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VEGETATION COMPOSITION OF INLAND SALTMARSHES IN WESTERN EGYPT IN RELATION TO EDAPHIC FACTORS

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Abstract: The vegetation-environment relationship in the inland saltmarshes of Siwa and Dakhla, two geographically distant oases of the Western Desert of Egypt, are described. Two data sets (25 species x 68 relevés for Siwa Oasis, 29 species x 89 relevés for Dakhla Oasis) were analysed by multivariate procedures. Two-way indicator species analysis (TWINSPAN) was used to classify the plant communities of the study areas, whereas detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA) were used to examine the relationship between the vegetation and selected edaphic factors (soil reaction, electric conductivity, calcium carbonate, organic matter, moisture content and fine fractions). Twelve halophytic plant communities linked to two main habitats (wet-moist and dry-mesic) were identified. In the two oases the most common communities are those of *Alhagi graecorum, Tamarix nilotica, Cressa cretica, Juncus rigidus* and *Phragmites australis*. Communities of *Cyperus laevigatus, Suaeda aegyptiaca, Suaeda vermiculata, Typha domingensis* and *Aeluropus lagopoides* are recorded from Dakhla Oasis; *Cladium mariscus* and *Arthrocnemum macrostachyum* communities are recorded from Siwa Oasis. The most important edaphic factors affecting distribution and structure of these plant communities are salinity, moisture content and fine fractions; $CaCO_3$ content seems to be more effective in the Dakhla Oasis.

Introduction

Saline lands are widely distributed globally and make up c. 10% of the Earth's terrestrial surface (O'Leary & Glenn 1994). Compared to studies of coastal marshes, little attention has been paid to inland saline landscapes (Krügger & Peinemann 1996). The inland saltmarshes of the Western Desert of Egypt are found in the form of Sabkhas (Zahran 1982) around the lakes, springs and wells of the oases, e.g. Siwa, Dakhla, Kurkur, Dungul, etc. and the depressions, e.g. Qattara, Wadi El-Natrun, El-Fayum, etc. (Fig. 1). Being lower in level than the surrounding territories, the inland saltmarshes are characterized by a shallow underground water table.

In some cases the underground water is exposed forming lakes of brackish water (Zahran & Girgis 1970; Zahran 1972). The formation of these salines is due to the uncontrolled spilling of water and flooding of the plains, or to the water table which is being close to the ground (Migahid *et al.* 1960). Under the severe arid conditions of the oases and the lack of a drainage system, flooding of the soil with slightly saline artesian water increases rapidly its salinity. In contrast to the littoral saltmarshes, these salines can be considered as secondary. The vegetation has a patchy structure: different patches contain different species (sometimes only one species) and even different growth forms (Abu-Ziada 1980; El-Hadidi 1993). The halophytes constitute the vegetation of extensive areas of Egypt. However, the halophytic flora consists of only 80 species from 17 families (Batanouny & Abo Sitta 1977), mainly perennial grasses, rushes, (dwarf-) shrubs, and some annuals which are recorded in saline environments, e.g., *Frankenia pulverulenta, Lotus corniculatus, Solanum nigrum, Asphodelus tenuifolius, Bassia muricata, Anagallis arvensis* s.l., *Conyza bonariensis* and *Ambrosia maritima*.

Although the autecology, synecology and ecophysiology of several coastal saltmarshes of the Western Desert of Egypt have been dealt with in a large number of publications (e.g. Ayyad & El-Ghareeb 1974 & 1982, Fahmy 1986, Shaltout & El-Ghareeb 1992, Zahran *et al.* 1996), the studies identifying the major environmental factors correlated with vegetation patterns in the inland saltmarshes are scarce. These have attempted to elucidate, by various means, factors causing the differences in communities both within and among marshes. In the present study objective methodology and quantitative procedures have been applied using classification

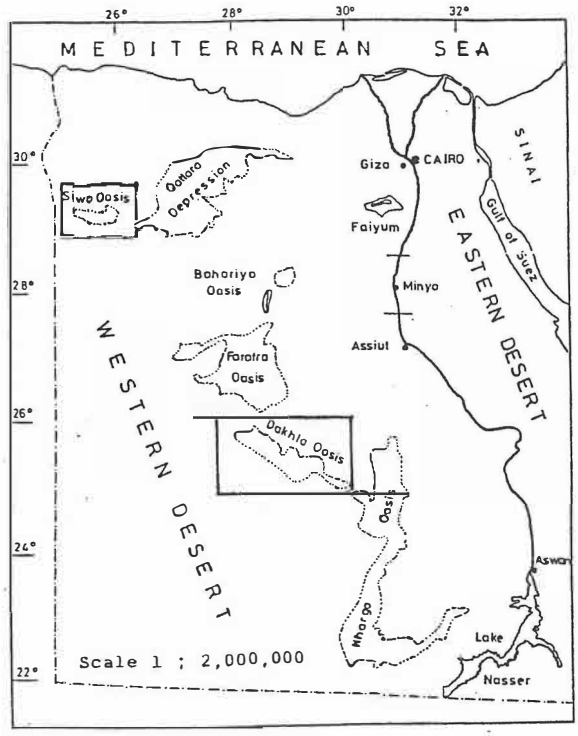

Fig. 1 - Location map of the study areas.

and ordination techniques. Recently, some studies in different parts of the country (Dargie & El-Demerdash 1991; Shaltout *et al.* 1995; Moustafa & Zaghloul 1996; Abd El-Ghani 1998, 1999; Springuel *et al.* 1997) based on multivariate approach to plant community analysis were carried out.

The purpose of this study is to document and describe the plant species composition of the inland saltmarshes in two geographically distant oases of the Western Desert of Egypt, and to relate the species distribution patterns to some soil factors. It should be kept in mind, however, that by the beginning of the 21st century the plant life in the oases of Egypt will be dramatically changed: about 500,000 acres are expected to be reclaimed and cultivated after transferring the Nile water to these areas through the "Toschka canal" from Lake Nasser (South of Aswan on the Nile Valley) to Kharga Oasis, and to Farafra Oasis in the Western Desert.

