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Regular research paper

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RELATIONSHIPS BETWEEN VEGETATION ZONATION AND EDAPHIC FACTORS IN A SALT-MARSH COMMUNITY (BLACK SEA COAST)

ABSTRACT: The effects of pH, electrical conductivity (EC), soluble cations (Na^+, K^+, Ca^{2+}, Mg^{2+}), and soluble anions (HCO_3^-, Cl^-, SO_4^{2-}) on vegetation zonation in a salt-marsh community (Black Sea coast) were investigated on two localities at Black Sea Coast differing as to the altitude, community composition and zonation. Three zones (25–80 m wide) – lower, middle and upper were distinguished in each locality along 150 m transect and according to the vegetation types which were analysed with Braun-Blanquet method. The dominant species were following: *Juncus acutus* L., *Salicornia prostrata* Pall., *Spergularia marina* (L.) Gris, *Hordeum geniculatum* All., *Plantago coronopus* L. subsp. *coronopus*, *Carex capitellata* Boiss. and Bal, *Artemisia santonicum* L. and *Juncus littoralis* C. A. Mey. Soil samples were taken down to 50 cm. The results of soil analysis were evaluated by using Canonical Correspondence Analysis (CCA) from winter 1999 to autumn 2000. HCO_3^- concentration and inundation depth (2.22–21.44 cm) are the environmental variables that correlate the best with axis 1, whereas K^+ concentration and inundation depth (2.22–21.44 cm) correlate the best with axis 2 during the study period. During winter 1999, HCO_3^- concentration showed the highest correlation with the canonical axis 1 and associated zone was *H. geniculatum*. In spring, summer and autumn 2000, inundation depth (3.44–19.11 cm) was the most prominent factor correlated with the first and second axes, respectively, with associated zone of *C. capitellata*. EC, Na^+ and Cl^- concentrations were decreased during autumn in all vegetation zones except for *C. capitellata* and *Artemisia santonicum* zones in which Na^+ and Cl^- concentrations and EC, respectively were increased during autumn. The *C. capitellata* (Cyperaceae) zone was located on the positive site of axis 1 during autumn 2000 and followed the gradient of inundation depth. *S. prostrata*, *S. marina*, *H. geniculatum* and *P. coronopus* subsp. *coronopus* seems to be adapted to the most saline soils, whereas *C.capitellata* indicates the wettest soils in the studied salt marsh. The *Juncus littoralis* zone followed the gradient of maximum salinity during autumn of the year 2000, but the zone was not related to the measured increase in soil salinity during winter, summer and spring. In both localities EC, Na^+ and Cl^- concentrations were tended to decrease at upper zones. Inundation regime, K^+ concentration, and HCO_3^- concentration are key factors affecting vegetation zonation in studied salt marshes.

KEY WORDS: coastal salt marshes, Cyperaceae, inundation regime, Juncaceae, soil salinity, zonation patterns

1. INTRODUCTION

Coastal salt marshes comprise areas of land bordering the sea largely covered with vegetation and subject to periodic tidal inundation. These areas have certain features, related to the proximity to the sea, that distinguish them from inland salt marshes (Asri and Ghorbanli 1997, Onaindia and Amezaga 1999). Salt marshes constitute some of the most diverse and biologically productive habitats of coastal regions and perform many important functions, including nutrient and organic matter production and transport, nutrients and pollutants removal, reduction of wave energy during storms, as well as inundation and sediment trapping (Niedowski 2000). Such ecosystems are generally dominated by halophytic species that have developed the mechanisms to avoid and resist salt stress, such as salt accumulation in tissues, osmotic adjustment, and selective ion uptake by roots (Kruger and Peinemann 1996, Kutbay and Demir 2001).

Salt marshes constitute example of an ecosystem that comprises stable species-poor or mono-specific communities with distributions that are related to environmental physical and chemical gradients. Pennings and Callaway (1992) proposed the 'new paradigm' concept related to the zonation of salt-marsh plants, whereby upper limits are set by competition in relatively low-stress environments, whereas lower limits are set by tolerance to harsh physical conditions (Sánchez *et al.* 1998).

The composition and distribution of plant communities in salt marshes is related to the ability of individual species to tolerate environmental conditions that are associated with flooding, salinity and nutrient limitation. Salt-marsh vegetation typically forms distinct and predictable zones that are superimposed on soil gradients. Sharp physical gradients in these communities allow close examination of the effects of physicochemical factors on species interactions (Pennings and Callaway 1992, Bertness and Hacker 1994, Van Wijnen and Bakker 1999).

Salt-marsh communities are generally dominated by a small number of species that are spatially segregated into pronounced vegetation zones. The problems faced by salt-marsh plants have been identified by Bertness and Allison (1987), Bertness (1991) and Bertness *et al.* (1992). Floristic structure of the study area selected in North Turkey is similar to the other Mediterranean salt marshes. *Salicornia* species are widespread in abandoned salt pans in western France (Bouzillé *et al.* 2001), such as is the case in the present study area. Succulence is a common phenomenon in the vegetation of saline habitats (Abd El-Ghani 2000a).

The success of salt-marsh plants is affected by several factors, most common of which are edaphic factors and flooding. These factors are often considered to determine the establishment and zonal patterns of species in salt marshes (Pennings and Callaway 1992, Ungar *et al.* 1979). Inundation causes long-term changes in salt-marsh vegetation (Leendertse *et al.* 1997). Vegetation zonation in salt-marsh environments may also reflect biotic interactions, such as interspecific competition and symbiotic activity. In addition, pressure by herbivores and parasites may play additional important roles in shaping salt-marsh vegetation (Ungar 1998).

