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THE GRASSLANDS OF THE FLOODING PAMPA (ARGENTINA): FLORISTIC HETEROGENEITY OF NATURAL COMMUNITIES OF THE SOUTHERN RIO SALADO BASIN

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Abstract. This study defines and describes the floristic heterogeneity of the natural grasslands of the southern region of the Río Salado Basin (Province of Buenos Aires, Argentina), one of the regional subdivision of the Flooding Pampa. Vegetation data were obtained through preferential sampling of stands located through photointerpretation. Vegetation relevés were analysed using classification and ordination techniques. An average linkage clustering yielded 14 vegetation units; a phytosociological summary table with 26 floristic groups was produced using correspondence analysis. The ordination of relevés through correspondence analysis allowed to relate plant communities to two main ecological gradients: topographical position and soil salinity. The plant communities were described primarily on the basis of floristic groups, dominant species and position along the major environmental gradients. The different environmental conditions along these gradients determine the vegetation heterogeneity at community-level present in this area.

Abbreviations: PS= Percentage Similarity; B.H.C.= Basic Homotoneity Coefficient; asl= above sea level.

Nomenclature: For names of taxa follow Cabrera (1963-1970), Cabrera & Zardini (1978) and Burkart (1969-1987).

Introduction

The Flooding Pampa (León 1992) (Fig. 1A), a region of around 90.000 km^2, which includes the Río Salado Basin (Vervoorst 1967) and the Laprida Region (Etchevere 1961), is part of the Pampean Province (Parodi 1947). Grasslands are the predominant vegetation type, with cattle raising its main agricultural activity. Less than 10% of the total area is dedicated annually to cropping (León et al. 1984). Although physiognomically fairly uniform, the region offers a considerable ecological heterogeneity, which necessarily conditions its pastoral potential.

The objective of this study is to characterize the floristic heterogeneity of the grasslands of the southern region of the Río Salado Basin, describing the plant communities present and identifying the main vegetation gradients.

Study area

The study area is a 40 km-wide transect (56° 35'W to 58° 30'W and 36°50'S to 37°10'S), with a very gentle E-W topographic gradient (mean slope: 0.6%; Fig. 1B), accompanied by changes in geomorphology, hydrology and soils. West of the 20m contour line ("derrames", Tricart 1973), numerous streams flow from the foothills to the plains (Fig. 1B). The predominant soils are Brunizems, with calcareous concretions or a subjacent continuous, calcareous layer (Moscatelli & Scoppa 1983). In the flat plain to the east of this contour line, the drainage system becomes anarchic, only active during large rainfall events, with numerous small, natural ponds scattered through the landscape (Dominguez & Carballo 1983). This area is dominated by solonetz, solodized solonetz and subhumid gley soils. In the lower plain, influenced by the Quaternary marine ingressions (below 5m asl), the soils are a complicated mosaic of planosols, saline-alcaline humic gleys and rendzinas on fossil shell debris shores (Borello 1968; Cappanini 1968; Tricart 1973).

The climate is warm temperate, with mean annual temperature ca. 14°C and mean annual rainfall ca. 900 mm. Species growth is restricted by: (1) a positive water balance during autumm, winter and early spring, with flooding of the lower areas (Paruelo & Sala 1990), (2) periods of negative water balance which cause drought conditions during late spring and summer (Sala 1992), and (3) salinity of the soil profile or temporary salinity associated with evaporation after flooding (Lavado & Taboada 1987). Grasslands are under continuous grazing by beef cattle, with stocking rates of about 0.6 head/ha (Cauhepé et al. 1982).

