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EDAPHIC GRADIENTS AND SPECIES ATTRIBUTES INFLUENCING PLANT DISTRIBUTION IN LITTORAL SALT MARSHES OF QATAR

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تأثير منحدرات التربة وصفات الأنواع النباتية على توزيع النباتات في السبخات الساحلية بدولة قطر

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أثبتت دراسة توزيع الفلورا أن منحدرات الماء والملوحة في التربة تمثل إجهادات بيئية حرجة تؤثر على حياة نباتات السبخات الساحلية . فاشتملت المجتمعات النباتية في مناطق السبخة المنخفضة القريبة من الخليج حيث تسود ظروف الاجهاد الملحي على أنواع نباتية متجنبة للملوحة تسلك مسلكا ثلاثي الكربون لتثبيت ثاني أكسيد الكربون في البناء الضوئي، بينما اشتملت المجتمعات النباتية في مناطق السبخة المرتفعة البعيدة عن الخليج حيث تسود ظروف الاجهاد المائي على حوليات شتوية تسلك أنواعها مسلكاً ثلاثي الكربون لتثبيت ثاني أكسيد الكربون في البناء الضوئي . أما المناطق الانتقالية حيث تسود ظروف قاسية من الاجهاد المائي والملحي معا فقد كان لأنواعها النباتية صفات ومميزات الأنواع ذات المسلك رباعي الكربون لتثبيت ثاني أكسيد الكربون في البناء الضوئي . هذا وقد أشارت نتائج الدراسة إلى أن الصفات التركيبية (تشريح الضفيرة) والوظيفية (كفاءة إستخدام الماء) الخاصة بنباتات المسلك رباعي الكربون لها أهمية كبيرة في حياة هذه النباتات التي توجد في المناطق الانتقالية بالسبخات الساحلية .

Key words: C4 syndrome, Edaphic gradients, Salt marsh flora.

ABSTRACT

Edaphic gradients of moisture and salinity are critical environmental stresses that seriously influence littoral salt marsh flora, and determine the zonation of coastal vegetation. Shoreline communities subjected to severe salt stress consisted of salt avoiding C_3 hygrohalophytes exhibiting syndromes such as halosucculence and salt secretion. Marsh communities further inland subjected to severe water stress during the dry season consisted of C_3 xeromorphic winter annual species. Plants inhabiting the transition zones between the low and high marsh areas were subjected to a double stress consisting of seasonal water and salt stresses. These transition zones were strictly inhabited by species exhibiting the C_4-syndrome. Structural and functional attributes associated with the C_4-syndrome appeared to be crucial for the life of species in these transition zones. Electron transport and chlorophyll fluorescence studies showed that the C_4 species of the transition zone possessed moderate tolerance to salt stress and a remarkably high degree of tolerance to water stress.

INTRODUCTION

Salt marshes of the supralittoral zone and mangrove swamps of the midlittoral zone form distinct ecosystems in coastal habitats. Soil water and salinity are of prime importance for the spatial distribution of vegetation in such habitats [1]. This distribution involves zonation of species that are structurally adapted to be principal colonists of such inimical brine environments [2]. Syndromes such as halosucculence and salt secretion represent important adaptations in salt marsh flora [3]. Moreover, this zonation involves functional adaptations of which the C_4-syndrome [4,5] appears to represent a competetive advantage for some floristic elements [6]. The work presented in this paper aimed at studying the distribution of littoral salt marsh flora as influenced by soil moisture and salinity. Differential responses of the dominant species to water and salt stresses were also investigated. Results were discussed in view of the importance of the C_4-syndrome for survival of perennial species in salt marsh transition zones.

MATERIALS AND METHODS

Study Sites

Two littoral salt marshes along the coastline of Qatar (Arabian Gulf) were physiognomically mapped and their vegetation was surveyed by the belt transect method [7]. Sites were located at Doha (25° 15' N, 51° 30' E) and at Dakhira (25° 45' N, 51° 30' E). Transects (10 m wide) were surveyed starting at the Gulf frontier and ending 1.0 km inland at the uppermost point of the salt marsh. Zones of vegetation along the transects were named after the dominant species.

Vegetation

Recorded species exhibiting life forms (LF) described as grasses (G), herbs (H), succulent shrubs (S), and trees (T) were identified and their growth habits (GH) as summer annuals (SA), winter annuals (WA), and perennials (P) were determined [8]. The CO_2-fixation mechanisms (CFM) of these species were determined by referring to previously published $\delta^{13}C$ values of samples collected in the Middle East [6,9,10,11,12,13]. Leaf anatomy with respect to the C_4-syndrome was described as Kranz (K) and non-Kranz (NK).