Vince and Snow (1984) found that vegetation zones within a salt marsh vary with respect to inundation and salinity. It has also been suggested that electrical conductivity determines the coarse patterns of plant-community composition, whereas ionic composition is responsible for the fine scale pattern (Cantero *et al.* 1998).

The present study addresses the following objectives: (i) to determine the effects of selected soil parameters on the zonation of plant communities and (ii) to determine the interactions between salinity and plant zonation. An understanding of the effects of soil conditions on plant zonation will contribute to the correct utilization and rehabilitation of salt marshes.

2. STUDY AREA

The study area is a main route for bird migration; it was decleared as a protected area, the object of a management plan of proper conservation in the region (Yarar and Magnin 1997). The study area is situated on the east bank of the Kızılırmak River in the northern and northeastern parts of Bafra Town (41°42′17″ and 41°31′46″N, and 36°05′40″ and 36°03′01″E), North Turkey, in the central Black Sea region. The study area comprised two different localities, four zones in each of them the eight zones in total (Fig. 1).

The 1° locality, which contains four different zones, is situated near the Cernek Lake (covers a 589 ha area) and extended 2 km west of this lake (Fig. 1). Cernek Lake is quite shallow (about 3 m depth) and almost at sea level. The flat nature of the Kızılırmak delta's topography ensures that relatively small changes in water level cause substantial changes in the areal extent of Cernek Lake. The sources of Cernek Lake water feeding are: groundwater originating from the Kızılırmak river, inputs of surface and local groundwater from the channels, surface run-off from the delta plain, groundwater flow derived from the dunes, direct precipitation on the lake, and seep up of seawater. According to a classification the surface water of Cernek Lake is of salt-brackish water type (Samsunlu *et al.* 2002, Taş *et al.* 2002).

The first zone (20 m) which extends towards Cernek Lake (Fig. 1), is inundated during spring, and is dominated by monospecific stand of *Juncus acutus* L. The second zone (70 m) is located to the west of the first zone and is dominated by mixed stands of *Salicornia prostrata* Pall. and *Spergularia marina* (L.) Gris; the zone includes salt-pans due to excess evaporation during summer months. The third (35 m) and fourth zones (25 m) are dominated by monospecific stands of *Hordeum geniculatum* All. and *Plantago coronopus* L. subsp. *coronopus*, respectively. The second zone was never inundated during the study similar to the the third and fourth zones (Fig. 2).

The 2° locality is situated 1 km east of the mouth of the Kızılırmak River (Fig. 1). A channel lies at the edge of the area. Four different zones are also present at this locality. The first zone (25 m) is connected to the channel, and is inundated during most of the year; it is dominated by monospecific stands of *Carex capitellata* Boiss. and Bal. The second zone (30 m) is located to the rear of the first zone and is dominated by mixed stands of *S. prostrata* and *S. marina*. The third (35 m) and fourth zones (60 m) are dominated by monospecific stands of *Artemisia*

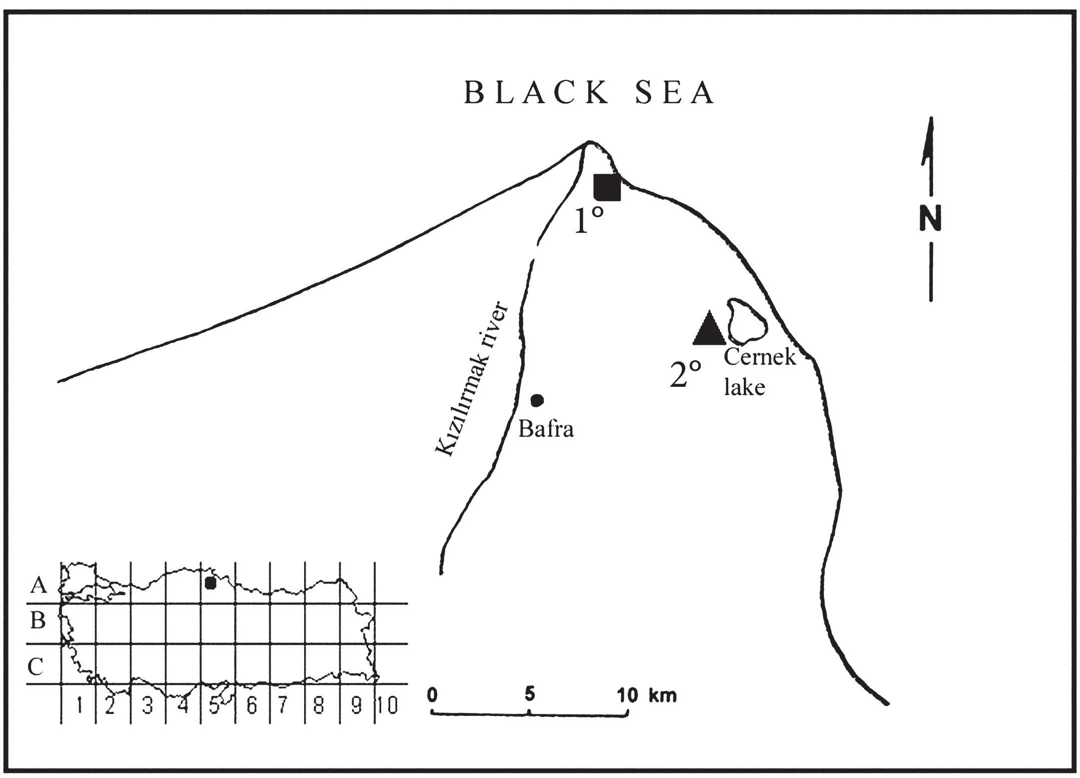

Fig. 1. Map of the study area with localisation of 1° and 2° study localities.