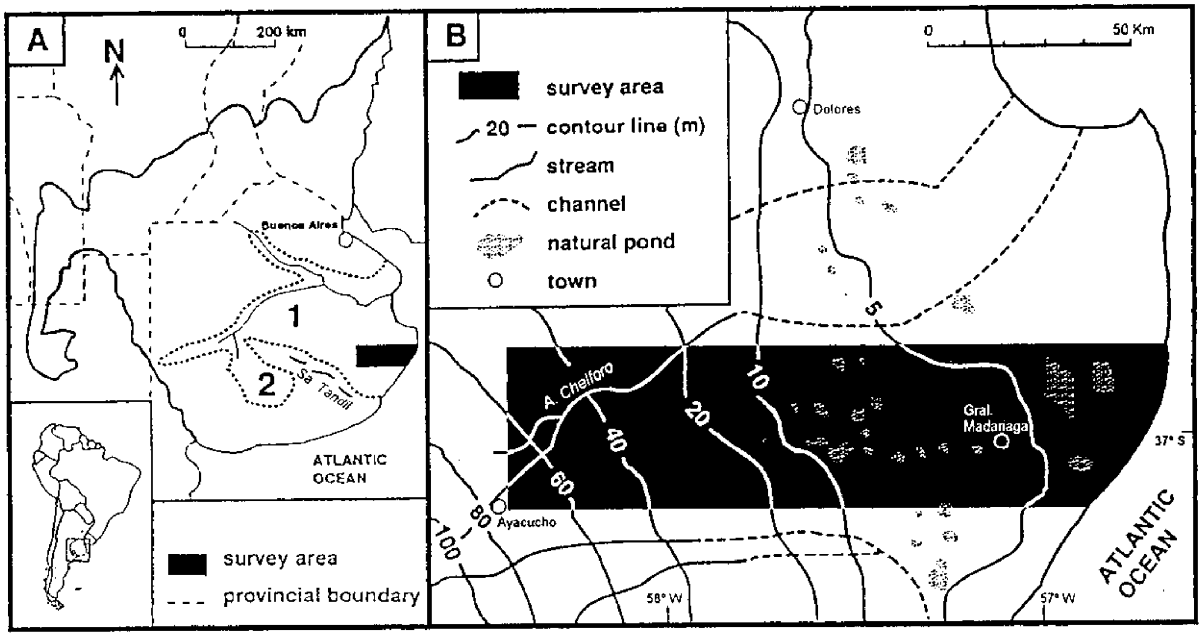

Figure 1. A) Map of the Pampean Region (-----) and the Flooding Pampa (....) with its two divisions: the Río Salado Basin (1) and the Laprida Region (2). B) Map of the study area.

Methods

Vegetation data were obtained by preferential sampling (Gauch 1982) of stands located through photointerpretation (van Zuidam & Cancelado 1979). In each sample site (25 m^2), cover-abundance values were given to each species present using the Braun-Blanquet scale (Mueller-Dombois & Ellenberg 1974)) for values under 5%, and in steps of 5% for higher cover. Vegetation sampling was carried out during late spring and summer, when the two dominant groups of species of this region: cool- and warm season species (Sala et al. 1981) can be easily identified.

The floristic heterogeneity was defined using a combination of classification and ordination methods. A raw table with 167 relevés and 285 species was used to obtain a primary matrix after excluding 6 species of very low constancy (<2%). Secondary similarity matrices were obtained using Sorensen's Qualitative Similarity Index and Czekanowski's Quantitative Percentage Similarity (Goodall 1973). Relevés were classified using Average Linkage Clustering (Digby & Kempton 1987). Because of the amplitude of the vegetation gradients (β-diversity calculated for the entire set of relevés = 6.5), presence-absence data were used. Constancy values of all species present in the defined phytosociological units were calculated and differential species were included in a constancy matrix used in the Correspondence Analysis. The first axis of this ordination was used to generate a summary table of phytosociological units. Plant communities and their variants were named on the basis of species constancy, cover and fidelity (Table 1). The primary matrix of relevés was subjected to Correspondence Analysis to determine the main directions of variation in species composition.

The internal homogeneity of vegetation units obtained by classification was determined through the Basic Homotoneity Coefficient (Moravec 1971), Whittaker's β-diversity index (Westhoff & van der Maarel 1973), and the Mean qualitative and quantitative Percentage Similarity between relevés (Ceska 1966).

Results and Discussion

Classification

Classification of vegetation relevés yielded 14 vegetation units: 10 plant communities and variants to three of these (Fig. 2). The units that merge with similarity values close to or greater than 50% were considered as variants of a given community. Relevés of communities S, R and P join with similarity indices greater than 50% showing high internal homogeneity; while T, V, M, N and K were more heterogeneous, with similarity values ranging from 35% to 45%.

At a higher level of classification, four community complexes were identified, including 13 of the defined units. Community T was excluded because it joined at a lower similarity value than the one to which complexes 1 and 2 merged, although it is closer to these than to communities of

Table 1. Names of plant communities and their variants. Symbols as used throughout the text.

Plant communities and variants	Symbol
Solidago chilensis-Hordeum leporinum	T
Cynodon dactylon-Hybanthus parviflorus	U
Stipa trichotoma-Margyricarpus pinnatus	
- with *Diodia dasycephala*	S_1
- with *Piptochaetium montevidense*	S_2
- with *Aristida murina*	S_3
Lolium multiflorum-Cynodon dactylon	V
Distichlis spicata	
- with *Panicum bergii*	R_1
- with *Stipa formicarum*	R_2
Stipa papposa-Paspalum vaginatum	
- with *Stipa neesiana*	P_1
- with *Baccharis pingraea*	P_2
Sporobolus pyramidatus-Lepidium parodii	L
Salicornia ambigua-Spatina densiflora	K
Alternanthera philoxeroides-Leersia hexandra	M
Glyceria multiflora-Polygonum punctatum	N