Study areas

The two oases are separated by a distance of about 600 km in a NW-SE direction (Fig. 1). Siwa Oasis is located in the northern part of the Western Desert of Egypt, some 65 km east of the Libyan border and 300 km south of the Mediterranean coast, between 25° 18' - 26° 05' E and 29° 05'- 29° 20' N. Groundwater is one of the Siwa Oasis most valuable resource. It is tapped from the Miocene fractured limestone through ca. 150 springs and flowing wells (total discharge is at least 200,000 m^3 day^{-1}). The water of Siwa springs is warm, ranging between 26.5 °C and 30 °C. However, due to the misuse of groundwater, a continuous rise of the level of subsoil water is widespread. According to Misak *et al.* (1997), in 1962-1977 the rate of rise was 1.33 cm $year^{-1}$ while in 1977-1990 it was 4.6 cm $year^{-1}$. Consequently, extensive patches are converted into salt marshes as the soils are subjected to deterioration and salinization. The oasis floor is below sea level, ranging from zero to -18 m, and displays numerous landforms: salt marshes (Sabkhas), salt lakes and cultivated lands (orchards). The bounding uplands are represented by the northern tableland (up to + 150 m) and the southern sand dunes (up to + 80 m). The climate exhibits extreme aridity, with very low rainfall (average 9.6 mm $year^{-1}$), high evaporation (17 mm day^{-1} in July to 5.2 mm day^{-1} in December) and high summer temperature (maximum 37.7 °C in July). Intermittent floods, originating from the northern tableland, take place rarely. In the last 60 years, floods took place in 1928, 1985 and 1987.

Dakhla Oasis is located c. 120 km west of Kharga Oasis and about 300 km west of the Nile Valley between 28° 48'- 29° 21' E and 25° 28' - 25° 44' N. The artesian groundwater discharges to the

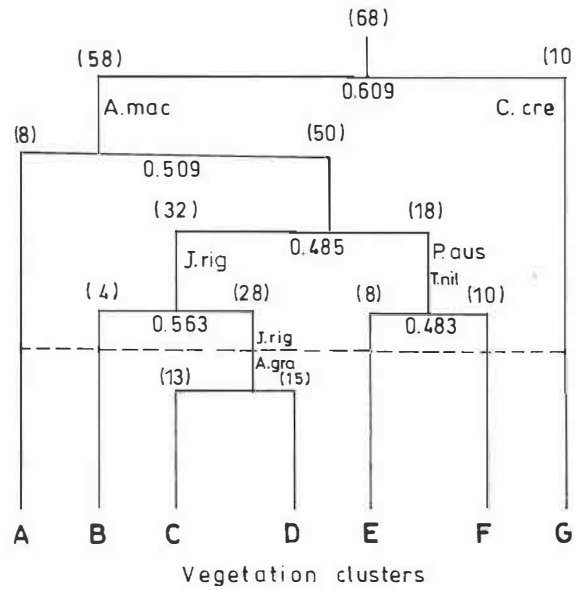

Fig. 2 - TWINSPAN classification of the 7 vegetation clusters of the Siwa Oasis inland saltmarshes. For abbrevations of indicator species, see Appendix.

Tab. 1 - Floristic composition of the vegetation clusters in the inland saltmarshes of Siwa Oasis. For each species frequency and mean cover class are included. Frequency classes: I = 1-20, II = 21-40, III = 41-60, IV = 61-80 and V = 81-100%. For cover classes, see text.

Vegetation cluster	**A**	**B**	**C**	**D**	**E**	**F**	**G**
Number of stands	8	4	15	12	9	10	10
Total number of species	4	5	11	9	10	15	3
Arthrocneum macrostachym	V.8				II.1		
Cladium mariscus		V.6					
Cyperus laevigatus		III.2					
Inula crithmoides		IV.2	II.3	III.2	III.2		
Juncus rigidus	II.2	III.I	V.7	III.3	II.1		
Cynanchum acutum			I.2			II.1	
Nitraria retusa			I.I	II.2			
Atriplex leucoclada			I.1		I.2		
Zygophyllum coccineum			II.2	II.2			
Imperata cylindrica			II.2			II.1	I.1
Phoenix dactilifera			I.1	II.1			
Alhagi graecorum	II.1			V.6	II.3	I.2	
Amaranthus graecizans				III.2	II.1	I.1	
Chenopodium album				II.1	I.1	I.1	
Tamarix nilotica			II.2	III.3	V.9	II.2	III.2
Phragmites australis	II.1	II.1	II.2		III.5	V.8	
Typha domingensis						III.4	
Sonchus maritimus						II.3	
Chenopodium murale						II.2	
Echinochloa colona						II.1	
Echinochloa crusgalli			I.1			I.2	
Portulaca oleracea						I.2	
Cynodon dactylon						II.2	
Frankenia pulverulenta					I.1	I.1	
Cressa cretica							V.7

surface through springs, shallow wells and modern deep wells in which the depth ranges from 300 to 1220 m (Himida 1966). A serious drop of groundwater pressure in the existing wells and consequently a drop in the discharge of the flowing wells has been emphasized (Abu-Ziada 1980). The lowest point of Dakhla Oasis is about 100 m above sea level and its surface rises gradually towards the rim. Altitudes range from 110 to 140 m above sea level. Geological evidences indicate that an economically potential deposit of the lower phosphatic horizon exists at the south-east corner of Abu-Tartur plateau, at depths ranging from 150 to 250 m from its top surface. Said (1962) reports also the occurrence of a number of mineral substances including ochre, bayrates and epsomites, which are found in fibrous crystalline forms. Dakhla Oasis belongs to the rainless part of the country. The hottest months are June, July and August (mean maximum temperature: 37.7 °C) and the coldest is January (mean minimum temperature: 4.0 °C). The evaporation rate attains the highest value in June (24.8 mm day^{-1}) and the lowest in January (7.7 mm day^{-1}).

Data and methods

157 relevés, each of 10 x 10 m (corresponding to the mean minimum area of the prevailing plant communities), were selected from representative sites of the inland saltmarshes of the two study areas, 68 in Siwa and 89 in Dakhla. The first relevé was selected at least 50 m from the edge of the marsh, and the other relevés were randomly distributed. In each relevé, a reasonable degree of homo-

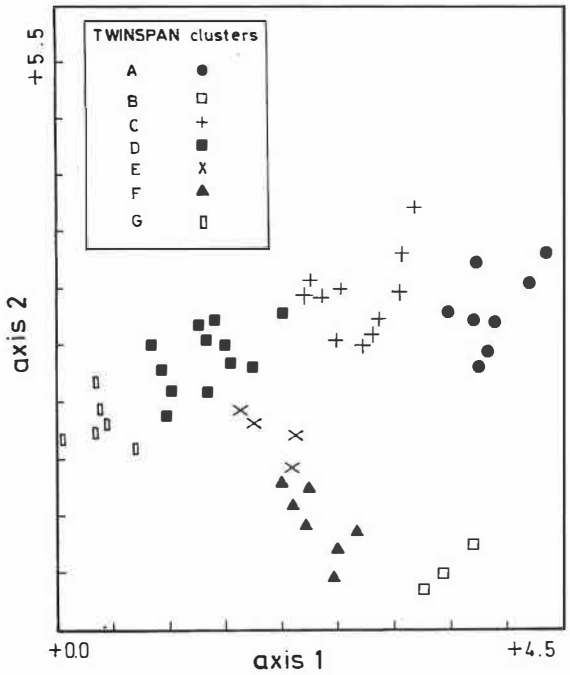

Fig. 3 - DCA ordination of the 68 relevés of Siwa Oasis on DCA axes 1 and 2 as classified by TWINSPAN.

geneity was ensured. Within each relevé, species present were recorded. Nomenclature follows Täckholm (1974), updated by Boulos (1995, 1999). Plant cover was estimated quantitatively using the line intercept method (Canfield 1941). For this purpose, 10 parallel lines each 10 m long were laid out in each relevé. The cover data were transformed using nine-point scale: 1 = 5-15, 2 = 16-25, 3 = 26-35, 4 = 36-45, 5 = 46-55, 6 = 56-65, 7 = 66-75, 8 = 76-85, 9 = 86-100%.

