

HALOPHILOUS COMMUNITIES AND SPECIES DISTRIBUTIONS ALONG ENVIRONMENTAL GRADIENTS IN SOUTHEASTERN SANTA FE PROVINCE, ARGENTINA*

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Abstract: Vegetation and soil samples were taken over a transect in the Saladillo River valley of southeastern Santa Fe. The set of data was analyzed using principal components analysis and the method of dynamic clouds. The ordination of samples on species was similar to that on soil variables. The samples were grouped in three communities: 'flechillar', 'espartillar', and halophilous prairie. The first and third ones of these were in turn divided into two variants each. Most soils factors as well as community distributions are correlated with elevation. Species have independent distributions along the transect. Dispersion profiles were constructed of twelve species over intervals of the best correlated and contrasting soil variables. In several cases these profiles segregate a response of the species to soil factors from another response that may be owing to the interactions of the species themselves.

Introduction

The three groups of plant communities which characterize southeastern Santa Fe are the *Stipa* grasslands, the halophilous grasslands and rushes, and the hygrophilous communities. The *Stipa* grasslands are on the best lands for agriculture, so most of their stands have disappeared altogether. The other groups are very difficult to analyse and characterize as they have a truly Gleasonian character (Gleason, 1926) and are around temporary ponds or small lakes which appear and disappear according to the amount of rainfall of a particular season (Lewis *et al.*, 1985).

The halophilous communities are well preserved and they thrive on extensive depressed land where the small rivers of the region are born, or in their valleys. The most important ones are the *Spartina argentinensis* and *Spartina densiflora* tall grasslands; prairies of *Distichlis spicata*; short rushes of *Scirpus americanus*, and peladales of very low general coverage where *Sporobolus pyramidatus* is usually the dominant species (Ragonese and Covas, 1947; Lewis *et al.*, loc. cit.).

In a previous paper Collantes and Lewis (1980) ordered the *Stipa* spp. grasslands ('flechillares') and halophilous communities of the Rosario district in the Province of Santa Fe in a coenocline associated with topography.

The river valley has a natural levee next to the river bed, then a shallow depression, and then an extended plain up to their boundary where there is a smooth, but

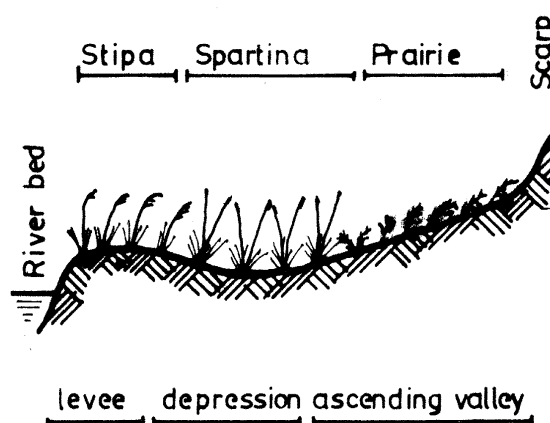


Fig. 1. Idealized profile of the Saladillo River valley. The main plant communities are shown.

noticeable scarp. Above the scarp, if it is not used by agriculture, there are different types of 'flechillares' and in the valley there are halophilous communities up to the levee where usually *Stipa hyalina* prairies appear (Fig. 1).

In this paper the results of a direct gradient analysis (Whittaker, 1978) are presented, where we try to verify if the halophilous communities are distributed along edaphic gradients associated with topography, and if this is so, which soil factors are correlated with species distributions.

Study area

The general characteristics of the region and its climate has been described elsewhere (Lewis *et al.*, 1985). The

* Taxonomic nomenclature follows Cabrera (1963, 1965a, b, 1967, 1968, 1970).

study area is located in the Saladillo River valley, about 10 km south of Sandford and Chabás in the Caseros district of the Province.

Next to the river there is a *Stipa hyalina* prairie, then a *Spartina densiflora* tall grassland, and farthest from the river, different types of halophilous prairies and meadows. Approximately on the limit of the river valley, beyond a fence, the land is or has been recently under cultivation. The entire area is grazed, alternating with periods when it is left fallow. The area has been periodically burnt, but it has never been cultivated.

Sampling

Every 25 m on a 650 m transect perpendicular to the river bed the relative topographic height was measured with an optical level. A 4 m² quadrat was laid at each of these points and in December 1983 all species were recorded and their cover/abundance was estimated using Braun-Blanquet's (1979) combined scale. A sample of the upper layer of the soil was taken from each quadrat and then they were sent to the Soil Laboratory of the Ministry of Agriculture of the Province where granulometric analyses were made, and pH, conductivity, total exchange capacity, total salt content, Cl⁻, SO₄⁼, CO₃⁼, HCO₃⁻, PO₄⁼, Na⁺, K⁺, Ca⁺⁺, Mg⁺⁺ and organic matter were determined. In some samples some values had to be estimated using stepwise and multiple regression (Kempthorne, 1952).

About 15 km further upstream two additional transects were laid, and data were collected in the same way. As the results of these transects were very similar to the first one, only short references will be made to them.

Data analysis

A 27 sample by 65 species matrix contains the vegetation data. The cover/abundance values were transformed into cover percentages using Braun-Blanquet's (1979) transformation scale. Samples were ordered through principal

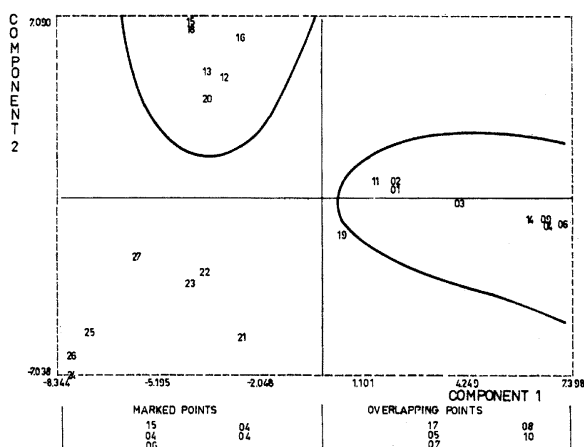


Fig. 2. Ordination of samples according to species (PCA). Axes are components. Numbers inside identify samples.

components analysis (PCA, Hotelling, 1933 a, b) using a covariance matrix of centered data (Pielou, 1984), and no data standardization was needed. Then they were classified using the method of dynamic clouds (Lebart *et al.*, 1977). Also a 27 sample by 29 variables matrix (soil characteristics and elevation) was analysed. The soil samples were also ordered by PCA using a correlation matrix obtained from standardized centered data. In both cases SPAD computing programs were used (Lebart & Morineau, 1982). The two sample ordinations were compared and a graph of species coverage over the transect was drawn.

