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A GENERALIZED MODEL OF THE EFFECTS OF GRAZING BY LARGE HERBIVORES ON GRASSLAND COMMUNITY STRUCTURE

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Why are certain plant communities very sensitive to grazing by large generalist herbivores and others not? Current models that relate predation, competition, or disturbance to community structure do not always answer this question or provide predictions consistent with data from grazing studies. A key element missing from current models is the evolutionary history of plant-herbivore interactions. The evolutionary history of grazing has had a large impact on the physiognomy of grasslands and on their ability to support grazing (Mack and Thompson 1982). The evolutionary history of grazing is not, however, a good single explanatory variable for the response of grassland communities to grazing. Very different, even opposite, responses to grazing occur within communities with either short or long evolutionary histories of grazing. We develop a model based on environmental moisture and the evolutionary history of grazing that explains grazer-grassland interactions over a wide range of communities.

The current models that do not adequately explain the response of grassland plant communities to grazing by large generalist herbivores are the predation hypothesis (Paine 1966, 1971), the intermediate-disturbance hypothesis (Grime 1973; Horn 1975; Connell 1978; Fox 1979), and the Huston hypothesis (1979, 1985). The predation hypothesis suggests that local prey diversity increases when predators prevent dominant species from monopolizing resources. The intermediate-disturbance hypothesis proposes a bell-shaped response of species importance along a stress gradient. Diversity is limited by stress at one extreme and by competitive exclusion at the other. Huston's model adds the important component of the reaction to, or recovery from, the disturbing force. Species diversity is related to "the dynamic balance . . . between the rate of competitive displacement and the frequency of population reduction," or population growth rates and disturbance intensity (Huston 1979, p. 97). The action and the reaction thus define the dimension of a window of relaxed competitive interactions after disturbance.

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The problems associated with applying the Huston model to grazing are twofold. First, numerous, very different types of disturbances are lumped together on a single axis. Grazing may or may not be a disturbance for a plant community depending on its evolutionary history. Thus, Huston's disturbance axis must be redefined as one proceeds along an evolutionary-time axis. Second, we show that interactions occur along gradients of environmental moisture and of the evolutionary history of grazing. These interactions influence not only the window of relaxed competition but also the manner in which the competitive relationships are expressed.

We first define terms and set bounds on the model. Second, we briefly review the state of knowledge of the effects of grazing on community structure and integrate these within the context of the gradients of moisture and of the evolutionary history of grazing. Third, we present a model of the effect of grazing on grassland community structure and present quantitative evidence that supports the model. Finally, we discuss the relationship of our model to other hypotheses.

DEFINITIONS AND BOUNDS OF THE MODEL

Grasslands can be categorized as climatically determined, successional, or agricultural (Lauenroth 1979). Climatically determined grasslands occur in areas having a period during the year when the availability of soil water falls below the requirements for forests yet is sufficient to sustain grasses (Poaceae) as the dominant or major component of vegetation. Here we consider savanna and shrub steppe (or the ecotone between grassland and forest) as climatically determined grassland. This category encompasses the potential natural vegetation of 25% of the earth's land surface (Shantz 1954); these areas receive 250–1000 mm of annual precipitation and have mean annual temperatures between 0° and 26°C (Lauenroth 1979). Successional and agricultural grassland, which often result from the removal of the original forest vegetation, are maintained by agronomic or other management practices. Most of the grasslands in Great Britain, Europe, Japan, eastern North America, and areas of Australia and Asia are successional or agricultural grasslands.

We constrain our model to climatically determined, nonanthropogenic grasslands because (1) the model is concerned with global-regional areas rather than small, isolated grasslands; (2) anomalies to the model may result from various management practices that override or mask the usual plant-animal interactions; and (3) the interactions that we describe between environmental moisture and the evolutionary history of grazing depend on the relationship between aboveground net primary production (ANPP) and measures of environmental moisture such as mean annual precipitation (Lauenroth 1979; Sala et al. 1988) or actual evapotranspiration (Rosenzweig 1968; Webb et al. 1978). The environmental-moisture axis of our model is thus interchangeable with ANPP. We speak primarily in terms of environmental moisture because we are concerned with plant adaptations. We term grasslands at the low end of the environmental-moisture range as *semiarid* and those at the high end as *subhumid*.

The effect that an herbivore has on plant community structure depends in part on its level of diet selectivity. Plant community structure can be affected quite differently by generalist herbivores and by specialist herbivores, depending on whether the specialist consumes competitively dominant or competitively inferior species (Lubchenco 1978). Our model applies to generalist herbivores. We examine studies across a wide range of grasslands where grazing by a large generalist ungulate or an assemblage of several more-specialized ungulates exerts a relatively uniform grazing pressure across plant species. The effects of these large ungulates are addressed conceptually in terms of herbivory, not in terms of the effects that they may have on community structure through other activities such as wallowing, trampling, and urine or fecal deposition.

Definitions of disturbance have been based on alterations in the level of competitive interactions (Grime 1973; Connell 1978; Huston 1979), changes in species composition (Sousa 1984; Loucks et al. 1985), forces counter to past selection pressures, or equilibrium–domain-of-attraction models (Holling 1973). All definitions of disturbance are wrought with ambiguities and complexities and lack objectivity (Connell and Sousa 1983; Sousa 1984). The model that we present raises questions about using the above definitions in the context of grazing, and it raises questions in addition to those presented by Connell and Sousa (1983) and Sousa (1984). We present part of our model in a form analogous to the Huston model and to the intermediate-disturbance hypothesis for three reasons: (1) these models are widely used; (2) gradients in level of disturbance or level of grazing are intuitively appealing; and (3) contrasting our model of grazing with disturbance models raises further questions about a proper definition of disturbance in terms of grazing. In the context of these models, we must temporarily adopt the definition of disturbance presented in Sousa: "[A] disturbance is a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established" (1984, p. 356).

