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Abstract. In order to understand the influence of edaphic factors on the spatial structure of inland halophytic plant communities, a 2.6 km^2 study site, located on the lower fringe of the alluvial fan of the Hutubi River, in an arid region of China, was sampled and mapped. 105 patches were found to be homogeneous in species composition. Plant species and their coverage were recorded in each patch. 45 patches were randomly selected for the measurement of edaphic variables. A map with quadrat locations and boundaries of patches was digitized into a GIS and related to the vegetation and edaphic data matrices. CCA was used to evaluate the relative importance of edaphic factors in explaining the variation of the species assemblages and to identify the ecological preferences of species. The spatial structure of the communities and the main edaphic factors were analyzed using correlograms, Mantel correlograms and clustering under constraint of spatial contiguity.

Gradient analysis showed that there are two distinct vegetation gradients in the study area, one of which is determined mainly by soil moisture (determined by depth to the water table), and the other by soil salinity (determined by electrical conductivity and hydrolytic alkalinity of the first soil layer). However, spatial analyses showed that at the sampling scale the halophytic communities in the study area are structured along one main spatial gradient determined by the water table level. Similar spatial autocorrelation structures between the factors related to the first soil layer and the communities, given our sampling scale, could not be detected. Our results suggest that the relative importance of the effects of different edaphic factors on the spatial structure of halophytic communities is scale-dependent. The partitioning of species variation indicates that in addition to edaphic factors, other factors, such as biotic interactions, may play an important role in structuring these communities.

Keywords: CCA; GIS; Indicator species; Mantel test; Soil salinity, Spatial autocorrelation; Variation partitioning; Xinjiang.

Abbreviations: CCA = Canonical Correspondence Analysis; GIS = Geographical information system.

Nomenclature: Anon. (1978) and references therein.

Introduction

A major goal of plant community ecology is to test hypotheses concerning the factors that may control the composition and structure of plant communities. It is now recognized that multiple factors must be invoked to explain the structure of communities (e.g. Quinn & Dunham 1983; Dunson & Travis 1991). It has also become apparent that different factors may affect community structure at different spatial and temporal scales (Wiens 1989; Allen & Hoekstra 1991; Levin 1992). One of the challenges of community ecology is to untangle the interactions among these factors. In inland saline ecosystems, the important role of edaphic factors in structuring plant communities has long been noted in a number of studies throughout the world (e.g. Waisel 1972; Chapman 1974; Ungar 1974; Anon. 1978; Sen & Rajpurohit 1982; Carnevale & Torres 1990; Burchill & Kenkel 1991; and many others). Many studies have revealed that species and plant community distribution follow a salinity gradient which reflects their degree of salt tolerance. However, some studies also showed that many halophytes have a wide amplitude for soil salinity, but a narrow one for soil moisture. Thus, some species with a common range of salinity tolerances are segregated on the basis of their water requirements (see Waisel 1972). No matter which edaphic factor is predominant, the influence of edaphic factors as a whole on the distribution of halophytic species and communities is important. Prior to the 1970s, there has been an emphasis on edaphic factors. Because of the strong relationships between halophytes and edaphic factors, certain species have been proposed as indicators of saline soil conditions. However, at the same time, researchers also noticed that many of the inland halophytic species can grow and reproduce under non-saline conditions, and that some indicator species were also found to be unreliable (Barbour 1970). Competitive exclusion may explain their elimination from moderate sites (Ungar 1974). Since the 1970s, the influence of competition has been emphasized and investigated. More and more field

transplantation and laboratory experiments have suggested that interspecific competition indeed exists in these stressed habitats, and that it is also important in structuring these communities (e.g. Barbour 1978; Ungar et al. 1979; Badger & Ungar 1990; Kenkel et al. 1991). Currently, it is clear that both edaphic and biotic factors (e.g. competition, dispersal, herbivory) must be used to explain the structure of inland halophytic communities. However, the relative importance of these factors still need to be tested in different halophytic communities. Furthermore, among the edaphic factors, factors other than salinity, such as soil moisture and alkalinity (because they often act synergistically with salinity) have received little attention.

