Journal of Vegetation Science 14: 433-440, 2003
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Temporal trends in species composition and plant traits in natural grasslands of Uruguay

Rodríguez, Claudia; Leoni, Elsa; Lezama, Felipe & Altesor, Alice[*]

Sección Ecología Terrestre, Facultad de Ciencias, Universidad de la República, Iguá 4225, 11400 Montevideo, Uruguay;
[*]Corresponding author; Fax +59825258616; E-mail aaltesor@fcien.edu.uy

Abstract. We report the successional trends of the major life-forms (graminoids and forbs) in natural grasslands of Uruguay over a 9-yr period after the removal of domestic herbivores. For the whole community, species richness and diversity decreased over the successional period. In graminoids we observed clear temporal trajectories in floristic composition; the rate of floristic change decreased with time and was associated with a shift in plant traits. The exclusion of large herbivores promoted erect and tall grasses with narrow leaves and greater seed length, vegetative growth constrained to the cool season and increased frequency of annual species. Forbs did not show a clear temporal trend in species composition, but there was, nevertheless, a plot-specific species turnover of this functional group that was reflected in their attributes. Species spreading by means of rhizomes, with vegetative growth restricted to the warm season. Species with larger seeds increased under grazing exclusion, as did annual and nitrogen-fixing forbs. The floristic changes induced by cattle exclusion occurred early in the succession. This early high rate of change has practical implications for management and conservation programs of the natural grasslands of Uruguay. Additionally, the shift in plant traits may be helpful in devising simple indicators of grazing impact.

Keywords: Biodiversity; Forb; Graminoid; Grazing exclosure; Plant functional type; Succession.

Nomenclature: Cabrera (1970).

Introduction

Temperate sub-humid grasslands cover the vast plains of central-eastern Argentina, Uruguay and southern Brazil, as an arc folded around the Rio de la Plata (Soriano 1991). Large areas have been replaced by crops but an important portion of the region is still occupied by natural or semi-natural grasslands grazed by domestic herbivores, mainly sheep and cattle (Soriano 1991; Altesor et al. 1998). The Flooding Pampa in Argentina and the Campos in Uruguay are one of the largest areas of natural temperate sub-humid grasslands in the world. The grasslands are structured as a matrix of perennial grasses with a second group of interstitial, less abundant species (subdominant grasses and forbs).

Grazing leads to changes in species richness, diversity and dominance over time (Collins 1990; Trémont 1994). In the Flooding Pampa of Argentina, grazing by domestic herbivores significantly increased the cover of cool-season exotic species (Facelli 1988; Facelli et al. 1988; Chaneton & Facelli 1991). In an Uruguayan grassland, Altesor et al. (1998) reported a decrease in forage quality after 55 yr of continuous grazing. Some palatable grasses decreased or disappeared and a large number of non-palatable species increased.

Plant functional types (PFTs) have been used recently as an alternative to floristic description in studies on grazing impact (Lavorel et al. 1997; McIntyre & Lavorel 2001). Five main PFTs can be identified in temperate grassland and shrublands areas: C_3 grasses, C_4 grasses, shrubs, forbs and succulents (Paruelo & Lauenroth 1996). The first three account for most of the biomass and show clear patterns across environmental gradients. Such PFTs are described on the basis of a number of structural and functional traits. The way species are grouped into PFTs depends on the traits considered and different grouping strategies will arise from different objectives. Several plant traits have been used as indicators of grassland responses to grazing. Landsberg et al. (1999) classified them as 'morphological traits' (height, lateral spread, habit, canopy structure, life form), 'grazing persistence traits' (leaf/stem ratio, spininess, regrowth potential, plasticity, specific area, toughness, hairiness) and 'regeneration traits' (seed size, dispersal aids, fecundity, life span, recruitment frequency, ability to reproduce vegetatively). Within this wide spectrum it is useful to identify those traits which can be easily measured and that consistently predict grazing response. A PFT definition aimed to describe the response of the plant community to grazing should emphasize on these traits. Describing the plant community dynamics at the PFT level is consistent with the approach outlined by Connell & Slatyer (1977) and Pickett et al. (1987)

which emphasizes the importance of autecology and life history attributes of individual species in determining plant succession.

Lavorel et al. (1997) proposed that the classifications of the response of plant functional groups to disturbance should be undertaken in a hierarchical way, with separated analyses for the different major life forms of a particular community.

