

Management and Restoration in African Savannas: Interactions and Feedbacks

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Savannas constitute one of the world's major biomes, covering about 33 million km², or nearly 20% of the earth's land surface. They cover more than half the area of the African continent, support a large fraction of its human population and a majority of its rangeland and livestock biomass, and are home to the greatest density and diversity of wild herbivores and carnivores of any ecosystem on Earth. Besides their obvious socioeconomic importance, savannas are also ecologically unique in featuring the coexistence of two contrasting plant life forms—trees and grasses—that share resources to a meaningful degree.

Savannas can be abstracted into a few components—trees, grasses, grazers, and browsers—the interactions among which are mediated by climate, biogeochemistry, fire, and humans. However, within these broad limits, African savannas display substantial variation in their physical and structural attributes at scales from the local to the regional. They exhibit differences in woody plant canopy cover and stature (sparsely treed to densely treed, shrub versus tree dominance), herbaceous characteristics (low or high grass biomass, vegetated versus bare patches), plant functional forms (fine leaved versus broad leaved trees, annual versus perennial grasses), vegetation spatial pattern (random, regular, or clumped), and soil and plant nutrient status (nutrient-poor, or dystrophic, savannas versus nutrient-rich, or eutrophic, savannas; House et al. 2003). These physical, structural, and compositional attributes of savannas in turn define many aspects of the functioning of these ecosystems, influencing such properties as net ecosystem production, carbon sequestration potential, herbivore carrying capacity, nutrient cycling, soil erosion, and hydrology (Padien and Lajtha 1992; Joffre and Rambal 1993; Belsky 1994; Aguiar et al. 1996; Schlesinger et al. 1996; Schulze et al. 1996; Rietkirk et al. 1997; Reid et al. 1999).

A Generalized Conceptual Model of African Savanna Function

Researchers studying African savannas have attempted to capture the complexity inherent in these systems with graphical, conceptual models that display complex interactions among various system components. Conceptual models of savanna structure and function, such as those of McNaughton (1983), Scholes and Walker (1993), and Venter et al. (2003), all suggest a constellation of forces “that act with varying intensity, interdependence, and predict-

ability” (McNaughton 1983). All such models share at least two fundamental similarities: (1) they are composed of similar sets of core variables that can be categorized as either “drivers” or response variables (i.e., of primary interest in restoration or management), and (2) all suggest that both positive and negative feedback loops are important in determining savanna structure and function.

We have attempted to represent the key drivers and responses in a general, simplified conceptual model that we believe applies to most African savannas (fig. 10.1). In this simple conceptual model, the nature of the effects (i.e., lines) are left unspecified and can take on a variety of shapes (linear versus nonlinear) and strengths (weak versus strong) and can be either positive or negative. In the following sections, we describe the various components of the model.

Response Variables

Management and restoration efforts in African savannas have focused largely on reducing bush encroachment or reversing desertification of rangeland habitats (Sinclair and Fryxell 1985; Smit 2004) and on reestablishing intact communities of large mammals, such as

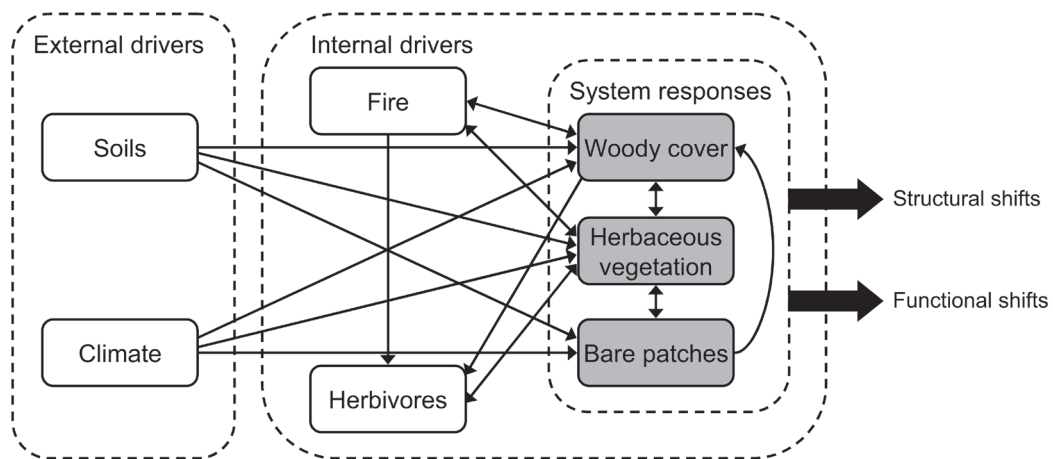


FIGURE 10.1. A generalized conceptual model of savanna function. Arrows connecting variables are assumed to represent the causal effect of one variable on another. Causal relationships can be unidirectional ($A \rightarrow B$) or reciprocal ($A \rightarrow B$ and $B \rightarrow A$). Relationships can be correlational rather than causal; such relationships are assumed to be the result of another, unmeasured variable and are represented with curved, double-headed arrows (none shown here). Soil and climate are typically considered external drivers and therefore not affected by the internal dynamics of the system over ecological time scales (i.e., soil parent material and mean annual rainfall). Fire and herbivory are typically considered internal driver variables, both controlling system responses and themselves influenced by external drivers. In many African savannas, human intervention has changed the internal nature of such variables (see text). Vegetation properties, also internal, are usually the responses of interest for purposes of management and restoration. Positive and negative feedbacks are generated by indirect paths connecting variables ($A \rightarrow B \rightarrow C \rightarrow A$). System responses can be structural, such as a change from herbaceous to woody cover, or functional, such as in the conversion of vegetated patches to bare soil. Note that structural shifts are often accompanied by shifts in functional properties.