Recently, Borcard et al. (1992) proposed a quantitative statistical approach, based on canonical correspondence analysis (CCA) (ter Braak 1986, 1987a), to discriminate among variables influencing species assemblages, which partition of the variation of species assemblages and allows one to measure the relative contribution of sets of explanatory variables. This method is conceptually linked to the idea that ecological heterogeneity in natural communities is explained by non-mutually exclusive abiotic and biotic factors that overlap in space and time. Geographical information system (GIS) methods and spatial statistical analyses provided powerful means to describe and detect the spatial patterns of communities and environmental factors (Johnson 1993; Legendre & Fortin 1989). The objective of this paper is to examine the influence of edaphic factors as a whole, as well as the influence of specific edaphic factors on the spatial structure of inland halophytic communities using these methods. We will first evaluate the relative importance of specific edaphic factors in explaining variation of species assemblages, and identify ecological preferences of the species. We will then analyze spatial patterns of communities and of major edaphic factors, and partition species variation among the different sources of assumed influence. Our research also emphasizes the use of halophytes and halophytic communities as indicators of soil properties and for soil mapping purposes. This investigation is intended to give some insight in the cause of the spatial structure of inland halophytic communities. This research will facilitate also the identification of soil properties and soil mapping using halophytes and halophytic communities, in order to improve vegetation management in the Xinjiang Autonomous Region of China.

Study site

The study site is located in the Xinjiang Autonomous Region of China, where a long-term ecological monitoring project on the dynamics of vegetation, soil water and salinity is in progress. Its geographic position is 86° 57'10" E, 44° 19'02" N. The annual average temperature is 6.8 °C, the monthly average temperature is – 16.9 °C in January and 25.6 °C in July. The annual precipitation is only ca. 170 mm, but the potential evaporation is ca. 2300 mm, giving a P:E ratio of 0.07. Geomorphologically, the study site is located on the lower fringe of the alluvial fan of the Hutubi River, which is part of the Zhungeer basin whose central portion is occupied by the Guerbantonggute desert.

The study site lies in a transition zone between oases and the desert. Temperate desert vegetation dominated by semi-shrub *Reaumuria soongorica* is distributed on the well-drained plain connected to the alluvial fan. On the upper and middle area of the alluvial fan both new and old oases are found. Due to the large amount of salt in the soil, as well as the relatively high water table, not only salt desert, but also salt marsh vegetation occur extensively in this transition zone. It provided an ideal location to analyze the relationships between the spatial structure of halophytic communities and edaphic factors. Moreover, because this is the only zone with high potential for agricultural development remaining in this extremely arid region, it has been the object of several research projects in grassland management and soil salinization control in China.