Following this hierarchical approach, the objectives of this article were to analyse the changes in diversity, floristic composition and plant traits of the major life forms (graminoids and forbs) in response to nine years of grazing exclosure in five Uruguayan grasslands.

Methods

The study site was located in a sedimentary plain in Cerro Largo, Uruguay (32°05' S, 54°30' W). Soils have a high organic matter content (> 3%) in the A-horizon and a moderate drainage capacity (Durán 1985). Rainfall is evenly distributed throughout the year and the annual mean is 1100 mm. Mean annual temperature varies from 10.7 °C in July to 22.7 °C in January (Anon. 1996). From a phytogeographical viewpoint the area is included into the Northern Campos subregion of the Rio de la Plata grasslands. In this area grazing usually leads to a two-strata system: a low and dense stratum, no more than 5 cm high, and a higher stratum of bunch grasses and small woody plants (Soriano 1991). Native C_4 grasses (*Poaceae*) dominated across the whole region. The main forb families include *Asteraceae*, *Fabaceae*, *Rubiaceae* and *Umbelliferae* (Gallinal et al. 1938; Rosengurtt 1943). The floristic composition and species frequency of five grazing exclosures (2500 m^2) set up between 1989 and 1990 were recorded annually in December until 1998 by the Dirección de Suelos of the Ministerio de Ganadería, Agricultura y Pesca (MGAP, Uruguay). No data were recorded in 1991 and 1997. Frequency values were obtained by recording all the species contacts in 50 points by a needle (Tothill 1978). In each site 25 observations were distributed regularly along two 50-m transects. We calculated richness (*S*), Shannon's diversity index (*H*) and evenness (*E*) for the whole community and we analysed the temporal trends of these synthetic descriptors using linear regression models.

We used Non-Metric Dimensional Scaling (NMDS) of sites (with the Bray-Curtis distance as dissimilarity measure) to analyse the species composition change over time. A Monte Carlo permutation test (199 random permutations of the samples in the species data) were included in the NMDS analysis. The analyses were performed using PCOrd (McCune & Mefford 1999). For the graminoid group (*Poaceae*, *Juncaceae* and *Cyperaceae*) the raw matrix contained 42 species and 35 observations (5 plots × 7 sampling periods). The matrix of the forb group contained 23 species and 35 observations. Only species with a relative frequency higher than 10% in a particular year and plot were included in the multivariate analysis.

Soil samples were taken from each plot during the 1990 sampling, and were air-dried and analysed in the laboratory. The soil features are summarized in Table 1. We correlated the scores of axis 1 and 2 of the NMDS against soil properties using Pearson's coefficient. Because each axis was analysed against 14 non-independent soil variables, we used a Bonferroni criterion to correct the threshold values for the acceptance of a significant association, making the test of the null hypothesis more stringent.

We also analysed the temporal changes of nine plant traits of the graminoid species. Three additional traits were added for the forb group (Table 2). The traits included morphological, physiological and ecological characteristics of the species that are expected to change in response to grazing. Traits were measured on ten individuals of each species randomly selected from the plots. Information from herbaria and floras was also utilized. The scales of measurement of the original traits where categorical or continuous. The whole range of continuous variables (e.g. plant height, width/length leaf ratio, seed length) was divided into three or four intervals. All categories and the resulting intervals of the continuous data were transformed into a binary scale for analysis. Therefore, the original traits resulted in 23 binary attributes for the graminoids and 33 for the forbs. The attributes were compiled into a graminoid-matrix of 42 species × 23 attributes and a forb matrix of 23 species × 33 attributes. For each group, we multiplied the matrix

Table 1. Soil attributes in each of the five plots, recorded during 1990. All values were measured in homogenized samples from the A-horizon, except for 'clay in B' which refers to % clay in the B-horizon.

