grass nitrogen content and deplete soil and grass phosphorus content in this system. Soil nitrogen was enriched under individual trees, consistent with results from other *Acacia* savanna systems (Belsky *et al.* 1993; Ludwig *et al.* 2004b), and this was in turn associated with increased grass production. Grass nitrogen content was not elevated under trees, which may be related to the increased grass production (and thus, dilution of nutrients on a tissue mass basis). Grass phosphorus was depressed under trees, leading to overall higher N : P ratios under trees. Similar patterns have been documented for grasses growing under and between *Acacia tortilis* trees (Ludwig *et al.* 2004b). In addition, preliminary results from an experimental manipulation of tree density indicate that leaf nitrogen is depressed and leaf phosphorus enhanced in former

sub-canopy areas after trees have been removed (C. Riginos, unpublished data).

Most *Acacia* species are capable of symbiotic biological N₂ fixation (DeFaria *et al.* 1989; Binkley & Giardina 1997), and rates of N₂ fixation can increase when *Acacias* compete with understorey grasses for soil nutrients (Cramer *et al.* 2007). Nitrogen-fixing species often have a reduced requirement for nitrogen uptake from the soil, but an increased requirement for phosphorus (Vitousek & Howarth 1991; Binkley & Giardina 1997). Although less is specifically known about nitrogen fixation and phosphorus demand for *A. drepanolobium*, our findings for sub-canopy grass nitrogen and phosphorus content are consistent with the expected effects of a nitrogen-fixing tree species.

Although not fully conclusive, our results also suggest that these effects of individual trees on grass and soil nutrients may translate to similar effects of increasing tree densities. Grass leaf N : P ratios were elevated in areas of high tree density, as under individual trees. At the same time, soil phosphorus was depleted at high tree densities. In terms of grass productivity, however, the positive effect of individual trees did not appear to scale up. Stand-wide grass productivity is significantly lower in sites with high *A. drepanolobium* cover than in sites with low tree cover ($r^2 = 0.39$, $n = 10$, $P = 0.05$; C. Riginos, unpublished data). This suggests that some factor other than soil nutrients drives grass productivity patterns across this gradient of tree cover. Soil moisture available to grasses may be reduced in areas with high tree cover due to increased competition with trees (Smit & Rethman 2000). This may explain the overall lower grass productivity in these areas – despite elevated grass productivity under individual trees.

CONSEQUENCES FOR UNGULATES

The results presented here suggest that the collective effects of many trees at the stand scale can oppose the effects of individual trees on forage quality and quantity. Two recent studies have demonstrated the positive effects of individual savanna trees on grass nutrients and digestibility and concluded that a loss of trees from the landscape would have negative consequences for wild ungulate populations (Treydte *et al.* 2007; Ludwig, de Kroon & Prins 2008). From these studies one might assume that the effects of individual trees scale up in the landscape and that an increase in the abundance of trees will have positive consequences for ungulates. While this may be true in savannas with low densities of large, isolated trees, our results illustrate that the effects of individual trees do not necessarily scale up in a landscape with high tree densities.

We found contrasting effects of trees on key grass nutrients. In terms of nitrogen and crude protein, areas of high tree density appear to be enriched; within one common species of grass (*B. lachnantha*), leaf nitrogen was as much as 50% higher in areas of high tree cover. These areas also had, on average, five times higher cover of *P. stramineum* – the species with the highest leaf crude protein content of all of the dominant grass species at this site (Sensenig 2007). In terms of grass leaf phosphorus, however, trees appear to have negative effects for herbivores. Grass leaf phosphorus at this site is well below

estimated requirements for pregnant and lactating female ungulates (Augustine 2004). Thus, if trees are depleting the phosphorus available to grasses, this could have negative repercussions for both wild and domestic ungulate populations.

Any positive effects of high tree cover on grass quality may also be counteracted by the negative effects of high tree cover on grass quantity and availability. Despite grass being more abundant under individual tree canopies (especially isolated trees), grass productivity in this study site is twice as high in the areas with the fewest trees relative to the areas with the most trees (C. Riginos, unpublished data). This is consistent with other studies that have shown a negative relationship between tree density and grass productivity (Scholes & Archer 1997; Smit 2005). Thus, the net effects of high tree cover on ungulate populations may be negative, if the quantity of available forage is limiting those populations. Perhaps even more importantly, areas of high tree cover may be effectively unavailable to ungulate herbivores. In a previous study, we found that wild herbivores preferred areas with low tree cover because of their ability to better detect predators in those areas (Riginos & Grace 2008). Thus it appears that, although a low density of scattered trees may provide some nutritional benefits to herbivores, the net effect of a high density of trees on many herbivore species is negative.