GRADIENTS OF MOISTURE AND OF THE EVOLUTIONARY HISTORY OF GRAZING: THE EFFECT ON GRASSLANDS' RESPONSE TO GRAZING

Convergent and Divergent Selection

The origin of nonanthropogenic grasslands is associated with regional climatic shifts toward aridity (Singh et al. 1983). Increasing specialization and adaptations to dry conditions among grasses occurred simultaneously with the development and radiation of large ungulate grazers (Stebbins 1972, 1981; Raven and Axelrod 1974). Consequently, ascertaining the original adaptive values of the traits is difficult (Gould and Lewontin 1979). Regardless of their origin, adaptations that enhance survival in semiarid environments may promote tolerance or avoidance of grazing. Coughenour (1985) discussed how basal meristems, small stature, high shoot density, deciduous shoots (high turnover), belowground nutrient reserves, and rapid growth allow grasses to evade or to tolerate both semiarid conditions and grazing.

Water stress and grazing stress are similar in that both periodically result in partial or total loss of organs. Tolerance to one necessarily includes tolerance to the other. Both drought and herbivory provide selection pressures to minimize the impact of the loss of individual plant organs (Orians and Solbrig 1977; Mooney and Gulmon 1982; Coughenour 1985). With respect to avoidance, the same characteristic that enables a plant to evade grazing can act to conserve or more effectively use moisture. For example, basal meristems, protected by basal sheaths, may better withstand drought as well as avoid grazing (Stebbins 1972; Barlow et al. 1980; Coughenour 1985). Expression of these characteristics increases with decreasing moisture and with an increasingly long evolutionary history of grazing, and there is an interaction of environmental moisture with grazing history. Thus, selection pressures in semiarid grasslands that have coevolved with large ungulate grazers are convergent. In this context, a convergent selection pressure is one that results in complementary effects on the plants' water-use efficiency and on response to herbivory.

In contrast, adaptations to grazing are divergent from other adaptations for survival that have evolved in species of subhumid grasslands. The moisture gradient from shortgrass steppe to mixed-grass prairie to tallgrass prairie in North America concurrently traverses gradients of low to high productivity, of short to tall stature in grasses, and of sparse to dense canopies with low to high competition for light. Tall growth forms, with relatively greater investment in aboveground rather than belowground production (Sims and Singh 1978), are adaptations that enhance the grasses' competitiveness for light but make them more vulnerable to grazing by large herbivores.

Competition and Regrowth

Current models predict an increase in diversity at intermediate levels of disturbance as a result of a reduction in competitive exclusion. However, plants respond to grazing in ways that may not necessarily decrease competition. In addition to reducing competition, grazing can change the relative importance of the mode of competition and can influence the longevity of the change in competitive relationships after the grazing event. These responses include regrowth and horizontal tillering or spread by rhizomes and stolons. Increased tiller numbers and regrowth of a grazed tiller have different effects on community structure, the subsequent mode of competitive relationships, and a plant's subsequent susceptibility to further herbivory.

Tillering response to grazing depends on the growth form and the grazing history of the species. Stimulated tillering or activation of rhizomes is more likely to occur among short-statured species (McNaughton et al. 1983; McNaughton 1984; Coughenour et al. 1985*a*). Rhizomatous or stoloniferous grasses are more prevalent in grasslands with long evolutionary histories of grazing (Mack and Thompson 1982). Unlike intermediate-height grasses and tallgrasses with a short grazing history, those with a long history of grazing may, however, produce many new tillers in response to defoliation (Caldwell et al. 1981; Hodgkinson et al. 1985). The total basal cover of grasslands grazed over a long period may increase or remain unchanged compared with basal cover in adjacent exclosures (Weaver and Albertson 1936; Costello and Turner 1941; Ellison 1960; Vogel and Van Dyne

1966; Pieper 1968; Thornton 1971; Holechek and Stephenson 1983; McNaughton 1984).

Competition need not be decreased by intermediate levels of grazing. In the shortgrass steppe and in the Serengeti, grazing increases tillering and spread by rhizomes and stolons, which does not result in reduced competition (McNaughton 1983*b*, 1984; Lauenroth and Milchunas, unpubl. data). Thus, grazing may not change competition for soil resources in communities with grazing-tolerant species, or it may shift the mode of competition from canopy resources to soil resources, depending on the intensity of grazing and on the proportions of tall, intermediate-height, and short grasses and of tolerant and intolerant grasses in the community. In contrast, tillering responses to grazing in communities of grazing-intolerant species are less well developed, rhizomatous and stoloniferous species are not prevalent, and defoliation results in reduced competitive interactions.

