

Long-term species change in a Uruguayan grassland

Altesor, A.^{1*}, Di Landro, E.², May, H.² & Ezcurra, E.³

^{1*}Unidad Ecología Funcional, Facultad de Ciencias, Universidad de la República; Iguá s/n, Montevideo, Uruguay; ²Dirección General de Recursos Naturales Renovables, Ministerio de Ganadería, Agricultura y Pesca, Montevideo, Uruguay; ³San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112 USA; E-mail eezcurra@sdnhm.org; *Corresponding author; Fax + 598 2 5258617; E-mail aaltesor@genetica.edu.uy

Abstract. This paper reports on species changes which occurred in plots in a Uruguayan grassland after 55 yr of continuous grazing. The study was based on the pioneering work of B. Rosengurt who sampled 10 plots in 1935; in 1990 we re-sampled five of them. Comparative studies were based on rank-frequency, diversity, evenness and multivariate analyses. Diversity was measured as species richness S , Shannon's index H and its exponential form $N = e^H$, evenness $E = N/S$ and Gini's coefficient of hierarchy G . Species-richness of the plots increased significantly. Species which entered the sites are mostly weedy species, while those that have decreased are mostly palatable forage species. Evenness, however, remained constant. Floristic change was chiefly associated with time, and secondarily with plot soil-type. During the 55 yr that elapsed between both observation periods, a dramatic floristic change has occurred in this grassland site.

Keywords: Community structure; Deterioration; Diversity; Evenness; Gini coefficient; Species-abundance; Weed.

Nomenclature: Lombardo (1984).

Introduction

The natural grasslands of the temperate South American plains in Uruguay, Brazil and Argentina have been considerably transformed by human intervention, particularly grazing and change of land-use into intensive agriculture. Unfortunately, very few efforts were made before this large transformation occurred to make an inventory of the original composition of the South American grasslands and follow its changes through time. Furthermore, few efforts have been made to establish permanent plots that may allow the evaluation of the rate of transformation of these ecosystems. In many cases, the extant native vegetation has been eliminated during recent decades to establish modern, high-input agricultural systems, frequently based on chemical tillage which completely change the original plant community – possibly beyond recovery.

In Uruguay, the area occupied by natural grasslands amounts to more than 140 000 km², of which about 90 % are used for extensive grazing by cattle and sheep. The introduction of domestic herbivores following settlement by Europeans significantly changed the original structure of these grasslands (Gallinal et al. 1938). While the ungrazed vegetation grows 40-50 cm tall and is dominated by tussock grasses, under the current grazing regime it is short turf less than 5 cm tall (Sala et al. 1986; Millot et al. 1987; Panario 1994).

Herbivore-induced shifts in species composition and ecosystem function have been well documented in grasslands from Argentina. In the flooded Argentinian Pampas, exotic species that grow primarily during winter and spring are significantly promoted by domestic grazing (Facelli et al. 1988; Facelli 1988; Chaneton & Facelli 1991). These grazed grasslands have suffered a major change in ecosystem function with a significant decline (ca. 40 %) in above-ground net primary production primarily during the warm season (Rusch & Oesterheld 1997). Additionally, changes in the architecture of the vegetation in response to anthropogenic disturbance (especially grazing pressure) have been reported in montane grasslands of Argentina with a progressive miniaturisation of photosynthetic structures and concentration of biomass close to the ground (Díaz et al. 1992).

In this paper we present evidence on how and to what extent the biological diversity and species composition of a native grassland in Northern Uruguay has changed during 55 yr, between 1935 and 1990, under traditional continuous grazing. We based our study on the pioneering work of Bernardo Rosengurt, who had the foresight to accurately describe the native grasslands of northern Uruguay in the early 20th century, by sampling and carefully mapping plots that can still be located in the field.

Methods

Study site

The study site was a native grassland on Cerro Largo, NW Uruguay, in the Estancia Palleros, a live-stock breeding ranch (32° 05' S, 54° 30' W). Geomorphologically, the site forms part of the sedimentary plains of NE Uruguay, near the Brazilian border, at an altitude of ca. 150 m a.s.l. The soil is a dark prairie soil type, developed on sediments derived from igneous and metamorphic materials, with a high content of organic matter (> 3%) in the A-horizon and a moderate drainage capacity. In the higher parts, the soil profile is more developed, with a deeper A-horizon and an argillic B-horizon. In the lower parts, poor drainage promotes the development of soils with less differentiation, with a higher pH, a more shallow A-horizon and a lower amount of clay in the B-horizon (Durán 1985).

Mean annual precipitation between 1961 and 1990 was 1098 mm. The rain is distributed evenly throughout the year (cf. Ezcurra & Rodrigues 1986). Mean annual temperature for the same period was 16.5 °C, ranging from a winter monthly mean of 10.7 °C in July to a summer mean temperature of 22.7 °C in January (Anon. 1996).

The dominant vegetation type is native grassland where the low herbaceous species are largely maintained by the grazing pressure of cattle. The normal height of the grassland canopy is around 5 cm, the dominant species are stoloniferous and caespitose grasses, and perennial herbs. In the non-grazed parts, some small woody shrubs and tussock grasses may appear (Rosengurtt 1943). In the region where our research site is located only 1.5 % of the area is used as cropland. Following the classification of grasslands of Milchunas et al. (1988), our study site corresponds to a subhumid grassland with a long history of grazing.