Conclusions

The results presented here suggest some of the ways in which the community characteristics of grasses found under isolated savanna trees may or may not scale up in a landscape of varying tree densities. Savanna systems are often considered to be simple two-phase mosaics of sub-canopy and inter-canopy patches (Jeltsch *et al.* 1997; Higgins, Bond & Trollope 2000; Caylor, Shugart & Rodriguez-Iturbe 2005). Surprisingly few studies have considered that connectivity between patches or dynamics operating at scales larger than these patches may affect the relationships between trees and grasses (Breshears 2006). Many savanna systems around the world are experiencing marked increases in the density and cover of woody species, while others (particularly in Africa) are experiencing declines in tree cover (Bond 2008). Attempts to predict the consequences of these changes for ecosystem services such as rangeland productivity, maintenance of wild ungulate populations and carbon sequestration will depend on our understanding of the reasons why local tree–grass interactions do or do not predict landscape-scale patterns. For the moment, however, it appears best not to assume that the local effects of trees will scale up to the landscape scale.

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References

- Archer, S., Schimel, D.S. & Holland, E.A. (1995) Mechanisms of shrubland expansion — land-use, climate, or CO₂. *Climatic Change*, **29**, 91–99.
- Augustine, D.J. (2003) Spatial heterogeneity in the herbaceous layer of a semi-arid savanna ecosystem. *Plant Ecology*, **167**, 319–332.
- Augustine, D.J. (2004) Influence of cattle management on habitat selection by impala on central Kenyan rangeland. *Journal of Wildlife Management*, **68**, 916–923.
- Augustine, D.J. & McNaughton, S.J. (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*, **41**, 45–58.
- van Auken, O.W. (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics*, **31**, 197–215.
- Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M. & Ali, A.R. (1993) Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology*, **30**, 143–155.
- Binkley, D. & Giardina, C. (1997) Nitrogen fixation in tropical forest plantations. *Management of Soil, Nutrients and Water in Tropical Plantation Forests*, vol. ACIAR Monograph No. 43. (eds E.K.S. Nambiar & A.G. Brown), pp. ACIAR, Canberra.
- Birkett, A. (2002) The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *African Journal of Ecology*, **40**, 276–282.
- Bond, W.J. (2008) What limits trees in C4 grasslands and savannas? *Annual Review of Ecology, Evolution & Systematics*, **39**, 641–659.
- Breshears, D.D. (2006) The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and the Environment*, **4**, 96–104.
- Breshears, D.D., Rich, P.M., Barnes, F.J. & Campbell, K. (1997) Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecological Applications*, **7**, 1201–1215.
- Caylor, K.K., Shugart, H.H. & Rodriguez-Iturbe, I. (2005) Tree canopy effects on simulated water stress in southern African savannas. *Ecosystems*, **8**, 17–32.
- Cramer, M.D., Chimphango, S.B.M., van Cauter, A., Waldram, M.S. & Bond, W.J. (2007) Grass competition induces N₂ fixation in some species of African Acacia. *Journal of Ecology*, **95**, 1123–1133.
- DeFaria, S.M., Lewis, G.P., Sprent, J.I. & Sutherland, J.M. (1989) Occurrence of nodulation in the Leguminosae. *New Phytologist*, **111**, 607–619.
- Georgiadis, N.J., Olwero, J.G.N., Ojwang, G. & Romanach, S.S. (2007) Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density and time. *Biological Conservation*, **137**, 461–472.
- Hewitt, J.E., Thrush, S.F., Dayton, P.K. & Bonsdorff, E. (2007) The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *The American Naturalist*, **169**, 398–408.
- Higgins, S.I., Bond, W.J. & Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology*, **88**, 213–229.
- House, J.I., Archer, S., Breshears, D.D., Scholes, R.J. & NCEAS Tree-Grass Interactions Participants (2003) Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography*, **30**, 1763–1777.
- Jeltsch, F., Milton, S.J., Dean, W.R.J. & van Rooyen, N. (1997) Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science*, **8**, 177–188.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.
- Ludwig, F., de Kroon, H. & Prins, H.H.T. (2008) Impacts of savanna trees on forage quality for a large African herbivore. *Oecologia*, **155**, 487–496.
- Ludwig, F., de Kroon, H., Prins, H.H.T. & Berendse, F. (2001) Effects of nutrients and shade on tree-grass interactions in an East African savanna. *Journal of Vegetation Science*, **12**, 579–588.
