Influence of different management alternatives of natural vegetation on perennial grass species richness and diversity in semiarid Argentina.

CARLOS A. BUSSO, HUGO D. GIORGETTI, OSCAR A. MONTENEGRO, GUSTAVO D. RODRIGUEZ AND ANA C. TABLAR

Key words: perennial grasses, species richness and diversity, Argentina grasslands, management alternatives.

Busso is Associate Professor, Departamento de Agronomía, Universidad Nacional del Sur (UNS) and research scientist, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Altos del Palihue, Bahía Blanca (8000), Argentina; Giorgetti, Montenegro and Rodríguez are research scientists, Chacra Experimental de Patagones, Ministerio de Asuntos Agrarios, cc 118, Carmen de Patagones (8504), Argentina; Tablar is teaching assistant, Departamento de Matemática, UNS.

Abstract

The influence of different management alternatives of natural vegetation was determined on species richness and diversity of perennial grasses in East-Central, semiarid Argentina (40° 39'S, 62° 54'W). Studies were effected in adjacent areas which received different treatments: (1) untreated control; (2) burning; (3) herbicide application (shrub control); (4) Old Field 1 or (5) Old Field 2 (areas previously exposed to different degrees of mechanical soil disturbance for 25 years); and (6) overgrazing. During 1984-1992, annual aboveground biomass was determined per perennial grass species within each treatament after clipping permanent plots (n=30). Species richness was calculated as the number of species sampled within each quadrat. Species diversity was calculated using the Simpson's index. Principal Coordinate Analysis, which used the association index of Morisita-Horn, showed that species composition was more similar among years within any treatment than among treatments in any given year. However, more than 69% of all perennial grass species were desirable perennial grasses in all treatments and years. Species both richness and diversity, which varied considerably among years within each treatment, were higher ($p<0.05$) at the Control or Burned area than at sites receiving a more severe or continuous grazing (Old Field 1 and Overgrazing). The Control, Shrub Control and Old Field 2 treatments had a similar ($p>0.05$) perennial grass species richness and diversity. Since species composition remained relatively constant among years within each treatment, variations in species diversity (1.46±0.14 ($\overline{X}$±1SE; 1989, Old Field 1)-3.19±0.17 (1986, Burning)) during the study period in these treatments were mainly due to changes in the species relative biomasses. From a parallel study, rainfall appeared to be the major factor

in accounting for most of the variation in herbage production between years in these rangelands.

Resumen

Se determinó la influencia de varias alternativas de manejo de la vegetación natural en la abundancia y diversidad de especies de gramíneas perennes en la región centro-este de Argentina (40° 39'S, 62° 54'W). Los estudios se efectuaron en áreas adjacentes que recibieron diferentes tratamientos: (1) Control no tratado; (2) Quema; (3) Aplicación de herbicidas para control de arbustos; (4) Campo abandonado 1 ó (5) Campo abandonado 2 (áreas previamente expuestas a varios grados de disturbio mecánico del suelo durante 25 años); y (6) Sobrepastoreo. Durante 1984-1992, se determinó la biomasa aérea anual por especie luego de cortar parcelas permanentes (n=30) dentro de cada tratamiento. La abundancia de especies se calculó como el número de especies presentes en dichas parcelas. La diversidad de especies se calculó usando el índice de Simpson. El Análisis de Coordenadas Principales, que usó el índice de asociación de Morisita-Horn, mostró que la composición de especies fue más similar entre años dentro de cualquier tratamiento que entre tratamientos en un año dado. Sin embargo, más del 69% de todas las especies de gramíneas perennes fueron gramíneas perennes deseables en todos los tratamientos y años. La abundancia y diversidad de especies, que varió considerablemente entre años dentro de cada tratamiento, fueron mayores ($p<0.05$) en las áreas Control y Quemada que en aquellas que recibieron un pastoreo más severo y continuo (Campo Abandonado 1 y Sobrepastoreo). Los tratamientos Control, Aplicación de herbicidas para control de arbustos y Campo

Abandonado 2 tuvieron una abundancia y diversidad de especies similar ($p>0.05$). Desde que la composición de especies permaneció relativamente constante entre años dentro de cada tratamiento, las variaciones en la diversidad de especies durante el período de estudio en estos tratamientos (1.46±0.14 ($\bar{X}$±1SE; 1989, Campo Abandonado 1)-3.19±0.17 (1986, Quema)) fue debido principalmente a los cambios en la biomasa relativa de las especies. Un estudio paralelo permitió determinar que la mayor parte de las variaciones en la producción de forraje entre años en estos pastizales fueron debidas a variaciones en la cantidad de lluvia anual.

Concern is increasing about the effects of range improvement practices on species richness and diversity (Lewis et al. 1988, West 1993). Cooperrider (1991) pointed out that range improvement projects typically emphasize increasing livestock forage while reducing plant species diversity. Other studies have reported that both selective and non-selective grazing or soil disturbance associated with grazer activity can potentially increase or decrease plant species diversity (Huntly 1991). Furthermore, grazers may interact with other processes operating at different spatial and temporal scales (e.g., fire, drought, species interactions) resulting in scale dependent effects (Coppock and Detling 1986, Grime et al. 1987). However, range improvement practices (e.g., woody plant control, appropriate grazing management) can be designed and planned in a manner to maintain or increase plant species richness and diversity (Milchunas et al. 1988, Fulbright 1996). Maintaining biodiversity, a concept which includes species both richness and diversity, is a desirable goal for range managers. This is because primary production is more resistant to and recovers more fully from disturbances (e.g., drought) in more diverse plant communities (McNaughton 1985, Tilman and Downing 1994). Biodiversity

components can also influence structural and functional attributes of grassland ecosystems (Archer and Smeins 1991, Tilman and Downing 1994), but factors affecting these components in rangelands remain poorly understood (West 1993).

Although effects of various management alternatives on perennial grass standing crop have been examined in the Phytogeographical Province of the Monte (Giorgetti et al. 1997), their influence on perennial grass species richness and diversity has not yet been reported: this is precisely the objetive of this study.