ungulate herbivores and their canid and felid predators, for the purposes of conservation, tourism, or game ranching (Treydte et al. 2006). Accordingly, we restrict our discussion here to response variables of relevance to these efforts. We concentrate largely on the dynamic responses of vegetation properties (fig. 10.1), such as the biomass, or cover, of woody compared to herbaceous plant species; the relative proportion of vegetated versus bare patches; and quantity and quality of herbaceous forage available to domestic or wild herbivores in African rangelands but also discuss the restoration of native animal communities given their importance to African conservation efforts (Hudson et al. 1989; Scholes and Walker 1993; Treydte et al. 2006).

Driver Variables

Climate, fire, and herbivory are considered to be the major drivers of savanna structure and function (fig. 10.1; Frost et al. 1986; Scholes and Walker 1993; Scholes and Archer 1997; Sankaran et al. 2004). Of these, climate is often considered the primary determinant of African savanna structure and function, while fire and herbivory are generally regarded as modifiers of the savanna state (Sankaran et al. 2004). In addition, soil properties are also thought to have major regulatory influences on savanna dynamics because they constrain the effects of different drivers (Frost et al. 1986; Scholes and Walker 1993; Scholes and Archer 1997).

Rainfall is widely considered the primary factor determining the distribution and functioning of tropical savannas, setting limits to the aboveground biomass that can be supported at any given site (Scholes and Walker 1993; Sankaran et al. 2005). Rainfall in many African savannas is highly variable in space and time, often occurring as large, unpredictable events, especially in the dry season (McNaughton 1985; Ellis and Swift 1988). Thus, rainfall variability, both interannual and intraseasonal, and dry season length are as influential as total annual precipitation in modulating savanna dynamics, with potentially significant implications for restoration efforts in these systems (Holmgren and Scheffer 2001; Holmgren, this volume).

Soil texture and fertility also play critical roles in defining savanna structure and function (Frost et al. 1986; Scholes and Archer 1997). Soil texture is important because it modifies plant-available water (i.e., soil water potential) and nutrient retention (Frost et al. 1986; Scholes and Archer 1997). The effects of soil nutrient availability, which often co-varies with texture, derives largely from its effects on vegetation quantity and quality and corresponding levels of herbivory. Soil fertility may also have direct effects on the tree–grass balance by regulating the competitive abilities of woody and herbaceous species, with grasses favored over woody shrubs under conditions of high nitrogen availability (Davis et al. 1999; Kraaij and Ward 2006).

Fire and herbivory have also played important historical and evolutionary roles in shaping African savannas by influencing the morphological and physiological traits of savanna vegetation (Stebbins 1981; Coughenour 1985; Bond and van Wilgen 1996). Although both remove aboveground components of plants and in this sense “compete” for biomass (Bond and Keeley 2005), they have different effects on savanna vegetation. Fire can be considered a “generalist herbivore” (Bond and Keeley 2005), consuming virtually any plant material given appropriate conditions. For obvious reasons, fire tends to remove biomass during the dry sea-

son, when plants are in a mature phenological and physiological state. Fire is often associated with shifts in woody cover because tree seedlings and saplings are especially vulnerable to fires even at low to moderate fire frequency and intensity. Fires also influence plant nutrient availability because they tend to volatilize nitrogen, carbon and sulfur, and, to a lesser degree, phosphorus and potassium (Frost and Robertson 1987). The effects of fire or its elimination from a system will depend largely on the historical fire regime and the fire tolerance and resprouting abilities of the species present (Hiesler et al. 2004; Briggs et al. 2005).

In contrast, herbivory can be selective or general in space and time. Selectivity can occur among individuals when herbivores select palatable over unpalatable species or within an individual when herbivores select different plant tissues (Augustine and McNaughton 1998). Selectivity also occurs with respect to plant functional type because grazers, browsers, and mixed feeders have diets that differ in woody and herbaceous components. In ecosystems dominated by native ungulates, herbivory often occurs in pulses synchronized with periods of elevated plant growth rates and tissue nutrient concentrations (McNaughton 1990). However, plant consumption in domestic livestock systems tends to be more chronic and less variable in time and space. Like fire, herbivory can influence rates of nutrient cycling and decomposition (McNaughton 1988; McNaughton et al. 1997). Fire and herbivory are, however, not mutually exclusive events (Hobbs et al. 1991; Hobbs 1996), each influencing the occurrence probabilities and characteristics of the other. By reducing plant standing crop and thereby fuel load, herbivory can influence the frequency, intensity, and extent of fires (Frost and Robertson 1987; McNaughton 1992; Hobbs 1996). Conversely, fires can influence the nature and frequency of subsequent grazing events by impacting the quality of available forage for different-sized herbivores (Wilsey 1996).

Researchers have often tended to categorize different drivers of savanna structure as either being external (exogenous) or internal (endogenous) to the system (fig. 10.1). However, what is internal or external to the system is largely in the “eye of the beholder” and contingent on the spatial and temporal scales of inquiry. Further, variables that may be considered endogenous in some savannas may be treated as exogenous in others. As an example, fire and grazing may be considered endogenous variables in “natural” savannas that are largely devoid of human presence or activity. Yet when humans take control of managing when and where herbivores graze or fires occur, as in pastoral systems throughout Africa, these drivers (fires and grazing) are no longer under regulation of internal control by the system (Mayer and Rietkerk 2004).