For each sampled relevé, three soil samples were collected along profiles of 0-50 cm. Soil texture was determined with a Bouyoucos hydrometer, and the results used to calculate the percentage of fine fractions (silt and clay). Moisture content and organic matter were determined by drying and ignition at 600 °C for 3 hours, and total $CaCO_3$ by the Collin's calcimeter (Wright 1939). Soil-water extract (1:5) was prepared for the estimation of electrical conductivity (EC) using an electric conductivity meter and soil reaction using a pH meter.

Two-Way Indicator Species Analysis (TWINSPAN) was applied to classify the two data sets (25 species x 68 relevés for Siwa Oasis and 29 species x 89 relevés for Dakhla Oasis), using species cover data; species with less than 5% cover were excluded. TWINSPAN is a divisive hierarchical programme that uses indicator species, i.e. species which are supposed to have clear ecological preferences to characterize and separate the classes (Hill 1979; (Økland 1990). All the default settings were used except for the cut levels (0, 5, 10, 30, 40, 50, 70, 80 and 90 were chosen). The non-parametric Mann-Whitney test was used to compare the means of all environmental factors for the two groups separated at each split in the classification. This statistical treatment, carried out with the package student SYSTAT (STUSTATW 5.0; Berk 1994), follows Zar (1984).

Tab. 2 - Means of the soil characteristics (± 1SD of the stands supporting the 7 vegetation clusters (A-G) derived from the application of TWINSPAN. TSS = total soluble salts, OM = organic matter, MC = moisture content, S+C = silt + clay.

Soil variables	Vegetation clusters							F ratio	*P*
	A	B	C	D	E	F	G		
pH	7.52 ± 0.4	7.52 ± 0.3	7.61 ± 0.55	7.79 ± 0.42	7.77 ± 0.46	8.01 ± 0.33	7.43 ± 0.42	2.06	0.07
EC mS cm^{-1}	8.24 ± 2.01	1.7 ± 0.94	6.24 ± 2.82	4.1 ± 1.48	3.62 ± 1.58	2.12 ± 0.62	2.68 ± 0.57	15.32	0.0001
$CaCO_3$ (%)	12.36 ± 4.04	20.35 ± 2.8	18.25 ± 7.64	16.42 ± 7.9	9.91 ± 2.75	13.01 ± 4.14	14.98 ± 2.2	3.24	0.008
OM (%)	4.7 ± 3.29	0.75 ± 0.87	5.07 ± 3.25	3.44 ± 2.22	2.97 ± 1.31	3.19 ± 2.25	1.88 ± 1.18	3.03	0.012
MC (%)	15.66 ± 6.1	2.52 ± 0.77	12.06 ± 5.03	6.84 ± 5.46	4.55 ± 1.62	10.33 ± 7.37	2.80 ± 1.44	7.67	0.0001
S +C (%)	16.25 ± 6.52	9.75 ± 2.5	18.31 ± 6.68	15.07 ± 4.54	12.0 ± 2.73	13.7 ± 5.49	9.3 ± 2.5	8.17	0.005

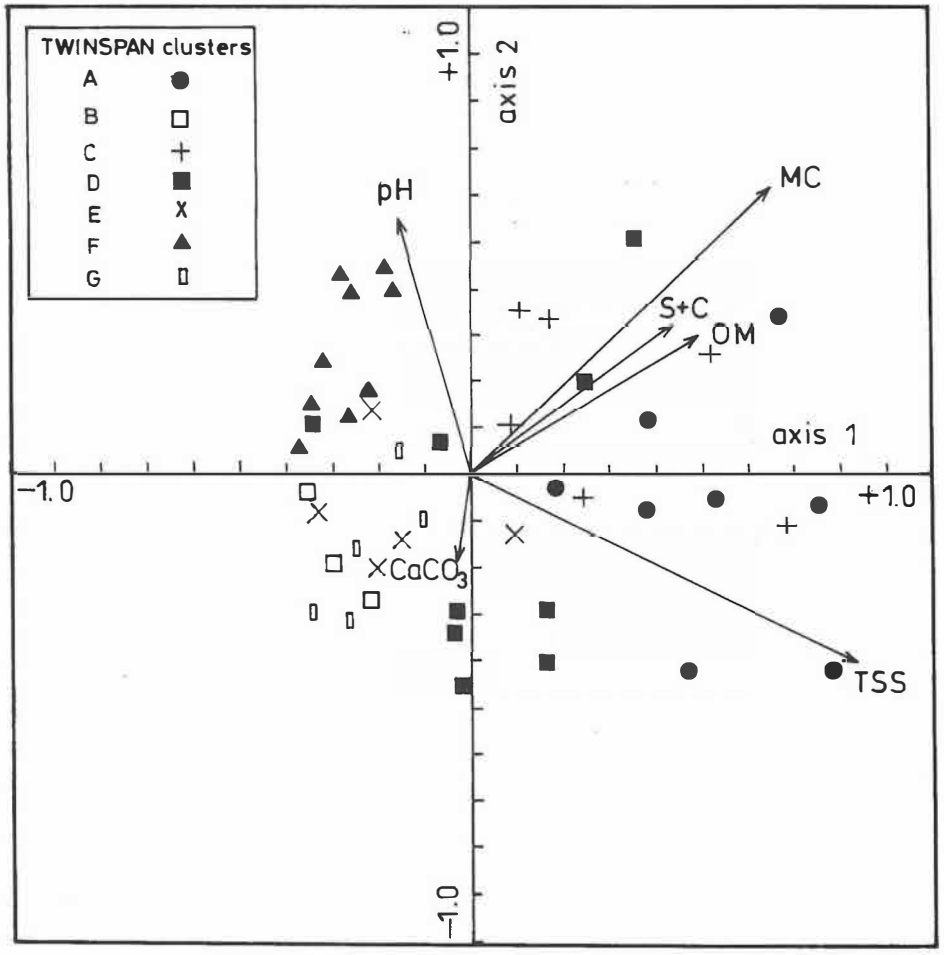

Fig. 4 - DCCA ordination of the first two axes showing the distribution of the relevés of Siwa Oasis with their TWINSPAN cluster and soil variables.