Data collection

The Palleros sites were first sampled in the summer of 1935 by B. Rosengurtt and collaborators (Gallinal et al. 1938). 10 plots were located in different parts of Estancia Palleros with the purpose of evaluating the species composition of the local native grasslands. Each plot was marked in the field as a 12 m × 12 m square. Botanical composition and species frequency were determined in each plot by locating 25 random quadrats 0.5 m × 0.5 m in size. In each quadrat, the presence of all species was recorded. The frequency of occurrence in the 25 quadrats was used as a measure of the relative abundance of the species in each plot. The first results were published shortly afterwards (Gallinal et al. 1938; Rosengurtt 1943). Since then, five of the plots have been lost, as they have been planted with *Eucalyptus* or have become flooded through water management. In 1990

we re-sampled the remaining plots, using exactly the same procedure that had been used by Rosengurtt et al. in 1935. The plots were relocated using the original maps, the 25 frequency quadrats were placed at random inside each plot. During the 55 yr that have elapsed between both samples, the fields were managed under traditional continuous grazing, with Hereford cows and sheep at a density of about one animal unit (i.e. one cow-equivalent) per 2 ha.

Data analysis

A species-by-plot matrix was prepared that included the species frequencies in the five plots in 1935, and in the same five plots in 1990. The matrix contained a total of 121 species (a magnetic copy of the complete data set can be obtained from the first author). For each plot, we counted the total species richness (S), calculated Shannon's diversity index (H) and its exponential diversity number ($N = e^H$), as well as the evenness ($E = N/S$; Hill 1973c) and Gini's coefficient of hierarchy (G ; Weiner & Solbrig 1984). Because S , H , N , E and G are synthetic community descriptors that were measured in the same plot at two different times, they constitute a case of repeated measures with no replicates at the plot level. Differences in these values between the two years were evaluated by means of a procedure suggested by Mead (1988; see also Gurevitch & Chester 1986 and von Ende 1993) for the case of repeated measurements. We first calculated, for each plot, the differences between the values observed in 1935 and in 1990. Thus, for each community variable (i.e. S , H , N , E , and G) we obtained a vector of five difference-values. Under the null hypothesis of no change in the descriptor, we would expect the differences between the two years to be random deviates with expected mean equal to zero. We tested by means of a t -test the mean of each difference vector, under the null hypothesis that the mean difference between the two years should not be significantly different from zero.

We also ranked the species abundances in each plot and plotted the resulting rank-frequency curves on both an arithmetic and a logarithmic scale. Differences between these curves were evaluated by means of a log-linear model on the rank-ordered frequency matrix, taking the rank of the species, the year and the plot as predictors of the species frequencies.

To evaluate the importance of purely floristic changes, a Principal Component Analysis (non-standardized, with Gower's double centring procedure; see Gower 1966; Noy-Meir 1973; Noy-Meir et al. 1975; Ezcurra 1987) was performed on the whole data matrix with presence-absence data. To evaluate the importance of changes in species abundances in the plots, we also carried out a Correspondence Analysis on the same

matrix with the complete frequency data. We used ORDEN version 2.0 for these analyses. To avoid distortion of the CA by rare species (i.e. the 'rare-species effect', see Gauch 1982), we eliminated from this second analysis all species that were present in only one plot and all species that were present in more than one plot but that showed low frequencies in the plots in which they were present (technically, the exact criterion we used was to eliminate all species that had expected values below unity in the frequency table, calculating the expected value in the standard way for contingency tables, i.e. row total \times column total / table total; see Everitt 1977). The resulting matrix contained 72 species. In both the Component Analysis and the Correspondence Analysis we evaluated the significance of the axes by comparing the percentage variance explained by each axis against the predicted values of the broken-stick distribution (Jackson 1993). In the case of correspondence analysis, we also calculated the χ^2 -value of each axis (calculated as the product of the axis' eigenvalue times the sum of all frequencies in the matrix; see Legendre & Legendre 1983) as a measure of significance. By means of an Analysis of Variance we evaluated the relationship between the axes and time as a predictive factor. Finally, the trajectories between 1935 and 1990 of the five plots in the reduced multivariate space were drawn on the ordination graphs to highlight differences and similarities in the vegetational changes between the plots.

Soil samples were taken from each plot during the 1990 sampling, and were air-dried and analysed in the laboratory (no soil samples were taken in 1935). After the laboratory analyses were completed, the soil features were summarised into a data table for statistical analysis, in which we included: (a) the thickness of the A-horizon, (b) the content of sand, loam and clay in the A-horizon, (c) the content of clay in the B-horizon, (d) the ratio of clay in the A-horizon to clay in the B-horizon, (e) pH, (f) monovalent and bivalent cations (Ca, Mg, Na and K) and (g) the K/Na ratio as an indicator of soil fertility. We assigned the same values to both the 1935 and 1990 plots, as these soil variables are relatively constant in time. We excluded from the analysis other soil variables such as organic matter, nitrogen and phosphorus contents in the A-horizon, as their values may have changed substantially with time and with the management of the pasture. We calculated the correlation coefficients between the soils attributes and axes 1 and 2 of both the Component Analysis and the Correspondence Analysis. Because each axis was analysed against 12 non-independent soil variables, we used a Bonferroni criterion to correct the threshold values for the acceptance of a significant association, thus making the test of hypothesis more stringent (to

calculate the corrected probabilities we used the Dunn-Šidák method as described in Ury 1976, and in Sokal & Rohlf 1995).