Materials and Methods

Study Site

Research was conducted at the field site of the Experimental Farm of Patagones (40° 39'S, 62° 54'W; 40 m a.s.l.) which is located 22 km North of Carmen de Patagones. This site is within the Phytogeographical Province of the "Monte" (Cabrera 1976). The community is characterized by an open shrubby layer which includes herbaceous species where the perennial grass component is dominant (Giorgetti et al. 1997). Giorgetti et al. (1997) have recently reported the major species composition of the studied community. In this study, perennial grasses were classified following Cano (1988) according to their degree of acceptance by livestock as desirable (*Bromus brevis* Nees, *Koelleria permollis* Nees, *Pappophorum subbulbosum* Arech., *Piptochaetium napostaense* (Speg.) Hack., *Poa lanuginosa* Poir., *P. ligularis* Nees ex Steud., *Sporobolus cryptandrus* (Torr.) A. Gray, *Stipa clarazii* Ball, *S. papposa* Nees and *S. tenuis* Phil.), intermediate (*Aristida pallens* Cav., *A. spegazzinii* Arech., *A. subulata* Henrard, *A. trachyantha* Henrard, *Stipa speciosa* Trin. & Rupr.; grazed when desirable species are not available) or undesirable (*Sporobolus rigens* (Trin.) Desv., *Stipa ambigua* Speg., *S. brachychaeta* Godron, *S.*

trichotoma Nees; only cut off when a better forage is not available). Except for the warm-season *Sporobolus*, *Aristida* and *Papphophorum* species, all other C_3 perennial grasses regrow in fall, stay vegetative during winter, and flower and set seed during spring and early summer. Regional topography is typically a plain. Major soil physical and chemical characteristics at the site are given in Table 1.

Long-term (1901-1950) mean annual values are 331 mm for rainfall, 14.6° C for temperature, 60% for relative humidity and 13 km h^{-1} for wind speed. Absolute minimum (August) and maximum (January) temperatures are -7.6 and 43° C, respectively. A meteorological station at the study site provided various climatic parameters during 1981-1992 as shown in Fig. 1.

Treatments

The plant community was characterized (n=20 stands) on 1 November 1977, before imposition of treatments, by using the abundance-dominance/sociability index of Braun Blanquet (Mueller-Dombois and Ellenberg 1974). Species with the highest index were *Chuquiraga erinacea* D. Don ($\bar{X}$=2.3), *Condalia microphylla* Cav. ($\bar{X}$=1.1), *Schinus fasciculatus* (Gris) I.M. Johnston ($\bar{X}$=1.1), *Lycium chilensis* Miers ex DC. var. *minutifolia*($\bar{X}$=1.1) and islands of *Geoffroea decorticans* (Gill. ex Hook. & Arn.) Burkart [$\bar{X}$=(4.4)] for the shrubby layer; *Baccharis ulicina* Hook. & Arn. ($\bar{X}$=1.2) for the forb layer, and *S. tenuis* ($\bar{X}$=4.4), *S. clarazii* ($\bar{X}$=2.3), *P. ligularis* ($\bar{X}$=1.2) and *P. napostaense* ($\bar{X}$=1.2) for the grass layer. The community was then classified as an open shrubland of *Ch. erinacea* and *C. microphylla* with islands of *G. decorticans* within a continuous herbaceous layer of *S. tenuis*.

Different management alternatives were imposed thereafter on areas which had been previously exposed to continuous grazing by cattle and sheep. Trees and undergrowth were cleared from one area (20 ha) which was then cropped during 1951-1975. Previous to cultivation, greater proximity to a water source for animals determined that half of this area (Old Field 1) received a more severe grazing than the other half (Old Field 2). During this period, and adjacent, non-cleared area (95 ha) was grazed by cattle and sheep. Access of domestic herbivores was then excluded in both areas during 1975-1993. The 95 ha area, however, was exposed to three different managements between December 1977 and March 1978: one site (34 ha) remained untreated (Control), another site (37 ha) was burned (Burned), and herbicides were applied on a third site (24 ha) for Shrub Control. The last studied area was an adjacent site (168 ha) which had been severely overgrazed (Overgrazing) until 1981, and then excluded from domestic herbivory grazing until 1993.

Burning was effected on 3 March 1978 when maximum and mean air temperatures were 23.5 and 14.4° C, respectively, mean relative humidity was 49%, mean wind speed was 22 km h^{-1}, and dry weight of fine fuel load was 438±56.5 kg ha^{-1}. At this time, mean regrowth height was 12 cm for perennial grasses, and shrubs were at the maturation and dissemination stage of development. One year after burning, ≥50% of plants of *G. decorticans*, *C. microphylla*, *L. chilensis*, *Ch. erinacea*, *Larrea divaricata* Cav. and *S. fasciculatus* had produced basal regrowth.

Digiuni (1983) has already reported characteristics for chemical shrub control in this study. Briefly, an aerial application of Tordon 213 (2 l ha^{-1}) and 2,4,5-T (4 l ha^{-1}) was effected on 29 December 1977. At this time, minimum, maximum and mean air temperatures were 13.6, 21.2 and 18.7° C, respectively, mean air relative humidity was

58%, mean wind speed at 4 m height was 14 km h^{-1}, accumulated rainfall during December was 108.2 mm, and shrubby vegetation was at the reproductive developmental stage. Immediately after their application, herbicides produced death or total defoliation with no basal regrowth in *C. microphylla*, *G. decorticans*, *L. chilensis* and *L. divaricata*, and less than 50% defoliation in *Ch. erinacea*. Sixteen months later, regrowth had not been produced by 80-90% of *C. microphylla* and *G. decorticans* plants. The remaining plants, however, and those of *L. chilensis*, *Ch. erinacea* and *L. divaricata* were less than 50% defoliated. Lack of manpower prevented from studying shrub recovery afterwards.

Sampling procedures

By mid-November 1978, percentage cover was determined per species within the herbaceous layer in each treatment (n=50) by randomly distributing quadrats (0.2 x 0.2 m) following Daubenmire (1959). In 1978, maximum above-ground standing crop was also measured (n=50) at the Control ($\overline{X}$=1867 kg ha^{-1}), Old Field 1 ($\overline{X}$=2120 kg ha^{-1}), Old Field 2 ($\overline{X}$=3804 kg ha^{-1}), Burned ($\overline{X}$=967 kg ha^{-1}) and Shrub Control ($\overline{X}$=2390 kg ha-1) treatments, and at these and the Overgrazing treatment from 1984-1992. Unfortunately, change of research scientists due to political reasons at the Experimental Farm of Patagones in 1978 left us with only mean values for percentage cover and maximum aboveground standing crop in the different treatments at this time. Maximum aboveground standing crop was obtained by hand clipping live+recent dead herbage by late December or early January, when major forage species reched maturity. Economic constraints also precluded from doing determinations in all treatments during 1979-1983. At harvesting time during 1984-1992, 30 randomly distributed, permanent plots (0.5 x

0.5 m) were clipped to 3-5 cm stubble height in each treatment. Except in 1978, when only total herbaceous standing crop was measured, herbage was separated by species, dried in a forced draft oven at 70° C until constant weight, and weighted.

