

THE EFFECT OF HERBIVORY ON VEGETATION STRUCTURE

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Abstract

Grazing by large herbivores is one of the major determinants of the structure of grasslands. The objectives of this paper are: (1) to assess the effect of grazing by large domestic herbivores upon the structure of grasslands using as an example the subhumid grassland of the flooding pampa in Argentina; (2) to evaluate the mechanisms involved in the changes of structure determined by grazers; (3) to compare the effect of grazing upon vegetation structure along different temporal and spatial scales.

One of the largest responses to grazing in the flooding pampa was observed in the vertical and horizontal distribution of leaves in the canopy. Total values of basal cover or leaf area changed very little with grazing. Changes in structure were accounted for by the changes in vigor as well as by changes in species composition. Grazing resulted in the introduction of a large number of exotic species.

In subhumid grasslands the response to grazing is related to changes in the light quality underneath the canopy which modifies the rate of tillering, tiller elongation and seed germination.

Responses to herbivory at different time scales are not independent but form a hierarchy. Slow responses, in evolutionary time constrain fast responses in ecological and ontogenetical time.

Based upon evolutionary grazing history and moisture conditions a model is presented of the effect of grazing upon vegetation structure. Contrasting examples in which grazing increased or decreased spatial heterogeneity are presented along with hypotheses explaining these differences.

Introduction

Herbivores are one of the major determinants of the structure of vegetation. Their effect varies across vegetation types and it is maximum in grasslands. Unlike forests, where loss of biomass to herbivores is usually less than 10%, grasslands are frequently characterized by herbivory rates of 50% or more of the above-ground net primary production (McNaughton 1976, 1985) and perhaps 25% of the belowground productivity (Coleman *et al.* 1976; Ingham and Detling 1984; Scott *et al.* 1979). Herbivores affect the structure of vegetation in at least two ways: directly through consumption and indirectly through a variety of mechanisms such as regeneration of limiting nutrients or changes in the light environment (Deregisus *et al.* 1985; Sterner 1986).

Most of the grassland management techniques modify vegetation structure (Harper 1971; Stoddart *et al.* 1975). Burning, chaining or spraying selective herbicides are often aimed at decreasing the shrub component, which supposedly will increase grass production. Fertilization, depending upon the concentration of major elements, usually affects the life-form composition besides modifying total productivity.

There is a tight link between the structure of grasslands and their function. Vegetation structure is the result of adaptations to the environment by the biotic components and their influences on the abiotic conditions. Vegetation structure

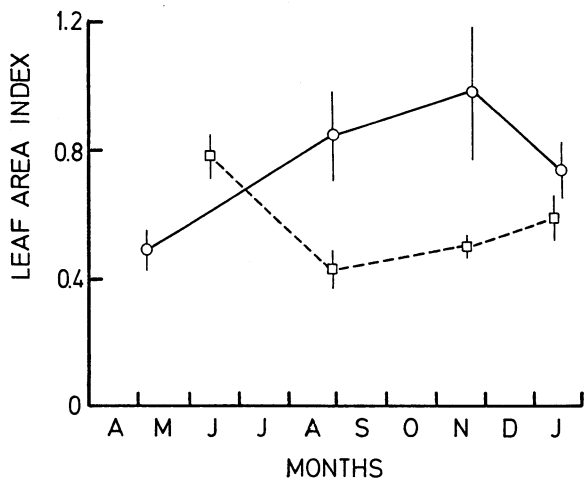


Fig. 1. Leaf area index (± 1 standard error) through the year for the grazed (\square ---) and ungrazed areas (\circ —).