Results

Changes in species diversity

The log-linear model indicated that the rank-frequency plots differed significantly ($p < 0.0001$) between years. A significant ($p < 0.0001$) quadratic effect of the rank was also detected, a fact that highlights the notable convex shape of the rank-frequency curves on a logarithmic scale (Fig. 1). Finally, significant (although quantitatively less important when compared to the between-years effect) differences were also found between plots. These results were confirmed by the values of diversity and evenness (Table 1). Both Shannon's diversity index H and the diversity number N increased significantly with time ($t = 50.2$; $p < 0.0001$, d.f. = 4; and $t = 25.6$; $p < 0.0001$, d.f. = 4, respectively). However, when diversity was decomposed into species richness (S) and evenness (E), it was found that species richness increased significantly ($t = 42.0$; $p < 0.0001$, d.f. = 4) in all plots between 1935 and 1990, but that evenness did not change in a significant way ($t = 2.6$; $p = 0.06$, d.f. = 4). A statistical analysis of Gini's coefficient (G) also failed to detect any significant change ($t = 1.7$; $p = 0.16$, d.f. = 4) in the degree of hierarchical dominance of the rank-frequency curves between 1935 and 1990. This would be expected since both indices measure the evenness of the hierarchical distribution of species, a very high correlation was also found between E and G ($r = 0.99$; d.f. = 8; $p < 0.0001$).

In short, the species richness of the five plots in-

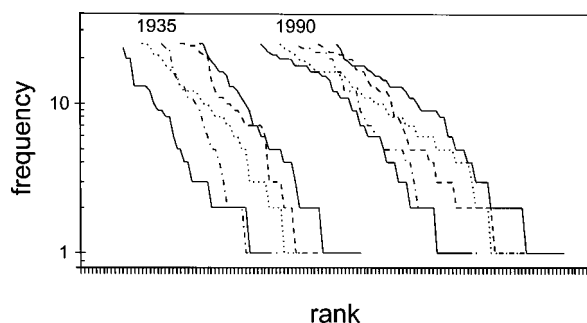


Fig. 1. Rank-frequency plots showing distribution curves for the five plots of Estancia Palleros in 1935 and 1990. Frequencies are shown on a logarithmic scale. All curves start from rank 1, and have been separated for clarity. (—) plot a; (.....) plot b; (- · - · -) plot c; (- - -) plot d; (—) plot e (same symbol as plot a).

Table 1. Shannon's diversity index (H) and its exponential diversity number (N), species richness (S), evenness (E), and Gini's coefficient of hierarchy (G) for the five plots of Estancia Palleros in 1935 (lower case) and 1990 (upper case).

Plot and year	H	N	S	E	G
a 1935	3.26	26.14	39	0.67	0.536
b "	3.44	31.23	43	0.73	0.582
c "	2.96	19.35	31	0.62	0.504
d "	3.23	25.40	37	0.69	0.555
e "	3.33	27.83	43	0.65	0.511
A 1990	3.67	39.23	56	0.70	0.560
B "	3.89	49.01	65	0.75	0.603
C "	3.44	31.06	48	0.65	0.514
D "	3.60	36.48	56	0.65	0.512
E "	3.74	42.17	60	0.70	0.557

creased ca. 50 % between 1935 and 1990, from a mean value of 38.6 species per plot (S.E. = 2.3) to a mean value of 57.0 species per plot (S.E. = 2.8). In contrast, the evenness of the species abundance distribution remained constant at a mean value of 0.68 (S.E. = 0.02). From the point of view of their biological diversity, the main change that has occurred during the last 55 yr, has been a large increase in the number of species in the native grassland, but no significant change has occurred in the patterns of species dominance or in the distribution of relative abundances within the grassland community.

Changes in species composition

The first two axes of the principal component analysis explained 32 % and 18 % of the variation in the data, and were either above or very near the values derived from the predictions of the broken-stick distribution under the null hypothesis of random variation (29 % and 19 %, respectively, for axes 1 and 2). All other axes were well below the predictions of the random model, and were hence considered 'non-significant' axes. Furthermore, the first component was significantly related to time as a discrete factor ($F_{(1,8)} = 55.76$; $p < 0.0001$), while the second component was significantly correlated with the percentage of clay in the B-horizon ($r = 0.86$, uncorrected $p = 0.0014$; Bonferroni-corrected $p = 0.016$) and more weakly related to other variables such as depth of the A-horizon, pH, Na and K/Na (although the uncorrected r -values were significant for all these variables, the Bonferroni-corrected significances were slightly above the 0.05 threshold). That is, the Principal Component Analysis of the presence-absence data produced a first axis that highlights the floristic variation in time and a second axis that emphasises floristic differences in space (Fig. 2). The second axis clearly detected a soil gradient going from plot b (an acidic site located in an elevated part of the plain with a deeper A-horizon, a

relatively high fertility as indicated by its high K/Na ratio, and a strongly argillic B-horizon that derives from its higher internal drainage) to plot a (a lightly alkaline site located in a topographic depression with a shallower A-horizon, relatively high sodium content and poor internal drainage; see Table 2). Thus, the secondary significant source of variation is basically associated with the level of profile development and internal drainage of the dark prairie soils. The dramatic change in species richness described in the previous section was clearly reflected in the component analysis, where the within-site floristic differences in time explained a larger proportion of the floristic variation than the differences between sites in space.

