Effect of grazing on native gramineae in Concepción, Santa Cruz, Bolivia

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Abstract

The effect of intensive grazing on 57 species of Gramineae was studied in 4 vegetation types (cerrado, seasonally inundated savanna, valley-side campo, and semideciduous forest) near Concepción, Santa Cruz, Bolivia. The relative abundance of each species was estimated from paired stands (relevés) along fence rows dividing grazed and ungrazed ranches. Thirteen species were significantly less abundant and 4 species were more abundant in grazed stands when compared to ungrazed stands. In cerrado, the total number of species in grazed stands was significantly reduced and the unpalatable grass, *Elionurus muticus*, was the dominant species in both grazed and ungrazed stands. The relatively palatable grasses, *Thrasya petrosa, Schizachyrium microstachyum,* and *Schizachyrium sanguineum* were important constituent species of cerrado and were the most negatively affected by selective grazing. Savanna wetland and semideciduous forest communities lack a single dominant grass species and differences in species richness were not significant between grazed and ungrazed stands.

Resumen

El efecto del pastoreo intensivo sobre 57 especies de Gramineae fué estudiado en 4 asociaciones vegetales (cerrado, sabana estacionalmente inundada, ladera de filtración y bosque semideciduo) en Concepción, Santa Cruz, Bolivia. La abundancia relativa de cada especie fue estimada mediante el uso de relevés en parcelas apareadas en estancias adyacente pastoreadas y no pastoreadas. En las parcelas pastoreadas, trece especies de gramíneas fueron significantemente menos abundantes, mientras que cuatro especies fueron más abundantes. En el cerrado, el pastoreo disminuyó el número total de especies, mientras que el pasto no palatable, Elionurus muticus, *fue la especie dominante en parceles pastoreadas y no pastoreadas. Los pastos palatables,* Thrasya petrosa, Schizachyrium microstachyum *y* Schizachyrium sanguineum, *fueron especies importantes del cerrado y las gramíneas más reducidas por el efecto del pastoreo selectivo. Las comunidades húmedas sabanales y el bosque semideciduo no mostraron una especie dominante y las diferencias entre el número total de especies en parcelas pastoreadas y no pastoreadas no fue significativa.*

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Introduction

Savanna vegetation covers an estimated 172 million ha or 21% of the land surface in tropical South America (Cochrane *et al.* 1987). Range management practices for these naturally occurring grasslands are rudimentary and consist of continuous grazing, coupled with fire to annually renovate the grass sward. A major reason for low levels of economic productivity can be attributed to the coarse and unpalatable nature of many savanna bunch grasses (Minson 1981; Skiles 1984). Nonetheless, savannas of the tropical regions of the western hemisphere (i.e., the Neotropics) are floristically diverse and some grass species are more palatable than others. The composition of the grass flora has been studied in parts of the Llanos savannas of Colombia and Venezuela (Sarmiento *et al.* 1971) but relatively little has been reported on the herbaceous stratum for the savanna communities in central South America. Identification of key savanna species of high forage quality is a prerequisite to the development of range management strategies which improve the productivity of these grasslands.

This report provides preliminary observations on the floristic composition of the grass sward in several different vegetation types for an important cattle producing region in eastern lowland Bolivia. Differences in the relative abundance of individual species in grazed and ungrazed stands are used to identify the more palatable native grasses.

Description of study area

Concepción (16°03'S; 62°10'W; altitude 500 m) is situated on the western edge of the Brazilian (Precambrian) Shield in northeastern Santa Cruz, Bolivia. The area has a typical savanna climate with a 5 month dry season coinciding with the austral winter. Mean annual precipitation is about 1200 mm, with yearly totals ranging from 700–1500 mm. Mean daily temperature varies only slightly throughout the year reaching a maximum of 26 °C in November and a minimum of 21 °C in June. Cold fronts sweep through the region during the dry season and can cause the temperature to drop to 10 °C for short periods; maximum temperatures of about 33 °C are common in November at the beginning of the rainy season.

Concepción lies on a dissected Tertiary planation surface which overlies the Precambrian Shield. Highly weathered ferralitic soils have developed on the ancient sediments of the flat uplands. Well-drained savanna is associated with red, distrophic ultisols and oxisols (pH 4.8–5.5), while forest islands occur over mesotrophic, dark brown alfisols (pH 5.2–6.0). Entisols, inceptisols, or histosols predominate in valley bottoms and on erosional surfaces associated with savanna wetlands. Soil pH, texture, and nutrient status of soil profiles in wetland habitats are variable and depend upon the position of the soil profile on the moisture gradient (Guamán and Valverde 1982; Killeen *et al.* 1990).

