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ZONATION AND PHOTOSYNTHETIC PATHWAYS OF HALOPHYTES ON THE RED SEA COAST NEAR TAWWAL (SAUDI ARABIA)

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ABSTRACT. This study presents the analysis of a transect in the halophytic vegetation of the coastal region of the Tihama near Tawwal, 80 km north of Jeddah, Saudi Arabia. The ecological factors at various sites are recorded, and relationships between anatomy and ecology are investigated. The halophytic communities on the coastal strip can be grouped according to physiognomic and ecological characteristics as follows: Mangrove forests, Halophytic semi-woody shrub communities, Open salt meadows and Perennial halophytic forb communities. On the basis of vegetation analysis these units can be correlated with the *Avicennia marina, Halopeplis perfoliata, Aeluropus lagopoides* and *Limonium axillare* associations. As in the case of previously investigated saline areas in Southwest Asia, comparison of photosynthetic type and distribution of halophytes shows a definite correlation between soil salinity, soil moisture and photosynthetic pathway: this is the first record of such a phenomenon on sea shores. C_3 plants are dominant at the margin with the sea and thus within hygrohalophytic formations (here the *Avicennia marina* and *Halopeplis perfoliata* associations), whereas xerohalophytic formations (here the *Aeluropus lagopoides* and *Limonium axillare* associations) are characterized by C_4 species.

STUDY SITES AND PHYSIOGNOMIC-ECOLOGICAL VEGETATION UNITS

The coastal land of the Tihama is characterized along the entire west coast of Saudi Arabia by halophytic communities of varying area, seawards of which there are stands of mangroves, some of them extensive. These mangroves, which are typical of tropical sea coasts, form large stands especially in the southern coastal region (near Jizan). Although they are sparser in the northern extratropical region, they are still well-developed on the coral reefs off the coast near Al Qunfudah, Tawwal, Rabigh and Hanak.

The halophytic communities of the coastal area of Tawwal lying 80 km north of Jeddah form the following physiognomic-ecological units (vegetation units corresponding to the classification scheme of Frey & Probst, 1977): Halophytic semi-woody shrub communities (14.1), Open salt meadow (14.22). Very open desert-like formations (14.4) and a Perennial halophytic forb community (14.32). Seagrass meadows which are widespread along the Red Sea coast of Saudi Arabia (Aleem, 1979), are not developed in the area studied near Tawwal. Phytogeographically, the whole area of the halophytic communities on the west coast of Saudi Arabia belongs to the Nubo-Sindian province of the Sudanian region.

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Fig. 1 shows the location of our transects in the halophytic communities near Tawwal and distribution of the vegetation units. The Perennial halophytic forb community (14.32) is degraded in the area of Tawwal and a transect in this community was sited at Obhor (40 km N of Jeddah) so that a more complete sampling of the halophytic communities of the Tihama could be obtained.

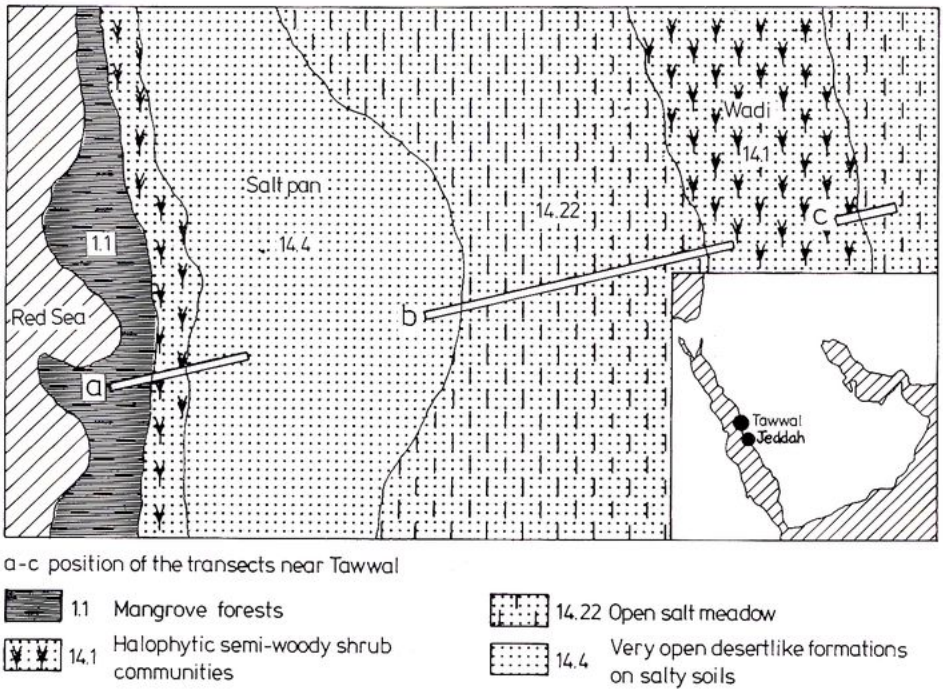


FIG. 1. Vegetation map of the area studied near Tawwal (the vegetation units follow the classification scheme of Frey & Probst, 1977).

