New Perspectives on Sustainable Grazing Management in Arid Zones of Sub-Saharan Africa

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Rangelands of sub-Saharan Africa have undergone dramatic changes in terms of development policy and land degradation during the past three decades (Behnke et al. 1993, Scoones 1994, Niamir-Fuller 1995). Between the 1960s and the 1980s, international donor communities and agencies (e.g., Western donor countries, US Agency for International Development, the World Bank, United Nations Food and Agriculture Organization, and international nongovernmental organizations) invested millions of dollars into range and livestock projects in the arid zones of sub-Saharan Africa for three reasons: to improve livestock production after droughts of the 1960s and the 1970s; to improve the economies of the sub-Saharan countries by putting in infrastructure and developing water for livestock use, increasing veterinary services, settling nomads, and imposing systems of grazing based on the experiences of commercial ranching, especially in the United States and Australia; and to strengthen the pastoral economy and reverse land degradation linked to overgrazing problems of the Sahelian rangelands (Sinclair and Fryxell 1985).

Despite the millions of dollars that have been invested in rangeland development projects during the last three decades, grazing projects in the arid zones of sub-Saharan Africa have generally been a failure, leading major donors to either scale down their involvement or withdraw entirely from the drylands of Africa. But the projects, by changing traditional patterns of land use, weakened the indigenous pastoral production system, thus creating a cycle of economic decline and land degradation. The failed projects, land degradation, recurrent drought, and donor withdrawal from development projects in the drylands of sub-Saharan Africa created a syndrome that has been termed a "pastoral crisis" (Scoones 1994, Niamir-Fuller 1995).

The rangeland development projects failed because they are based on four assumptions perpetuated by ecological models that appear to be inappropriate for sub-Saharan Africa (Ellis and Swift 1988): that changes in grazing systems and in patterns of pastoralist land use will improve range production; that if grazing is rotated by developing water in specific areas of the range, degradation will be reversed; that long-term grazing exclusion will reverse range degradation; and that sub-Saharan pastoralists have traditionally maintained more livestock than can be supported by the range (Breman and de Wit 1983). Indeed, it

A NEW PERSPECTIVE ON INTERACTIONS AMONG CLIMATE, PLANTS, AND HERBIVORY SUGGESTS THAT RANGELANDS INFLUENCED BY HIGHLY STOCHASTIC WEATHER AND GRAZING DISTURBANCE ARE DEGRADED, NOT BY CONTINUOUS GRAZING, BUT RATHER BY THE LONG-TERM ABSENCE OF GRAZING.

has been suggested, especially following the Sahelian droughts of the 1960s, the 1970s, and the 1980s, that high livestock mortality resulted from increased livestock density (Sinclair and Fryxell 1985).

These assumptions about sub-Saharan Africa arise from the prevailing equilibrium view of rangelands, which was originally developed for wet environments. According to this view, if rangelands are stocked at greater than carrying capacity (i.e., if the number of stock exceeds available forage), then grazing-induced degradation will occur (Lamprey 1983, Sinclair and Fryxell 1985, Milton et al. 1994). Range degradation due to grazing has been defined in various ways: as a progressive process leading to reduced grass cover, soil compaction, and loss of woody cover (Lamprey 1981); as a progressive loss of grasses followed by bush encroachment (Bosch and Theunissen 1992); as a temporary or permanent change in plant density and composition (Grainger 1992); and as a change leading to perma-

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nent economic losses (Abel and Blaike 1989). Thomas and Middleton (1994) have suggested that degradation leads to desertification, which they defined as the "creation of desert-like conditions" that are irreversible except through massive technical and capital investments.

Grazing programs based on assumptions from equilibrium systems have failed in arid zones in general, and in sub-Saharan Africa in particular, because these assumptions do not apply to plant production patterns and land use in these regions. Grazing exclusion and unplanned water establishment alter traditional land-use patterns and have severe environmental consequences because they induce desertification and create food scarcity for livestock (Sinclair and Fryxell 1985, Ellis and Swift 1988, Dodd 1994). Contrary to the equilibrium view of most grazing programs, pastoralists' traditional land use is appropriate from environmental and management points of view. First, pastoral systems of land use involve a high degree of opportunism to cope with unpredictable rainfall and highly fluctuating forage distribution (Ellis and Swift 1988, Dodd 1994). Livestock mobility relieves areas of concentration and allows herds to exploit grazing resources that are unevenly distributed in time and space. Second, a strategy of managing multiple livestock species—sheep, cattle (grazers), goats, and camels (browsers)—allows optimal use of these highly variable grazing resources (Figure 1). Third, pastoral management strategies are aimed at exploiting multiple vegetation states at a landscape level.

These approaches to land use are similar to those recommended by non-equilibrium grazing models, such as those incorporating multiple states and thresholds (Friedel 1991), state-and-transition (Westoby et al. 1989), and rangeland health (NRC 1994). An assumption underlying all non-equilibrium models is that plant production dynamics in arid zones are influenced more by rainfall than by grazing. Consequently, these models neglect the important role of herbivory and do not treat herbivory and climate as interacting ecological processes. These models, like equilibrium models, therefore fail to fully capture the processes that occur on arid rangelands.

In this article, we present new perspectives on arid rangeland dynamics, focusing on a conceptual model for interactions among climate, plants, and herbivory. This model predicts that in arid zones, interactions between rainfall, plants, and grazing explain the responses of plants to grazing better than grazing or rainfall alone (i.e., better than state-and-transition or rangeland health models). We also offer empirical evidence in support of this model. In contrast to the equilibrium view, the climate–plant–herbivory interaction model predicts that the removal of grazers (e.g., both domestic and wild ungulates) will not improve range production or range condition (i.e., range health, as described by NRC 1994) in the long term (i.e., greater than 5 years). Rather, an extended lack of grazing may result in the accumulation of "old" vegetation, a

decline in live plant cover, the loss of species diversity, and reduced plant production. Our model also suggests that some plant species in arid environments require regular grazing. Arid rangeland plants that are grazed continuously may have lower residual biomass and ground cover, but they may also have greater production and better survival than ungrazed plants. Consequently, grazing, rather than being destructive, is necessary for proper management of arid zone pastures.

To put our overview in perspective, it is necessary to clarify some specific definitions at the outset. We use the term "grazing exclusion" to refer to long-term removal of grazing animals from the range (which has been done in the hope of reversing range degradation) and the term "grazing strategies" to refer to the way land is used in indigenous grazing. Although livestock grazing movement is seasonally regulated in traditional grazing systems, total exclusion is absent. Thus, when we refer to grazing exclusion we imply a deferred grazing system (as in equilibrium grazing models), in which some areas are left ungrazed for long periods of time (at least 5 years). We use the terms "grazing models" to refer to relationships between theoretical concepts (such as succession and state-and-transition) and actual land use (e.g., grazing). Equilibrium grazing models describe management techniques in which stocking rates and carrying capacity are established to match vegetation change, whereas non-equilibrium grazing models describe opportunistic land-use strategies in response to unpredictable disturbance (e.g., climate, fire, and grazing) and resulting changes in forage production.

Sub-Saharan grazing lands

Sub-Saharan Africa is predominately arid and semi-arid (Le Houérou 1989). The region south of the Sahara is tropical, whereas the northern- and southernmost tips of Africa are Mediterranean (Ellis and Galvin 1994). Eastern Africa receives bimodal rainfall—that is, rainfall occurs from April to June and from October to November, whereas West Africa and the Sudano–Sahel zone receive rainfall during the hot summers. Rainfall in the Sahel and West Africa is influenced by the Inter-Tropical Convergence Zone, which is associated with tropical atmospheric pressure systems (Nicholson et al. 1990). In eastern and southern Africa, rainfall is influenced by trade winds from the Indian Ocean and by weather patterns associated with sea surface temperatures and the El Niño Southern Oscillation (Ellis and Galvin 1994). The Mediterranean regions receive rainfall during the winter months, whereas the summers are dry (Figueroa and Davy 1991). Multi-year droughts are frequent in the Sahel, lasting from a few years to a decade (Ellis and Galvin 1994, Turner 1998).