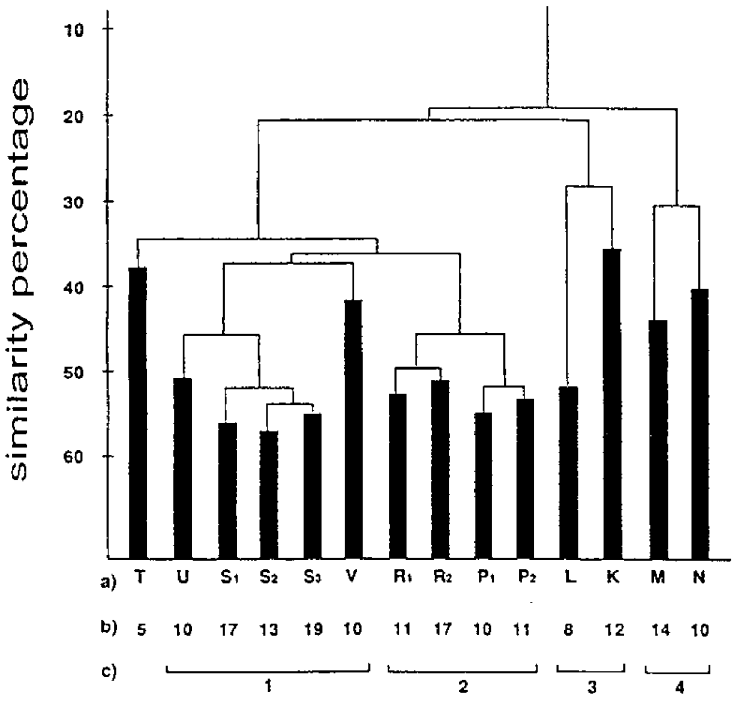

Figure 2. Hierarchical classification of vegetation relevés through average linkage clustering, using Sorensen's similarity index. a) vegetation unit; b) number of relevés; c) community complex.

the other complexes. The relevés of complexes 3 and 4 merged with the rest at similarity values of 20%, indicating their markedly different floristic composition.

The plant communities are defined by 26 floristic groups (Table 2). Groups I to IX characterize complex 1, indicating differences between its communities and/or variants. Group XXI is exclusive to complex 4. At community level, four floristic groups appear in a single community (I, T; III, U; XXII, N; XXVI, K), the remaining are common to several.

Table 2. Phytosociological summary table. Constancy values (Braun-Blanquet scale, except values <20%: I=10-20%, (.)<10%) of the differential species in the phytosociological units. Bold boxes: exclusive floristic groups in a plant community. Other boxes: taxa preferential to various plant communities.

T= *Solidago chilensis-Hordeum leporinum* community
S= *Stipa trichotoma-Margyricarpus pinnatus* comm.: S_1= with *Diodia dasycephala*, S_2= with *Piptochaetium montevidense*, S_3= with *Aristida murina*
U= *Cynodon dactylon-Hybanthus parviflorus* comm.
V= *Lolium multiflorum-Cynodon dactylon* comm.
R= *Distichlis spicata* comm.: R_1= with *Panicum bergii*, R_2= with *Stipa formicarum*
M= *Alternanthera philoxeroides-Leersia hexandra* comm.
N= *Glyceria multiflora-Polygonum punctatum* comm.
P= *Stipa papposa-Paspalum vaginatum* comm.: P_1= with *Stipa neesiana*, P_2= with *Baccharis pingraea*
L= *Sporobolus pyramidatus-Lepidium parodii* comm.
K= *Salicornia ambigua-Spartina densiflora* comm.

Floristic Group	Plant community / Variant / no. of releves	T 5	S 1 17	U 10	S 2 13	S 3 19	V 10	R 1 11	R 2 17	M 14	N 10	P 1 10	P 2 11	L 8	K 12
I	*Solanum sisymbriifolium*	IV													
	Hordeum leporinum	IV		II	.				.						
	Dactylis glomerata	III			.										
	Picris echioides	II								.					
	Cestrum parqui	III			.										
	Amaranthus sp.	II													
	Jodina rhombifolia	II													
	Scutia buxifolia	II													
	Araujia hortorum	III													
II	*Solanum chenopodioides*	III	I												
	Celtis spinosa	IV	II												
	Chenopodium multifidum	II	II												
	Sida rhombifolia	V	IV												
	Diodia dasycephala	IV	V		.										
	Stipa bertrandii	II	II	I											
	Cyperus eragrostis	III	III		.	.				I	I				
	Solidago chilensis	V	I		.	I									
III	*Facelis retusa*			V	.										
	Carex phalaroides			III	I										
	Scutellaria racemosa			III	I					I	I				
	Turnera pinnatifida			II											
	Triodanis biflora			II											
	Modiola caroliniana			II											
	Soliva pterosperma	.	.	III		.									
IV	*Carduus pycnocephalus*	II	II	III	.	.									
	Silybum marianum	III	II	IV	II										
	Ammi majus	V	IV	IV	I	.									
	Oxypetalum solanoides	III	V	IV	II	.									
	Echium plantagineum	II	III	II	II		I								
	Bromus unioloides	V	III	II	II										

Table 2 (continued).