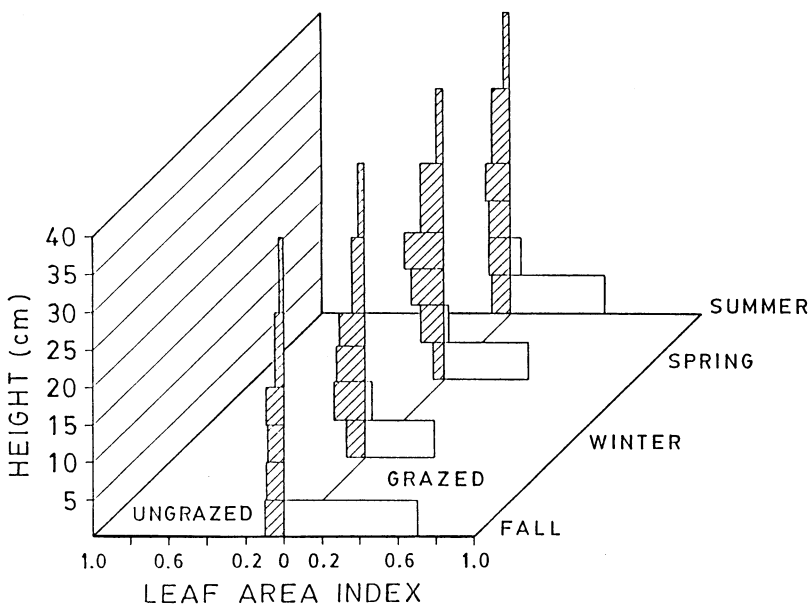


Fig. 2. Leaf area index for different layers from soil level up to 40 cm for the ungrazed areas (shaded bars) and grazed areas (empty bars) along the four seasons.

is one of the influential determinants of ecosystem processes which in turn shape the structure of vegetation.

The objectives of this paper are: (1) to describe the effects of grazing by large domestic herbivores upon vegetation structure; (2) to evaluate the mechanisms involved in the changes in structure determined by grazers and (3) to compare the effect of grazing upon vegetation structure along different temporal and spatial

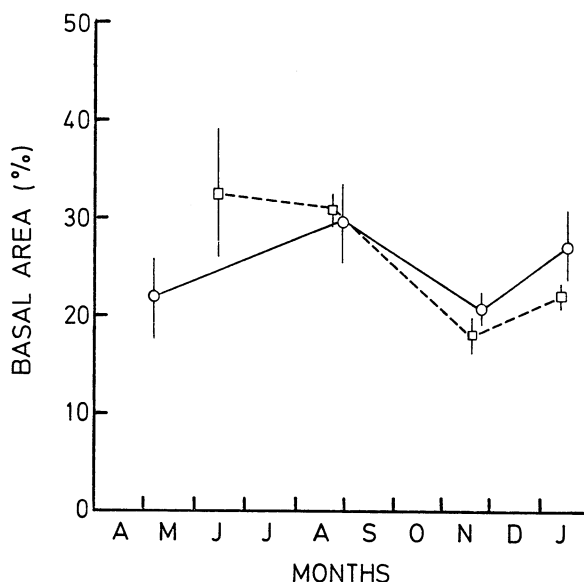


Fig. 3. Basal area (± 1 standard error) through the year for the grazed (\square ---) and ungrazed areas (\circ —).

scales. To accomplish these objectives the paper will focus on a particular grassland located in the flooding pampa in Argentina. First, I will describe the effect of large herbivores upon leaf area index, basal area and species composition as well as their vertical and horizontal distribution. Second, I will look at possible mechanisms which may account for a fraction of the observed changes in structure. Thirdly, I will compare the response of grasslands to grazing at three time scales and two spatial scales emphasizing the relationships among scales.

A description of the effects of herbivores upon vegetation structure: the case of the flooding pampa

The flooding pampa is a region in the eastern portion of Argentina of approximately 5 million ha which is covered in 80% of its area by native grasslands (León *et al.* 1984). It is a temperate region with a mean annual precipitation of 920 mm and mean monthly temperatures ranging from 7°C in July–August to 22°C in January. Mesic conditions and the small range between winter and summer temperatures are mainly the result of its proximity to the ocean. Flat topography, along with low hydraulic conductivity in the B horizon, determine the frequent occurrence of both flooding events and droughts.