The rangelands of the Sudano–Sahel and West Africa are dominated by annuals and dwarf shrubs, but perennial grasses may occur in depressions, where soil moisture is high (Breman and de Wit 1983). In the drier zones of East Africa, annuals and dwarf shrubs account for a greater

Equilibrium system	Non-equilibrium system
Ecological implications	
Climate stability	Climatic variability
Predictable primary productivity	Variable primary productivity
Livestock population controlled by density-dependent factors	Livestock population controlled by density-independent factors
Change in stocking density creates predictable changes in plant composition	Livestock track unpredictable forage production
Potential carrying capacity can be predicted and stocking density can be regulated according to potential carrying capacity	Prediction of potential carrying capacity not useful; uncertainties dominate future events
Management implications	
Management oriented toward a single species of livestock	Management of multispecies herds: sheep, goats, camels, cattle, and donkeys
Conventional range management appropriate	Opportunistic land use more suited
Grazing can be ascribed to planned systems	Grazing follows opportunistic strategies; mobility is an adaptive strategy
Strict regulation of stocking rates	Opportunistic stocking
Resources secure from land reforms	Resources have user rights
Land has collateral value	Resources lack collateral value
Clementsian succession and other equilibrium models suited	State-and-transition and the climate–plant–herbivory interactive models apply
Development implications	
Economic goals are commercial	Mostly subsistence economy
Management goals may be influenced by market	May be averse to market forces
Benefits are in financial terms	Benefits are in reproductive capital

Table 1. Distinguishing characteristics of equilibrium and non-equilibrium ecosystems.

proportion of the diet of the nomadic pastoralists' livestock than perennial grasses (Coughenour et al. 1990). The vegetation of southern Africa is mostly savanna, whereas in the Mediterranean zones, annual grasses and trees are important components (Le Houérou 1989). Indigenous land use in arid zones of sub-Saharan Africa is mostly grazing by livestock of nomadic and agro-pastoralists. In West Africa, indigenous transhumant grazing follows a centuries-old grazing route northward to the borders of the Sahara Desert and southward to the moist savanna during the wet and dry seasons, respectively (Turner 1998). In East Africa, indigenous grazers often move between key resources, such as mountain pastures, during the dry season, whereas in the wet season the population disperses over wide areas (Lusigi and Glaser 1984). These indigenous grazing systems have largely been replaced throughout sub-Saharan Africa with grazing systems that are appropriate for equilibrium systems.

Grazing models

Equilibrium (based on range succession) and non-equilibrium grazing models (e.g., state-and-transition, rangeland health, and climate–plant–herbivory models) have influenced rangeland policy and management worldwide. The two types of models differ in their characterization of range ecology, grazing systems, and development (Table 1). Although the distinction between them is not always clear (Scoones 1994), they form two ends of a gradient. Non-equilibrium ecosystems are predominant in arid zones, whereas equilibrium ecosystems tend to exist in moist environments. Equilibrium systems function through negative feedback, whereas non-equilibrium systems are highly fluctuating in response to disturbances such as grazing, fire, and drought (Walker 1993).

In equilibrium systems, successive years with favorable rainfall lead to progressive increases in livestock density until their numbers "overrun" forage production in subsequent years of below-average rainfall and they crash (Noy-Meir 1973, Lamprey 1981). For example, Van de Koppel et al. (1997), using catastrophic vegetation modeling (which may be considered an equilibrium grazing model, provided that the catastrophes do not occur too frequently), suggested that grazer density in the Sahel would continue to increase even as plant availability declined, thereby contributing to irreversible vegetation destruction. In non-equilibrium systems, by contrast, fluctuating forage production in response to variable rainfall creates corresponding fluctuations in animal numbers (Ellis and Swift 1988). Drought accentuates declines in forage quantity and quality and reduces forage availability. As forage becomes scarce, the body conditions of the animals decline and their numbers plummet before plants are overrun (Scoones 1994).

Equilibrium grazing models. In equilibrium grazing systems, managers aim to stock the range below carrying capacity (Heady and Child 1994). Stocking rates usually refer to the ability of graminoids to support cattle (Walker 1993). Range ecologists often consider perennial grasslands to be desirable for both grazing and conservation, whereas annuals, forbs, dwarf shrubs, and trees are less valuable. In equilibrium systems, grazing is planned

according to stages of range succession and condition, in which the vegetation improves as a result of management, changing from poor to excellent condition (Westoby et al. 1989, Milton et al. 1994). Therefore, the goal of range managers is to sustain a vegetation composition that is dominated by perennial grasses while minimizing invasion by less desirable species. Shifts in plant species composition from poor to excellent range conditions reflect this change: A grazing-desirable species becomes a decreaser (i.e., a species that decreases with grazing pressure), which is then replaced by an undesirable increaser (i.e., a species that increases with grazing pressure) or an invader (i.e., a species that is rare under low grazing pressure but becomes predominant with heavy grazing; Heady and Child 1994). Using the increaser, decreaser, and invader criteria, range managers maintain grazing at or near range conditions characterized by an abundance of decreaser plant species (Westoby et al. 1989).

Application of this mainstream equilibrium grazing model in arid zones in general, and sub-Saharan Africa in particular, has been criticized on several grounds. First, in rangelands where multiple species of livestock (e.g., cows, camels, goats, sheep, and donkeys) are managed, each with different forage requirements (i.e., browsers and grazers), a single stocking rate based on the needs of cattle is not appropriate. Second, ungulate grazing can actually improve productivity of grazing-tolerant plant species at moderate grazing intensities (McNaughton 1992). Third, the succession model views the prevalence of annual grasses as a sign of degradation, whereas in Sahelian zones and Mediterranean ecosystems, annual grasses persist in the presence of grazing and serve as a principal livestock forage (Le Houérou 1989). Fourth, range degradation may occur in arid zones without livestock grazing (Omar 1991, Oba 1992, Savory and Butterfield 1999). Fifth, a lack of long-term range monitoring makes it difficult to identify different succession stages in arid zones. The difficulty of identifying succession stages reflects the fact that pristine conditions on historically grazed rangelands are nonexistent (Cornelius and Schultka 1997).

Finally, vegetation cover and plant productivity in arid and semi-arid rangelands may be regulated by rainfall variability rather than herbivore density (Ellis and Swift 1988). For example, the dynamics of the Sahelian rangelands are due more to episodic rains than to grazing pressure. During the multiple droughts of 1980–1984, range production in the Sahelian zone decreased progressively as compared to that in years of above-average rainfall (Tucker et al. 1991). In northern Kenya during a decade when rainfall totals ranged from 50 mm (i.e., drought year) to 350 mm (i.e., above-average rainfall), a corresponding recovery of vegetation was reported under grazing by pastoralists' livestock (Lamprey and Yussuf 1981). These changes in vegetation are clearly the features of non-equilibrium systems.

Non-equilibrium grazing models. Whereas equilibrium grazing systems can be designed in accordance with predetermined goals, the erratic rainfall and consequent high variability of vegetation productivity in non-equilibrium grazing systems does not normally allow time-related management plans. Therefore, in non-equilibrium grazing models, livestock carrying capacity is impossible to predict with certainty. Furthermore, because of frequent multiple-year droughts, livestock population is allowed neither to overshoot the carrying capacity nor to die off entirely (Ellis and Swift 1988, Behnke and Scoones 1993, Dodd 1994). Thus, the optimal system of land use in non-equilibrium systems is through livestock and ungulate tracking of rainfall and forage production. However, the equilibrium grazing models that have been used in the past did not take into account the high variability of rainfall. Indeed, these models associated the spatial and temporal changes in vegetation in arid zones of sub-Saharan Africa with rangeland degradation.

Misconceptions about the effects of grazing on sub-Saharan arid zones have, therefore, resulted from the failure to distinguish non-equilibrium–related range dynamics from the negative feedback processes that are characteristic of equilibrium systems (Walker 1993). Moreover, the subcontinental-level range deterioration that is often cited as being responsible for the pastoral land use crisis in Africa has not been verified by long-term research (Prince et al. 1998).

Indeed, vegetation dynamics in response to grazing in arid zones of Africa occur in discrete states and transitions (Westoby et al. 1989). Vegetation changes from one state to another by going through different transient states. Reversing vegetation states after certain thresholds (i.e., distances between states) are crossed may be impossible. The vegetation instead assumes new transitory states that may not persist. The National Research Council (NRC 1994) used the state-and-transition model and threshold ideas to describe rangeland health. They considered rangelands to be healthy if productivity, soil, and watershed integrity were maintained through sustainable management. According to this model, rangelands at risk are those in which degradation has occurred but can still be reversed with improved management (Busby et al. 1995). However, as deterioration progresses, rangelands are transformed irreversibly into an unhealthy state. Milton et al. (1994) proposed that such a stepwise degradation model shows that once healthy rangelands (usually represented by commercial ranches worldwide) have retrogressed irreversibly, desertification eventually results.