Floristic Group	Plant community / Variant / no. of releves	T 5	S 1 17	U 10	S 2 13	S 3 19	V 10	R 1 11	R 2 17	M 14	N 10	P 1 10	P 2 11	L 8	K 12
V	*Noticastrum diffusum*		III		II	.									
	Teucrium cubense		I		II	.									
	Verbena montevidensis		III		II										
	Oenothera sp.		I	II	I										
	Torilis nodosa		I	II	I										
VI	*Cuphea glutinosa*		III	III	II	II									
	Melica brasiliana		II	IV	IV	III									
	Margyricarpus pinnatus		IV	IV	IV	II									
	Stipa trichotoma		IV	V	V	IV									
	Bromus sp.		III	III	I	II		I							
	Alchemilla parodii		II	II	.	I									
	Briza subaristata		I	II	II	I									
	Hordeum stenostachys			III	II	II									
VII	*Aristida murina*		.		III	IV									
	Eragrostis lugens				II	II									
	Micropsis spathulata				II	III		.	I						
	Conyza chilensis		.		II	II									
	Chevreulia sarmentosa		.		III	II									
	Stenandrium sp.				II	I									
VIII	*Eryngium elegans*	II	IV		I	II		.				II			
	Hypochoeris radicata	III	V	V	V	II									
	Berroa gnaphalioides	III	IV	III	IV	V		.	I						.
IX	*Physalis viscosa*	V	V	II	IV	I	I								
	Centaurea calcitrapa	V	V	IV	IV	III	I		I			II			
	Carthamus lanatus	IV	III	III	III	II	II								
	Convolvulus hermanniae	V	V	V	IV	II	III	.							
	Carduus acanthoides	V	V	V	V	III	III			.					
	Anthemis cotula	IV	I	III	.		III			I					
	Silene gallica		III	V	IV	II	IV		.						
	Sonchus asper	IV	.	IV	.	.	III			.					
X	*Crepis setosa*	III	.	III	.	.	II	I	.						
	Piptochaetium bicolor	II	V	V	V	V	III	II	.				.		
	Hybanthus parviflorus	II	III	V	II	.	II	II	I						
	Conyza blakei	II	II	III	IV	I	III	II			I				
	Eleusine tristachya	III	I		II	.		I	.	.					
XI	*Medicago polymorpha*	I	III	IV	II	II	IV	II	I	.		II			
	Bromus mollis	II	V	V	V	IV	IV	I	I	I		II		I	I
	Oxalis sp.	II	III	V	III	I	II	II	I			II			
	Stipa neesiana	IV	V	V	V	III	V	IV	II			IV	I		
	Taraxacum officinale	IV	I	IV	IV	III	II	I	.			II	I		
	Bothriochloa laguroides	IV	V	III	IV	V		IV	.			II			
	Juncus capillaceus	IV	II	IV	IV	II		II	.						
	Panicum bergii	II	III		V	II		IV	II			II	I		

Ordination

The ordination of relevés along the first two ordination axes (Fig. 3), showed species composition changing gradually across plant communities. Two vegetation gradients are evident in the ordination. Complex 1 is a common extreme to both gradients whose other extremes are communities N (complex 4, axis 1) and L (complex 3, axis 2), with complex 2 (R and P) occupying the centre of the ordination plane (Fig. 3), showing where both gradients diverge. Communities from complexes 3 and 4 show maximum dispersion among relevés, consistent with their low homoteneity coefficients and high β-diversity values (Table 3). Communities U, T and

Table 2 (continued).

Floristic Group	Plant community / Variant / no. of releves	T 5	S 1 17	U 10	S 2 13	S 3 19	V 10	R 1 11	R 2 17	M 14	N 10	P 1 10	P 2 11	L 8	K 12
XII	*Glandularia dissecta*		III	V	III	I	III	I	II						
	Adesmia bicolor		V	V	V	III	III	V	II			II			.
	Relbunium richardianum		I	IV	III	II	II	III	I					II	
	Eclipta bellidioides		I		II	I		III	II						
	Piptochaetium montevidense		I	II	V	III	II		.					I	
	Trifurcia lahue		IV	V	IV	V		V	I	.					
	Vulpia sp.		IV	V	IV	IV	IV	V	II	.		II			
XIII	*Danthonia montevidensis*			II	I	I		III	II			II			
	Polygala australis			II	I	I		III	III			III			
XIV	*Stipa papposa*	IV	IV	III	III	V	III	I	I	.		V	IV	II	I
	Cynodon dactylon	III	I	IV	II	I	V	I				II	I	III	
	Lepidium spicatum		.	III	III	III	II	I	II	.		II	III	IV	
	Melilotus indicus		.	IV	II	I	IV	I	.			IV	V	IV	I
	Conyza bonariensis	III	IV	III	IV	III		II	II	II		IV	II	II	.
	Anagallis arvensis	II	II	V	IV	II	IV	I	I			III	IV	I	.
XV	*Setaria geniculata*	III	IV		IV	III		V	IV	III		III			
	Paspalum dilatatum	IV	V	III	V	III		V	I	II	I	II			
	Trifolium repens	IV	III	III	II		II	IV	III	II		II			
XVI	*Cerastium glomeratum*	III	III	II	.	II		I	.	II					I
	Carex bonariensis	V	II	II	II	II	II	IV	III	III					
	Juncus microcephalus		IV		II	II		II	II	III					
	Cyperus reflexus		IV	II	III	I			III	I					
XVII	*Distichlis spicata*				I	III		IV	V	III	I	V	V	V	III
	Paspalum vaginatum				I	II		IV	IV	III	I	V	V	IV	III
	Chaetotropis elongata			I	II	III	III	IV	V	IV	II	V	V	IV	V
	Malvella leprosa					II	II	II	V	IV	IV	II	I		IV
XVIII	*Baccharis pingraea*					II		I	I			II	IV		.
	Hordeum pussillum		I		.	II	III		.			III	V	V	III
	Plantago myosurus		I		II	II	III	I	IV	.		III	IV	V	.
	Distichlis scoparia				II	III	II		I			II	IV	V	I
XIX	*Stipa formicarum*							II	IV	II					.
	Panicum gouinii		I			I		I	II	IV	II				.
	Leersia hexandra		.					II	II	IV	V				
XX	*Eleocharis macrostachya*					.			III	IV	II				.
	Phalaris angusta		.		.		I		III	IV	II				I
	Paspalidium paludivagum								IV	III	II				.
	Alternanthera philoxeroides	II				.			III	IV	V				.
	Pamphalea bupleurifolia							.	III	III	I				
	Polypogon monspeliensis		.			.			II	III	II				III
	Gratiola peruviana								I	I	I				
	Rorippa bonariensis				.				II	II	I				
	Agrostis avenacea								III	III	II			I	.
	Euphorbia serpens								II	I	I				.