For detecting underlying factors and to isolate the trended components of variation from random component, analysis of concentration was performed (Feoli and Orlóci, 1979, 1985, Orlóci 1981). Dispersion profiles were constructed of twelve species, including *Paspalum vaginatum*, *Distichlis spicata*, *Ranunculus cymbalaria*, *Chaetotrops chilensis*, *Apium sellowianum*, *Spartina densiflora*, *Rumex pulcher*, *Stipa hyalina*, *Paspalum distichum*, *Phyla canescens*, *Cynodon dactylon* and *Carex sororia* over intervals of the best correlated and contrasting soil variables. In both cases the Orlóci and Kenkel (1985) programs were used.

Results

When the species by samples matrix is ordered by PCA the first two axes account for most of the variation (47.4% and 27.1%). In Figure 2 the order of the samples according to the two axes is given. Axis 1 segregates two groups: on the positive side, the samples of the halophilous prairies, and on the negative side all the others. The latter ones are divided by axis 2 into two further groups, 'flechillar' (*Stipa hyalina* prairie) below and 'espartillar' (*Spartina densiflora* tall grassland) above, leaving the halophilous prairies between the two.

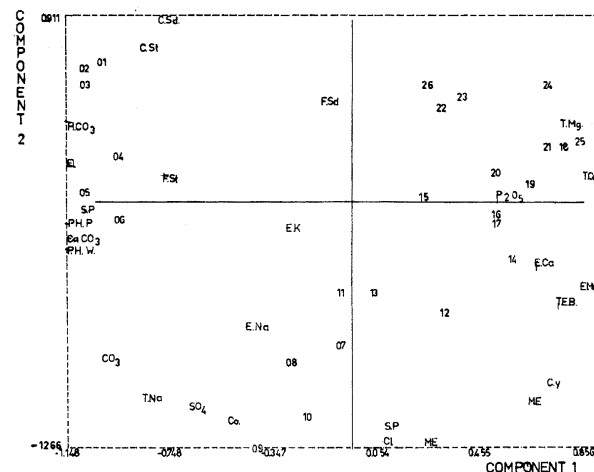


Fig. 3. Ordination of samples according to soil variables (PCA), and soil variables according to samples. Axes are components. Numbers inside identify samples and symbols soil variables.

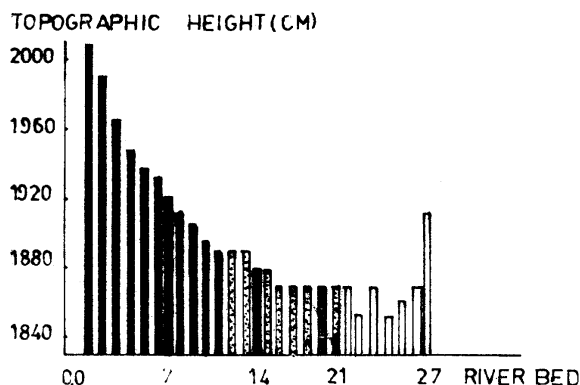


Fig. 4. Elevation gradient along the transect. Black, halophilous prairie; dotted, 'espartillar'; empty, 'flechillar'; hatched, sample 19.

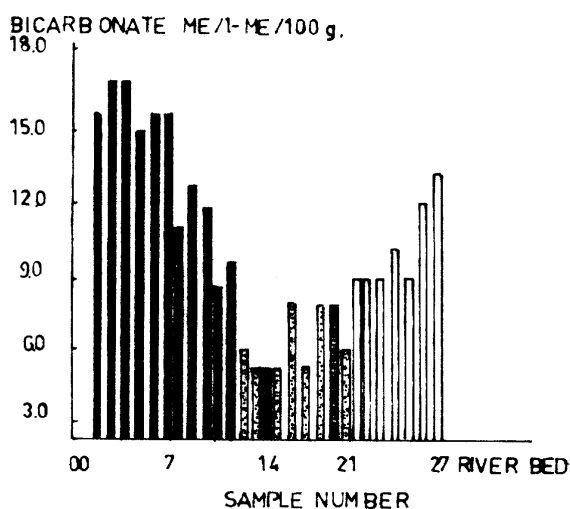


Fig. 6. Bicarbonate gradient along the transect. Symbols as in Figure 4.

The most abundant species of the halophilous prairies are *Paspalum vaginatum* and *Distichlis spicata*, accompanied by *Ranunculus cymbalaria*, *Chaetotropis chilensis* and *Apium sellowianum*. *Stipa hyalina*, *Paspalum dilatatum* and *Phyla canescens* are the most abundant species of the 'flechillar', but also *Paspalum vaginatum* and *Cynodon dactylon* are present, though less abundant. *Spartina densiflora* is the dominant of the 'espartillar' where *Rumex pulcher*, *Heliotropium curassavicum* and *Petunia parviflora* are present as well, though far less abundant. The species lists for each community are given in Appendix 1. Sample 19 is not included. It is transitional between the 'espartillar' and 'flechillar'.

If samples are classified in three clusters, they are identical to the above mentioned communities. If the fourth cluster is obtained, the halophilous prairie is divided into a variant where *Paspalum vaginatum* is the dominant and *Ranunculus cymbalaria* and *Distichlis spicata* are present, although their abundance is lower, and a variant with *Paspalum vaginatum* and *Distichlis spicata* where *Spartina*

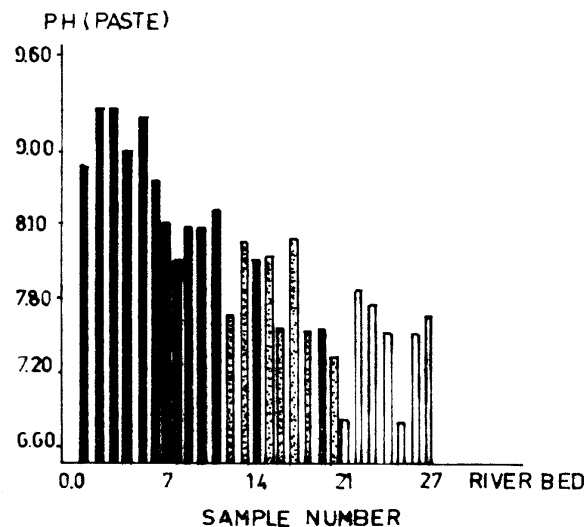


Fig. 5. pH (soil paste) gradient along the transect. Symbols as in Figure 4.

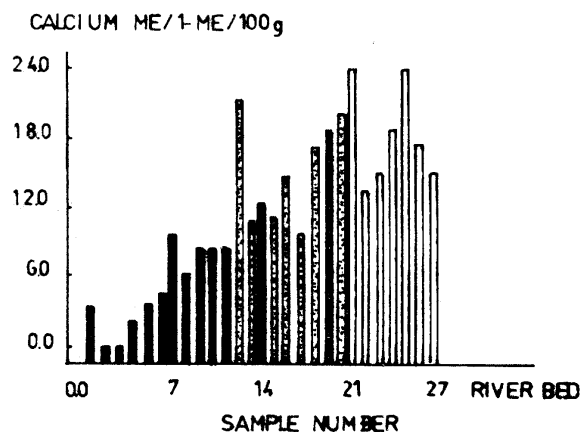


Fig. 7. Total calcium gradient along the transect. Symbols as in Figure 4.

argentinensis is also present. When the fifth cluster is obtained a 'flechillar' variant comes out where *Paspalum dilatatum* is the dominant while *Stipa hyalina* and *Phyla canescens* have a significantly lower coverage, and the original 'flechillar' remains with very high coverage of *Stipa hyalina* and *Phyla canescens* accompanied by *Paspalum dilatatum* and *Paspalum vaginatum* with very low coverage. The sixth cluster segregates only one sample from the 'flechillar', but this division is meaningless.

