

Grass competition suppresses savanna tree growth across multiple demographic stages

CORINNA RIGINOS^{1,2,3}

¹Department of Plant Sciences, University of California, Davis, California 95616 USA

²Mpala Research Centre, P.O. Box 555, Nanyuki, 10400, Kenya

Abstract. Savanna ecosystems, defined by the codominance of trees and grasses, cover one-fifth of the world's land surface and are of great socioeconomic and biological importance. Yet, the fundamental question of how trees and grasses coexist to maintain the savanna state remains poorly understood. Many models have been put forward to explain tree–grass coexistence, but nearly all have assumed that grasses do not limit tree growth and demography beyond the sapling stage. This assumption, however, has rarely been tested. Here I show that grass can strongly suppress the growth of trees. I removed grass around trees of three size classes in an *Acacia drepanolobium* savanna in Laikipia, Kenya. For even the largest trees, grass removal led to a doubling in growth and a doubling in the probability of transitioning to the next size class over two years. These results suggest that grass competition in productive (nutrient-rich) savannas may limit tree growth as much as herbivory and fire (the main factors thought to determine tree demography within a rainfall region) and should be incorporated into savanna models if tree–grass coexistence and savanna dynamics are to be understood.

Key words: *Acacia drepanolobium*; black cotton; bush encroachment; competition; Laikipia, Kenya; tree–grass interactions; woody encroachment.

INTRODUCTION

The coexistence of trees and grasses in savanna systems is one of the most intensely studied topics in terrestrial ecology (reviewed in Sarmiento 1984, Scholes and Archer 1997, House et al. 2003, Sankaran et al. 2004, 2005). Savannas cover one-fifth of the world's land surface and are home to most of the world's rangelands, livestock, and large wild herbivores (Sankaran et al. 2005), most of which depend on the maintenance of the mixed tree–grass state. The relative abundance of trees and grasses can affect important aspects of ecosystem function, including hydrology, carbon and nitrogen storage and cycling, and grass and herbivore productivity (Scholes and Archer 1997, Jackson et al. 2002, House et al. 2003). Trees and shrubs can provide numerous ecosystem services such as enhanced forage quality for grazing herbivores in subcanopy areas (Treydte et al. 2007, Ludwig et al. 2008) and structural and habitat diversity that facilitates a variety of terrestrial and arboreal species (Scholes and Archer 1997, House et al. 2003). A high density of trees and shrubs, however, can have strong negative effects on grasses, rangeland productivity, and wild herbivores (Scholes and Archer

1997, Riginos and Grace 2008; C. Riginos, J. B. Grace, D. J. Augustine, and T. P. Young, *unpublished manuscript*). Savanna systems the world over are threatened by increasing densities of woody plants (Archer 1995, van Auken 2000, Roques et al. 2001, Moleele et al. 2002), which can, in extreme cases, lead to ranch failure and apparently irreversible landscape degradation (Scheffer et al. 2001, Tobler et al. 2003).

Although the maintenance of the mixed tree–grass state is essential to the functioning of savanna ecosystems, the mechanisms allowing trees and grasses to coexist remain poorly understood (Scholes and Archer 1997, House et al. 2003, Sankaran et al. 2004, 2005). Attempts to answer the “savanna problem” (Sarmiento 1984) have generally fallen into two categories (Sankaran et al. 2004). Competition-based models typically invoke niche partitioning mechanisms by which trees and grasses avoid competition, usually for water. Demographic models, in contrast, invoke factors that limit tree growth and survival. These factors include precipitation, fire, herbivory, and combinations thereof (Sankaran et al. 2004). Both types of explanations assume that larger (post-sapling) trees are superior competitors to grasses, and that grasses have a minimal effect on the growth and survival of these trees (Scholes and Archer 1997). Surprisingly, however, this assumption has rarely been tested.

Of the numerous demographic and spatially explicit simulation models that have been put forward to explain variation in savanna tree abundances (e.g., Dublin et al.

Manuscript received 5 March 2008; revised 19 September 2008; accepted 23 September 2008. Corresponding Editor: L. Gough.