Regime Shifts, Transitions, and Thresholds in African Savannas

Interactions and feedbacks between different savanna drivers results in the occurrence of a diverse array of savanna types across the African continent, spanning a range of structural and functional states (Scholes and Archer 1997; House et al. 2003). However, these “states” are not static properties of the system; rather, they represent the dynamic outcomes of interactions between different driver variables. In recent years, many African savannas appear to have undergone structural and functional transitions, some gradual and others abrupt, toward less productive or desirable states (United Nations Environment Programme [UNEP] 2002). Given the importance of savannas to human welfare and economy, identifying the

factors underlying these transitions and their attendant impacts on the provisioning of ecosystem services by these biomes is of obvious management concern.

In the following sections, we discuss three common transitions frequently observed in African savannas: transitions between grass and woody dominance, vegetated and bare states, and high and low grass biomass states. There has been considerable debate in the literature whether these observed transitions represent slow-moving transient dynamics characterized by gradual continuous models or whether they in fact represent “regime shifts” involving multiple stable states that require management interventions (Suding and Hobbs, this volume). Although the importance of multiple stable states is firmly established in the theoretical savanna literature and is supported by empirical evidence from some savanna ecosystems (Noy-Meir 1975; Walker et al. 1981; Westoby et al. 1989; Rietkerk et al. 1996; van de Koppel et al. 2002), their ubiquity in explaining the observed transitions in African savanna ecosystems and their importance to management remain debated (Illius and O’Connor 1999; Oba et al. 2000; Sullivan and Rohde 2002; Schröder et al. 2005; Ward 2005; Groffman et al. 2006). Given that African savannas are extremely diverse ecosystems, displaying substantial variation in both structure and function, identifying the environmental conditions under which different savannas are likely to display regime shifts characterized by threshold dynamics or, alternately, exhibit slow transient dynamics represents an important challenge facing savanna ecologists today.

Regime shifts, where they occur, are typically driven by changes in a driver, or “trigger,” and are initiated when the value of the trigger crosses a certain “threshold” level (Briske et al. 2006). Below this threshold, negative feedbacks between system components act to “absorb” changes in the trigger, thus preserving savanna structure and function. However, when the level of the trigger passes the threshold, it causes a reorganization of the internal relationships and a switch from the predominance of negative feedbacks to positive feedbacks that enable structural and functional shifts in the savanna (Briske et al. 2006). Commonly observed structural shifts in savannas include changes in the relative representation of woody versus herbaceous vegetation, cover of vegetated versus bare patches, and changes in species composition. These structural changes are, in turn, associated with functional shifts in savanna ecosystem processes, such as changes in hydrology, nutrient cycling, and primary production (Briske et al. 2006).

Regime Shifts between Open and Woody Vegetated States

Over the past several decades, evidence has accumulated suggesting that many of the world’s savannas are showing a trend of increasing woody cover or “bush encroachment” (Archer 1995; Smit 2004; Ward 2005). Bush encroachment is associated with an increase in unpalatable woody species at the expense of palatable grasses, often resulting in lowered livestock carrying capacity, survival rates, calving rates, and milk production (Oba et al. 2000). The problem is particularly acute in southern Africa, where bush encroachment has drastically reduced the grazing capacity of vast tracts of savannas to the extent that many ranching and livestock production areas that were once profitable are now no longer considered economically viable (Milton and Dean 1995, Smit 2004).

Despite decades of research, the phenomenon of bush encroachment is still not well understood (Smit 2004; Ward 2005). Overgrazing, fire suppression, browser population

declines, and climate change have all been implicated as causal agents in the transitions from open, grassy states to dense, wooded savannas. In the overgrazing scenario, woody establishment is promoted through herbivore dispersal of woody seeds and by grazer suppression of grass biomass, resulting in reduced grass competition and increased water availability for deep-rooted woody plants (Brown and Archer 1987; Archer 1995; Scholes and Archer 1997; Roques et al. 2001; Smit 2004). Attendant changes in fire regimes as a result of reduced grass-fuel loads further promotes woody dominance, eventually leading to a wooded savanna incapable of supporting frequent fires or high ungulate biomass. Bush encroachment has been linked to overgrazing in many savannas of southern and eastern Africa (van Vegten 1983; Skarpe 1990; Moleele and Perkins 1998; Tobler et al. 2003) but not in others (Ward 2005; Wiegand et al. 2005).

Fire suppression has likewise been argued to trigger a similar sequence of events leading to eventual woody dominance and loss of livestock production potential, even in the absence of overgrazing (Smit 2004; Briske et al. 2006). Bush encroachment in some African savannas, particularly within protected areas, has also been linked to reduced browsing pressure following ungulate population crashes (Dublin et al. 1990; Prins and van der Juegd 1993).

Altered precipitation regimes and elevated CO₂ levels have also been invoked as explanations for large-scale trends of bush encroachment in African savannas (Polley et al. 1997; Bond and Midgley 2000). In contrast to the previously described scenarios, bush encroachment in response to altered climate represents a gradual continuous change rather than a regime shift. Bush encroachment in the Limpopo province of South Africa is widespread and has occurred regardless of grazing history, strongly suggesting a large-scale environmental driver such as climate change (Smit and Rethman 1992). However, effects of smaller-scale drivers may be superimposed on larger-scale patterns, as evidenced by the greater rate of increase in heavily grazed areas (Smit and Rethman 1992).