The first two axes of the correspondence analysis of the frequency data explained 29.1 % and 21.7 % of the variation in the quantitative data set, and were considered significant by the criteria of both the broken-stick and the χ^2 tests. In total agreement with the component analysis of the presence-absence data, the correspondence analysis detected primarily variation in time, and secondarily it also detected a spatial gradient from plot a in one extreme to plot b in the other (in the correspondence analysis, however, the Bonferroni-corrected correlations between multivariate axes and soil variables were, in all cases, higher than 0.05 and hence only very weakly significant). In short, for our data set the statistical relationship between the multivariate axes and time and soil variables was, in all cases, higher for the presence-absence component analysis than for the correspondence analysis with frequency data, indicating that

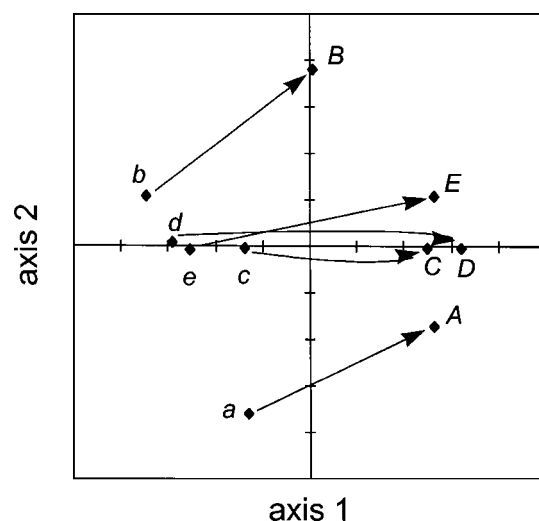


Fig. 2. Principal Components Analysis of the presence-absence data for the five plots belonging to 1935 (lower case) and 1990 (upper case) samples. The arrows indicate temporal trajectories for each plot.

in this grassland site the analysis of floristic variation in simple terms of presence-absence data is more robustly associated to long-term change than the analysis of relative frequencies of the dominant species.

Finally, using the species classification derived from the multivariate axes, we classified and listed the species that disappeared, decreased, increased or appeared in the sampling plots during the 55-yr period (App. 1).

Discussion

Based on the description by Rosengurt (1979) of ecological, morphological and productivity traits of prairie plants in Uruguay, the species in our study area can be classified into three simple categories:

- I Palatable species: graminoids and herbs, presenting soft leaves throughout their life span and usually highly palatable. These plants tend to decrease in their frequency of occurrence as grazing increases.
- II Species of intermediate palatability: Graminoids and herbs with fibrous leaves when old and with medium to low palatability. These plants tend initially to increase in their frequency of occurrence as grazing pressure increases (although they may eventually decrease in heavily overgrazed plots).
- III Weedy species: Herbaceous plants and shrubs, usually unpalatable, inaccessible or toxic for herbivores. These are opportunistic species that generally colonise disturbed or heavily overgrazed sites.

For the discussion of the results, Rosengurt's classification was superimposed onto the results of the multivariate analyses (App. 1). In the 1935 sample, 79 % of the recorded species were grasses. By 1990, the *Poaceae* had decreased to 48 % of the total species richness. One species (*Piptochaetium panicoides*) which was common in 1935 had completely disappeared by 1990. Twenty other species that were relatively rare in 1935 were extinct by 1990 (the second group in App. 1), 90 % of them belonging to the *Poaceae*. Most of the grasses that disappeared were native perennials with a caespitose growth form and high forage quality (categories I and II). Furthermore, the whole set of species that decreased (the third group in App. 1) belongs to forage categories I and II, and is formed by graminoids and legumes with a caespitose growth form.

In the group of species that remained common between 1935 and 1990 (group 4 in App. 1) five grasses: *Paspalum notatum*, *Setaria geniculata*, *Axonopus affinis*, *Bothriochloa laguroides* and *Coelorhachis selloana* are still dominant, together with a weedy composite (*Chevreulia sarmentosa*) that appeared in the 1990 census.

Most (64 %) of the 28 species that were absent or rare in 1935 and are now common (group 5) are weeds or low-palatability forbs belonging to category III. Only five (18 %) of these immigrant species belong to the *Poaceae*. One of them is an introduced and cultivated forage species (*Lolium multiflorum*) and another is *Cynodon dactylon*, an aggressive invader characteristic of overgrazed grasslands (Lorenzi 1991; Ríos & Giménez 1992). A similar trend was observed in the 15 species that were absent in 1935 and are now present (but not abundant): 80 % of these belong to the type-III category, and only two of them (13 %) are grasses. Among these weedy newcomers a variety of different morphologies is found, ranging from rosette plants with below-ground storage organs and planophyllous leaves such as *Chaptalia piloselloides*, to shrubby species such as *Baccharis trimera*.

Some species remained throughout the period as good indicators of soil quality, and their presence was largely independent of the changes in species composition through time, as indicated by the second ordination axis. *Andropogon ternatus*, *Aristida murina*, *Aristida venustula*, *Desmanthus depressus*, and *Schizachyrium spicatum* (all of them belonging to types I and II), were common in 1935 and only remained in 1990 in plot b, a meadow with a well-developed soil, a deep A-horizon and comparatively high fertility. Another group of species only increased or appeared in this plot (see groups seven and eight of App. 1).

