

THE RELEVANCE OF PHYSICAL FACTORS ON SPECIES DISTRIBUTIONS IN INLAND SALT MARSHES (ARGENTINA)

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Abstract. The objective of this paper is to describe the factors that affect vegetation pattern on continental saline lowlands around rivers. Three transects were laid perpendicular to the River Saladillo (S.E. Santa Fe, Province, Argentina). Vegetation and soil data were collected and analysed based on indirect canonical correlation, Spearman rank correlation coefficient and Pearson correlation coefficient. Three plant communities were detected: Flechillar of *Stypa hyalina*, Espartillar of *Spartina densiflora* and a Halophilous prairie. Flechillar was positively correlated with soil texture and exchangeable ions, Mg, Ca, CO₃ and P₂O₅; the Halophilous prairie with elevation, HCO₃, pH, Na and CO₃; and the Espartillar clearly with none of the examined edaphic variables. Characteristic species, in contrast to rare species, show correlation with edaphic variables for all three transects. No correlations for rare species can be related to plasticity.

Introduction

Halophytes can withstand a wide range of salinity (Jefferies and Pitman 1986) and there is general agreement that the physical factors are more important than the biotic ones for plant species distribution in marshes (Bertness and Ellison 1987). However, several authors suggest that biotic interaction may be important as well (Silander and Antonovics 1982; Bertness and Ellison 1987).

The plant communities of SE Santa Fe have been analysed by Lewis *et al.* (1985) and Collantes and Lewis (1980). They suggested that plant community distribution follows environmental (edaphic) gradients. In a previous paper (Carnevale *et al.* 1987) we analysed plant species distributions along environmental gradients in a marsh at the River Saladillo (Province of Santa Fe, Argentina). We found three distinct communities: the Flechillar, the Halophilous prairie, and the Espartillar. We also found that species distributions along the gradient respond to physical (edaphic) factors, but there was another response component that could be correlated with species interactions.

The objective of this paper is to discover how far different physical factors determine plant species distributions, as a first approximation to understanding the causes which mold vegetation pattern (Ernst 1978) on continental marshes of river valleys.

Material and methods

Three transects, 650, 675 and 850 m long, were laid across the River Saladillo valley near Chabás and Sandford. Vegetation and soil data were obtained from 26, 28 and 27 plots over the transects in the same way as in Carnevale *et al.* (1987). In all, 29 soil variables were analysed and 66, 55 and 65 species were recorded. Soil

and vegetation data were analysed by PCA (Principal Component Analysis) using SPAD programs (Lebart and Morineau 1982). Then for each transect, vegetation and soil data were correlated in indirect canonical analysis (Lagonegro and Feoli 1985) using CANCOR (Orlói and Kenkel 1985). The Spearman rank correlation coefficient (Siegel 1980) and Pearson correlation coefficient (Snedecor and Cochran 1979) were also calculated.

Results

The three plant communities that we already mentioned appear in all transects (see Appendix 1), and always there is *Phyla canescens*, *Stipa hyalina* and *Paspalum vaginatum* in the Flechillar, *Paspalum vaginatum* in the Halophilous prairie and *Spartina densiflora* in the Espartillar. Different variants of the Halophilous prairie occur in the different transects and differences exist in companion species of *Spartina densiflora* in the espartillares. The transects were analysed separately. Canonical correlations are shown in Figure 1 (a, b and c). The principal component values of species and soil variables for calculating canonical variables are in Appendix 2.

The Flechillar is highly correlated with organic matter (0.87), clay (0.73), exchangeable Mg (0.76) and total exchangeable bases (0.69) on transect 1 (Fig. 1a); with silt, fine sand, and to a lesser degree, CO₃, total and exchangeable Ca, total exchangeable bases and clay on transect 2 (Fig. 1b); and with exchangeable Mg (0.92), total Ca (0.90), total exchangeable bases (0.85), total Mg (0.83), exchangeable Ca (0.79), P₂O₅ (0.68), clay (0.63), organic matter (0.55), medium sand (0.76) and silt (0.62) on transect 3 (Fig. 1c). On transect 1 (Fig. 1a) the Halophilous prairie is associated with pH, both water extraction and paste (−0.80), HCO₃ (−0.82), CO₃ (−0.68), Na percentage (−0.77), and elevation (−0.86); and the