³ Present address: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA. E-mail: criginos@princeton.edu

1990, Menaut et al. 1990, Jeltsch et al. 1997, Higgins et al. 2000, van Langevelde et al. 2003, Holdo 2007), only a handful include pathways by which grass competition may limit trees. In these few cases, grasses are assumed to suppress tree seedling establishment (Menaut et al. 1990, Jeltsch et al. 1997) but not to have competitive effects on larger trees. Empirical studies, however, indicate that the rooting zones of these two guilds can overlap substantially (Knoop and Walker 1985, Smit and Rethman 2000), suggesting that even large trees may be competing with grasses for limited soil moisture. A number of studies have shown the inverse, that large trees can suppress grasses (Belsky 1994, Ludwig et al. 2004), and others have shown that grasses can suppress tree seedling and sapling establishment (Weltzin and McPherson 1997, Jurena and Archer 2003, Riginos and Young 2007). One previous study examined the effects of grass competition on the growth of larger trees (Knoop and Walker 1985). To our knowledge, however, no previous study has simultaneously examined the effects of grasses on trees for a range of tree demographic stages (Midgley and Bond 2001, Sankaran et al. 2004).

Here, I report the results of an experimental test of the effects of grass on *Acacia drepanolobium* tree growth in a Kenyan savanna system. I conducted a grass-removal experiment on trees ranging in height from 30 cm to 4.4 m. With this two-year experiment, I set out to address three main questions: (1) Does grass competitively suppress tree growth? (2) If so, does the effect of grass competition vary with tree size?, and (3) Does grass competition affect the likelihood of trees transitioning from one demographic stage to the next?

MATERIALS AND METHODS

This study was conducted at the Mpala Research Centre (37°53' E, 0°17' N; mean annual rainfall ~500 mm), in the Laikipia region of Kenya. The study area is underlain by poorly drained, high clay content "black cotton" soil. Black cotton soils make up nearly one-half of the land area in Laikipia and are widespread over large areas of East Africa, including much of southern Ethiopia and parts of the Serengeti-Mara ecosystem, and support some of the most productive rangelands in the region. Across all of semiarid Africa, black cotton soils and other, similar vertisols cover ~8–10% of the land area (Deckers et al. 2001).

This site, like many underlain by black cotton soils, is dominated by the whistling thorn acacia (*Acacia drepanolobium*), which accounts for 97% of the woody cover (Young et al. 1998). Individual trees can grow up to 10 m in height (Coe and Beentje 1991), but at this site the vast majority (92–95%) of trees are <4 m tall (Young et al. 1997). Individual trees are typically occupied by one of four species of symbiotic ants (Young et al. 1997, Palmer et al. 2000). Because the identity of the ant occupant can influence various demographic characteristics of the trees (Palmer et al. 2008), I limited this

experiment to trees occupied by the most common ant species, *Crematogaster mimosae*.

The herbaceous layer at this site is dominated by five species of perennial bunchgrass, which together make up >90% of the herbaceous cover (Young et al. 1998). Although a number of forb species are present at this site, they make up <3% of the total herbaceous cover; thus, I use the term "grass" to refer to all herbaceous species. The Mpala Research Centre property is managed for both cattle production and wildlife conservation. Common wild herbivores include plains zebras (*Equus burchelli*), Grant's gazelles (*Gazella granti*), hartebeest (*Alcelaphus buselaphus*), giraffes (*Giraffa camelopardalis*), elephants (*Loxodonta africana*), buffalos (*Syncerus caffer*), oryx (*Oryx gazella*), eland (*Taurotragus oryx*), and steinbuck (*Raphicerus campestris*).

In September 2005, I located 180 trees within an area ~200 × 200 m. These trees ranged from 0.3 to 4.4 m in height. True seedlings (recently germinated trees) are very rarely encountered in this ecosystem; thus, I focused this study on trees in three size classes: sapling (<1 m tall), juvenile (1–2.5 m tall), and adult (>2.5 m tall). I located 60 individuals within each size class, one-half of which were randomly assigned to a grass-removal treatment and one-half to a control treatment. For each grass-removal tree, I clipped and sprayed with glyphosate (Roundup, Monsanto, St. Louis, Missouri, USA) all herbaceous vegetation under the tree's canopy in late September 2005. Canopy diameter was strongly correlated with stem diameter ($r^2 = 0.77$, $n = 180$ trees, $P < 0.0001$), and stem diameter is strongly correlated with biomass (Okello et al. 2001). Thus by killing the grass under each tree's canopy, I attempted to standardize the treatment level to the tree's size. All clipped grass was removed from the site. Smaller trees were wrapped in plastic during the herbicide spraying to prevent the herbicide from affecting the trees.