Detrended Canonical Correspondence Analysis (DCCA) or direct gradient analysis (Jongman *et al.* 1987), combined with calculation of t-values associated with the regression coefficients and a Monte Carlo permutation test (99 permutations) for the significance of the first canonical axis (p-value at 0.01-significance level), was used to ordinate the vegetation relevés with the environmental variables. Detrended Correspondence Analysis (DCA), an indirect gradient analysis, was also performed to examine the species composition without the constraints imposed by the environmental factors. The computer program CANOCO 3.12 (ter Braak 1988, 1990) was used for all ordinations and the plots were drawn by CANODRAW 3.0 (Smilauer 1993).

The percentage of life forms per community (Fig. 8) was calculated according to Raunkiaer (1973).

Results

Siwa Oasis

Vegetation

The vegetation data of Siwa Oasis, ordered according to the results of the TWINSPAN analysis (Fig. 2), are reported in Tab. 1. The TWINSPAN analysis grouped the relevés into 7 vegetation clusters, each cluster representing a specific plant community which can be characterized by the species with the highest cover values. These are: (A) *Arthrocnemum macrostachyum*, (B) *Cladium mariscus*, (C) *Juncus rigidus*, (D) *Alhagi graecorum*, (E) *Tamarix nilotica*, (F) *Phragmites australis*, and (G) *Cressa cretica*. Some clusters have a single characteristic species (A, B and G), while the others have three-four species. Three clusters are dominated by a single species (A, C and G), of which one is restricted to the dry-mesic habitat. No one species is

Soil variables	Siwa Oasis		Dakhla Oasis	
	Axis 1	Axis 2	Axis 1	Axis 2
pH	- 0.152	0.530	0.038	0.286
EC	0.832	-0.394	0.325	-0.255
$CaCO_3$	-0.014	-0.173	-0.439	0.072
OM	0.496	0.293	0.297	-0.297
MC	0.666	0.628	0.547	0.025
Silt + clay	0.453	0.305	0.101	-0.370
Species-environment correlation	0.832	0.626	0.786	0.682
% cumulative variance	44.2	63.9	39.8	61.7

Tab. 3 - Weighed correlation matrix of stand ordination along the first two DCCA axes with soil variables in the study areas. For abbreviations and units, see Tab. 2.

present in all clusters. The first TWINSPAN dichotomy differentiates the 68 relevés into two main groups according to soil moisture content and fine material (silt and clay) with p values of 0.003 and 0.001, respectively. A distinct community (*Cressa cretica*) associated with the driest saline habitat is separated on the right side of the dendrogram (Fig. 2) while the left side is heterogeneous. At the second hierarchical level, the "wet-moist" group is split into two subgroups related to the same factors mentioned above, in addition to soil salinity (p values of 0.0001, 0.004 and 0,0001 for moisture content, fine material and soil salinity, respectively). Another distinct community (*Arthrocnemum macrostachyum*) of the wettest habitat is separated. Among the relatively less "wet-moist" group two further subdivisions distinguish communities that differ primarily in calcareous deposits.

An ordination plot of relevés on the first two axes (eigenvalues: 0.744 and 0.474) of Detrended Correspondence Analysis (DCA) is shown in Fig. 3; the seven TWINSPAN clusters are superimposed. The first and second axes account for 17.1% and 10.9%, respectively, of the overall floristic variance. A well-defined gradient in soil moisture content (r = 0.939) was found on the first axis, reflected in the species composition from dry to wet sites. Communities of the wet-moist group appear on the right side of the first axis, while those of the dry-mesic group appear on the left side. The second axis is positively correlated (r = 0.809) with salinity indicating a gradient from sites with low to sites with high salt contents.

Vegetation-environment relationship

Soil characteristics of each of the 7 vegetation clusters identified by TWINSPAN are summarized in Tab. 2. The mean values of the soil variables show high significant variation between clusters, except soil reaction. The soil lime content show a significant inverse relationship with salinity, moisture content and fine material (r = 0.297, 0.274 and 0.333, respectively). Soil salinity is significantly correlated with fine material (r = 0.370), moisture content (r = 0.359) and organic matter (r = 0.254). With increasing the amount of fine fractions, organic matter content increases (r = 0.718). In addition, organic matter increases with moisture content (r = 0.527), which is positively correlated with soil salinity (r = 0.359); this means that the distribution patterns of organic matter and soil salinity gradually decreases from the wet-moist towards the dry-mesic communities.

The ordination diagram produced by DCCA is shown in Fig. 4. The length and the direction of an arrow representing a given environmental variable provides an indication of the importance and direction of the gradient of that variable, within the set of samples measured. The Monte Carlo permutation test showed that the overall effect of the environmental variables on species and the first canonical axis are significant (p = 0.01). About 64% of the cumulative variance of specie-environment relations is explained by the first (eigenvalue 0.426) and second axis (eigenvalue 0.173). This suggests that environmental variables other than those examined in this study, are likely to play a role in explaining

further the distribution of plant communities in the target areas. The pattern of ordination is very similar to that of the floristic DCA (Fig. 3), with most of the samples remaining in their respective TWINSPAN clusters.

Soil salinity, organic matter, moisture content and fine material are higher in *Arthrocnemum macrostachyum* and *Juncus rigidus* communities than any of the other communities (significant at $p = 0.0001$). Both communities are present in the wettest relevés of the shallow depressions, and form monotypic relevés with high cover values (80-90%). However, whereas the *Arthrocnemum* community shows the lowest number of species, the *Juncus* community is richer in species (Tab. 1). The relevés of the swampy community of *Phragmites australis* is associated with high moisture content, pH and low salinity levels. It usually dominates the vegetation around the wells, where it forms dense growth typical of reed swamps. This community includes species growing in both wet-moist and dry-mesic conditions (e.g. *Chenopodium murale, Typha domingensis, Echinochloa colona*, *E. crusgalli, Sonchus maritimus* and *Frankenia pulverulenta*). The driest relevés are occupied by *Cladium mariscus* and *Cressa cretica* with relatively high amounts of calcareous sediments. Zahran & Willis (1992) report that *Cladium mariscus* is a very rare halophyte, and its domination is recorded only in Siwa Oasis where it occurs in the marshy land about the springs where the water level is very shallow (c. 5 cm). In this study, it inhabits the lime-rich saline flats far from the wells or at the feet of some sand dunes in the extreme western part of the oasis (Al-Maraqi area). The dry-mesic communities of *Alhagi graecorum* and *Tamarix nilotica* associated with flat or convex plains. As a result of the high evaporation rate, a thick crust of salt on the soil surface is formed.

The weighed correlations between the environmental variables and the first two axes of DCCA are given in Tab. 3. These data indicate that the distribution of plant species is strongly influenced by soil salinity and moisture content. The weighed correlations of the first axis with organic matter and fine material are also high. The second axis is significantly correlated with soil reaction and moisture content.