Table 1. Climatic data of the study area in North Turkey (Fig. 1).

Variable	Value
Mean annual precipitation (P)	806 mm
Mean precipitation values for successive seasons (Wi. Au. Sp. Su.)	262.4 mm, 241.3 mm, 178.4 mm, 123.9 mm
Precipitation regime	Wi. Au. Sp. Su.
Mean annual temperature (T)	13.7°C
Mean temperatures for successive seasons (Wi. Au. Sp. Su.)	6.63°C, 15.06°C, 11.26°C, 21.5°C
Maximum temperature for the warmest month (M)	33.8 °C (July)
Minimum temperature for the coldest month (m)	–2.6°C (February)
Pluviometric quotient (Q)	77
Mean annual relative humidity (%)	79.8

Wi: Winter, Au: Autumn, Sp: Spring, Su: Summer

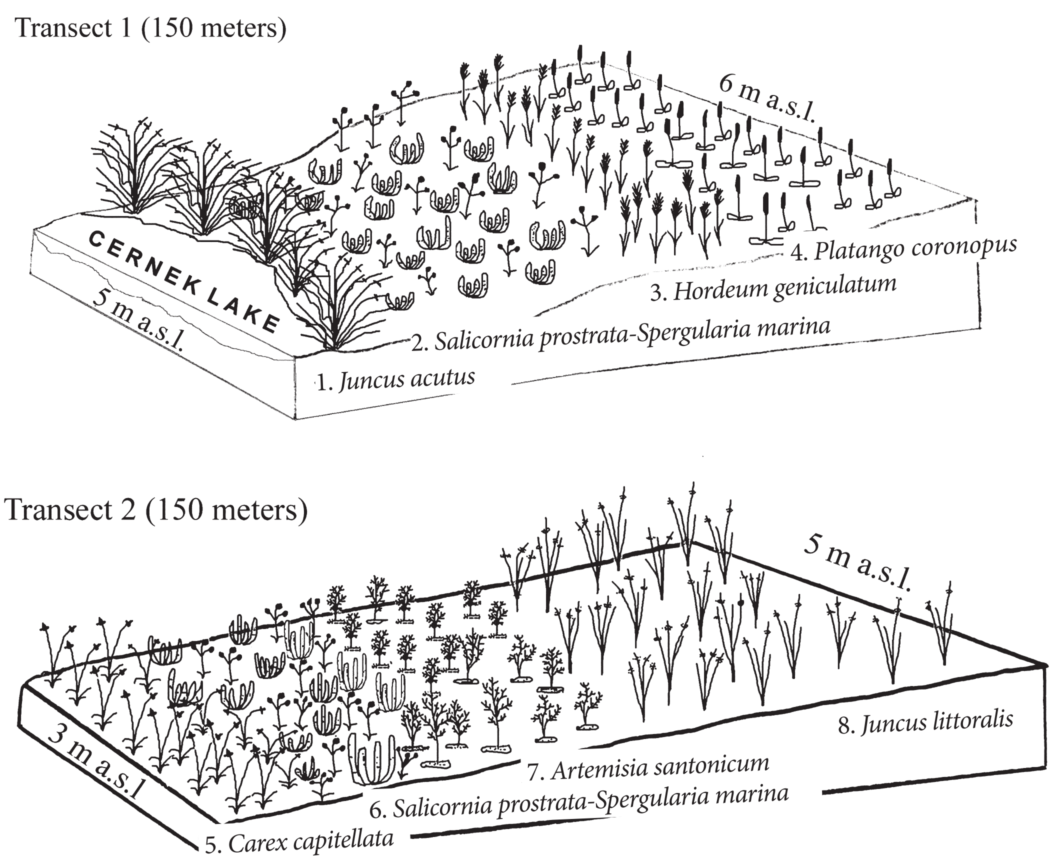

Fig. 2. Diagram of the transect 1 (near to Cernek Lake) and transect 2 (near to Black Sea) showing plant zonation in the study area.

santonicum L. and *Juncus littoralis* C. A. Mey, respectively. The third zone is dominated by *J. littoralis*. The third and fourth zones are situated at a slightly higher elevation than the first and second zones and are inundated during winter, although they are further from the Black Sea than the first and second zones (Fig. 2).

On the basis of the climatic data and the classification of Daget (1977), the area can be considered as belonging to semi-humid Mediterranean climate (Table 1) and, the precipitation regime is characteristic for Mediterranean region (Turkish Ministry of Agriculture 2002).

The mean annual rainfall in the study area is more than expected for an arid environment. However, excess evaporation that occurs during summer months, and the highest potential evapotranspiration rate is found in June namely 102 mm (Koksal 1972, Engin *et al.* 1988). These high evaporation rates reduce the natural accumulation of surface water (Wadie 2002). Inundation takes place from winter to autumn especially in the 2° study locality and dissolved salts have been raised to the surface. In the 1° locality inundation is irregular. Saline soils are dominant in the study area (Avcı *et al.* 2000). Taxonomic nomenclature of plants follows that of Brummitt and Powell (2001).