I measured tree growth in three ways: change in height, change in stem diameter (measured at 5 cm above ground level), and change in total branch length of four permanently marked branches per tree (which were averaged for each tree). Trees were measured in September 2005 just before the grass-removal treatment was applied, and again in September 2006 and 2007.

Growth data for each of the three growth metrics were initially analyzed using a two-factor repeated-measures ANOVA with tree size class and grass treatment as fixed factors. There were significant effects of year for all growth metrics, which was not surprising given that total rainfall was substantially lower in the first year of the study than in the second year (353 mm in 2005–2006 vs. 674 mm in 2006–2007). There were no interactions, however, among year, tree size class, and treatment. Because growth responses were qualitatively similar for both years of the study, I subsequently used simple two-factor ANOVAs to analyze the total growth of trees over the two-year duration of the experiment. Also,



FIG. 1. Representative trees from the study: these two *Acacia drepanolobium* trees had the same height (1.4 m) and similar basal diameters (grass-removal tree, 2.9 cm; control tree, 3.4 cm) when the experiment began in 2005. After two years, the grass-removal tree (right) had increased in height by 0.3 m, whereas the control tree (left) had only increased in height by 0.07 m.

because branch length results were virtually identical to height and diameter results, I present only the height and diameter results. Trees that died or died back and subsequently coppiced ($n = 8$ trees, five grass-removal and three control trees) were excluded from all analyses. All data met ANOVA assumptions.

To illustrate the effects of grass treatment on the likelihood of trees transitioning from one size class to the next, I divided trees into four 1-m increment size classes: <1, 1–2, 2–3, and 3–4 m. I calculated the percentage of trees in each size class and grass treatment that advanced to the next size class (including a 4–5 m size class) over the two-year duration of the experiment. I then used χ^2 tests to examine the effect of grass removal on transition likelihood within each of the four size classes.

RESULTS

Over two years, grass-removal trees grew more than twice as much as control trees in height (Figs. 1 and 2a; main effect of grass treatment, $F_{1,165} = 17.21$, $P < 0.0001$) and nearly twice as much as control trees in basal diameter (Fig. 2b; main effect of grass treatment, $F_{1,165} = 27.42$, $P < 0.0001$). Although there were significant effects of tree size on tree growth (height, $F_{2,165} = 18.36$, $P < 0.0001$; diameter, $F_{2,165} = 5.91$, $P = 0.003$), there were no significant interactions between tree size and grass treatment for either of the growth

metrics (height, $F_{1,165} = 0.97$, $P = 0.38$; diameter, $F_{1,165} = 1.37$, $P = 0.26$). In other words, the effects of grass removal were substantial and significant for even the largest trees in the experiment.

Grass-removal trees were also twice as likely to make the transition from one 1-m increment size class to the next over the two-year duration of the experiment (Table 1; $P < 0.05$ in χ^2 tests for 1–2, 2–3, and 3–4 m size classes). The only exception was for trees <1 m tall, which had a very low transition probability ($\chi^2 = 0.001$, $df = 1$, $P = 0.98$) regardless of grass treatment. Trees in the intermediate size classes exhibited the greatest amount of vertical growth for both grass treatments and were most likely to make the transition from one size class to the next (Table 1).

DISCUSSION

The results presented here demonstrate that grass competition can substantially reduce the growth and demographic transition probability of trees, regardless of demographic stage or rainfall. These results suggest that grass competition may be far more important in limiting savanna trees than previously thought.