Although theoretical models attest to the possibility of savannas existing in alternate stable states (open versus wooded), supporting empirical evidence for the same is equivocal. This is because the long life spans of woody species have thus far precluded determining whether the wooded state is self-sustaining and can persist for more than a single generation (Schröder et al. 2005). Ecologists have also argued that bush encroachment in arid and semiarid savannas is a natural phenomenon resulting from patch-dynamic processes (Ward 2005; Wiegand et al. 2005). Here, events lead to pulses of woody recruitment in different patches at different times, with the entire landscape consisting of patches in different degrees of transition between woody and grassy dominance (Ward 2005; Wiegand et al. 2005).

From a management perspective, identifying the ultimate trigger or combination of triggers responsible for bush encroachment in any given savanna is critical because it provides insights into whether the observed changes represent a gradual continuous transition (e.g., in response to climate change) or a regime shift (e.g., in response to overgrazing or fire suppression). It should be noted, however, that isolating the ultimate “trigger(s)” responsible for bush encroachment in any savanna is complicated by the fact that many “triggers” invariably act in concert (Oba et al. 2000). At present, such data are lacking for most African savannas. In addition, as noted earlier, the parameter space wherein savannas are likely to display regime shifts toward alternate stable states in response to different triggers remains unknown.

For savannas that are likely to display threshold dynamics, quantifying different components of thresholds (triggers, structural and functional) is of particular relevance to conservation and restoration efforts because it can provide an early warning of the need for management interventions to prevent or reverse “regime shifts.” A qualitative description of threshold characteristics is provided in table 10.1. However, quantitative data on trigger levels at which regime shifts are likely to be initiated are lacking for most African savannas. For example, little data are available on the specific grazing intensities at which any given savanna is likely to undergo a switch from an open to a wooded state and how this varies across broad environmental gradients. Because of time lags between structural shifts and changes in levels of triggers, the exceeding of a trigger threshold by itself does not imply an irreversible shift, and intervention may still reverse woody encroachment (Folke et al. 2004). For managers, the problem becomes acute once structural thresholds have been surpassed, such as when grass-fuel loads can no longer support fires capable of regulating the density and spatial distribution of woody vegetation through mortality (table 10.1).

Regardless of the actual trigger, common structural thresholds appear to exist for managing bush encroachment (table 10.1), linked to tree densities above which grass-fuel contiguity becomes insufficient to support frequent, intense fires. Even where bush encroachment represents a gradual directional change (e.g., in response to climate change) rather than a regime shift, fires can nevertheless serve as a management tool to maintain the savanna in an open state. Given this commonality, the monitoring of structural states represents the simplest option available for managers concerned with bush encroachment. In particular, the use of spatially explicit fire models that account for fire intensity, tree demographics, and fire behavior (Higgins et al. 2000; Liedloff and Cook 2007) might help identify tree densities above which fire management is unlikely to prove effective in countering bush encroachment. Managers must exercise caution, however, since fire can exacerbate bush encroachment in some cases by favoring the spread of exotic or fire-resistant species (Smit 2004). When fire is not an option, the long-lived nature of woody species implies that natural mortality is unlikely to occur within time frames of relevance for restoration efforts, necessitating the use of costly chemical or mechanical efforts to reduce tree densities (Smit 2004).

Regime Shifts between Vegetated and Bare-Soil States

Besides bush encroachment, the loss of savanna vegetation, or desertification, is also a major issue in African rangelands. United Nations experts recently called desertification “the greatest environmental challenge of our time,” affecting as many as 2 billion people, many in Africa (Adeel et al. 2006). The maintenance of high-quality grass forage is necessary to sustain many rural Africans that depend on domestic livestock; pastoral lands with managed domestic livestock account for >20% of the African continent (Fritz and Duncan 1994). Overgrazing of rural lands has been blamed for the degradation of savanna throughout the continent (UNEP 2002, 2007). A cycle of grazing, vegetation loss, soil erosion, and eventual vegetation collapse has been documented in several arid regions (Bremen and de Wit 1983; Sinclair and Fryxell 1985; Milton and Dean 1995; Rietkerk et al. 1996).

As a result, research developed to understand what triggers desertification in savannas (Rietkerk et al. 1996). Theoretical models suggest that in arid and semiarid areas, vegetation

TABLE 10.1.
Threshold characteristics associated with different regime shifts in African savannas.

Transition	Trigger	Threshold	Structural Aspects of Threshold
Grassy to woody	Overgrazing	Off-take levels above which the ability of grasses to compensate for tissue removal is impaired	Density and spatial distribution of woody vegetation in savanna above which the amount and contiguity of grass-fuel loads in the system are insufficient to support fires of the necessary intensity and frequency to suppress woody establishment
	Fire suppression	Fire-return interval is long enough for seedlings to establish and grow to a fire-resistant size	
	Browser and mixed-feeder population declines	Densities below which browsers are incapable of effectively suppressing woody seedling establishment and growth to a fire-resistant size	
Vegetated to bare soil		Patch scale: biomass removal above which the ability of grasses to compensate for tissue removal is impaired	Reduction of plant standing crop to levels where surface runoff increases and infiltration into soils decreases below sustainable levels, which in turn is contingent on site rainfall and soil characteristics
	Overgrazing	Systemwide scale: as above plus redirection of herbivores to remaining patches	Area of vegetated relative to bare patches in the landscape below which increased off-take levels in vegetated patches becomes unsustainable; function of rainfall, soil characteristics, herbivore biomass, mobility, and selectivity

continued

TABLE 10.1.
Threshold characteristics associated with different regime shifts in African savannas, continued.