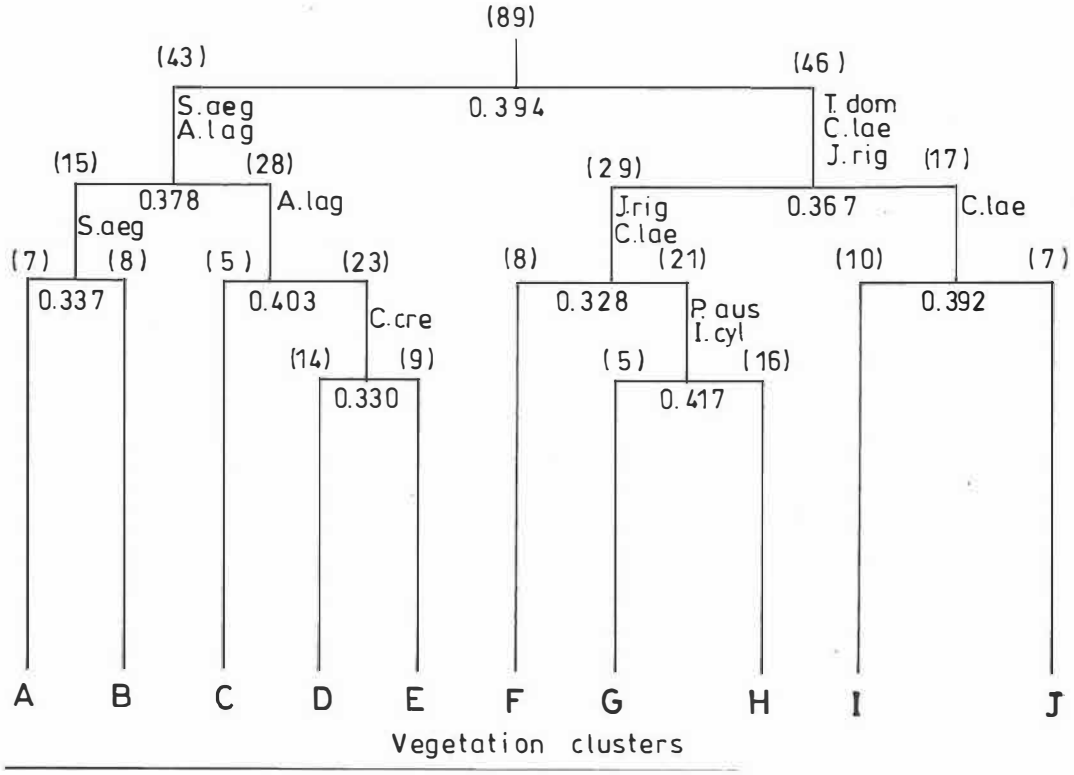

Fig. 5 - TWINSPAN dendrogram of the 89 relevés in Dakhla Oasis inland saltmarshes. For abbreviations of indicator species, see Appendix.

Tab. 4 - Floristic composition of the 10 vegetation clusters of the inland saltmarshes in Dakhla Oasis. For each species frequency and mean cover class are given. For frequency classes, see Tab. 1.

Vegetation cluster	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**
Number of stands	7	8	5	14	9	8	5	16	10	7
Total number of species	8	9	5	9	4	9	14	9	7	6
Suaeda aegyptiaca	V.8	II.2								
Atriplex leucoclada	III.2	I.1					II.1	I.2		
Centaurium spicatum	III.1									
Zygophyllum coccineum	II.1						I.3	II.2		
Chrozophoa obliqua	II.2			I.2						
Ammi majus	III.1				II.2					
Aeluropus lagopoides	III.4	V.7								
Sonchus oleraceus							II.1			II.1
Polypogon monspeliensis		III.2								II.2
Bassia indica		III.1	I.1							
Cynodon dactylon		II.2				II.2			III.1	
Phoenix dactilifera		II.1		II.1		II.1		II.3		
Suaeda vermiculata			V.8							
Sarcocornia fruticosa						III.2				
Polygonum equisetiforme			II.2			II.1	III.2			
Spergularia marina						II.2				
Alhagi graecorum				V.7	II.3	III.2	III.1	III.2		
Prosopis farcta				II.1				I.2		
Echinochloa colona				II.1			I.2			
Cressa cretica		II.1		III.2	V.8					
Juncus rigidus		II.1	IV.2	II.1			III.1	III.3		
Phragmites australis				II.2	III.1	V.9	V.6	III.2	IV.5	
Cyperus rotundus						III.2	II.2		III.3	II.2
Tamarix nilotica	II.4		III.3	II.3			IV.3	V.9	II.2	
Imperata cylindrica				II.1			II.1	II.3		
Typha domingensis							III.2		V.7	
Panicum repens									I.1	II.1
Scirpus maritimus							I.1		I.2	I.2
Cyperus laevigatus						III.2	II.3			V.8

Dakhla Oasis

Vegetation

The vegetation data of Dakhla Oasis, ordered according to the results of the TWINSPAN analysis (Fig. 5), are reported in Tab. 4. Ten communities were recognized at the fourth division of the TWINSPAN classification of 89 relevés. They are characterized by: (A) *Suaeda aegyptiaca*, (B) *Aeluropus lagopoides*, (C) *Suaeda vermiculata*, (D) *Alhagi graecorum*, (E) *Cressa cretica*, (F) *Juncus rigidus*, (G) *Tamarix nilotica*, (H) *Phragmites australis*, (I) *Typha domingensis*, and (J) *Cyperus laevigatus*. The first level in the TWINSPAN separates the relevés according to the soil moisture content (p = 0.003) and fine material (p = 0.005). At the second level, further divisions correspond to additional partitioning of the moisture content, fine material, salinity and calcareous deposits (p = 0.002, 0,004, 0.001 and 0.003, respectively). Lower levels distinguish communities that differ in pH, and all the aforementioned soil variables.

The wet-moist communities include *Suaeda aegyptiaca* community which is widespread on waste land which was formerly cultivated and left fallow due to salinization. The *Suaeda vermiculata* community shows similarities to that of *S. aegyptiaca*, but has a high frequency of *Juncus rigidus* (Tab. 4). The *Juncus rigidus* community forms thickets of dense growth. It dominates the saline flats in the saline-neglected land that were formerly under cultivation. The plant cover is dense (>80% on the ave-

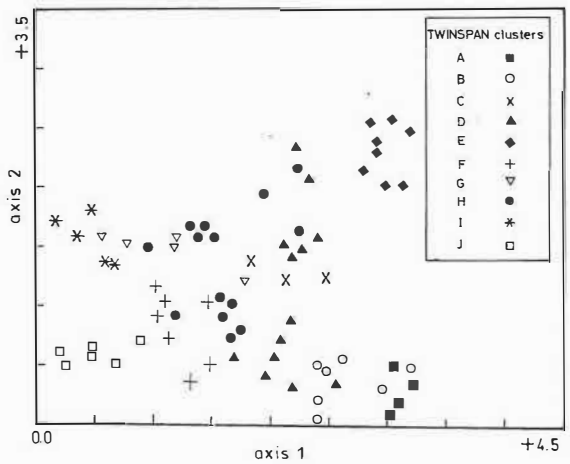

Fig. 6 - DCA ordination of the 89 relevés of Dakhla Oasis on DCA axes 1 and 2 as classified by TWINSPAN.