V are not shown as they overlap with relevés of community S.

These two main directions of change have been related to topography (axis 1) and to soil salinity (axis 2). Along the topographic gradient the sequence of plant communities is S-R-M-N. The second direction of change arranges the communities in the sequence R_1-P-L. Community K presents an intermediate position between the humid and salinity extremes. Our interpretation of the associations between plant communities and landscape heterogeneity in topography and soils has been portrayed as a block diagram (Fig. 4), includ-

Table 2 (continued).

Floristic Group	Plant Variant no. of	T 5	S 1 17	U 10	S 2 13	S 3 19	V 10	R 1 11	R 2 17	M 14	N 10	P 1 10	P 2 11	L 8	K 12
XX	*Marsilea concinna*									I	II				
	Trifolium									II	I				
	Cerastium									I	I				
	Ludwigia									I	III				
XXI	*Glyceria multiflora*										V				
	Scirpus californicus										III				
	Polygonum punctatum										IV				
	Xanthium cavanillesii	II									IV				
XXII	*Eryngium ebracteatum*					I		II	III	II	II	II			
	Solanum glaucophyllum	II					I	II	III	IV	V	III			
	Hydrocotyle bonariensis									III	IV	II			II
XXI	*Nostoc*					I	II		I				III	III	
	Parapholis incurva					II	III	I					II	III	
	Spergula						III		II				II	III	
XX	*Lepidium*												II	V	
	Sporobolus pyramidatus												II	IV	
	Monerma cylindrica												III	I	
XXV	*Salicornia ambigua*								II						V
	Apium									I					III
	Hordeum jubatum														III
	Cressa														II
	Heliotropium curassavicum														II
	Spartina densiflora														III
	Sesuvium portulacastrum														III
	Atriplex hastata														III

Additional species: with total constancy > 40%: *Ambrosia tenuifolia, Apium leptophyllum, Bupleurum tenuissimum, Centaurium pulchellum, Dichondra microcalyx, Eryngium echinatum, Gamochaeta* sp., *Gerardia communis, Juncus imbricatus, Leontodon taraxacoides, Lolium multiflorum, Mentha pulegium, Phyla canescens, Sisyrinchium* sp., *Spilanthes stolonifera, Sporobolus indicus, Stenotaphrum secundatum.*

20 - 40%: *Aster squamatus, Briza minor, Cirsium vulgare, Lythrum hyssopifolia, Medicago lupulina, Paronychia brasiliana, Poa annua, Rumex* sp.

5 - 20%: *Agropyron* sp., *Agrostis jürgensii, Asclepias mellodora, Centunculus minimus, Cynara cardunculus, Grindelia discoidea, Hypochoeris* sp., *H. microcephala, Juncus acutus, Lactuca serriola, Lepidium aletes, Lotus tenuis, Plantago* sp., *Puccinellia glaucescens, Rebulnium* sp., *Samolus valerandi, Senecio burchelii, Spergula levis, S. ramosa, S. villosa, Veronica arvensis.*