Vegetation is composed of an intricate mosaic of plant communities associated to small differences in topographical position (15–20 cm). Two communities mainly form this mosaic; one characterized by *Piptochaetium montevidense*, *Ambrosia tenuifolia*, *Eclipta bellidiodes* and *Mentha pulegium* which is located on

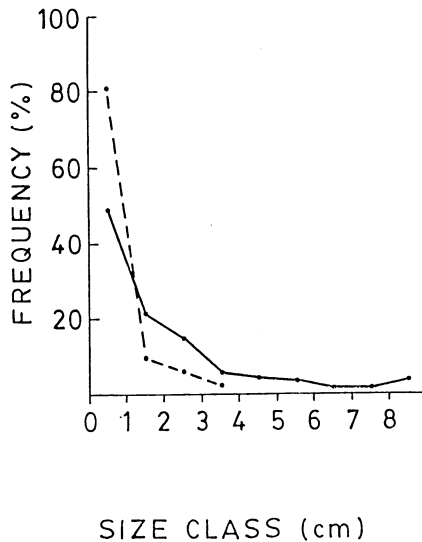


Fig. 4. Frequency distribution of size classes of the interception of individual plants with the line used to estimate basal area. Frequency distribution of size classes of interception is related with the frequency distribution of classes of diameter of individuals at the base level. For the grazed (□---) and ungrazed areas (○—).

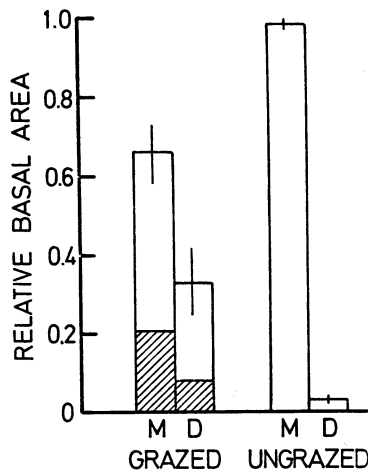


Fig. 5. Relative basal area of monocots (M) and dicots (D), annuals (shaded bars) and perennials (empty bars) for the grazed and ungrazed areas.

the uplands and the other by *Mentha pulegium*, *Leontodon nudicaulis* and *Paspalidium paludivagum* located on the lowlands (León 1975; nomenclature follows this publication and Cabrera 1968).

Cattle usually graze these grasslands year long. This has been a pervasive practice throughout the region, leaving no relict grasslands. Experiments aimed at as-

Table 1. Basal area by species (± 1 standard error) for grazed and ungrazed areas of the upland community. Boxes show the species which decrease in the ungrazed condition. Species with no values entered were not recorded in the spring sampling but in another season.