	Plots				
	A	B	C	D	E
Thickness of A (cm)	25	53	28	25	34
Sand (%)	44.5	30.3	59.3	55.2	61.5
Loam (%)	32.6	34.0	21.1	23.3	16.7
Clay (%)	23.3	35.6	19.6	21.4	22.3
Clay in B (%)	30.5	46.8	40.3	38.8	38
pH	7.3	5.9	5.6	5.9	5.8
Ca (meq/100g)	18.9	22.8	4.6	5.0	7.7
Mg (meq/100g)	3.5	2.4	1.5	1.7	1.1
Na (meq/100g)	0.9	0.3	0.2	0.3	0.2
K (meq/100g)	0.3	0.5	0.3	0.4	0.4
K/Na	0.3	1.8	1.5	1.2	1.8
Organic matter (%)	5.1	6.6	3.1	3.4	2.8
P (ppm)	5.0	4.5	4.0	4.0	3.5

Table 2. Traits recorded on the most frequent species of natural Uruguayan grasslands. Text in bold indicates traits or attributes recorded only for graminoid species, text in italics indicates traits or attributes recorded only for forbs.

Traits	Description	Attributes
Persistence	Life span[1,5]	Annual, perennial
Habit	Mode of growth[1,5,8]	Erect, prostrate, *rosette*
Height	Vegetative height of adults[1,5,9]	Categories (cm): cat I < 30, $30 \leq$ cat II ≤ 60, $60 <$ cat III ≤ 100, **cat IV >100**
Vegetative spread	Capacity and mode of production of clones[1,4,5,8]	Absent, rhizome, stolon, *bulb*
Growth period	Season of active growth[1,5,7]	Cool-season, warm-season
Leaf form	Leaf length/ width ratio[1,5,10]	Categories: 1= ratio < 50; 2 = 50 - 100; 3 = > 100
Leaf pubescence	Presence of hairs[1,5,10]	High, medium, glabrous.
Seed length (cm)	Higher diameter[1,2,3,4,5,10]	Categories: 1 = < 0.3; 2 = 0.3 - 0.5; 3 = > 0.5
Palatability	Livestock preference[7]	High palatability, medium palatability, *unpalatable*
Stem type	*Stem woodiness*[1,5,8]	*Woody, herbaceous*
Nitrogen fixation	*N-fixation root nodules*[1]	N^+, N^-
Dormant buds	*Dormant bud position*[5,8]	*Chamaephytes, hemicryptophytes, geophytes, therophytes*

[1]Lombardo (1984); [2]Cabrera (1970); [3]Correa (1978); [4]Burkart (1969); [5]Rosengurtt et al. (1970); [6]Watson & Dallwitz (1992); [7]Rosengurtt (1979); [8]Field observation; [9]Field measurement; [10]Laboratory measurement or observation.

of *plots* × *species* frequencies by the *species* × *attributes* matrix and we obtained a *plots* × *attributes* matrix. We analysed by linear regression the changes through time of the relative frequencies of each attribute.

Results

Floristic and diversity changes

Over the whole length of the study, we recorded a total of 72 species of graminoids and 59 species of forbs. The average number of species observed per year was higher for graminoids than forbs (graminoid mean = 21.1 species, forbs mean = 12.9 species). The mean relative frequency (RF) per year of graminoids was also higher than forbs (graminoids RF mean = 0.74; forbs RF mean = 0.26). For the whole community, species richness S and Shannon's diversity index H decreased significantly through time ($r = -0.40$, $P < 0.05$ and $r = -0.39$, $P < 0.05$, respectively) but evenness (E) did not change ($r = -0.31$, NS).

Site ordination (NMDS, Bray-Curtis distances, graminoid species composition) showed a clear temporal pattern. The directional change reflected by axis 1 (Fig. 1a), and the results of the Monte Carlo test indicate that there was a highly significant trend ($P < 0.005$) in species composition across the entire period. NMDS plot suggests that the greatest species turnover occurred between 1989-1990 and 1992. Under grazing, all plots were dominated by *Paspalum notatum*, *Botriochloa laguroides*, *Axonopus affinis* and *Sporobolus platensis* with frequencies higher than 20%. All of them decreased or disappeared during the first years of exclusion. These species were replaced by a group of species that increased during the first years of the successional