rage) mainly by the dominant rush. It represents one of the most common halophytic communities in Dakhla Oasis. The swampy vegetation types represented by *Phragmites australis* and *Typha domingensis* occupy the wettest relevés within the study area. This habitat is characterized by a rich and continuous flow of fresh or brackish water from springs or irrigated land (Zahran & Willis 1992). Some water-loving species were recorded: *Cyperus laevigatus, Scirpus maritimus* and *Cyperus rotundus*. The *Phragmites australis* community inhabits the shallow swamps that result from the flow of springs or drainage water, while *Typha domingensis* community forms dense growth in the deeper water fringed with *Phragmites australis* towards the periphery of the swamp. Moist pastures dominated by the severely grazed *Cyperus laevigatus* are common in the wet saline flats associated with a shallow (or exposed) underground water.

The dry-mesic communities include *Aeluropus lagopoides*, not recorded from Siwa Oasis, and occupies the flat saline relevés covered by a thin crust of salts. Whereas *Cressa cretica* community inhabits saline fallow land with occasional deposition of sheets of sand, *Alhagi graecorum* community occurs in sand plains overlying saltmarsh beds, and *Tamarix nilotica* community occupies the saltmarshes with deep sand deposits. The latter plant is considered a climax species of saltmarsh vegetation (Abu-Ziada 1980). It is subjected to destructive cutting for fuel and other household purposes in almost all Egyptian oases. The floristic composition of the *Cressa* community is the poorest, while those of *Alhagi* and *Tamarix* are the richest (Tab. 4).

Tab. 5 - Means of the soil characteristics (± 1SD) of the stands supporting the 10 vegetation clusters derived from TWINSPAN analysis. For abbreviations and units, see Tab. 2.

Soil variable	Vegetation clusters										F (ratio)	*p*
	A	B	C	D	E	F	G	H	I	J		
pH	8.3 ± 0.5	7.9 ± 0.8	8.1 ± 0.5	8.1 ± 0.5	8.1 ± 0.4	8.2 ± 0.1	8.7 ± 0.3	8.0 ± 0.3	8.5 ± 0.6	7.8 ± 0.3	2.01	0.05
EC	4.6 ± 1.5	4.3 ± 1.2	4.1 ± 1.4	2.3 ± 1.4	1.3 ± 1.4	3.2 ± 1.1	2.1 ± 0.7	2.3 ± 1.7	3.3 ± 4.0	4.7 ± 3.0	3.49	0.001
$CaCO_3$	28.2 ± 8.2	8.5 ± 3.2	15.3 ± 4.5	16.2 ± 5.5	17.0 ± 4.8	28.5 ± 7.9	13.8 ± 6.4	17.3 ± 8.8	11.4 ± 2.5	9.7 ± 4.4	8.49	0.0001
OM	1.6 ± 1.3	1.6 ± 1.1	1.2 ± 0.9	1.7 ± 1.4	1.1 ± 0.9	1.4 ± 0.6	0.3 ± 0.2	1.8 ± 1.7	1.5 ± 1.4	2.8 ± 2.5	1.58	0.134
MC	16.2 ± 5.5	6.4 ± 4.2	18.2 ± 7.1	6.5 ± 4.9	8.8 ± 6.3	17.8 ± 7.8	21.6 ± 7.9	7.3 ± 4.8	18.3 ± 7.3	20.5 ± 8.9	7.78	0.0001
S + C	13.7 ± 4.7	11.5 ± 4.9	11.6 ± 5.8	8.7 ± 5.1	6.7 ± 2.9	17.1 ± 5.9	12.8 ± 7.6	12.6 ± 4.3	9.2 ± 5.3	13.7 ± 6.2	2.70	0.008

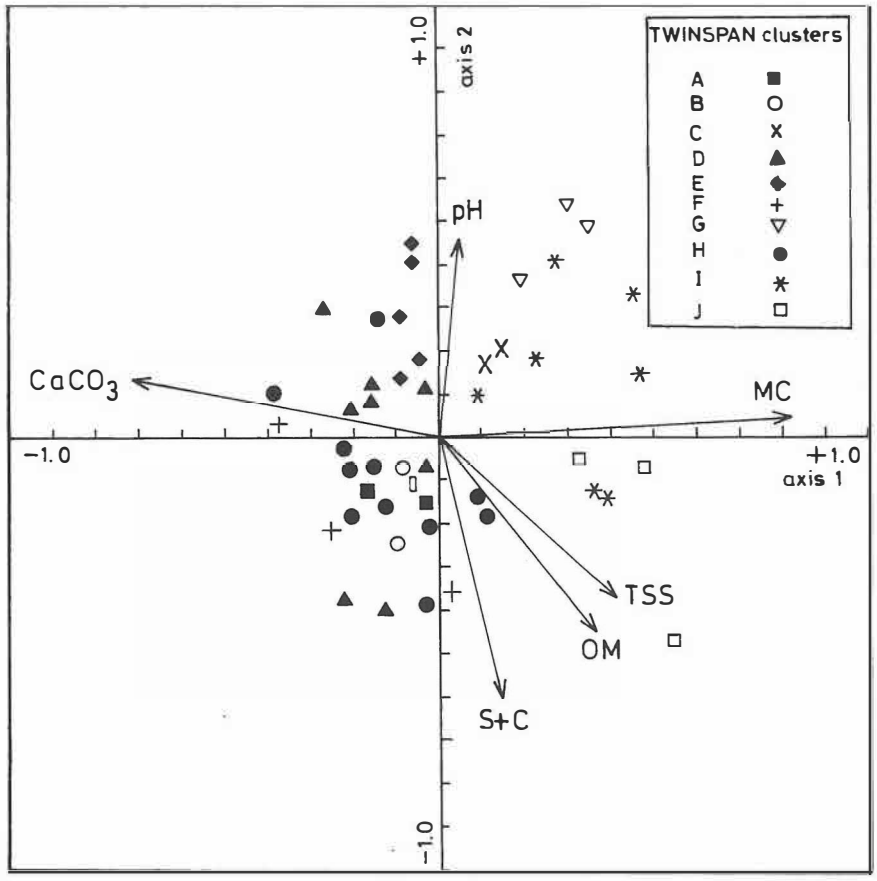

Fig. 7 - DCCA ordination of the first two axes showing the distribution of the relevés of Dakhla Oasis with their TWINSPAN cluster and soil variables.