CLIMATE

The climatic diagram of Jeddah (Fig. 2) provides a picture of conditions in the coastal region of the Tihama. Since the study area in the vicinity of Tawwal is only 80 km from Jeddah, the diagram may be considered valid there as well. The region is characterized by a hot, arid, desert climate with very low annual precipitation and often very high humidity. Temperatures vary little in the course of the year (with an annual fluctuation of about 9°C), although extremes of more than 40°C are not unusual. The absolute temperature minima are seldom below 12°C. In Jeddah the absolute temperature maximum was 49°C (June 1979), and the absolute minimum was 11·4°C (January 1977). Total annual precipitation is around 70 mm, with the maximum occurring in the 'winter' months (November–February).

From this it may be seen that the vegetation of the coastal area must suffer water-stress most of the year. Life is only possible by means of morphological and physiological adaptive strategies that enable plants to achieve a positive water-balance.

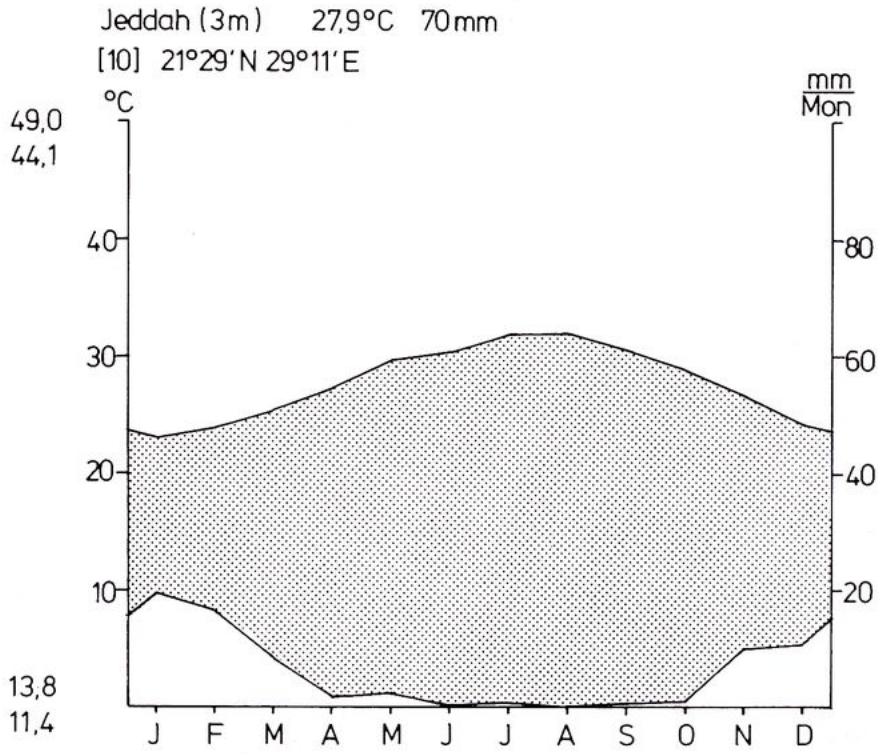


FIG. 2. Climatic diagram of Jeddah.

MATERIAL AND METHODS

The halophytic communities in the vicinity of Tawwal were analysed with the aid of quantitative techniques (Kürschner, 1982, 1983). For this purpose we marked out quadrats (2×2 m) at intervals of 3 m on transects along an ecological gradient of salt and moisture content (see Figs 1 & 4) and recorded all species occurring on them. The resulting binary data were subjected to an association analysis in order to separate the heterogeneous halophytic communities into homogeneous ecological groups. The associations were mapped and classified according to physiognomic and ecological criteria with the aid of the classification and mapping scheme of Frey & Probst (1977). To study soil conditions, samples were taken from the areas of the characteristic associations and examined for their contents of NaCl, $CaCO_3$, and moisture.