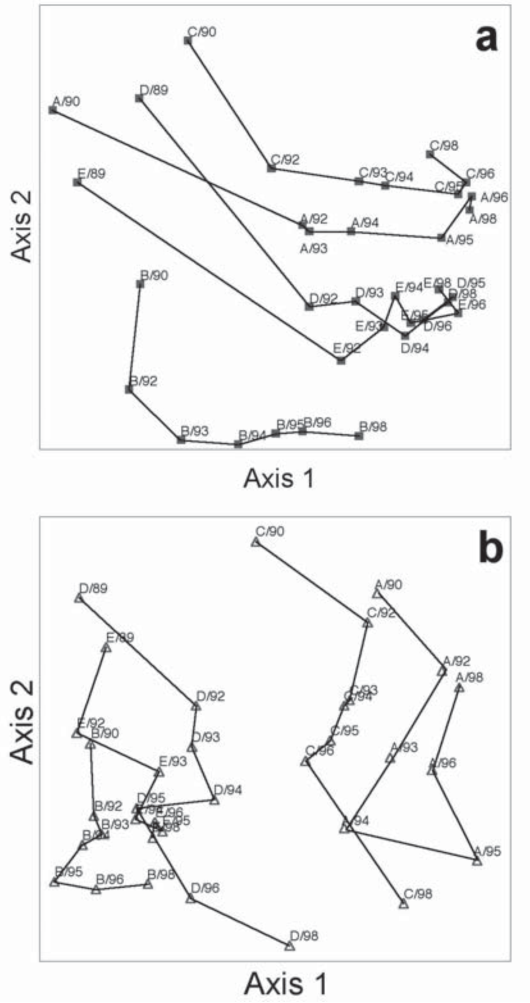

Fig. 1. Configuration of (frequency) samples of graminoids (**a**) and forbs (**b**) in a two-dimensional Non-Metric Multidimensional Scaling (NMDS) representation of the Bray-Curtis distances. The trajectories of the same plot through time are represented by lines; points indicate the plots at each sampling date.

period. Among them *Paspalum plicatulum* and *Briza subaristata* were present at all sites, with frequencies ranging between 43-68% and 23-60%, respectively, depending on the plot. The species turnover continued over the successional period and in the last years all plots were dominated by *Coelorhachis selloana* with frequencies ranging from 78 to 98%. For graminoids the floristic dissimilarity between contiguous sampling dates (Bray-Curtis distance) decreased throughout the succession ($r = -0.795$, $P < 0.001$) (Fig. 2).

The second axis distinguished the spatial differences among sites. This axis clearly detected a soil gradient going from plot B (an argillic soil with a deeper A-horizon and high organic matter content) to plot C (a sandy soil, with a shallow A-horizon and low organic matter content).

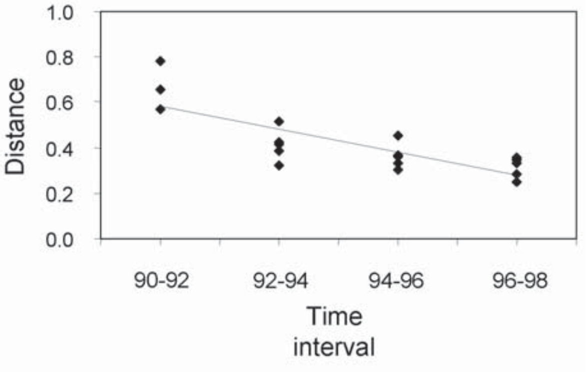

Fig. 2. Relationship between the Bray-Curtis distances among sampling dates for the graminoid group for the periods 1990-1992 to 1996-1998 throughout the succession. For the first interval (90-92) only plots A, B and C were included.