When the matrix of samples by soil factors is analyzed in PCA the first axis accounts for 42.2% of the total variance. Figure 3 gives the order of samples on soil variables and Table 1 contains the loadings on the first axis. In general terms the order based on soil variables is similar to the order based on species. Halophilous prairies are on left and the 'flechillar' and 'espartillar' on the right.

In relation to the distance from the river, the soil factors behave in different ways. Elevation increases with the distance to the river, however, its lowest point is not at the river, but where the 'flechillar' and 'espartillar' meet (Fig.

Table 1. Loadings of soil variables on the first axis of PCA.

1. pH (soil paste) pHp	-0,92
2. pH (water extract) pHw	-0,91
3. Elevation - El	-0,91
4. Calcium carbonate - CaCO ₃	-0,85
5. Bicarbonate - HCO ₃	-0,84
6. Sodium percentage - NaP	-0,82
7. Carbonate - CO ₃	-0,74
8. Silt (50 u) - C.St.	-0,63
9. Total sodium - T.Na	-0,61
10. Coarse sand - C.Sd.	-0,55
11. Silt (20 u) - F.St.	-0,54
12. Sulfate - SO ₄	-0,50
13. Total salts - T.S.	-0,40
14. Total potassium - T.K.	-0,39
15. Conductivity - Co.	-0,38
16. Exchangeable sodium - E.Na	-0,30
17. Exchangeable potassium - E.K	-0,15
18. Fine sand - F.Sd.	-0,04
19. Saturation percentage - S.P	0,05
20. Chloride - Cl.	0,07
21. Moisture equivalent - M.E.	0,25
22. Organic matter - O.M.	0,55
23. Clay - Cy.	0,63
24. Posphate - P ₂ O ₅	0,68
25. Exchangeable calcium - E.Ca	0,97
26. Total magnesium - T.Mg	0,92
27. Total exchangeable bases - T.E.B.	0,85
28. Total calcium - T.Ca	0,90
29. Exchangeable magnesium - E. Mg	0,92

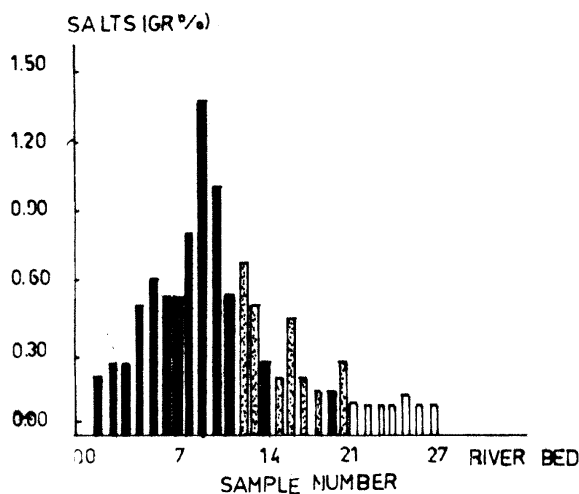
4). pH, whether for the water extract or the soil paste, total carbonates and CaCO₃ increase with the distance to the river (Fig. 5), however, CaCO₃ varies on a gradient slightly approaching the elevation gradient. Bicarbonates vary on a gradient very similar to the elevation gradients (Fig. 6). Total Ca and Mg change opposite to pH (Fig.7), that is, they decrease with distance from the river. However, exchangeable Mg, and even more, exchangeable Ca and total exchangeable bases, although very low farthest from the river, do not have their highest values close to the river; in fact, changes in these bases mirror the changing elevation. Conductivity, total salts, Cl, SO₄=, saturation percentage, total Na and total K have highest values in the centre of the halophilous prairie, but their values decrease whether the distance to the river increases or decreases from this point (Fig. 8). Exchangeable Na, and to a lesser extent ex-

changeable K, follow a gradient similar to bicarbonates, but neither of these gradients are very clear.

The variation of other factors with distance from the river are not always easy to explain. For instance, phosphates decrease with increasing distance with very low concentration, on average where the halophilous prairies thrive. However, the point with highest concentration of phosphates is at a point in the middle of halophilous prairie. Very little can be said of the textural variation in the soils along the transect. Although the soils are clayish, there are points very far from the river bed where the proportion of clay is low, but silt is comparatively high.

In Figure 9 the distribution and coverage of the twelve already mentioned species over the transect is shown. Although the communities are ordered along the transect in an edaphic coenocline, the species seem to have more independence. However, there are edaphic factors correlated with species distributions, which might be any of the soil variables, but other factors can also be influential, independent of the soil variables, such the interactions among the species themselves.

Dispersion profiles (Feoli and Orlóci, 1985) of the species listed above were constructed for eight edaphic variables chosen for their loadings and clear cut gradients. Class intervals for each variable are in Table 2. In Figure

**Fig. 8. Total salts gradient along the transect. Symbols as in Figure 4.****Table 2. Class intervals of soil variables and elevation used in species dispersion profiles.**

Class	I	II	III	IV	V	
pH water)	7.28	7.77	8.26	8.75	9.24	9.73
pH (paste)	6.98	7.47	7.96	8.45	8.94	9.43
Salts (gr %)	0.055	0.313	0.571	0.829	1.087	1.345
Sulfate (me/1 - me/100 g)	0.0	20.49	40.98	61.47	81.96	102.45
Bicarbonate (me/1 - me/100 g)	5.18	7.53	9.88	12.23	14.58	16.93
Calcium (me/1 - me/100 g)	0.0	4.49	8.98	13.47	17.96	22.45
Magnesium (me/1 - me/100 g)	0.38	2.47	4.56	6.65	8.74	10.83
Relative elevation -cm-	0	29	58	87	116	145

10 are the dispersion profiles for pH (E, total deviation from random expectation; C_1 , C_2 , C_3 and C_4 , the components of E). C_1 usually have a monotone ascending or descending shape which suggests the type of relationship that exists between the species and the soil variable concerned, or a flat shape when there is no response. C_2 may have a convex or concave shape which suggests interaction among the species over the factor or a flat shape when no such interaction happens. However, the interpretation of profiles is not always straight forward, as other variables may interact with the variable under analysis. C_3 and C_4 components usually have a flat or seesaw shape which suggests no response or random response. In Figures 11,

12 and 13 are C_1 and C_2 dispersion profiles for the other soil variables. C_3 and C_4 components have been omitted. Table 3 summarizes the results of the analysis and the response of different species to the soil variables.