The state-and-transition model and its derivative, the rangeland health model, can be used to characterize the conditions of different vegetation states in sub-Saharan and Mediterranean rangelands (Westoby et al. 1989), which feature high turnover of vegetation cover (Noy-Meir 1973). For much of the year, the vegetation exists as a soil seed bank (Figueroa and Davy 1991, O'Connor

Figure 1. The grassland of the plains of Diida Galgallu in northern Kenya supports high livestock stocking density (e.g., camels) during the wet season. Similarly, the arid zone grasslands of sub-Saharan Africa may be highly productive when rainfall is above average. The huge biomass produced during such periods supports greater stocking rates than in dry years, when the landscape may be almost bare.

1994). Thus, on annual grasslands, the dominating vegetation states (i.e., plants versus seed bank) may change dramatically among seasons or years (George et al. 1992, Turner 1998). On perennial grasslands and dwarf shrublands, by contrast, short-term grazing (i.e., less than 5 years) is unlikely to explain changes in vegetation states; grazing for longer periods (more than 20 years) may be needed to establish vegetation states (Allen-Diaz and Bartolome 1998).

The state-and-transition model is, therefore, better for arid zone rangelands than equilibrium models because it focuses on the idea of multiple states and opportunities for managing states. The weakness of the state-and-transition model for arid zone rangelands in general is, however, its failure to account for vegetation changes due to spatial variability of the landscape or to acknowledge episodic changes that result in rapidly changing transient vegetation states or the existence of vegetation states in the form of seed banks. By contrast, pastoralists' strategies of manipulating grazing strategies by exploiting vegetation through fine tuning of management at the landscape scale does account for these phenomena. Thus, it is clear that making good management decisions in sub-Saharan rangelands requires a better understanding of how interactions among climate, plants, and grazing influence the dynamics of the vegetation in these rangelands.

New perspectives: A climate–plant–herbivory interactive model

The linkages among climate, plants, and herbivory serve as ecological drivers that influence the dynamics of sub-Saharan rangelands. The principal driver is the climate, with its variability having a direct impact on the variability of plant cover and biomass. Herbivory influences biomass, species diversity, and the efficiency with which plants use rainwater. Hence, by taking into consideration the inter-linkages between climate, plants, and herbivory, the new model contributes to an improved understanding of the dynamics of sub-Saharan rangelands. Furthermore, the new model provides an opportunity to interpret more effectively the causes of land degradation in arid zones in general and those of sub-Saharan Africa in particular.

In arid zones of sub-Saharan Africa, vegetation growth depends on soil moisture (Pickup 1994), structure, and water storage capacity (Rietkerk et al. 1997); rainfall patterns over several years (O'Connor 1994); amounts of effective rainfall released; and duration of rainfall and sea-

Figure 2. Heavy browsing shapes the dwarf shrub Indigofera spinosa, *which is abundant in the arid zone shrublands of sub-Saharan Africa. The shrub is highly adapted to herbivory and responds to persistent goat and sheep browsing by growing interlocking twigs covered with spines. The spines serve as a defense against herbivory. Flowering is not hindered by heavy browsing. (a) Heavily browsed and (b) moderately browsed plants in flower.*

son (Ellis and Swift 1988). For example, in the Sahel, interannual differences in rainfall explain 17% of the variation in herbaceous vegetation cover and production (Turner 1998). For the arid zones of northern Kenya, surveys conducted during the wet season of 1982 (followed by the wet and dry seasons of 1983) showed highly variable herbaceous vegetation cover: During the 1982 wet season, mean herbaceous cover was approximately 36%, whereas during the 1983 wet and dry seasons, herbaceous cover changed from approximately 22% to 4% (Lusigi et al. 1986). The drop of herbaceous species cover from the wet season of 1982 to that of 1983 was reflected by the decline in rainfall. By comparison, the high drop in herbaceous cover between the wet season and the dry season implies that most of the plant species were annuals that survived only during the wet season and persisted as soil seed banks during the dry season. Thus, whereas the equilibrium grazing models interpret changes of annual grasslands in the arid zone of Africa as land degradation, the new model interprets the changes as temporal dynamics, driven mainly by rainfall variability, with grazing having a lesser influence.

Premises of the climate–plant–herbivory interactive model.

The synergistic effects of rainfall and grazing on plant production can, therefore, be viewed from two angles. First, rainfall, by increasing plant growth, increases food availability to herbivores. Second, moderately intense herbivory promotes productivity that is higher than in the absence of grazing (Noy-Meir 1973). Arid zone plants persist in the face of grazing of domestic and wild ungulates because they have coevolved over millions of years (Frank et al. 1998). In Mediterranean ecosystems, grazing "stabilizes" adapted plant populations, whereas the absence of grazing destabilizes the system (Perevolotsky and Seligman 1998).

Interactions among climate, plants, and herbivores occur at the scales of regions, landscapes, grazing patches, and individual plants (Senft et al. 1987). At the regional and landscape levels, rainfall controls spatial and temporal distribution in plant production (Coughenour 1992). At the landscape scale, spatially variable rainfall promotes migratory movement of ungulates. Opportunism is a necessary strategy for exploiting discontinuous vegetation production. At these scales, biomass production is related to effective rainfall and number of growing days (Noy-Meir 1979). During drought, plant productivity is zero; therefore, grazers have no influence on future plant growth (Le Houérou 1989). However, when rainfall returns, herbivore grazing at moderate grazing pressure stimulates production of new plant biomass (McNaughton 1992).

The regrowth creates grazing patches to which grazers return. Stretches of nutritionally rich grazing mats or "grazing lawns" (McNaughton 1983, Belsky 1986) support much greater grazing pressure than would be estimated from stocking rate studies (Hierneux and Turner 1996). Among the migratory ungulates of the East African savan-

na, grazing by coarse grazers (e.g., buffalos, zebras, elephants) facilitates grazing by concentrate feeders (e.g., grant gazelle, Thomson's gazelle, eland), thus allowing grazing sequences by different ungulate species at the landscape scale (Bell 1971). On the tallgrass prairie of North America, repeated grazing by bison creates patches of grazing lawns that have greater photosynthetic rates than the ungrazed patches (Knapp et al. 1999). Similar patterns of grazing at the patch level have been reported for the arctic Alaskan ranges grazed by caribou (Post and Klein 1996). In the Sahelian rangelands, grazing creates patches that are frequented more often than ungrazed patches (Hiernaux and Turner 1996). Grasses in grazed patches are more productive (McNaughton 1983), of better nutritional quality (Post and Klein 1996), and live longer (Eldoroma 1981) than ungrazed grasses.

The effect of ungulate grazing at the individual plant level depends on the intensity and season of grazing (Frank et al. 1998). The outcome of herbivory also depends on the plants' adaptive morphological and growth features. Plants that are highly adapted to herbivory are those with meristems below the level of grazing. In shrubs, the characteristic "hedging" provides a mechanical barrier against herbivory (Figure 2), whereas in grasses, grazing favors prostrate species (Belsky 1986). Herbivory reduces surface area from which plants lose water (Briske 1991). Removal of the transpiring surface by grazing improves soil moisture and consequently increases the chances of plants to sustain growth (Archer and Smeins 1991).

Attributes of the climate–plant–herbivory interactive model.

The findings that we have cited so far show the need to recognize the links between rainfall and grazing. Understanding the interactions among climate, plants, and grazing—rather than trying to separate their effects—would improve understanding of the dynamics of sub-Saharan rangelands. Thus, it is essential that the climate–plant–herbivory interactive model conform to the criteria of a functional model, including being able to predict system changes within a time frame that is relevant to resource users; to predict changes within rangeland components that influence resource use; to help resource managers make appropriate decisions about where, when, and how long to graze rangelands; to help resource managers implement actions that might lead to improvement of grazing; and to enhance communication among scientists, resource users, technicians, and the wider public about the links between climate, plants, and herbivory (Brown 1994). The climate–plant–herbivory interactive model conforms to these criteria: it has components that describe responses of the rangelands to climate and grazing; it addresses linkages between components that describe the functions of grazing ecosystems; and the components are linked through complex, interactive ecological and physiological processes that serve as diagnostic parameters for