Species	Grazed Spring	Ungrazed Spring
Natives		
Cool-season species		
<i>Stipa neesiana</i>		0.6 \pm 0.6
<i>Danthonia montevidensis</i>	1.8 \pm 0.7	3.8 \pm 1.2
<i>Heleocharis</i> sp.	0.4 \pm 0.1	0.3 \pm 0.3
<i>Briza subaristata</i>	0.9 \pm 0.1	3.5 \pm 0.7
<i>Carex phalaroides</i>	1.0 \pm 0.1	4.3 \pm 3.3
<i>Stipa papposa</i>	0.2 \pm 0.2	
<i>Sisyrinchium platense</i>	0.2 \pm 0.1	
<i>Gamochaeta spicata</i>	0.6 \pm 0.6	
<i>Trifurcia labue</i>	0.1 \pm 0.1	
<i>Cypella herbertii</i>		
<i>Eryngium ebracteatum</i>	0.1 \pm 0.1	
<i>Lilaea scilloides</i>	0.1 \pm 0.1	
Warm-season species		
<i>Sporobolus indicus</i>	0.6 \pm 0.1	1.1 \pm 0.8
<i>Bothriochloa laguroides</i>	2.2 \pm 0.6	0.1 \pm 0.1
<i>Leersia hexandra</i>		0.1 \pm 0.1
<i>Paspalum vaginatum</i>		
<i>Panicum gouinii</i>	0.1 \pm 0.1	
<i>Ambrosia tenuifolia</i>	0.5 \pm 0.1	0.3 \pm 0.1
<i>Paspalidium paludivagum</i>		
<i>Distichlis scoparia</i>		4.8 \pm 2.2
<i>Panicum milioides</i>		0.2 \pm 0.1
<i>Stenotaphrum secundatum</i>	0.1 \pm 0.1	
<i>Dichondra repens</i>	0.2 \pm 0.1	
<i>Eclipta bellidiodes</i>	0.2 \pm 0.1	
<i>Aster squamatus</i>	0.1 \pm 0.1	
<i>Paspalum dilatatum</i>		
<i>Chaetotropis elongata</i>		
<i>Setaria geniculata</i>	0.1 \pm 0.1	
<i>Gerardia communis</i>		
<i>Spilanthes stolonifera</i>	0.1 \pm 0.1	
<i>Phyla canescens</i>	0.1 \pm 0.1	
<i>Apium leptophyllum</i>		
Exotics		
Cool-season species		
<i>Plantago lanceolata</i>	1.5 \pm 0.3	
<i>Leontodon taraxacoides</i>	0.8 \pm 0.6	
<i>Mentha pulegium</i>	0.8 \pm 0.8	
<i>Lolium multiflorum</i>	1.7 \pm 0.5	
<i>Oxalis</i> sp.		
<i>Vulpia dertonensis</i>	1.5 \pm 0.2	
<i>Briza minor</i>	0.1 \pm 0.1	
<i>Linum usitatissimum</i>	0.2 \pm 0.1	
<i>Medicago polymorpha</i>		
<i>Lytbrum hyssopifolia</i>	0.1 \pm 0.1	
Warm-season species		
<i>Bupleurum tenuissimum</i>		

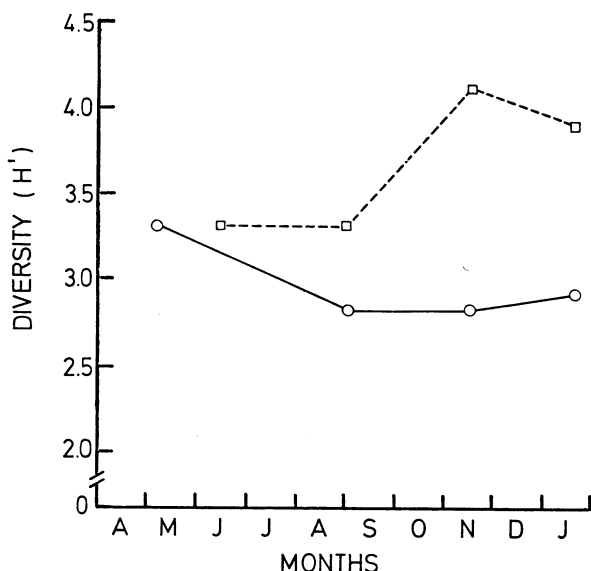


Fig. 6. Species diversity (H') through the year for the grazed (\square ---) and ungrazed areas (\circ —).

sessing the effect of grazing upon vegetation structure were based on the comparison between grazed areas and exclosures.

One of the effects of excluding large domestic herbivores has been a small increase in total leaf area index (LAI) (Fig. 1) (Sala *et al.* 1986). Annual average LAI increased 30% after four years of exclosure. The distribution of leaves in the canopy presented a larger effect of grazing than total LAI (Fig. 2). In the grazed area, most of the green material was concentrated in the 0–5 cm layer whereas in the ungrazed area the largest portion of the leaf area was in the 10–30 cm layer. The small difference in total LAI and biomass between the grazed and ungrazed areas along with the large difference in vertical distribution resulted in a sharp decrease of biomass concentration (2.3 to 0.5 mg cm^{-3} , respectively).

Total basal area presented no differences between grazed and ungrazed areas (Fig. 3). The major effect of grazing upon basal area was observed, as in the case of LAI, not on the total value but on its distribution. The average size of tussocks was higher on ungrazed than on grazed areas (Fig. 4). Grazing exclusion resulted in the replacement of a large number of small tussocks by few large ones.