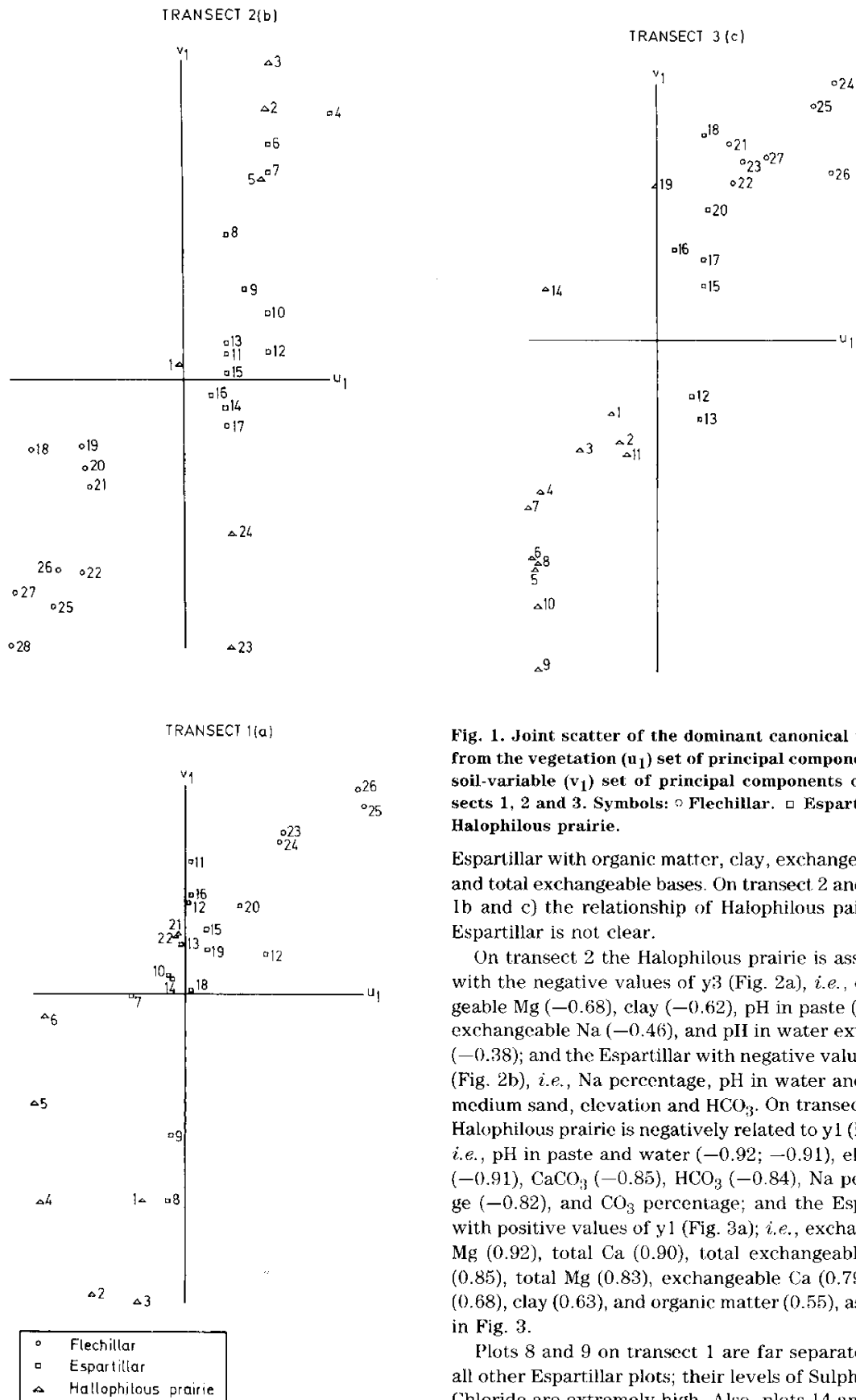


Fig. 1. Joint scatter of the dominant canonical variates from the vegetation (u_1) set of principal components and soil-variable (v_1) set of principal components on Transects 1, 2 and 3. Symbols: \circ Flechillar, \square Espartillar, \triangle Halophilous prairie.

Espartillar with organic matter, clay, exchangeable Mg and total exchangeable bases. On transect 2 and 3 (Fig. 1b and c) the relationship of Halophilous prairie and Espartillar is not clear.

On transect 2 the Halophilous prairie is associated with the negative values of y_3 (Fig. 2a), *i.e.*, exchangeable Mg (-0.68), clay (-0.62), pH in paste (-0.48), exchangeable Na (-0.46), and pH in water extraction (-0.38); and the Espartillar with negative values of y_2 (Fig. 2b), *i.e.*, Na percentage, pH in water and paste, medium sand, elevation and HCO_3 . On transect 3, the Halophilous prairie is negatively related to y_1 (Fig. 3a), *i.e.*, pH in paste and water (-0.92 ; -0.91), elevation (-0.91), CaCO_3 (-0.85), HCO_3 (-0.84), Na percentage (-0.82), and CO_3 percentage; and the Espartillar with positive values of y_1 (Fig. 3a); *i.e.*, exchangeable Mg (0.92), total Ca (0.90), total exchangeable bases (0.85), total Mg (0.83), exchangeable Ca (0.79), P_2O_5 (0.68), clay (0.63), and organic matter (0.55), as shown in Fig. 3.