< 5%: *Agrostis montevidensis, Amphibromus scabrivalvis, Atriplex* sp., *Baccharis notosergila, Bacopa monnieri, Brachystele dilatata, Bromus auleticus, Centaurea solstitialis, Cerastium* sp., *Chaptalia* sp., *Chenopodium album, Chevreulia acuminata, Chloraea* sp., *Cotula* sp., *Cuscuta* sp., *Cypella herbertii, Datura ferox, Digitaria sanguinalis, Erodium cicutarium, Eryngium pandanifolium, Euphorbia supina, Festuca arundinacea, Gaudinia fragilis, Geranium dissectum, G. molle, Glandularia peruviana, Hordeum vulgare, Hydrocotyle* sp., *H. modesta, Hymenoxys anthemoides, Hypochoeris megapotamica, Jaborosa* sp. *Lilaeopsis* sp., *Limonium brasiliense, Matricaria* sp., *Medicago arabica, Mikania micrantha, Myriophyllum brasiliense, Nothoscordum inodorum, Panicum milioides, P. sabulorum, Paspalum distichum, P. nicorae, P. quadrifarium, Petunia parviflora, Picrosia longifolia, Piptochaetium stipoides, Plantago tomentosa, Pluchea sagittalis, Polygonum aviculare, P. brasiliense, Portulaca oleracea, Ranunculus* sp., *Raphanus sativus, Rapistrum rugosum, Scirpus olneyi, Sisymbrium* sp., *Spergula grandis, Sporobolus platensis, Stenandrium diphyllum, Stipa bonariensis, S. clarazii, S. philippi, Trifolium bonannii, T. dubium, Triglochin striata, Verbena* sp., *V. bonariensis, V. intermedia, Vernonia echioides, Vicia graminea, Wahlenbergia linarioides.*

ing some assumed influence of anthropogenic disturbance on vegetation heterogeneity.

Species richness and Homogeneity

Relevés of complex 1 have higher floristic richness than the mean (Table 3). S_1, S_2 and U are the richest, with an average of over 50 species/relevé. Complex 3 is the poorest, with a mean of 18 species/relevé. At the complex level, the classification reduced the β-diversity of the whole set of relevés by 40%. The B.H.C. values show that complexes 1 and 2 are better described through species constancy than complexes 3 and 4. Communities L and N show different in-

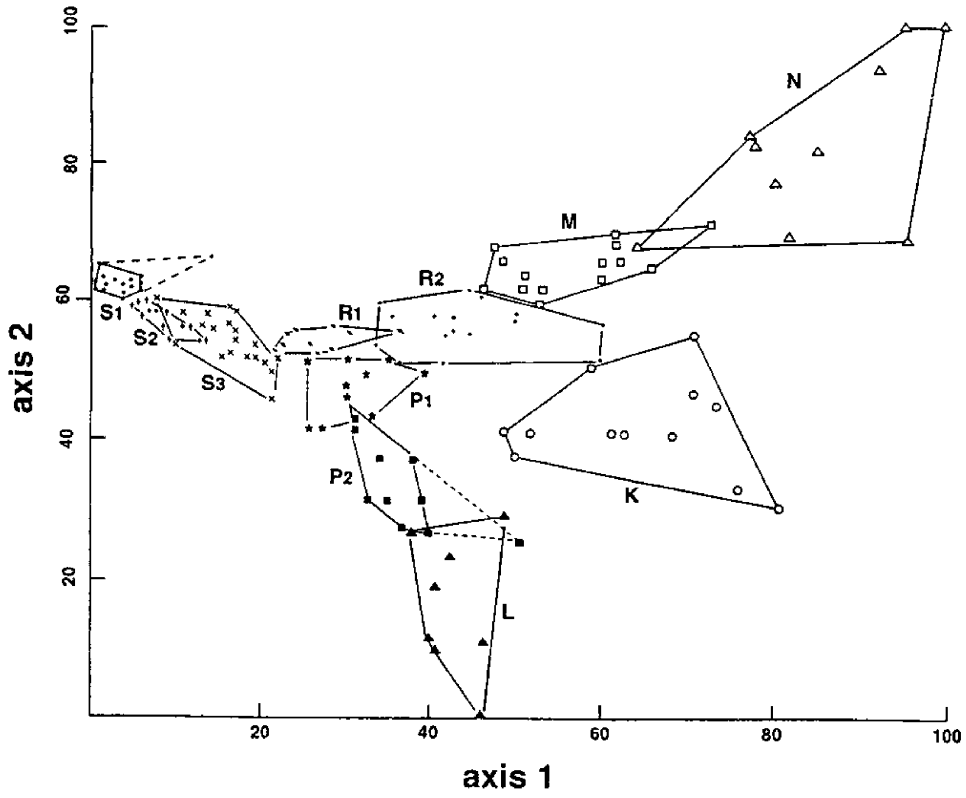

Figure 3. Ordination of vegetation relevés through correspondence analysis. Relevés from the same vegetation unit are drawn with the same symbol. Communities T, U, V are not shown as they overlap with community S. Letters as in Table 1.

Table 3. Floristic richness and internal homogeneity of community complexes in the southern grasslands of the Río Salado Basin. Internal homogeneity determined through Whittaker's β-diversity index and the Basic Homotoneity Coefficient.

