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ENVIRONMENTAL RELATIONSHIPS OF VEGETATION PATTERNS IN SALTMARSHES OF CENTRAL ARGENTINA

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Abstract: We describe vegetation-environment relationships in the saltmarshes of central Argentina. Gradient analysis (Detrended canonical correspondence analysis, DCCA) was performed involving 14 parameters of the groundwater that account for most of the variation in plant communities. We used a stepwise multivariate procedure to classify the vegetation data into 8 clusters, named according to the most abundant characteristic species: *Chloris canterai, Cynodon dactylon, Distichlis spicata, Spartina densiflora* and *Paspalum vaginatum* clusters, containing relevés of tall grassland communities, and *Atriplex undulata, Cyclolepis genistoides* and *Heterostachys ritteriana* clusters, containing relevés from scrub. Our interpretation of DCCA ordinations suggests that vegetation pattern is primarily related to a salinity-moisture gradient. There is a strong relationship between vegetation type and the amount of salt in the groundwater and the pattern of its variation during the year. The depth of the groundwater and the conditions of submersion are also related to the compositional variation of the vegetation. Although flooding causes some differences between sites, the most important discriminant variable, and therefore the best predictor of floristic variation, is salinization.

INTRODUCTION

Saline lands are widely distributed globally and make up about 10% of the Earth's terrestrial surface (O'LEARY & GLENN 1994). Compared to studies of coastal marshes, considerably less research has been carried out on inland saline landscapes (ADAM 1990, KRUEGGER & PEINEMANN 1996). The inland saltmarshes of central Argentina cover approximately 2.5 million ha, of which about 20 percent is made up of saline lakes (1440 permanent and semipermanent lagoons) and about 80 percent of a mosaic of different plant communities. However, there is only limited information available about these communities. The vegetation has a patchy structure – different patches contain different species and even different growth forms (PERELMAN et al. 1982, LEWIS et al. 1985, CHANETON et al. 1988, CANTERO & LEON 1996). The halophytic flora is poor in species and mainly consists of perennial grasses, rushes, (dwarf-) shrubs and some annuals, which are exclusively found in saline environments (like *Prosopis humilis* GILL. ex HOOK et. ARN., *Leptoglossis linifolia* (MIERS) GRIS., *Sclerophylax spinescens* MIERS and *Lippia salsa* GRIS) (CANTERO et al. 1996). CANTERO & LEON (unpubl. data) have suggested a broad classification of salt marsh vegetation of the Argentinian Inland Pampa.

Until now, the number of studies identifying the major environmental factors correlated with vegetation patterns in the inland saltmarshes of central Argentina is very small, although it is generally known that two main gradients, viz. soil moisture and salinity, account for the compositional pattern (BURKART et al. 1990, CHANETON et al. 1988, LEWIS et al. 1985). CANTERO & LEON (1996) suggested that the groundwater depth and electrical conductivity determine the coarse pattern in plant community composition, while ionic composition is responsible for the fine grain pattern. The fine pattern of plant communities and small-scale variation in species richness in inland saltmarshes of central Argentina have been described by CANTERO et al. (1998). However, information concerning which factors determine the variation of species composition at a community level, is lacking. The purpose of this study was to examine the relationships between vegetation and an array of environmental parameters of hydrology and soil chemistry, using techniques of direct gradient analysis.

MATERIAL AND METHODS

Study site

The study area was located in the southeastern part of the province of Cordoba, Argentina (Fig. 1). It is a plain of 2.5 × 106 ha with interconnected lagoons, derived from paleo-fluvial activity. The topography varies from catenas of different slope and length, to hydrologically connected shallow depressions. The climate is temperate, subhumid. The mean annual rainfall is 725 mm and it has a so-called monsoon distribution, where most of the rain is concentrated in the spring-summer (October–April) and the winter is dry. The average temperature for the year is 16 °C. The hydric balance shows an excess period in autumn (February–April), in which general flooding of the area may occur, two deficit periods (April–June and November–January) and an equilibrium period (June–October). The vegetation is seminatural – the region has been grazed at an intensity of roughly 0.2 cows per ha for at least the last 100 years.

The hydrohalomorphic soils of the study area are complex because they were formed by interactions of fluvial processes and eolic geomorphological processes (CANTU & DEGIOVANNI 1984). The soils are classified as (SOIL SURVEY STAFF 1975): Typic Natracualf; Typic Fragiacualf, Typic Duracualf and Thapto Fragic Haplacuoll. All soils are saline – sodic, not alkaline.

Data collection

We selected a study area near Pacheco de Melo as a representative area which is characterized by a high diversity of habitat conditions and plant communities. Aerial photographs at a scale of 1:50,000, 1:40,000 and 1:20,000 were used for the preliminary survey of the landscape (ANTROP 1983). We also used information about the topography, drainage network and soil parent material to characterize site conditions. On this basis we selected eight sampling sites in different parts of the landscape mosaic, each characterized by 5 to 8 relevés. In total 56 relevés of 4 × 4 m were described in patches of relatively homogeneous vegetation. In each 16 m^2 relevé the cover of vascular species was assessed using a seven-point ordinal scale (7=>75% cover; 6=51–75%, 5=26–50%; 4=6–25%; 3=3–5%; 2=1–2%; 1=a few plants, with small cover). The nomenclature of vascular plants follows CANTERO & BIANCO (1986).