Plots 8 and 9 on transect 1 are far separated from all other Espartillar plots; their levels of Sulphate and Chloride are extremely high. Also, plots 14 and 19 on

TRANSECT 2

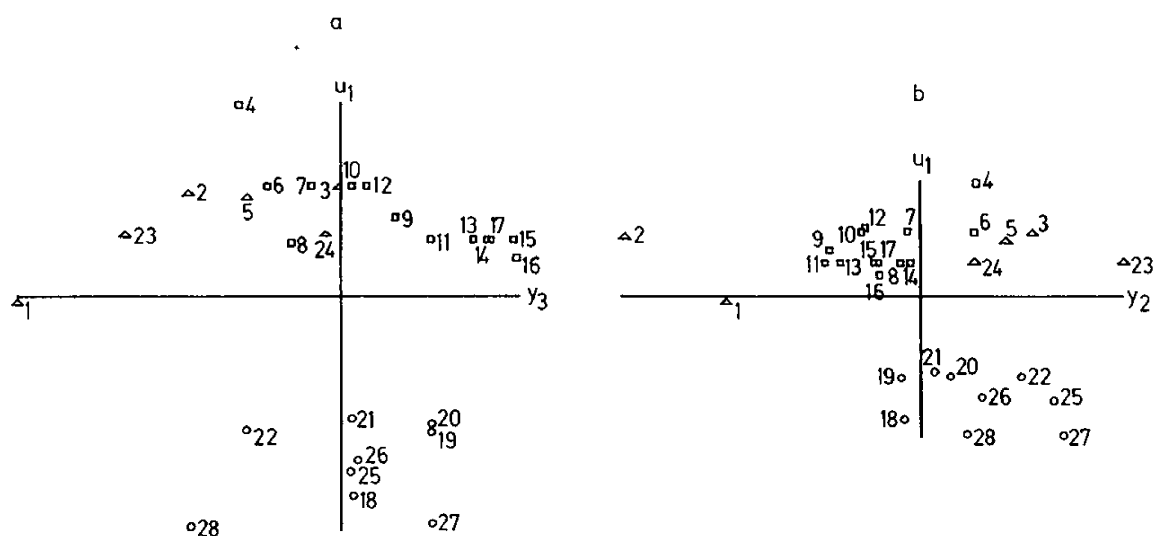


Fig. 2. Joint scatter of the dominant canonical variate from the vegetation (u_1) set of principal components and the 2nd and 3rd soil-variable principal components on Transect 2. Symbols: \circ Flechillar. \square Espartillar. Δ Halophilous prairie.

transect 3 are anomalous, although both are Halophilous prairies, the former has *Stipa hyalina* and *Phyla canescens* which are Flechillar species and the latter has *Salicornia ambigua* and *Rumex pulcher* which are common in the Espartillar.

Table 1 shows a matrix of high correlation coincidences for species, common to the three transects, and soil variables. There is a higher number of coincidences in high correlations between species of transects 1 and 3 and soil variables than between species of transect 2 and the same soil variables. Also, there is an evident

similarity between the communities physiognomy of transects 1 and 3, except for the Flechillar, as it shown by their Euclidean distances (Table 2).

The Spearman rank correlation coefficients between characteristic and common species for all communities and edaphic variables are alike for all transects. These species are always correlated with less than 50% of soil variables ($p > 0.95$) (Table 3). There are no correlations between rare species and edaphic variables on either transects in terms of the Pearson correlation coefficient.

Discussion

If the results from the three transects are compared, it can be seen that there are some differences in canonical correlations between vegetation and soil variables due to local differences in both types of variables. However, in spite of these local differences, the results are consistent among themselves.

The Flechillar of the three transects has *Stipa hyalina* and *Phyla canescens* like any other stand of the same community within the region, but while in transects 1 and 2 *Phyla canescens* is dominant, accompanied by *Stipa hyalina* and *Paspalum vaginatum*, in the third transect, the dominant is *Stipa hyalina* accompanied by *Phyla canescens* and *Paspalum vaginatum*; *Paspalum dilatatum* is an important species as well. Also, in all cases, this community is significantly correlated with soil texture, i.e., the proportion of clay, silt and fine sand, as well as with exchangeable ions, Mg and Ca, CO_3 , and P_2O_5 .

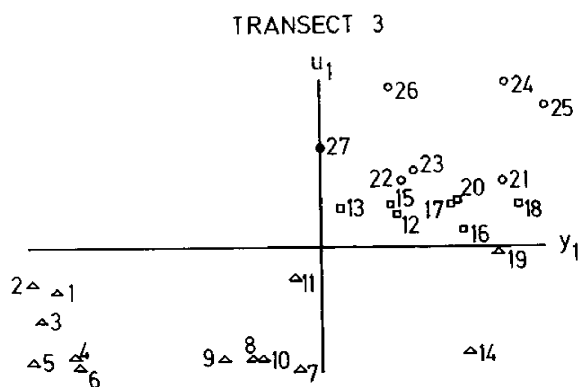


Fig. 3. Joint scatter of the dominant canonical variate from the vegetation (u_1) set of principal components and the 1st soil-variable principal component on Transect 3. Symbols: \circ Flechillar. \square Espartillar. Δ Halophilous prairie.