Figure 3. The state-and-transition model provides one way to describe the effects of grazing in arid shrublands. This version of the model, based on grazed and ungrazed treatments, shows four transient vegetation states and 12 transitions in the dwarf shrub–annual grass association in the arid zone of Kenya. In transient State I, livestock browsing reduces vegetation cover but has no adverse effect on recruitment of the shrubs Indigofera cliffordiana *and* Sedera hirsuta *(T1). Seedling mortality in the grazed area is caused by desiccation rather than by grazing. Total shrub cover fluctuates less than annual grass cover between wet and dry cycles because growth of annual grasses is dependent on immediate rainfall, whereas shrubs rely mostly on moisture that percolates deep into the soil. Range rehabilitation*

by exclusion of livestock for 5 years (State II) was initially successful (Oba 1992). After 5 years of grazing exclusion, shrub cover more than doubled, litter cover increased, and bare ground decreased substantially (T3). Forb cover (dominated by Mullogo ceriana, Tribulus terrestris, Blepharis linariifolia, and Chloris virgata) fluctuated following episodic rainfall (T4). Following protection from grazing for more than 5 years combined with drought (T5), dwarf shrub cover was lost (State III). Such a loss is a risk of over-resting the dwarf shrub–annual grass association (i.e., of excluding grazing from the association for so long that shrubs become moribund). Over-resting from grazing for more than 5 years led to loss of the dwarf shrub cover, whereas annual grass (T6) and annual forb cover (T7) fluctuated between seasons. State IV occurred 8 years after the loss of dwarf shrub cover (Gufu Oba, unpublished data). Bare ground increased following loss of episodic forb cover and litter (T8). State IV is vulnerable to soil erosion by wind and periodic surface runoff (T9). The condition is not reversible and might result in desertification (T10). It is unlikely that State IV would be reversed to States II and III (i.e., T11 and T12) more than 8 years after the loss of dwarf shrub cover without intervention, because loss of mature I. cliffordiana—and the likely loss of soil seed reserves—would mean that even when growth conditions are improved, an extended period would be needed to reestablish dwarf shrub cover. However, it may be possible to reestablish shrub cover if watering techniques are used for improving soil moisture (T11) and reseeding (T12), followed by management (State II). Once established, the arid zone dwarf shrub ecosystem is persistent (States I–II). Brief periods of grazing deferral (State II) allow shrub cover and litter to increase. Management of arid zone grazing lands should therefore be aimed at the transient states sustained under pastoral land use (States I–II).
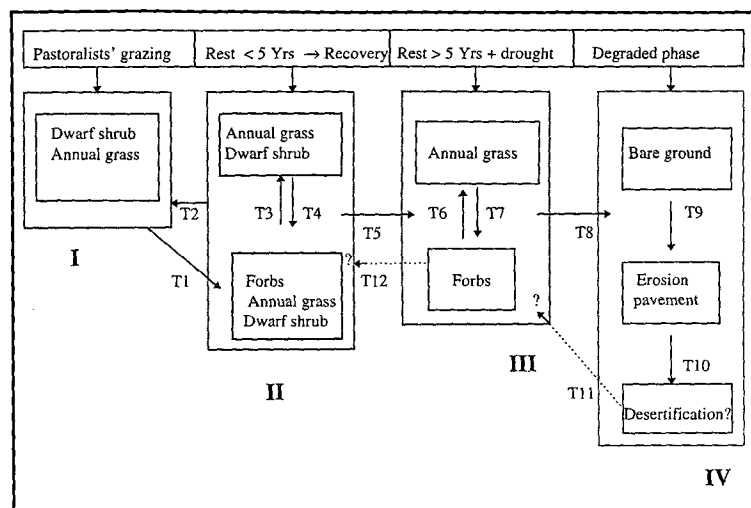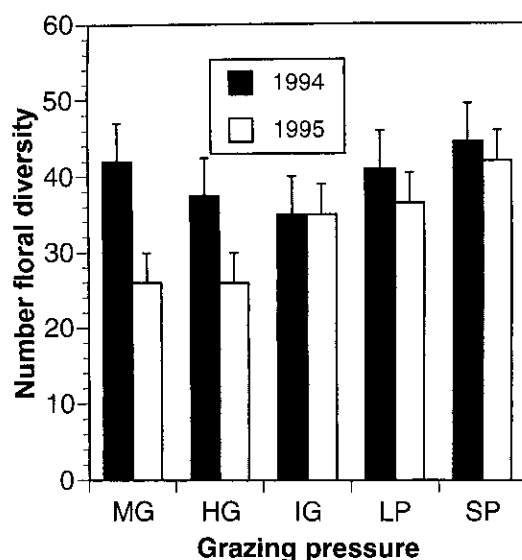
measuring and monitoring responses of plants to rainfall and grazing.

A number of diagnostic parameters may be used in the climate–plant–herbivory interactive model. Responses of plants to long-term grazing may be measured using species composition or species diversity and cover. Short-term responses to rainfall and grazing may be ascertained by rainfall use efficiency, which is the ratio of annual primary production and annual rainfall (Le Houérou 1989), or water use efficiency, which is the measure of dry matter increment per amount of water transpired by vegetation. Water use efficiency (Fischer and Turner 1978) is related to infiltration, runoff, and soil storage. Other useful parameters include relative growth rates (a physiological growth function that influences the responses of individual plants to herbivory; Hilbert et al. 1981), and net primary productivity, which is directly correlated with rainfall (Le Houérou 1984). We briefly describe empirical evidence in support of the climate–plant–herbivory interactive model using these diagnostic parameters. Other

diagnostic parameters that are not discussed include nutrient uptake, carbon assimilation, biomass allocation below and aboveground, and plant reproductive success.

Long-term grazing exclusion leads to loss of plant cover.
Long-term grazing exclusion studies attempt to test the hypothesis that grazing causes degradation. Hence, the most revealing experiments are those in which grazing is either regulated (i.e., indigenous grazing), such that grazing patterns are changed according to resource availability or season, or controlled (i.e., grazer exclusion), as in ranch grazing, in which grazing is deferred until the desired range conditions are achieved. Several studies comparing the effects of excluding grazing with those of continuous grazing have been conducted worldwide, including in arid zones of sub-Saharan Africa, for more than half a century.

In many studies, exclusion of grazing has not increased range production in arid zones any more than continuous or short-duration rotational grazing or grazing strategies

as used by the pastoralists. For example, in the arid zones of North America, 50 years of grazing exclusion did not result in succession beyond cyclic annual communities (Hironaka 1986), nor did it influence changes in species composition (Blydenstein et al. 1957). Twenty-two years of grazing exclusion did not increase grass cover in ungrazed as compared to grazed areas (Bock and Bock 1993), and 17 years of grazing exclusion in velvet mesquite (*Prosopis juliflora* var. *veluta*)–grass savanna had no effect on tree–grass dynamics (Glendening 1952). A decade of controlled grazing in arid grasslands was followed by a decline in perennial grass cover and the accumulation of grass litter; by contrast, in lightly grazed areas, grass cover was high and less litter was accumulated (Kleiner 1983). Similarly, three decades of grazing exclusion of livestock in desert shrubs resulted in the disappearance of the initially dominant species, whereas these species persisted on the grazed sites (Shreve and Hinckley 1937). After 50 years and 20 years of grazing exclusion, respectively, plant cover in arid zones of south-central Mexico and Australia did not increase, but the vegetation did respond to changes in rainfall (Wright and Van Dyne 1976, Austin et al. 1981). Similarly, desert communities protected from grazing for 100 years showed rapid changes in vegetation in response to cycles of wet and dry years (Turner 1990).

In the Negev, Noy-Meir and Seligman (1979) reported that 5000 years of grazing had resulted in no substantial changes in vegetation structure but that the vegetation responded to periodic fluctuations in rainfall patterns. Because of co-adaptation with grazing, the vegetation of the Negev, like that of sub-Saharan Africa, is highly resilient to grazing (Perevolotsky and Seligman 1998). On the Arabian peninsula, as well as on semi-arid rangelands of sub-Saharan Africa, long-term grazing exclusion does not increase forage production as compared with continuous grazing because forage production and cover are influenced more by rainfall than by herbivory and because

herbivory sustains range productivity (Omar 1991, Turner 1998). Moreover, in Sahelian rangelands that are continuously grazed by agro-pastoralist livestock, 9 years of monitoring showed rapid recovery of the herbaceous biomass production once the rains returned (Hiernaux 1998). In fact, according to Pierre Hiernaux, Peder N. de Leeuw, and Lassine Diarra (unpublished manuscript), grazing pressure is not the cause of the pastoral crisis; indeed, they say, the continuing productivity of the primary resource base has helped to stabilize the pastoral economy in the Sahelian zone.

In a related study in the Sahelian rangelands, Hiernaux (1998) has reported that plant species that tolerate herbivory disappeared in the absence of grazing, whereas grazing-intolerant species became dominant. Furthermore, studies in the Serengeti ecosystems have shown that, in the absence of ungulate grazing, species composition and plant growth forms changed relative to those present under grazing (McNaughton et al. 1988). Some important grass species, such as *Andropogon greenwayi*, disappeared after 18 years of protection in the Serengeti and yet persisted outside the exclosure, where they were subject to grazing (Belsky 1986). Following a decade of monitoring of the Kargi paddock in northern Kenya, *Indigofera cliffordiana* disappeared from an ungrazed portion of the paddock but remained in the grazed area (Walter Lusigi, personal observation).