The capacity for regrowth after grazing results, in many cases, from mechanisms that increase the relative availability of resources such as water, nutrients, and light to remaining plants or tissues (McNaughton 1979*b*, 1983*a*; Dyer et al. 1982; Deregibus et al. 1985; Sterner 1986). This indicates the presence of a temporal window of relaxed competitive interactions. The degree and rate of regrowth influences the degree and longevity of competitive relaxation. Slower regrowth means that a given level of disturbance creates a longer temporal window (Huston 1979). Therefore, less frequent or lower levels of defoliation are necessary to achieve a given change in a slowly regrowing community, and the opportunity for establishment of invader species is greater. The degree and rate of regrowth is relatively greater in short species and in grazing-tolerant species (McNaughton et al. 1983; Wallace et al. 1984; Coughenour et al. 1985*a*,*b*; Richards and Caldwell 1985).

THE MODEL

Selection pressures resulting from grazing and from environmental moisture through evolutionary time are two important forces that have shaped the present structure (composition and physiognomy) of grasslands and their relative abilities to withstand grazing (fig. 1). The action of grazing results in both injury to individual plants and changes in community physiognomy. The community reacts to the grazing event directly by death or by regrowth in response to injury and indirectly by a regrowth response to the altered physiognomy. The mode and magnitude of the grazing action and of the community reaction are functions of the past history of the community; these actions and reactions feed back to become part of the history of the community (fig. 1).

Environmental moisture and the evolutionary history of grazing are continuous variables that intersect to form a two-dimensional space exemplified by four extreme cases. The response of plant communities to grazing is mediated through an interaction of convergent or divergent selection pressures along the moisture gradient and factors relating to a tolerance or an intolerance of grazing along the evolutionary-history-of-grazing gradient.

We have chosen data sets from areas representing the four boundary cases of

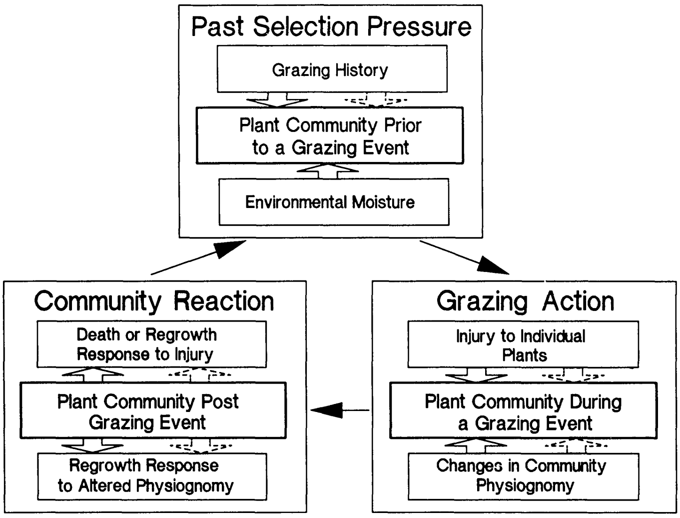


FIG. 1.—Illustration of past selection pressures that shape grassland community structure, the effect of grazing during a grazing event, and the plant community response to the grazing event. The force of the grazing actions and the community reactions can be strong (*solid arrow*) or weak (*dashed arrow*) or a mixture of strong and weak within a box, depending on where the community lies along the axes of environmental moisture and of evolutionary history of grazing. The four boundary cases are examined in the text and illustrated in figures 2 and 3.

the moisture gradient and the evolutionary-history-of-grazing gradient. Examples of the response of plant communities to grazing by large generalist herbivores in grasslands with long evolutionary histories of grazing are examined for the semiarid North American shortgrass steppe and the subhumid grasslands of Africa (table 1). The bunchgrass steppe region of the northwestern United States and the Patagonian steppe represent the semiarid grasslands with short histories of grazing, and the pampa region of Argentina the subhumid grasslands (table 1). We present the model and the experimental evidence for each of the four boundary cases. Finally, we suggest how the model behaves for grasslands between these four boundary cases, and we examine the response to grazing of a grassland that falls outside the definitions of the model.

Semiarid grassland communities with a long history of grazing are dominated by relatively short grasses that have developed in response to the convergent selection pressures of herbivory and semiaridity (fig. 2). Competition is mainly for soil resources. Occupancy of aboveground space is maximized horizontally rather than vertically. Grazing has relatively small effects on community composition and physiognomy because (1) changes in canopy structure are usually insignificant and there is no shift in competitive interactions between soil and canopy resources; and (2) grazing pressures have selected for rapid regrowth following defoliation, thus ensuring a short duration in the relaxation of competitive interactions. The lack of competitive release from the established dominants in the

TABLE 1

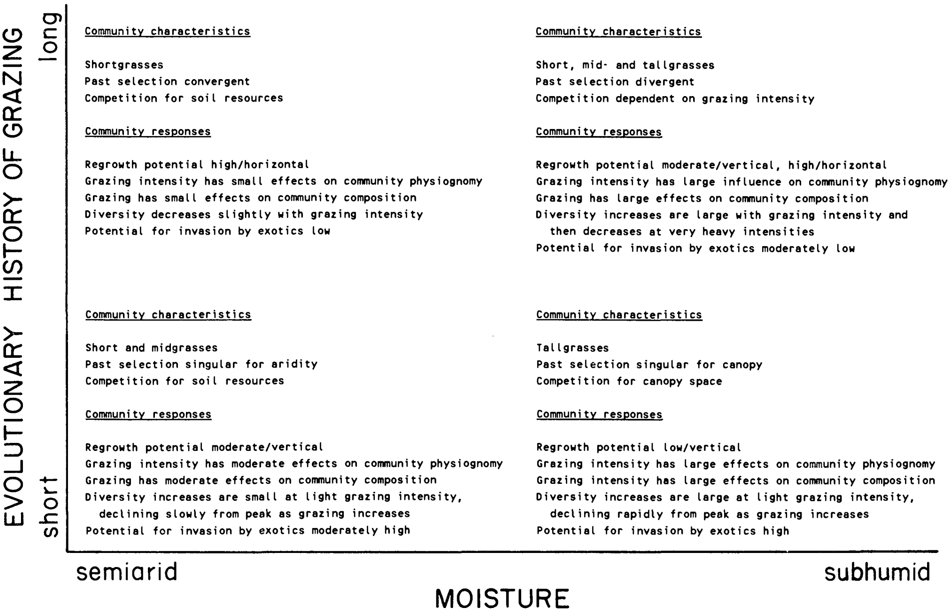
CHARACTERISTICS OF GRASSLANDS REPRESENTING THE FOUR BOUNDARY CASES ALONG GRADIENTS OF THE EVOLUTIONARY HISTORY OF GRAZING AND OF MOISTURE