Table 1. Matrix of correlation coincidences for species common to the three transects and soil variables.

	10H	2CY	3FS	4CS	5CSd	6FSd	7CO ₃	8B	9SP	10TS	11Co	12PHw	13PHp	14CL	15SO ₄	16CO ₃	17HCO ₃	18TCa	19TMg	20TNa	21TK	22ECa	23EMg	24ENa	25EK	26TEB	27P ₂ O ₅	28NaP	29EL
1 DISP	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
2 PAVA	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
3 HOEU	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
4 CHCH	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
5 HYAN	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
6 PLMY	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
7 PEPA	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
8 SPRA	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
9 LEPI	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
10 LOMU	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
11 SCAM	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
12 COBO	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
13 APSE	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
14 RACY	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
15 PILO	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
16 SAAM	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
17 ASSO	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
18 SPDE	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
19 HECU	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
20 CRTR	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
21 SEPO	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
22 PHCA	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
23 SHYH	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
24 POLY	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
25 SEGE	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
26 BRUN	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
27 APLE	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
28 POBR	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
29 LIBR	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
30 ELTR	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
31 RUCR	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
32 AHVI	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
33 CYDA	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
34 HYMI	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△
35 MOGI	△	○	○	■	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△	△

○ Transect 1 (121 correlations); △ transect 2 (87 correlations); □ transect 3 (146 correlations); ◻ transects 1 and 2 (43 coincidences); ◻ transects 1 and 3 (83 coincidences); ◻ transects 2 and 3 (47 coincidences); ■ transects 1, 2 and 3 (83 coincidences).

1 - Organic matter OM; 2 - Clay Cy; 3 - Silt (20 u) F St; 4 - Silt (50 u) C St; 5 Coarse and CSd; 6 - Fine sand FSd; 7 - Calcium Carbonate Ca CO₃; 8 - Moisture equivalent ME; 9 - Saturation percentage SP; 10 - Total salts TS; 11 - Conductivity Co; 12 - Water extract Pilw; 13 - Soil paste Pilp; 14 - Chloride Cl; 15 - Sulfate SO₄; 16 - Carbonate CO₃; 17 - Bicarbonate HCO₃; 18 - Total calcium TCa; 19 - Total magnesium TMg; 20 - Total sodium TNa; 21 - Total potassium TK; 22 - Exchangeable calcium ECa; 23 - Exchangeable magnesium EMg; 24 - Exchangeable sodium ENa; 25 - Exchangeable potassium EK; 26 - Total exchangeable bases TEB; 27 - Phosphate P₂O₅; 28 - Sodium percentage NaP; 29 - Elevation.

Table 2. Euclidean distances.

Halophilous prairie of transect 1 and transect 2=378.21
Halophilous prairie of transect 1 and transect 3=304.56
Halophilous prairie of transect 2 and transect 3=351.60
Espartillar of transect 1 and transect 2=495.84
Espartillar of transect 1 and transect 3=178.66
Espartillar of transect 2 and transect 3=431.78
Flechillar of transect 1 and transect 2= 332.57
Flechillar of transect 1 and transect 3=1745.25
Flechillar of transect 2 and transect 3=2433.43

Table 3. Species common to the three transects and their correlation (expressed as percentages) with physical factors.