Soil Analysis

Five soil samples (20 cm deep) were randomly collected from each zone of vegetation along the transects, and were separately analyzed. Soil water content was determined after oven drying (105 °C) to a constant weight. Soil chloride content, pH, and electrical conductivity were measured using standard techniques [14].

Electron Transport

Responses to salt stress of the dominant species were examined by testing the effect of increased NaCl concentration on whole-chain electron transport in isolated thylakoids. Plants were transferred to the laboratory and thylakoids were immediately isolated [15]. Whole-chain electron transport was measured by assessing the rate of oxygen uptake associated with the flow of electrons from water to methyl viologen in an oxygen electrode (Rank Brothers, Cambridge, UK) at 25 C°, 200μE m^{-2} s^{-1}, and 100 μg cm^{-3} chlorophyll. Sodium chloride was incorporated into the assay medium [16] to give concentrations in the range of 25-400 mol m^{-3}. Measurements made in the absence of added NaCl were considered to be 100% control values.

Chlorophyll Fluorescence

Responses of the dominant species to water stress were examined by monitoring water stress-induced changes in *in vivo* chlorophyll fluorescence induction using a plant productivity fluorometer (SF 20, Richard Branker, Canada). Individuals of each dominant species were separately transferred together with a sample of their natural soil (50 cm^3) to a plastic container and soil water potential was measured for each sample using a the Wescor C-52 Sample Chamber and HR 33 Dew Point Microvoltmeter (Wescor, Utah, USA). The soil samples were then left to dry under natural conditions, and soil water potential was measured daily. Water stress responses of chlorophyll fluorescence induction kinetics were measured after a 10 min dark incubation at 25°C as FR, the maximal rate of the induced rise in chlorophyll fluorescence [17,18,19].

RESULTS

The study sites belong to the subtropical arid desert with a mild winter, hot summer, and low irregular rainfall. The transects contained 22 species, half of which had Kranz cell anatomy and $\delta^{13}C$ values of -15.6 to -10.9% . Other species had no Kranz anatomy and $\delta^{13}C$ of -29.0 to -24.3% (Table 1).

The transect at Doha consisted of six zones (Fig.1a). The survey of species (Fig.1b) indicated that Zone-I was a bare salt desert, subject to semidiurnal tidal inundation. Monospecific stands of the perennial succulent shrubs *Halocnemum strobilaceum*, and *Halopeplis perfoliata* dominated Zones II and III, respectively. Zones IV and V were salt meadows inhabited by C_4 species (*Cynodon dactylon, Eremopogon foveolatus,* and *Salsola Baryosma*) and dominated by the perennial grasses *Aeluropus lagopoides* and *Sporobolus arabicus*, respectively. Xeromorphic annual forms (*Helianthemum lippi, Heliotropium kotschyi, Polypogon monspeliensis, Trigonella hamosa,* and *Stipa capensis*) inhabited the semidesert shrubland of Zone-VI, which was dominated by perennial shrubs of *Zygophyllum qatarense.*

The transect at Dakhira consisted of six zones (Fig.2a). The bare Zone-I was followed by a mangrove (*Avicennia marina*) swamp (Zone-II) divided by intertidal channels (Fig.2b). The mangrove was followed by monospecific stands of perennial succulent shrubs of *Arthrocnemum glaucum* (Zone-III), and by Zone-IV (with *H. perfoliata* and *Limonium auxillare*). Zone-V was a salt meadow occupied by perennial species (*A. lagopoides, Anabasis setifera, Atriplex leucoclada, S. arabicus, Suaeda vermiculata*). Zone-VI was inhabited by (*Cassia italica, H. lippi, H. kotschyi, L. hirsutus, Trigonella stellata*) and was dominated by perennial succulent shrubs of *Zygophyllum qatarense.*

Table 1

Growth habit (GH), life form (LF), anatomy (A), CO_2 fixation mechanism (CFM), $\delta^{13}C$ of the recorded species as reported by references (R) in the literature. (Refer to Materials And Methods for explanation of other symbols).