In general, the results from the other two transects were consistent with these results, but in one of them the behaviour of two additional species, *Salicornia ambigua* and *Coniza bonariensis*, were investigated. A response to organic matter could be detected. *Salicornia ambigua* in relation to soil factors in a similar manner as *Spartina densiflora*. *Stipa hyalina*, *Phyla canescens*, and to a lesser degree *Cynodon dactylon* and *Coniza bonariensis* are positively correlated with organic matter while the reverse

Table 3. Distribution of species over class intervals of the eight soil factor analyzed. Class intervals as in table 2.

Class intervals of soil factors					
Soil Factors	I	II	III	IV	V
Topographic height	<i>Stipa hyalina</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>	<i>Ranunculus cymbalaria</i> <i>Apium sellowianum</i>	<i>Ranunculus cymbalaria</i> <i>Apium sellowianum</i>	<i>Distichlis spicata</i> <i>Paspalum vaginatum</i> <i>Chaetotropis chilensis</i>	<i>Paspalum vaginatum</i> <i>Chaetotropis chilensis</i> <i>Distichlis spicata</i>
pH (water)	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i> <i>Distichlis spicata</i>	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>	<i>Spartina densiflora</i> <i>Rumex pulcher</i>	<i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i> <i>Distichlis spicata</i>	<i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i> <i>Distichlis spicata</i>
pH (paste)	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i> <i>Distichlis spicata</i>	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>	<i>Spartina densiflora</i> <i>Rumex pulcher</i>	<i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i> <i>Paspalum vaginatum</i> <i>Distichlis spicata</i>	<i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i> <i>Paspalum vaginatum</i> <i>Distichlis spicata</i>
Salts	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>	<i>Spartina densiflora</i> <i>Rumex pulcher</i> <i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i>	<i>Spartina densiflora</i> <i>Rumex pulcher</i> <i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i>	<i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i>	<i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i> <i>Distichlis spicata</i>
Magnesium	<i>Paspalum vaginatum</i> <i>Distichlis spicata</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i>	<i>Paspalum vaginatum</i> <i>Distichlis spicata</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i>	<i>Spartina densiflora</i> <i>Rumex pulcher</i>	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>
Calcium	<i>Paspalum vaginatum</i> <i>Distichlis spicata</i> <i>Apium sellowianum</i> <i>Chaetotropis chilensis</i> <i>Ranunculus cymbalaria</i>	<i>Paspalum vaginatum</i> <i>Distichlis spicata</i> <i>Apium sellowianum</i> <i>Chaetotropis chilensis</i> <i>Ranunculus cymbalaria</i>	<i>Spartina densiflora</i> <i>Rumex pulcher</i>	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>
Bicarbonate	<i>Spartina densiflora</i> <i>Rumex pulcher</i>	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i> <i>Ranunculus cymbalaria</i>	<i>Ranunculus cymbalaria</i> <i>Paspalum dilatatum</i>	<i>Ranunculus cymbalaria</i> <i>Distichlis spicata</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i> <i>Paspalum vaginatum</i>
Sulfate	<i>Stipa hyalina</i> <i>Paspalum dilatatum</i> <i>Phyla canescens</i> <i>Cynodon dactylon</i> <i>Carex sororia</i>	<i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i> <i>Spartina densiflora</i> <i>Rumex pulcher</i>	<i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i> <i>Spartina densiflora</i> <i>Rumex pulcher</i>	<i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i>	<i>Paspalum vaginatum</i> <i>Ranunculus cymbalaria</i> <i>Chaetotropis chilensis</i> <i>Apium sellowianum</i> <i>Distichlis spicata</i>

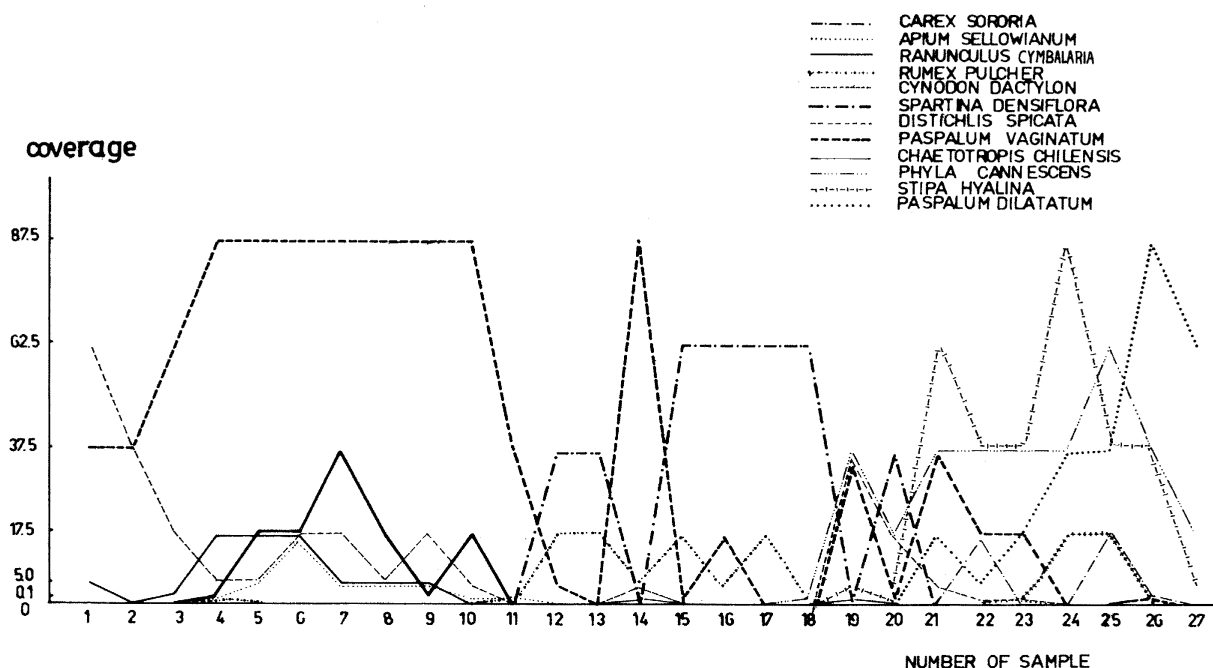


Fig. 9. Species distribution along the transect.

happens with *Distichlis spicata*, *Paspalum vaginatum* and *Apium sellowianum*. *Spartina densiflora* is in an intermediate position between these two groups of species in face of organic matter content. In the third transect also *Salicornia ambigua* as well as *Hordeum euclaston* and *Sporobolus pyramidatus* were investigated. *Sporobolus pyramidatus* and *Salicornia ambigua* behave in a similar way as *Paspalum vaginatum* and *Distichlis spicata*, while *Hordeum euclaston* behaves in the opposite way.