Grassland Type	Site	Evolutionary History of Grazing Reference	Precipitation ($\bar{x}$ annual, mm)	Above-ground NPP* (g/m^2)	Canopy Height (cm)	Experimental Grazing Intensity†	Years of Treatment	Study
Long history Semiarid	Colorado shortgrass steppe	Stebbins 1981; Mack & Thompson 1982; Coughenour 1985	310	103 ± 23	grazed, 3–5	heavy (60%)	14	Klipple & Costello 1960
						moderate (40%)	24	Hyder et al. 1966
					ungrazed, 5–10	light (20%)	31	Hyder et al. 1975
						none	45	Milchunas & Lauenroth, MS
Long history Subhumid	Serengeti	Raven & Axelrod 1974; Sinclair 1983; Coughenour 1985	500–1000^a	400–1200^a	shortgrass^b grazed, 2 ($\bar{x}$), 3 (max); ungrazed, 12 ($\bar{x}$), 39 (max) mid-height grazed, 9 ($\bar{x}$), 45 (max); ungrazed, 21 ($\bar{x}$), 58 (max)	none	12	McNaughton 1979*a*, 1983*b*
						?		
	Uganda *Themeda*/*Heteropogon*		714	?				Thornton 1971
	Uganda *Sporobolus*/*Setaria*		?	?		none	3	Spence & Angus 1970
						?	24	Hatton & Smart 1984
Short history Semiarid	Washington bunchgrass steppe	Osborne 1953; Daubenmire 1970	250	50–70 live biomass		none moderate	4	Rickard 1985
	Oregon bunchgrass steppe	Mack & Thompson 1982; Markgraf 1985		100^c		none ?	36	Sneva et al. 1984
	Argentina Patagonian arid steppe		138	66		none light heavy	20	Schlichter et al. 1978
Short history Subhumid	Argentina flooding pampa	Stebbins 1981; Markgraf 1985	924	532		none moderate	4	Sala et al. 1986

SOURCE.—*a*, McNaughton 1985; *b*, McNaughton 1984; *c*, Lauenroth 1979.

* Net primary production.

† The experimental grazing intensities apply to all studies at each site.



Community characteristics

Shortgrasses
Past selection convergent
Competition for soil resources

Community responses

Regrowth potential high/horizontal
Grazing intensity has small effects on community physiognomy
Grazing has small effects on community composition
Diversity decreases slightly with grazing intensity
Potential for invasion by exotics low

Community characteristics

Short, mid- and tallgrasses
Past selection divergent
Competition dependent on grazing intensity

Community responses

Regrowth potential moderate/vertical, high/horizontal
Grazing intensity has large influence on community physiognomy
Grazing has large effects on community composition
Diversity increases are large with grazing intensity and then decreases at very heavy intensities
Potential for invasion by exotics moderately low

Community characteristics

Short and midgrasses
Past selection singular for aridity
Competition for soil resources

Community responses

Regrowth potential moderate/vertical
Grazing intensity has moderate effects on community physiognomy
Grazing has moderate effects on community composition
Diversity increases are small at light grazing intensity, declining slowly from peak as grazing increases
Potential for invasion by exotics moderately high

Community characteristics

Tallgrasses
Past selection singular for canopy
Competition for canopy space

Community responses

Regrowth potential low/vertical
Grazing intensity has large effects on community physiognomy
Grazing intensity has large effects on community composition
Diversity increases are large at light grazing intensity, declining rapidly from peak as grazing increases
Potential for invasion by exotics high

FIG. 2.—Grassland community characteristics and responses to grazing along gradients of moisture and of evolutionary history of grazing.

community reduces the capacity for invasion by exotics. Therefore, the function describing diversity with increasing grazing intensity is linear with a small negative slope (fig. 3). Rare species that are less tolerant of grazing are eliminated as grazing intensity increases, but the major components of the plant community do not shift.