3. METHODS

Two transects 150 long were drawn across the 1° and 2° localities (Fig. 2). Along each transect, three plots were placed within each zone, and the size of plots were determined as the minimal areas of relatively uniform stands (Mueller-Dumbois and Ellenberg 1974). Hence, nine plots were sited along Transect 1 and nine along Transect 2. Cover data of species (in %) were analysed according to the Braun–Blanquet scale, as proposed by Van Der Maarel (1979), using standard methods of relevés. Soil samples were taken from December 1999 to November 2000. In the zones of *S. prostrata–S. marina*, *C. capitellata* and *H. geniculatum–P. coronopus*, soil samples were taken from 0.5 m × 0.5 m (0.25 m^2) plots. For the *J. acutus*, *A. santonicum* and *J. littoralis* zones (Fig. 2), soil samples were taken from 4 m × 4 m (16 m^2) plots. Five soil cores were taken in each plot and each zone to a depth of 50 cm using a 7 cm diameter auger. The soil cores were mixed. The samples were air-dried, crushed and sieved using a 2-mm mesh (Ortiz *et al.* 1995).

Soil pH was measured in soil-water extracts at 1:1 (w:v) with a Beckman pH meter. Electrical conductivity (dS m^{-1}) was determined in soil-water extracts at 1:1 (w:v) using a Jenway analyser. Both exchangeable and soluble cations were leached from 25 g of dry soil samples with 100 ml of neutral (pH 7.0) 1.0 mol l^{-1} ammonium acetate. Na^+ and K^+ (meq l^{-1}) were determined using a Perkin Elmer atomic absorption spectrophotometer. Ca^{2+} and Mg^{2+} (meq l^{-1}) were determined using EDTA (disodium dihydrogen ethylenediamine tetraacetate) and murexide indicator for calcium and eriochrome black indicator for calcium and magnesium together. HCO_3^- (meq l^{-1}) was determined by titration with sulphuric acid, whereas Cl^- and SO_4^{2-} (meq l^{-1}) were determined by gravimetric and turbidimetric methods, respectively (Black 1965, Allen *et al.* 1986, Abbas e*t al.* 1991, Kılınc *et al.* 2006, Onkware 2000). Inundation was measured from soil surface to the upper level of water surface as cm by a meter stick.

To examine the relationships between plant communities and soil variables, Canonical Correspondence Analysis (CCA) was applied (Jongman *et al.* 1995) using the MVSP version 12c (2000) and ECOM version 1.33 (Henderson and Seaby 2001) of software programmes. pH, electrical conductivity (EC), soluble cations (Na^+, K^+, Ca^{2+}, Mg^{2+}), soluble anions (HCO_3^-, Cl^-, SO_4^{2-}) and inundation (2.22–21.44 cm) were included as environmental variables. The Monte Carlo permutation test was used to test the significance of canonical axes (P <0.01 and P <0.05). The cover-abundance symbols of the Braun-Blanquet scale (r, +, 1, 2, 3, 4 and 5) were replaced by values according to van der Maarel (1979): 1, 2, 3, 5, 7, 8, and 9, respectively (Focht and Pillar 2003). Cover data for plant species were log-transformed to improve normality and homogeneity of variance.

One-way ANOVA was used to test for significant differences in environmental factors between different vegetation zones.

Tukey's Honestly Significance (HSD) test was also used to compare the groups for means following analysis of variance using SPSS version 10.0 software (1999). The data were divided into sets (pools) for successive seasons as winter (December–February) 1999, spring (March–May) 2000, summer (June–August) 2000 and autumn (September–November) 2000.

4. RESULTS

In the 1º locality, Na^+ concentration (meq l^{-1}) in lower zone was remarkably changed and ranged from 58.00 to 326.30. Similarly Cl^- concentration (meq l^{-1}) was ranged from 32.35 to 427.83. Remarkable changes were also found in the 2º locality in middle zone regarding Na^+, Cl^- and HCO_3^- concentrations. Na^+ (meq l^{-1}) concentration was ranged from 63.88 to 188.83. Cl^- and HCO_3^- (meq l^{-1}) concentrations were ranged from 23.31 to 318.72 and 22.91 to 116.38, respectively (Tables 2 and 3).

Na^+ and Cl^- were the most prevalent ions in soils of the study area (Tables 2, 3). EC, Na^+ and Cl^- concentrations were considerably higher in the *S. prostrata* and *S. marina* zone than in other zones, whereas inundation depth (21.44 cm) was higher in the *C. capitellata* zone than in other zones. Similarly, Ca^{2+}, Mg^{2+}, SO_4^{2-}, Na^+ and K^+ concentrations were also higher in the *S. prostrata*–*S. marina* zone. HCO_3^- concentration was higher in the *A. santonicum* and *J. littoralis* zones, respectively (Tables 2, 3).

Table 2. Range of mean values of selected soil variables for four seasons in different zones of locality 1º. (Figs 1, 2).

Variable	Lower	Middle	Upper
pH	7.66–8.02	7.45–7.91	7.58–8.11
EC (ds m^{-1})	2.00–15.88	1.86–14.35	3.39–5.78
Na^+ (meq l^{-1})	58.00–326.30	55.55–136.00	78.72–114.00
K^+ (meq l^{-1})	2.95–6.52	2.38–6.97	3.00–4.02
Ca^{2+} (meq l^{-1})	14.16–80.41	22.50–89.16	19.72–29.54
Mg^{2+} (meq l^{-1})	19.30–84.86	25.41–69.58	17.77–28.02
HCO_3^- (meq l^{-1})	37.50–57.77	24.16–62.50	34.50–68.88
Cl^- (meq l^{-1})	32.35–427.83	23.83–207.94	45.22–108.77
SO_4^{2-} (meq l^{-1})	14.94–52.68	13.11–47.61	5.61–44.08
Inundation depth (cm)	0.00–3.44	0.00–0.00	0.00–0.00

Table 3. Range of mean values of selected soil variables for four seasons in different zones of locality 2º. (Figs 1, 2).