Discussion

As the gradient segment under study is short, and the communities are closely related to each other, it can be assumed that the data set has a relatively high homogeneity, that is, a low beta diversity; so PCA is a suitable ordination method (Orlóci, 1978; Whittaker and Gauch, 1978). The results confirmed this.

As far as we know dynamic clouds (mobile centres) have not been used in phytosociological or botanical research. However, Jancey (1965a, b) used a similar method for the genus *Phyllota*, which according to Clifford and Stephenson (1975) appears to show «considerable promise». The procedure in both methods is the same, but while in Jancey's method reclustering is repeated automatically until there is no more regrouping, in the present method the user states the number of repetitions based on the knowledge of the data, the results from PCA in our case. The advantage of this method is that the results have more general validity. In fact the results were very consistent with field observations. However, the results of this part of the analysis do not add too much to our knowledge as the clusters or communities are almost evident anyway.

Nevertheless it adds objective confirmation.

Most of the soil variables analysed are correlated with topography and the distribution of species and communities within the valley can be correlated with these factors. The lowest part of the valley is not close to the river bed, but further away from it; and this point is regularly flooded during the wet season or after rainfalls. From this point towards the river the soil water table seems to drop, while in the opposite direction it is located near the soil surface. This may explain the soil reaction gradient.

Stipa hyalina, *Paspalum dilatatum*, *Phyla canescens*, *Carex sororia* and *Cynodon dactylon* are the less halophilous species, and most of the other species are more or less *halophytes*; but among them *Paspalum vaginatum*, *Distichlis spicata*, *Apium sellowianum*, *Chaetotropis chilensis* and *Ranunculus cymbalaria* are dispersed over more alkaline soils than *Spartina densiflora* and *Rumex pulcher*.

Spartina densiflora, although an *halophyte* does not seem to tolerate high pH as *Paspalum vaginatum* and *Distichlis spicata* do. Although these two latter species may thrive where *Spartina densiflora* grows, are far less abundant or absent where *Spartina densiflora* is abundant. It should be taken into account that the physiological response of a species to an environmental factor is not the same as the ecological response to the same factor (Austin and Austin, 1980). The first two components of the dispersion profiles in some cases appear to segregate these two responses; however, this should be tested experimentally. *Spartina densiflora* has a different growth form than *Distichlis spicata* and *Paspalum vaginatum*; the former has tall tussocks which form a dense canopy while the other two are creeping rhizomatous species, therefore the shade cast on them prevents their growth in that segment of the

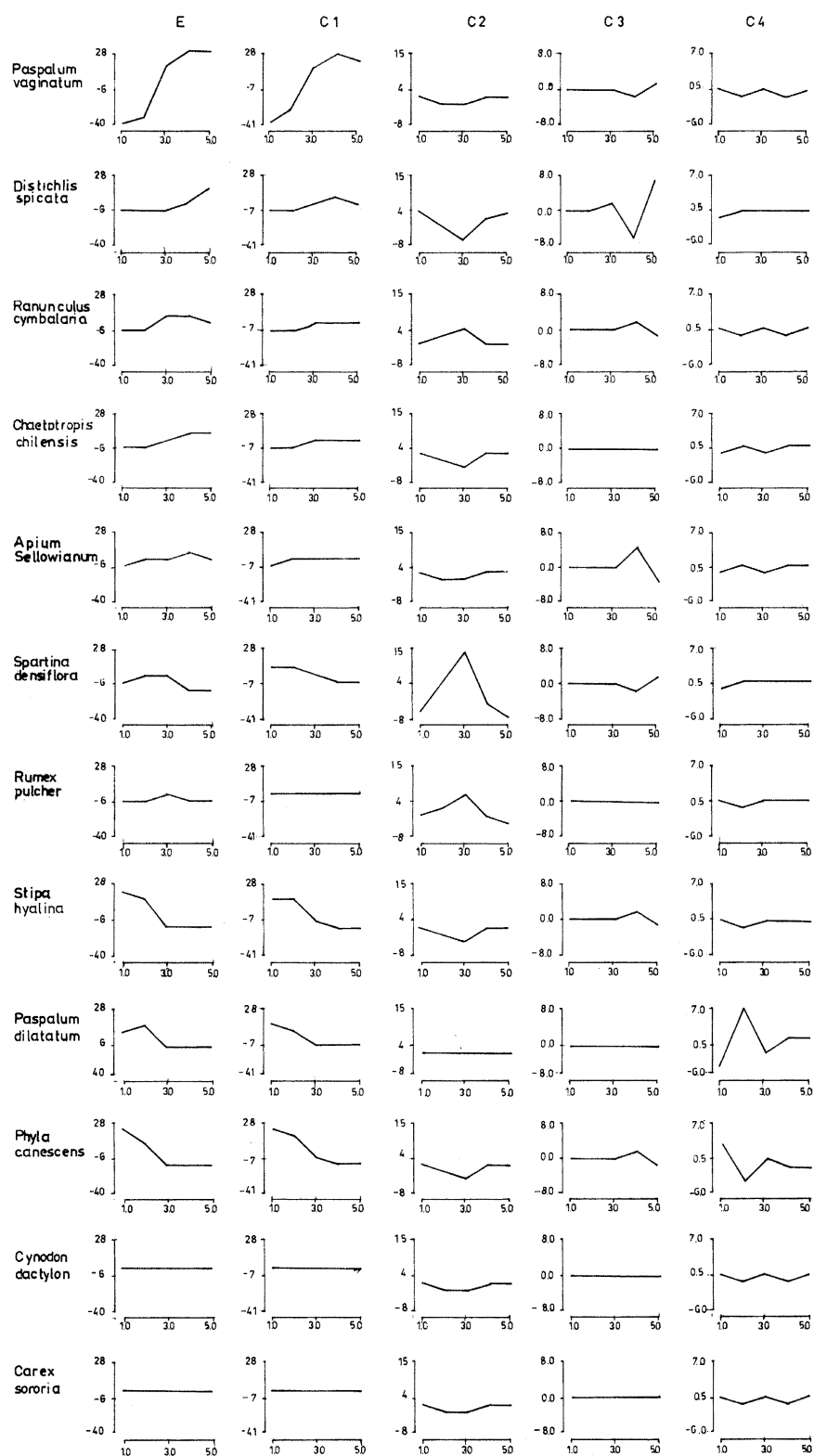


Fig. 10. Dispersion profiles of 12 species for pH (horizontal scale). Vertical scale indicates deviations from expectation. E, total deviation; C₁, C₂, C₃, C₄ deviation in successive lattices defined by canonical variables. Percentage of total chi-squares accounted for by lattices: C₁-76, C₂-14, C₃-5, C₄-2, E-100.