Principal coordinate analysis was used to detect possible species associations among years and/or treatments. With this purpose, biomasses of each of the 19 perennial grass species were averaged over the 30 quadrats, and its relative contribution to total biomass was calculated giving a proportion vector for each treatment and year. The Morisita-Horn index was then calculated for any pair of proportion vectors as follows:

$$Mo(i,j) = \frac{2 \sum_{k=1}^{19} p_{ik} \; p_{jk}}{\sum_{k=1}^{19} p_{ik}^2 + \sum_{k=1}^{19} p_{jk}^2} \quad \text{(Pielou, 1977)}$$

where $(p_{i1},\ldots,p_{i19})$ and $(p_{j1},\ldots,p_{j19})$ corresponded to any combination of treatment and year for species (k) 1 through 19. This index takes into account species dominance: it detects greater association between vectors sharing a dominant species that between those which share species of similar importance. Vectors are represented as points within a space where distance among them represents a measure of its association: closer points then represent a greater association between them.

Species richness will refer to the number of species sampled within each quadrat and will be expressed for each treatment and date. Species diversity, which includes both richness and evenness or equitability of species'relative biomass components, was calculated for each quadrat within each treatment and year using the Simpson's index

$(1/\sum_{k=1}^{19} p_{ik}^2)$ where p is the relative biomass of species k (Pielou 1977).

Simpson's index was used since it is implicitly considered in the algorithm of the association index of Morisita-Horn.

Statistical analysis

Statistical differences in species richness or diversity between treatments within each year were assessed with a Kruskal-Wallis test ($p<0.01$) (Miller 1981). Pairwise comparisons were made on treatment means using Tukey's test ($p<0.05$), which was applied on rank averages. These analysis were performed using BMDP New System for Windows.

Results

Stipa tenuis, *P. ligularis*, *P. napostaense* and *S. clarazii* represented altogether >31% cover in the Control, Burned and Shrub Control treatments in 1978, when there was a high amount of bare soil in the Burned treatment (Table 2). At this time, percentage cover for these species was <8% in the Old Field treatments, where annuals or other undesirable perennial species (e.g., *Stipa ambigua* Speg., *Baccharis gilliesii* A. Gray) were more abundant (Table 2).

Principal Coordinate Analysis showed that species composition was more similar among years within any treatment than among treatments in any given year (Fig. 2). However, more than 69% of all perennial grass species corresponded to desirable perennial grasses in all treatments and years (Fig. 3).

The Old Field 1 and Overgrazing treatments had a similar ($p>0.05$) perennial grass species richness during the study period (Fig. 4). This variable, however, reached lower ($p<0.05$) values in these treatments than in the Control in 1988-1992 (Fig. 4). Undesirable grasses were mainly present in the Old Field 1 and Overgrazing treatments where they contributed 5.8 (1987, Overgrazing)-32.6% (1984, Old Field 1) to total perennial grass species number. Contribution of intermediate perennial grasses to this total, which were almost exclusively restricted to the Old Field 2 (Fig. 3), varied from 21.4 (1991)-39.8 %(1985) in this treatment. The Control, Shrub Control and Old Field 2 treatments had a similar ($p>0.05$) species both richness and diversity of perennial grasses during the study period (Figs. 4 and 5); the only exceptions to this occurred in 1984 for the Old Field 2 treatment and in 1987 for the Shrub Control treatment, when perennial grass species richness was lower or higher, respectively, than in the untreated Control (Fig. 4).

Except in 1992 where the Burned and Old Field 1 treatments had a similar ($p>0.05$) perennial grass species diversity, this variable was always lower ($p<0.05$) in the Old Field 1 than in the Burned and Control treatments (Fig. 5). Similarly, perennial grass species diversity was similar ($p>0.05$) or lower ($p<0.05$; 1986-1987 and 1989-1992) in the Overgrazing than in the Control and Burned treatments (Fig. 5). Perennial grass species diversity was also lower ($p<0.05$) in the Old Field 1 than in Shrub Control treatment during 1985-1989, and similar ($p>0.05$) or lower ($p<0.05$), but not higher, in the Old Field 1 than in the Old Field 2 treatment (Fig. 5). The Old Field 1 and Overgrazing treatments had a similar ($p>0.05$) perennial grass species diversity in all years, except in 1984 where it was lower ($p<0.05$) in the first than in the lattest treatment (Fig. 5). In the same manner, Control and Burned treatments always had a similar

(p>0.05) perennial grass species richness and diversity (Figs. 4 and 5). Species both richness and diversity of perennial grasses varied among years within each treatment (Figs. 4 and 5). However, and at the same time species composition remained quite similar, relative biomasses of each species changed considerably among years within each treatment (Fig. 3).

Discussion

One year after treatments, percentage cover of desirable perennial grasses was higher in the Control, Burned and Shrub Control treatments than in both Old Fields (Table 2). At this time, annuals were mostly abundant in these Old Fields (Table 2). In a parallel study, Giorgetti et al. (1997) reported a lower contribution of *P. napostaense*, *P. ligularis*, *S. clarazii*, *S. papposa* and *S. tenuis* to desirable perennial grass standing crop in the Old Field 2 than in the Control treatment. These authors also found a similar desirable perennial grass standing crop in the Control and Burned treatments during 1984-1992. Annual grasses have been shown to increase with soil disturbance in the Great Basin (Klemmedson and Smith 1964) and South Dakota (Gartner et al. 1986).

Despite species composition was more similar among years within any treatment than among treatments in any given year (Fig. 2), most (>69%) perennial grass species were desirable in all treatments. At this study site, annual rainfall was closely related to desirable perennial grass standing crop in most treatments, and it accounted for most of the variation in herbage production between years (Giorgetti et al. 1997).

Bóo et al. (1993) and Distel and Bóo (1996) reported that *P. ligularis* and *S. clarazii* are the most highly preferred by cattle in semi-arid rangelands of Central Argentina, and tend to dissapear from the pastures with heavy grazing. These species

contributed the least to total perennial grass standing crop in the Overgrazing treatment in our study (Fig. 3). Proper grazing management aids recruitment and persistance of desired species, whereas poor management hastens their replacement by other, less desirable species (Jones and Mott 1980).