Within in each plot site (56), we evaluated the groundwater (GW) level and took water samples for determining chemical parameters through a series of observation holes (PIZARRO 1978). Two bore holes were sunk to an impenetrable clay layer in each site. The bore holes were cased by plastic tubes with filters and capped. The depth of the GW (GWD) was recorded

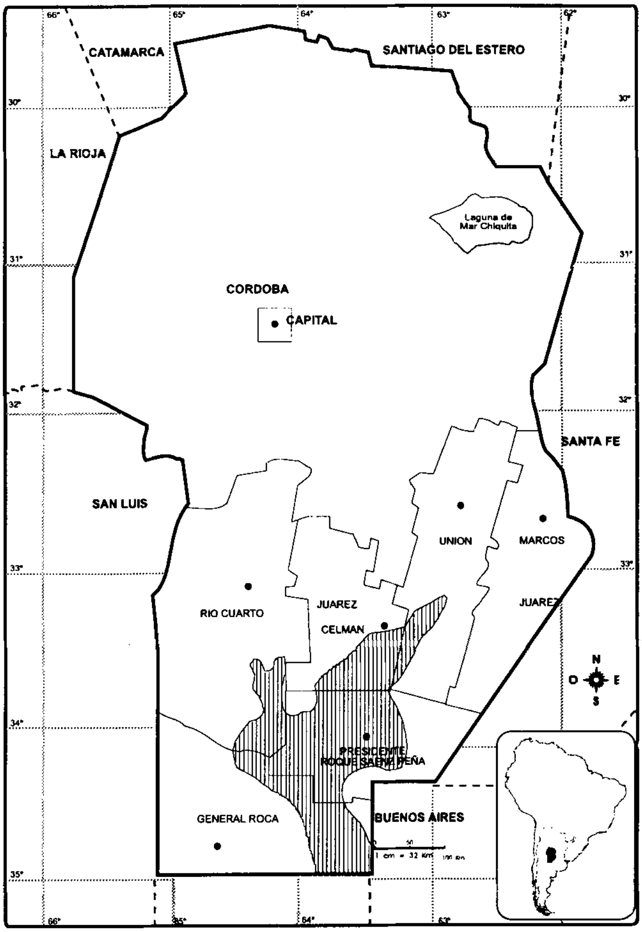

Fig. 1. Study area.

every month from September 1986 to December 1989. We also characterized the GW fluctuation regime from the local hydrologic balance and recorded the existence of additional recharge sources (local runoff or hypodermic flow). The GW chemical analysis was made according to RICHARDS (1973). Electrical conductivity (EC) and anion/cation concentration were also measured. The following two scalar indices were used to integrate the environmental variables data base: sodium adsorption ratio (SAR) and chloride/sulphate ratio (Cl/SO_4). The environmental data were organized as a three-way table, where each entry X_{ijk} corresponds to the object i, attribute j and time k. We standardized all values according to:

$$y = (100\,x)\,/\,x_{max} \qquad (1).$$

Abbreviations used: DCCA = Detrended canonical correspondence analysis; GW = groundwater; CO_3H = concentration of carbonates and bicarbonates; Cl = concentration of chlorides; SO_4 = concentration of sulfates; GWD = depth of the groundwater table; EC = electrical conductivity of the groundwater; SAR = sodium adsorption ratio.

Data analysis

Numerical analysis of the compositional variation

In order to classify the vegetation we performed an analysis in accordance with the proposals of WILDI (1989). The description of algorithms for the different methods used (agglomerative clustering, PCA and CA, analysis of concentration, discriminant analysis) can be found in ORLOCI (1978), WILDI & ORLOCI (1983, 1990), ORLOCI & KENKEL (1987). We executed multivariate numerical procedures with the MULVA-5 package (WILDI & ORLOCI 1990, WILDI 1994) running cluster analysis of the relevés and species with Euclidean distance as a resemblance measure and minimum variance as a clustering algorithm. The scalar transformation was the square root of the absolute value and relevé vectors were adjusted to unit length. We define a cluster (called also nodum by ORLOCI & STANEK 1979) as a coherent group of relevés characterized by the presence of constant species (present in at least 80% of the relevés). The block structure derived in cluster analysis was analysed using concentration analysis and the internal order of species and relevés within the groups was derived through correspondence analysis. By means of variance ranking, species exhibiting high power of resolution were selected to print the structured vegetation table

Vegetation-environment relationships

We performed ordination by using the default options of CANOCO (TER BRAAK 1987a,b,c, 1988), combined with polynomial detrending, calculation of t-values associated with the regression coefficients and a Monte Carlo permutation test (99 permutations) for the significance of the first canonical axis (P-value at the 0.01-significance level). Detrending-by-polynomials (TER BRAAK 1988, TER BRAAK & PRENTICE 1988) was used to correct the non-linear dependence between axes. Species ordination diagrams performed with CanoDraw LITE illustrate the results of DCCA (ŠMILAUER 1992). We also applied a constrained ordination to the variation in the community data which remained after known environmental variables had been fitted by regression. We partialled out the effect of EC and GWD from the ordination (TER BRAAK & PRENTICE 1988). This enabled us to draw a complete image of the relation between species data and the explanatory data set. We performed Monte Carlo permutation tests within each DCCA to assess the trace significance.