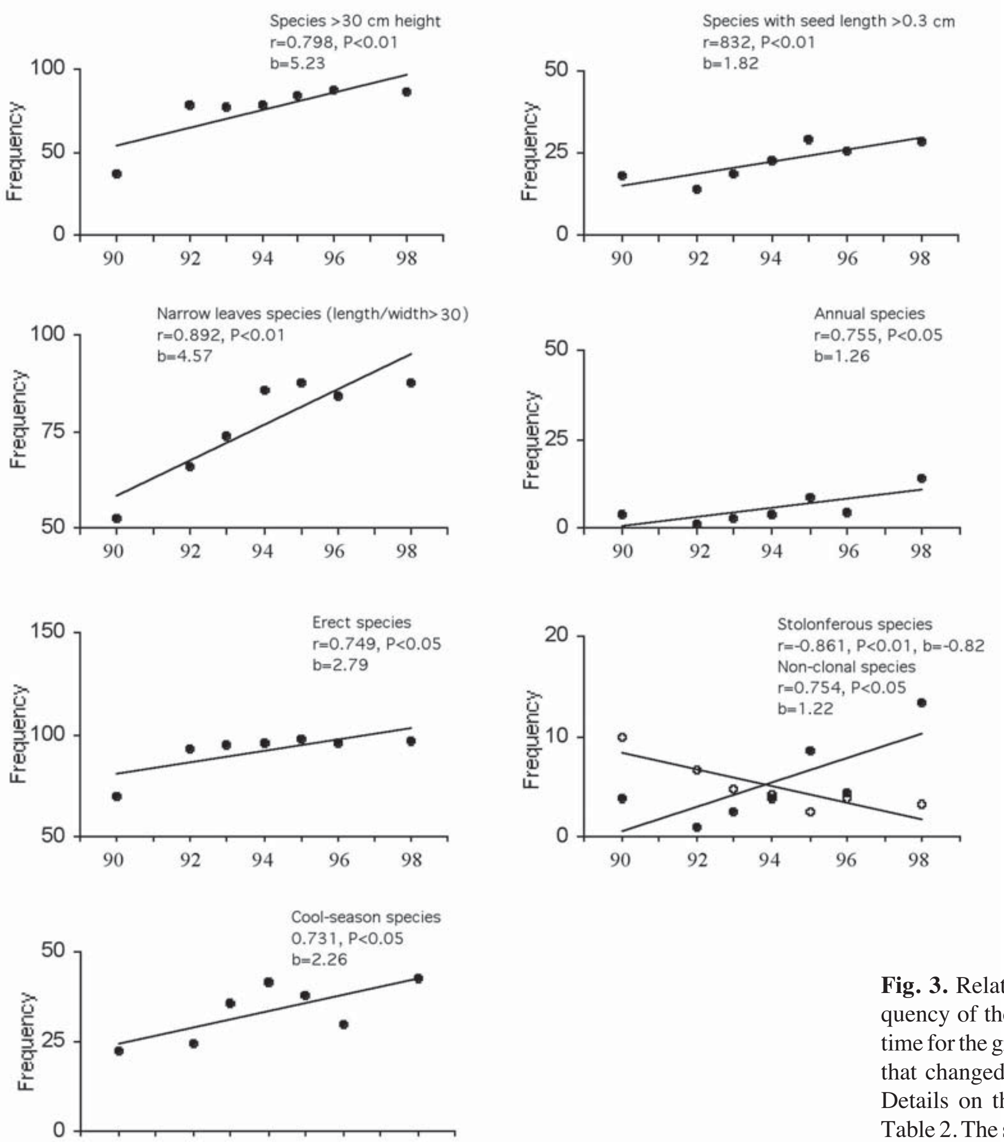

Fig. 3. Relationship between the frequency of the different att ributes and time for the graminoids. Only attributes that changed significantly are shown. Details on the traits are presented in Table 2. The scale of the *y*-axis changes among graphs.