Commnity complex	Mean floristic richness α	ß-Diversity	B.H.C.
1 (S,V,U)	47	3.8	6.8
2 (R,P)	36	3.8	7.3
3 (L,K)	18	4.3	2.9
4 (M,N)	26	3.9	4.8
Entire set of relevés	36	6.5	0.9

ternal homogeneity. Although both have low species richness, L exhibited high mean percentage similarity (PS) values (PS quali= 56.0; PS quanti= 49.2), while N had a particularly low quantitative PS (=23.3; PS quali= 45.6), indicating a greater between-stand variability in floristic composition. In community L, soil salinity should impose a restriction to plant growth, where few species of low competitive ability would be able to survive (Grime 1973). On the other hand, community N is subjected to frequent disturbance by flooding. We suggest there is an important chance component determining species composition of these stands. The regime of water availability and flooding constitute more stochastic restrictions along time than the one imposed by soil properties derived from parent material (community L). Moreover, considering their position in the landscape, neighbouring communities might contribute species to the colonization of microsites open by the frequent floods, which would be otherwise unable to retain a viable population in such restrictive environment (Shmida & Wilson 1985).

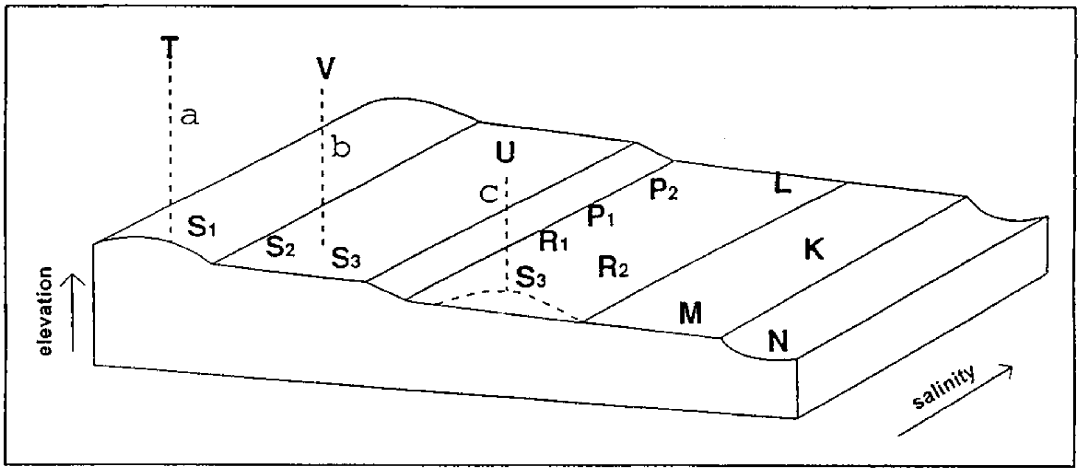

Figure 4. Landscape block diagram showing the relative position of plant communities and their variants in relation to topography and soil salinity. Replacement communities as the result of: a) the replacement of Celtis tala forest; b) alternate cropping and grazing; c) overgrazing and trampling. Letters as in Table 1.

The plant communities

The plant communities included in complex I (S, U and V) and community T occupy the highest terrain of this area. Some of the species that characterize this group of communities (*Celtis tala, Sida rhombifolia, Diodia dacycephala, Carduus pycnocephalus, Silybum marianum, Oxypetalum solanoides, Echium plantagineum, Facelis retusa, Ammi majus, Verbena montevidensis, Melica brasiliana, Margyricarpus pinnatus, Stipa trichotoma, Conyza chilensis, Chevreulia sarmentosa*) are associated with poligenetic thaptoargic hapludols, deep non-saline soils (Batista 1991).

The three variants of community S form a topographical gradient within the positive areas of this region. They can be distinguished by floristic groups II, IV and VII. Half the species from groups XVII and XVIII (*Distichlis spicata, D. scoparia, Chaetotropis elongata, Hordeum pusillum* and *Plantago myosurus*), associated with shallow and saline soils (Batista 1991) and absent in S_1, would indicate salinity conditions in stands of S_2 and S_3.

Stands of community V are poor in species, with a mean of 34 species/relevé. Their dominant species (*Lolium multiflorum* in the upper layer, and *Cynodon dactylon* in the lower one) invade and dominate post-agricultural communities (D'Angela et al. 1986; Omacini et al. 1995) and are present in sown pastures during the first years of succession (Oesterheld & León 1987, León & Oesterheld 1982). Although its maximum similarity is with U (PS=42.1), these facts and the similar topographical position and vicinity to stands of S_3, suggests that V could be a replacement community of these stands. The fact that land use seems to cause greater floristic changes than those accounted for by topographic differences (Sala et al. 1986; Chaneton, 1995) is consistent with the above hypothesis. Except for the dominant species, the floristic composition of community V is very variable, with one of the highest mean quantitative and one of the lowest mean qualitative PS values. Cool-season annuals (*Plantago myosuros, Hordeum pusillum, Parapholis incurva*), which are successful on soils with low vegetation cover (León et al. 1979), have medium constancy values in this unit.

Community T has the maximum floristic similarity (PS= 42.1) and species cover values with S_1, although lower species richness (mean number species/relevé: 51 and 40, respectively). The presence of species from the neighbouring Celtis tala forest (*Celtis tala, Jodina rhombifolia, Araujia hortorum, Scutia buxifolia, Cestrum parqui, Stipa hyalina*, Parodi 1940) in some of its stands, would indicate the replacement of the forest by this grassland.