CODE	SPECIES	PERCENTAGES		
		T1	T2	T3
DISP	<i>Distichlis spicata</i>	44.83	48.27	41.38
SPDE	<i>Spartina densiflora</i>	24.14	58.62	24.14
STHY	<i>Stipa hyalina</i>	27.59	27.59	37.93
SEGE	<i>Setaria geniculata</i>	48.27	17.24	20.69
RUCR	<i>Rumex crispus</i>	31.03	13.79	17.24
(characterics species)				
PAVA	<i>Paspalum vaginatum</i>	20.69	31.45	65.51
HOEU	<i>Hordeum euclaston</i>	6.90	6.90	10.34
CHCH	<i>Chaetotropis chilensis</i>	44.83	6.90	51.72
HYAN	<i>Hymenoxis anthemoides</i>	0	6.90	17.24
PLMY	<i>Plantago myosurus</i>	17.24	0	20.69
PEPA	<i>Petunia parviflora</i>	13.79	13.79	10.34
SPRA	<i>Spergularia ramosa</i>	10.34	13.79	68.96
LEPI	<i>Lepidium sp.</i>	72.41	13.79	24.14
LOMU	<i>Lolium multiflorum</i>	3.45	20.69	34.48
SCAM	<i>Scirpus americanus</i>	62.07	75.86	55.17
COBO	<i>Coniza bonariensis</i>	10.34	24.14	13.79
APSE	<i>Apium sellowianum</i>	62.07	41.38	51.72
RACY	<i>Ranunculus cymbalaria</i>	72.41	65.52	62.07
PILO	<i>Picrosia longifolia</i>	51.72	10.34	37.93
SAAM	<i>Salicornia ambigua</i>	48.27	44.83	48.27
ASSQ	<i>Aster squamatus</i>	31.03	0	27.59
HECU	<i>Heliotropium curassavicum</i>	0	44.83	34.48
CRTR	<i>Cressa truxilensis</i>	24.14	82.76	37.93
SEPO	<i>Sesuvium portulacastrum</i>	10.34	13.79	31.03
PHCA	<i>Phyla canescens</i>	48.27	41.38	44.83
POLY	<i>Polygonum sp.</i>	58.62	20.69	37.93
BRUN	<i>Bromus unioides</i>	27.59	20.69	27.59
APLE	<i>Apium leptophyllum</i>	34.48	13.79	20.69
POBR	<i>Polygonum brasiliense</i>	55.17	37.93	37.93
LIBR	<i>Limonium brasiliense</i>	27.59	13.79	86.21
ELTR	<i>Eleusine tristachya</i>	58.62	13.79	31.03
AMVI	<i>Ammi viznaga</i>	55.17	31.03	41.38
CYDA	<i>Cynodon dactylon</i>	17.24	34.48	27.59
HIMI	<i>Hipchoeris microcephala</i>	10.34	10.34	34.48
MOGI	<i>Modiolastrum gillesii</i>	48.27	48.27	65.52

The Halophilous prairie is correlated with elevation, HCO₃, pH (paste), and percentage Na and CO₃ in transects 1 and 3, while in transect 2, it is significantly correlated only with pH among the mentioned variables. In all cases *Paspalum vaginatum* is the dominant or co-dominant species of the community, but in transect 1 and 3 *Distichlis spicata* is abundant as well as *Phyla canescens* in the latter, while in transect 2 *Ranunculus cymbalaria* is important. These suggest that the Halophilous prairie is more humid on transect 2 than on the other transects (Cabrera 1967).

The Espartillar is not correlated with any of the soil variables. Both, in transect 1 and 3, it is correlated with the same variables as the Flechillar, while in transect 2 it is correlated with the same variables as the Halophilous prairie. The Espartillar is always in the lowest

segment of the elevation gradient (Carnevale *et al.* 1987), and therefore, it is periodically flooded. In transect 2, as it was pointed out above, the Halophilous prairie could be more humid than in the other transects. Flooding or periodical water excess may explain the behaviour of the Espartillar in relation to soil variables in any transect and the Halophilous prairie in transect 2. However, soil moisture and water table fluctuations were not measured, only inferred from water accumulation above the soil surface.

There seems to be good agreement between the soil variables and vegetation distribution. Transplantation experiments show that some of the species, with closely related ones in the New England shore marshes, grow better in environments different from where they naturally occur. This fact is linked to interspecific competition (Bertness and Ellison 1987). Nevertheless, although correlations do not imply causality, in two out of the three transects coincidences between species and soil factors were more similar where the same factors were correlated to the same species. So, it can be concluded that physical factors determine species distribution at least in the extreme segments of their gradients but where there is flooding, all other measured edaphic factors become less important. Under these conditions, *Spartina* becomes dominant. However, in transitional environments, certain species of very different growth form are excluded. Interestingly, the Feoli and Orlóci (1987) species dispersion profiles segregate response to soil factors from response to other variables (Carnevale *et al.* 1987). There is some inferential evidence that these "other" variables may be interactions among species.

According to interpretation of the Pearson correlation coefficient, rare species are not correlated with the measured soil variables. Although halophytes generally have a high plasticity level (Jefferies and Pitman 1986), rare species seem to be even more plastic. A high plasticity level constrains specialization within communities and may be inversely correlated with competitive ability (Pickett and Bazzaz 1978). The plastic species, the generalists, contrast with the characteristic species, the specialists, confined to competitive refugia which make them rare within the communities.

However, species like *Paspalum vaginatum* has low correlations with physical factors in transects 1 and 2 and a high correlation in transect 3, and although it is a characteristic of Halophilous prairies, it appears in other communities as well. This independent distribution may be correlated with varying local plasticity. It should be investigated if there are different genotypes of this species along the environmental gradient.

As a final remark it can be said that although species distribution is determined by physical factors in certain segments of their gradients, in other segments, other factors such as species interactions and species

plasticity or genetic variation may be important.

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Appendix 1.

Species composition of communities by transect.