Variable	Lower	Middle	Upper
pH	7.79–8.27	7.51–8.48	7.78–8.11
EC (ds m^{-1})	2.09–5.04	1.37–12.90	0.64–1.87
Na^+ (meq l^{-1})	72.50–127.80	63.88–188.83	5.27–30.19
K^+ (meq l^{-1})	4.25–6.66	2.31–7.81	2.27–4.03
Ca^{2+} (meq l^{-1})	7.33–18.19	19.44–98.75	13.97–40.36
Mg^{2+} (meq l^{-1})	23.11–26.72	17.47–85.41	16.69–32.40
HCO_3^- (meq l^{-1})	42.27–66.38	22.91–116.38	27.16–48.46
Cl^- (meq l^{-1})	34.16–74.97	23.31–318.72	3.72–36.38
SO_4^{2-} (meq l^{-1})	16.69–54.05	5.97–57.05	7.14–42.13
Inundation depth (cm)	5.33–21.44	0.00–17.33	0.00–2.22

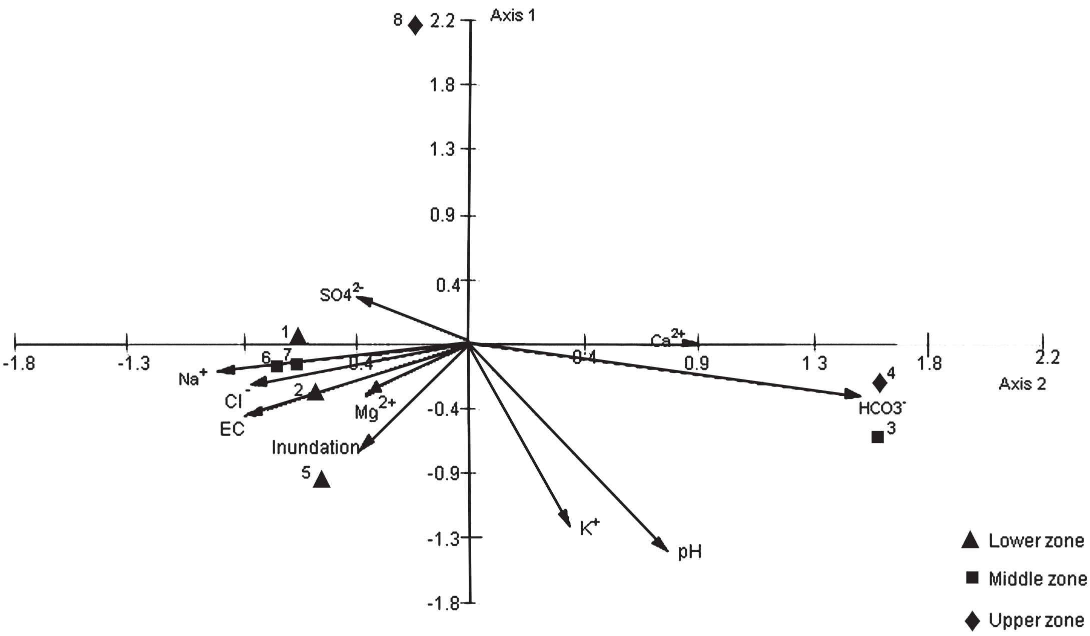

Fig. 3. Soil-plant species data ordination in lower, middle and upper zones of salt marsh community (Canonical Corespondense Analysis (CCA) diagram for winter 1999). For zone information see Fig. 2.

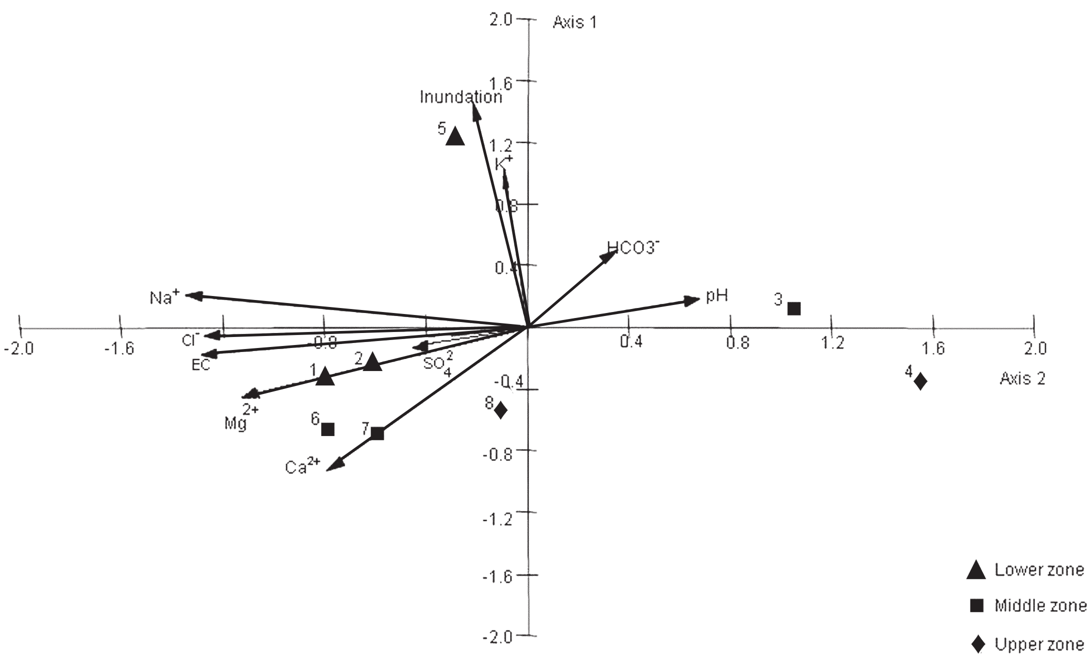

Fig. 4. Soil-plant species CCA diagram in salt marsh community for spring 2000. For the detailed description of zones see Fig. 2.