The study site extends over a 2.6 km^2 area (Fig. 1). The topography is undulating and elevation varies between 446.0 and 449.5 m above sea level; the southeastern part of the area being at a higher altitude than the western part. In the upper part, the water table is 1.5 - 2.5 m below the soil surface, in the lower part 0.7-1.5 m below the soil surface. Salt content in the ground water varies from 2.3 to 38.5 g/L. Soil salinity varies spatially. Electrical conductivity of the first soil layer (0 - 30 cm) ranges between 0.1 and 0.9 S/m. Salts are generally sodium sulfates or sodium chlorides. In some areas where the pH and alkalinity are relatively high, there are also sodium carbonates. The pH of the first soil layer is 8.2-9.9 and hydrolytic alkalinity is 0.1-1.8 meq/100g soil. Soil texture is usually fine sand or light loam with a clay layer occurring at 30 - 120 cm depth. The thickness of the clay layer varies from 25 to 120 cm. The spatial variation of the plant communities in the study area is notable. The extremely xerohalophytic species such as *Reaumuria soongorica, Nitraria sibirica* and *Suaeda physophora*, occur in the upper parts, while in the lower parts the communities are dominated by hydrohalophytic species such as *Aeluropus littoralis, Limonium gmelinii* and *Tamarix ramosissima*. Between the upper and lower parts, xerohalophytic species such as *Kalidium foliatum* and *Halocnemum strobilaceum* dominate most of the area.
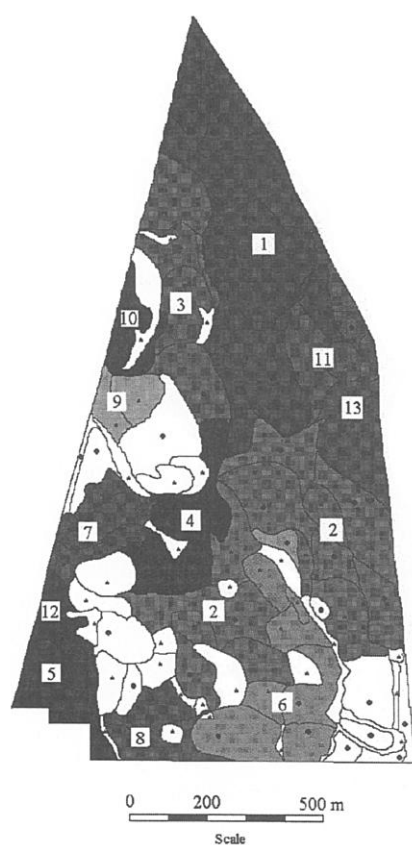
Fig. 1. Locations of the sampled quadrats (points), homogeneous patches, and vegetation structure obtained by agglomerative clustering (see Methods). ● and * represent quadrats with and without sampled edaphic data, respectively. Vegetation group 1 is dominated by *Suaeda physophora* and *Halocnemum strobilaceum*; groups 2, 5 and 7 by *Halocnemum strobilaceum*; group 3 by *Nitraria sibirica* and *Phragmites communis*; group 4 and 6 by *Kalidium foliatum*; group 8 by *Phragmites communis* and *Aeluropus littoralis*; group 9 is dominated by *Nitraria sibirica*; group 10 by *Achnatherum splendens*; group 11 by *Artemisia schrenkiana*; group 12 by *Tamarix ramosissima*; group 13 by *Suaeda physophora*. Unclustered quadrats (white) are not labelled.

Methods

Sampling and mapping

A 10 m × 10 m grid (x: east-west; y: south-north direction) was established over the entire area in order to record the coordinates of the sampling points and draw the boundaries of homogeneous patches. Patches which were homogeneous in species composition were determined by surveyors and the boundaries were delineated on a base map. In some locations where the boundaries are not easy to determine, the homogeneous patches were defined by as small an area as possible, in order to emphasize details of the spatial structure. In order to

record the species present and their coverage in each homogeneous patch, a single quadrat was placed at random in each of the patches. Quadrat size was 1 m^2 for herb-dominated patches and 25 m^2 for shrub-dominated patches. 105 patches were found to be homogeneous in species composition, and thus 105 quadrats were sampled in the study site (Fig. 1). 29 species were recorded. Among the 105 quadrats, 45 were selected randomly to record edaphic variables (Fig. 1). The eight selected edaphic factors were: electrical conductivity, pH and hydrolytic alkalinity of the first soil layer (0 - 30 cm); depth to the water table; total salt content and pH of the ground water; and the depth and thickness of the clay layer. The map with quadrat locations and boundaries of patches was digitized into a GIS system and related to the vegetation and edaphic data matrices. The elevation map of the study site was also digitized into this system. By visually comparing the spatial pattern of the species, patches and communities to the topography and spatial patterns of the edaphic factors, the GIS allowed us to check the validity of the relationships uncovered by the following statistical methods. The GIS system was also used to map soil properties by interpolating the edaphic data for the other unsampled quadrats using the data of the 45 quadrats sampled.