One way in which species may adapt to extreme environments of this kind is in their photosynthetic pathway (Frey & Kürschner, 1983; Kürschner, 1983; Shomer-Ilan, Nissenbaum & Waisel, 1981; Winter, 1981; Winter & Troughton, 1978) and species were identified as C_3 or C_4 plants by looking for Kranz anatomy (C_4 syndrome), which is a morphological feature of C_4 plants. To do this the leaves were boiled in distilled water, bleached in sodium hypochlorite solution, and examined in cross-section under a light microscope. As a further criterion $\delta^{13}C$ values obtained from the literature were employed.

Results and Discussion

Four associations may be distinguished in the halophytic vegetation along the coast near Tawwal (Figs 1, 3, 4; Table 1). Owing to differences in the factors determining the habitat, they form more or less clearly defined zones (Figs 1, 4) which coincide with those near Rabigh, published by Mahmoud, El-Sheikh & Isawi (1982) and the vegetation units recognized by Kassas & Zahran (1967) on the Red Sea coast of Egypt.

Table 1. Species composition of the associations near Tawwal

(an asterisk indicates the most characteristic species of the association and brackets the dominant species).

Association	1	2	3	4	0
Total no. of quadrats	16	21	65	63	42
Avicennia marina	—	(21*)	—	—	—
Limonium axillare	(16*)	—	—	—	—
Suaeda pruinosa	(16)	—	—	—	—
Suaeda monoica	—	—	(8)	—	—
Halopeplis perfoliata	4	—	(65*)	—	—
Aeluropus lagopoides	3	—	17	(63*)	—
Zygophyllum album	3	—	9	(10)	—

Other species present (in less than 3 quadrats): *Arthrocnemum macrostachyum* (Assoc. 3), *Atriplex farinosa* (Assoc. 3), *Lycium shawii* (Assoc. 1, 4), *Salsola baryosma* (Assoc. 1), *Sporobolus spicatus* (Assoc. 4).

The first zone is occupied by Mangrove forests (1.1), made up exclusively of *Avicennia marina** (*Avicennia marina* association). *Rhizophora mucronata* which is reported by Hagra (1978), Kassas & Zahran (1967) and Zahran (1976) from different places on the African Red Sea coast was not observed in the Tawwal area. These mangroves, which have only a shrub-like level of development because of the northern location, are protected by coral reefs which break the impact of the waves and thus create the conditions for mangrove colonization. They grow on extremely moist, oxygen-poor, mud soils which are periodically exposed by the changing tide. Seagrass meadows of *Cymodocea rotundata, Halophila ovalis, Halodule uninervus* which often form a characteristic submerged belt outside the mangroves were not observed near Tawwal.

The mangrove zone is followed by a narrow, lime-rich shore dune, on which *Halopeplis perfoliata* and *Suaeda monoica* form a *Halopeplis perfoliata* association (Halophytic semi-woody shrub communities, 14.1) (see figs 1, 4). This dune, consisting of fine sand and sea shells, lies directly at the water margin at high tide. It is dry at the surface but becomes increasingly moist at depths reached by roots. The NaCl content ranges from 2·6% at the surface to 0·7% at 30 cm. Adjoining this shore dune there is a region of extensive clay pan which is deficient in lime and very saline. On account of the high NaCl content (9·2% at the surface) and the soil structure, plants are unable to germinate on it. It is therefore

*Authorities for the species recorded on the transects are given in Table 3.