Undesirable perennial grasses were mostly found in the Old Field 1 and Overgrazing treatments (Fig. 3). These species represented up to 35% of total herbaceous standing crop in these treatments at the study site during 1984-1992 (Giorgetti et al. 1997). Species of this group, such as *S. ambigua*, *S. brachychaeta* and *S. trichotoma*, are indicative of previous grazing mismanagement conducive to rangeland deterioration (Cano 1988, Distel and Bóo 1996). Standing crop of these species, for example, was greater at the Old Field 1 than at the Old Field 2 treatment (Giorgetti et al. 1997). This, and the lower perennial grass species diversity in the Old Field 1 than in the Old Field 2 treatment (Fig. 5), was probably due to the greater proximity of the Old Field 1 site to a water source for cattle, with a subsequent more severe and continuous grazing.

Intermediate perennial grasses were mostly present in the Old Field 2 treatment (Fig. 3) where they represented 14-45% of total herbaceous standing crop during 1984-1992 (Giorgetti et al. 1997). Contribution of these grasses to total herbaceous standing crop in the other treatments was very low (Giorgetti et al. 1997), and it included *Aristida* species (e.g., *A. subulata*) which may indicate rangeland overuse (Cano 1988). This suggests that the Old Field 2 site may have been exposed to severe overgrazing previous to cultivation.

Species both richness and diversity were higher at the Control or Burned area than at sites receiving a more severe or continuous grazing (Old Field 1 and

Overgrazing) (Figs. 4 and 5). Maintenance of biodiversity allows primary productivity to recover more fully from and be more resistant to disturbances such as drought (McNaughton 1985, Tilman and Downing 1994), a common environmental stress in our study region (Giorgetti et al. 1997). Recent evidence has also shown that plant species diversity and the compositional and production stability of grassland plant communities are positively related (Hartnett et al. 1996). In agreement with our results, Agnew et al. (1986) found higher plant species richness in uncolonized mixed-grass prairie than in prairie dog colonies. Also, Kucera (1956) in Missouri tallgrass prairie sites or Noy-Meir (1995) on Mediterranean grasslands reported decreased plant species either diversity or richness, respectively, when grazing was very heavy for many years. Long-term exclusion of grazers from east African grasslands, however, has resulted in floristically poor plant communities dominated by a few grass species (Smart et al. 1985). Bonham and Lerwick (1976) and Archer et al. (1987) reported that diversity was usually greater in prairie dog colonies than in nearby uncolonized sites on short- and mixed-grass prairies. Hartnett et al. (1996) also found greater plant species diversity on sites moderately grazed by bison relative to ungrazed sites which supported specific predictions of the intermediate disturbance hypothesis and the generalized model of Milchunas et al. (1988). Similarly, Noy-Meir (1995) obtained a higher mean species richness and diversity at sites grazed (burnt or unburnt) mostly moderately than at those kept ungrazed on Mediterranean grasslands. In sub-humid grasslands, theoretical models also predict greater plant species diversity under moderate grazing than under ungrazed conditions (Milchunas et al. 1988). The increase in species both richness and diversity under moderate grazing is likely due to the generation of greater habitat heterogeneity. The mosaic of habitat patches generated by herbivory grazing and non-grazing activities

likely increases the diversity of colonization and establishment opportunities for several species that are otherwise excluded from the community by the strong competitive effects of the matrix dominant species (Hartnett et al. 1996). In fact, Huntly (1991) reported that both selective and non-selective grazing or soil disturbance associated with grazer activity can potentially increase or decrease plant species diversity. Furthermore, grazers may interact with other procceses operating at different spatial and temporal scales (e.g., fire, drought) resulting in scale dependent effects (Kucera 1956, Coppock and Detling 1986, Collins 1987, Grime et al. 1987, Noy-Meir 1995, Hartnett et al. 1996). Despite the Old Field 1 and Overgrazing treatments had a similar perennial grass species both richness and diversity, severe overgrazing followed by a couple of cropping decades (i.e., Old Field 1) appeared to have the least perennial grass species both richness and diversity among all treatments.

Herbivores can mediate species diversity through differentially utilizing plants variously suceptible to defoliation; the capacity of competitive dominants to exclude other species is decreased, and gaps available for occupation by other species are created (Archer and Smeins 1991, Hartnett et al. 1996). Initial conditions, climatic regimes, intensity and duration of grazing impact, and grazer selectivity for specific food items can also be important determinants of either increases or decreases in plant species diversity in response to grazing (Harper 1969, Milchunas et al. 1988). Thus, when reporting on the effects of grazing on species both richness and diversity we need to be cautious, for example, that different either herbivory types or management conditions may have different effects on these community components (e.g., see Hartnett et al. 1996). Systems managed with cattle within the Phytogeographical Province of the Monte typically involve year-round grazing with minimal or none grazing management (Busso

1997). In other rangelands managed for livestock production, however, grazing is often seasonal. Thus differences in the temporal and spatial patterns of grazing may differ considerably among studies and contribute to the observed differences in vegetation responses.

Species richness and diversity varied considerably among years within each treatment, and were similar in the Control and Burned areas during the study period (Figs. 4 and 5). These treatments also had a similar total herbaceous standing crop during 1984-1992 (Giorgetti et al. 1997). Our results are similar to those of Noy-Meir (1995) on Mediterranean grasslands where species richness and diversity varied considerably between years within each category of grazing and fire treatment. However, this author reported that the effect of fire on species richness and diversity in pairs of adjacent sites was much less consistent than that of grazing: in ungrazed areas, a single fire was about as likely to decrease species richness as to increase it. Noy-Meir (1995) reported that in grasslands with a strong perennial component, like ours (see Giorgetti et al. 1997), there was a significant trend of increased richness in the three years after a single fire in grazed areas. This response was attributed to stimulation of germination by fire in some Mediterranean herbaceous species (e.g., González-Rabanal et al. 1994). Economic constraints during a few years immediately after treatment application, however, precluded us from the possibility of observing this trend. Direct negative effects of hot fires on propagule populations of some species may outbalance, however, the gap creation and stimulation effects of fire (Noy-Meir 1995). Belsky (1992) also found a tendency for increased diversity in response to fire in East African grasslands, but the effect was not consistent over communities and grazing treatments.