Transition	Trigger	Threshold	Structural Aspects of Threshold
High-biomass to low-biomass states	<p>Decline in herbivore population densities</p> <p>Human activities associated with pastoral practices</p>	<p>Reduction of grazing to levels insufficient to suppress dominant light competitors</p> <p>Inputs of nutrients and organic matter to soils that favor the growth of high-quality lawn grasses</p>	<p>Stand biomass levels and/or ratio of unpalatable to palatable biomass levels above which herbivory is discouraged</p> <p>Quality of forage in patch relative to matrix above which herbivore selectivity, nutrient inputs to patches, and stimulation of nutrient cycling in patches is sufficient to maintain patches in an elevated nutrient state; thresholds are likely to be contingent on matrix fertility; probability of fires, which can alter matrix forage nutrient status; and herbivore behavior, such as the use of low-biomass patches as an antipredator strategy</p>

can exist in a two-phase mosaic consisting of vegetated and bare-soil patches, each representing an alternate stable state (Rietkerk et al. 1997; Rietkerk and van de Koppel 1997; van de Koppel et al. 1997). The argument underlying these models is that interactions between plant density and water infiltration (or soil resources) control regime shifts from vegetated to bare states (Rietkerk et al. 1997; van de Koppel et al. 1997; table 10.1). Reductions in plant density can result in increased runoff of rainwater, lower water infiltration into soils, and increased loss of nutrients via soil erosion. Factors such as grazing can trigger local vegetation collapse by reducing plant density below a threshold level necessary to regrow under limited resources (nutrients or water). Impaired recruitment in bare patches due to low water availability, harsher temperatures, and soil capping or crusting can result in the persistence of bare patches in the habitat (Rietkerk and van de Koppel 1997).

The previous scenario accounts for the origin of bare patches on small scales but not systemwide vegetation collapse. An additional model that incorporates water redistribution as runoff and more complex grazer responses attempts to account for the coarse scale vegetation decline observed in arid African grazing systems (van de Koppel et al. 2002). The model assumes that surface water runoff from bare patches supplies water to surrounding vegetated patches. Remaining vegetated patches experience enhanced plant growth because of increased water and infiltration as surrounding patches are eliminated, creating a feedback that further enhances growth in vegetated patches and vegetation loss in bare patches. However, as grazers are increasingly redistributed to the vegetated patches, it can lead to an eventual systemwide vegetation collapse as grazers remove more biomass from fewer vegetated patches.

Crucial assumptions underlie these models. For example, as herbivory increases, so too does the minimum requirement of resources (water or nutrients) necessary to sustain plant growth. This assumption can be violated in two important ways: first, when herbivory causes the replacement of species with a lower minimum nutrient requirement and, second, when herbivores increase nutrient inputs. We suggest that the degree to which these assumptions are violated is related to the adaptation of plant species to grazing at a particular site (Milchunas et al. 1988) and the magnitude of novel disturbances (e.g., climate change, exotic species). For example, in a study conducted in the Serengeti, in which vegetation in fenced and unfenced plots was completely excavated at sites differing in rainfall, plots were observed to return to their original biomass and species composition within five years regardless of grazing treatment or severity of disturbance (Belsky 1986). Consistent with our suggestions, the results were attributed to the lack of exotic species, the capacity for vegetative reproduction in the native species, and the evolutionary adaptation of species to significant disturbance (Belsky 1986).

Although observations from some African savannas document the presence of bare and vegetated patches that seem to be consistent with theory (Rietkerk et al. 2000; Augustine 2003b), these need not necessarily always represent alternate stable states. Two-phase mosaics in the Serengeti have been observed to disappear with the exclusion of large herbivores (McNaughton 1983; Belsky 1986; Rietkerk and van de Koppel 1997). Such responses are likely related to the characteristics of the resident plant species, the nature of the resource limiting plant growth, and the potential for runoff dynamics in the underlying soils (Rietkerk et al. 1997; Bestelmeyer et al. 2006). Theoretical models predict that vegetation collapse and

regime shifts are more likely to occur on clay soils when plant growth is water limited and on sandy soils when plant growth is nutrient limited (Rietkerk et al. 1997).

Transitions between High and Low Grass Biomass States

Some savannas can show transitions between states of low grass biomass characterized by high levels of herbivory and high grass biomass states with low levels of herbivory (table 10.1). Apparently, the potential for the occurrence of these states is a function of the interaction between site productivity and herbivore body size distributions (van de Koppel et al. 1996; Ritchie and Olff 1999; Sankaran and McNaughton 2005). Theory predicts that in areas of intermediate productivity dominated by small herbivores, the plant–herbivore system can either exist in a state where herbivores maintain a low standing crop or be characterized by dense vegetation unsuitable for herbivores (van de Koppel et al. 1996). Such dynamics result from a decrease in foraging efficiency of herbivores with increasing plant standing crop and the inability of small-bodied herbivores to tolerate low-quality forage (van de Koppel et al. 1996; Ritchie and Olff 1999). When herbivore numbers are high, vegetation is maintained at low standing biomass. However, reduction of grazing can trigger a shift to a high plant biomass state unsuitable for small-bodied herbivores. Given the foraging constraints of small-bodied herbivores, the vegetation can remain poorly utilized even following herbivore reintroduction. Reversal of trends in such cases would require an additional driver such as fire. Although theoretically possible in African savannas, evidence for such transitions comes largely from temperate systems with small herbivores, such as geese (Bazely and Jeffries 1986; van de Koppel et al. 1996; van der Wal et al. 1998; Person et al. 2003).