The semiarid shortgrass steppe of the North American Great Plains is dominated by *Bouteloua gracilis* and *Buchloe dactyloides*, two clonal species that are tolerant of drought and grazing and grow to an average height of only 3–10 cm. Long-term controlled-grazing experiments (table 1) were established in north-central Colorado at the Central Plains Experimental Range in 1939 on areas that were not previously overgrazed (Klipple and Costello 1960). No grazing or light-, moderate-, or heavy-grazing treatments did not differ in community composition in 1940–1942, 1946–1948, 1952–1953, or 1962–1963 (Klipple and Costello 1960; Hyder et al. 1966). Sampling from 1964 to 1966 continued to reveal no significant effects of grazing, with only minor alterations detected in 1967–1970 (Hyder et al. 1975). These studies suggest that grazing did not affect plant community composition. Our recent studies of these grazing treatments indicate that subtle changes in community composition are still occurring after 45 years. Basal cover of the dominant grasses and total vegetation increased, whereas those of forbs decreased with heavy grazing. The increase of grasses with grazing was not all at the expense of a decrease in cover of other species because total cover increased. McNaughton (1979*a*) termed these other grass species *grazophiles*. Diversity (H')

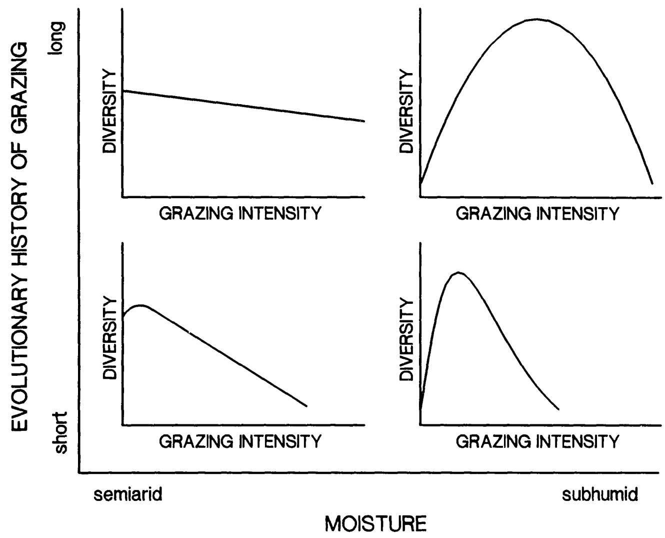


FIG. 3.—Plant diversity of grassland communities in relation to grazing intensity along gradients of moisture and of evolutionary history of grazing. Increments in the diversity axis are equal in all cases, but equal specific values are not implied; that is, relative response, not absolute diversity, is implied.

increased as grazing intensity decreased as a result of both decreased dominance and increased richness.

Subhumid grasslands with a long history of grazing are composed of intermediate-height, short, and tall grasses as a result of divergent past selection for grazing tolerance and canopy dominance (fig. 2). In the absence of grazing, a few tall species dominate the community. Moderate grazing creates a mosaic pattern, with shortgrasses predominating in relatively heavily grazed patches, mixtures of grasses in moderately grazed patches, and tallgrasses where ungrazed growth deters grazing because of high ratios of stem tissues to leaf tissues or dead to live tissues. The mixture of shortgrasses and tallgrasses and, therefore, of canopy structure, regrowth potential, and mode of regrowth by horizontal spread or vertical reestablishment results in a mosaic pattern in the duration of competitive relaxation, in the mode or mixtures of modes of competitive interactions, and in the potential for the establishment of exotics. Diversity is low at low grazing intensities because a few species dominate the canopy (fig. 3). Diversity is high at moderate grazing intensities because of the mosaic of growth forms. With increasingly heavy grazing, diversity declines as shortgrasses dominate a greater proportion of the community.

Changes in community physiognomy and species composition inside and outside grazing exclosures in African grasslands differ from those observed in the shortgrass steppe of North America. McNaughton (1979*a*, 1983*b*) assessed vegetation inside and outside 12-yr exclosures in several communities of the Serengeti grasslands and observed that organization and structural properties had changed radically because of protection; in some cases, species composition had changed almost completely. Low-growing prostrate and short caespitose species dominated heavily grazed areas, whereas protected areas were dominated by "stemmy species capable of overtopping less erect species and thereby eliminating the latter by competition for light" (McNaughton 1979*a*, p. 62). Belsky (1986*b*) observed that mats of *Andropogon greenwayi* disappeared from within an exclosure, whereas *Pennisetum stramineum* tallgrass, which was sparse in the grazed community, made up nearly 50% of the cover. The rapid switching from plants maximizing horizontal occupation of space near the ground to canopy competitors has also been reported in other African grasslands. The extermination of hippopotamuses in Queen Elizabeth National Park, Uganda, resulted in large decreases in the basal cover of grasses and increased bare ground after only 1 yr (Thornton 1971). Four years after the removal of the hippopotamuses the basal cover of "carpet grass" decreased greatly with a concurrent increase in bunchgrass cover. Large changes in species composition and canopy structure have also been reported for *Sporobolus-Setaria* grasslands in Murchison Falls National Park, Uganda, after only 2 yr (Spence and Angus 1970) or after 24 yr (Hatton and Smart 1984) of exclosure from grazing. Working in *Themeda* grasslands of Uganda, Kenya, and Tanzania, Heady (1966) observed that dominance by intermediate-height, tall, or short grasses was not closely related to soils or climate but was primarily a result of grazing intensity. Tall *Themeda* plants were present and abundant in parts of each study area, and conversely, even thick stands of tallgrasses usually contained a few shortgrass individuals. Belsky, however, concluded that "although moisture, grazing, and soil were the major determinants of vegetational composition at the regional and catenary scales in the Serengeti ecosystem, termite activity and growth habits of the plants were dominant locally" (1983, p. 150).