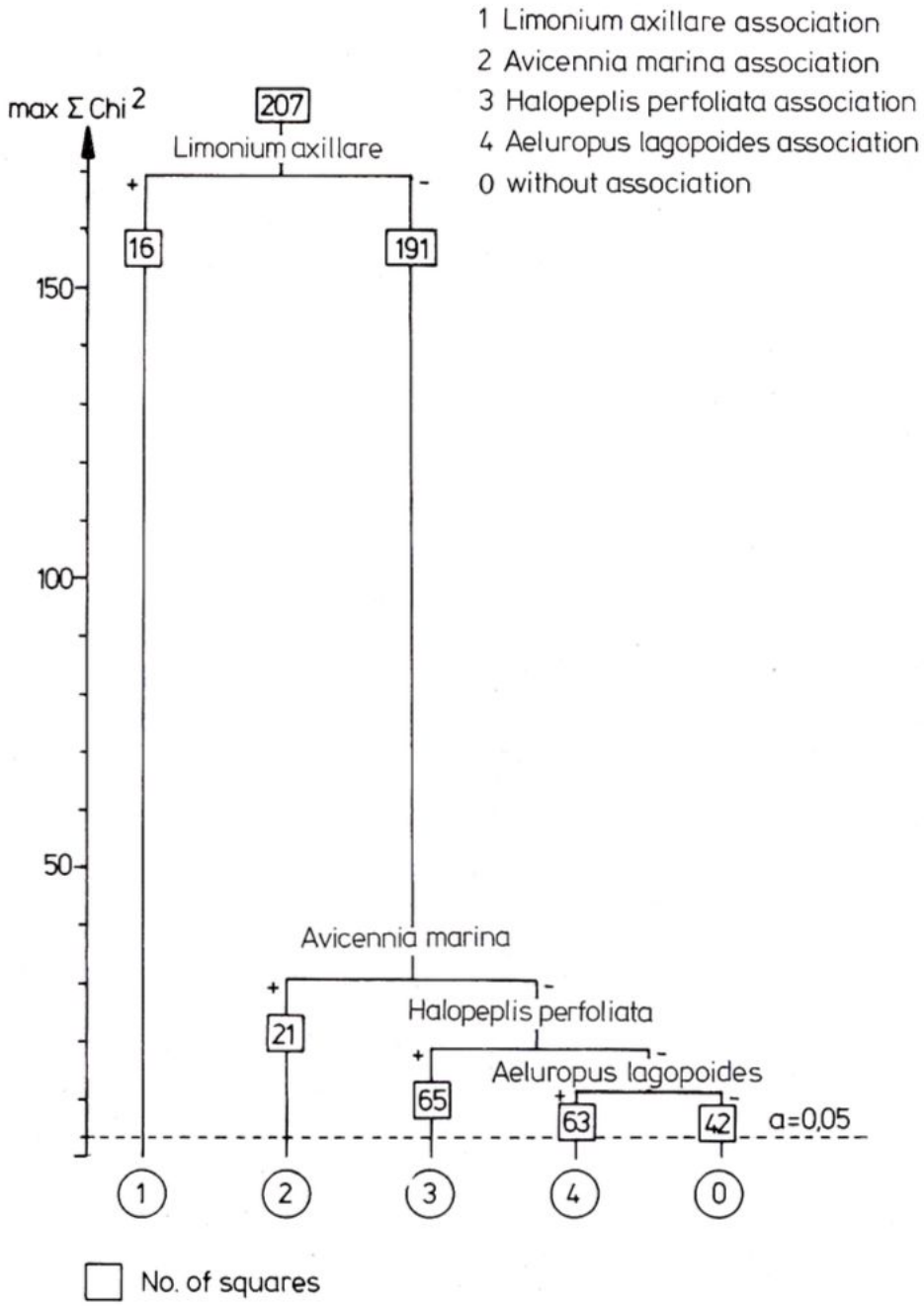