Halophilous prairie				Espartillar			
	T1	T2	T3		T1	T2	T3
<i>Paspalum vaginatum</i>	65.62	79.17	70.19	<i>Spartina densiflora</i>	48.57	68.27	51.78
<i>Phyla canescens</i>	9.37	5.83	2.88	<i>Phyla canescens</i>	6.78		2.51
<i>Distichlis spicata</i>	9.07	4.58	17.89	<i>Salicornia ambigua</i>	5.92	3.29	2.54
<i>Apium sellowianum</i>	6.27	0.03	2.91	<i>Coniza bonariensis</i>	3.78	0.04	0.01
<i>Cynodon dactylon</i>	4.37			<i>Paspalum vaginatum</i>	1.97	7.12	3.23
<i>Plantago myosurus</i>	3.16	1.72	1.21	<i>Limonium brasiliense</i>	1.81	0.01	0.01
<i>Chaetotropis chilensis</i>	2.51	0.03	5.60	<i>Plantago myosurus</i>	1.48	0.04	0.01
<i>Picrosia longifolia</i>	2.21	0.02	0.79	<i>Hymenoxis anthemoides</i>	1.12	0.42	0.75
<i>Stipa hyalina</i>	1.25		0.38	<i>Verbena gracilenscens</i>	1.11		1.46
<i>Salicornia ambigua</i>	0.70	0.85	1.18	<i>Distichlis spicata</i>	1.08	0.38	2.50
<i>Carex sororia</i>	0.64			<i>Apium sellowianum</i>	0.78	0.41	
<i>Coniza bonariensis</i>	0.62		0.01	<i>Heliotropium curassavicum</i>	0.77	0.03	3.26
<i>Apium leptophyllum</i>	0.62	0.02		<i>Rumex pulcher</i>	0.74		10.71
<i>Hordeum euclaston</i>	0.07		0.39	<i>Cressa truxilensis</i>	0.71	0.01	0.04
<i>Hipochaeris microcephala</i>	0.07	0.05		<i>Aster squamatus</i>	0.41	0.03	0.01
<i>Spergularia ramosa</i>	0.06		0.01	<i>Sporobolus pyramidatus</i>	0.36	0.01	
<i>Hymenoxis anthemoides</i>	0.05	0.02	0.01	<i>Teucrium cubescens</i>	0.36		
<i>Lolium multiflorum</i>	0.05	0.02	0.02	<i>Stipa philippii</i>	0.36		
<i>Heliotropium curassavicum</i>	0.04	0.02	0.01	<i>Chaetotropis chilensis</i>	0.07	0.02	
<i>Rumex crispus</i>	0.02	0.02		<i>Sesuvium portulacastrum</i>	0.03	0.02	0.03
<i>Sesuvium portulacastrum</i>	0.02	0.03		<i>Picrosia longifolia</i>	0.03	0.44	0.03
<i>Ranunculus cymbalaria</i>	0.02	9.18	8.28	<i>Melilotus sp.</i>	0.03		
<i>Cirsium vulgare</i>	0.02			<i>Petunia parviflora</i>	0.03	1.19	2.86
<i>Aster squamatus</i>	0.02	0.02	0.01	<i>Senecio pinnatus</i>	0.03		
<i>Limonium brasiliense</i>	0.02			<i>Hordeum euclaston</i>	0.02	0.01	
<i>Sporobolus pyramidatus</i>	0.01	0.83		<i>Hipochaeris microcephala</i>	0.02	0.01	
<i>Spergularia platensis</i>	0.01			<i>Rumex crispus</i>	0.02		
<i>Scirpus americanus</i>	0.01	0.85	2.88	<i>Lepidium sp.</i>	0.02	0.01	0.06
<i>Trifolium repens</i>	0.01			<i>Cirsium vulgare</i>	0.01		0.01
<i>Melilotus sp.</i>	0.01		0.01	<i>Samolus valerandii</i>	0.01		
<i>Spartina densiflora</i>	0.01			<i>Carex sororia</i>	0.01		
<i>Petunia parviflora</i>	0.01		0.01	<i>Melica macra</i>	0.01		
<i>Juncus balticus</i>	0.01			<i>Sida rhombifolia</i>	0.01		
<i>Cyperus reflexus</i>	0.01			<i>Polypogon monspeliensis</i>	0.01		0.03
<i>Cyperus cayenensis</i>	0.01			<i>Medicago sp.</i>	0.01		
<i>Bromus unioloides</i>	0.01	0.02		<i>Spergularia ramosa</i>	0.01		
<i>Anthemis cotula</i>	0.01			<i>Lolium multiflorum</i>	0.01		
<i>Gratiola peruviana</i>		0.85		<i>Chenopodium almu</i>	0.01		
<i>Small rose</i>		0.85		<i>Salpichroa sp.</i>	0.01		
<i>Triglochin striata</i>		0.83	1.93	<i>Melilotus officinalis</i>	0.01		
<i>Dichondra microcalyx</i>		0.83		<i>Deyeuxia viridiflavescens</i>	0.01		
<i>Sonchus asper</i>		0.02		<i>Solanum sp.</i>	0.01		
<i>Medicago lupulina</i>		0.02		<i>Dichondra microcalyx</i>	0.01		
<i>Ammi viznaga</i>		0.02		<i>Stipa papposa</i>	0.01		
<i>Matricaria chamomila</i>		0.02		<i>Euphorbia serpens</i>		1.75	0.06
<i>Solidago chilensis</i>		0.02		<i>Ranunculus cymbalaria</i>		0.01	
<i>Spartina argentinensis</i>			5.19	<i>Polygonum brasiliense</i>		0.01	0.01
<i>Cyperus laevigatus</i>			2.88	<i>Anthemis cotula</i>		0.01	
<i>Rumex pulcher</i>			0.40	<i>Spartina argentinensis</i>			0.01
<i>Lepidium sp.</i>			0.40	<i>Senecio grisebachii</i>			0.01
<i>Polypogon monspeliensis</i>			0.01	<i>Stipa hyalina</i>			0.01
<i>Chenopodium macrospermum</i>			0.01	<i>Setaria geniculata</i>			0.01
<i>Cressa truxilensis</i>			0.01	<i>Bromus unioloides</i>			0.01
<i>Verbena gracilenscens</i>			0.01	<i>Apium leptophyllum</i>			0.01
<i>Juncus sp.</i>			0.01	<i>Trifolium sp.</i>			0.01
<i>Polygonum sp.</i>			0.01	<i>Nicotiana longifolia</i>			0.01
<i>Setaria geniculata</i>			0.01				