RESULTS

Vegetation types and their environment

Seventy nine vascular plant species were identified altogether. Vegetation classification by MULVA-5 showed that 8 distinct clusters formed by 21 species groups exist. We gave the eight clusters names according to the most abundant characteristic species (Tab. 1): *Chloris canterai*, *Cynodon dactylon*, *Atriplex undulata*, *Cyclolepis genistoides*, *Heterostachys ritteriana*, *Spartina densiflora*, *Paspalum vaginatum* and *Distichlis spicata*.

Tab. 2 characterizes the hydrology and chemical parameters of the GW in sites where the relevés belonging to the above mentioned clusters were described. It was possible to distinguish the following GW fluctuation regimes: (a) GW with a mean fluctuation greater than 100 cm, which is associated with flat or convex plains, (cluster *Chloris canterai*); (b) GW with a mean fluctuation less than 100 cm, which is associated with flat positions in the landscape, and more or less balanced inflow and runoff (clusters *Cynodon dactylon* and *Heterostachys ritteriana*); (c) GW with a mean fluctuation up to 80 cm, either without flooding or with relatively short flooding periods of 60 days or less per year; such conditions are usually found in shallow depressions or gentle slopes in the landscape (clusters *Atriplex undulata*, *Cyclolepis genistoides* and *Heterostachys ritteriana*); and (d) GW with a mean fluctuation up to 80 cm with relatively long flooding periods (60 or more days per year); these conditions occur in shallow depressions in the landscape (clusters *Distichlis spicata*, *Spartina densiflora* and *Paspalum vaginatum*).

Two GW types were distinguished according to their chemical characteristics (Tab. 2). The first type is characterized by EC < 18 dS/m. Such conditions prevail in sites where the relevés of the following clusters are located: *Chloris canterai*, *Cynodon dactylon* and *Paspalum vaginatum*. In this case, the value of EC is relatively low for saltmarsh conditions and there is a significant positive correlation between GWD and EC, reflecting a strong dilution effect by rainfall. Even though the correlation does not show statistical significance in the case of the *Paspalum vaginatum* cluster, EC always remains below 8 dS/m. In the case of the other two clusters, dilution corresponds to a recharge in soils of greater permeability and relatively high topographic positions, which do not receive saline runoff. The phenomenon of dilution is also associated with the presence of locally perched GW, which is hydrologically independent of the highly saline GW prevailing in the deeper horizons. This occurs because of the cemented soil horizons (fragipans and hardpans) at different depths, which considerably decrease the vertical hydraulic conductivity.

The second type of GW has EC > 18 dS/m. It is a typical situation in sites where relevés of clusters *Atriplex undulata*, *Cyclolepis genistoides*, *Distichlis spicata*, *Spartina densiflora* and *Heterostachys ritteriana* are located. In this case, no correlation between EC and GWD exist, indicating the relatively smaller significance of rain-borne dilution (Tab. 2). This is a result of the particular hydrological conditions associated with sites occupying intermediate or low topographic positions, receiving highly saline runoff and hypodermic flows which do not have an important dilution effect. The soils also have good capillary linkage with the highly mineralized groundwater.

Compositional and environmental gradients

The DCCA ordination (Fig. 2, Tab. 3) revealed contrasting environmental situations. The variations in the content of bicarbonates, sulfates, sodium, etc. in the groundwater is closely related to the pattern of floristic variation in groups 4, 5, 9, 12, and 13 (clusters *Chloris canterai* and *Cynodon dactylon*). Some species groups (10, 11 and 14, cluster *Cyperus corymbosus*), which are located far from the center on the graph, are associated with the lowest values of GWD. This is an indication of the particular habitat conditions there: these are sites with a GW fluctuating close to the surface, which are flooded temporarily or for extended periods, and which have moderately saline waters (EC = 2–10 dS/m). Two other environmental variables – pH and CO_3H – are associated with cluster *Paspalum vaginatum* but also with cluster *Cynodon dactylon*. The Cl/SO_4 ratio, which has the highest negative correlation with axis 2, separates cluster *Paspalum vaginatum* from the others. The lowest values of chlorides and sulfates (30 meq/l) for all the sites occur in the small depressions where stands classified into cluster *Cyperus corymbosus* are typically found. The variable GWD distinguishes cluster *Cynodon dactylon* from cluster *Chloris canterai*. In the third quadrant of Fig. 2, species group 21 (cluster *Heterostachys ritteriana*) is located separately. Site conditions for this community are characterized by the highest values of SAR, Cl, EC and Na content and by the highly saline GW fluctuating near the surface. Species groups 8,

Table 1. Vegetation table documenting the communities of salt marsh landscapes from Central Argentina. Starred numbers indicate individual floristic groups sensu WILDI & ORLOCI 1990. A – *Chloris canterai*, B – *Cynodon dactylon*, C – *Paspalum vaginatum*, D – *Spartina densiflora*, E – *Distichis spicata*, F – *Atriplex undulata*, G – *Cyclolepis genistoides*, H – *Heterostachys ritteriana*.