Table 4. Eigenvalues, species-soil correlation coefficients and percentage cumulative variance during the study period.

	Axis 1	Axis 2
(1) Eigenvalues		
Winter 1999	0.884	0.603
Spring 2000	0.782	0.708
Summer 2000	0.730	0.648
Autumn 2000	0.676	0.463
(2) Species-environment correlation coefficients		
Winter 1999	0.956	0.876
Spring 2000	0.913	0.909
Summer 2000	0.870	0.907
Autumn 2000	0.879	0.759
3) Percentage cumulative variance		
Winter 1999	29.3	49.4
Spring 2000	25.2	48.1
Summer 2000	23.7	44.8
Autumn 2000	20.1	35.3

Table 5. Intraset correlation coefficients of soil environmental variables with the first two axes of CCA ordination (Figs 3–6) during the studied seasons. Statistically significant correlations are marked in bold.

Variable	Seasons	Axis 1	Axis 2
pH	Winter 1999	0.33	**–0.62**
EC	Spring 2000	**–0.71**	–0.10
	Summer 2000	**–0.64**	–0.42
Na^+	Spring 2000	**–0.74**	0.11
	Summer 2000	**–0.64**	–0.41
K^+	Winter 1999	0.17	**–0.54**
	Spring 2000	–0.05	**0.56**
Ca^{2+}	Spring 2000	–0.43	**–0.52**
Mg^{2+}	Spring 2000	**–0.62**	–0.11
HCO_3^-	Winter 1999	**0.66**	–0.16
Cl^-	Spring 2000	**–0.70**	–0.03
	Summer 2000	**–0.56**	**–0.50**
Inundation depth	Spring 2000	–0.11	**0.81**
	Summer 2000	–0.25	**0.64**
	Autumn 2000	**0.76**	–0.45

The lowest EC and Na^+ and Cl^- concentrations occurred in the *J. littoralis* zone (Tables 2, 3). According to the Monte Carlo permutation test, the eigenvalues of the first and second axes were highly significant (P <0.01; Table 4). The cumulative percentage of variance explained by the first axis accounted for 20–29%, whereas the cumulative percentage of variance explained by the second axis accounted for 35–49%. The eigenvalues were significant for the study period (winter 1999 to autumn 2000) (Table 4).

During winter 1999, HCO_3^- concentration showed the highest correlation with the canonical axis 1 (Table 5) and associated zone was *H. geniculatum* (Fig. 3). In spring and summer 2000, inundation depth (3.44–19.11 cm) was the most promi-

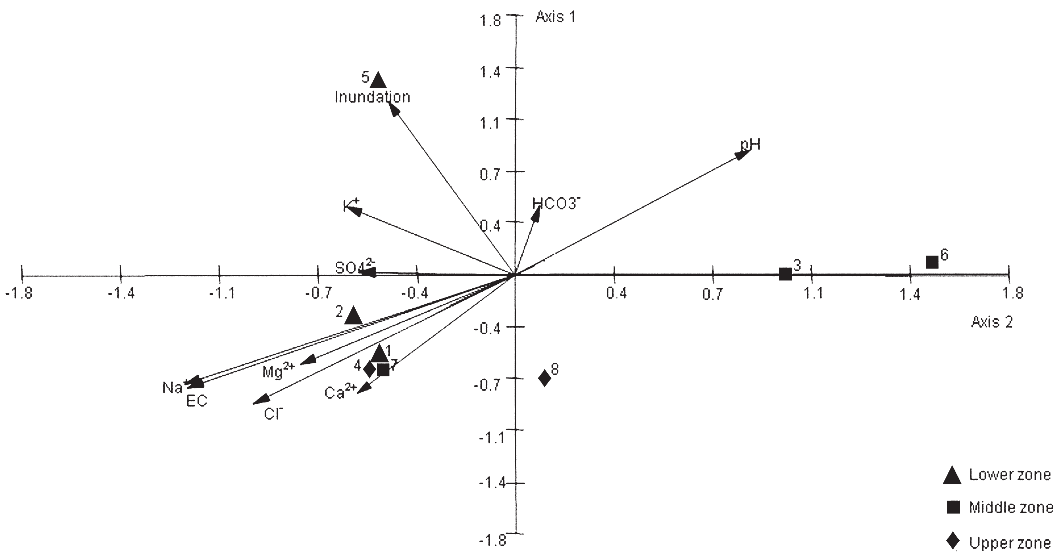

Fig. 5. Soil-plant species CCA diagram in salt marsh community for summer 2000. For the detailed description of zones see Fig. 2.