Statistical methods

Our analyses were mainly carried out using CANOCO (ter Braak 1986, 1987b) and the R-package (Legendre & Vaudor 1991). Rare species (frequency < 2%) were removed before any analysis. CCA was used to obtain an ordination of the vegetation data in the 45 quadrats, constrained by the edaphic variables. The root mean squared deviation of the species was used to identify the realized niche width of the species in the environmental space, as well as to determine the indicator species. Monte Carlo permutation tests were performed to assess the significance of the canonical axes showing the relationships between species and the selected edaphic factors. Partial CCA produced constrained ordinations while controlling for the effect of a number of edaphic variables. Partitioning the variation of the species data between edaphic and spatial components was obtained by partial CCA (Borcard et al. 1992). The spatial data consisted in the x and y geographic coordinates of the quadrats, as well as the other terms of a third-degree surface trend polynomial equation of the x and y coordinates (Legendre 1990); significant terms of that polynomial were selected using the forward selection procedure available in the CANOCO program. The variation partitioning yielded four fractions of the species data variation: (a) local species variation, explained by the edaphic factors independently of any spatial structure, (b)

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spatial structure in the species data which is shared by the edaphic factors, (c) spatial structure in the species data which is not shared by the edaphic factors, and (d) unexplained variation (Borcard et al. 1992; Borcard & Legendre 1994). Although CCA has been proven to be robust to highly skewed species data (Palmer 1993), we still made several runs with different log-transformed data in order to get the most appropriate result. Considering the lax convergence criterion in the CANOCO program, which may cause instability of the results (Oksanen & Minchin 1997), the analysis was repeated using a CCA-program written by one of us (P. Legendre), which uses a more strict convergence criterion. Weighted average scores were used to draw the ordination diagram of the quadrats.

The R-package was used to analyze the spatial structure of the communities and edaphic factors. To describe the spatial structure of the edaphic factors, we used the 45 quadrats with edaphic data to compute correlograms (with Moran's I) of each factor. We used proportional-linked agglomerative clustering with spatial contiguity constraint (Legendre & Fortin 1989) and a Mantel correlogram to describe the spatial structure of the communities within the 105 quadrats. The Mantel test was used to test the significance of the relationship between the community similarity matrix and the geographical distance matrix, and to study niche segregation of the two most widely distributed species, *Kalidium foliatum* and *Halocnemum strobilaceum*. Both of these species are widely distributed between the upper and lower topographic positions. One of the two species, or both, are present in 39 of the 45 quadrats. The differences in their edaphic preferences needed to be determined. A model similarity matrix among quadrats was constructed, containing 1s for pairs of quadrats that were dominant for the same species and 0s for pairs of quadrats differing as to the dominant species. Using the Mantel test, this matrix was compared to a similarity matrix computed from the edaphic variables. A series of *a posteriori* tests were used to determine the significant factors. Steinhaus's coefficient (Legendre & Legendre 1983) was used to compute this similarity matrix.

Results

### Gradient analysis of species assemblages and edaphic factors

The results of CCA with different transformations of the data gave comparable results. We adopted the data set with log-transformed electrical conductivity and alkalinity of the first soil layer, and log-transformed total salt content of the ground water because it is biologically more reasonable (Palmer 1993). The stability of our results with CANOCO was confirmed by repeating the run with P. Legendre's program. The results of CCA are shown in Fig. 2 and in Tables 1 and 2. A Monte Carlo permutation test of the trace (i.e. the sum of all canonical eigenvalues; 999 permutations) confirmed the overall significance of the canonical ordination ($p < 0.001$). Three main edaphic factors, depth to the water table, electrical conductivity, and alkalinity of the first soil layer, explained 70 % of the variance. The first CCA-axis is positively correlated with depth to the water table, while the second axis is negatively correlated with electrical conductivity and hydrolytic alkalinity of the first soil layer. Other factors have comparatively little effect on the two major vegetation gradients. Monte Carlo permutation tests confirmed the significance of the first two axes ($p < 0.001$).

The ordination of quadrats (Fig. 2) clearly distinguishes the edaphic conditions of the five main community types pre-defined by the single dominant species. Three *Aeluropus littoralis* stands are located on the left of the diagram, where the characteristic edaphic conditions are shallow but saline and alkaline ground water. These stands are distributed locally in the lower part, topographically, of the study sites. The coverage of *A. littoralis* can reach up to 50 %. *Suaeda physophora* stands are located in the lower right corner of the diagram where the edaphic conditions are high aridity and high salinity. Stands of *S. physophora* are found only in the upper parts of the study site with 2 - 10 % of total coverage. Two *Phragmites communis* stands are located in the upper part of the

Table 1. Results of CCA. Eigenvalues (λ) and species-to-explanatory-variable correlations (γ) for the first two axes, significance of trace and of the first two canonical axes (Monte Carlo permutation tests), the sum of all canonical eigenvalues of CCA (Sumλ) and their percentage of the sum of all eigenvalues of CA (i.e. total species variation) (Percent Sumλ) as well as fractions in variation partitioning are shown.