Species	GH	LF	A	CFM	$\delta^{13}C$	R
Aeluropus lagopiodes (L.) Trin. ex Thw.	P	G	K	C4	-13.3	13
Anabasis setifera Moq.	P	S	K	C4	-12.8	10
Arthrocnemum glaucum (Del.) Ung.-Strenb.	P	S	N	C3	-26.7	11
Atriplex leucoclada Boiss.	SA	S	K	C4 -	15.6	10
Avicennia marina (Forssk.) Vierh.	P	T	N	C3	-27.2	12
Cassia italica (Mill.) Lam. ex Steud.	SA	H	N	C3	-28.9	12
Cynodon dactylon (L.) Pers.	SA	G	K	C4	-15.6	13
Eremopogon foveolatus (Del.) Stapf.	P	G	K	C4	-10.9	13
Halocnemum strobilaceum (Pall.) M.B.	P	S	N	C3	-25.6	10
Halopeplis perfoliata Forssk.	SA	S	N	C3	-26.3	11
Helianthemum lippi (L.) Pers.	WA	H	N	C3	-28.3	12
Heliotropium kotschyi (Bge.) Guerke	WA	H	N	C3	-27.8	12
Lasiurus hirsutus (Forssk.) Boiss.	SA	G	K	C4	-11.7	12
Limonium auxillare (Forssk.) Ktze.	SA	S	N	C3	-25.3	9
Polypogon monspeliensis (L.) Desf.	SA	G	N	C3	-29.0	12
Salsola baryosma Roem. et Schult	SA	S	K	C4	-14.7	10
Sporobolus arabicus Boiss.	P	G	K	C4	-12.4	6
Stipa capensis Thunb.	WA	G	N	C3	-25.1	13
Suaeda vermiculata Forssk. ex Gmel.	P	S	K	C4	-14.2	10
Trigonella hamosa L.	WA	H	N	C3	-28.6	6
Trigonella stellata Forssk.	WA	H	N	C3	-28.7	6
Zygophyllum qatarense Hadidi	P	S	K	C3	-	-

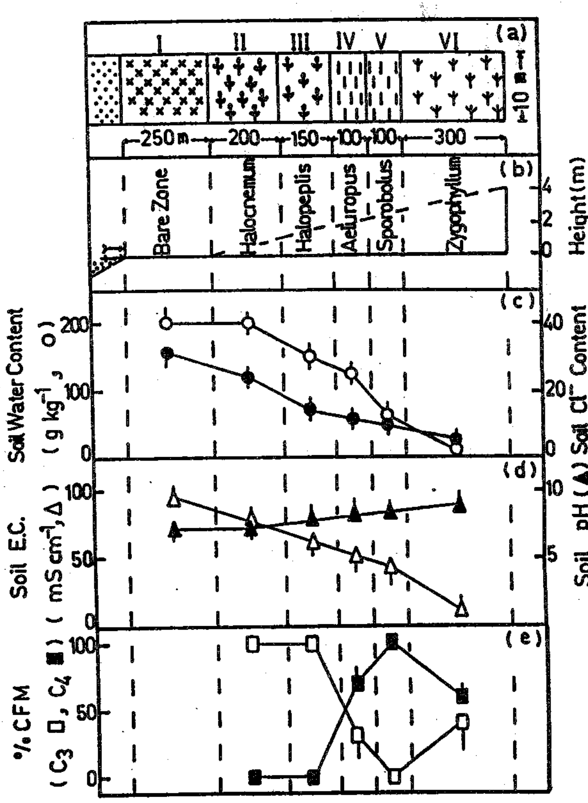

Fig.1: Vegetation zonation (a), transect profile (b), edaphic gradients of water, chloride, electric conductivity, and pH (c,d), and % C_3 and C_4 species (e) along the transect at Doha (± SE, n = 5). ⊡ Arabian Gulf, ⊠ salt desert, ⊞ perennial succulent shrubs, ◫ salt meadows, ⊞ xeromorphic shrublands, ➔ high tide mark, ⟶ low tide mark.