The vegetation in the vicinity of Concepción is a mosaic of forest, savanna, and savanna wetland. The savannas in well-drained soils are floristically related to the cerrado vegetation of central Brazil (Killeen *et al.* 1990). The term cerrado refers to a complex of intergrading communities which range from low forest to open grassland. The cerrado vegetation has been well-studied and its ecology has been described by Eiten (1972, 1978). Physically associated with cerrado is a treeless savanna wetland that forms a clinal sequence along a gradient of increasing water surplus. These "valley-side campos" occur wherever a fluctuating, perched water table intersects the surface of the landscape (Goldsmith 1974; Eiten 1978). In larger valleys with a flat bottom, impeded drainage or the overflow of a stream leads to the formation of a seasonally inundated savanna complex. Scattered across these open grasslands are raised earth platforms associated with termite mounds which support cerrado vegetation (Diniz de Araujo Neto *et al.* 1986). Detailed phytosociological studies of similar savanna wetland complexes in Bolivia have been conducted by Beck (1984) in the Beni and by Haase (1990a, 1990b) in northern La Paz. Semideciduous forest occurs as islands surrounded by cerrado vegetation. The canopy rarely exceeds 25 m in height and a continuous vegetation gradient exists between "high forest" and cerrado.

Materials and methods

Seven localities within 15 km of Concepción were visited near the end of the rainy season between April 10 and May 1, 1986. Each locality consisted of an intensively grazed estancia (cattle ranch) situated next to an inactive estancia. In several instances, the fence row dissected 2 or more vegetation types and a total of 21 paired stands were sampled. Paired stands were classified as cerrado (n = 13), semideciduous forest (n = 4), seasonally inundated savanna (n = 2), or valley-side campo (n = 2). Stocking rates on grazed estancias ranged from 0.2–0.5 animal units/ha (1 animal unit = 400 kg) and varied seasonally depending upon the short-term needs of individual owners. It was not possible to obtain more precise information on past practices for "intensively grazed" estancias but all had been continuously grazed for several years. Ungrazed estancias were temporarily inactive due to bankruptcy or probate of an estate but none had been intensively grazed for at least 3 years.

The grass sward in each stand was sampled by making a visual estimate of its floristic composition (i.e., relevés) in an area adjacent to the fencerow approximately 500 m^2. The relative abundance of each grass species was recorded using a modified Braun-Blanquet cover-abundance scale (0.5 < 1%, 1 = 1–5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, and 5 = 76–100%; Mueller-Dombois and Ellenberg 1974). The data

Table 1. Mean cover-abundance values (*C*) for grasses in four vegetation types and the mean difference in cover-abundance values between ungrazed and grazed paired stands (*D*).