Fulbright (1996) reported that plant species richness and diversity within a patch created by woody plant control may be similar to, lower than, or greater than plant species richness and diversity on nonmanipulated rangeland following treatment depending on various factors including the treatment method, composition of the plant community before treatment, soil series, and rainfall before and after treatment. In our study, perennial grass species richness and diversity were similar in the Control, Shrub Control and Old Field 2 treatments (Fig. 4 and 5). This result is similar to that of Nolte et al. (1994) in the western Rio Grande Plain where plant species richness and diversity was similar in ephemeral drainages chained (about 40 years earlier) and then root plowed (about 30 years earlier) than in untreated rangeland.

Since species composition remained relatively constant among years within each treatment (Fig. 3), changes in species diversity among years within these treatments (Fig. 5) were mainly due to changes in the relative biomasses of the studied species (Fig. 3). Giorgetti et al. (1997) demonstrated that rainfall appeared to be the major factor in accounting for most of the variation in herbage production between years in these rangelands. The positive relationship between rainfall and herbage standing crop, and the great year to year variations in rainfall which can occur in the east-central rangelands of Argentina continually pose a challenge for land managers. Special management skills are needed for maintenance of a viable livestock industry in this region due to large and rapid changes in forage production (Giorgetti et al. 1997).

Literature Cited

Agnew, W., D.W. Uresk, and R.M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. J. Range Manage. 39:135-139.

Archer, S., M.G. Garret, and J.K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio 72:159-166.

Archer, S. and F.E. Smeins. 1991. Ecosystem-level processes, p. 109-140. *In*: R.K. Heitschmidt and J.W. Stuth (eds.) Grazing management: An Ecological Perspective. Timber Press, Portland, Ore.

Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. J. Veg. Sci. 3:187-200.

Bonham, **C.D. and A. Lerwick. 1976.** Vegetation change induced by prairie dogs on shortgrass range. J. Range Manage. 29:221-225.

Bóo, R.M., L.I. Lindstrom, O.R. Elía, and M.D. Mayor. 1993. Botanical composition and seasonal trends of cattle diets in central Argentina. J. Range Manage. 46:479-482.

Busso, C.A. 1997. Towards an increased and sustainable production in semi-arid rangelands of central Argentina: Two decades of research. J. Arid Environ. 36:197-210.

Cabrera, A. L. 1976. Regiones fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería. Tomo II. Editorial ACME S.A.C.I., Buenos Aires.

Cano, E. 1988. Pastizales naturales de La Pampa. Descripción de las especies más importantes. Tomo 1. Convenio AACREA-Provincia de La Pampa, La Pampa.

Collins, S.L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecol. 68:1243-1250.

Cooperrider, A. 1991. Conservation of biodiversity on western rangelands, p. 40-53. *In*: W.E. Hudson (de.), Landscape linkages and biodiversity. Island Press, Washington, D.C.

Coppock, D.L. and J.K. Detling. 1986. Alteration of bison and black-tailed prairie dog grazing interaction by prescribed burning. J. Wildlife Manage. 50:452-455.

Daubenmire, R. 1959. A canopy-coverage method for vegetation analysis. Northwestern Scientist 33:43-64.

Distel, R.A. and R.M. Bóo. 1996. Vegetation states and transitions in temperate semiarid rangelands of Argentina, p. 117-118. *In:* N.E. West (ed.), Proc. Fifth International Rangeland Congress. Soc. Range Manage. Denver, Colo.

Digiuni, **D. 1983.** Métodos de desmonte y su impacto sobre el pastizal natural en el noroeste de Rio Negro. Estación Experimental IDEVI, Serie Técnica 11:1-73.

Fulbright, T.E. 1996. Viewpoint: A theoretical basis for planning woody plant control to maintain species diversity. J. Range Manage. 49:554-559.

Gartner, **F.R., E.M. White, and R.I. Butterfield. 1986.** Mechanical treatment and burning for high quality range forage, p. 135-140. South Dakota Beef Report. Animal and Range Sciences Dept., Agriculture Experiment Station and Coop Extension Service. South Dakota State University, Brookings.

Giorgetti, H.D., O.A. Montenegro, G.D. Rodríguez, C.A. Busso, T. Montani, M.A. Burgos, A.C. Flemmer, M.B. Toribio, and S.S. Horvitz. 1997. The comparative influence of past management and rainfall on range herbaceous

standing crop in east-central Argentina: 14 years of observations. J. Arid Environ. 36:623-637.

González-Rabanal, F., M. Casal, and L. Trabaud. 1994. Effects of high temperatures, ash and seed position in the inflorescence on the germination of three Spanish grasses. J. Veg. Sci. 5:289-294.

Grime, J.P., J.M.L. Mackey, S.H. Hiller, and D.J. Read. 1987. Floristic diversity in a model system using experimental microcosms. Nature 328:420-422.

Harper, J.L. 1969. The role of predation in vegetation diversity. *In:* Diversity and stability in ecological systems. Brookhaven Symp. in Biology 22:48-62.

Hartnett, D.C., K.R. Hickman, and L.E. Fischer Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. J. Range Manage. 49:413-420.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Ann. Rev. Ecol. Syst. 22:477-503.

Jones, R.M. and J.J. Mott. 1980. Population dynamics in grazed pastures. Trop. Grassl. 14:218-224.

Klemmedson, J.O. and J.G. Smith. 1964. Cheatgrass (*Bromus tectorum* L.). Botanical Review 30:226-262.

Kucera, C.L. 1956. Grazing effects on composition of virgin prairie in north-central Missouri. Ecol. 37:389-391.

Lewis, C.E., B.F. Swindel, and G.W. Tanner. 1988. Species diversity and diversity profiles: concept, measurement, and application to timber and range management. J. Range Manage. 41:466-469.

McNaughton, S.J. 1985. Ecology of a grazing ecosystem: The Serengeti. Ecol. Mon. 55:259-294.

Milchunas, D.G., O.E. Sala, and W.K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. Amer. Natur. 132:87-105.

Miller, R.G. 1981. Simultaneous statistical inference. Springer-Verlag, New York.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York.

Nolte, K.R., T.M. Gabor, M.W. Hehman, M.A. Asleson, and T.E. Fulbright. 1994. Long-term effects of brush management on vegetation diversity in ephemeral drainages. J. Range Manage. 47:457-459.

Noy-**Meir, Y. 1995.** Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. J. Veg. Sci. 6:701-710.

Pielou, E.C. 1977. Mathematical Ecology. John Wiley and Sons, New York.

Smart, N.O.E., J.C. Hatton, and D.H.N. Spence. 1985. The effect of long-term exclusion of large herbivores on vegetation in Murchison Falls National Park, Uganda. Biol. Conserv. 33:229-245.