In more productive areas, shifts between low and high grass biomass states are controlled mainly by large-bodied herbivores (Ritchie and Olff 1999). Plant competition in these areas is primarily for light, and as a result dominant plants are tall, of low nutritional quality, and utilized mostly by large-bodied herbivores (Ritchie and Olff 1999). Large-bodied herbivores can reduce the dominance of good light competitors, facilitating the coexistence of high-quality subdominant plants and selective, small-bodied herbivores. A loss of large-bodied herbivores induces the dominance of tall unpalatable grasses and corresponding reductions in small herbivores (Ritchie and Olff 1999). Because even large-bodied herbivores preferentially feed on high-quality forage, reintroducing them following removals might not cause the system to revert to a palatable, low grass biomass state without an additional factor such as fire. Evidence for unpalatable tallgrass dominance following the exclusion of bulk-feeding herbivores comes from the Ngorongoro crater in Tanzania, where removal of pastoralists and their livestock caused a switch toward a coarser sward with less palatable species and declines in the densities of native herbivores (Runyoro et al. 1995).

High and low grass biomass states are typical on and around so-called herbivore hot spots (sensu McNaughton and Banyikwa 1995)—dense patches of ungulates that punctuate regions otherwise devoid of herbivores. Hot spots are often associated with heavily grazed, prostrate grasses forming densely packed “grazing lawns” (sensu McNaughton 1984) that are maintained by herbivory and can be stable for decades. In the Serengeti, underlying soil differences were ruled out as a cause for hot-spot formation because total soil nutrient concentrations were similar between lawns and adjacent high biomass areas (McNaughton

1988), leading to speculations that they may represent alternate states brought on by some set of threshold behaviors.

Another explanation is that an episodic event, such as a fire followed by heavy rains, creates optimum foraging conditions in a patch that is then fertilized by ungulates through urine and dung deposition. Nutrient inputs, coupled with suppression of tall-statured grasses and shifts in the soil microbial community, push the system toward a new state of higher nutrient mineralization and forage nutritive quality. In a similar fashion, long-term grazing lawns in many East African savannas appear to be the result of traditional pastoral practices that involve enclosing large numbers of cattle inside fenced “bomas” as protection from predators (Reid and Ellis 1995; Augustine 2003a). The high animal densities result in enormous nutrient inputs to bomas, which, following abandonment, support a dense lawn of high-quality grass stable for more than 40 years (Reid and Ellis 1995; Augustine 2003b). Wild herbivores occupy the lawns postabandonment and maintain them in a low-biomass state, even importing nutrients from the surrounding habitat (Augustine et al. 2003). The importance of such patches can be far greater than their extent in the landscape, potentially serving to enhance herbivore carrying capacity at larger scales by providing key areas where herbivores can meet their nutritional requirements (Augustine 2003a). However, the factors that enable hot-spot formation and maintenance, while highly germane to animal conservation in African savannas, remain unclear.

A Multivariate Perspective of Woody Cover in African Savannas

Theoretical explorations of threshold dynamics and regime shifts in savanna ecosystems have witnessed significant advances in recent years, but empirical evidence for the same has lagged behind. In large part, this is because identifying and characterizing threshold behavior in these systems, particularly in terms of bush encroachment, is difficult given the long-lived nature of savanna trees. Despite a substantial body of research on the effects of different drivers on savanna structure and function, we still lack an integrated understanding of the environmental conditions under which different savannas are likely to display threshold behaviors and how different drivers interact to influence threshold dynamics in any given savanna.

Ultimately, African savannas are diverse ecosystems the structure and function of which are regulated by a suite of interacting drivers. Effective understanding and management these biomes is best achieved through the use of synthetic, multivariate studies that are spatially and temporally extensive and that span a range of variation in driver variables. For example, a recent spatially extensive continental scale analysis of woody cover in African savannas, consisting of nearly 850 sites across the continent, documented an upper bound in woody cover in savannas that receive between 150 and 650 mm mean annual precipitation (fig. 10.2). Within this rainfall range, maximum realizable woody cover increases linearly with rainfall but appears unrelated to other variables, such as fire frequency, levels of herbivory, soil texture, or soil nutrients (Sankaran et al. 2005). The existence of an upper bound on woody cover suggests that bush encroachment in these arid and semiarid savannas, regardless of whether they result from threshold behaviors or represent gradual continuous change in response to environmental drivers, might in fact be a bounded process, ultimately limited