One group of species (*Ambrosia tenuifolia*, *Eleocharis* sp., *Eragrostis bahiensis*, *Hydrocotyle* sp., *Rhynchospora luzuliformis* and *Spilanthes decumbens*; most of them of type III) only appeared or increased in plot a, on slightly alkaline soil with a less-developed profile, a more shallow A-horizon (25 cm) and the highest proportion of interchangeable sodium. In contrast with the characteristic species of plot b, most of the plants that had a distinctive distribution in plot a were unpalatable weeds.

Table 2. Main soil attributes in each of the five plots, measured during the 1990 sampling. All values were measured in homogenized samples from the A-horizon, except for 'clay in B' which refers to % clay in the B-horizon.

Plot	Thickness (cm)	Sand	Loam	Clay (%)	Clay in B	pH	Ca	Mg	Na (meq/100 g)	K	K/Na
A	25	44.5	32.6	23.3	30.5	7.3	18.9	3.5	0.9	0.3	0.33
B	53	30.3	34.0	35.6	46.8	5.9	22.8	2.4	0.25	0.45	1.8
C	39	46.9	32.5	20.5	40.7	5.7	6.7	1.3	0.4	0.2	0.5
D	28	59.3	21.1	19.6	40.3	5.6	4.6	1.45	0.2	0.3	1.5
E	25	55.2	23.3	21.4	38.8	5.7	5.0	1.65	0.3	0.35	1.17

Most of the species recorded, including a large proportion of the species that have colonized the area since 1935, are native to Uruguay. 86 % of the now widespread weedy invaders which were totally absent in 1935 are native to the region. These species include herbaceous composites, sedges, umbellifers and plantains of high dispersal capacity. Although there is no information on their original habitat, we assume that these plants have evolved as opportunists growing in disturbed areas, and have become colonizers of grazed pastures with the growing development of animal husbandry in Uruguay.

It should be noted that both the data for 1935 and for 1990 were obtained in a single season and we do not know whether these years were typical or atypical years. Thus, we have no means of differentiating within our data set short-term variation from long-term trends. From a biological viewpoint, however, the trend seems consistent, as most of the species that have changed in the plots are perennials and it does not seem likely that their extinction or appearance could be attributed to short-term trends. However, more detailed monitoring is necessary to confirm the preliminary trend described in this paper. Long-term monitoring sites are needed in the Uruguayan grasslands, and we are in the process of establishing such a longer-term project to follow floristic change in the Palleros plots.

Conclusions

Between 1935 and 1990 there has been a marked deterioration in the pasture quality of the Palleros grassland site: some palatable grasses have decreased or disappeared and a large number of low-quality invaders has immigrated into the plots. The species-richness of the plots has increased significantly, while the evenness of the species-abundance distribution has remained constant. The newcomers are mostly unpalatable weeds, while the species that have decreased are mostly palatable forage species.

The most significant change observed was in floristic composition, as the guild of dominant species remained relatively constant. A similar trend has been reported by other authors (e.g. Milchunas et al. 1988). Within the group of dominant species, the most abundant were prostrate species such as *Paspalum notatum* and *Axonopus affinis*. These are rhizomatose and stoloniferous plants that can spread horizontally at ground level, and thus avoid the effects of intense grazing.

Some palatable grasses have disappeared or decreased and many low-quality forbs have immigrated or increased their frequency in the plots. These plants belong mostly to category III, usually have a small leaf area and

storage structures close to the ground. Their growth form may be rosettophyllous (e.g. *Plantago myosurus*), shrubby (e.g. *Gamochaeta spicata*) or prostrate, in many cases with horizontal spread through stolons and rhizomes (e.g. *Richardia humistrata*, *Cyperus* sp., *Chevreulia sarmen-tosa*). As pointed out by Díaz et al. (1992), these morphological traits could be responses to the pressure of herbivores. Many of these plants can avoid herbivory through physical or chemical defences such as spiny, sclerophyllous or fibrous tissues (e.g. *Eryngium horridum*), or unpalatable secondary compounds (*Baccharis coridifolia*). In strong contrast with the high number of exotic invaders that have colonised the grasslands of the flooded Pampas (Sala et al. 1986; Facelli et al. 1988; Facelli 1988; Chanton & Facelli 1991; Rusch & Oesterheld 1997), most of the invading species found in Palleros are native to the region.

Although there were no exclosures established as control plots in 1935 when this experiment was initiated, the comparative results strongly suggest that a large part of the floristic change observed is caused by cattle grazing. The establishment of permanent plots with exclosures is needed to evaluate whether the deterioration of these plots is reversible through a more adequate management of the grazing regime. However, other mechanisms contributing to the strong floristic change observed in Palleros cannot be discarded. Among these, we can mention an increased taxonomic knowledge which may have introduced formerly unidentified species into the 1990 sample, the possible existence of long-term climatic trends, or the effect of landscape alterations linked to animal husbandry, agriculture, new forms of land-use and transportation. In particular, a regional increase in transportation and in agriculture may have contributed substantially to the dispersal of weedy species into the pasture plots, further accentuating the floristic changes induced by grazing.