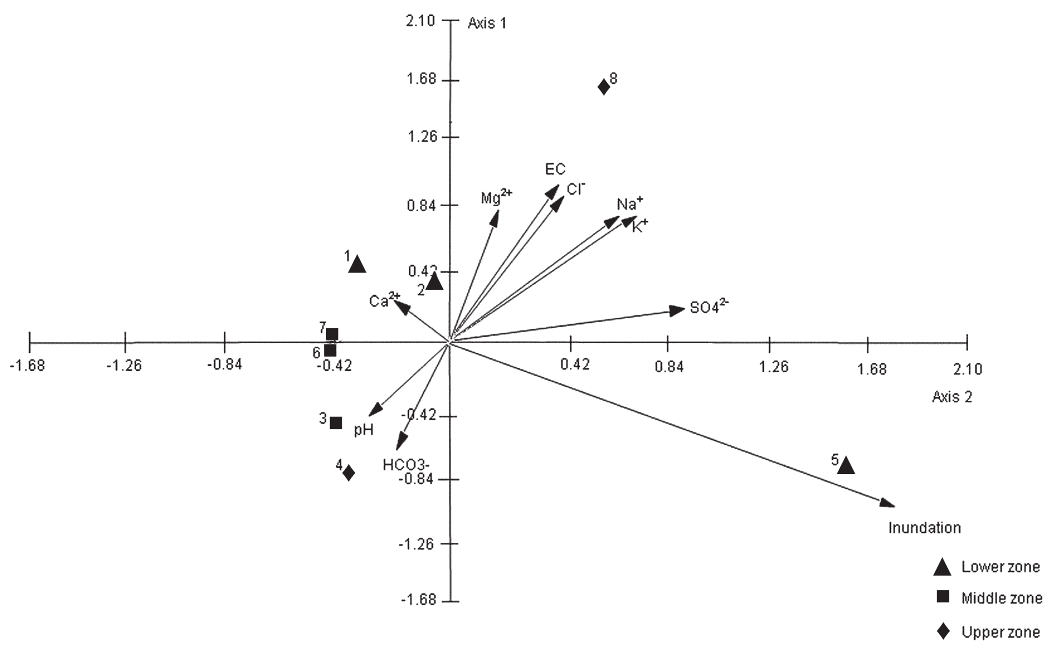

Fig. 6. Soil-plant species CCA diagram in salt marsh community for autumn 2000. For the detailed description of zones see Fig. 2.

nent factor correlated with the first and second axes, respectively (Table 5), with associated zone of *C. capitellata* (Figs 4 and 5), and the same was observed in autumn 2000 (10.33 cm) (Fig. 6).

HCO_3^- concentration and inundation depth (2.22–21.44 cm) are the environmental variables that best correlate with axis 1, whereas K^+ concentration and inundation depth (2.22–21.44 cm) best correlate with axis 2 during the study period (Table 5).

Significant negative correlations were also found. EC, Cl^-, Na^+ and Mg^{2+} concentrations were negatively correlated with the first axis during spring and summer 2000, whereas Ca^{2+} concentration was negatively correlated with the second axis during spring 2000. Similarly, soil pH, K^+ and Cl^- concentrations were negatively correlated with the second axis during winter and summer 2000, respectively (Table 5). Negative correlations were associated with the *J. acutus*, *S. prostrata and A. santonicum* zones during spring 2000, whilst they were associated with *S. prostrata* and *A. santonicum* zones during summer 2000 (Figs 3–5).

5. DISCUSSION

Plant zonation in salt marshes is affected by physical stress and nutrient limitation, and these factors can result in modification of the pattern of plant zonation (Barbour *et al.* 1987, Bertness 1991, Levine *et al.* 1998). In a previous study, inundation up to depth 10.70 cm was observed to persist for 170 days in the same area (Kutbay and Demir 2001). However, during the present study period, a twofold increase was observed and inundation depth up to 21.44 cm continued for 330 days. This is mainly due to existence of connection channel between the Kızılırmak River and the sea. Consequently, inundation up to 5.33 cm continued over the summer months (especially in summer 2000), and the growth period of saline species *C. capitellata* was extended. Channels between the river and the sea influence the distribution and composition of salt-marsh vegetation as they generate the gradients of soil salinity (Sanderson *et al.* 2000).

According to Tukey's HSD test, the *C. capitellata* zone is significantly different from other zones in terms of inundation. The difference in inundation frequency creates an environment for subsequent steps in marsh development leading to this striking zonation pattern of vegetation (Dijkema *et al.* 1990). Changes that occur in community structure in salt marshes mainly depend on inundation regime and salinity (Baldwin *et al.* 1996). Duration of inundation and Na^+ concentration are important factors for vegetation diversity at the landscape scale (Sanderson e*t al.* 2000, Bouzillé *et al.* 2001). Inundation has a pronounced regulatory effect on the distribution and abundance of plant species (Deegan and Harrington 2004).

The zonation of salt-marsh vegetation is influenced by the duration of inundation and is modified by the process of sedimentation (Vince and Snow 1984). In the lower marsh zone near the sea level, annual species are usually widespread. Perennial species are usually situated further from the sea, which is rarely flooded and therefore receives a small volume of sediment. Sediments are supplied by perennial species such as *Juncus* species (Watkinson and Davy 1985, Houwing *et al.* 1999). In the 2° locality, annual *S. prostrata* is situated near the sea, whereas perennial *J. littoralis* is situated further from the sea. *Salicornia* species are extremely tolerant to inundation (Davy *et al.* 2001). The *S. prostrata–S. marina* zone is inundated during winter months. *Salicornia* plants themselves may facilitate colonization by dominant, perennial halophytes in physically stressed marshes, by reducing evaporation from the sediment surface and controlling the salinity stress (Hacker and Bertness 1999). The second zone in the 2° locality includes salt-pan areas due to excess evaporation during summer months. Such salt pans are dominated by annual *S. prostrata* and *S. marina* among dense vegetation of perennial *J. acutus*. These salt pan areas are assumed to be indicative of extreme conditions (Duke and Mackenzie 2006). *Salicornia* (Chenopodiaceae) species are regarded as fugitive species of hypersaline bare patches and salt pans, because of their inability to compete with the dominant perennials (Bertness *et al.* 1992). Barrett (2006) stated that chenopods are often associated with very saline conditions.