Changes in LAI and basal area due to grazing were accounted for by changes in vigor and growth form as well as by changes in species composition. As a result of the exclusion of large herbivores, monocotyledoneae increased from 65% to 95% of total cover (Fig. 5). This compares well with results of Willems (1983) from chalk grasslands where monocotyledoneae contributed 40% to total above-ground phytomass in sheep-grazed sites as against 85% in exclosures. In the exclosure in the flooding pampa annuals, both dicots and monocots, were replaced by perennials. The major effect of the exclosure upon species composition was observed in a drastic reduction of all exotic species along with native planophiles (Table 1). In contrast, there was an increase of major native perennial grasses. The

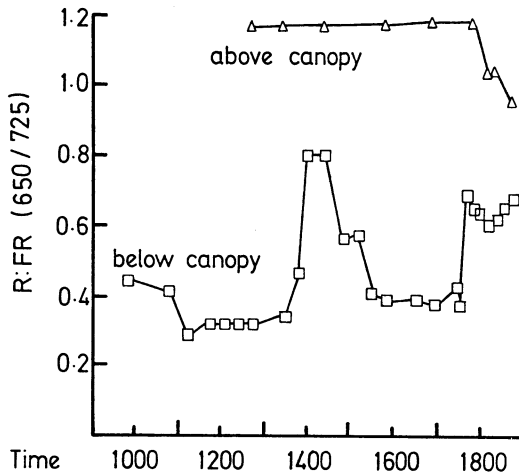


Fig. 7. R:FR quantum flux ratio above and below the canopy of a temperate grassland on a clear day in the fall. Redrawn from Deregibus *et al.* 1985.

same species which occurred on the ungrazed area, occurred on the grazed area. The difference between these two areas was given by a set of species presumably adapted to grazing which appeared on the grazed conditions. The exotic species which responded to grazing were cool-season species originating in the Mediterranean region. Diversity was higher on grazed areas than on ungrazed areas (Fig. 6). There are several examples in which grazing determines higher species diversity (McNaughton 1979; Picket 1980; During and Willems 1984).

Mechanisms of the changes in structure caused by grazing

The major changes in structure caused by grazing in the flooding pampa were observed in the distribution of leaf area and basal area and they were the result of changes in growth form and species composition. Changes in growth form are mainly the result of indirect effects of herbivory. Grazing determines better water supplies, better nutrient supplies and, at the same time, increases light intensity and modifies its quality for the remaining tissues. These indirect effects lead to compensatory growth (McNaughton 1983a). The importance of these three factors, water, nutrients and light, varies among systems and among processes within a system (McNaughton *et al.* 1983).

The effect of herbivory upon growth form in the flooding pampa occurs mainly as a result of alterations of light quality. There is evidence for crops and grasslands that light intensity and quality change throughout the canopy (Holmes and Smith 1977; Deregibus *et al.* 1985). The light beneath the canopy is poorer in red than above the canopy. For an ungrazed grassland in the flooding pampa, which intercepted 80% of the incoming radiation, the red (R): far red (FR) ratio had a daily average of 1.2 above the canopy and 0.4 beneath the canopy (Fig. 7). The same

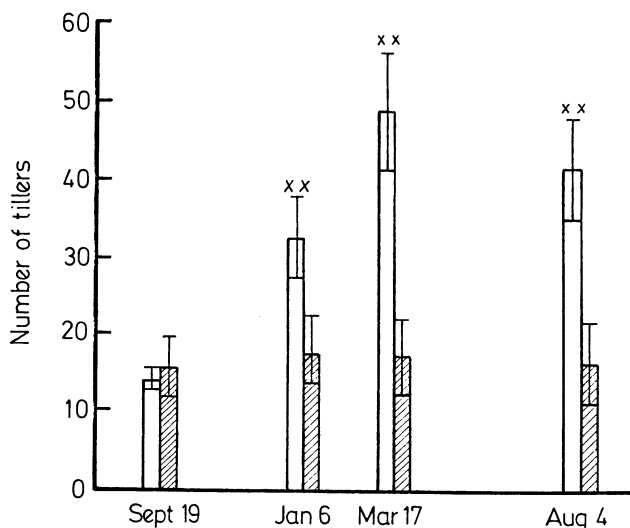


Fig. 8. Tiller populations per plant (± 1 standard error) for *Paspalum dilatatum* as affected by increased red light conditions beneath the canopy. Significant treatment differences ($p < 0.01$) are indicated by xx. Additional red light empty bars and control shaded bars. Redrawn from Deregibus *et al.* 1985.