Tilman, **D. and J.A. Downing. 1994.** Biodiversity and stability in grasslands. Nature 367:363-365.

West, N.E. 1993. Biodiversity of rangelands. J. Range Manage. 46:2-13.

Table legends

Table 1. Physical and chemical soil characteristics at different depths on the exclosure in the Phytogeographical Province of the Monte.

Table 2. Percentage cover of herbaceous species, litter and bare soil in the Control, Burned, Shrub Control, Old Field 1 or Old Field 2 treatment on 15 November 1978. Each value is the mean of n=50.

Figure legends

Fig. 1. (a) Mean monthly maximum and minimum, and mean monthly air temperatures, (b) mean monthly soil temperatures at 0.05-0.5 cm depth; temperatures were taken at 0.05, 0.10, 0.20, 0.30, 0.40 and 0.50 cm depth, and averaged over the 0.05-0.50 cm soil depth range, (c) mean monthly maximum and minimum, and mean monthly relative humidities, (d) mean monthly pan evaporation and (e) daily rainfall during 1981-1992 at a meteorological station located at the study site in the Phytogeographical Province of the Monte.

Fig. 2. Results of Principal Coordinate Analysis after using the Morisita-Horn index. Distance among symbols either within or among treatments represents a measure of its association: a greater association is obtained among closer than distant points.

Fig. 3. Percentage contribution of desirable, intermediate and undesirable grass species to total perennial grass standing crop in the different treatments during 1984-1992.

Fig. 4. Species richness in the different treatments during 1984-1992. Each histogram is the mean of n=30. Vertical bars represent +1SE of the mean.

Fig. 5. Simpson species diversity index in the different treatments during 1984-1992. Each histogram is the mean of n=30. Vertical bars represent +1SE of the mean.

Table 1.

		Soil depth (cm)				
		0-3	3-20	20-28	28-43	43-100
% Clay		25.94	28.77	38.28	17.54	24.38
%Loam (2-20μ)		9.56	8.23	5.22	10.21	10.62
%Loam(20-50μ)		7.88	6.73	7.99	16.88	9.31
% Sand		56.62	56.27	48.52	55.37	55.70
% Organic carbon		0.954	0.642	0.611	1.445	1.699
% Calcium carbonate		0.239	0.113	0.185	0.362	0.915
pH		8.0	8.7	9.1	9.0	9.1
% Total Nitrogen		0.076	0.052	0.053	0.112	0.123
Available phosphorus(ppm)		28.7	9.9	9.8	5.3	4.0
Exchangeable Cations cmol Kg-1 soil	Ca^{2+}	10.3	12.5	10.1	10.6	11.7
	Mg^{2+}	3.72	3.81	4.60	4.72	3.63
	Na^{+}	0.41	0.81	1.76	3.61	6.06
	K^{+}	1.41	1.15	1.03	0.92	0.60
Soluble Cations meq100gL^{-1}	Ca^{2+}	5.16	3.17	4.03	11.64	23.21
	Mg^{2+}	3.56	1.40	1.41	6.07	14.21
	Na^{+}	3.09	4.04	5.90	30.74	84.24
	K^{+}	1.03	0.41	0.35	0.58	0.94

Table 2.

	Control	Burned	Shrub Control	Old Field 1	Old Field 2
Vegetation					
Perennial					
Desirable grasses					
Bromus brevis Nees	0.2	0	0	0	0.7
Pappophorum caespitosum Fries	0	2.2	0	0	0
Piptochaetium napostaense	0	8.6	10.5	5.6	0
Poa lanuginosa Poir.	1.0	0	0	0	0
P. ligularis	12.0	7.8	23.2	0	0
Stipa clarazii	9.6	9.5	12.3	0	0
S. papposa Nees	0	2.2	0	0	0
S. tenuis	28.0	6.0	17.1	0	7.7
Intermediate grasses					
Aristida spegazzinii Arech.	0	2.2	0	0	0
Stipa speciosa Trin. & Rupr.	0	0	2.2	0	0
Undesirable grasses					
Stipa ambigua	0	0	0	10.5	26.7
Undesirable forbs					
Baccharis gillesii	0	0	0	13.3	4.5
Annual					
Desirable grasses					
Hordeum murinum L.	0	0.3	0.2	3.7	3.7
Schismus barbatus (L.) Thellung	0	0	0	2.7	3.4
Vulpia megalura (Nutt.) Rydb.	0.7	2.5	0.3	0	0
Bromus catharticus Vahl	0	0	0	7.7	0
Desirable forbs					
Erodium cicutarium (L.) L'Hér.	0	0	0	3.7	11.5
Medicago minima (L.) Grufberg	0	0	0	15.9	0
Litter	13.8	7.5	20.1	12.2	23.1
Bare soil	26.1	49.5	15.8	21.5	18.5