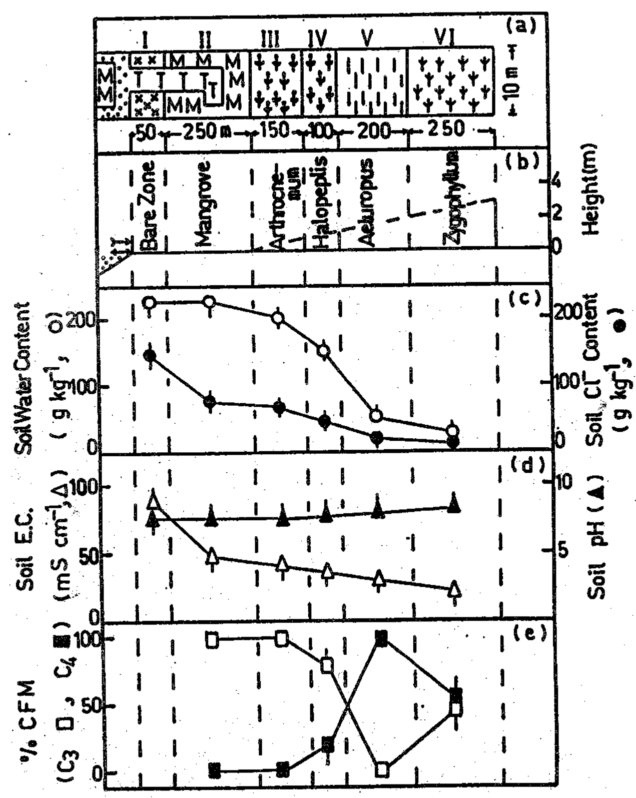

Fig.2: Vegetation zonation (a), transect profile (b), edaphic gradients of water, chloride, electric conductivity, and pH (c,d), and % C_3 and C_4 species (e) along the transect at Dakhira (± SE, n = 5). ⊡ Arabian Gulf, ⊠ salt desert, ⊞ perennial succulent shrubs, ◫ salt meadows, ⊞ xeromorphic shrublands, ➔ high tide mark, ⟶ low tide mark. ⊟ mangrove swamp, ⊡ intertidal channels.

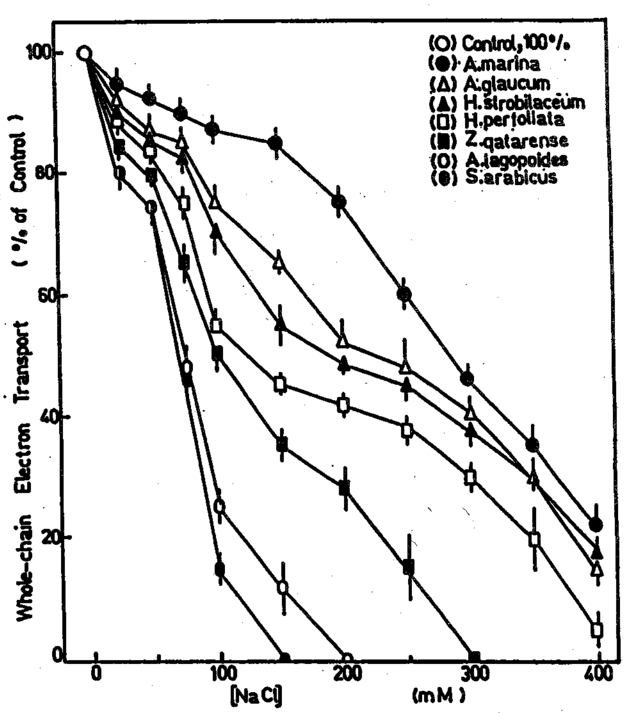

Fig.3: Effect of NaCl on photosynthetic whole-chain electron transport in thylakoids isolated from (●) *A.marina*, (Δ) *A. glaucum*, (▲) *H. strobilaceum*, (□) *H. perfoliata*, (■) *Z. qatarense*, (O) *A. lagopoides*, (●) *S. arabicus*. Rates expressed as percentages of the (O) Control rates (85-95 umol O_2 consumed mg^{-1} Chl h^{-1}) measured in absence of exogenously added NaCl (±SE, n = 5).

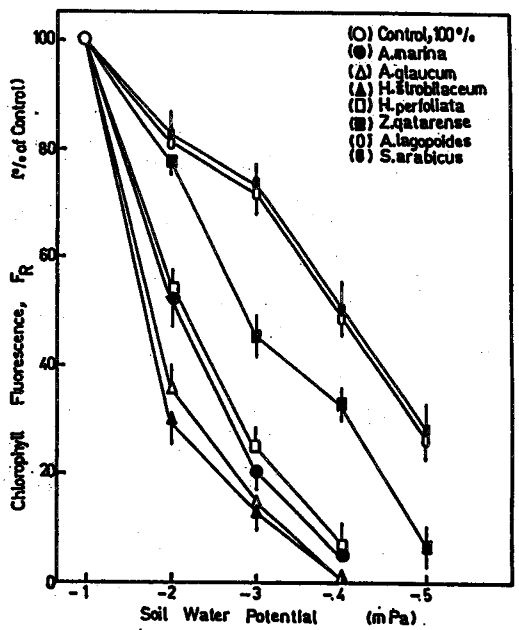

Fig.4: Effect of soil water potential on the maximal rate of the induced rise of prompt Chl a fluorescence induction kinetics (F_R) in leaves of (●) *A. marina*, (Δ) *A. glaucum*, (▲) *H. strobilaceum*, (□) *H. perfoliata*, (■) *Z. qatarense*, (O) *A. lagopoides*, (●) *S. arabicus*. Recorded relative units expressed as percentages of those (O) Control Values measured at an initial soil water potential of -1 mPa (± SE, n = 5).