values were measured in an ungrazed chalk grassland in the Netherlands (Willems 1983). This sharp decrease of the ratio throughout the canopy is caused by the preferential absorption by green leaves of R compared to FR wavelengths. In contrast, the R:FR ratio at the soil level of the grazed area averaged 1.0.

There is evidence indicating that the light quality received at the base of plants influences the rate of tillering in grasses (Deregibus *et al.* 1983). An increase in the R:FR ratio, without significantly modifying the photosynthetically active radiation, resulted in an increase in tiller production in *Lolium* plants cultivated in a growth chamber. The enrichment with red light beneath the canopy of an ungrazed grassland also resulted in an increase in the tillering rate of two native grasses, *Paspalum dilatatum* and *Sporobolus indicus* (Fig. 8) (Deregibus *et al.* 1985).

These changes in the spectral composition of light which occur throughout the canopy profile also modify shoot extension in grasses (Casal *et al.* 1987). A low R:FR of light reaching the base of grasses resulted in longer shoots and leaves.

An increase in grazing intensity increases the R:FR ratio of the light reaching the base of plants as a consequence of the direct effects of removal and trampling. This change in light quality results in shorter leaves and more numerous tillers which will further increase the R:FR ratio. There is a shift in the allocation of resources. As a result of grazing the investment in new tillers increases and the investment in elongation of the tillers already formed decreases.

The effect of herbivory upon species composition is the result of changes in mortality rate and in the establishment of new individuals. There are morphological and physiological traits which confer capacity to tolerate or evade grazing (Coughenour 1985). Differential mortality under grazing conditions is the result of presence or absence of these traits.

Grazing affects establishment of new individuals by controlling seed production and availability of safe-sites (Harper 1971). Changes in light intensity and quality due to grazing may regulate germination rate from seed banks (Silvertown 1980; Fenner 1980; Verkaar 1986). Results from the flooding pampa indicated that grazing exclusion decreased seedling establishment for a rosette plant *Leontodon taraxacoides* and for one of the dominant grasses *Danthonia montevidensis* (Oosterheld and Sala unpublished). These experiments indicated the relative importance of availability of seeds and safe-sites under different grazing conditions. For example, the seed bank of the rosette species was depleted after six years of exclosure as a consequence of the negative balance of seed production, germination and disappearance.

The effect of herbivory at different scales

Time scales

Up to this point, I have discussed changes in vegetation structure which occur in months or years. However, the effects of herbivory occur in a broader range of time scales, from days to centuries. McNaughton (1983a) described responses to herbivores in ontogenetical, ecological and evolutionary time. In the first class are those responses which occur within an individual and during its life cycle. The most important responses at this time scale include compensatory growth and defensive chemical mobilization. The ecological time includes changes in population demographics and encompasses successional studies related to grazing. Changes in evolutionary time occur at a coarser scale. The effect of herbivory is reflected in traits which evolve throughout long periods of time and are engraved in genetic codes.

These responses to herbivory at different time scales are not independent of each other but form a hierarchy. Responses are ordered in this hierarchy from fast to slow. After establishing a hierarchy, deductions can be drawn from hierarchy theory and applied to this case (Allen and Starr 1982; O'Neill *et al.* 1986). Slow responses at the higher level in the hierarchy constrain fast responses which occur at lower levels in the hierarchy. Responses in evolutionary time constrain responses in ecological and ontogenetical time.

Evolution set the limits of what can occur in plant demographics. One of the aspects of succession is a sequential replacement of species. These species possess traits which have already evolved. Similarly, responses in ontogenetical time depend upon species composition which is the result of succession.