A 5-year experiment involving exclusion of livestock grazing from a dwarf shrub–annual grass association dominated by *I. cliffordiana* and *Aristida mutabilis* in the arid zone of Turkana, northwestern Kenya, displayed several identifiable transient states (i.e., as in the state-and-transition model). The *I. cliffordiana* dwarf shrub persisted under grazing (Oba 1992). In response to the absence of grazing and variations in rainfall, the dwarf shrub–annual grass vegetation fluctuated between different transient states (Figure 3). Allowing the dwarf shrub and annual grass community to rest from grazing for less than 5 years (State II; Figure 3) led to improved dwarf shrub cover and to a healthier range than was seen under
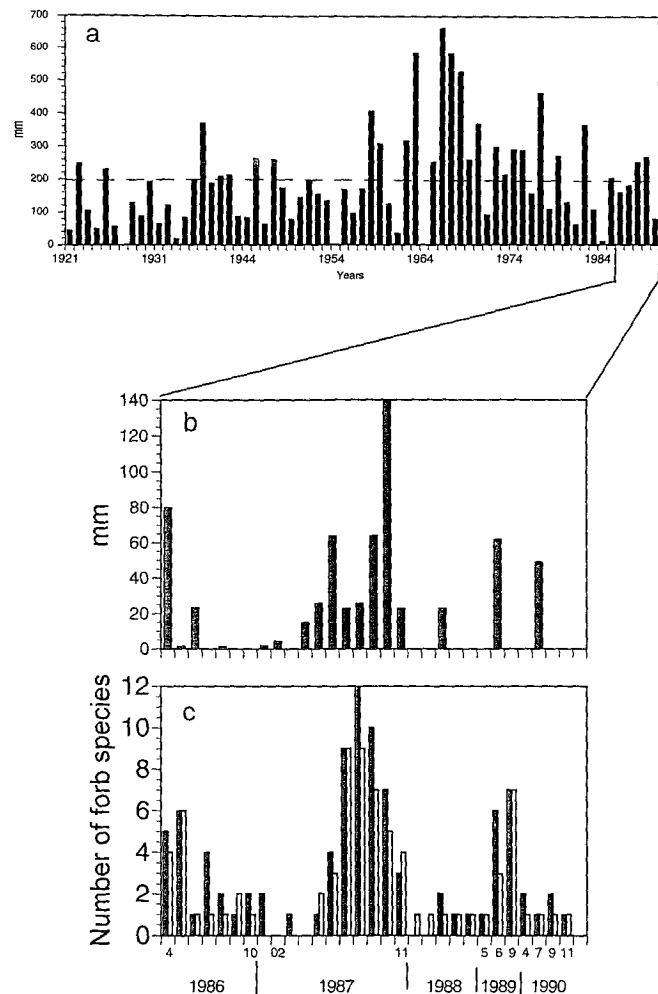
Figure 5. Relationship between rainfall and dynamics of forb species composition in central Turkana, northwestern Kenya. (a) Long-term annual rainfall recorded at the town of Lodwar from 1921 to 1990. (b) Patterns of monthly rainfall from April 1986 to December 1990. (c) Changes in the number of annual forb species on ungrazed (open bars) and grazed (shaded bars) areas between 1986 and 1990. The forb species richness is closely related to monthly rainfall, implying closer links to rainfall than to grazing (Gufu Oba, unpublished data).

continuous grazing. However, protection exceeding 5 years, combined with drought, resulted in the elimination of *I. cliffordiana* through dieback and increased dominance of *A. mutabilis* and annual forbs (State III, Figure 3), leading to a less healthy range condition. Permanent loss of the dwarf shrub cover indicates that the threshold for shrub cover has been crossed (cf., NRC 1994). These findings are contrary to the stepwise (i.e., equilibrium) model of range degradation (Milton et al. 1994), which assumes that it is long-term overgrazing that causes desertification. Yet in the dwarf shrub–annual grass study (Oba 1992), grazing by livestock did not degrade the dwarf shrub cover. Indeed, the study of grazing exclusion from the arid dwarf shrub–annual grassland might suggest that if removal of grazing results in loss of cover of the key plant species (i.e., dwarf shrub), then this particular arid zone ecosystem should be considered degraded.

Grazing does not harm plant diversity. Indeed, grazing on the Mediterranean, sub-Saharan, and other sub-tropical rangelands at moderate intensities promotes plant species diversity (Van Dyne et al. 1978, Perevolotsky and Seligman 1998, Pucheta et al. 1998, Knapp et al. 1999). In the Sahelian rangelands, neither continuous grazing nor long-term protection had a lasting effect on plant species diversity (Hiernaux and Turner 1996). Moreover, grazing gradient (i.e., from light to intensive grazing) did not substantially change the numbers of herbaceous plant species (Figure 4), although protection from grazing for 3 years increased herbaceous plant species diversity more than did 14 years of protection from grazing. Instead, interannual variations in herbaceous plant species diversity are influenced by rainfall (Hiernaux 1998). Thus, when rainfall fails, as it often does throughout the Sahelian zone, the herbaceous plant species diversity is dramatically changed. However, vegetation recovers rapidly after the rains return (Laweson 1990), suggesting strong causal links between herbaceous species richness and rainfall (Breman and Cissé 1977, de Fabrégues 1992).

However, when rainfall is not limiting, the absence of grazing has an important influence on plant species diversity. For example, in an area of Uganda's Queen Elizabeth National Park, in which rain is abundant, 20 years of graz-

ing exclusion resulted in high density but low diversity of grass species, and thicket cover was greater on ungrazed than grazed sites (Lenzi-grillini et al. 1996). This outcome can be explained as follows: In savanna ecosystems, two alternating ecological changes occur in response to herbivore grazing. First, tree cover is promoted; second, as tree cover increases, the diversity of herbaceous species under the thicket canopy declines. By contrast, where grazing is excluded, herbaceous species density increases, increasing competition for soil resources and thereby suppressing growth of thickets. Yet, whereas the sites from which herbivores are excluded support a few abundant species, the grazed areas support more, rare species. For example, when elephants and other ungulates were excluded from a *Sprobolus–Setaria* grassland for 14 years, the result was a marked increase in tree density, a decrease in herbaceous vegetation cover, and poor species diversity (Smart et al. 1985). Excluding large herbivores resulted in the disappearance of important forage species, such as *Glycine javonica* and *Brachira brizantha*, which persisted on the grazed area.

Additional evidence of the response of plant species diversity to grazing and protection from grazing comes

a

b

Available water (cm³ x 10⁻⁴ / growing season)
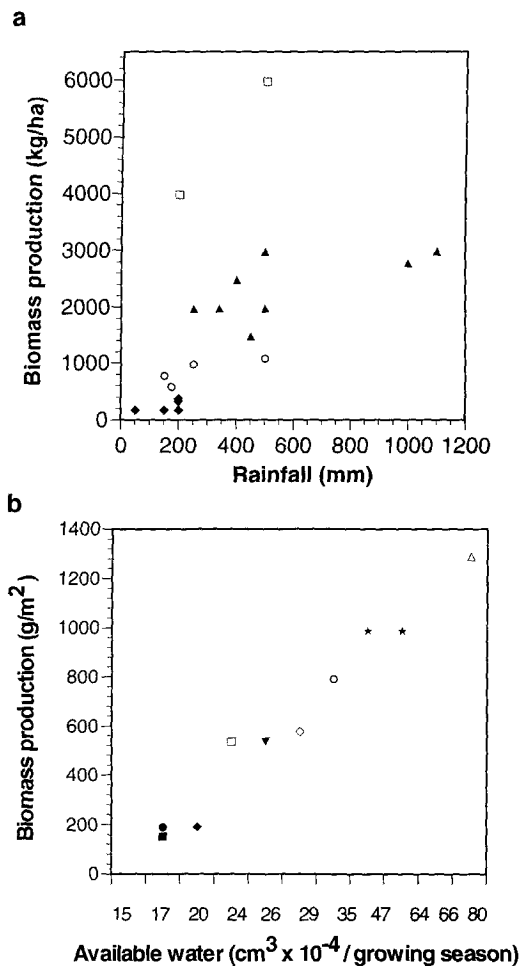
Figure 6. Water use efficiency of the world's grasslands, in terms of total biomass production. (a) Correlation between rainfall and biomass production at several sites in sub-Saharan Africa, representing the arid and very arid (solid diamonds), semi-arid (open circles), sub-humid (solid triangles), and humid savanna (open squares). Data from UNESCO (1979). (b) Correlation between available water and biomass production in North American grassland types, including shrub–steppe (open square), low mountain (solid diamond), high mountain (solid circle), northern mixed prairie (solid stars), northern shortgrass prairie (open diamond), southern mixed prairie (open circle), tallgrass prairie (open triangle), southern shortgrass prairie (solid triangle), and desert grassland (solid square). Based on data in Van Dyne et al. (1978).

the year because their cover varied greatly between growth and dormancy months (Oba 1992). Similarly, in a South African study, O'Connor and Roux (1995) showed that annual rainfall variability had a greater influence on annual forb abundance than grazing. In Serengeti ecosystems, ungrazed perennial grasses declined in the absence of grazing (McNaughton et al. 1988).