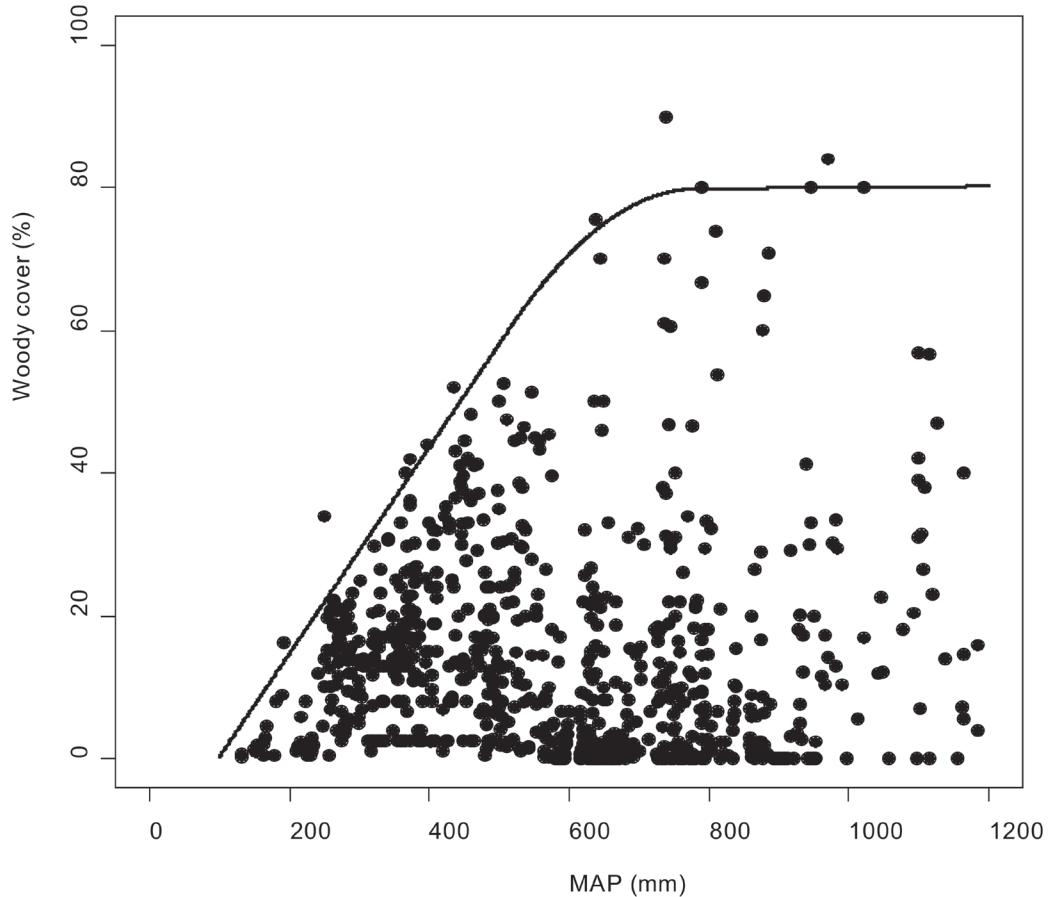


FIGURE 10.2. Relationships between woody cover and mean annual rainfall (MAP) in African savannas. These data from 852 sites suggest an upper bound to tree cover in sites with 150–650 mm MAP. The fitted line represents the 99th quantile based on a piecewise linear regression model. Maximum potential tree cover is attained at approximately 650 mm MAP, while trees are excluded below 101 mm MAP. The line quantifying the upper bound on tree cover between 101 and 650 mm MAP is $\text{Cover (\%)} = 0.14 (\text{MAP}) - 14.2$. Reproduced with permission from Sankaran et al. (2005).

by water availability (Sankaran et al. 2005). For sites close to or at the climatic bound, global change factors such as altered precipitation regimes and increased atmospheric CO_2 concentrations, rather than overgrazing, may be the primary factors of concern with respect to bush encroachment. Nevertheless, bush encroachment still remains a concern in most savannas, as even modest increases in bush cover can have significant economic impacts. For East African systems, it has been estimated that a 10% increase in shrub cover can reduce grazing by 7%, with bush cover becoming a problem when it exceeds 30% (Oba et al. 2000).

At present, it is unclear if savanna sites below the climatic envelope (fig. 10.2) are stable end points in the multidimensional axes of rainfall, geomorphology, and disturbances or if they merely represent sites in “transition” where woody cover is prevented for attaining its climatic potential because of the frequent leveling impacts of disturbances such as fires

and browsing. The fact that that different savanna sites occupy more or less the entire state space beneath the climatic envelope (fig. 10.2) suggests that African savannas can exist in a wide range of structural states at any given rainfall level, highlighting the need for more detailed site-specific studies, both observational and experimental, to determine which of these savannas, if any, are characterized by threshold dynamics. Further, it reinforces the need for a more multivariate view of the dynamics of African savannas, as suggested by earlier conceptual models (McNaughton 1983; Scholes and Walker 1993; Venter et al. 2003). As an example of what such a view would look like, we conducted a partial reanalysis of a subset of data from Sankaran et al. (2005) using structural equation modeling (SEM), an analytical technique that combines the familiar approaches of regression, path analysis, and factor analysis in a framework that evaluates a system of interacting variables in one analysis (Grace 2006). Results of the SEM are displayed in figure 10.3. Interestingly, fire-return interval was the single most important variable associated with realized woody cover in sites, consistent with our observations (table 10.1) that changes in fire frequency seems to be the dominant feedback regulating woody encroachment in savannas. Other factors exert effects on woody cover but largely via their indirect effects on fire-return interval, suggesting that fire manipulation might provide a particularly effective and convenient option for managers interested in manipulating savanna woody cover. A more exhaustive analysis that additionally considers other factors, such as herbaceous biomass, measures of fire severity, and so on, will no doubt allow for better predictive and forecasting capabilities.