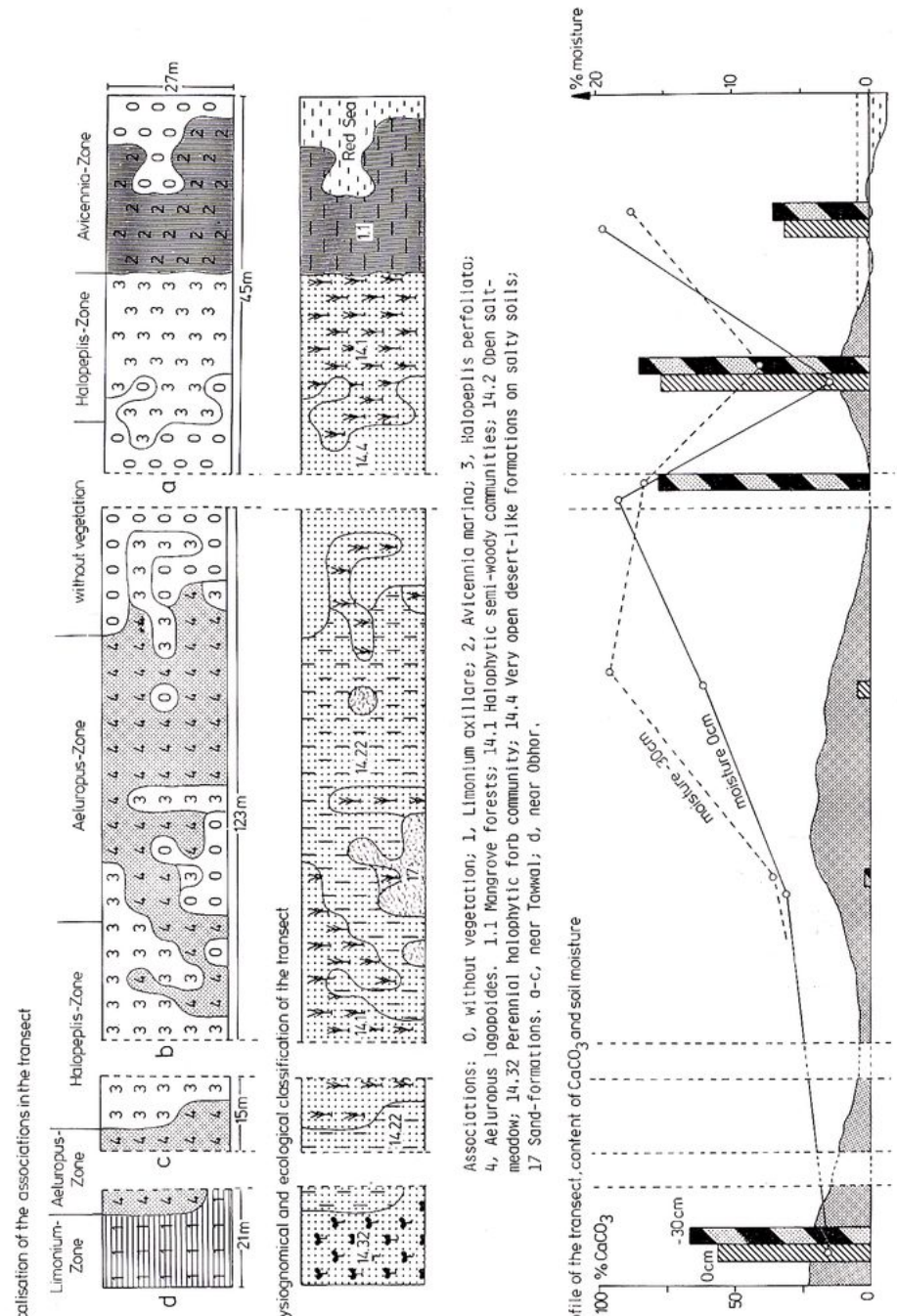