Vegetation cluster	A	B	C	D	E	F	G	H
Relevé number		111111	11112222	22222233	3333	333344444	4444444	5555555
	1234567	89012345	67890123	45678901	2345	678901234	3456789	0123456
Chloris canterai	6777777	....	....	....	....	....	....	....
Schizachyrium condesatum	43655..	....	....	....	....	....	....	....
Cenchrus myosuroides	32.....	....	....	....	....	....	....	....
Geranium dissectum 1*	4454544	....	....	....	....	....	....	....
Briza subaristata	5454434	....	....	....	....	....	....	....
Verbena bonariensis	2	....	....	....	....	....	....	....
Bowlesia incana	2.232..	....	....	....	....	....	....	....
Physalis viscosa	3..3..3	....	....	....	....	....	....	....
Senecio pampeanus 2*	3322..4	....	....	....	....	....	....	....
Panicum bergii	33.....	....	....	....	....	....	....	....
Sisyrinchium iridifolium	....	1	....	....	....	....	....	....
Stipa trichotoma	3444446	....	....	....	....	....	....	....
Stipa tenuissima	4......	....	....	....	....	....	....	....
Eustachys retusa 3*	..34...	....	....	....	....	....	....	....
Plantago tomentosa	...34..	....	....	....	....	....	....	....
Sporobolus rigens	....	....	....	21......	....	2........	....	....
Cirsium vulgare	344443.	....	....	....	....	....	....	....
Ammi majus	234..2.	....	....	....	....	....	....	....
Setaria parviflora 4*	24.....	....	....	....	....	....	....	....
Conyza bonariensis	22..12.	2......1	....	....	....	....	....	....
Cynodon dactylon	2322111	7676777.	....	....	....	....	....	....
Muhlenbergia asperifolia	..4....	....	....	....	....	....	....	....
Hypochoeris chillensis	...12..	....	....	....	....	....	....	....
Aster squamatus	....	554555..	333.4...	....	....	....	....	....
Parapholis incurva	....	3.3..3..	....	....	....	....	....	....
Chaetotropis elongata 5*	....	46434.5.	....	....	....	....	....	....
Hypochoeris microcephala	....	....44..	....	....	....	....	....	....
Sisyrinchium pachyrhizum	....	.....1..	....	....	....	....	....	....
Medicago lupulina	....	.....1..	....	....	....	....	....	....
Verbena montevidensis	....	......3.	3.......	....	....	....	....	....
Cyperus reflexus	....	......2.	4.......	....	....	....	....	....
Ammi viznaga	....	......1.	....	....	....	....	....	....
Daucus pusillus	342.1..	....	....	....	....	....	....	....
Lolium multiflorum 6*	434..2.	....	....	....	....	....	....	....
Anthemis cotula	....	......1.	....	....	....	....	....	....
Melilotus indicus	..43...	....	....	....	....	....	....	....
Eragrostis lugens	.232223	....	....	....	....	....	....	....
Pappophorum caespitosum 7*	..3...2	....	....	....	....	....	....	....
Baccharis stenophylla	3	....	....	....	....	....	..3..4.	.11....
Distichlis scoparia	...1114	....	....	....	....	....	.2...33	4......
Plantago myosurus 8*	....	444434..	....	....	....	....	....	....
Lepidium spicatum	....	42......	....	....	....	....	....	....
Chloris halophila	....	44.54...	....	....	....	....	....	....
Spergula ramosa	1	....	....	....	....	....	....	....
Centaurium pulchellum 9*	....	..1.....	....	....	....	....	....	....
Polygonum stypticum	....	2..22...	455.44.4	....	....	....	....	....
Sporobolus pyramidatus 10*	....	.33.....	....	....	....	....	....	....

Vegetation cluster	A	B	C	D	E	F	G	H
Relevé number		111111	11112222	22222233	3333	333344444	4444444	5555555
	1234567	89012345	67890123	45678901	2345	678901234	3456789	0123456
Poa resinulosa	....	.1..1.23	....	....	....	....	....	....
Cyperus corymbosus 11*	....	..1.....	7677775.	....	....	....	....	....
Paspalum vaginatum	....	....	5	....	....	....	....	....
Euphorbia serpens 12*	....	3.......	....	....	....	....	....	....
Hoedeum stenostachys 13*	....	......3.	....	....	....	....	13	....
Pappophorum philippianum	....	....	....	....	....	....33...	.22423.	....
Eleocharis nodulosa	....	......5.	443557..	....	....	....	....	....
Eryngium ebracteatum 14*	....	....	.....3..	....	....	....	....	....
Rumex crispus	....	....	....44..	....	....	....	....	....
Diplachne uninervia	....	......2.	45554.3.	....	....	....	....	....
Spartina densiflora 15*	....	....	....76..	65556...	....	....	....	....
Baccharis pingraea	5535654	....	....	....	....	....	....	....
Boopis anthemoides 16*	34.34..	....	....	....	....	....	....	....
Tessaria dodonaefolia	....	....	....	....	....	....	....4..	....
Heliotropium curassavicum	....	2312221.	....	.21.....	....	2........	....	....
Sesuvium portulacastrum	....	3.......	....	....	...2	.4...3...	..12..1	....
Distichlis spicata	....	..3.....	44	34444777	7777	4445543..	4543444	4......
Sporobolus indicus 17*	....	3544	....	....	....	....	.2...2.	..3..43
Cressa truxillensis	....	....	34	34434344	4444	1223.....	2......	42.2...
Salicornia perennis	....	1321....	43	45436423	3555	5555656..	4544534	44443..
Frankenia pulverulenta	....	....	....	....	....	.....2...	....	....
Suaeda patagonica 18*	....	....	....	.....4..	....	....	....	....
Trichloris crinita	....	....	....	....	....	..3......	..3421.	....
Psila tenella 19*	....	....	....	....	....	....	443..43	....
Lippia salsa	....	....	....	....	....	....	5444634	....
Schinus fasciculatus	....	....	....	....	....	....	65313.1	....
Limonium brasiliense	....	....	....	....	1.11	....	3223123	.3.....
Atriplex undulata	....	....	....	....	....	6667677..	4565554	1..343.
Lycium tenuispinosum 20*	....	....	....	....	....	.3...3...	222443.	....
Cyclolepis genistoides	....	....	....	....	....	..1......	5677755	....
Maytenus vitis-idaea	....	....	....	....	....	....	44543.4	....33.
Heterostachys ritteriana 21*	....	....	....	....	....	....	5	655655.