Differences in plant diversity inside and outside of exclosures were observed for several community types in the Serengeti (McNaughton 1983*b*; Belsky 1986*c*). Diversity declined in all exclosures. Equitability dropped sharply, although species richness was not significantly different. McNaughton attributed this to replacement by tall species in ungrazed areas formerly dominated by short species when the area had been grazed. Pattern diversity, rather than point diversity, was found to be the major contributor to stand diversity.

The response of subhumid African grasslands to changes in grazing intensity contrasts with the response observed in the shortgrass steppe of North America. Large changes in species composition and community physiognomy occur rapidly after changes in grazing regimes in African grasslands, whereas changes in the shortgrass steppe are slow and subtle. In these two grasslands with their long histories of grazing, grazing has resulted in opposite changes in diversity.

Belsky (1986*a*) raised questions concerning the effects of grazing on compensatory growth of plants. Our model is not based on absolute overcompensation; rather, it is based on relative differences in rates and modes of regrowth and the influence of these on competitive relationships among plants. It demonstrates the difficulty of generalizing along single gradients of environmental moisture or of the evolutionary history of grazing.

Although often considered semiarid, the driest grasslands of the Serengeti have nearly double the precipitation and four times the ANPP of the shortgrass steppe (table 1). The shortgrass region of the Serengeti falls between mixed-grass and tallgrass prairies in North America in terms of ANPP and precipitation (see the table; Sims and Singh 1978; Sims et al. 1978), suggesting that this region of the Serengeti would support tall growth forms in the absence of heavy grazing. We have temporarily lumped the Serengeti grasslands (500–1000 mm of precipitation) for the general comparison with the shortgrass steppe, even though we would expect different responses to grazing within Serengeti grasslands. We address this when we describe intermediate locations along the axes of figures 2 and 3.

Semiarid grasslands with a short history of grazing are dominated by shortgrasses and intermediate-height grasses that have been selected for their tolerance to drought. Semiaridity limits development of full canopy structure; therefore, grazing has moderate effects on community physiognomy. Since adaptations for drought tolerance also confer some degree of grazing resistance, but regrowth potential is low and does not occur through horizontal spread, changes in community composition with grazing are moderate. We term changes in physiognomy and composition moderate in this community because they are less than what occurs in the subhumid type with a short evolutionary history of grazing but greater than what occurs in semiarid grasslands with a long history of grazing (figs. 2, 3). The potential for invasion by exotics is moderately high because of the relatively low rate of regrowth by dominants. This community type exhibits a small increase in diversity at low grazing intensities, declining slowly from the peak as grazing intensity increases.

The semiarid regions of the northwestern United States and southwestern Canada are grasslands with a short evolutionary history of grazing (table 1). Before the introduction of cattle, these grasslands were dominated by caespitose grasses and contained few rhizomatous grasses (Tisdale 1947; Daubenmire 1970). The inability of these grasses to cope with heavy grazing allowed the invasion and eventual dominance of many areas by Eurasian weeds (Daubenmire 1940, 1970; Ellison 1960; Mack 1981; Mack and Thompson 1982).

Heavy grazing of the bunchgrass steppe of western North America was extensive during the early 1900s. Few areas remained in a relatively undisturbed condition. Community composition in one such undisturbed grassland after 4 yr of moderate grazing was not significantly altered (Rickard 1985). The invasion of exotics occurred only in areas around watering tanks that were heavily grazed and trampled. After 36 yr of moderate grazing and grazing-exclosure treatment in *Artemisia-Agropyron* habitat in eastern Oregon, species composition inside and outside the exclosures showed parallel temporal changes (Sneva et al. 1984). Although these grasslands can be invaded by exotics if heavily grazed, moderate grazing does not produce the large, immediate effects on community composition or physiognomy that are observed in subhumid grasslands. Changes in community structure are, however, much greater than those that occur in semiarid grasslands with long evolutionary histories of grazing.

Changes in diversity with grazing intensity were not reported for studies in the northwestern United States. However, the Patagonian steppe in southern Argentina is another example of a semiarid grassland with a short evolutionary history of grazing (Markgraf 1985). Comparison between 20-yr-old exclosures and areas subjected to light and heavy grazing showed a clear decrease in species number, species diversity, and equitability with grazing intensity (Schlichter et al. 1978).

Subhumid grasslands with a short evolutionary history of grazing have the greatest potential for being altered by grazing (fig. 2). These communities are composed of tallgrasses that do not tolerate well grazing or aridity. In the past, there was primarily a single selection pressure for canopy dominance, but grazing significantly affects canopy structure. Slow rates of regrowth and a lack of flexibility in the modes of regrowth following defoliation result in a high potential for invasion by exotics. The response of inferior canopy competitors to canopy removal and the increase in exotics produce large increases in diversity at relatively low grazing intensities (fig. 3). Diversity declines rapidly thereafter as grazing mortality becomes a relatively greater force than the relaxation of competitive interactions in shaping community composition.