Analysis[a]	λ_1	λ_2	γ_1	γ_2	p(trace)	p(λ_1)	p(λ_2)	Sumλ	Percent Sumλ	Fractions
1. CCA (ED)	0.460	0.394	0.858	0.859	0.001	0.001	0.001	1.357	1.357/3.377 = 40.20	a+b
2. CCA(SPA)	0.424	0.307	0.817	0.810	0.001	0.001	0.02	1.114	1.114/3.377 = 32.98	b+c
3. CCA(ED)[SPA]	0.269	0.186	0.870	0.823	0.002	0.056	0.29	0.751	0.751/3.377 = 22.24	a
4. CCA(SPA)[ED]	0.138	0.116	0.749	0.762	0.045	0.61	0.45	0.507	0.507/3.377 = 15.01	c

[a] ( ) represents the constraint variables, [ ] represents the covariables. ED = edaphic variables, SPA = spatial variables.
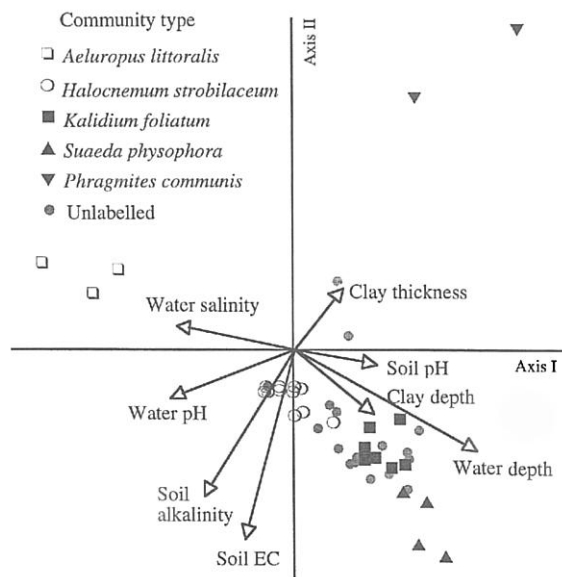
Fig. 2. CCA ordination of the 45 quadrats. The five main community types were predefined by the single dominant species. Some community types with few stands and those dominated by two or more species are unlabelled. Edaphic variables are represented as arrows. Abbreviations: Soil EC = Electrical conductivity of the first soil layer; Soil pH = pH of the first soil layer; Soil alkalinity = Hydrolytic alkalinity of the first soil layer; Water depth = Depth to the water table; Water salinity = Total salt content of the ground water; Water pH = pH of the ground water; Clay depth = Depth of the clay layer; Clay thickness = Thickness of the clay layer.

diagram where the edaphic conditions are characterized by low salinity. They are distributed in-between the upper and lower parts of the site, and have a high coverage (60 %). Stands dominated by *Kalidium foliatum*, *Halocnemum strobilaceum,* or both, are widely distributed between the upper and lower parts of the sites. CCA-results reveal that stands dominated by *H. strobilaceum* are located in areas with a higher water table than stands dominated by *K. foliatum.* Segregation of their niches was confirmed by the Mantel test ($p < 0.05$). Surprisingly, the significant edaphic factors are salt content and pH of the ground water. The roles of other factors are not significant. Since these two species usually occur where there is a relatively shallow water table, they are not normally considered to be phreatophytes. Our results indicate that salinity of the ground water plays a significant role, and that in certain seasons the two species may obtain water from the water table. From the positions of the species in the ordination diagram, the ecological preferences of the species to the main edaphic factors were identified (not shown here). In addition, five species, *Aeluropus littoralis, Alhagi sparisifolia, Halimodendron halodendron, Nitraria sibirica* and *Suaeda physophora*

were selected as indicators of the different degrees of soil aridity and salinity, because they have the lowest standard deviations of species scores along the first two ordination axes, and were recorded in more than 10 of the 45 quadrats.