The scatter diagram for the first two DCA axes (eigenvalues: 0.549 and 0.389) is shown in Fig. 6. The ten TWINSPAN clusters are superimposed, and show some overlap between related clusters. The largest clusters D and H (14 and 16 stands, respectively) are confined to the centre of the diagram and merge into other clusters; they are the most common dry-mesic communities in this area. The first DCA axis is negatively correlated with soil moisture content (r =-0.64) and positively correlated with lime content (r =0.51), indicating a gradient from wet relevés with low calcareous deposits to those dry with high calcareous sediments. This axis is also correlated with a gradient in organic matter (r =-0.51). The second DCA axis does not show such clear correlations with the environmental variables, but is only correlated with moisture content (r =-0.51).

Vegetation-environment relationship

Soil data for each of the 10 TWINSPAN clusters are presented in Tab. 5. There is a narrow spectrum of soil reaction and organic matter content. The mean values of soil salinity, calcium carbonate, moisture content and fine fractions show high significant variation between clusters. In contrast to those correlations between soil variables in Siwa Oasis (results not shown), soil reaction is significantly negatively correlated with salinity (r =-0.215) and organic matter (r =-0.300), and positively correlated with lime content (r =0.245). In addition, soil salinity does not correlate with fine fractions, but it is positively correlated with organic matter and moisture content. The soil lime content is negatively correlated with organic matter (r =-0.434) and positively with fine material (r =0.263), and the latter is strongly correlated with moisture content (r =0.534). Therfore, calcium carbonate seems to play an important role in characterizing the dry-mesic communities from the wet-moist ones .

In Fig. 7 the relevés are distributed along the first two DCCA axes. The percent of species-envi-

ronment variance accounted for by the first two axes (and their eigenvalues) are respectively, 39.8 (0.306) and 21.9 (0.168). The species-environment correlations are slightly higher for the DCCA axes, being 0.786 (first axis) and 0.682 (second axes). This is expected as the axes in DCCA are calculated on the basis of species and environmental variables. Correlation coefficients indicate that the measured environmental variables do account for some of the species variation. However, the eigenvalues for the DCCA axes are substantially lower than for DCA suggesting that further important site variables were not considered. The first canonical axis primarily reflects a soil moisture-lime content gradient; the moisture content is strongly correlated with this axis, and soil salinity and organic matter are also correlated. A Monte Carlo permutation test suggests that the relations between vegetation variation and environmental factors revealed by the first axis is significant (p =0.01). The second canonical axis reflects the gradient of soil reaction and fine fractions. Soil salinity and organic matter are inversely related to this axis (Tab. 3).

The mutual position of relevés in the DCCA diagram of Fig. 7 is similar to the DCA ordination of Fig. 6, although the dispersion of relevés is different. Notably, most of the wet-moist communities, except that of *Suaeda aegyptiaca*, are located on the right hand side and their relevés are closely associated with pH, moisture content, salinity and fine materials. On the left hand side of the diagram, almost all the dry-mesic communities are separated. The relevés of these communities are highly affected by $CaCO_3$, pH, fine materials and organic matter, while the relevés of *Phragmites australis* and *Cressa cretica* communities are associated with soil reaction; relevés of *Cyperus laevigatus, Typha domingensis* and *Suaeda vermiculata* communities are affected by soil salinity and moisture content.

Discussion

The vegetation distribution pattern in the two study areas is mainly related to gradients in salinity, soil moisture content and fine fractions. Concentration of calcareous deposits, especially in Dakhla Oasis, is also important. Although poor in species, the vegetation is here a mosaic of twelve plant communities. *Alhagi graecorum, Tamarix nilotica, Cressa cretica, Juncus rigidus* and *Phragmites australis* are ubiquitous species with wide ecological ranges. Communities of *Cyperus laevigatus, Suaeda aegyptiaca, Typha domingensis, Suaeda vermiculata* and *Aeluropus lagopoides* are recorded from Dakhla Oasis only, whereas the *Cladium mariscus* and *Arthrocnemum macrostachyum* communities are recorded from Siwa Oasis. Most of these communities have analogues in the northern (Ayyad & El-Ghareeb 1982) and southern (Abu-Ziada 1980; Sheded & Hassan 1998) parts of the Western Desert of Egypt. Some of the dominant plant species are known to be of economic importance, e.g. for mats and good-quality paper (Zahran *et al.* 1979), sand dune fixation (Batanouny 1979), protection from coastal erosion (Zahran 1977), and sustaining animal life (Boulos 1983).

The life-form spectra reported in Fig. 8 provide information which may help in assessing the response of vegetation to variations in environmental factors. Chapman (1960), on the basis of the percentage of species from different geographical regions, indicates that the saltmarsh is fundamentally a hemicryptophyte habitat, but with a tendency for chamaephytes and therophytes to be more abundant in eastern Europe and Asia. The present study provide evidence that chamaephytes and therophyte form about 63% in most of the communities identified in the investigated areas. Their relative percentages, however, vary from one habitat to another, with chamaephytes acquiring dominance in more saline and therophytes in less saline habitats. Most chamaephytes are succulents and/or mound-forming. The succulence is common in plants of saline habitats. However, five growth forms can be distinguished: (a) rhizomatous growth form, e.g. *Juncus rigidus, Typha domingensis, Cyperus laevigatus* and *Cladium mariscus*, (b) stoloniferous growth form as in *Aeluropus lagopoides* and *Phragmites australis*, (c) non-succulent perennial herb growth form e.g. *Cressa cretica*, (d) non-succulent frutiscents as in *Tamarix nilotica* and *Alhagi graecorum* and (e) succulent frutiscents as in *Arthrocemum macrostachum, Suaeda aegyptiaca* and *Suaeda vermiculata*.

The distribution of the reed swamp vegetation in the two oases is remarkable: their growth is usually confined to the areas around the waterholes of the springs in the central and western parts where numerous wells and springs occur. The present study reveals that *Typha domingensis* has a very limited range of distribution in the saltmarshes of Siwa Oasis, and does not form a discrete community. Simpson (1932) stated that "*Typha domingensis* is more sensitive to salt than *Phragmites australis* as the latter forms well into Lake Mariut while *Typha* is present only where the Lake receives fresh water from Mahmudiya canal". Analysis of the soil samples representing swamps indicate that *Typha*