FIG. 3. Association analysis of the halophytic vegetation near Tawwal. (*Note*: squares = quadrats).


1. Localisation of the associations in the transect
Limonium-Zone
Aeluropus-Zone
Halopeplis-Zone
Aeluropus-Zone
without vegetation
Halopeplis-Zone
Avicennia-Zone
21m
15m
123m
45m
27m
2. Physiognomical and ecological classification of the transect
Red Sea
Associations: 0, without vegetation; 1, Limonium axillare; 2, Avicennia marina; 3, Halopeplis perfoliata; 4, Aeluropus lagopoides. 1.1 Mangrove forests; 14.1 Halophytic semi-woody communities; 14.2 Open salt-meadow; 14.32 Perennial halophytic forb community; 14.4 Very open desert-like formations on salty soils; 17 Sand-formations. a-c, near Tawal; d, near Obhor.
3. Profile of the transect, content of $CaCO_3$ and soil moisture
% $CaCO_3$
100
50
0
-30cm
0cm
moisture -30cm
moisture 0cm
% moisture
20
10
0

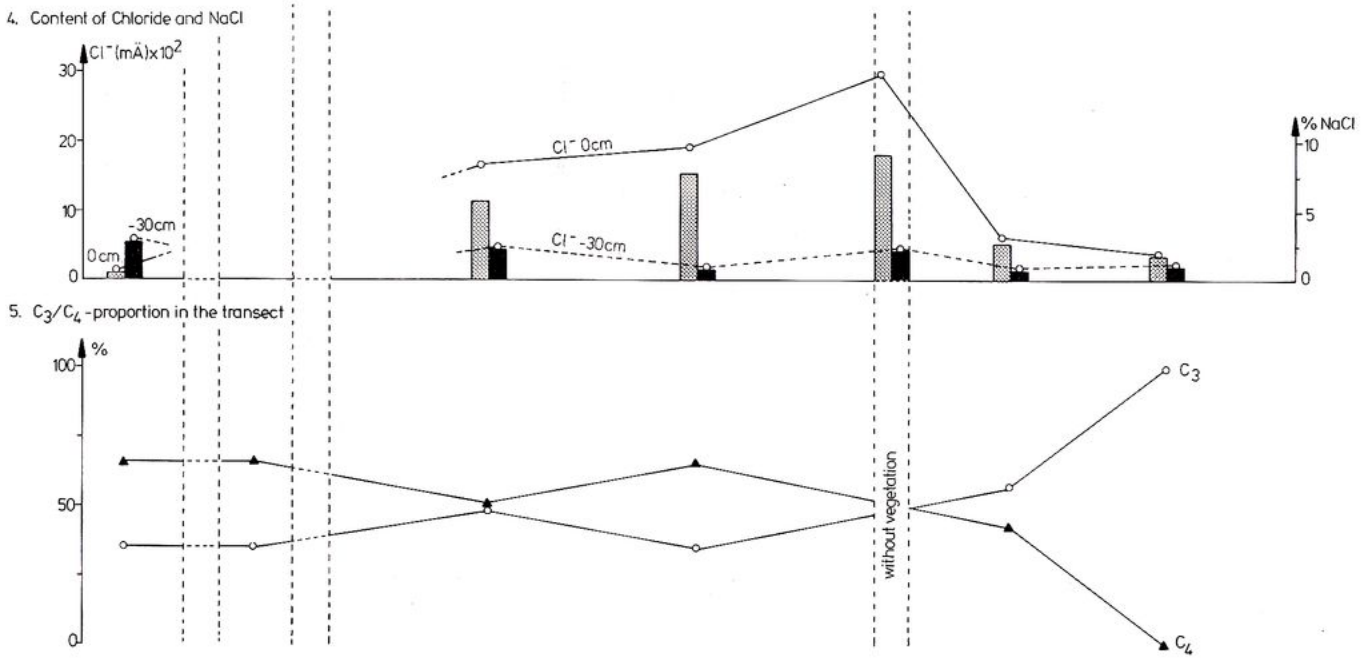


FIG. 4. Location of associations, physiognomic-ecological classification, edaphic factors and C_3/C_4 proportion in the halophytic vegetation of the transect near Tawwal. Sea on right.

completely free of vegetation (Very open desert-like formations on salty soils, 14.4).

The salt pan is followed by an *Aeluropus lagopoides* association (Open salt meadow, 14.22) growing on lime-free sands. Here too, the content of moisture is much higher in the root zone than at the surface. The NaCl content is between 7·8% and 5·7% at the surface but declines to between 2·2% and 0·7% at greater depths. Near Tawwal, this extensive *Aeluropus lagopoides* association is dissected by a wadi system which is dominated by *Halopeplis perfoliata (*Halophytic semi-woody shrub communities, 14.1) together with *Zygophyllum album* and *Aeluropus lagopoides* (Table 1). Inland of the wadi the Open salt meadow (14.22) continues. It covers a large area here but is shown in Fig. 4 only in part. The last zone to be mentioned here is formed by a *Limonium axillare* association (Perennial halophytic forb community, 14.32) consisting of *Limonium axillare* and *Suaeda pruinosa* (Table 1). It grows on lime-rich, relatively dry sandy soils in which salt enrichment has occurred in the lower layers (NaCl content 2·8% at 30 cm) as a result of leaching of salts from the upper layers (NaCl content 0·45% at the surface).

This *Limonium axillare* association is well-developed at Obhor, 40 km N of Jeddah, but at Tawwal it is degraded almost to the point of disappearance. It is nevertheless characteristic of the coastal region of the Tihama and has therefore been included in the description here in order to illustrate the potential succession of halophytes.

At some locations on the coast of the Tihama there are sand-dunes dominated by *Panicum turgidum, Stipagrostis obtusa* and *Cyperus conglomeratus*. However, they were not recorded in the vegetation survey.

Table 2 presents a compilation of the various site factors and vegetation conditions. A clear picture emerges of the factors which are ecologically relevant for the *Halopeplis perfoliata, Aeluropus lagopoides* and *Limonium axillare* associations. Whereas the *Halopeplis perfoliata* association is restricted to the coastal dunes and wadi sediments and is dependent, like the *Limonium axillare* association, on a calcareous substrate, the *Aeluropus lagopoides* association colonizes only sands which contain no lime. The first two associations are apparently confined in the study area and in the Tihama to the shore banks and their wadis, which consist of erosion products of coral and sponge reefs from the past and present. The area occupied by the *Limonium axillare* association, which is relatively far from the present-day coast (c.500–800 m), appears to have been an upper shore zone in previous times. In contrast, the *Aeluropus lagopoides* association colonizes the almost lime-free weathering products which have been washed and blown in from the Hejaz mountains.