Spatial structure and variation partitioning

The result of the variation partitioning shows that 40 % of the variation (a+b in Table 1) has been explained by edaphic factors, while 33 % of the variation (b+c in Table 1) has been explained by spatial variables. In the analysis of the relationships between the species and spatial variables, the selected monomials were x, y, xy, y^2, x^2y, x^3 and y^3. The high eigenvalues and species to explanatory variable correlations (Table 1, step 2) indicate that the community has an obvious spatial structure. A Monte Carlo permutation test of the trace statistic confirmed the significance of the canonical relationship between the species and spatial variables ($p < 0.001$). Fraction b, found by subtracting a from a + b in Table 1 (40.2 % - 22.2% = 18.0 %), represents 18 % of the species variation. This fraction represents the spatial variation which has been explained by the edaphic factors. Therefore, nearly half of the variation explained by the spatial matrix is independent of edaphic factors (compare b and c in Table 1). On the other hand, 22 % of the variation explained by the edaphic factors is local variation (compare a and b in Table 1). After removing the effect of spatial structure, the correlation of hydrolytic alkalinity of the first soil layer with the first axis greatly increased (right-hand part of Table 2). The importance of hydrolytic alkalinity was confirmed by significance tests ($p < 0.01$) for partial CCA. The role of depth to the water table was significant also at the 0.05 level. Variance explained by these two variables occupied 51 % of the variance explained by all of the eight variables. This shows that the two variables contribute considerably to the determination of the local species variation.

The correlograms of the edaphic factors (Fig. 3) show that the three ground water factors – depth to the water table, pH, and total salt content of the ground water – have obvious gradient structures; at the $\alpha = 5$ % level, depth to the water table, in particular, has a significant positive autocorrelation within distance classes 2, 3, 4 and 5, and a significant negative autocorrelation within the distance classes from 8 to 12. However, the three factors of the first soil layer – electrical conductivity (correlogram not shown), hydrolytic alkalinity, and pH – do not have obvious spatial structures. Hydrolytic alkalinity and pH of the first soil layer are only significant for distance class 2 (no quadrat pairs were located within distance class 1) and electrical conductivity is not significant for any distance class. The Mantel correlogram (Fig. 3f) shows that the communities had a spatial autocorrelation structure very

Table 2. Correlations of edaphic factors with the first and second canonical axes of CCA.

Edaphic factor	1. CCA(ED)		3. CCA(ED)[SPA][1]	
	Axis I	Axis II	Axis I	Axis II
Soil EC	− 0.178	− 0.711	− 0.321	0.516
Soil pH	0.312	− 0.048	− 0.438	0.111
Soil alkalinity	− 0.331	− 0.556	− 0.769	0.343
Water depth	0.694	− 0.373	0.409	0.389
Water salinity	− 0.423	0.098	− 0.213	− 0.319
Water pH	− 0.457	− 0.178	− 0.221	− 0.454
Clay depth	0.300	− 0.232	− 0.137	0.258
Clay thickness	0.192	0.240	− 0.219	− 0.078

[1] ( ) represents the constraint variables, [ ] represents the covariables. ED = edaphic variables, SPA = spatial variables.

similar to that of the three ground water factors. The Mantel test also confirmed the overall significant spatial autocorrelation ($p < 0.05$) of the plant communities. From these results we see that at the sampling scale, the spatial structure of the communities is mainly determined by the water table. The result of clustering with spatial contiguity constraint (level 0.54, connectedness 0.5; Fig. 1) clearly shows that the communities have a spatial structure that follows relative elevation (elevation map not shown). In the flat locations (east), the clusters of vegetation patches are large, whereas in the undulating portion (west and southeast) the clusters are small, with several patches remaining unclustered at the selected level. Different topographic positions create variation in the water table level and the communities probably respond by a similar variation pattern.