16, 19 and 20 (clusters *Cyclolepis genistoides* and *Atriplex undulata*) are most abundant in sites with GW fluctuating between 40–60 cm and where the GW is highly saline (EC = 20–30 dS/m), but less so than in sites of cluster *Heterostachys ritteriana*. The location of species groups 15 and 17 on the diagram, characteristic for clusters *Spartina densiflora* and *Distichlis spicata*, coincide with low values of GWD and high values of the content of different ionic complexes in the GW.

High Ca content is associated with the occurrence of extreme halophytic species groups. The relevés belonging to clusters *Chloris canterai*, *Cynodon dactylon* and *Cyperus corymbosus*, are typically described in sites with a lower Ca concentration in the GW (10 meq/l). Among the groups of halophytic species, this variable is particularly useful for separating clusters *Distichlis spicata* and *Spartina densiflora*, which represent communities in sites with a Ca concentration higher than 15 meq/l.

Table 2. Some groundwater chemical characteristics in the sites where relevés of the eight clusters were located (averaged values ± s.d.). r (GWD, EC) is the correlation between the depth and electrical conductivity of the groundwater, d.f. = 27.

Variable/ cluster	*Atriplex undulata*	*Distichlis spicata*	*Spartina densiflora*	*Cynodon dactylon*	*Cyclolepis genistoides*	*Paspalum vaginatum*	*Chloris canterai*	*Heterostachys ritteriana*
Depth (cm)	51.8 ± 24	45.3 ± 32	21.8 ± 18	83.3 ± 34	72.2 ± 31	30.0 ± 32	106.1 ± 23	23.1 ± 18
EC (dS/m)	32.9 ± 4.9	20.8 ± 5.3	30.7 ± 4.3	4.1 ± 3.3	24.6 ± 4.5	4.9 ± 2.0	12.0 ± 6.3	38.8 ± 5.8
pH	7.9 ± 0.4	8.2 ± 0.4	8.1 ± 0.5	8.0 ± 0.4	8.4 ± 0.2	8.6 ± 0.2	8.3 ± 0.2	8.1 ± 0.2
CO_3 (g/l)	0.02 ± 0.04	0.04 ± 0.05	0.09 ± 0.16	0.02 ± 0.05	0.12 ± 0.10	0.03 ± 0.05	0.04 ± 0.06	0.05 ± 0.06
CO_3H (g/l)	0.52 ± 0.6	0.48 ± 0.4	0.68 ± 0.6	0.27 ± 0.1	0.92 ± 0.6	0.46 ± 0.2	0.52 ± 0.4	0.70 ± 0.4
Cl (g/l)	11.3 ± 2.7	6.8 ± 1.7	9.5 ± 1.9	0.8 ± 0.8	6.5 ± 0.5	0.7 ± 0.3	3.3 ± 1.8	15.7 ± 3.8
SO_4 (g/l)	11.5 ± 2.5	6.6 ± 3.8	11.5 ± 3.0	0.8 ± 0.8	7.9 ± 0.5	0.9 ± 0.4	2.4 ± 1.3	10.6 ± 2.4
Na (g/l)	10.7 ± 2.4	6.2 ± 3.2	10.4 ± 2.3	0.6 ± 0.5	7.1 ± 0.9	0.9 ± 0.4	2.8 ± 1.6	13.5 ± 3.0
K (g/l)	0.24 ± 0.08	0.14 ± 0.09	0.25 ± 0.19	0.06 ± 0.07	0.14 ± 0.04	0.04 ± 0.04	0.11 ± 0.18	0.25 ± 0.17
Ca (g/l)	0.48 ± 0.11	0.24 ± 0.14	0.32 ± 0.11	0.10 ± 0.08	0.15 ± 0.04	0.06 ± 0.05	0.09 ± 0.05	0.34 ± 0.12
Mg (g/l)	0.87 ± 0.29	0.54 ± 0.36	0.62 ± 0.23	0.07 ± 0.05	0.44 ± 0.15	0.03 ± 0.01	0.22 ± 0.14	1.48 ± 0.28
SAR	67.2 ± 27.0	45.9 ± 32.4	77.5 ± 28.3	11.4 ± 11.0	66.6 ± 15.2	9.2 ± 6.4	35.8 ± 24.9	87.2 ± 34.0
r (GWD, EC)	0.37 *	0.08 ns	0.02 ns	0.57 **	0.19 ns	0.25 ns	0.85 **	0.49 **