The occurrence of dissimilar responses to herbivory in different grasslands led Milchunas *et al.* (1988) to develop a conceptual model of the effect of herbivores on grassland structure. The model is focused on the effects of herbivory in ecological time. It uses two explanatory variables: evolutionary grazing history and environmental moisture.

Sites with different evolutionary grazing history will have different responses to herbivory in ecological and ontogenetical time. As an example, I will compare the response in ecological time of two grasslands with presumably different evolu-

tionary grazing history, the flooding pampa and the Serengeti grasslands. Grasslands of the flooding pampa evolved under light grazing conditions (Webb 1978) and so remained until the arrival of Europeans in the 16th century who introduced domestic herbivores and the frequent use of fire. In contrast, grasslands of the Serengeti have a long evolutionary grazing history. In both grasslands, grazing exclusion resulted in large changes in canopy structure. In the Serengeti, these changes were accounted for primarily by changes in the growth form of native species since exotic species were not observed neither in grazed nor in ungrazed areas (McNaughton 1979, 1983b). In the grasslands of the flooding pampa, structural changes were accounted for by changes in the growth form of native species as well as by the presence or absence of exotic species. It suggests that native grasslands of the flooding pampa did not have the ecotypes or species adapted to the heavy grazing conditions imposed by Europeans.

Adaptations that enhance survival in arid environments promote tolerance or avoidance of grazing. Coughenour (1985) examined how basal meristems, small stature, high shoot density, deciduous shoots, and belowground nutrient reserves allow grasses to evade or tolerate both arid 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. With respect to avoidance, the same characteristic can conserve moisture as well as evade grazing. For example, basal meristems protected by basal sheaths may better withstand drought as well as avoid grazing (Stebbins 1972; Barlow *et al.* 1980).

Milchunas *et al.* (1988) based their model on the idea that adaptations to grazing are divergent from adaptations to humid environments. In contrast, selection pressures in arid grasslands that have coevolved with large grazers are convergent. A relaxation of the grazing pressure in a humid or subhumid grassland will result in a complete shift in the selection pressure. In contrast, excluding grazing in an arid or semiarid grassland will not change the direction of selection pressure. Large changes in the structure of grasslands as a result of grazing are expected in humid and subhumid regions and relatively small changes in arid to semiarid regions.

This model focuses on the effect of grazing on diversity. Arid and semiarid grasslands with a long grazing history are dominated by relatively short grasses that have developed in response to the convergent selection pressures of herbivory and aridity. The semiarid shortgrass steppe of the North American Great Plains is an example of this type of grassland. Grazing has relatively small effects on species composition and diversity, decreasing slightly with increased grazing intensity, as rare and less-grazing tolerant species are eliminated.

Humid and subhumid grasslands with a long grazing history are composed of short, mid- and tallgrasses as a result of divergent selection for grazing tolerance and canopy dominance. In the absence of grazing, a few tall species dominate the community. Moderate grazing creates a mosaic pattern, with shortgrasses predominating in heavily grazed patches, mixture of grasses in moderately grazed patches, and tallgrasses where ungrazed growth deter grazing. Grasslands of the Serengeti are one example of grasslands of this type.

Arid and semiarid grasslands with a short grazing history are dominated by short- and midgrasses that have been selected for their drought tolerance which

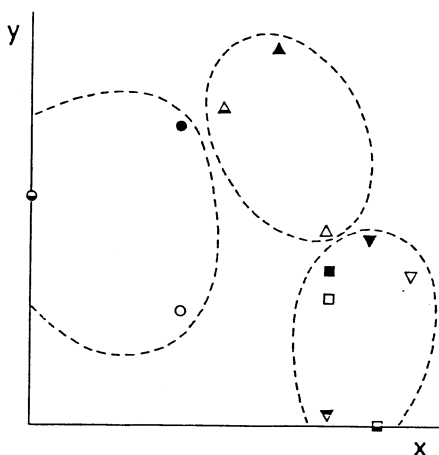


Fig. 9. Ordination of vegetation samples collected in fall (open symbols), in spring (half shaded), and summer (dark symbols) for \square = upland community grazed; \circ = upland community ungrazed; ∇ = lowland community grazed, and Δ = lowland community ungrazed.

also confer some degree of grazing resistance. Structural changes due to grazing are moderate, less than what occurs in the humid-short evolutionary grazing history type, but greater than what occurs in arid grasslands with a long history of grazing. Diversity exhibits a small increase at low grazing intensities and slow decrease throughout most of the range of grazing conditions. Examples of grasslands of this type are the semiarid steppe of northwestern United States and the Pantagonian steppe in southern Argentina (Mack and Thompson 1982; Markgraf 1985).