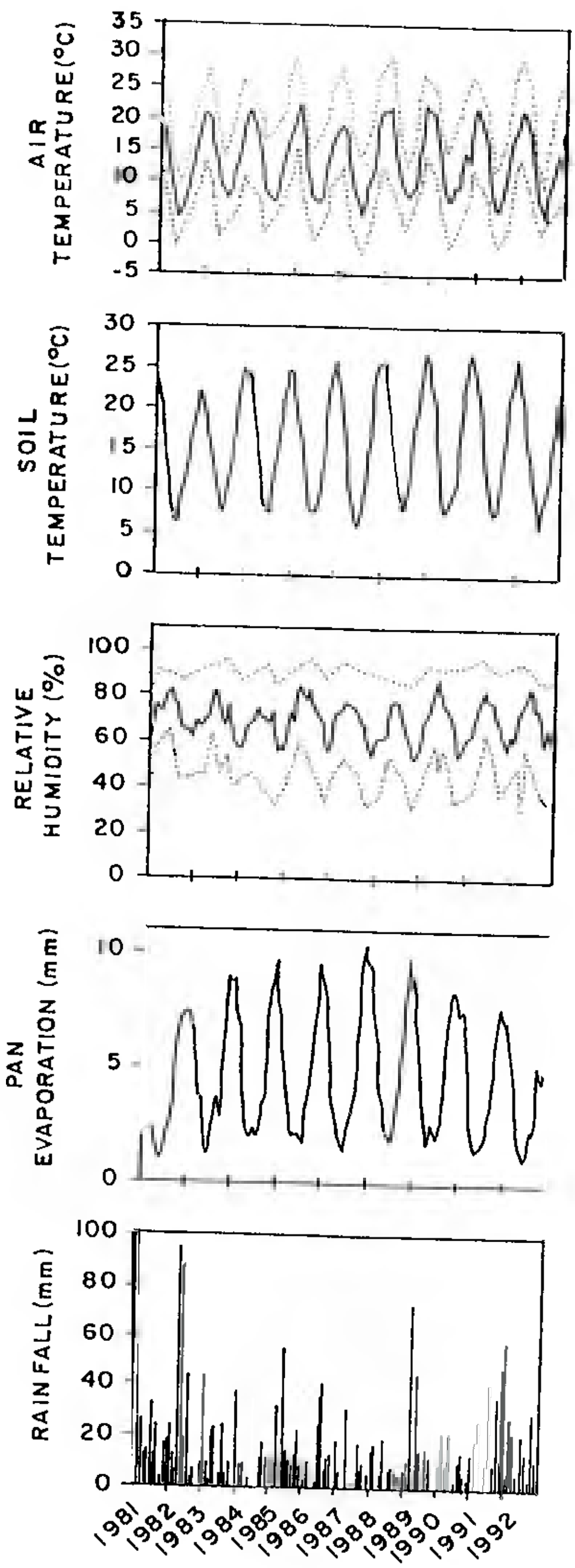

Fig. 1

Busso, Giorgetti, Montenegro, Rodriguez & Tabler

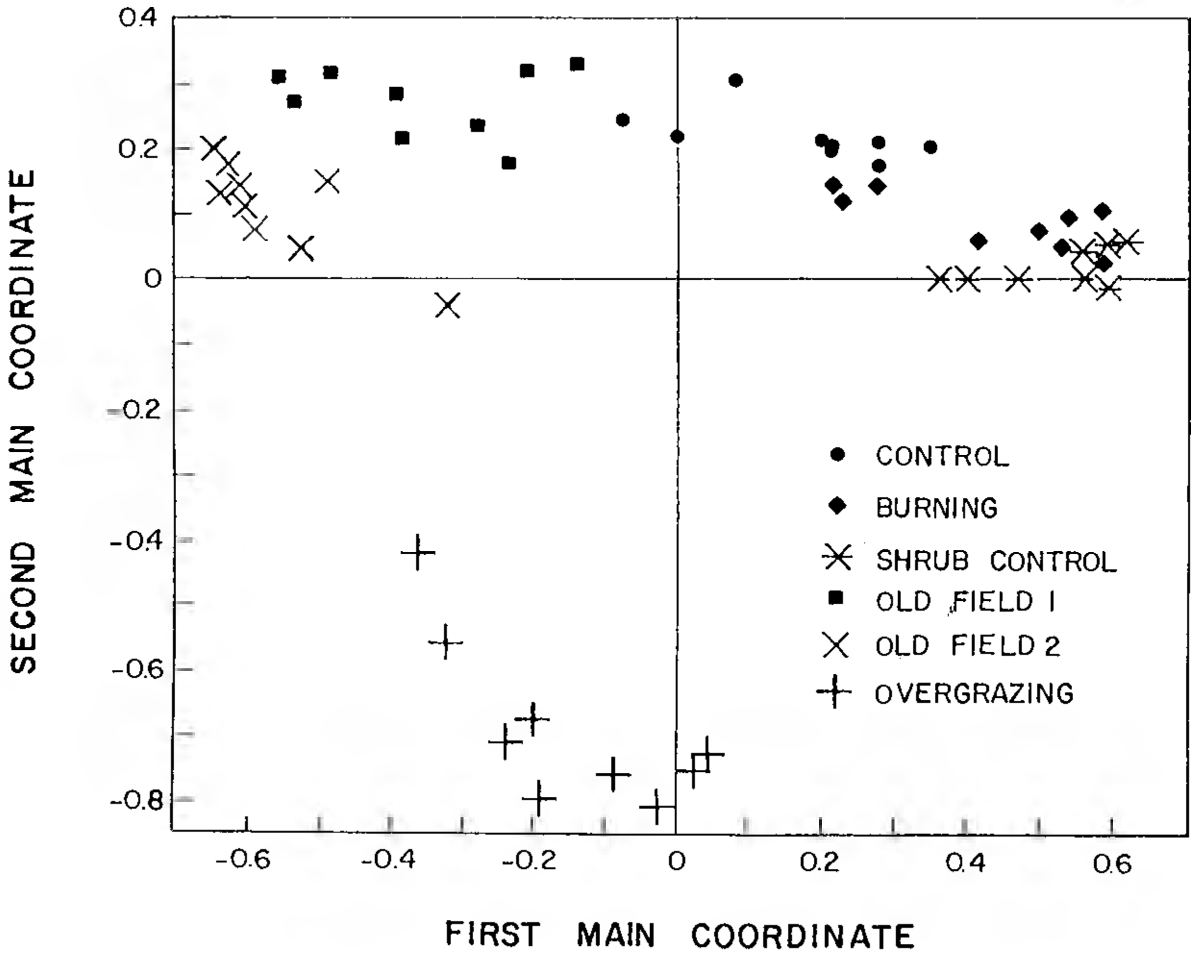

Fig. 2
Busso, Giorgetti, Montenegro, Rodriguez & Tablar

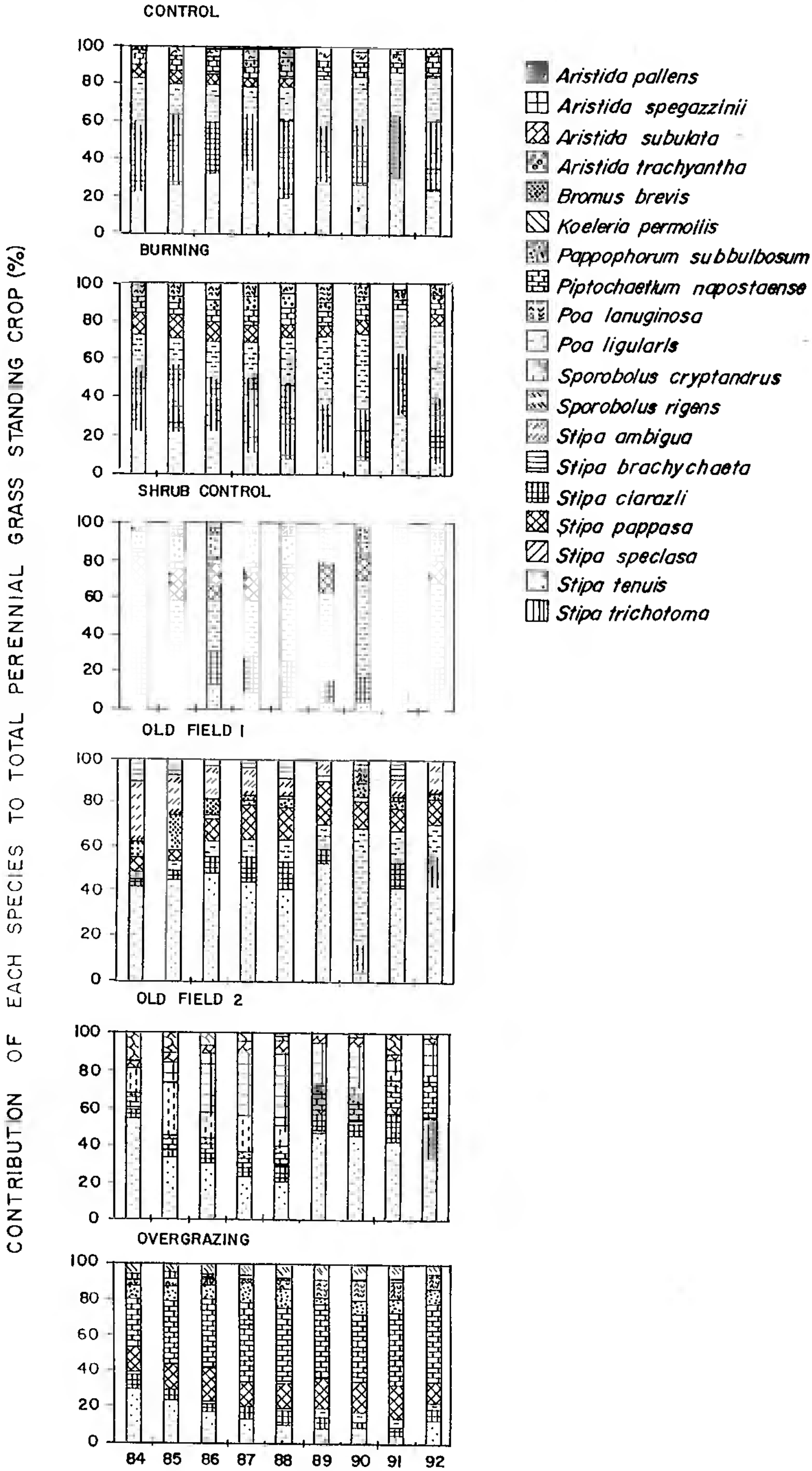

Fig. 3