Finally, it is important to remark that the temperate grasslands of Uruguay, Brazil and Argentina are one of the ecosystems in the region that have received little attention in terms of the establishment of protected areas. Our data show that significant biological change has been occurring in these ecosystems even in areas that have been subject to a traditional, non-agricultural management. The protection of what remains of these grassland communities is of the highest importance.

Acknowledgements. We are grateful to the Gallinal family, owners of the Estancia Palleros, and to manager Enrique Sanner, for making this study possible. We thank the late César Álvarez for his contribution in the field work. The help in many ways of several colleagues, Julio Campo, Stella Grun, Fabiana Pezzani, Daniel Panario and Claudia Rodríguez is gratefully acknowledged.

References

- Anon. 1996. *Normales Climatológicas*. Dirección Nacional de Meteorología, Ministerio de Defensa, Montevideo.
- Chaneton, E.J. & Facelli, J.M. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. *Vegetatio* 93: 143-155.
- Díaz, S., Acosta, A. & Cabido, M. 1992. Morphological analysis of herbaceous communities under different grazing regimes. *J. Veg. Sci.* 3: 689-696.
- Durán, A. 1985. *Los suelos del Uruguay*. Ed. Hemisferio Sur, Montevideo.
- Everitt, B.S. 1977. *The analysis of contingency tables*. Chapman and Hall, London.
- Ezcurra, E. 1987. A comparison of reciprocal averaging and non centred principal component analysis. *Vegetatio* 71: 41-48.
- Ezcurra, E. & Rodrigues, V. 1986. Rainfall patterns in the Gran Desierto, Sonora, Mexico. *J. Arid Environ.* 10: 13-28.
- Facelli, J.M. 1988. Response to grazing after nine years of cattle exclusion in a Flooding Pampa grassland, Argentina. *Vegetatio* 78: 21-25.
- Facelli, J.M., León, R.J.C. & Deregibus, V.A. 1988. Community structure in grazed and ungrazed grassland sites in the Flooding Pampa, Argentina. *Am. Midl. Nat.* 121: 125-133.
- Gallinal, J., Bergalli, L., Campal, E., Aragone, L. & Rosengurt, B. 1938. *Estudios sobre praderas naturales del Uruguay. Primera Contribución*. Imprenta Germano Uruguaya, Montevideo.
- Gauch, H.G. Jr. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge.
- Gower, J.C. 1966. Some distance properties of latent roots and vector methods used in multivariate analysis. *Biometrika* 53: 323-338.
- Gurevitch, J. & Chester, S.T. 1986. Analysis of repeated measurements. *Ecology* 67:251-255.
- Hill, M.O. 1973c. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427-432.
- Jackson, D.A. 1993. Principal component analysis: how many components are nontrivial and interpretable? *Ecology* 74: 2204-2214.
- Legendre, L. & Legendre, P. 1983. *Numerical ecology*. Elsevier, Amsterdam.
- Lombardo, A. 1984. *Flora montevidensis*. Tomos I, II, III. Intendencia Municipal de Montevideo, Montevideo.
- Lorenzi, H. 1991. *Plantas daninhas do Brasil*. Ed. Plantarum, São Paulo.
- Mead, R. 1988. *The design of experiments*. Cambridge University Press, New York, NY.
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.* 132: 87-106.
- Millot, J.C., Risso, D. & Methol, R. 1987. *Relevamiento de pasturas naturales y mejoramientos extensivos en áreas ganaderas del Uruguay*. Informe Técnico, Ministerio de Ganadería, Agricultura y Pesca, Montevideo.
- Noy-Meir, I. 1973. Data transformations in ecological ordination: I. Some advantages of non-centering. *J. Ecol.* 61: 329-341.
- Noy-Meir, I., Walker, D. & Williams, W.T. 1975. Data transformations in ecological ordination: II. On the meaning of data standardization. *J. Ecol.* 63: 779-800.
- Panario, D. 1994. Evolución y tendencia de la vegetación nativa uruguaya I. La pradera. In: *Contribución de los estudios edafológicos al conocimiento de la vegetación en la República Oriental del Uruguay*. Boletín Técnico N 13, Ministerio de Ganadería, Agricultura y Pesca, Montevideo.
- Ríos, A. & Gimenez, A. 1992. Ecofisiología de malezas. *Rev. INIA Invest. Agron.* 1: 157-166.
- Rosengurt, B. 1943. *Estudios sobre Praderas Naturales del Uruguay. 3era. Contribución*. Casa Barreiro y Ramos, S.A. Montevideo.
- Rosengurt, B. 1979. *Tablas de comportamiento de las especies de plantas de campos naturales en el Uruguay*. Dirección General de Extensión Universitaria, División Publicaciones y Ediciones. Facultad de Agronomía, Montevideo.
- Rusch, G.M. & Oesterheld, M. 1997. Relationship between productivity, and species and functional group diversity in grazed and non-grazed Pampas grassland. *Oikos* 78: 519-526.
- Sala, O.E., Oesterheld M., León, R.J.C. & Soriano, A. 1986. Grazing effects upon plant community structure in sub-humid grasslands of Argentina. *Vegetatio* 67: 27-32.
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry*. 3rd ed. W.H. Freeman and Company, New York, NY.
- Ury, H.K. 1976. A comparison of four procedures for multiple comparisons among means (pairwise contrasts) for arbitrary sample sizes. *Technometrics* 18: 89-97.
- von Ende, C.N. 1993. Repeated-measures analysis: Growth and other time-dependent measures. In: Scheiner, S.M. & Gurevitch, J. (eds.) *Design and analysis of ecological experiments*, pp. 113-137. Chapman & Hall. New York, NY.
- Weiner, J. & Solbrig, O.T. 1984. The meaning and measurement of size hierarchies in plant populations. *Oecologia (Berl.)* 61: 334-336.