Persistence under grazing is also shown by *Indigofera spinosa*, which is widely distributed throughout northern Kenya, northeastern Africa, and the Red Sea coast (Thulin 1982). Approximately 30 years of photographic monitoring of *I. spinosa* in northern Kenya (Shantz and Turner 1958, Gufu Oba, unpublished data) confirmed that this dwarf shrub persists under continuous livestock grazing. The persistence under grazing of both *I. spinosa* and *I. cliffordiana* may be due to both herbivory tolerance and the ability to cope with water loss by increasing dieback of the current year's growth (Oba 1995). Thus, droughts are probably less harmful to grazed dwarf shrub than to shrubs that are protected from grazing (Oba 1994, 1995). Generally, during dry years, productivity of the dwarf shrub declines, whether grazed or ungrazed (Coughenour et al. 1990, Oba 1995). Because of the dieback, the ungrazed shrubs accumulate dead standing material that further reduces plant production. Sahelian pastures protected from livestock grazing for 12 years similarly accumulated dead standing material, preventing plant growth and lowering productivity (Brigitte et al. 1995).

Thus, the evidence suggests that the lack of grazing may degrade rangelands in sub-Saharan Africa. Therefore, during non-drought years, grazing exclusion does not produce a long-term improvement of vegetation cover, production, or diversity compared to what is produced during short-term rest from grazing or continuous, moderately intensive grazing. Instead, long-term deferral of grazing results in either no significant changes in species composition or in lowered diversity caused by the disappearance of herbivory-adapted species. Therefore, if the removal of ungulate grazing results in the loss of principal species from the plant community, then this ecosystem may be

from a study on the arid plains of central Turkana, northwestern Kenya, during which most years received below-average rainfall (Figure 5a). Six years of grazing exclusion resulted in more than 60% mortality of the principal dwarf shrub, *Indigofera cliffordiana*, compared to 6% mortality in a grazed area. Therefore, *I. cliffordiana* is not a decreaser in the sense of the classical succession model; rather, it decreases in the absence of grazing (Oba 1992). In the absence of grazing, *I. cliffordiana* plants responded to water stress by dieback of the current year's production. Protection from grazing for longer than 5 years led to complete mortality of the ungrazed *I. cliffordiana* plants.

By contrast, the effects of more than 5 years of controlled grazing on forb species composition were indistinguishable from those of continuous grazing. Forbs were irruptive and regulated more by rainfall than by herbivory (Figures 5b and 5c). During years with above-average rainfall, forb regeneration was greater in the grazed than in the ungrazed area. The annual grass *A. mutabilis* was also unaffected by herbivory and was regulated by rainfall. *A. mutabilis* increased on ungrazed areas by taking advantage of the increase in soil water that resulted after the shrub cover declined due to mortality. However, annual grass and forbs did not sustain ground cover throughout

Figure 7. Rainfall use efficiency (RUE) values. (a) RUE of different vegetation communities in the arid zones of Africa: wet savanna (solid squares), East African grasslands (open squares), Sudan savanna (solid diamond), Namibia (solid circle), and Turkana, Kenya (solid triangle). Based on these data, RUE can be calculated as follows: $RUE = 4.382 - 4x^{8.65}$ ($r^2 = 0.876$, $P < 0.05$). Rainfall and biomass data for calculating RUE are from UNESCO (1979). (b) A 10-year RUE profile ($RUE = 1.00 + ln(x)^{-3.86}$, $r^2 = 0.934$, $P < 0.005$) of the herbaceous vegetation sampled at a ranch in Ferlo, Senegal (Sahel). Rainfall and biomass data used for calculating RUE at this site were adapted from Brigitte et al. (1995).

considered to have been degraded in the absence of grazing. Consequently, we suggest that contrary to the definitions that relate to equilibrium systems, the term "range degradation" should be defined as the loss of a key plant assemblage from a grazing ecosystem, and "desertification," by inference, should be defined as a change that cascades through the ecosystem, severely altering rangeland productivity and accelerating losses of the grazing potential. In both cases, the efficiency with which range vegetation exploits soil moisture might decline.

Water use efficiency. In arid zones, herbaceous plant production is linearly related to rainfall (Figure 6a). In the Sahel, production increases to 600–2000 $kg \cdot ha^{-1} \cdot yr^{-1}$ when rainfall increases from 200 mm to 800 mm (Le Houérou and Host 1977). Amounts, sequences, and season of rainfall as well as drought affect plant production by influencing soil moisture and, therefore, water use efficiency. Desert ecosystems have the lowest water use efficiency, and humid grasslands the greatest (Figure 6b). The lower water use efficiency of arid zone plants probably reflects the sparseness of vegetation and greater water loss through transpiration (Singh et al. 1980). For the grasslands of the arid zone, water use efficiency varies from 0.37 $g \cdot m^{-2} \cdot mm^{-1}$ to 1.25 $g \cdot m^{-2} \cdot mm^{-1}$ (Webb et al. 1978). Generally, in arid zones, the water use efficiency for grasses (1.3 $g \cdot m^{-2} \cdot mm^{-1}$) is greater than that for dwarf shrubs and trees (0.65 $g \cdot m^{-2} \cdot mm^{-1}$; Coughenour 1992).

Dwarf shrubs respond rapidly to water input, up to a point beyond which additional water does not increase production. For example, Coughenour et al. (1990) reported that irrigation with up to 8 mm of water per week induced *I. spinosa* shrubs to green, whereas an additional 15 mm per week did not increase production. Approximately 36 mm of rain in a single bout is necessary to break drought dormancy of *I. spinosa* shrubs. Also, Coughenour (1991) showed that grazing on *I. spinosa* had the least impact on plant biomass when the intervals between watering were longer rather than shorter. Conversely, additional water stimulated clipped *I. spinosa* to produce more biomass than clipped plants that were not watered (Keya 1997). The biomass of grazed *I. spinosa*
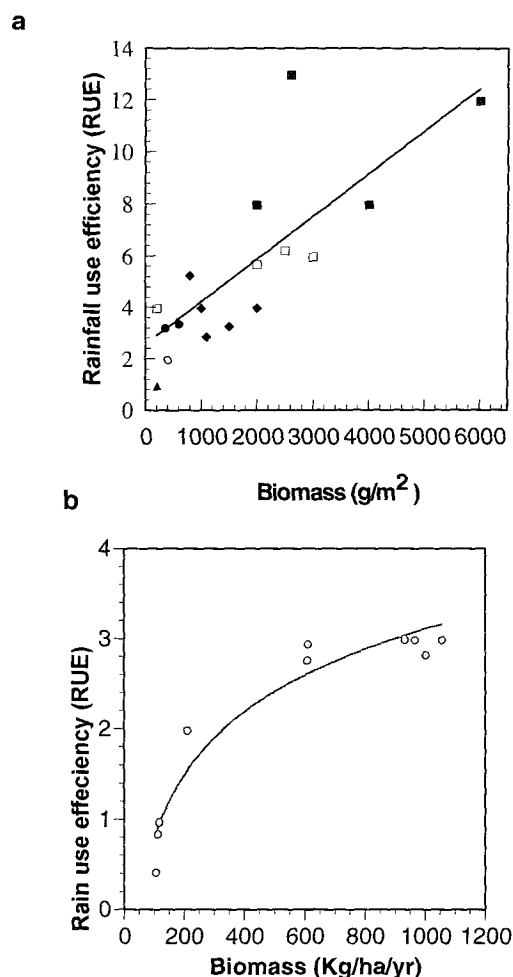
increased substantially on the grazed, as compared with the ungrazed, plants in years of average rainfall. Browse yields were lower during years of below-average rainfall, whereas greater production was associated with years of above-average rainfall (Oba 1994, 1995).