Effect of covariables

Partial DCCA showes that the remaining floristic variation in the vegetation after the adjustment of the two covariables is significant ($P < 0.01$). The highest correlations between the sets of environmental variables and axes is for Cl/SO_4 (Fig. 3). When comparing the graphs in Fig. 2 with those in Fig. 3, differences appear among the configurations of environmental variables CO_3H, pH, Cl/SO_4, Cl, SAR, Mg and content of Na. Consequently, these parameters are the most important determinants of variability after eliminating the effect of covariables. Some relationships inferred from Fig. 2 are more evident. Thus, CO_3H and pH are clearly associated with cluster *Paspalum vaginatum*, Cl, Mg and Ca distinguish the principal variation trends for cluster *Cynodon dactylon*, Na for cluster *Distichlis spicata*, Cl/SO_4 for clusters *Heterostachys ritteriana* and *Chloris canterai*, SO_4 for clusters *Cyclolepis genistoides* and *Spartina densiflora* and K for cluster *Atriplex undulata*.

DISCUSSION AND CONCLUSIONS

The vegetation pattern in central Argentinian saltmarshes primarily relates to gradients of salinity and moisture conditions. There is an evident relationship between plant community composition and the GW salt concentration. Depth of the GW and the duration and frequency of flooding are also of great importance. Although poor in species, the vegetation is a true mosaic of eight plant communities, which occur in locally different landscape units, characterized by different habitat conditions.

It is possible to distinguish five contrasting environmental situations: (a) Sites where chlorides and sodium dominate the ionic composition of the GW, the depth of which fluctuates between 0–40 cm. In these conditions, relevés of the cluster *Heterostachys ritteriana* are located; (b) Sites where the mineralization of the soil is extremely high and sulfates and calcium predominate over chlorides and sodium in the ionic composition of the GW. Relevés of the clusters *Atriplex undulata* and *Cyclolepis genistoides* are located there, while in the case of the first cluster, site conditions are characterized by the relatively higher sulfate content

Table 3. Correlation coefficients of abiotic variables (characteristics of the groundwater) with 1st and 2nd canonical axes of DCCA ordination. Environmental data averaged over time, vegetation data in quantitative form.

Abiotic Variable (GW)	No covariables		GWD, and EC as covariables	
	Axis 1	Axis 2	Axis 1	Axis 2
GWD	-0.69	-0.27	-	-
EC	0.72	-0.43	-	-
pH	-0.01	-0.21	-0.11	-0.38
CO_3H	0.12	-0.47	-0.13	-0.28
Cl	0.66	-0.37	0.06	0.47
SO_4	0.81	-0.26	0.57	-0.21
Na	0.74	-0.37	0.25	0.16
K	0.53	-0.22	-0.38	-0.03
Ca	0.66	-0.09	0.25	0.30
Mg	0.70	-0.34	0.31	0.23
SAR	0.67	-0.47	-0.20	-0.42
Cl/SO_4	-0.23	-0.40	-0.64	0.21

in the GW; (c) Relevés, which are classified into the clusters *Spartina densiflora* and *Paspalum vaginatum*, are located in sites where flood pulses have a high frequency of recurrence and duration (more than 45 days). However, in the second case, the capillary link between the highly mineralized groundwater is inhibited due to the presence of a hardpan – a cemented soil horizon; (d) Sites which are flooded no longer than 45 days – cluster *Distichlis spicata*; and, (e) Sites with considerable GW fluctuations (60–150 cm) – clusters *Chloris chanterai* (sites with highest GW fluctuations) and *Cynodon dactylon* (sites with slightly less fluctuations).

The role of soil salinity in determining the distribution of plant species in saltmarshes has been stressed by several authors (UNGAR 1968, 1970, 1972, WAISEL 1972, FLOWERS 1975, CALLAWAY & SABRAW 1994, CABALLERO et al. 1994, MARYAM et al. 1995). UNGAR (1965, 1974a,b) has shown that the distribution of inland halophytes in the United States is mainly dependent on the salinity gradient, while local climate, topography, soil moisture and biotic factors are less important. SYKORA et al. (1987) suggested that for saltmarshes in Ireland the main factors responsible for the floristic differences between the communities were the duration of waterlogged conditions and the salinity of the soil. RAGONESE & COVAS (1947) described the interrelation of the salinity gradient and vegetation in northern Argentinian saltmarshes – from *Paspalum vaginatum* + *Distichlis spicata* communities in alkaline soils to *Salicornia ambigua* + *Sesuvium portulacastrum* in the most saline acid soils. In the same region, LEWIS et al. (1985) also noted strong relationships between vegetation pattern and the soil moisture-salinity gradient. When studying the coastal communities of Argentina, KRUEGGER & PEINEMANN (1996) found that grassland vegetation with sparse shrubs dominated by *Heterostachys ritteriana* was present in soils with high salinity while *Geoffroea decorticans* communities occurred in soils with low salinity. However, the concrete role of particular ecological factors varies between different ecosystems. In the inland saltmarshes of central Argentina, the GW salinity and its annual variation are the primary determinants of the plant community composition. The depth of the GW and its annual variation account for a smaller amount of compositional variation.

The relationship between vegetation and environment is not unidirectional in saltmarshes. In the present study area, CISNEROS et al. (unpubl.) found that vegetation modifies the hydrophysical properties of saline soils, especially the speed of infiltration and the capillary flow of salt towards the surface. These parameters, in turn, change the species composition of plant communities.