Humid or subhumid grasslands with a short evolutionary grazing history have the greatest potential for being altered by grazing. Grasslands of the flooding pampa are an example of this type of grasslands (Sala *et al.* 1986). Species were selected primarily for canopy dominance. Communities are made up of tall-grasses that are not tolerant of grazing. The increase of exotic species produce large increases in diversity at relatively low grazing intensities. Diversity declines rapidly thereafter as grazing intensity increases.

Spatial scales

Throughout this paper the discussion and observations of the effect of herbivory upon vegetation structure have been concentrated at the scale of plant or stand. In this section I will explore the effect of herbivory upon vegetation at a coarser scale. I will analyze the effect of herbivory at the scale of landscape.

The grasslands of the flooding pampa are made up of a mosaic of mainly two plant communities which are located in different topographical positions. Although topographical differences are only 15–20 cm, they are enough to determine differences in the duration of floods, in soil properties and in vegetation.

Under conditions of light grazing the two communities were floristically very different (Fig. 9). For example, the upland community was dominated by cool-

season species whereas the lowland community was dominated by warm-season species. Grazing erased the floristic differences between these two communities or phases of the mosaic (Fig. 9). The differences due to environmental factors such as topography and frequency or duration of floods were overshadowed by the effect of grazing.

The Serengeti offers a contrasting example; spatial pattern apparently is caused and maintained by grazing animals (McNaughton 1983b; Belsky 1986). This is also the case of a two-phase grassland mosaic. The *Andropogon* phase is strongly dominated by the grass *Andropogon greenwayi* Napper, which forms large, dense mats while the *Chloris pycnothrix* Trin. phase is sparsely vegetated by a species-rich mixture. Overgrazing and disturbances by large herbivores produce the mosaic by breaking up continuous *Andropogon greenwayi* mats (McNaughton 1983b). Sown grasslands in The Netherlands provide another example of grazing dependent pattern. In this case, sheep grazing in a very small pasture created small scale spatial pattern (Bakker *et al.* 1984).

McNaughton (1983b) suggested that landscape pattern may facilitate foraging efficiency and promote coexistence of diverse grazing animals. If a preferred food source is concentrated in a stand instead of being randomly distributed in several stands, animals can walk from stand to stand to feed. In this manner animals save time and foraging efficiency is facilitated. Different grazing animals with different preferred foods can coexist in the same grassland with minimal competition, by exploiting different vegetation patches (McNaughton 1983b).

These apparently contrasting examples, from the flooding pampa and the Serengeti, suggest that there is a hierarchy of factors which create spatial heterogeneity. One of these factors is grazing. The hierarchy encompasses fine to coarse grained heterogeneities. The pattern of grazing can be finer or coarser than the pattern generated by environmental factors. If the pattern of grazing is coarser, grazing erases the environmental pattern. In contrast, grazing generates pattern if it is finer than the environmental pattern.

Large herbivores generate spatial patterns at different scales as a result of different activities (Senft *et al.* 1987). Fecal pats and the action of hooves create microscale pattern (Coffin and Lauenroth 1988). Preferential grazing in selected stands and seasonal movements of animals create large-scale pattern. Herbivory may be a factor generating pattern at one scale and erasing pattern at another scale.

Evidence that animals generate or erase pattern in grasslands with long or short evolutionary grazing history respectively, suggests that foraging facilitation resulting from the ability of animals to create and maintain pattern may have been a trait selected in evolutionary time. This may be a case similar to the development and maintenance of grazing lawns (McNaughton 1984).

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