taxa	Cerrado		Semidecidous forest		Valley-side campo		Seasonally inundated		
	ungrazed C^1	grazed C^1	ungrazed C^1	grazed C^1	ungrazed C^1	grazed C^1	ungrazed C^1	grazed C^1	D^2
Cerrado									
Elionurus muticus	2.85	3.92	0.25	0.38	0.25	0.25			0.85**
Thrasya petrosa	1.89	0.54							−1.35**
Schizachyrium microstachyum	1.65	0.39	0.13						−1.31**
Schizachyrium sanguineum	1.58	0.62			1.5	0.5			−1.15*
Paspalum erianthum	1.04	0.27							−0.96**
Aristida riparia	0.89	0.42				0.25			−0.42*
Axonopus barbigerus	0.69	0.23					0.25	0.25	−0.50
Paspalum plicatulum	0.62	0.15							−0.60**
Hyparrhenia rufa	0.58	0.12							−0.93**
Imperata brasiliensis	0.58	0.62	0.25	0.25					−0.56
Schizachyrium scabriflorum	0.50	0.31							−0.31
Axonopus chrysoblepharis	0.36	0.39			0.75				−0.23
Digitaria neesiana	0.35	0.00							−1.13+
Gymnopogon spicatus	0.31	0.19							−0.42
Panicum olyroides	0.31	0.12							−0.42*
Trachypogon plumosus	0.31	0.23				0.5			−0.60
Panicum quadriglume	0.23	0.04							−0.42*
Sorghastrum minarum	0.19	0.12							−0.30
Melinis minutiflora	0.08	0.00							−1.00
Aristida recurvata	0.04	0.15							0.75
Eragrostis polytricha	0.04	0.04							−0.00
Eriochloa grandiflora	0.04	0.00			0.25		0.75	0.25	−0.50
Eragrostis articulata		0.27							0.70**
Microchloa indica		0.15							−1.00
Valley-side campo									
Paspalum malmeanum					2.00	1.50	0.50		−0.67
Andropogon selloanus	0.04	0.04			1.50				−1.00
Axonopus fissifolius	0.00	0.19			0.25	2.50			1.75+
Sacciolepis angustissima					1.25	0.75	0.50	0.50	−0.25
Eriochrysis cayanensis					0.50	0.25			−0.25
Eriochloa distachya					0.50	0.25			−0.50
Seasonally inundated savanna									
Leersia hexandra							2.50	2.00	−0.50
Coelorhachis aurita							2.00	0.25	−1.75
Hyparrhenia bracteata					0.50	0.25	2.00	1.00	−0.83
Panicum stenodes							1.50	1.25	−0.25
Panicum laxum							0.75	0.75	−0.00
Gymnopogon fastigiatus							0.50	0.25	−0.50
Otachyrium versicolor							0.25	0.25	−0.00
Misc. wetland species									
Loudetia flammida					1.50	0.50	1.25	0.75	−0.75
Andropogon virgatus					1.50	0.75	0.75	0.75	−0.38
Paspalum stellatum	0.23	0.23			1.00	1.50	1.50	0.75	−0.15
Andropogon bicornis	0.19	0.04			1.00	0.25	0.25	0.50	−0.39*
Paspalum lineare						0.50	0.50	0.50	0.50
Ichnanthus procurrens					0.50	1.00	0.25	0.50	0.75
Paspalum lenticulare					0.50	0.25	0.25		−0.33
Saccharum trinii					0.50	0.50	0.25	0.25	−0.00
Sacciolepis myuros					0.50		0.25	0.25	−0.50

was summarized by calculating mean cover-abundance values (*C*) in each vegetation type (Table 1). The effect of grazing on individual species was estimated by calculating the mean difference in the cover-abundance values between grazed and ungrazed paired stands (*D*). Wilcoxson's signed rank test for paired comparisons of nonparametric data (Hollander and Wolfe 1973) was used to determine if the value of *D* was significantly different than 0 (i.e., no effect of

Table 1 continued

taxa	Cerrado ungrazed C^1	Cerrado grazed C^1	Semidecidous forest ungrazed C^1	Semidecidous forest grazed C^1	Valley-side campo ungrazed C^1	Valley-side campo grazed C^1	Seasonally inundated ungrazed C^1	Seasonally inundated grazed C^1	D^2
Forest									
Olyra ciliatifolia	0.08	0.04	0.88	0.63					−0.25
Lasiacis sorghoidea			0.63	0.13					−0.83
Guadua paniculata	0.08	0.00	0.63	0.13					−0.60*
Paspalum malacophyllum	0.19	0.00	0.38						−1.00+
Oplismenus hirtellus			0.34	0.38					−0.00
Setaria vulpiseta			0.25						−1.00
Axonopus compressus	0.12	0.35	0.13	0.63					0.57+
Ichnanthus pallens			0.13						−0.50
Panicum millegrana			0.13						−0.50
Paspalum conjugatum				0.13					−0.50
Rhipidocladum racemiflorum			0.13						−0.00

1. mean cover-abundance value; $C = \Sigma\ c/n$, where c = cover–abundance values; n = number of stands.
2. mean difference in cover abundance values; $D = \Sigma\ (c_u - c_g)/x$, where x = the number of stands in all vegetation types; stands were excluded from the calculation when both c_u and $c_g = 0$;
statistical significance of D determined with Wilcoxson's signed rank test (** $P < 0.01$; * $P < 0.05$; + $P < 0.10$).

grazing). A similar test was conducted to determine the effect of grazing on grass species richness for each vegetation type (Table 2).

The previous year had been spent conducting an exhaustive inventory of the Gramineae for the region. Most grasses included in this study were in bloom or had senescent flowering culms during the sampling period and could be identified easily in the field. However, several species were identified in the vegetative state, particularly the dominant grass, *Elionurus muticus*. Voucher specimens, as well as taxonomic authorities, synonyms, and other annotations are cited in Killeen (1990).