Busso, Giorgetti, Montenegro, Rodriguez & Tablar

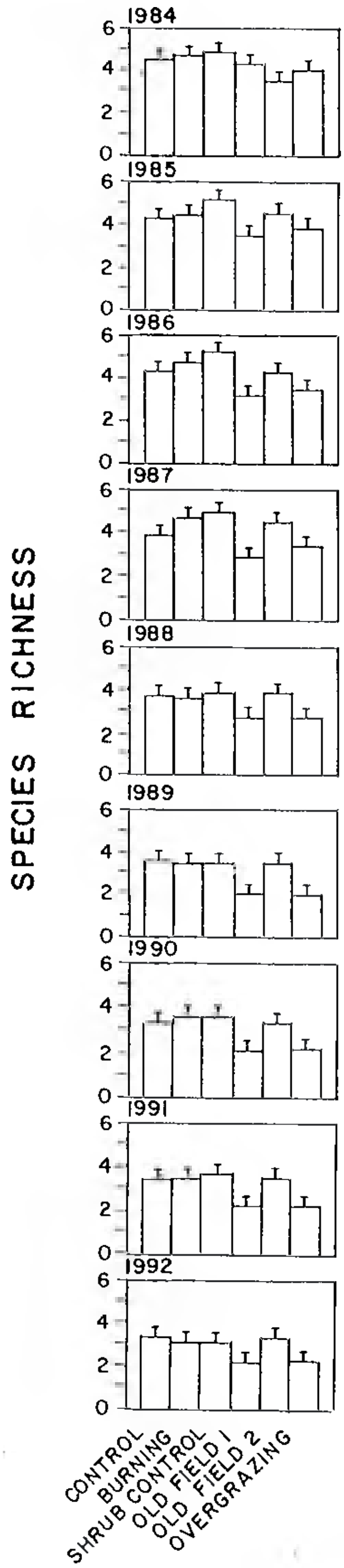

Fig. 4
Busso, Giorgetti, Montenegro, Rodríguez & Tablar

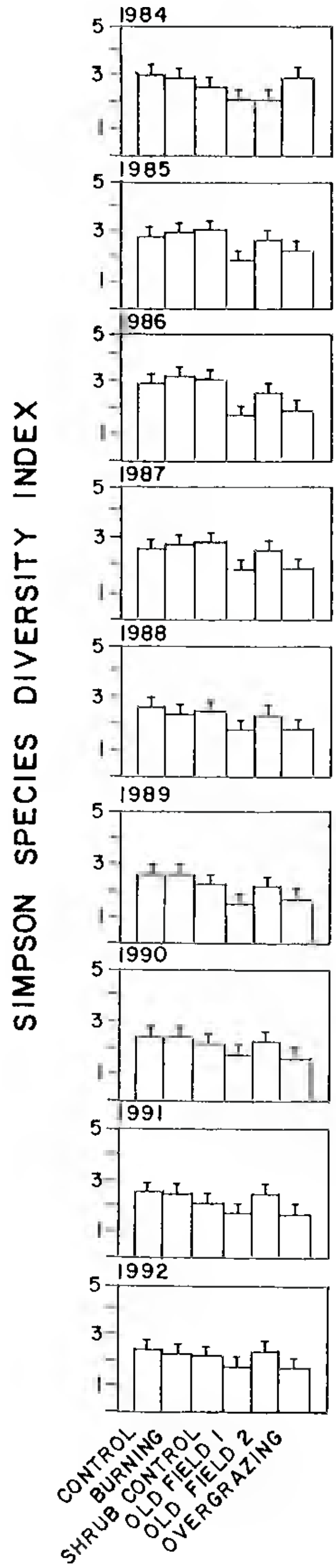

Fig. 5

Busso, Giorgetti, Montenegro, Rodríguez & Tablar