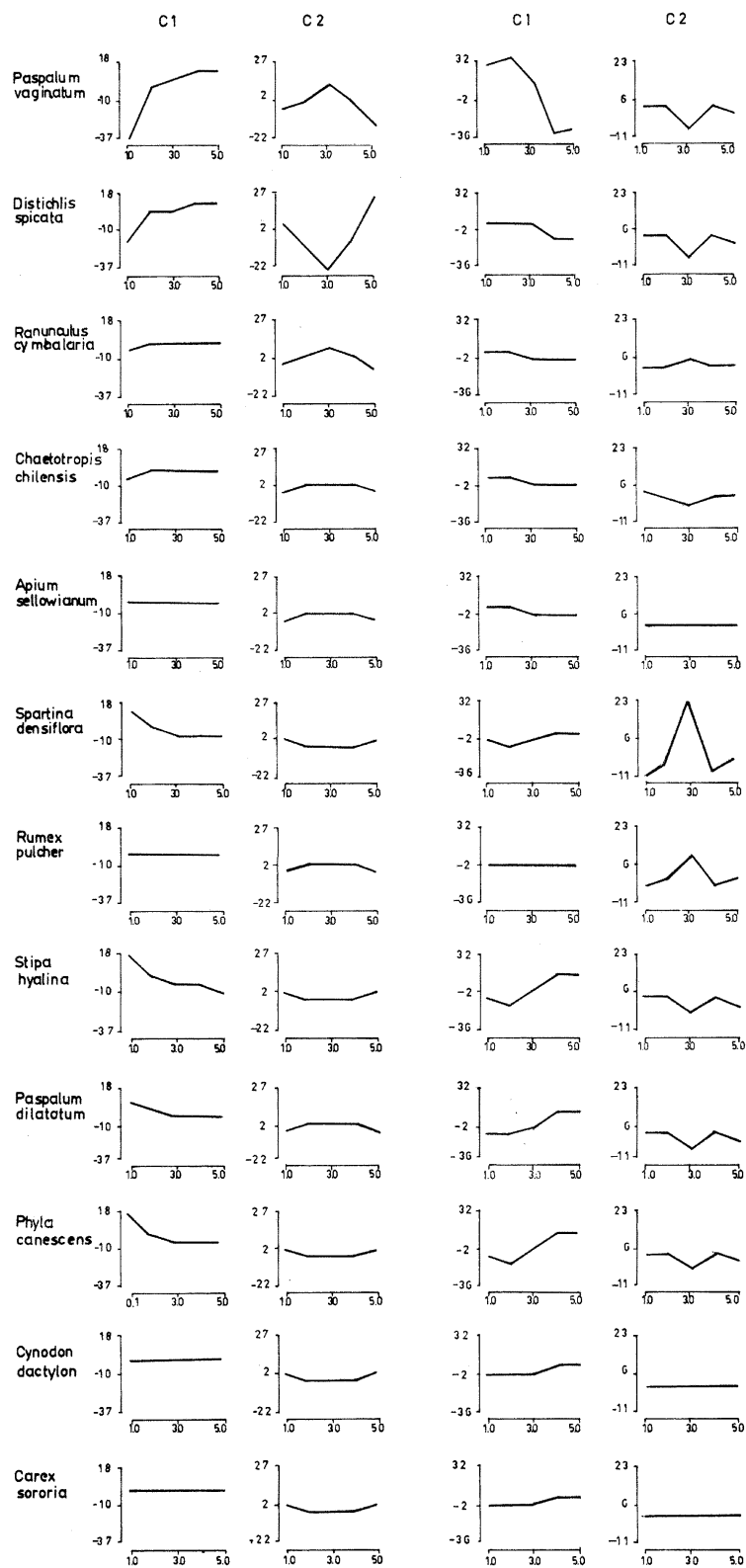


Fig. 11. C_1 and C_2 dispersion profiles of the same 12 species as in figure 10 for elevation (left) and total calcium (right). Percentage of total chi-squared accounted for by lattices (left), C_1 -56, C_2 -25, and by lattices (right): C_1 -69; C_2 -22.

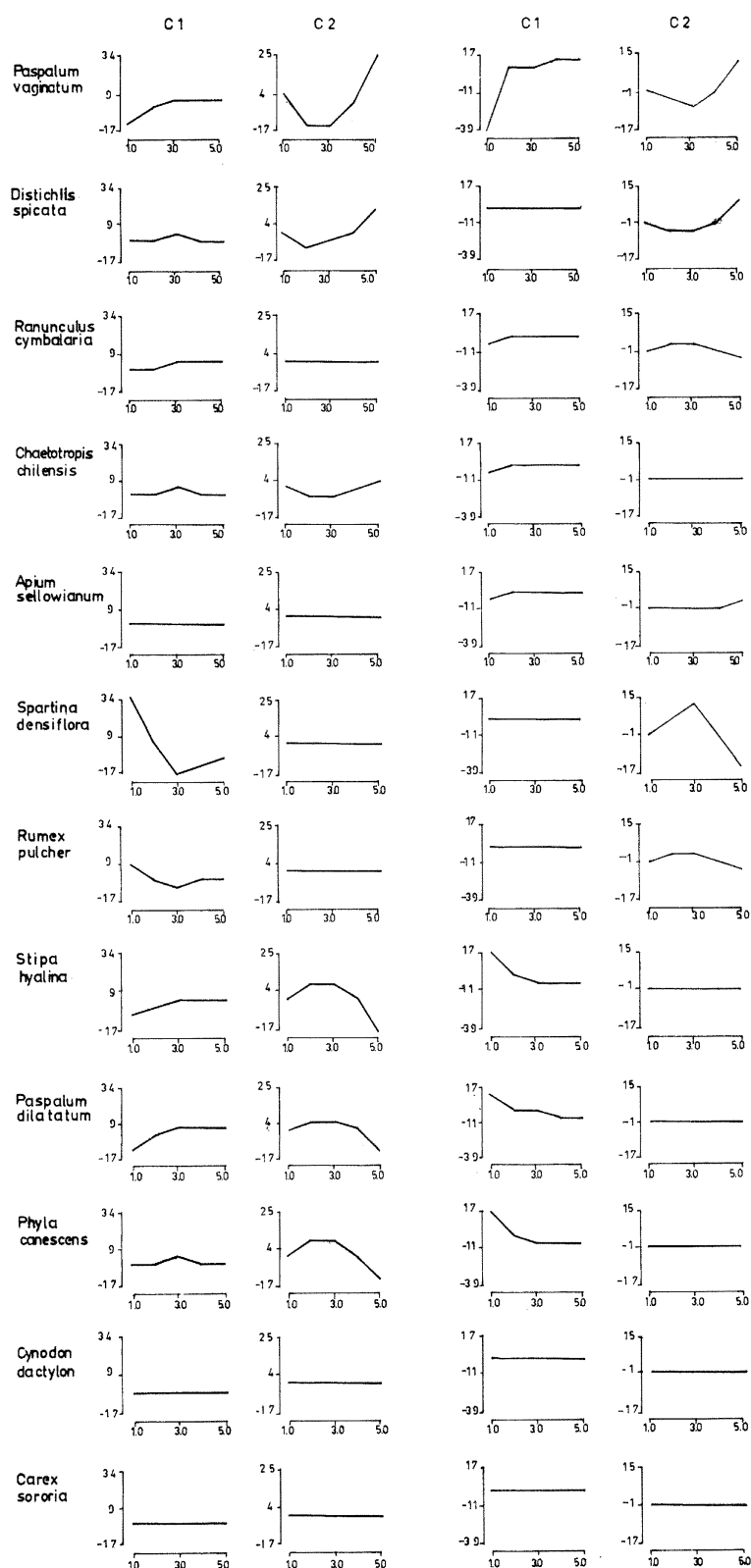


Fig. 12. C_1 and C_2 dispersion profiles of the same 12 species of figure 10 for bicarbonate (left) and sulfate (right). Percentage of total chi-squared accounted for by lattices (left): C_1 -57, C_2 -28, and by lattices (right): C_1 -70, C_2 -17.