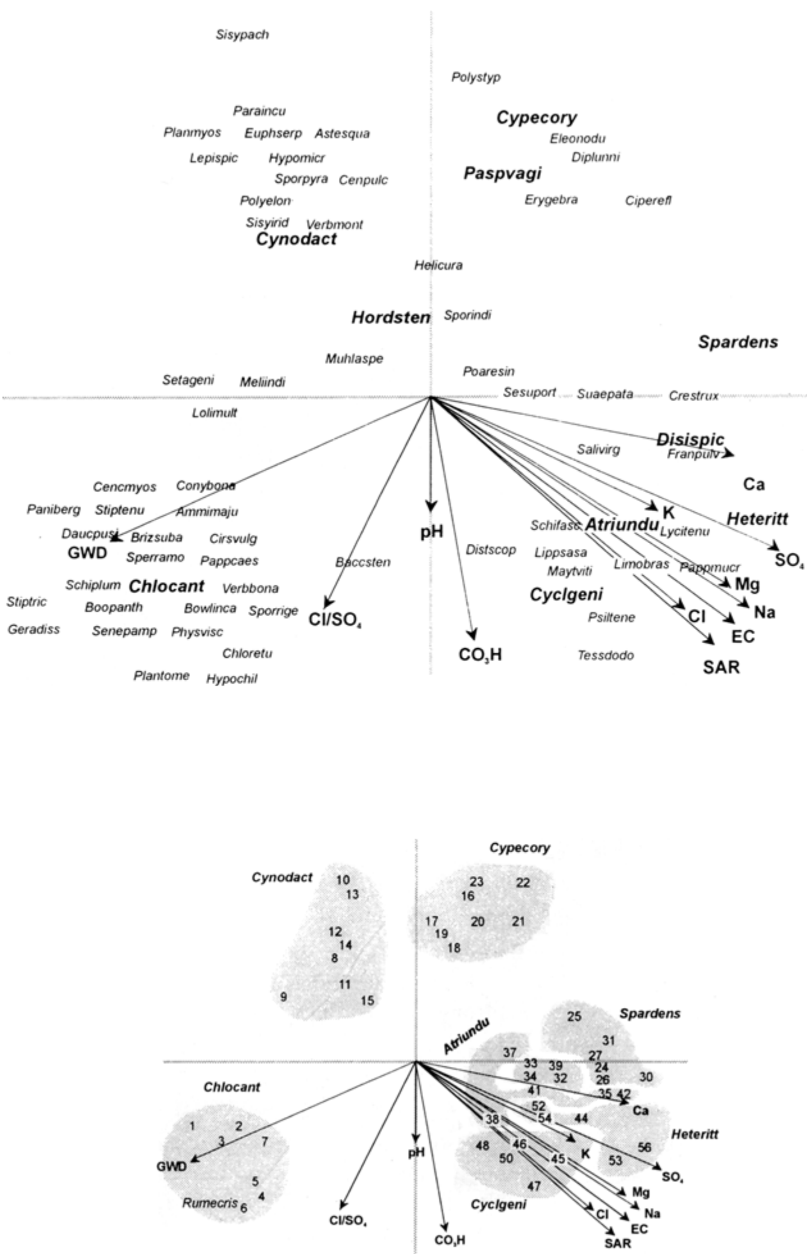

Fig. 2. DCCA ordinations (relevés and species) of environmental data averaged for all the sampling periods and of the vegetation data in quantitative form. Numbers represent the relevés and arrows represent the abiotic variables. Species names in boldface represent vegetation clusters (for abbreviations see Fig. 3). Eigenvalue: axis 1, 0.72; axis 2, 0.57. Species-environment correlations: axis 1, 0.92; axis 2, 0.87; 83% variance accounted for the first two axes. Monte Carlo test significant ($P < 0.01$).

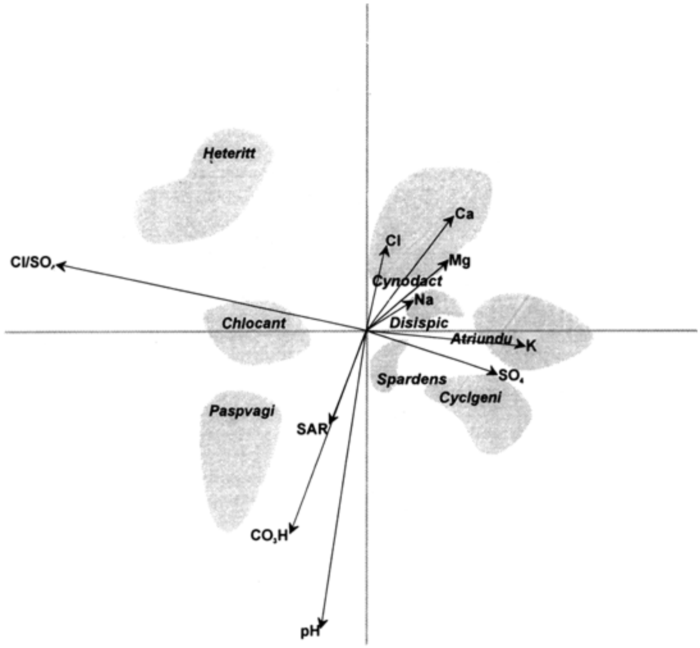

Fig. 3. Partial DCCA ordination of environmental data averaged for all sampling period and the vegetation data in quantitative form (groundwater table depth and groundwater table electrical conductivity as covariable). Eigenvalue: axis 1, 0.35; axis 2, 0.25. Species-environment correlations: axis 1, 0.77; axis 2, 0.72; 73% variance accounted for the first two axes. Monte Carlo test significant ($P < 0.01$).