Flechillar

	T1	T2	T3
Phyla canescens	43.75	40.28	38.21
Stipa hyalina	28.75	14.45	43.57
Paspalum vaginatum	10.00	8.33	10.37
Cynodon dactylon	4.37	6.11	5.01
Plantago myosurus	2.50	0.08	0.04
Hipchoeris microcephala	1.32	0.05	0.03
Apium leptophyllum	1.32	0.07	0.04
Bromus unioloides	1.32	1.98	0.04
Aster squamatus	1.30	0.07	
Carex sororia	1.30		5.01
Anthemis cotula	1.27	0.58	
Spergularia villosa	1.27	0.01	
Spergularia ramosa	1.25	0.60	
Dichondra microcalyx	1.25	2.50	
Trifolium sp.	1.25		0.03
Lolium multiflorum	0.07	0.59	2.20
Limonium brasiliense	0.07	0.59	
Juncus balticus	0.05		0.03
Setaria geniculata	0.05	0.59	0.74
Modiolastrum gillesii	0.05	0.02	0.71
Hordeum euclaston	0.02	5.87	0.73
Rumex crispus	0.02	0.03	0.08
Coniza bonariensis	0.02		0.77
Sida rhombifolia	0.02		
Eleusine tristachya	0.02	1.97	0.04
Polygonum sp.	0.02	0.03	0.01
Sonchus oleraceus	0.02	0.01	
Sonchus asper	0.02		
Medicago hispida	0.02		
Polygonum brasiliense	0.02	0.01	0.01
Ammi viznaga	0.02	0.01	0.03
Sporobolus pyramidatus		7.24	
Distichlis spicata		0.57	0.74
Chaetotropis chilensis		0.57	
Hymenoxis anthemoides		0.07	0.01
Lepidium sp.		0.04	
Petunia parviflora		0.03	
Salicornia ambigua		0.02	0.01
Euphorbia serpens		0.02	0.03
Sporobolus indicus		0.02	
Small rose		0.02	
Trifolium repens		0.02	
Sesuvium portulacastrum		0.01	0.01
Apium sellowianum		0.01	0.01
Heliotropium curassavicum		0.01	
Triglochin striata		0.01	
Picrosia longifolia		0.01	0.01
Spartina densiflora		0.01	
Solidago chilensis		0.01	
Senecio pinnatus		0.01	
Brassica hirschfeldia		0.01	
Carduus acanthoides		0.01	0.03
Undetermined vegetative		0.01	
Anoda cristata		0.01	
Paspalum dilatatum			37.86
Alternanthera philoxeroides			2.50
Stipa brachichaeta			2.50
Sida leprosa			2.14

Hirschfeldia sp.	1.43
Ambrosia tenuifolia	0.71
Cressa truxilensis	0.07
Verbena gracilescens	0.04
Carex bonariensis	0.04
Teucrium cubescens	0.01
Anthemis sp.	0.01
Physalis viscosa	0.01
Medicago lupulia	0.01
Melilotus officinalis	0.01

Appendix 2. Canonical function and components by transect and variables.