The flooding pampa of Argentina is representative of subhumid grasslands with a short evolutionary history of grazing (table 1). Grazing in this system resulted in a relatively small reduction in total leaf area, whereas the largest response was observed in the distribution of leaves in the canopy (Sala et al. 1986). In the grazed areas, most of the green material was concentrated in the 0–5-cm layer, but in the ungrazed treatments, the largest portion of the leaf area was in the 10–30-cm layer. Many small tussocks characteristic of the grazed areas were replaced by a few large ones in the ungrazed areas. These changes in canopy structure resulted in changes in the microenvironment. The quantity of light reaching the soil surface increased by 50% (Deregibus et al. 1985). The effect of grazing on leaf area and basal cover was accounted for by changes in species composition and in the structure of existing species. After 4 yr of exclosure, cover of grasses and sedges increased, dicot and monocot annuals were replaced by perennials, and exotic species were greatly reduced. Grazed areas had higher diversity than ungrazed areas, primarily because of the greater numbers of forbs. In contrast, reduced dominance by grasses and increased number of forb species were the primary reasons for the greater diversity of ungrazed areas of the shortgrass steppe.

Figures 2 and 3 represent the boundary cases of moisture and grazing history for climatically determined grasslands. Many grasslands are at intermediate locations along the environmental-moisture axis or the axis of the evolutionary history of grazing. Smooth or punctuated, linear or nonlinear transitions from one case, through the intermediate zones of the model axes, to the other case are possible. Changes in plant community response to grazing with increasing environmental moisture are based on the increasing importance of competition for light, the greater potential for a grazing event to alter community physiognomy and for plants to respond to this alteration, and the relatively greater intolerance of grazing by many tallgrasses. The change in model conditions from semiarid to subhumid can be described as a function of canopy development with increasing moisture. We envision this function as a sigmoid curve. Increasing moisture from semiarid conditions would at first involve increases in both basal cover and canopy height. A region of moisture would be reached where small increases would have relatively large effects on light intensity within the canopy. When light compensation points are reached, additional increments in moisture influence only the length of time in which light within the canopy is below the compensation point. Therefore, the expected rate of change in model conditions from semiarid to subhumid would be parabolic.

In our discussion of African grasslands, we temporarily lumped Serengeti grasslands receiving 500–1000 mm of precipitation for the purpose of general comparison with the boundary case of the semiarid shortgrass steppe. The drier regions of the Serengeti were described as comparable to productive mixed-grass prairies of North America in terms of ANPP and precipitation. In exclosures on shortgrass Serengeti grasslands, canopy heights lie between those for shortgrass steppe and tallgrass Serengeti grasslands (table 1). Greater diversity in grazed areas compared with exclosures has been reported for both shortgrass Serengeti grasslands (McNaughton 1983*b*; Belsky 1986*c*) and the mixed-grass prairie of North America (Collins and Barber 1985). Data comparing the response of vegetation to levels of grazing within these grasslands, or between grasslands of different environmental moisture, are not available. On the basis of our model, we predict a diversity curve with a peak that is lower and left-skewed compared with that for the subhumid case with a long history of grazing described in figure 3, and we predict differences in changes in community composition and physiognomy that are intermediate between those described for semiarid and subhumid grasslands with long histories of grazing in figure 2.

The transition in responses to grazing across the evolutionary-history-of-grazing axis in figures 2 or 3 are not easily described. In a review of theoretical models, Roughgarden (1983) examined some of the many factors that may determine the rate and outcome of coevolution in the context of the effect of coevolution on traits that determine how populations interact and on the abundance and distribution of the interacting populations. Roughgarden concluded that "there is a glaring shortage, even absence, of good models for many kinds of coevolutionary situations, including the plant-herbivore and plant-pollinator interactions" (1983, p. 64). Experimental evidence is also lacking. This would require controlled, consistent, multi-intensity grazing experiments across a range of levels of environmental moisture and evolutionary history of grazing. Our inability to predict transitions across the evolutionary-history-of-grazing axis is a weakness of our current model.

Are there examples of climatically determined grasslands that do not respond according to the predictions of our model? Although we do not know of any, two situations are possible. In the first situation, factors other than environmental moisture may operate with the evolutionary history of grazing to determine the response of the plant community to grazing. The exclosure of grazing animals from sugar-limestone outcrops on a plateau summit in England did not result in substantial changes in community structure, even though precipitation is high (Elkington 1981). The sandy, mineral-nutrient-poor soil and low temperatures were the factors contributing to the lack of change in exclosures. This edaphically controlled, isolated grassland occurs in an area that climatically would not be grassland (see Walter 1979). It is possible that the combined effects of semiaridity and a severe mineral-nutrient deficiency in the soil could result in a sparsely populated community in which competitive exclusion would not occur even in the absence of disturbance. However, substantial evidence indicates that competition among plants is both common and strong enough to be readily detected in dry grassland and even deserts (Fowler 1986). Furthermore, we are not comparing the importance of competition across a moisture gradient. Rather, we are comparing the relative importance of the modes of competition within a community and then comparing this across a moisture gradient. In the second situation, frequent fires or other disturbances may maintain a plant community at its potentially peak diversity. The additional effect of grazing would decrease diversity by causing a shift toward population reduction.

RELATIONSHIP TO OTHER HYPOTHESES

Disturbance Models

The Huston, predation, and intermediate-disturbance hypotheses of species diversity predict the occurrence of a frequency of disturbance at which diversity is greatest. Our model is consistent with this prediction. However, it is difficult to define grazing as a disturbance across communities with different histories of grazing or within communities having a long evolutionary history of grazing. If the lack of grazing is considered a disturbance in a community that has evolved with grazing, then diversity should increase when grazing is reduced from the nominal. Although this is true for the shortgrass steppe, it is not for the Serengeti. However, if grazing is considered a disturbance in a community that has evolved with grazing, then current disturbance hypotheses do not accurately predict the responses of the shortgrass steppe to grazing. Disturbance hypotheses predict an increase in diversity at a level of disturbance that is predicated on a decrease in competitive exclusion. Grazing may not always decrease competition.