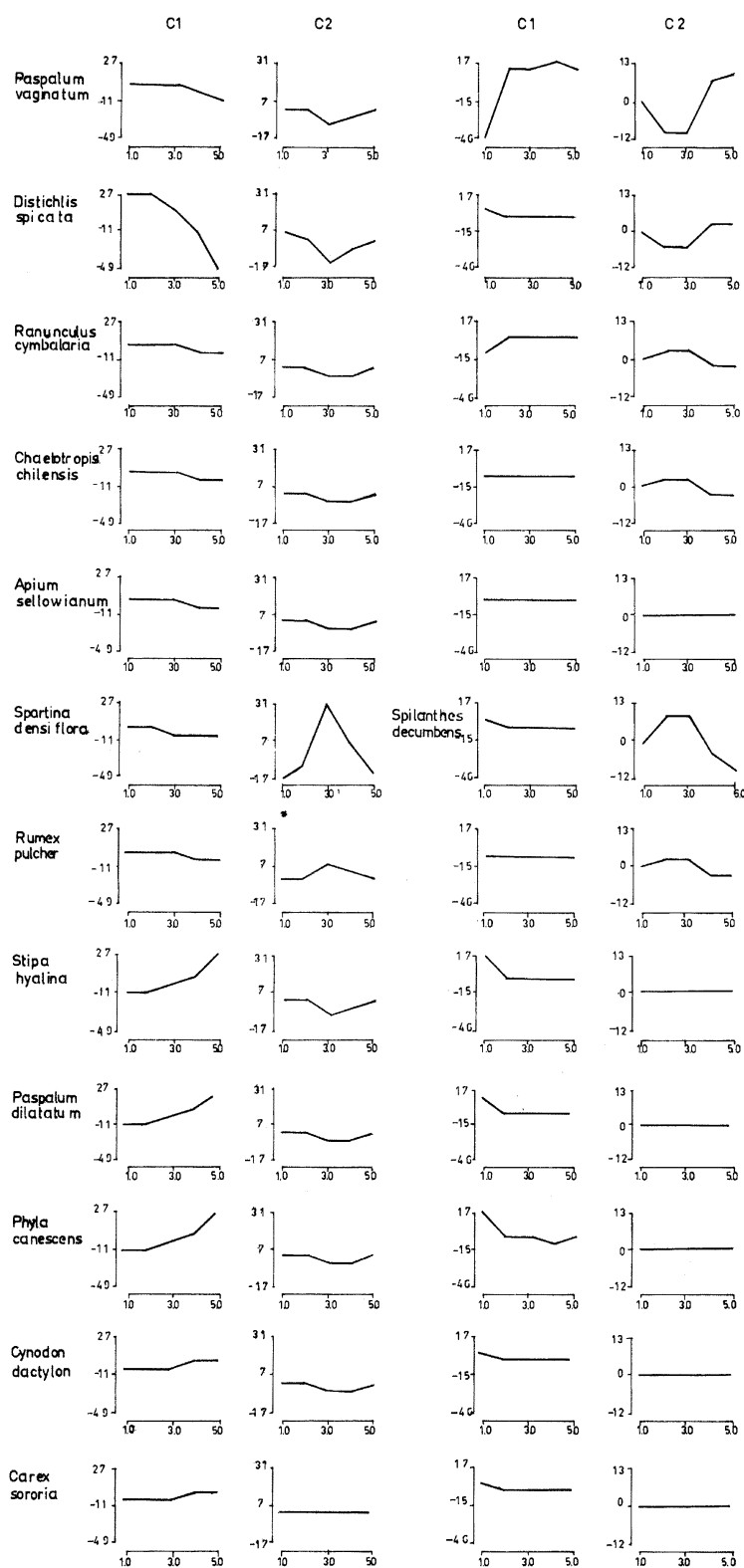


Fig. 13. C_1 and C_2 dispersion profiles of 12 species for total magnesium (left) and total salt (right). Percentage of total chi-squared accounted for by lattices (left): C_1 -65, C_2 -31, and by lattices (right): C_1 -75, C_2 -74. (For magnesium, the same species as in figure 10; for total, salts, *Spartina densiflora* omitted, and *Spilanthes decumbens* was also investigated).

gradient. At the other extreme of the transect both *Phyla canescens* and *Cynodon dactylon* suffer from the interference of *Stipa hyalina* and *Paspalum dilatatum*, although the latter seems to be more shade tolerant than the former.

Spartina densiflora and *Rumex pulcher* apparently behave similarly in the face of different soil variables, but a warning should be in order. Mature tussocks of *Spartina densiflora* have a growth form with central gap like a monk's tonsure. Whether this tonsure develops through *Spartina*'s self inhibition, soil depletion or accumulation of dead organic matter we can not tell. But the soil conditions inside it may differ from other parts of the quadrat where the soil sample may have been taken, and *Rumex pulcher* finds there an adequate environment to grow. Therefore the distribution of *Rumex pulcher* along the transect may be more correlated with the presence of the gaps in the *Spartina* tussocks than the surrounding soil characteristics.