Acacia drepanolobium trees were suppressed by the presence of grass across three size classes and in both a relatively low rainfall year and a relatively high rainfall year. Saplings (trees <1 m tall) appeared to be more strongly suppressed by grass than larger trees in terms of

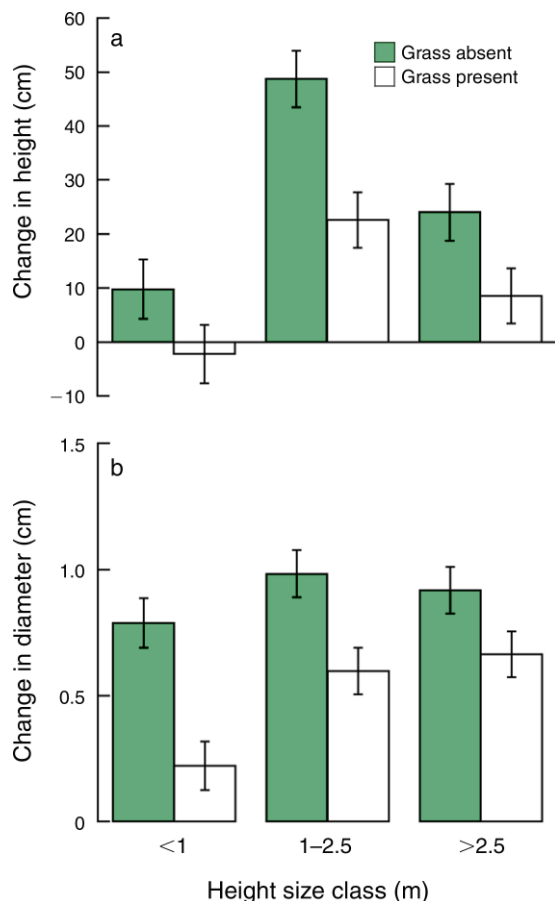


FIG. 2. Growth of *Acacia drepanolobium* trees (mean \pm SE) over two years with and without the subcanopy grass removed. Growth is measured as (a) change in height and (b) change in stem diameter.

growth (Fig. 2), but there were no significant interactions between grass treatment and tree size class. Interestingly, however, saplings had a very low likelihood of making the transition to the next demographic size class, regardless of grass treatment (Table 1). Among control saplings, in fact, mean vertical growth was negative, apparently because of senescence among larger branches (*personal observation*) rather than browse damage, which is low among control saplings relative to grass-removal saplings (Riginos and Young 2007). It is possible that, at this stage, trees are allocating more resources to belowground biomass accumulation than to vertical growth. Four years of data from a companion study (the first two years of which are presented in Riginos and Young 2007), show that, even though very few saplings escape from the <1 m size class, the likelihood of trees making this transition is significantly higher among grass-removal saplings (grass-removal, 4%; control, 1.5%; $\chi^2 = 3.8$, $n = 337$, $df = 1$, $P = 0.05$). Thus, although there appear to be other factors that strongly limit sapling growth, the

effect of grass competition on saplings is consistent with its effect on larger trees.

These negative effects of grasses on trees may be widespread in space and time. In a previous study, Knoop and Walker (1985) found that grass competition affected trees in a fertile savanna but not in an infertile system, and in a high rainfall year but not a low rainfall year. Replication in this study, however, was limited ($n = 3$ trees per treatment per ecosystem), which may explain its equivocal results. The present study clearly demonstrates that grass competition can be an important factor limiting tree growth in fertile savannas, even under low rainfall conditions (353 mm in the first year of the study). It is possible that the effects of grass competition are weaker in less fertile systems, where grass cover is lower. Fertile savannas, however, make up some 44% of African savannas (which themselves cover 52% of the continent; Justice et al. 1994, du Toit and Cumming 1999), suggesting that grass-on-tree competition may be important in at least a substantial proportion of savanna systems.

These findings have important implications for both of the prevailing models of savanna tree–grass coexistence. Competition-based models generally assume that tree seedling and sapling recruitment may be limited by grass but that this competitive asymmetry switches direction for larger (post-sapling) trees (Scholes and Archer 1997). In the present study, saplings (<1 m tall) may have experienced slightly stronger competition from grasses than larger trees in terms of growth (Fig. 2), but tree growth in both the juvenile (1–2.5 m tall) and adult (>2.5 m tall) size classes were also substantially suppressed by grasses. Although I did not test the magnitude of tree effects on grasses, the strong effects of grasses on trees demonstrated here do not support niche partitioning between these two guilds. This adds to the emerging consensus that niche partitioning may not be sufficient to explain tree–grass coexistence in savannas (Jeltsch et al. 2000, Ludwig et al. 2004, Sankaran et al. 2004).