Discussion

Our gradient analyses not only confirmed the important role of edaphic factors on the species and community distribution as a whole, they also showed that two distinct vegetation gradients exist, one of which is determined mainly by soil moisture (determined by depth to the water table), and the other by soil salinity (determined by electrical conductivity and hydrolytic alkalinity of the first soil layer). Although salt stress is physiologically difficult to distinguish from water stress (Osmond et al. 1987), we found that plants and communities reacted to two distinct stresses. In some sites with basin-shaped topography, the water table is highly correlated with salinity, i.e. there is a gradient from dry, less saline areas to moister, more saline areas. That may explain why the water table has not received much attention previously. However, in some sites with undulating topography, spatial variation of salinity is usually not correlated with water table level, and thus a single gradient does not exist. Actually, plants in the salt desert need to develop tolerance mechanisms to both water- and salinity stress. No-

ticing that most of the laboratory experiments on competition of halophytes have concentrated on one edaphic factor, i.e. salinity, our results suggest that at least two edaphic factors, i.e. soil moisture and salinity, must be included when studying xerohalophytes.

Although alkalinity is highly correlated with salinity, we included alkalinity in our analysis because we wanted to verify which factor best explained species and community distribution and also because a CCA-ordination diagram is not in any way hampered by high correlations between environmental variables (ter Braak 1987b). In fact, such redundancy is probably beneficial because some errors in measuring environmental data may be averaged out (Palmer 1993). It seems that alkalinity and salinity are measuring essentially the same thing, ion concentration. However, alkalinity usually has deleterious effects on the physical and chemical properties of soils (Shainberg 1975). Therefore, alkalinity would appear to be a better integrating and comprehensive index of saline soil properties. In soil science these two factors are combined to classify different types of saline soils (Waisel 1972; Shainberg 1975). Our CCA-results not only show that both salinity and alkalinity play significant roles and were highly correlated with the second axis of the CCA-ordination, but also that alkalinity plays a more important role than salinity on the local fraction of variation (fraction a in Table 1). Waisel (1972) stated that halophytes do not respond only to salinity, but are also more tolerant than glycophytes to the entire complex of physical, chemical, and biological modifications induced in the soil by salt. The important role of alkalinity in the local fraction of variation confirmed his statement to some extent.