Results

The mean cover-abundance values for 57 species of Gramineae in grazed and ungrazed stands are shown in Table 1. The most abundant species in cerrado vegetation are all caespitose perennial grasses which form characteristic "bunches" 5–30 cm wide at ground level and which form a closed herbaceous stratum approximately 1 m in height. The dominant species in all grazed and ungrazed cerrado stands was *Elionurus muticus*. Along forest margins or in densely wooded savannas the rhizomatous species *Imperata brasiliensis* increases in abundance but *E. muticus* remains a co-dominant of the herbaceous stratum.

If one assumes that a statistically significant decrease in cover-abundance values between ungrazed and grazed stands is indicative of selective grazing, then 12 cerrado species can be considered to be relatively palatable and subject to selective grazing (Table 1). The most negatively affected species are *Thrasya petrosa, Schizachyrium microstachyum, Schizachyrium sanguineum*, and *Digitaria neesiana*. However, local ganaderos (cattlemen) indicate that certain genotypes of the apomictic species *Paspalum plicatulum* (camalote) provide the best quality forage in native cerrado. Nonetheless, *P. plicatulum* is a relatively uncommon species and, based on both palatability and relative abundance, *T. petrosa, S. microstachyum,* and *S. sanguineum* can be considered to be the principal forage resources of the cerrado savannas of the Brazilian Shield region of Bolivia.

In contrast, *E. muticus* was significantly more abundant in grazed stands when compared to ungrazed stands. *E. muticus* is an extremely unpalatable grass and is only grazed for 2–4 weeks after the annual burn when its rapid regeneration provides young, succulent forage in the dry season. During the remainder of the year this coarse species was not observed to be grazed at all. The local name "paja carona" refers to the traditional use of the highly sclerified foliage to weave saddle-pads (i.e., caronas) for pack-horses. *E. muticus* has a lemon-like odor and is sometimes referred to as "pasto amargo" (i.e., sour grass).

Only 3 other species were significantly more abundant in grazed stands in all vegetation types. The annual grass, *Eragrostis articulata*, grows on exposed lateritic outcrops in cerrado vegetation where superficial soils have become denuded of their perennial grass sward by cattle trampling. *Axonopus compressus* a weedy, stoloniferous perennial forms colonies along cow-paths in forest and cerrado. Mack and Thompson (1982) report that species with similar life-forms are tolerant of disturbance by large-hoofed ungulates. *Axonopus fissifolius* occurs most frequently in seasonally humid sandy soils and, paradoxically, is considered to be palatable by ganaderos. It was observed to be grazed by cattle on numerous occasions and anatomical examination of leaf blades revealed relatively small amounts of sclerification (i.e., the species is not coarse). *A. fissifolius* will rarely produce stolons and forms a dense, low growing turf when grazed. These later 2 characteristics provide an explanation for the increase in the relative abundance of this apparently palatable grass in intensively grazed stands. *A. fissifolius* is closely related to *Axonopus purpusii*, which has a similar life form and habitat preferences. *A. purpusii*, like its sister taxon, is very palatable and has been reported to be an important forage resource in shallowly inundated regions of the Gran Pantanal (Allem and Valls 1987).

Differences in cover-abundance values between grazed and ungrazed stands for most wetland grasses were not found to be statistically significant. This was due primarily to small sample size (n = 2) for both valley-side campos and seasonally inundated savanna. Only those species with populations in other habitats had sufficient replication to demonstrate statistical significance. Nonetheless, *Coelorachis aurita* and *Andropogon selloanus* showed a dramatic decrease in relative abundance and these species are probably selectively grazed (Table 1). The savanna vegetation which develops in seasonally inundated, flat valley bottoms has a rich grass flora which lacks a single dominant species. *Leersia hexandra, Hyparrhenia bracteata, Panicum stenodes, Paspalum stellatum* and *C. aurita* predominate at the these 2 localities. However, other seasonally inundated savanna complexes in the region had abundant *Paspalum limbatum, Paspalum lenticulare, Paspalum intermedium,* and *Andropogon virgatus*. Seasonally inundated savanna is highly prized by ganaderos in the region for its high quality forage. This can be attributed to the increased succulence (and therefore palatability) of many aquatic or semi-aquatic species. *L. hexandra* (arrocilla) and *P. lenticulare* (camalote del agua) are the most important forage resources of this vegetation type.