Demographic models have achieved greater success in explaining tree–grass coexistence by considering a variety of factors that can limit tree population growth across a number of demographic stages. Competitive suppression by grass, however, is rarely considered. Instead, grass density and biomass in these models are typically parameterized to affect trees indirectly, by

TABLE 1. Probability of making the transition from one 1-m increment size class to the next for *Acacia drepanolobium* trees in the Mpala Research Centre, Laikipia, Kenya, with and without the subcanopy grass removed.

Transition	Grass present (%)	Grass removed (%)
<1 to 1–2 m	2	2
1–2 to 2–3 m	17	35
2–3 to 3–4 m	11	22
3–4 to 4–5 m	5	11



PLATE 1. By eating down the grass, cattle may release savanna trees from competition, eventually leading to an increase in tree cover. Photo credit: C. Riginos.

providing more fuel for the fires that kill them (Higgins et al. 2000, van Langevelde et al. 2003, D'Odorico et al. 2006, Holdo 2007). However, the results here indicate that even a partial reduction in grass density (for example, due to grazing or fire) could have substantial positive effects on the growth of savanna trees. This could partially or fully offset the effects of fire or browsing herbivores in suppressing tree biomass and population growth.

Range managers have frequently blamed heavy or prolonged cattle grazing for reducing the cover and/or density of competitor grasses, thereby causing increases in woody vegetation (van Vegten 1984, Archer 1995, van Auken 2000, Roques et al. 2001; see Plate 1). Given the magnitude of the woody encroachment problem, and its consequences for the biodiversity and economic productivity of savanna ecosystems, it is surprising that so few experimental studies have tested the effects of grasses on trees or incorporated these effects into models of tree demography (Midgley and Bond 2001, Sankaran et al. 2004). Future experimental research should focus on testing the effects of grasses on a variety of savanna tree species and demographic stages (includ-

ing seedling survival and adult reproduction), for a variety of grass densities, and over a variety of edaphic and climatic conditions. Only by directly comparing empirically derived estimates of the magnitude of the various determinants of tree demography will we further our understanding of tree–grass coexistence and the dynamics and management of savanna systems.

ACKNOWLEDGMENTS

I thank John Lochukuya, Jackson Ekadeli, Frederick Erii, Patrick Etelej, Kari Veblen, and Lauren McGeogh for their assistance in the field, and the staff of the Mpala Research Centre for their logistical support. I also thank Truman Young, Kevin Rice, Maureen Stanton, Robert Pringle, and two anonymous reviewers for comments on this manuscript. This research was funded by a National Science Foundation Graduate Research Fellowship to C. Riginos and National Science Foundation LTREB BSR-03-16402 to T. P. Young.

LITERATURE CITED

- Archer, S. 1995. Tree–grass dynamics in a *Prosopis*–thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2:83–99.
- Belsky, A. J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree–grass competition. *Ecology* 75:922–932.