Abbreviations and symbols in Figs. 2 and 3: The abiotic variables represented by arrows: Cl/SO4 – chlorides/sulfates ratio; SO4 – sulfates; GWD – water table depth; pH – pH; CO3H – carbonates and bicarbonates; Cl – chlorides; Ca – calcium; Mg – magnesium; Na – sodium; K – potassium; EC – electrical conductivity; SAR – sodium adsorption ratio. Species abbreviations: Ammimaju – *Ammi majus*, Astesqua – *Aster squamatus*, Atriundu – *Atriplex undulata*, Baccsten – *Baccharis stenophylla*, Boopanth – *Boopis anthemoides*, Bowlinca – *Bowlesia incana*, Brizsuba – *Briza subaristata*, Cencmyos – *Cenchrus myosuroides*, Cenpulc – *Centaurium pulchellum*, Cirsvulg – *Cirsium vulgare*, Ciperefl – *Cyperus reflexus*, Chlocant – *Chloris canterai*, Chloretu – *Eustachys retusa*, Conybona – *Conyza bonariensis*, Crestrux – *Cressa truxillensis*, Cyclgeni – *Cyclolepis genistoides*, Cynodact – *Cynodon dactylon*, Cypecory – *Cyperus corymbosus*, Daucpusi – *Daucus pusillus*, Diplunni – *Diplachne uninervia*, Distscop – *Distichlis scoparia*, Disispic – *Distichlis spicata*, Eleonodu – *Eleocharis nodulosa*, Erygebra – *Eryngium ebracteatum*, Euphserp – *Euphorbia serpens*, Franpulv – *Frankenia pulverulenta*, Geradiss – *Geranium dissectum*, Helicura – *Heliotropium curassavicum*, Heteritt – *Heterostachys ritteriana*, Hypochil – *Hypochoeris chillensis*, Hypomicr – *Hypochoeris microcephala*, Lepispic – *Lepidium spicatum*, Limobras – *Limonium brasiliense*, Lippsasa – *Lippia salsa*, Lolimult – *Lolium multiflorum*, Lycitenu – Lycium *tenuispinosum*, Maytviti – *Maytenus vitis-idaea*, Meliindi – *Melilotus indicus*, Muhlaspe – *Muhlenbergia asperifolia*, Paniberg – *Panicum bergii*, Pappmucr – *Pappophorum philippianum*, Pappcaes – *Pappophorum caespitsum*, Paraincu – *Parapholis incurva*, Paspvagi – *Paspalum vaginatum*, Physvisc – *Physalis viscosa*, Planmyos – *Plantago myosurus*, Plantome – *Plantago tomentosa*, Poaresin – *Poa resinulosa*, Polystyp – *Polygonum stypticum*, Polyelon – *Chaetotropis elongata*, Psiltene – *Psila tenella*, Rumecris – *Rumex crispus*, Salivirg – *Sarcocornia perennis*, Schifasc – *Schinus fasciculatus*, Schiplum – *Schizachyrium condensatum*, Senepamp – *Senecio pampeanus*, Sesuport – *Sesuvium portulacastrum*, Setageni – *Setaria parviflora*, Sisyirid – *Sisyrinchium iridifolium*, Sisypach – *Sisyrinchium pachyrhizum*, Spardens – *Spartina densiflora*, Sperramo – *Spergularia ramosa*, Sporindi – *Sporobolus indicus*, Sporpyra – *Sporobolus pyramidatus*, Sporrige – *Sporobolus rigens*, Suaepata – *Suaeda patagonica*, Stiptenu – *Stipa tenuissima*, Stiptric – *Stipa trichotoma*, Tessdodo – *Tessaria dodonaefolia*, Verbbona – *Verbena bonariensis*, Verbmont – *Verbena montevidensis*. The vegetation clusters are indicated in boldface: **Atriundu**, *Atriplex undulata*; **Chlocant**, *Chloris canterae*; **Cyclgeni**, *Cyclolepis genistoides*; **Cynodact**, *Cynodon dactylon*; **Cypecory**, *Cyperus corymbosus*; **Disispic**, *Distichlis spicata*; **Heteritt**, *Heterostachys ritteriana*; **Hordsten**, *Hordeum stenostachys*; **Paspvagi**, *Paspalum vaginatum*; **Spardens**, *Spartina densiflora*.

The results of our study show that salinity and flooding act as ecological filters that reduce plant diversity in the saltmarsh. The highest species richness (cluster *Chloris canterai*) is associated with the lowest soil salinity level and conversely, the lowest species richness (cluster *Heterostachys ritteriana*) is associated with the highest soil salinity. Similar results have been obtained for the inland saltmarshes of North America – UNGAR (1972) found that lower species richness and standing crop were characteristic of communities on more saline soils. GARCIA et al. (1993) have shown that in a Mediterranean inland saltmarsh, the salinity was negatively correlated with species richness. We suggest that communities belonging to clusters *Chloris canterai* and *Cynodon dactylon*, associated with higher topographic positions, have a different origin, compared to the rest of the vegetation – they more closely resemble grassland communities on non-saline soils.

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