Community U is characterized by floristic group III. Some of its species (*Facelis retusa, Soliva pterosperma, Triodanis biflora*) are planophiles, low-growing, annual forbs, that predominate in overgrazed environments. Stands of community U are seldom cultivated, due to their position in the landscape, restricted convex areas in a flat landscape where their most common disturbance is grazing and trampling, especially during flooding of the surrounding low areas.

The units of community complex 2 (P and R) occupy an intermediate topographical position (Fig. 4). Plant community R shares floristic group XIX with the units of the humid environments (M and N), and group XII, with the communities present on higher terrain (S, U and V). The variants of this community represent two successive steps in the topographical gradient: R_1 has maximum mean qualitative similarity with S_3 (PS=49.7) and R_2 with M (PS=47.3). These differences are reflected in their floristic composition (Table 2). Floristic group XX, present in communities M, N and R_2, is absent in R_1, while group X, present in the higher extreme of the topographical gradient, is barely represented in R_2. Some species of groups XI and XII (*Stipa neesiana, Bothriochloa laguroides, Panicum bergii, Trifurcia lahue,*

Vulpia sp., *Adesmia bicolor*), associated to the higher terrains (Vervoorst 1967) have high constancy values in R_1.

The variants of community P are part of the salinity gradient, whose extreme is community L (Fig. 3). The highest mean qualitative and quantitative similarity indices of P_1 and L are with P_2 (quali PS=49.9 and 43.2, quanti PS= 30.8 and 34.5, respectively), showing its intermediate position along this gradient. Their floristic richness (mean species/relevé: P_1=32, P_2=28) is also intermediate between community S (49 species/relevé), present on the higher terrains, and L with 18. Floristic group XI, well represented in the communities of complex 1, show decreasing constancy values in P and is absent in L (Table 2). Differences between the two variants are given by the presence or absence of floristic groups XI, XIII and XXIII. P_1 stands are dominated by *Paspalum vaginatum, Stenotaphrum secundatum* and *Sporobolus indicus*, while in P_2 stands, *Distichlis spicata* and *Paspalum vaginatum* form a lawn with patches of the tussock-grass *Chaetotropis elongata.*

The units included in community complex 3 (L and K), are the poorest in species (Table 3), and the ones with highest quantitative PS values (L=49.2, K=48.2). This is due to the presence of species with high constancy and mean cover values (*Distichlis scoparia*, 25%; *D. spicata*, 13% in L; *D. spicata* 27% and *Paspalum vaginatum* 29% in K). Community K is characterized by floristic group XXVI. The presence of some species of groups XX and XXIII indicate a slightly more hydromorphic condition than in L. Community K appears only to the east of the 10m contour line (Fig. 1B), coinciding with the western boundary of the marine ingressions (Tricart 1973). Community L does not have exclusive floristic groups, sharing groups XXIV and XXV with P_2, whose species indicate saline-alcaline soils and high surface salt concentration (Batista 1991).

The plant communities of complex 4 (M and N) are defined by a group of species (group XXI) with low constancy but high fidelity. Three species associated with hydromorphic conditions (*Alternanthera philoxeroides, Solanum glaucophyllum* and *Leersia hexandra*) (Collantes et al. 1988) have high constancy in these units. Community N, the lower end of the topographical gradient although poor in species (mean species/relevé= 20) has an exclusive floristic group (XXII). Values of internal qualitative and quantitative similarity are very different (45.6 and 23.3, respectively), which is the result of different dominant species in each stand. It shows low qualitative similarity with most units (PS<18), except with R_2 (PS=27.2) and M (PS=37.7). Although communities M and N have an exclusive floristic group (XXI), M has its highest mean quantitative and qualitative similarity with R_2 (PS=30.5 and 47.3, respectively), sharing with this variant floristic group XVI, a group of species of wide ecological amplitude but absent in N.

Conclusions

The vegetation survey of this area provides a basis for the identification and understanding of community-level floristic heterogeneity of these natural grasslands.

We used a combination of techniques that provided an objective means for obtaining a phytosociological table and for detecting critical species groupings which can be used for community identification, an essential pre-requisite for studies of grassland function and management in an area of such ecological heterogeneity. The present study established the floristic relationships among plant communities, and showed how variation in grassland species composition across the landscape may be linked to two major ecological gradients associated to topographic position and soil salinity.

The topography gradient, with the sequence of plant communities S-R-M-N, corresponds to the positive, convex terrains in the landscape as one extreme, and the low, flat to concave areas on the other, meaning potential differences in soil water regime, including depth and duration of seasonal flooding events. The gradient of soil salinity arranges some of the communities present in the topographically intermediate to low, flat areas, following the sequence R_1-P-L.

The floristic composition of the communities related to hydromorphic and/or saline soils seem to be similar to the ones present in the Laprida region (Batista et al. 1988) and in the centre of the Flooding Pampa (Burkart et al. 1990), while in the communities related to deep, well-drained soils there seems to be a greater floristic heterogeneity (Perelman 1996).

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