Rainfall use efficiency. Rainfall use efficiency is a derivative of rainfall and biomass production. It is linearly correlated with a rainfall gradient varying from very arid sites to the sub-humid savanna in the sub-Sahara (Figure 7a). In the Sahel, rainfall use efficiency (in terms of dry matter production per mm of water) averages between 2.5 $kg \cdot ha^{-1} \cdot yr^{-1} \cdot mm^{-1}$ and 1.0 $kg \cdot ha^{-1} \cdot yr^{-1} \cdot mm^{-1}$ (Le Houérou 1989). However, for a given vegetation type, rainfall use efficiency may vary between wet and dry years and between grazed and ungrazed treatments (Le Houérou et al. 1988). Rainfall use efficiency of ungrazed and grazed *I. spinosa* (1.66 $kg \cdot ha^{-1} \cdot mm^{-1} \cdot yr^{-1}$ and 1.3 $kg \cdot ha^{-1} \cdot mm^{-1} \cdot yr^{-1}$, respectively) in Turkana, northwestern Kenya (Oba 1994), were within the range given for the Sahelian rangelands (Le Houérou et al. 1988). In the Sahelian rangelands, rainfall use efficiency of grazed vegetation was lower than that of ungrazed vegetation (Le Houérou 1989). Generally, the rainfall use efficiency of herbaceous

a

b
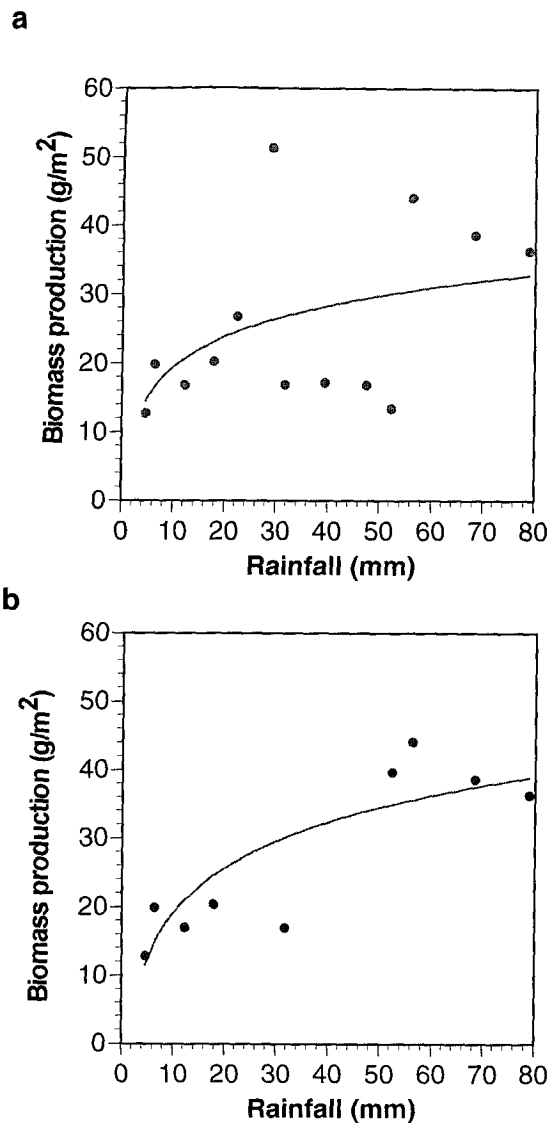
Figure 8. Regression between rainfall of the previous month and the current month's biomass of Indigofera spinosa *in ungrazed and grazed plots. (a) Ungrazed plots: Biomass = 6.412 + ln(x)$^{4.720}$, r^2 = 0.20, P > 0.05. (b) Grazed plots: Biomass = 9.64 + ln(x)$^{-3.241}$, r^2 = 0.71, P < 0.005.*

species have different critical minimum moisture requirements. Herbaceous plants have a critical minimum rainfall requirement for growth of 25–75 mm annually (Noy-Meir 1981). Above the critical moisture level of 75 mm of rainfall, biomass yield (on a dry matter basis) increases by 0.5–2.0 mg per g of water. For the ungrazed *I. spinosa*, however, critical moisture from previous months' rainfall stored in the soil is approximately 6 mm, whereas critical rainfall for grazed plants is approximately 4 mm (Figures 8a and 8b). This finding suggests that, by concentrating biomass, grazing improves rainfall use efficiency in *I. spinosa* plants. The increased efficiency may be related to the fact that the ungrazed *I. spinosa* plants accumulate standing dead necromass due to dieback, whereas the grazed plants concentrate biomass that is efficient in converting rainfall into dry matter production. In the Sahelian rangelands, therefore, because of the close relationship between rainfall use efficiency and plant production, changes in rainfall use efficiency provide an important criterion for determining overall trends in vegetation production. In particular, downward trends in rainfall use efficiency may signify deteriorating range condition. Following 9 years of monitoring on the Sahelian rangelands, Prince et al. (1998) found no evidence of a reduction in rainfall use efficiency but rather an increase, dispelling fears of desertification.

Relative growth rates. Relative growth rates of shrubs and trees are much lower than those of herbaceous vegetation (Le Houérou et al. 1988). Both grazing and rainfall have important influences on relative growth rates. However, the role of herbivory in plant production has been the subject of much controversy, with some evidence that herbivory reduces productivity and reproductive success of rangeland plants (Painter and Belsky 1993) and some evidence that herbivory at moderate levels increases biomass production and survival of grazing-tolerant plant species (McNaughton 1983).

Generally, light to moderate grazing may stimulate plant production, leading to biomass that is more concentrated than in ungrazed plants (McNaughton et al. 1988, Oba 1994). For example, in several grassland study sites in the United States, growth rates of grasslands that were rested (i.e., kept free of grazers) for short durations during 1970–1971 ranged from 0.82 g·m^{-2}·d^{-1} to 0.67 g·m^{-2}·d^{-1} on average, whereas growth rates of grasslands that had been rested for longer durations but were measured during 1970–1971 ranged from 0.96 g·m^2·d^{-1} to 0.90 g·m^2·d^{-1} on average, showing no significant differences (F = 1.251, P = 0.272; Singh et al. 1980). Similarly, Frank et al. (1998)

vegetation varied from year to year, increasing when rainfall was increased and biomass production was greater (Figure 7b). By contrast, rainfall use efficiency values of both grazed and ungrazed *I. spinosa* shrubs were greater during dry years than wet years (Oba 1995). This finding suggests that dwarf shrubs have evolved greater abilities than herbaceous vegetation to conserve water and increase photosynthetic efficiency under environmental stress.

In the case of dwarf shrubs (e.g., *I. spinosa*), productivity is more strongly linked to moisture stored deeper in the soil and to grazing intensity than is the case with herbaceous plants, whose shallow roots cannot access moisture stored in the deeper soil profile but that are more responsive than dwarf shrubs to immediate rainfall. This difference would explain different plant survival strategies, whereby herbaceous plant species production fluctuates with rainfall but production in shrubs is sustained as long as soil moisture lasts.

Thus, in arid zones, herbaceous and perennial plant

Figure 9. (a) Long-term defoliation of Indigofera spinosa *that were clipped during the wet season, the dry season, and the full year. The clipping regimes were 0% (control), 30% (light), 50% (moderate), 70% (severe), and 90% (very severe) of the aerial biomass. Defoliation of individual plants was sustained for a period of 5 years (1986–1990). For each level of clipping intensity, there were 20 treatment plants. At the termination of the study, all of the residual biomass (i.e., remaining plant parts) was harvested. By adding the initial biomass (i.e., biomass initially clipped), regrowth biomass (i.e., biomass defoliated), and residual biomass, we obtained total aboveground biomass production (g/plant) of* I. spinosa *that were individually defoliated under the five regimes. In the dry-season defoliation treatments, plants under the light grazing regime overcompensated by approximately 340% compared to the controls, whereas those under the moderate grazing regime overcompensated by 210%. Plants grazed at the light regimes during the dry season displayed greater overcompensation for three reasons. First, this level of grazing stimulated more biomass production. Second, the plants were left with higher residual biomass at all times relative to the controls. Third, plants are rested during the wet season, thus taking advantage of rainfall to increase biomass production. At greater grazing pressure, the residual biomass was low, which means that individual plants grazed continuously for 5 years lacked sufficient residual biomass to increase regrowth compared to the controls. (b) Percent mortality of* I. spinosa *defoliated under the different grazing regimes for 5 years during the wet season, dry season, and the full year (Oba 1994, Oba et al. in press a). (c) Ungrazed and grazed treatments comparing dead standing necromass (g·m⁻²·yr⁻¹) of* I. spinosa *that was protected from grazing or was continuously grazed. Data from Oba (1995).*

showed a substantial increase in biomass production following wild ungulate herbivory in both the Yellowstone National Park and Serengeti ecosystems. In addition, McNaughton (1976) showed that in the Serengeti ecosystem, wildebeest grazing stimulated grass productivity, whereas in an area protected from grazing, grass productivity declined. In the Kalahari region of Botswana, unbrowsed shrubs produced 14 g/m² of browse, compared with 39 g/m² under moderate to heavy grazing (Skarpe 1992). In *I. spinosa* pastures, however, dry matter production in ungrazed pastures (1.37 g·m⁻²·d⁻¹) was not significantly different from that of grazed pasture (1.09 g·m⁻²·d⁻¹; Oba 1995).