Although the CCA-analysis revealed two gradients, our spatial analyses showed that, at the sampling scale used, halophytic communities in the study area are structured along one main spatial gradient, i.e. water table level. We did not detect a similar spatial autocorrelation structure between the factors related to the first soil layer and the communities, given our sampling scale. This indicated that factors of the first soil layer influence the community structure at some different spatial scale. Here we have clearly shown that alkalinity in the first soil layer played an important role in determining the local fraction of variation. The local fraction of variation usually reflected the finer scale ecological pattern than the sampling scale. Furthermore, the spatial autocorrelations of hydrolytic alkalinity and pH of the first soil layer are significant for distance class 2. These results indicate that the community and the factors of the first soil layer may have a similar spatial autocorrelation structure at some finer scale than the one used in this study. In addition, if we only examine two close-neighbouring species, other factors are also important, for instance both salt content and pH of the ground water – as shown by our analysis on
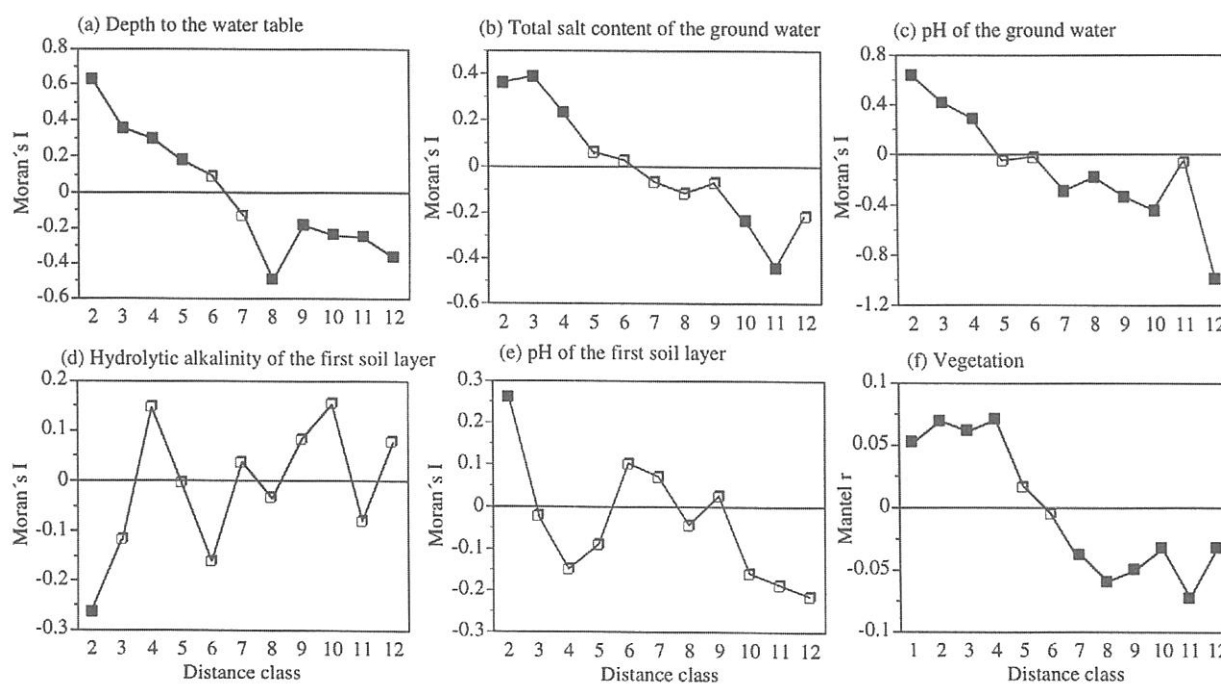
Fig. 3. a-e. All-directional spatial correlogram of some edaphic variables; **f.** Mantel correlogram for the structure of halophytic communities. Abscissa: distance classes, one unit of distance is 98.6 m on average for the correlograms and 97.2 m on average for the Mantel correlogram. Dark squares correspond to significant values ($p < 0.05$) of Moran's I (a-e) or Mantel r ($p < 0.05$) (f). Gower's coefficient was used to compute the similarity matrix for the Mantel correlograms.

niche segregation of *Kalidium foliatum* and *Halocnemum strobilaceum*. The discrepancy between the importance of soil salinity and soil water regime could be due to the different spatial scales in which the sampling was conducted. Our results suggest that the relative importance of different edaphic factors on the spatial structure of halophytic communities is scale-dependent.

While noticing that many of the inland halophytic species can grow and reproduce under non-saline conditions, other researchers tested the hypothesis that salt-tolerant species are excluded from areas of no or low salinity, through competitive exclusion by less salt-tolerant, but faster growing glycophytes. However, the growth of dicot halophytes is frequently stimulated by salt, that of most monocot halophytes is not (Flower et al. 1986). In salt deserts, dicot plants usually dominate. Therefore, evaluating the relative importance of edaphic and biotic factors has important implications in the salt desert. In inland saline systems, vegetation discontinuities are often not linked to environmental discontinuities (e.g. Ungar 1974; Burchill & Kenkel 1991). This feature has been assumed as evidence for competition. In our study area, we have observed both sharp and diffuse boundaries when we determined homogeneous patches. Some of the sharp boundaries followed topographic undulations, while oth-

ers did not. With our spatial polynomial, not only the linear gradient patterns in the species data were extracted, but also more complex features like patches or gaps (Legendre 1990). Our results showed that nearly half of the variation explained by the spatial matrix is independent of the edaphic factors (compare b and c in Table 1). This result indicates that other factors, such as biotic interactions, may play an important role in structuring these communities, although the influence of other factors such as disturbance may also be reflected in fraction c. Nevertheless, the strong relationships between the distribution of halophytes and halophyte communities and some critical edaphic factors will facilitate the forecasting and mapping of soil properties such as moisture and salinity. This is indeed a rapid and economical way to proceed compared to using instrumental measurements (Tóth et al. 1995). Because the study area has a potential for reclamation for agriculture, the indicator species of different soil salinity levels are of high practical value.

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