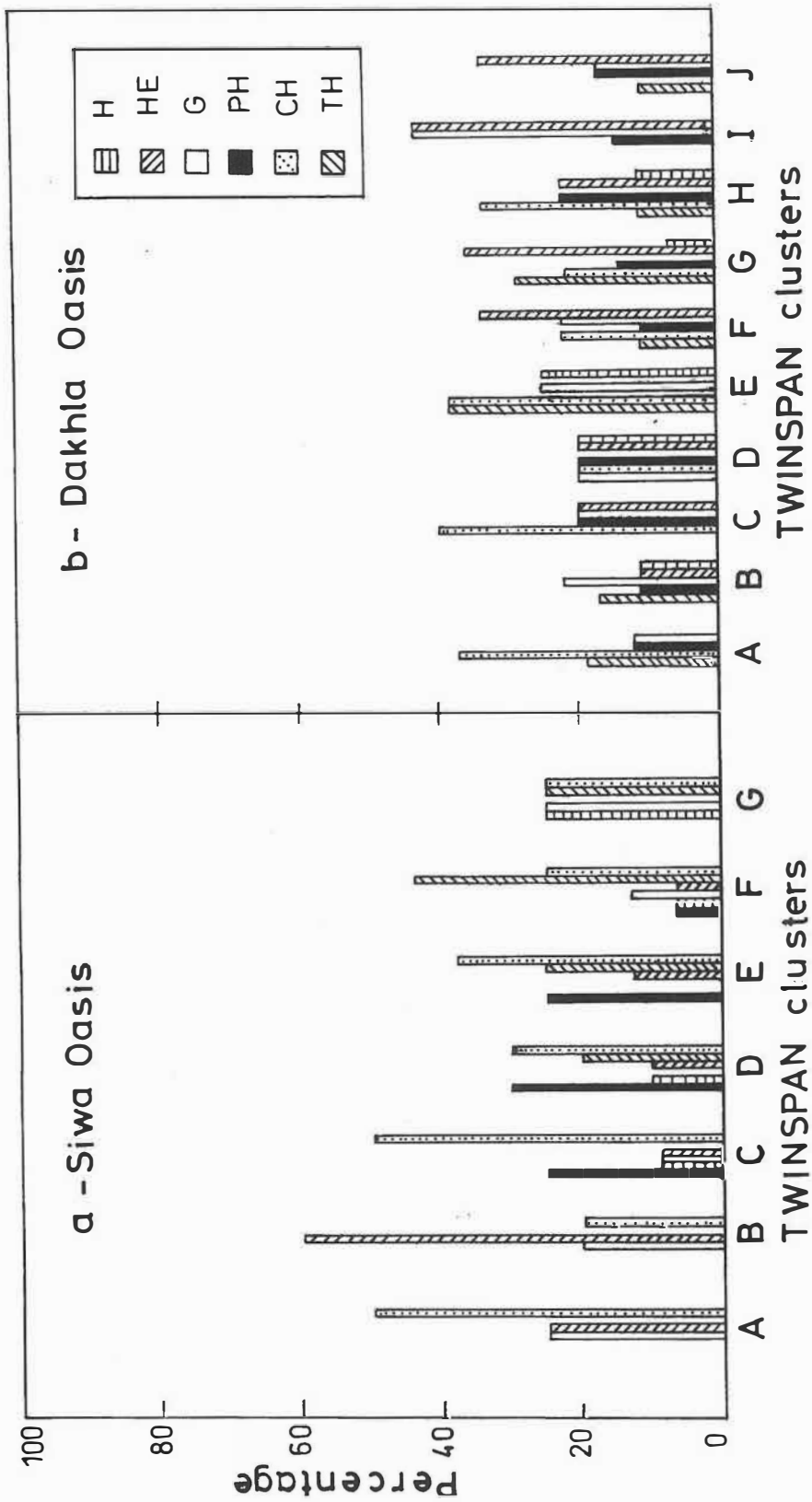

Fig. 8 - Life form spectrum according to Raunkiaer of the TWINSPAN clusters in the inland saltmarshes of the study areas. H = Hemicryptophytes, HE = Halophytes, G = Geophytes, PH = Phanerophytes, CH = Chamaephytes, and TH = Therophytes.

domingensis and *Phragmites australis* communities are confined to levels of salinity lower than any of the other wet-moist habitat communities. Available records for the groundwater analysis indicate that salinity in the springs water of Siwa Oasis are much higher (1900-8200 ppm; Zahran 1972) than those of the Dakhla Oasis (440 ppm; Worsley 1930). This may explain, to some extent, the formation of a well-defined community of *Typha domingensis* in the northern Oasis. This conclusion is consistent with that of Zahran & Girgis (1970) in Wadi El-Natrun, and Girgis *et al.* (1971) in the Moghra Oasis.

The relationship between vegetation and environment is not unidirectional in saltmarshes. In this study, the high clay, silt and organic matter, and the flatness of the marsh surface result in frequent or almost continuous waterlogging. Salinity promotes waterlogging by lowering the water vapour pressure, so depressing evaporation, and by affecting the organization of clay particles so that a largely structureless soil with a low hydraulic conductivity is produced (Long & Mason 1983). These parameters, in turn, change the species composition of plant communities. This is also in agreement with the findings of Fahmy (1986) in a saltmarsh on the western Mediterranean coast of Egypt, and those of Shaltout *et al.* (1995) in the Mediterranean region of Nile Delta. The role of soil moisture as a key element in the distribution of the plant species in the saltmarshes is known in other adjacent regions, such as the Dead Sea region of Israel (Zohary & Orshan 1949), the Al-Kharg springs of Saudi Arabia (El-Sheikh & Yousef 1981), the inland saltmarsh of Al-Qassim area of Saudi Arabia (El-Sheikh *et al.* 1985), and the Jordanian saltpan of Al Azraq Oasis (Winter 1990).

The zonation of saltmarsh vegetation is a universal phenomenon. Concentric zonation of halophytic communities in small lakes and saltmarshes of the Egyptian oases was described by Kassas (1971). Kehl *et al.* (1984) also describe the ring-shaped vegetation formations in NW-Egypt resulting from different habitat gradients. In his account on the vegetation and flora of Qara Oasis (-70 m, on the SW edge of Qattara depression), Abd El-Ghani (1992) recognizes four concentric zones of plant communities bounding the oasis, established on previously cultivated land but now salinized or desertified. A detailed account on the zonation of the vegetation in the present study in relation to different edaphic, topographic and climatic variations will be the subject of a forthcoming paper.

Appendix

Names and abbreviations of the indicator species displayed in Figs. - 3 and 6: *Alhagi graecorum* Boiss.: **A. gra**; *Aeluropus lagopoides* (L.) Trin. ex Thwaites: **A. lag**; *Arthrocnemum macrostachyum* (Moric.) K. Koch: **A. mac**; *Cressa cretica* L.: **C. cre**; *Cyperus laevigatus* L.: **C. lae**; *Imperata cylindrica* (L.) Raeusch.: **I. cyl**; *Juncus rigidus* Desf.: **J. Rig**; *Phragmites australis* (Cav.) Trin. & Steud.: **P. aus**; *Suaeda aegyptiaca* (Hasselq.) Zohary: **S. aeg**; *Typha domingensis* (Pers.) Poir. ex Steud.: **T. dom**; *Tamarix nilotica* (Ehrenb.) Bunge: **T. nil.**

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