Transect 1. The following equations represent the first pair of canonical variables:

$$u_1 = -0.41 x_1 + 0.91 x_2$$

$$v_1 = 0.99 y_1 + 0.10 y_2$$

$$r = 0.71$$

Variables x_1 , x_2 and y_1 , y_2 below are principal components for species and soil factors respectively:

$$x_1 = \dots - 28.78 \text{ Paspalum vaginatum} + \dots + 23.57 \text{ Spartina densiflora} + \dots$$

$$x_2 = \dots - 10.41 \text{ Paspalum vaginatum} - 10.37 \text{ Spartina densiflora} + \dots + 16.32 \text{ Phyla canescens} + 9.62 \text{ Stipa hyalina} + \dots$$

$$y_1 = \dots - 0.86 \text{ elevation} - 0.82 \text{ bicarbonate} - 0.80 \text{ pH (water extract)} - 0.80 \text{ pH (soil paste)} - 0.77 \text{ sodium percentage} - 0.68 \text{ carbonate} + \dots + 0.87 \text{ organic matter} + 0.75 \text{ exchangeable magnesium} + 0.73 \text{ clay} + 0.69 \text{ total exchangeable bases} + \dots$$

$$y_2 = \dots - 0.90 \text{ chloride} - 0.89 \text{ sulfate} - 0.89 \text{ conductivity} - 0.88 \text{ total salts} - 0.88 \text{ total sodium} - 0.87 \text{ total magnesium} - 0.84 \text{ total potassium} - 0.79 \text{ exchangeable calcium} - 0.76 \text{ total calcium} + \dots + 0.66 \text{ carbonate} + 0.50 \text{ coarse sand} + 0.50 \text{ sodium percentage} + \dots$$

Transect 2. The following equations represent the first pair of canonical variables:

$$u_1 = 0.40 x_1 - 0.91 x_2$$

$$v_1 = -0.91 y_1 - 0.41 y_2 - 0.09 y_3$$

$$r = 0.75$$

Variables x_1 , x_2 and y_1 , y_2 , y_3 below are principal components for species and soil factors:

$$x_1 = \dots - 22.93 \text{ Paspalum vaginatum} - 9.19 \text{ Phyla canescens} + \dots + 34.27 \text{ Spartina densiflora} + \dots$$

$$x_2 = \dots - 22.53 \text{ Paspalum vaginatum} - 10.45 \text{ Spartina densiflora} + \dots + 14.94 \text{ Phyla canescens} + 8.30 \text{ Stipa hyalina} + \dots$$

$$y_1 = \dots - 0.94 \text{ sulfate} - 0.94 \text{ sodium} - 0.93 \text{ conductivity} - 0.92 \text{ total magnesium} - 0.91 \text{ total salts} - 0.88 \text{ saturation percentage} - 0.87 \text{ moisture equivalent} - 0.86 \text{ calcium carbonate} - 0.85 \text{ potassium} - 0.85 \text{ chloride} + \dots + 0.59 \text{ silt (50 u)} + 0.54 \text{ fine sand}$$

+ ...

$y_2 = \dots - 0.88$ sodium percentage -0.83 pH (water extract) -0.69 pH (soil paste) -0.67 coarse sand -0.65 elevation -0.56 bicarbonate + ... $+0.83$ carbonate $+0.71$ exchangeable calcium $+0.70$ total calcium $+0.65$ total exchangeable bases $+0.64$ clay + ...

$y_3 = \dots - 0.49$ total calcium -0.40 elevation + ... $+0.68$ exchangeable magnesium $+0.62$ clay $+0.48$ pH (soil paste) $+0.46$ exchangeable sodium $+0.38$ pH (water extract) + ...

Transect 3. The following equations represent the first pair of canonical variables:

$$u_1 = -0.98 x_1 - 0.17 x_2 \quad r = 0.87$$

$$v_1 = -0.76 y_1 + 0.65 y_2$$

Variables x_1 , x_2 and y_1 , y_2 below are principal components

for species and soil factors:

$x_1 = \dots - 12.51$ *Stipa hyalina* -12.50 *Paspalum dilatatum* -11.25 *Phyla canescens* -9.33 *Spartina densiflora* + ... $+34.92$ *Paspalum vaginatum* + ...

$x_2 = \dots - 15.40$ *Stipa hyalina* -12.33 *Paspalum dilatatum* -12.17 *Phyla canescens* -8.09 *Paspalum vaginatum* + ... $+20.35$ *Spartina densiflora* + ...

$y_1 = \dots - 0.92$ pH (soil paste) -0.91 pH (water extract) -0.91 elevation -0.85 calcium carbonate -0.84 bicarbonate -0.82 sodium percentage -0.74 carbonate + ... $+0.92$ exchangeable magnesium $+0.90$ total calcium $+0.85$ total exchangeable bases $+0.83$ total magnesium $+0.79$ exchangeable calcium $+0.68$ phosphate $+0.63$ clay $+0.55$ organic matter + ...

$y_2 = \dots - 0.93$ moisture equivalent -0.92 chloride -0.88 saturation percentage -0.87 total potassium -0.86 total salts -0.85 conductivity -0.78 sulfate + ... $+0.76$ coarse sand $+0.62$ silt (50 μ) + ...