On valley-side campos, *A. fissifolius, P. stellatum, A. selloanus,* and *Paspalum lineare* predominate in a narrow band of seasonally humid, gleyed sandy soils at the top of the soil moisture gradient. Downslope, the extremely coarse and unpalatable species *Paspalum malmeanum* and *Rhynchospora emaciata* (Cyperaceae) form a dense sward in a bog-like community where an organic mat develops over the acidic sandy soil (pH 4.2–4.5). Valley-side campos are considered to be of little value as a forage resource by local ganaderos but are an important water source during the dry season.

Forest vegetation has an important role in cattle management. During the early dry season, when savanna grasses become increasingly senescent, livestock move into the forest in search of understory plants which remain green throughout the year. This is particularly true of the C_3, panicoid forest grasses, such as *Lasiacis sorghoidea, Ichnanthus pallens, Oplismenus hirtellus,* and *Panicum millegrana*, which are collectively referred to as taquarilla (a misnomer meaning "little bamboo"). The change in foraging habits also coincides with the onset of the austral winter, when cattle seek shelter in the forest from cold fronts (surazos).

The negative effect of grazing on grass species richness is shown in Table 2. The most depauperate stands were located on 2 estancias (i.e., the grazed half of localities B and D), which were stocked at more than twice the recommended rate of 0.2 animal units/ha (Paterson 1984). These 2 estancias showed additional evidence of overgrazing, including an appreciable amount of bare soil and an abundance of the weedy shrub *Vernonia ruficoma.*

Discussion

The grass sward in the cerrado vegetation near Concepción is exuberant, but the dominance of the extremely coarse and unpalatable *E. muticus* severely limits the ability of ganaderos (cattle owners) to harvest the productivity of these tropical grasslands. No data was gathered on

Table 2. Effect of grazing on total number of grass species

Stand pair	Locality	Ungrazed stands	Grazed stands	Difference (# species/stand)
Cerrado				
1	A	12	13	−1
2	B	14	1	13
3	C	19	14	5
4	D	17	11	6
5	E	15	14	1
6	F	13	11	2
7	G	12	10	2
8	B	11	6	5
9	D	11	6	5
10	D	16	6	10
11	D	13	6	7
12	E	14	12	2
13	E	10	4	6
			mean difference =	4.85**
Valley-side campo				
20	A	14	15	−1
21	B	13	5	8
			mean difference =	3.5
Seasonally inundated savanna				
18	A	16	16	0
19	B	14	10	4
			mean difference =	2.0
Semideciduous forest				
14	D	6	6	0
15	D	5	6	−1
16	E	10	12	−2
17	E	3	4	−1
			mean difference =	−1.0

biomass production during this study, but Sarmiento and Vera (1979) showed that above ground dry matter production in Venezuelan savannas with similar climatic, edaphic and floristic characteristics ranged from 2.3-6.0 t/ha/yr (extrapolated from data presented as g/m²/year). Such levels of productivity should support higher stocking rates than currently realized.

Fire may be partially responsible for the dominance of the unpalatable species *E. muticus* in cerrado. Not only is the vegetative growth of this grass stimulated by fire, but plants bloom 3 to 4 weeks after being burned; if populations are not burned, plants will not flower (Killeen 1990). This fire-dependent phenological strategy ensures that diaspores escape fire and are deposited on the soil surface shortly after the input of mineral-rich ash. Although fire is a naturally occurring phenomenon in lowland Bolivia, most fires are deliberately set to provide a flush of new, green foliage at the end of the dry season (August, September, and October). It is important to note that the reproductive cycles of the most palatable cerrado grasses (e.g., *T. petrosa, S. microstachyum, S. sanguineum,* and *P. plicatulum*) are not stimulated by fire. These species flower toward the end of the rainy season and there is evidence that their reproduction from seed is impeded by frequent fire (Silva and Castro 1989).

Range management strategies which decrease the relative abundance of *E. muticus* are essential to increasing the stocking rates in cerrado savannas. Range managers have often emphasized the eradication of undesirable woody plants, particularly exotic species which invade grasslands as a consequence of grazing. There is less information available on practices for changing the composition of the herbaceous flora by either grazing or burning strategies. A period of rest is often recommended as a solution for restoring the productivity of degraded grasslands (Brady *et al.* 1988; Paton and Rickert 1989). "Ungrazed" estancias near Concepción have a long history of

exploitation and have probably been intensively grazed at some point in the past. These results indicate that certain species in the cerrado grass sward are selectively overgrazed and this has led to a decrease in the relative abundance of those species. Ungrazed estancias benefited from a rest, which allowed the palatable grasses to increase in relative abundance.