- Ludwig, F., Dawson, T.E., Kroon, H., Berendse, F. & Prins, H.H.T. (2003) Hydraulic lift in *Acacia tortilis* trees on an East African savanna. *Oecologia*, **134**, 293–300.
- Ludwig, F., Dawson, T.E., Prins, H.H.T., Berendse, F. & de Kroon, H. (2004a) Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecology Letters*, **7**, 623–631.
- Ludwig, F., de Kroon, H., Berendse, F. & Prins, H.H.T. (2004b) The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, **170**, 93–105.
- Morgan, J.A., Milchunas, D.G., LeCain, D.R., West, M. & Mosier, A.R. (2007) Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in a shortgrass steppe. *Proceedings of the National Academy of Sciences, USA*, **104**, 14724–14729.
- Odadi, W., Young, T.P. & Okeyo-Owuor, J.B. (2007) Effects of wildlife on cattle diets in Laikipia rangeland, Kenya. *Rangeland Ecology and Management*, **60**, 179–185.
- Okello, B.D., Young, T.P., Riginos, C., Kelly, D. & O' Connor, T.G. (2008) Short-term survival and long-term mortality of *Acacia drepanolobium* after a controlled burn. *African Journal of Ecology*, **46**, 395–401.
- Olsen, S. & Sommers, L. (1982) Determination of total phosphorus in soil using simple Kjeldahl digestion. *Methods of Soil Analysis: Part 2. Chemical and Microbiological Properties*, vol. 2 (eds A. Page, R. Miller & D. Keeney), pp. 403–430. American Society of Agronomy, Madison, WI, USA.
- Palmer, T.M. (2003) Spatial habitat heterogeneity influences competition and coexistence in an African acacia ant guild. *Ecology*, **84**, 2843–2855.
- Pratt, D.J. & Gwynne, M.D. (1977) *Rangeland Management and Ecology in East Africa*. Hodder and Stoughton, London.
- Riginos, C. & Grace, J.B. (2008) Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology*, **89**, 2228–2238.
- Roques, K.G., O' Connor, T.G. & Watkinson, A.R. (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, **38**, 268–280.
- Sankaran, M., Ratnam, J. & Hanan, N.P. (2004) Tree-grass coexistence in savannas revisited — insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, **7**, 480–490.
- Sankaran, M., Hanan, N.P., Scholes, R.P., Ratnam, J., Augustine, D.L., Cade, B.S. *et al.* (2005) Determinants of woody cover in African savannas. *Nature*, **438**, 846–849.
- Scholes, R.J. & Archer, S.R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.
- Sensenig, R.L. (2007) *Spatial ecology of fire in an East African savanna: effects of burn size and patchiness on the foraging ecology of herbivores of varying body size*. PhD Thesis, University of California, Davis, CA, USA.
- Smit, G.N. (2004) An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *Journal of Environmental Management*, **71**, 179–191.
- Smit, G.N. (2005) Tree thinning as an option to increase herbaceous yield of an encroached semi-arid savanna in South Africa. *BMC Ecology*, <http://www.biomedcentral.com/content/pdf/1472-6785-5-4.pdf>.
- Smit, G.N. & Rethman, N.F.G. (2000) The influence of tree thinning on the soil water in a semi-arid savanna of southern Africa. *Journal of Arid Environments*, **44**, 41–59.
- Taylor, M. (2000) Determination of total phosphorus in soil using simple Kjeldahl digestion. *Communications in Soil Science and Plant Analysis*, **31**, 2665–2670.
- Thomas, R., Sheard, R. & Moyer, J. (1967) Comparison of conventional and automated procedures for nitrogen phosphorus and potassium analysis of plant material using a single digestion. *Agronomy Journal*, **59**, 240–243.
- Tobler, M.W., Cochar, R. & Edwards, P.J. (2003) The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *Journal of Applied Ecology*, **40**, 430–444.
- Treydte, A.C., Heitkonig, I.M.A., Prins, H.H.T. & Ludwig, F. (2007) Trees improve grass quality for herbivores in African savannas. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 197–205.
- Veblen, K.E. (2008) Season- and herbivore-dependent competition and facilitation in a semiarid savanna. *Ecology*, **89**, 1532–1540.
- van Vegten, J.A. (1984) Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio*, **56**, 3–7.
- Vitousek, P.M. & Howarth, R.W. (1991) Nitrogen limitation on land and in sea: how can it occur? *Biogeochemistry*, **13**, 87–115.
- Western, D. & Maitumo, D. (2004) Woodland loss and restoration in a savanna park: a 20-year experiment. *African Journal of Ecology*, **42**, 111–121.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
- Young, T.P., Stubblefield, C.H. & Isbell, L.A. (1997) Ants on swollen-thorn acacias: species coexistence in a simple system. *Oecologia*, **109**, 98–107.
- Young, T.P., Okello, B.D., Kinyua, D. & Palmer, T.M. (1998) KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage Science*, **14**, 94–102.

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