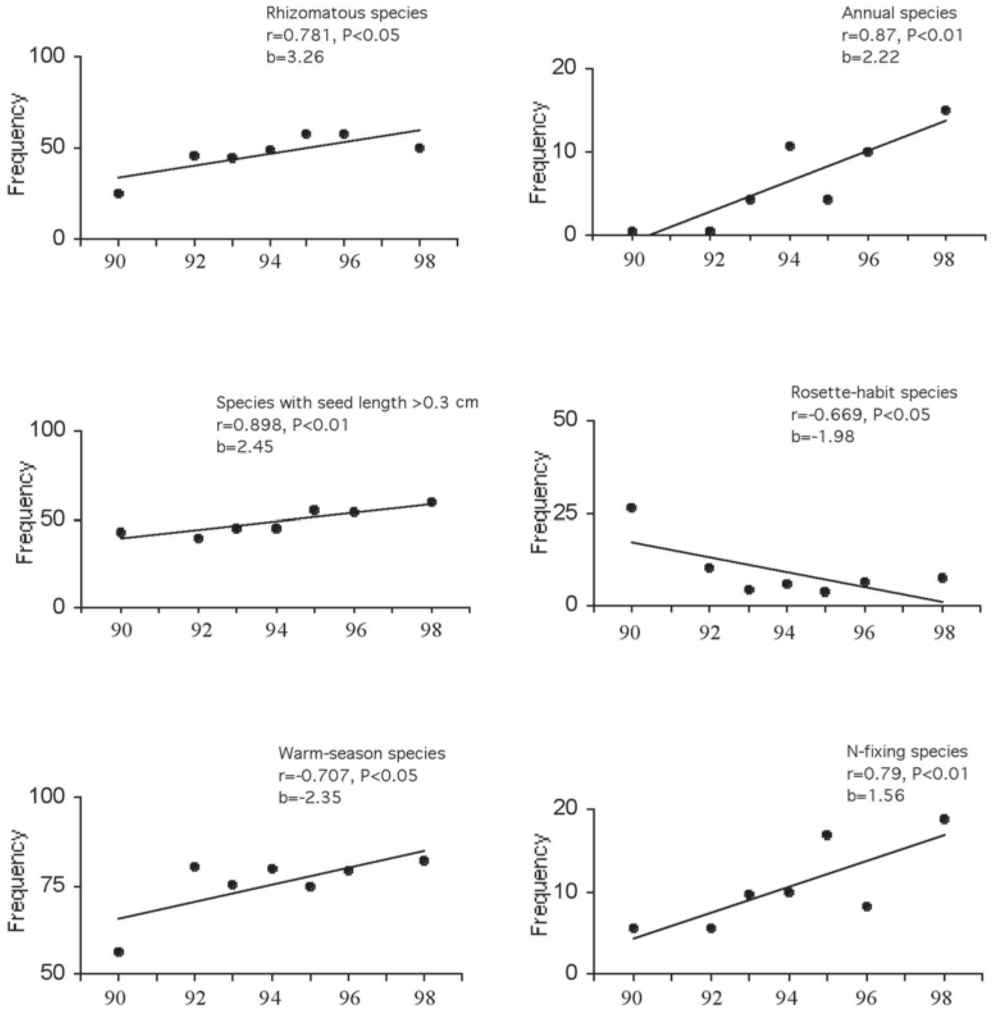

Fig. 4. Relationship between the frequencies of the attributes and time for the forbs. Only attributes that changed significantly are shown. Details on the traits are presented in Table 2. The scale of the *y*-axis changes among graphs.

Soil variables showed no significant correlation with axis 1, but thickness, percentage of clay and the potassium content of the A-horizon were significant correlated with axis 2 scores ($r = -0.905$, $P < 0.05$; $r = -0.903$, $P < 0.05$; $r = -0.910$, $P < 0.05$ respectively). Site ordination for the forb group did not reveal any temporal trend and the Bray-Curtis distance between sampling dates did not show any significant relationship with time (Fig. 1b). In contrast to the graminoid group, axis 1 revealed differences among plots. We found that the thickness of the A-horizon, the percentage of clay in the A-horizon and the potassium content were significantly correlated with the axis 1 scores ($r = 0.937$, $P < 0.05$; $r = 0.877$, $P < 0.05$; $r = 0.969$, $P < 0.01$ respectively). No significant relationships were observed between axis 2 scores and soil variables.

Attribute changes

Height, habit, seed length, vegetative spread, leaf form, growth period and persistence were the traits that changed significantly over time for the graminoid group (Fig. 3). Plants taller than 30 cm increased their frequencies rapidly, their rate of change was twice that of the rest. At the beginning of the succession (1989 and 1990) all sites were characterized by C_4 prostrate grasses with small seeds and broad leaves that spread horizontally by means of long rhizomes or stolons. Excluding large herbivores favoured erect and tall plants with larger seeds, narrow leaves and a vegetative growth constrained to the cool season. The significant increase of annual species was due to the increase of the exotic grass *Lolium multiflorum* in some plots.

Of the 12 traits analysed for the forb group, six of them changed significantly in response to herbivore exclosure: vegetative spread, seed length, growth period, persistence, habit and nitrogen fixation (Fig. 4). Cattle exclosure favoured rhizomatose, warm-season species with larger seeds, as well as annuals and nitrogen fixing species. The rosette habit decreased significantly. The rates of change of frequency ranged from $3.26.yr^{-1}$ for the rhizomatose habit to $1.56.yr^{-1}$ for legumes.

Discussion

Nine years after removing large herbivores the diversity index of the whole community decreased. The same pattern was described for different grasslands (e.g. Trémont 1994; Collins et al. 1998; Altesor et al. 1998). Grazing may increase diversity by reducing the dominance of superior competitors.