Received 4 June 1997;

Revision received 8 December 1997;

Accepted 9 January 1998.

App. 1. List of species that changed significantly between 1935 and 1990, as inferred from their values on the multivariate axes. The species have been classified according to their tendency to invade or disappear from the plots. The ‘family’ column indicates the taxonomic family, ‘life-cycle’ indicates whether the plant is annual or perennial, ‘type’ shows the forage quality of the species (I: palatable, II: intermediate and III: unpalatable weed), and ‘origin’ indicates whether the species is native or alien.

Species	Family	Life-cycle	Type	Origin	Species	Family	Life-cycle	Type	Origin
Species that were common in 1935 and became extinct by 1990									
<i>Piptochaetium panicoides</i>	Poaceae	perennial	I	native	<i>Plantago myosurus</i>	Plantaginaceae	annual	III	native
Species that were present in 1935 and became extinct by 1990									
<i>Agrostis tandilensis</i>	Poaceae	annual	I	native	<i>Relbunium richardianum</i>	Rubiaceae	perennial	II	native
<i>Andropogon lateralis</i>	Poaceae	perennial	II	native	<i>Richardia humistrata</i>	Rubiaceae	perennial	III	native
<i>Aristida pallens</i>	Poaceae	perennial	II	native	<i>Richardia stellaris</i>	Rubiaceae	perennial	III	native
<i>Calamagrostis viridiflavescens</i>	Poaceae	perennial	I	native	<i>Scoparia montevidensis</i>	Scrophulariaceae	perennial	III	native
<i>Eragrostis</i> sp.	Poaceae	perennial	II	native	<i>Apium leptophyllum</i>	Apiaceae	annual	II	alien
<i>Eriochloa montevidensis</i>	Poaceae	perennial	I	native	<i>Eryngium horridum</i>	Apiaceae	perennial	III	native
<i>Eustachys bahiensis</i>	Poaceae	perennial	I	native	<i>Glandularia selloi</i>	Verbenaceae	perennial	III	native
<i>Leptocoryphium lanatum</i>	Poaceae	perennial	I	native	<i>Verbena litoralis</i>	Verbenaceae	perennial	III	native
<i>Panicum bergii</i>	Poaceae	perennial	II	native	Species that were absent in 1935 and are now present				
<i>Panicum</i> sp.	Poaceae	perennial	I	native	<i>Aster squamatus</i>	Asteraceae	perennial	III	native
<i>Paspalum quadrifarium</i>	Poaceae	perennial	II	native	<i>Baccharis trimera</i>	Asteraceae	perennial	III	native
<i>Phalaris platensis</i>	Poaceae	annual	I	native	<i>Chaptalia piloselloides</i>	Asteraceae	perennial	III	native
<i>Piptochaetium bicolor</i>	Poaceae	perennial	I	native	<i>Chevreulia acuminata</i>	Asteraceae	perennial	III	native
<i>Polygomon monspeliensis</i>	Poaceae	annual	III	alien	<i>Conyza bonariensis</i>	Asteraceae	annual	II	native
<i>Stipa nutans</i> var. <i>quinqueciliata</i>	Poaceae	perennial	I	native	<i>Soliva pterosperma</i>	Asteraceae	annual	III	native
<i>Stipa philippii</i>	Poaceae	perennial	I	native	<i>Vernonia</i> sp.	Asteraceae	perennial	III	alien
<i>Stipa</i> sp.	Poaceae	perennial	I	native	<i>Evolvulus sericeus</i>	Convolvulaceae	perennial	III	native
<i>Tridens brasiliensis</i>	Poaceae	perennial	I	native	<i>Geranium albicans</i>	Geraniaceae	perennial	III	native
<i>Sisyrinchium</i> sp.	Iridaceae	annual	III	native	<i>Digitaria aequiglumis</i>	Poaceae	annual	I	native
<i>Margyricarpus pinnatus</i>	Rosaceae	perennial	III	native	<i>Schizachyrium tenerum</i>	Poaceae	perennial	II	native
Species that decreased between 1935 and 1990					<i>Heimia salicifolia</i>	Lythraceae	perennial	III	native
<i>Aira caryophyllea</i>	Poaceae	annual	II	native	<i>Oxalis</i> sp.	Oxalidaceae	perennial	III	native
<i>Briza minor</i>	Poaceae	annual	I	alien	<i>Anagallis minima</i>	Primulaceae	annual	III	native
<i>Chascolytrum subaristatum</i>	Poaceae	perennial	I	native	<i>Gerardia communis</i>	Scrophulariaceae	annual	III	native
<i>Eragrostis lugens</i>	Poaceae	perennial	II	native	Common species in 1935 that now only remain in plot b				
<i>Eragrostis neesii</i>	Poaceae	perennial	II	native	<i>Andropogon ternatus</i>	Poaceae	perennial	I	native
<i>Panicum milioides</i>	Poaceae	perennial	I	native	<i>Aristida murina</i>	Poaceae	perennial	II	native