- Coe, M., and H. Beentje. 1991. A field guide to the acacias of Kenya. Oxford University Press, Oxford, UK.
- Deckers, J., O. Spaargaren, and F. Nachtergaele. 2001. Vertisols: genesis, properties and soilscape management for sustainable development. Pages 3–20 in J. K. Syers, F. W. T. Penning de Vries, and P. Nyamudeza, editors. The sustainable management of vertisols. CABI, Wallington, UK.
- D'Odorico, P., F. Laio, and L. Ridolfi. 2006. A probabilistic analysis of fire-induced tree–grass coexistence in savannas. *American Naturalist* 167:E79–E87.
- Dublin, H. T., A. R. E. Sinclair, and J. McGlade. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59: 1147–1164.
- du Toit, J. T., and D. H. M. Cumming. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* 8:1643–1661.
- Higgins, S. I., W. J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology* 88:213–229.
- Holdo, R. M. 2007. Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications* 17:558–568.
- House, J. I., S. Archer, D. D. Breshears, and R. J. Scholes. and NCEAS Tree–Grass Interactions Participants. 2003. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography* 30:1763–1777.
- Jackson, R. B., J. L. Banner, E. G. Jobbagy, W. T. Pockman, and D. H. Wall. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418:623–626.
- Jeltsch, F., S. J. Milton, W. R. J. Dean, and N. van Rooyen. 1997. Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science* 8:177–188.
- Jeltsch, F., G. E. Weber, and V. Grimm. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree–grass coexistence. *Plant Ecology* 150:161–171.
- Jurena, P. N., and S. Archer. 2003. Woody plant establishment and spatial heterogeneity in grasslands. *Ecology* 84:907–919.
- Justice, C., R. J. Scholes, and P. Frost. 1994. African savannas and the global atmosphere: research agenda. IGBP report number 31. International Geosphere-Biosphere Programme, Stockholm, Sweden.
- Knoop, W. T., and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* 73:235–253.
- Ludwig, F., T. E. Dawson, H. H. T. Prins, F. Berendse, and H. de Kroon. 2004. Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecology Letters* 7:623–631.
- Ludwig, F., H. de Kroon, and H. H. T. Prins. 2008. Impacts of savanna trees on forage quality for a large African herbivore. *Oecologia* 155:487–496.
- Menaut, J., J. Gignoux, C. Prado, and J. Clobert. 1990. Tree community dynamics in a humid savanna of the Cote-d'Ivoire: modelling the effects of fire and competition with grass and neighbors. *Journal of Biogeography* 17:471–481.
- Midgley, J. J., and W. J. Bond. 2001. A synthesis of the demography of African acacias. *Journal of Tropical Ecology* 17:871–886.
- Moleele, N. M., S. Ringrose, W. Matheson, and C. Vanderpost. 2002. More woody plants? The status of bush encroachment in Botswana's grazing areas. *Journal of Environmental Management* 64:3–11.
- Okello, B. D., T. G. O'Connor, and T. P. Young. 2001. Growth, biomass estimates, and charcoal production of *Acacia drepanolobium* in Laikipia, Kenya. *Forest Ecology and Management* 142:143–153.
- Palmer, T. M., M. L. Stanton, T. P. Young, J. R. Goheen, R. M. Pringle, and R. Karban. 2008. Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna. *Science* 319:192–195.
- Palmer, T. M., T. P. Young, M. L. Stanton, and E. Wenk. 2000. Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia* 123:425–435.
- Riginos, C., and J. B. Grace. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology* 89:2228–2238.
- Riginos, C., and T. P. Young. 2007. Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. *Oecologia* 153:985–995.
- Roques, K. G., T. G. O'Connor, and A. R. Watkinson. 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., et al. 2005. Determinants of woody cover in African savannas. *Nature* 438:846–849.
- Sankaran, M., J. Ratnam, and N. P. Hanan. 2004. Tree–grass coexistence in savannas revisited—insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* 7:480–490.
- Sarmiento, G. 1984. The ecology of neotropical savannas. Harvard University Press, Cambridge, Massachusetts, USA.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folkes, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591–596.
- Scholes, R. J., and S. R. Archer. 1997. Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517–544.
- Smit, G. N., and N. F. G. Rethman. 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.
- Tobler, M. W., R. Cochar, and P. J. Edwards. 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., I. M. A. Heitkonig, H. H. T. Prins, and F. Ludwig. 2007. Trees improve grass quality for herbivores in African savannas. *Perspectives in Plant Ecology, Evolution and Systematics* 8:197–205.
- van Auker, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197–215.
- van Langevelde, F., C. A. D. M. van de Vijver, L. Kumar, J. van de Koppel, N. de Ridder, J. van Andel, A. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M. Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84:337–350.
- van Vegten, J. A. 1984. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* 56:3–7.
- Weltzin, J. F., and G. R. McPherson. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* 112:156–164.
- Young, T. P., B. D. Okello, D. Kinyua, and T. M. Palmer. 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage Science* 14:94–102.
- Young, T. P., C. H. Stubblefield, and L. A. Isbell. 1997. Ants on swollen-thorn acacias: species coexistence in a simple system. *Oecologia* 109:98–107.