Net primary productivity. Under long-term (i.e., 5 years) clipping regimes, *I. spinosa* individuals defoliated during the dry season produced more biomass than those defoliated during the wet season or all year-round (Figure 9a). However, *I. spinosa* plants defoliated during the entire year produced less biomass than nondefoliated controls. Overall, compared to the nondefoliated controls, *I. spinosa*
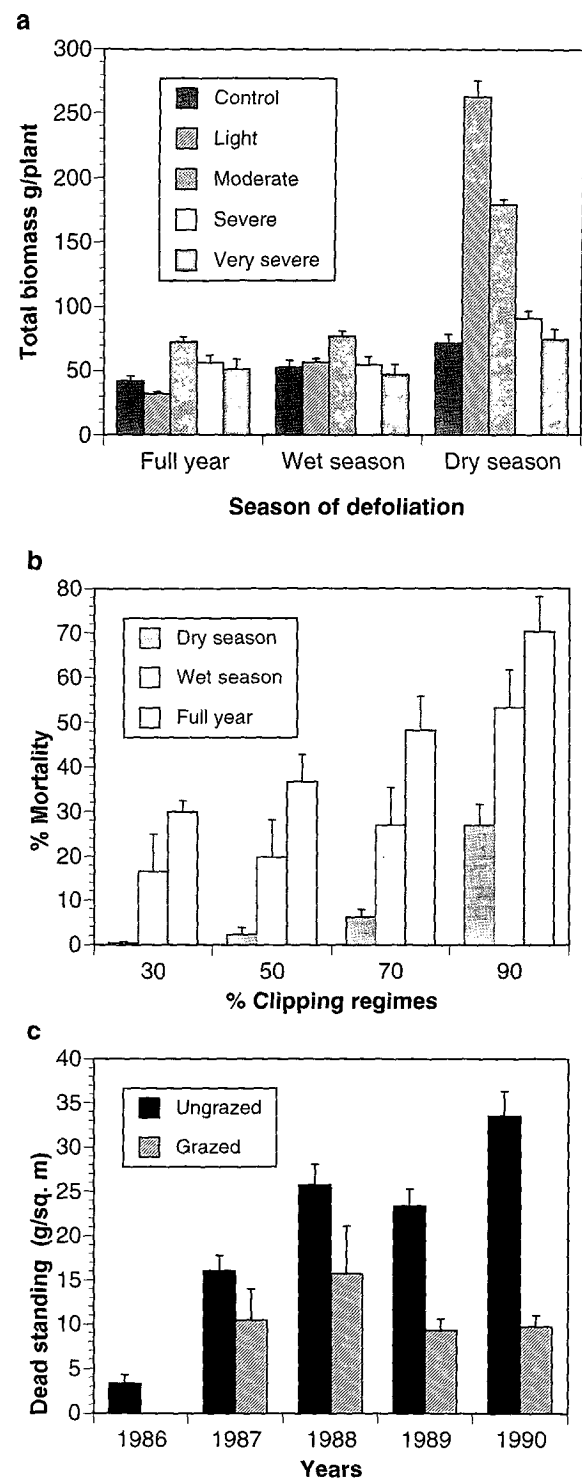
defoliated under the light grazing regime overcompensated for the biomass continuously removed for 2–3 years in dry and wet seasons but undercompensated for the biomass removed during the entire year (Oba et al. in press a).

Mortality was also greater in the *I. spinosa* pastures that were protected from livestock grazing for 5 years than in pastures that were continuously grazed by pastoralists' livestock for 5 years (Figures 9b and 9c; Oba 1994). These

treatments imitated the traditional grazing systems in the arid zones of Africa. Usually, livestock of the sub-Saharan pastoralists use mobility in response to rainfall to graze rangelands during the wet season. Other rangelands that are preserved during the wet season are grazed in the dry season. However, since the imposition of equilibrium grazing models of range development programs three decades ago, decline in mobility has led to some rangelands being grazed for the entire year.

These findings therefore suggest that the majority of the plants of arid zones of Africa, especially dwarf shrubs such as *I. spinosa*, are highly adapted to herbivory. The adaptive features of *I. spinosa* may include rapid bud development from the axillary meristem, which compensates for the loss of the apical meristem (Coughenour et al. 1990). More rapid response to rainfall events in grazed *I. spinosa* plants than ungrazed plants suggests that grazed plants are more efficient in using rainfall (Coughenour et al. 1990, Oba 1994, 1995). By continuously removing live tissues and reducing the accumulation of standing dead material, herbivory functions to stimulate and sustain new biomass production. Grazed plants allocate more resources to live biomass than do ungrazed plants. Moreover, without herbivory, increased water stress is likely to result in the transfer of dry matter from live to standing dead, or from live to litter, compartments. By contrast, we have found that grazed shrubs transfer less production to the standing dead compartment than ungrazed shrubs, suggesting that protecting the shrub from grazing leads to a decline, rather than an increase, in productivity (Oba et al. in press b). Similarly, in the Ferlo rangelands in West Africa, herbaceous biomass production was greater with grazing than with grazing exclusion (Brigitte et al. 1995).

Management and policy implications

The empirical evidence and examples presented in this article show that sub-Saharan Africa's catastrophe scenario resulted from the imposed equilibrium grazing models rather than from the often assumed link between the inherent tendencies of indigenous land use and environmental degradation (Lamprey 1983, Sinclair and Fryxell 1985). Despite the lack of empirical evidence to directly link pastoralist grazing strategies to land degradation before the imposition of equilibrium grazing models, the catastrophic scenario known as the pastoral crisis in Africa has been perpetuated for the last three decades. This scenario has gained support as a result of experiences with equilibrium-oriented grazing schemes, enforced stocking rates, veterinary programs that were not followed by responsive marketing systems, and development of water in the rangelands without taking into consideration the traditional patterns of land use.

Even more worrisome is that recipient countries have not benefited from the long-term research findings that existed from the arid zones in sub-Saharan Africa (e.g., those accumulated by the International Livestock Center

for Africa. In certain cases, valuable research data accumulated over many years and used to develop range resource management guidelines have remained unimplemented (Lusigi 1984) because donors and recipient governments have not been forthcoming with funding. There are two reasons for the lack of funding. First, disappointments from failed rangeland projects (that were based on equilibrium models) discouraged donor and recipient countries from continuing to support rangeland grazing programs. Thus, commitments to sustainable development in the arid zones of sub-Saharan Africa have been substantially reduced since the 1980s. Second, and most important, lessons learned from new empirical evidence and appropriate policies promoted by non-equilibrium models have not been put into practice by development agencies or governments. Therefore, it is not surprising that the economic and ecological consequences of the application of incorrect equilibrium grazing models and the withdrawal of international donors from rangeland development projects have created a burden on the fledgling economies of sub-Saharan countries.

What we have called new perspectives on grazing management, however, raise optimism about the opportunity for improved management of arid zones in general and those of Africa in particular. The optimism arises from reevaluating past misconceptions, coupled with a growing body of scientific information that supports non-equilibrium grazing models. Resource administrators and some international donors (e.g., The World Bank; see De Haans 1995) are also beginning to acknowledge the validity of non-equilibrium models for arid zones of sub-Saharan Africa. As we have described, such models as climate–plant–herbivory interactive and state-and-transition provide a better understanding of the ecology of the arid zones than equilibrium grazing models. These non-equilibrium grazing models employ flexibility in resource management and combine climatic variability and grazing in the processes by which resource users and managers make decisions about opportunistic and flexible land use strategies. In the future, donors and governments should use these new perspectives to plan and improve range development and policy: by acknowledging the need to build opportunism into management plans; by training range technicians and local government personnel in the new ideas; by promoting uses of traditional institutions of self-regulation and management strategies to increase grazing management success; and, finally, by designing studies that address the high temporal and spatial variability and linkages between climate, plants, and herbivory to improve understanding of the ecology of non-equilibrium ecosystems and to promote sustainable grazing systems in the arid zones of Africa.

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