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REFERENCES

- AUSTIN, M.P. and AUSTIN, B.O. 1980. Behaviour of experimental plant communities along a nutrient gradient. *J. Ecology* 68: 891-918.
- BRAUN-BLANQUET, J. 1979. *Fitosociología*. H. Blume Ediciones, Madrid.
- CABRERA, A.L. (1963, 1965a, b, 1967, 1968, 1970. *Flora de la Provincia de Buenos Aires*. 6 vols. Colección Científica del INTA. Buenos Aires.
- CLIFFORD, H.T. and STEPHENSON, W. 1975. *An introduction to numerical classification*. Academic Press, New York.
- COLLANTES, M.B. and J.P. LEWIS. 1980. Ordenamiento de las comunidades herbáceas del departamento Rosario (Prov. de Santa Fe. Argentina) *Ecosur* 7: 171-184.
- FEOLI, E. and L. ORLÓCI. 1979. Analysis of concentration and detection of underlying factors in structured tables. *Vegetatio* 40: 49-54.
- FEOLI, E. and L. ORLÓCI. 1985. Species dispersion profiles of anthropogenic grassland in the Italian Eastern Pre-Alps. *Vegetatio* 60: 113-118.
- GLEASON, H.A. 1926. The individualistic concept of the plant association. *Toney Bot. Club Bull.* 53: 7-26.
- HOTELLING, H. 1933 a. Analysis of a complex of statistical variables into principal components. *J. Educ. Psych.* 24: 417-441.
- HOTELLING, H. 1933 b. Analysis of a complex of statistical variables into principal components. *J. Educ. Psych.* 24, 498-520.
- JANCEY, R.C. 1965 a. Multidimensional group analysis. *Aust. J. Bot.* 14: 127-30.
- JANCEY, R.C. 1965 b. The application of numerical methods of data analysis to the genus *Phyllota* Benth. in New South Wales. *Aust. J. Bot.* 14: 131-149.
- KEMPTHORNE, O. 1952. *The design and analysis of experiments*. John Wiley & Sons, New York.
- LEBART, L., MORINEAU, A. and N. TABARD. 1977. *Techniques de la description statistique*. Dunod, Paris.
- LEBART, L., MORINEAU, A. and J.P. FENELON. 1982. *Traitement des données statistiques*. Dunod, Paris.
- LEBART, L. and A. MORINEAU. 1982. SPAD. Cesia, Paris.
- LEWIS, J.P., COLLANTES, M.B., PIRE, E.F., CARNEVALE, N.J., BOCCANELLI, S.I., STOFELLA, S.L. and D.E. PRADO. 1985. Floristic groups and communities of southeastern Santa Fe, Argentina. *Vegetatio* 60: 67-90.
- ORLÓCI, L. 1978. Ordination by resemblance matrices. In: R.H. Whittaker (ed.), *Ordination of Plant Communities*, pp. 239-275. Junk, The Hague.
- ORLÓCI, L. 1981. Probing time series vegetation data for evidence of succession. *Vegetatio* 46: 31-35.
- ORLÓCI, L. and N. KENKEL. 1985. *Introduction to Data Analysis*. Statistical Ecology Monographs Vol. 1. International Cooperative Publishing House, Fairland, Maryland.
- PIELOU, E.C. 1984. The interpretation of ecological data. John Wiley & Sons, New York.
- RAGONESE, A.E. and G. COVAS. 1947. La flora halófila de la provincia de Santa Fe (Rep. Argentina). *Darwiniana* 7: 401-496.
- WHITTAKER, R.H. 1978. Direct gradient analysis. In: R.H. Whittaker (ed.), *Ordination of Plant Communities*, pp. 9-50. Junk, The Hague.
- WHITTAKER, R.H. and H.G. GAUCH. 1978. Evaluation of ordination techniques. In: R.H. Whittaker (ed.), *Ordination of Plant Communities*, pp. 277-336. Junk, The Hague.

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Appendix I - Floristic composition and average species coverage of plant communities

Halphilous prairie		Spartina densiflora tall grassland («Espartillar»)	
Paspalum vaginatum	70,19	Spartina densiflora	51,78
Distichlis spicata	17,89	Rumex pulcher	10,71
Ranunculus cymbalaria	8,28	Heliotropium curassavicum	3,26
Chaetotropis chilensis	5,60	Paspalum vaginatum	3,23
Spartina argentinensis	5,19	Salicornia ambigua	2,54
Scirpus americanus	2,88	Phyla canescens	2,51
Cyperus laevigatus	2,88	Distichlis spicata	2,50
Phyla canescens	2,88	Petunia parviflora	2,86
Triglochin striata	1,93	Verbena gracilescens	1,46
Salicornia ambigua	1,18	Hymenoxis anthemoides	0,75
Apium sellowianum	2,91	Lepidium sp.	0,06
Plantago myosurus	1,21	Picrosia longifolia	0,03
Picrosia longifolia	0,79	Polypogon monspeliensis	0,03
Rumex pulcher	0,40	Euphorbia serpens	0,06
Lepidium sp.	0,40	Sesuvium portulacastrum	0,03
Hordeum euclaston	0,39	Cressa truxilensis	0,04
Stipa hyalina	0,38	Plantago myosurus	0,01
Lolium multiflorum	0,02	Coniza bonariensis	0,01
Coniza bonariensis	0,01	Spartina argentinensis	0,01
Polypogon monspeliensis	0,01	Aster squamatus	0,01
Petunia parviflora	0,01	Senecio grisebachii	0,01
Aster squamatus	0,01	Cirsium vulgare	0,01
Hymenoxis anthemoides	0,0077	Stipa hyalina	0,01
Spergularia ramosa	0,0077	Setaria geniculata	0,01
Melilotus sp.	0,0077	Bromus unioloides	0,01
Chenopodium macrospermum	0,0077	Apium leptophyllum	0,01
Heliotropium curassavicum	0,0077	Trifolium sp.	0,01
Cressa truxilensis	0,0077	Limonium brasiliense	0,01
Verbena gracilescens	0,0077	Nicotiana longiflora	0,01
Juncus sp.	0,0077	Polygonum brasiliense	0,01
Polygonum sp.	0,0077		
Setaria geniculata	0,0077		
Stipa hyalina grassland («Flechillar»)		Stipa hyalina grassland («Flechillar»)	
Stipa hyalina	43,57	Trifolium sp.	0,03
Phyla canescens	38,21	Juncus balticus	0,03
Paspalum dilatatum	37,86	Ammi viznaga	0,03
Paspalum vaginatum	10,37	Hipchoeris microcephala	0,03
Carex sororia	5,01	Carduus acanthoides	0,03
Cynodon dactylon	5,01	Hymenoxis anthemoides	0,01
Lolium multiflorum	2,20	Apium sellowianum	0,01
Sida leprosa	2,14	Picrosia longifolia	0,01
Alternanthera philoxeroides	2,50	Salicornia ambigua	0,01
Stipa brachychaeta	2,50	Sesuvium portulacastrum	0,01
Coniza bonariensis	0,77	Polygonum sp.	0,01
Hirschfeldia sp.	1,43	Polygonum brasiliense	0,01
Distichlis spicata	0,74	Teucrium cubense	0,01
Setaria geniculata	0,74	Anthemis sp.	0,01
Hordeum euclaston	0,73	Physalis viscosa	0,01
Ambrosia tenuifolia	0,71	Medicago lupulina	0,01
Modiolastrum gillesii	0,71	Melilotus officinalis	0,01
Cressa truxilensis	0,07		
Rumex crispus	0,08		
Plantago myosurus	0,04		
Verbena gracilescens	0,04		
Bromus unioloides	0,04		
Apium leptophyllum	0,04		
Eleusine tristachya	0,04		
Carex bonariensis	0,04		
Euphorbia serpens	0,03		