<i>Panicum sabulorum</i>	Poaceae	perennial	I	native	<i>Aristida venustula</i>	Poaceae	perennial	II	native
<i>Paspalum plicatulum</i>	Poaceae	perennial	I	native	<i>Schizachyrium spicatum</i>	Poaceae	perennial	II	native
<i>Schizachyrium condensatum</i>	Poaceae	perennial	II	native	<i>Desmanthus depressus</i>	Fabaceae	perennial	II	native
<i>Sporobolus indicus</i>	Poaceae	perennial	II	native	Species that only appeared or increased in plot b				
<i>Juncus imbricatus</i>	Juncaceae	perennial	II	native	<i>Aspilia setosa</i>	Asteraceae	perennial	III	native
<i>Adesmia bicolor</i>	Fabaceae	perennial	I	native	<i>Conyza blakei</i>	Asteraceae	perennial	III	native
<i>Rhynchosia senna</i>	Fabaceae	perennial	I	native	<i>Fimbristylis ovata</i>	Cyperaceae	perennial	III	native
<i>Trifolium polymorphum</i>	Fabaceae	perennial	I	native	<i>Piptochaetium stipoides</i> var. <i>purpurascens</i>	Poaceae	perennial	I	native
Common species in both 1935 and 1990					<i>Stipa papposa</i>	Poaceae	perennial	II	native
<i>Bulbostylis capillaris</i>	Cyperaceae	annual	III	native	<i>Stipa pauciciliata</i>	Poaceae	perennial	I	native
<i>Carex bonariensis</i>	Cyperaceae	perennial	III	native	<i>Trachypogon montifari</i>	Poaceae	perennial	II	native
<i>Axonopus affinis</i>	Poaceae	perennial	I	native	<i>Galactia marginalis</i>	Fabaceae	perennial	III	native
<i>Axonopus suffultus</i>	Poaceae	perennial	I	native	<i>Stylosanthes montevidensis</i>	Fabaceae	perennial	I	native
<i>Bothriochloa laguroides</i>	Poaceae	perennial	II	native	<i>Cliococca selaginoides</i>	Linaceae	perennial	II	native
<i>Coelorrhachis selloana</i>	Poaceae	perennial	I	native	<i>Eryngium serra</i>	Apiaceae	perennial	III	native
<i>Danthonia cirrata</i>	Poaceae	perennial	I	native	Species that only appeared or increased in plot a				
<i>Eleusine tristachya</i>	Poaceae	perennial	II	native	<i>Ambrosia tenuifolia</i>	Asteraceae	perennial	III	native
<i>Melica rigida</i>	Poaceae	perennial	II	native	<i>Hypochoeris</i> sp.	Asteraceae	perennial	III	native
<i>Paspalum notatum</i>	Poaceae	perennial	I	native	<i>Spilanthes decumbens</i>	Asteraceae	perennial	III	native
<i>Setaria geniculata</i>	Poaceae	perennial	I	native	<i>Eleocharis</i> sp.	Cyperaceae	perennial	III	native
<i>Setaria vaginata</i>	Poaceae	perennial	I	native	<i>Rhynchospora luzuliformis</i>	Cyperaceae	perennial	II	native
<i>Stipa setigera</i>	Poaceae	perennial	I	native	<i>Eragrostis bahiensis</i>	Poaceae	perennial	II	native
<i>Vulpia australis</i>	Poaceae	annual	III	native	<i>Eragrostis retinens</i>	Poaceae	perennial	III	native
<i>Eryngium echinatum</i>	Apiaceae	perennial	III	native	<i>Sisyrinchium platense</i>	Iridaceae	perennial	III	native
<i>Eryngium nudicaule</i>	Apiaceae	perennial	III	native	<i>Hydrocotyle</i> sp.	Apiaceae	perennial	II	native
Species that were absent or rare in 1935 and are now common									
<i>Pfaffia tuberosa</i>	Amaranthaceae	perennial	III	native					
<i>Hypoxis decumbens</i>	Amaryllidaceae	perennial	II	native					
<i>Baccharis coridifolia</i>	Asteraceae	perennial	III	native					
<i>Chevreulia sarmentosa</i>	Asteraceae	perennial	III	native					
<i>Facelis retusa</i>	Asteraceae	annual	III	native					
<i>Gamochoaeta spicata</i>	Asteraceae	perennial	III	native					
<i>Dichondra microcalyx</i>	Convolvulaceae	perennial	III	native					
<i>Cyperus</i> sp.	Cyperaceae	perennial	III	native					
<i>Kyllinga odorata</i>	Cyperaceae	perennial	II	alien					
<i>Cynodon dactylon</i>	Poaceae	perennial	II	alien					
<i>Lolium multiflorum</i>	Poaceae	annual	I	alien					
<i>Paspalum dilatatum</i>	Poaceae	perennial	I	native					
<i>Piptochaetium montevidensis</i>	Poaceae	perennial	II	native					
<i>Sporobolus platensis</i>	Poaceae	perennial	II	native					
<i>Herbertia lahue</i> ssp. <i>amoena</i>	Iridaceae	perennial	II	native					
<i>Sisyrinchium minus</i>	Iridaceae	perennial	III	native					
<i>Juncus capillaceus</i>	Juncaceae	perennial	III	native					
<i>Scutellaria racemosa</i>	Lamiaceae	perennial	III	native					
<i>Cuphea glutinosa</i>	Lythraceae	perennial	III	native					