Inundation causes stressful conditions in salt marshes, especially near sea level (Curcó *et al.* 2002). *H. geniculatum* and *P. coronopus* zones were never inundated during the study period. Thus Na^+ and Cl^- concentrations were remarkably increased during summer as compared to winter and spring and then remarkably decreased during autumn again. Upper salt marsh zones are less frequently inundated as compared with lower marsh zones where more frequently inundated. As a result of this infrequency in inundation, soil surface regions in the upper marsh zones are prone to extreme saline environmental conditions during the dry summer periods when evaporative rates increase (Callaway *et al.* 1990). EC, Na^+ and Cl^- concentrations were decreased during autumn in all vegetation zones except for *Carex capitellata* and *Artemisia santonicum* zones in which Na^+ and Cl^- concentrations and EC, respectively were increased during autumn. The precipitation regime changes according to the season and the rains cause a reduction in the soil salinity in the topographically elevated parts of the salt marshes (Garcia *et al.* 1993, Álvarez-Rogel *et al.* 1997, Omer 2004**).** The lowest Na^+ and Cl^- concentrations were found in the *J. littoralis* zone. This adjustment presumably influences the species that colonize any particular zone of the salt marsh (Álvarez-Rogel *et al.* 1997).

The *Juncus littoralis* zone followed the gradient of maximum salinity during autumn of the year 2000, and this zone was not related to the measured increase in soil salinity during winter, summer and spring. The differences in concentrations of saline ions like Na^+ and Cl^- show important temporal variations. Saline ions may be moved upward due to excess precipitation and capillarity during autumn because the porosity of soils in the study area was low (Álvarez-Rogel *et al.* 1997). This zone was not related to the increase in soil salinity in winter, summer and spring. The dense network of rhizomes of *J. littoralis* might facilitate the percolation of water and remove salts more readily than in other zones (Álvarez-Rogel *et al.* 2000). *Juncus* L. species are classified as slow-growing plants with extensive below-ground reserves, and hence tend to respond slowly to changes in abiotic connections such as soil factors (Pennings *et al.* 2005). The evident zonation of *Juncus* must therefore be explained in terms of factors related to the vertical movements of water above the soil and in the soil and, likely, soil properties (Silvestri *et al.* 2005). Upper (*P. coronopus* subsp. *coronopus*) and middle (*H. geniculatum*) zones were associated with HCO_3^- concentration during winter and autumn, respectively. The *C. capitellata* (Cyperaceae) zone was located on the positive site of axis 1 during autumn 2000 and followed the gradient of inundation. *S. prostrata*, *S. marina*, *H. geniculatum* and *P. coronopus* subsp. *coronopus* seems to be adapted to the most saline soils, whereas *C. capitellata* indicates the wettest soils in the studied salt marsh. Inundation depth and associated changes of the edaphic conditions in salt marshes may play a role in the maintenance and persistence of the Cyperaceae (sedge) and Juncaceae (forb) zones. The soils of the sedge and forb zones seem to retain more water than adjacent areas, and thus dramatically reduce the amount of oxygen that is available for plant roots. Forb and sedge communities are the consequence of poor drainage and waterlogged soils (Ewanchuk and Bertness 2004a, b).

The mean annual rainfall in the study area accounts for more than expected for an arid environment. However, remarkable seasonal fluctuations occurred in the study area and the notable aspects of these fluctuations are, primarily, excess evaporation occurring during summer months due to the potential evapotranspiration rate and the growth of annuals, especially near sea level (Wadie 2002). Curcó *et al.* (2002) also stated that annual variability is considerably higher in Mediterranean-type salt marshes. Our findings are similar to the studies that have been carried out in arid and semi-arid lands. The relative concentrations of Na^+, Ca^{2+}, Mg^{2+}, SO_4^{2-} and Cl^- are found to be the most important factors in controlling the vegetational pattern in saline areas (Asri and Ghorbanli 1997), as in the current study. It has been indicated that ionic concentrations (mainly Na^+ and Cl^-) are the most important variables that affect the distribution and structure of the plant communities in several studies that have been carried out in arid and semi-arid environments (El-Demerdash 1996, Abd

El-Ghani 2000a, b, Álvarez-Rogel e*t al.* 2001, Jafari *et al.* 2003).

In both studied localities EC, Na^+ and Cl^- concentrations were tended to decrease at upper zones (*P. coronopus* subsp. *coronopus* and *Juncus littoralis* zones). Mean electrical conductivity declined with increasing distance from the sea and increasing altitude, in clear accordance with the principal pattern of vegetation zonation. Sánchez *et al.* (1998) stated that Na^+ and Cl^- concentrations decline with increasing distance from the sea, in clear accordance with the principal pattern of vegetation zonation. This indicates the existence of a gradient that is perpendicular to the coastline, which broadly coincides with vegetation zonation along the topographic profile. Soil salinity increases with soil elevation, it reaches a maximum just above mean high sea level and then decreases beyond it. These observations, indirectly linking the presence of halophytes to topographic elevation, have been explained by noting that duration of evaporation periods (occurring when the marshes are not flooded) increases with elevation and thus salts become increasingly concentrated (Silvestri and Marani 2004).

Additionally at high soil elevations soil water salinity tends to decrease due to progressively less frequent flooding of salt marshes and the associated reduced salt input. The dependence of soil salinity on elevation may thus partly explain zonation, since physiological responses of plants to salinity are heavily species-dependent (Silvestri *et al.* 2005).

The results of the present study indicate that inundation, K^+ concentration, and HCO_3^- concentration are the key factors related to vegetation zonation.

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