Soil water content, chloride content, and electrical conductivity decreased, while soil pH slightly increased with distance from the coast along both transects (Figs. 1 & 2 c-d). Changes of CFM in both transects involved a transfer from C_3-dominated seaward zones to C_3/C_4-shared inland zones, through C_4-dominated transition zones (Figs. 1 & 2, e).

Assessment of the effect of salt stress on whole-chain electron transport in thylakoids isolated from the dominant species showed that these species exhibited different responses. The mangrove (*A. marina*) and the perennial succulent shrubs (*A. glaucum, H. perfoliata*) of the seaward zones had a higher degree of tolerance to salt stress than the perennial grasses (*A. lagopoides, S. arabicus*) of the transition zones (Fig.3). On the other hand, assessment of water-stress-induced changes in F_R indicated that the grasses of the transition zones were much more tolerant than the succulent species of the seaward zones (Fig.4). Moreover, succulent shrubs of *Z. qatarense* of the inland zones showed somewhat intermediate responses to both salt stress and water stress (Figs. 3 & 4).

DISCUSSION

Highly saline shorelines subject to tidal flooding were bare salt deserts devoid of vegetation. On low reaches of the site at Dakhira, tidal flooding extended deeper inland in lagoons and tidal channels, and there were strong reducing conditions. These shores covered waterlogged, single-species mangrove swamps, in which vivipary [20], pneumatophore formation [21], and salt tolerance (Fig.3) constituted elements of a mangrove syndrome dominated by *A. marina* which is adapted to this anoxic saline environment. High chloride requirements for Photosystem II reactions in thylakoids isolated from other *Avicennia* species have previously been reported [22], and perhaps support the observed salt tolerance of *A. marina* (Fig.3).

Seaward sand formations regularly exposed to salt spray followed the salt desert and mangrove zones and were colonized by salt tolerant, C_3, perennial succulent shrubs. Halosucculence, a syndrome with which plants dilute increased internal ionic levels in large leaf cells with high water contents [3,23], was evident in species inhabiting these zones (i.e.*A. glaucum, H. strobilaceum,* and *H. perfoliata*). Salt secretion via salt glands [24,25] was linked to salt tolerance [2], and was also evident in (*A. leucoclada,* and *L. auxillare*) on seaward sand formations.

On the other hand, high marsh semidesert shrublands further inland with low water content and low salinity were inhabited by winter-annual, xeromorphic life forms. These annual species were mainly drought-avoiders that germinate during rainy winters and exclusively employ the C_3 photosynthetic pathway. In these high marsh zones the endemic C_3 perennial succulent *Z. qatarense*, a phreatophyte with roots reaching down to permanent water-tables [8] had access to water resources unavailable to other species and was consequently able to better manage its water economy. This species had, therefore, an advantage that enabled it to achieve dominance over other species growing in high marsh areas.

It was evident that perennial C_3 species survived salt stress in the foreshore zones by halosucculence and salt secretion. This observation agrees with the hypothesis that cytosolic enzymes are able to operate because active metabolic machinery is kept free from salinity by accumulation of salt within the cell vacoules [26]. Annual C_3 plants tended to evade hot dry summers by adopting a winter growth habit on the high marsh areas where water stress was prevalent.

Moreover, transition zone salt meadows with low water content were subject to seasonal saline conditions during periods of spring tides. Plants inhabiting these zones, experience, therefore, a double stress, namely drought and salinity. Transition zones were dominated by C_4 grass species (*A. lagopoides,* and *S. arabicus*). These salt marsh grasses among which the C_4-syndrome is prominent [1] have previously been reported to occupy maritime salt marsh transition zones [6].

Leaves of salt tolerant species carry on metabolic activities at low internal water potential and high salt content, although they do not appear to have enzyme systems that are particularly more salt tolerant than those of glycophytes. Furthermore, it has long been recognized that water use efficiency (WUE) of a C_4 plant is predominantly superior to, and can be double that, of a morphologically similar C_3 plant [27]. It can, therefore, be concluded that structural (Kranz anatomy) and functional (high WUE) attributes associated with the C_4-syndrome are important for the C_4 grasses to survive the double stress prevailing in littoral salt marsh transition zones.

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