Management Implications

Regime shifts, when they occur, are expensive and slow to revert and come at significant ecological and economical costs. More often than not, regime shifts in African savannas seem to occur when humans manipulate fire and grazing regimes directly and decouple them from internal control of system. An important consideration for the management and restoration of African savannas is that historical conditions of fire and herbivory were likely very different from the conditions under which African savannas are managed today. Because protected areas restrict the movement of wild ungulates (Boone et al. 2006), they create regions of human wildlife conflict (Sitati et al. 2003) and are subjected to higher fire frequencies than historically occurred (van Wilgen et al. 2004). Fire and grazing are now manipulated and intensified in ways that enhance feedback loops that can, in theory, create system instabilities that result directly from human management decisions. On the other hand, the ability to manipulate these forces provides managers with powerful tools to alter the trajectory of vegetation development, especially if thresholds are a property of the system of interest. Interventions, where needed, must be designed taking into account the broader canvas of environmental conditions, both past and present, prevailing at the site. It has been suggested that managers can take advantage of the high rainfall resulting from the El Niño Southern Oscillation to maximize restoration efforts and facilitate regime shifts, given appropriate prediction and response capabilities (Holmgren and Scheffer 2001). Furthermore, it is critical that restoration efforts in African savannas be based on a holistic view of these ecosystems, with the objective of restoring multifunctionality of ecosystem services rather than focusing on a single response variable (Smit 2004).

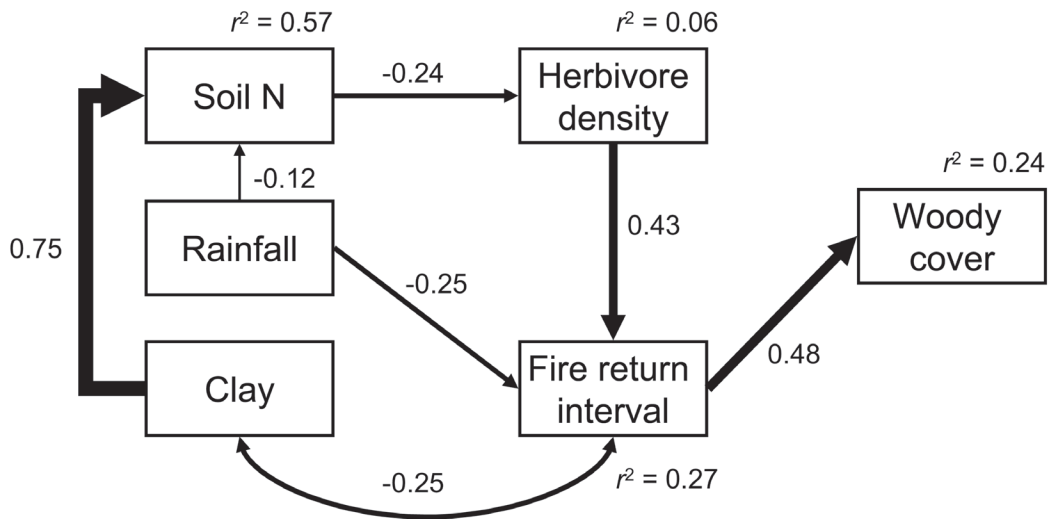


FIGURE 10.3. Final structural equation model (SEM) predicting percent of woody cover in African savannas. The data, from Sankaran et al. (2005), represented savanna sites across Africa ($n = 161$) and included measures of exogenous (climate and soil) and endogenous (herbivore numbers and fire return interval) drivers and vegetation responses (woody cover). The a priori model matched the generalized conceptual model of African savannas from figure 10.1 and was estimated with the SEM software AMOS (version 5.0). The analysis yielded a good fit between the model and observed data ($\chi^2 = 6.26$; $P = 0.62$; $df = 8$) but explained a relatively modest amount of the total variation in woody cover ($r^2 = 0.24$). Note that when the evaluating model fits a low χ^2 (and high P -value), it indicates no significant difference between model and observed data. Paths included in figure 10.1 but not in the final SE model were either not testable with the available data or not statistically significant at $\alpha = 0.05$. Fire return interval emerges as the single variable associated with woody cover; other factors exert effects on woody cover but only indirectly via their effects on fire return interval. The double-headed arrow between clay and fire return interval represents an unspecified correlation, while all other single-headed arrows imply direct effects. This exercise was intended to illustrate how an analytical model can evaluate multivariate conceptual models of savanna structure and function (i.e., fig. 10.1) rather than yield an exhaustive analysis of woody cover in African savannas.

Conclusions

In summary, savanna restoration will ultimately represent a long-term commitment rather than a one-off event (Smit 2004). In this regard, it would appear that prevention is definitely better than the cure. In particular, recent economic models of rangelands suggest that the optimal strategy from the perspective of long-term sustainability is to manage savannas conservatively, stocking the system at low levels and using fire to control tree–grass ratios (Higgins et al. 2007). In fact, the models also suggest that the need to manage more conservatively increases in systems that are more stochastic (Higgins et al. 2007). Moreover, for those analyzing data relevant to African savanna management, we advocate a multivariate perspective and a “systems” view of interacting processes (Grace 2006). Finally, we agree with Briske et al. (2005) that, in savanna ecosystems, sound management theory should consider both thresholds and continuous dynamics and responsible management practice regard both reversible and irreversible vegetation dynamics.

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