In the Serengeti, diversity declines with the exclusion of grazing. Removal experiments show that grazing does not eliminate competition between plant species (McNaughton 1983*b*); however, although intermediate levels of grazing may not reduce the overall level of competition, they may alter the modes of competition. Even though grazing is a disturbance to an individual grass plant, it is not a disturbance at the community level, because negative effects on tallgrasses are compensated for by positive effects on shortgrasses, and competitive interactions are not eliminated. Many of the species colonizing areas of human disturbance in the Serengeti were ruderals or weeds that rarely grew where natural disturbances had occurred, even when these occurred only a few meters from a seed source (Belsky 1987). The difference between this situation and that predicted by the Huston hypothesis is that the rapid regrowth and lack of a relaxation in competitive exclusion result in major, not minor, changes in community composition and diversity.

In the shortgrass steppe, diversity declines with increasing grazing intensity. Disturbance hypotheses predict that grazing initially decreases competitive exclusion and increases diversity. The increase in density of dominants and of total basal cover with grazing suggests that competitive interactions may not be lowered. Disturbance species occur at low densities on both the grazed and ungrazed treatments but in large numbers on small-mammal diggings, on ant mounds, around water-tank areas, and along roadsides. The opportunity exists for increases in disturbance species, but these species do not significantly contribute to the community composition of grazed or ungrazed areas.

Thus, moderate grazing may not be a disturbance on either the Serengeti or the shortgrass steppe, because neither the rapid switching capabilities of grasses on the Serengeti nor the increases in the heavily grazed dominants of the shortgrass steppe reduce competitive interactions. Alternatively, moderate grazing may be considered a disturbance in the Serengeti but not on the shortgrass steppe because semiaridity and adaptation to grazing are complementary selection pressures, but grazing and competition for light in subhumid communities are divergent selection pressures. In any case, defining grazing as a disturbance in different communities is a problem inherent in applying disturbance models to large-herbivore grazing of grasslands, but it is not inconsistent with our model. Our model is not a disturbance model but a grazing model. Contrasting it with disturbance models emphasizes the difficulty in defining grazing as a disturbance using even more liberal, safe definitions, such as changes in species composition or altered competitive relationships. Equilibrium–domain-of-attraction models suffer from the lack of objectivity in defining a threshold at which a periodicity becomes a disturbance (Karr and Freemark 1984; Sousa 1984). There is the additional problem of how the force interacts with the selection pressures that have shaped the community. That is, given two communities subjected to the same level, frequency, and duration of a particular force, the resulting adaptations and the manner in which the communities respond to an alteration of the force depend on the degree of convergent, neutral, or divergent adaptations to the particular force arising from the many other forces operating on the communities.

Predator-Mediated Coexistence Models

Caswell (1978) reviewed studies that failed to demonstrate predator-mediated coexistence or actually showed a decrease in the number of coexisting species under the impact of predation (Harper 1969; Paine and Vadas 1969; Hurlbert et al. 1972; Adicott 1974; Janzen 1976). Caswell developed and made comparisons between an open-cell, nonequilibrium model and a closed-cell, equilibrium model that explain these anomalies. Nonequilibrium models rely on the temporary action of predation. New cells are opened for colonization and then released from predation pressure to allow nonequilibrium population growth. If the predation pressure does not disappear periodically, the nonequilibrium effect will not be seen. Instead, within the cell, a new equilibrium is established, having no more and perhaps fewer species than occur in the absence of predation. As one example, Caswell used the situation in which grazing herbivores are in enclosed pastures. At high densities of grazers, the entire pasture is treated as a single cell, receiving uniformly high predation pressure, which results in a negative effect on coexistence.

Is the decline in diversity with grazing intensity on the shortgrass-steppe grazing treatments simply a result of a single-cell equilibrium effect? The lightly, medium-, and heavily grazed pastures are each 130 ha. Even in the heavily grazed pastures, large differences occur in grazing pressure between and within topographical position. Furthermore, grazing intensities on swales and ridgetops shift seasonally (Senft et al. 1985). These pastures can hardly be described as a single-cell equilibrium system.

SUMMARY

Current disturbance models do not adequately account for the wide range of responses by grassland plant communities to grazing by large generalist herbivores. The evolutionary history of grazing, an important factor in the response of grasslands to grazing, has not been explicitly addressed. Grazing history alone, however, is not a good predictor of plant-herbivore interactions. Interactions occur along gradients of convergent to divergent selection pressures with increasing environmental moisture and of intolerance to tolerance of grazing with increasingly long evolutionary histories of grazing.

We suggest that feedback mechanisms between plants and grazing animals are well developed in grasslands with long evolutionary histories of grazing. Feedback mechanisms are manifest in the rapid switching capabilities (of plant species and modes of competition) of subhumid grasslands with long evolutionary histories of grazing and divergent selection pressures. Switching capabilities do not exist in semiarid grasslands with long evolutionary histories of grazing and convergent selection pressures. Rather, for heavily grazed dominant species dominance increases. Feedback mechanisms are not well developed in systems with short evolutionary histories of grazing. In these cases, the differences in response to grazing by semiarid and subhumid situations arise primarily from differences in the grazing tolerance of plants adapted to semiaridity or of plants adapted to competition for light and from the different effects of grazing on canopy structure.

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