Studies of tropical or subtropical grassland communities have shown that grazing can lead to either an increase or decrease in species diversity depending upon a variety of environmental factors and the relative intensity of grazing. Facelli *et al.* (1989) reported that although spatial heterogeniety was greater in ungrazed exclosures, the total number of species actually decreased due to an increase in the cover of the dominant perennial bunch grasses. Moderate grazing can lead to an increase in species diversity by creating openings in the herbaceous stratum (McNaughton 1983, Facelli 1988). Much of the increase in species richness associated with grazing activities can be attributed to herbaceous and shrubby dicots, life-forms which were not included in this study. Heavily grazed pastures have been demonstrated to lead to a loss of grass species richness in a variety of grassland ecosystems (Crawley 1983). Important factors which may influence species richness are the density of animals and the frequency of grazing (McNaughton 1983; Savory 1988). In the savannas near Concepción, grass species richness in ungrazed stands was significantly greater in cerrado vegetation, with equivocal results for other habitats. Under the continuous grazing practices common to eastern Bolivia, selective grazing of the most desirable species may lead to the eradication of those species from the grass sward.

Development agencies and research institutions must orient resources to devise range management strategies for Neotropical savannas. Past policies have emphasized forage crop research, which in turn has stimulated tropical forest destruction. In the past 10 years, millions of hectares of cerrado landscapes have been converted to cropland by the application of lime and chemical fertilizers (Goedert 1983). If present trends continue, the biological diversity of the cerrado biome will soon be exterminated (Furley and Ratter 1988). Conservation organizations have dedicated their efforts in Latin America to tropical forest preservation. These agencies should promote the proper management of Neotropical savannas, so as to better ensure their maintenance as natural grassland ecosystems.

This research shows that cattle selectively graze specific grass species in the cerrado savannas near Concepción, Bolivia. Continuous grazing at high stocking rates has led to an impoverishment of the grass flora. This has caused a decline in its value as a forage resource. Grazing systems that incorporate a rest phase are necessary to promote a more floristically diverse grass flora and ensure the long-term productivity of these native grasslands.

Acknowledgements

This research was funded by a fellowship from the Organization of American States (OAS) and grants from the World Food Institute of Iowa State University. I thank Beth Middleton and Emilio Oyarzabal for critical reviews of the manuscript and the staff of the Instituto de Ecología (La Paz, Bolivia) for logistic support. I am indebted to the citizens of Concepción for their hospitality and assistance during my residence in their beautiful and historic community.

References

ALLEM, A.C. and VALLS, F.F.M. (1987) *Recursos Forrageiros Nativos do Pantanal Mato-Grossense.* (Empresa Brasileira de Pesquisa Agropecuária — EMBRAPA: Brasília.)

BRADY, W.W., STROMBERG, M.R., ALDON, E.F., BONHAM, C.D., and HENRY, S.H. (1989) Response of a semidesert grassland to 16 years of rest from grazing. *Journal of Range Management*, **42**, 284–288.

BECK, S.G. (1984) Comunidades vegetales de las sabanas inundadas de NE de Bolivia. *Phytocoenologia*, **12**, 321–350.

COCHRANE, T.T., SANCHEZ, L.G., AZEVEDO, L.G., PORRAS, J.A. and GARVER, C.L. (1985) *Land in Tropical America. Vol. I.* (Centro Internacional de Agricultura Tropical (CIAT) and Empresa Brasiliera de Pesquisa Agropecuária do Cerrados (EMBRAPA-CPAC): Cali, Columbia.)

CRAWLEY, M.J. (1983) *Herbivory. The Dynamics of Animal-Plant Interactions.* (Univ. California Press: Berkeley.)

DINIZ DE ARAUJO NETO, M., HARIDASAN, M.P.A., and JOHNSON, C.E. (1986) The murundus of the cerrado region of central Brazil. *Journal of Tropical Ecology*, **2**, 17–35.

EITEN, G. (1972) The cerrado vegetation of Brazil. *Botanical Review*, **38**, 201–341.

EITEN, G. (1978) Delimitation of the cerrado concept. *Vegetatio*, **36**, 169–178.