Graminoid ordination pointed out that most of the changes took place during the early stages of the succession. The magnitude of the floristic changes between successive sampling dates (Bray-Curtis distance) decreased from a rate of $0.335.yr^{-1}$ to $0.155.yr^{-1}$ (Fig. 2). A previous study in the same plots over 55 yr (1935-1990) of continuous grazing (Altesor et al. 1998) showed that the community maintained a 'stable' composition, at least in terms of dominant species. In 1990, 10 of the 13 dominant grasses in the 1935 samples maintained frequencies higher than 30% in 1990.

In contrast, forbs did not show clear temporal trends. The Bray-Curtis distances were more associated with soil quality than with a successional changes. This agrees with the general behaviour of forbs in temperate grasslands, where they conform a group of localized, less abundant, and less predictable interstitial group of species (Hartnett & Fay 1998), although they may become important in a phytosociological sense (Batista et al. 1988; Burkart et al. 1990; Perelman et al. 2001). In this Uruguayan grassland, it seems that forbs behave like subordinate or transient species (*sensu* Grime 1998) that are associated with specific habitats but did not show any clear association with particular dominant species. Our results suggest that their dynamics is regulated by processes other than grazing.

The floristic changes outlined for graminoids were coupled with a shift in plant traits. Plant height was the trait that showed the fastest response to grazing exclosure, possibly as a result of competition for light. Díaz et al. (2001), working with 83 species from Argentina and 19 from Israel, found that plant height was the trait more clearly associated to grazing. Previous studies also show that livestock grazing reduces the average plant height and leaf size of the community, and that it concentrates the biomass close to the ground (Noy-Meir et al. 1989; Díaz et al. 1992; Lavorel et al. 1999; Landsberg et al. 1999). Although the forb group did not show a clear turnover of species composition, certain attributes showed significant trends over time.

Large-seeded species, both graminoids and forbs, increased after fencing. Possibly many small-seeded forbs and grasses fail to establish under a tall and closed canopy. Changes in growth season period showed opposite trends for graminoids and forbs. Cool-season grasses (C_3), whose short rhizomes only allows an erect mode of growth, increased significantly after fencing. On the contrary, winter forbs – many of them with rosettes – decreased in the exclosures. These cool-season forbs which, under a grazing regime, occupied the gaps left by grasses, are all native. This is an important difference with the Pampa grasslands, where grazing promotes the invasion of alien cool-season forbs. Anyhow, being native or exotic, these winter forbs are replaced by tussock grasses after cattle exclusion.

Annual species were very scarce in the community. We only registered three annual grasses over the whole study period. Two of them decreased their frequencies after fencing (*Briza minor* and *Vulpia australis*) but *Lolium multiflorum*, an exotic grass that is usually sown to improve the forage quality of the grasslands, invaded three plots, reaching high frequencies during the succession. In the forb group, only three species were responsible for the significant increase of this attribute during succession. The legumes also increased their frequency after fencing. Legumes are often considered as a distinct functional group in grasslands. In this community they were represented by only three species with medium to low frequencies; consequently they were incorporated in the forb group.

The differences observed between groups reinforce the idea that the hierarchical approach improves the analysis of the communities' responses to grazing (Lavorel et al. 1997). Certain patterns that can be obscured when the analysis is performed at the whole community, become more evident when life-forms groups are treated separately.

Conclusions

The hierarchical approach of this study highlighted that in this community graminoids are good indicators of the management regime, showing a clear and consistent temporal pattern in all the plots. By contrast, forbs tend to be more tightly associated with particular environmental factors, being good descriptors of spatial heterogeneity.

The community showed significant changes in functional attributes during the succession. Our results indicate that in this region, grassland communities respond rapidly to grazing exclosure. After two or three years of fencing, a considerable turnover of species occurred. This provides an important empirical base to define management and conservation programs for the natural grasslands of Uruguay.

Acknowledgements. This work was partially supported by the Consejo Nacional de Investigaciones Científicas y Tecnológicas of Uruguay and by a IAI grant (CRN 012). Data were provided by C. Álvarez (in memoriam), H. May and E. Di Landro under the contract N° 4042 of BID-CONICYT. We are grateful to the Gallinal family, owners of the Estancia Palleros, and to manager E. Sunner, for making this study possible. The help in many ways of F. Pezzani, M. Texeira, D. Panario and B. Costa is gratefully acknowledged. We thank J.M. Paruelo for useful suggestions and comments on the manuscript.

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Received 21 January 2002;
Revision received 22 October 2002;
Final version received 3 December 2002;
Accepted 13 December 2002.
Coordinating Editor: E. Ezcurra.