Table 3 shows the photosynthetic pathways of the characteristic species. On the basis of concurring anatomical evidence (Kranz anatomy) and physiological-chemical evidence ($\delta^{13}C$ values), 50% of the species studied are identified as C_4 species. Most of them belong to the families Chenopodiaceae and Poaceae. Among the Chenopodiaceae only *Arthrocnemum macrostachyum* and *Halopeplis perfoliata,* which are characterized by extremely hyperhydric storage tissue (halophyte stem-succulence), are C_3 species; the other members possess the C_4 mechanism. The predominance of C_4 species among the Poaceae of the Nubo-Sindian region,

TABLE 2.

Ecological factors in the halophytic vegetation of the transect near Tawwal

Vegetation zone	Association	Soil	% Soil moisture		% $CaCO_3$		% NaCl	
			Surface	30 cm	Surface	30 cm	Surface	30 cm
1. Mangrove forests (1.1)	*Avicennia marina* association	Mud on coral reefs and on the beach area	19	17	31	35	1·8	1·1
			High		High			
2. Halophytic semi-woody shrub communities (14.1)	*Halopeplis perfoliata* association	Dunes (calcareous sand of destroyed coral reefs), calcareous wadi sands and gravel	3	8	77	84	2·6	0·7
			Low at surface, higher with increasing depth, as storage effect of sand and ground water					
3. Salt pan (without vegetation) Very open desert-like formations on salty soils (14.4)		Salty clay on calcareous lime-stone	18	16	0	77	9·2	2·2
							Very high at surface, salt crystals present owing to high evaporation	
4. Open salt-meadow (14.22)	*Aeluropus lagopoides* association	Non-calcareous sand	12	19	5	0	7·8–5·7	2·2–0·7
			Lower at surface, higher with, increasing depth, as storage effect of lower sand layers				Salt content in root area relatively low	
5. Perennial halophytic forb community (14.32)	*Limonium axillare* association	Calcareous sand	c. 3		57	67	0·45	2·8
			Low				Higher NaCl content in deeper layers	

TABLE 3

Life form, chorotype, anatomical characteristics, $\delta^{13}C$ values and photosynthetic type of species from Tawwal (Life form: P = Phanerophyte, CH = Chamaephyte, H = Hemicryptophyte. Chorotype: M = Mediterranean, SA = Saharo-arabian, SU = Sudanian, T = Tropical sea-shore. Anatomy: N = Non-Kranz anatomy, K = Kranz anatomy. $\delta^{13}C$ values after Shomer-Ilan et al., 1981; Winter, 1981; Winter & Troughton, 1978; Ziegler et al., 1981).

	Life form	Chorotype	Anatomy	$\delta^{13}C$(‰)	Photosynthetic Type
Chenopodiaceae					
Arthrocnemum macrostachyum (Moric.) Moris & Delponte	P, CH	M-SA	N	−26·7/−28·6	C_3
Atriplex farinosa Forssk.	P	SU	K	−14·7	C_4
Halopeplis perfoliata (Forssk.) Bge. ex Schweinf.	CH, H	SA-SU	N	−26·3	C_3
Salsola baryosma (Schult.) Dandy	CH	SA-SU	K	−13·0/−14·2	C_4
Suaeda monoica Forssk.	P	SU	K	−14·2/−14·3	C_4
Suaeda pruinosa Lange	CH	SU-SA	K	−14·8	C_4
Plumbaginaceae					
Limonium axillare (Forssk.) Ktze.	CH	SU	N	−25·3/−26·2	C_3
Poaceae					
Aeluropus lagopoides (L.) Trin. ex Thw.	H	SU	K	−14·5	C_4
Panicum turgidum Forssk.	H	SA-SU	K	−12·5/−12·9	C_4
Sporobolus spicatus (Vahl) Kunth.	H	SA-SU	K	−13·4	C_4
Stipagrostis plumosa (L.) Munro	H	SA-SU	K	−12·9/−14·1	C_4
Solanaceae					
Lycium shawii Roem. & Schult.	P	SA	N	−26·1	C_3
Verbenaceae					
Avicennia marina (Forssk.) Vierh.	P	T	N	−25·1/−27·3	C_3
Zygophyllaceae					
Zygophyllum album L.	CH	SA	N	−24·2/−26·5	C_3

which is in contrast to the situation in the Irano-Turanian salines (Frey & Kürschner, 1983), is a consequence of the hot, arid desert climate in which there are seldom minimum temperatures below 12°C. Under such conditions, C_4 monocotyledons can grow (Teeri & Stowe, 1976).