FACELLI, J.M. (1988) Response to grazing after nine years of cattle exclusion in a flooding pampa grassland. *Vegetatio*, **78**, 21–25.

FACELLI, J.M., LEON, R.J.C., and DEREGIBUS, A. (1989) Community structure in grazed and ungrazed grassland sites in the flooding pampa, Argentina. *American Midland Naturalist*, **121**, 125–133.

FURLEY, P.A. and RATTER, J.A. (1988) Soil resources and plant communities of the central Brazilian cerrado and their development. *Journal of Biogeography*, **15**, 97–108.

GOEDERT, W.J. (1983) Management of the Cerrado soils of Brazil: a review. *Journal of Soil Science*, **34**, 405-428.

GOLDSMITH, F.B. (1974) Multivariate analysis of tropical grassland communities in Mato Grosso, Brazil. *Journal of Biogeography*, **1**, 111-122.

GUAMAN C.A. and VALVERDE, C.M. (1982) Levantamiento integrado de los recursos naturales de la Provincia Ñuflo de Chavez (Sector Concepción). Estudio de Suelos. *CORDECRUZ, Santa Cruz, Bolivia.*

HAASE, R. (1990a) Plant communities of a savanna in northern Bolivia I. Seasonally flooded grassland and gallery forest. *Phytocoenologia*, **18**, 55-81.

HAASE, R. (1990b) Plant communities of a savanna in northern Bolivia I. Palm swamps, dry grassland, and shrubland, *Phytocoenologia*, **18**, 343-370.

HOLLANDER, M. and WOLFE, D.A. (1973) *Nonparametric Statistical Methods.* (John Wiley and Sons: New York)

KILLEEN, T.J. (1990). The grasses of Chiquitanía, Santa Cruz, Bolivia. *Annals of the Missouri Botanical Garden*, **77**, 125-201.

KILLEEN, T.J., LOUMAN, B.T., and GRIMWOOD, T. (1990) La ecología paisajística de Concepción y Lomerío, Santa Cruz, Bolivia. *Ecología en Bolivia*, **16**, 1-45.

MACK, R.N. and THOMPSON, J.N. (1982) Evolution in steppe with few large hoofed mammals. *American Naturalist*, **119**, 757-773.

MCNAUGHTON, S.J. (1983) Serengeti grassland ecology: The role of composite environmental factors and contingency in community organization. *Ecological Monographs*, **53**, 291-320.

MINSON, D.J. (1981) Nutritional differences between tropical and temperate pastures. In: Morley, F. H. W. (ed) *Grazing Animals.* pp. 143-156. (Elsevier: Amsterdam.)

MUELLER-DOMBOIS, D. and ELLENBERG, H. 1974. *Aims and Methods of Vegetation Ecology.* (John Wiley & Sons: New York.)

PATERSON, R.T. (1984) Investigación *y desarrollo de pastos tropicales, Santa Cruz, Bolivia. Final Report, Centro de Investigación Agricola Tropical y Misión Británica en Agricultura Tropical. Santa Cruz, Bolivia.*

PATON, C.J. and RICKERT, K.G. (1989) Burning, then resting reduces wiregrass (*Aristida spp.*) in black speargrass pastures. *Tropical Grasslands*, **23**, 211-218.

SARMIENTO, G. and VERA, M. (1979) Composición, estructura, biomasa y producción de diferentes sabanas en los Llanos de Venezuela. *Boletín de la Sociedad Venezolana de Ciencias Naturales*, **136**, 5-41.

SARMIENTO, G., MONASTERIO, and SILVA, J. (1971) Reconocimiento ecológico de los Llanos Occidentales. I. Las unidades ecológicas regionales. *Acta Científica Venezolana*, **22**, 52-60.

SAVORY, A. (1987) *Holistic Resource Management.* (Island Press: Washington.)

SILVA, J.F. and CASTRO, F. (1989) Fire, growth and survivorship in a Neotropical savanna grass *Andropogon semiberbis* in Venezuela. *Journal of Tropical Ecology*, **5**, 387-400.[1]

SKILES, J.W. (1984) A review of animal preference. In: *Natl. Res. Council/Natl. Acad. Sci., Developing Strategies for Rangeland Management* pp. 153-213. (Westview Press: Boulder, Colorado.)

1. *Andropogon semiberbis* is a synonym of *Schizachyrium sanguineum* of this study.

(Received for publication, November 10, 1990; accepted January 31, 1991)