Fig. 4 shows the occurrence of these different photosynthetic types along the transect as related to salt and moisture gradients. Here it can be observed that the characteristic succession of C_3 and C_4 types described by Kürschner (1983) and Frey & Kürschner (1983) is also valid for the

halophytes on the Red Sea coast: this is the first report of such a zonation on a sea-shore.

Within the first two zones, namely the *Avicennia marina* and *Halopeplis perfoliata* associations, C_3 species clearly predominate, while further inland in the adjoining *Aeluropus lagopoides* and *Limonium axillare* associations C_4 species are in the majority. Active salt-secretion through glands on the underside of the leaves, as in *Avicennia marina,* and halophyte stem-succulence, as in *Halopeplis perfoliata,* seem to be more effective adaptations to halophytic, moist biotopes than the C_4 mechanism, provided there is an adequate water supply. In habitats with constant water-stress, however, the C_4 mechanism becomes competitive. One can therefore conclude that the correlation which has elsewhere been observed between the C_3 pathway and hygrohalophytes, and between the C_4 pathway and xerohalophytes (Frey & Kürschner, 1983; Shomer-Ilan, Nissenbaum & Waisel, 1981), also exists for the halophytes of the Nubo-Sindian region along the Red Sea.

Two more transects (near Jizan and Qunfidah) dealing with the halophytic vegetation in the coastal region of the Tihama will be published in a dissertation by König. These transects were made on two further journeys to the Tihama (1982) and yielded similar results to those reported here.

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References

Aleem, A. A. (1979). A contribution to the study of seagrasses along the Red Sea coast of Saudi Arabia. *Proc. Saudi Biol. Soc.* 3:213–236.

Frey, W. & Kürschner, H. (1983). Photosyntheseweg und Zonierung von Halophyten an Salzseen in der Türkei, in Jordanien und in Iran. *Flora* 173:293–310.

—— & Probst, W. (1977). Gliederung der Vegetation und ihre Darstellung im Tübinger Atlas des Vorderen Orients und in den Beiheften zum Atlas. *Beih. Tübinger Atlas Vorderer Orient, Reihe A, Naturwissenschaften, 1, Wiesbaden.*

Hagra, H. (1978). Field study on the ecology of Avicennia marina along the Red Sea coast, Saudi Arabia. *Proc. Saudi Biol. Soc.* 2:83–95.

Kassas, M. & Zahran, M. A. (1967). On the ecology of the Red Sea litoral salt marsh, Egypt. *Ecological monographs* 37:297–315.

Kürschner, H. (1982). Vegetation und Flora der Hochregionen der Aladağları und Erciyes Dağı (Türkei). *Beih. Tübinger Atlas Vorderer Orient, Reihe A, Naturwissenschaften, 10, Wiesbaden.*

—— (1983). Vegetationsanalytische Untersuchungen an Halophytenfluren Zentralanatoliens (Türkei). *Beih. Tübinger Atlas Vorderer Orient, Reihe A, Naturwissenschaften, 11, Wiesbaden.*

MAHMOUD, A., EL-SHEIKH, A. M. & ISAWI, F. (1982). Ecology of the litoral salt marsh vegetation at Rabigh on the Red Sea coast of Saudi Arabia. *Journ. Arid Environment* 5:35–42.

SHOMER-ILAN, A., NISSENBAUM, A. & WAISEL, Y. (1981). Photosynthetic pathway and the ecological distribution of the Chenopodiaceae in Israel. *Oecologia (Berlin)* 48:244–248.

TEERI, J. A. & STOWE, L. G. (1976). Climatic patterns and the distribution of C_4 grasses in North America. *Oecologia (Berlin)* 23:1–11.

WINTER, K. (1981). C_4 plants of high biomass in arid regions of Asia. Occurrence of C_4 photosynthesis in Chenopodiaceae and Polygonaceae from the Middle East and USSR. *Oecologia (Berlin)* 48:100–106.

—— & TROUGHTON, J. H. (1978). Photosynthetic pathways in plants of coastal and inland habitats of Israel and the Sinai. *Flora* 167:1–34.

ZAHRAN, M. (1976). Biogeography of mangrove vegetation along the Red Sea coasts. *International Symposium of the Biology and Management of Mangroves (1974 (1976)), Honolulu, Hawaii* 8–13 & 101.