

## Relationships between vegetation and environmental characteristics in a salt-marsh system on the coast of Northwest Spain

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### Abstract

This study reports an investigation of relationships between environmental variables (electrical conductivity of groundwater, soil redox potential, water-table depth, and high-tide flooding depth) on vegetation zonation in a salt-marsh system on the coast of northwest Spain. Discriminant analysis indicated that conductivity (a measure of salinity) and redox potential are correlated with vegetation type within the study area. Conductivity declines with increasing altitude and distance from the sea, whereas redox potential does not vary along well-defined large-scale gradients. Soils with the most strongly oxidizing conditions (i.e. moderate salinity, with Eh greater than 200 mV and thus subtoxic levels of  $Mn^{2+}$ ,  $Fe^{2+}$  and  $S^{2-}$ ) are occupied by the *Halimione portulacoides* community. Communities dominated by *Juncus maritimus*, and *Phragmites australis* reedbeds, occur at more strongly reducing sites (Eh between 100 and 200 mV, with possibly toxic levels of  $Mn^{2+}$  but not of  $Fe^{2+}$ ); the presence of these communities may thus be limited by  $Fe^{2+}$  toxicity. The most strongly reducing sites (with Eh low enough for the reduction of  $Fe^{3+}$  to  $Fe^{2+}$ ) are occupied by *Spartina maritima* and *Scirpus maritimus* communities. These communities appear to be tolerant of  $Fe^{2+}$ , and even of low concentrations of  $S^{2-}$ .

### Introduction

Salt-marshes constitute a clear example of an ecosystem comprising stable species-poor or monospecific communities with distributions related to environmental physical and chemical gradients as well as biological interactions (see, for example, Adams 1963; Lefor et al. 1987). Vegetation zonation in intertidal habitats appears to be a universal phenomenon (see for example Adam 1990): such zonation broadly reflects the influence of position with respect to tides, through more proximate variables such as substrate salinity (Rozema et al. 1985a, b; Callaway et al. 1990) or oxygen availability (Huiskes 1990; Patterson & Mendelsohn 1991). The influence of tides is modulated by factors such as topography (Lefor et al. 1987; Orson & Howes 1992; Sánchez et al. 1996) and local climate (Olf et al. 1988; Dijkema et al. 1990; Huiskes 1990).

Vegetation zonation in salt-marsh environments may also reflect biotic interactions. In the words of Pennings & Callaway (1992), the 'new paradigm' for the zonation of marsh plants is that upper limits are set by competition in relatively low-stress environments, while lower limits are set by tolerances to harsh physical conditions (Snow & Vince 1984; Bertness 1991a,b). In some cases, especially at intermediate tidal zones, neighboring plants can ameliorate harsh physical conditions for other species that do not have the physiological tolerance for those zones. This facilitation can extend species distributions into zones that they could not normally occupy (Bertness & Shumway 1993; Pennings & Callaway 1992; Bertness & Hacker 1994; Hacker & Bertness 1995).

In the work reported here we investigated the relationships between a number of physical and chemical factors (namely electrical conductivity of groundwater, soil redox potential, water-table depth, and high-tide

flooding depth) and vegetation zonation in a salt-marsh system on the coast of northwest Spain.

## Material and methods

### Nomenclature

Taxa followed Castroviejo et al. (1986–1993) and Tutin et al. (1964–1980); syntaxa followed Izco et al. (1996).

### Study area

The marshes studied are in the rias of Ortigueira and Ladrado in Galicia (northwest Spain) (Figure 1). Both rias are classed as wetlands of international importance under the Ramsar Convention (Ramsar Convention Bureau 1990), and have been declared protected sites by the Galician regional government. Climate in the area is mesothermic and strongly oceanic on Thornthwaite's classification (Carballeira et al. 1983), and thermocoline (*termocolino*) on the classification of Rivas-Martínez (1987). On Rivas-Martínez's (1987) biogeographic zonation of the Iberian Peninsula, the study area falls within the Cántabro-Atlántica Province of the Eurosiberian Region.

The vegetation of the study area has been characterized in a previous study (Izco & Sánchez 1996). In the present study, we considered perennial-species communities occupying large areas of the marsh, with distributions previously shown to be related to altitude (Sánchez et al. 1996). Specifically, the communities studied were (from lowest to highest altitude) *Spartinetum maritimae* (henceforth SP), *Limonio-Juncetum maritimae* subass. *typicum* (LJ), *Bostrychio-Halimionetum portulacoidis* (BH), *Limonio-Juncetum maritimae* subass. *juncetosum gerardi* (JG), *Agrostio-Juncetum maritimae* (AJ), *Scirpetum maritimo-compacti* (SC) and *Phragmites australis* reedbed (PA).

### Sampling

At each of the two sites, one sampling point was selected in each community. Physical and chemical variables were determined at each sampling point at 29-day intervals over the period March 1992 to April 1993 inclusive, at low or high tide (see below) on the day of the new-moon spring tide.

For monitoring of water-table depth (measured at low tide), electrical conductivity of groundwater (like-

*Table 1.* Results of repeated-measures analyses of variance to investigate, for each of the four environmental variables, whether the variance in that variable can be explained by *location* and/or *syntaxon*. Environmental data were collected at each site on 15 occasions (see Material and methods). The syntaxon PA was excluded from this analysis because it is present at only one of the two locations.

Variable	Factor	<i>F</i>	df	<i>p</i>
Flooding depth	Location	11.11	1	0.008
	Syntaxon	41.86	5	0.00
Electrical conductivity	Location	0.01	1	0.98
	Syntaxon	87.96	5	0.00
Eh	Location	0.10	1	0.91
	Syntaxon	58.80	5	0.00
Water-table depth	Location	0.41	1	0.53
	Syntaxon	12.89	5	0.00

wise measured at low tide), and high-tide flooding depth, a borehole as specified by Soil Survey Staff guidelines (7 cm in diameter and 100 cm deep, lined with a PVC tube rising to a sufficient height to prevent submersion at high tide; Soil Survey Staff 1975, cited in Faulkner et al. 1989) was sunk at each sampling point. Water-table depth (cm below ground level, expressed as a negative value) and electrical conductivity (i.e., a measure of salinity) were determined within 15 min either side of low tide as predicted by the Spanish Navy (IHM 1992, 1993). Flooding depth (cm above ground level) was determined within 15 min either side of high tide. Additionally, soil redox potential was determined at all sites on all sampling days, within 2 h either side of low tide.

Water-table depth and flooding depth were measured with an accuracy of  $\pm 0.5$  cm. In cases where a site was not flooded at high tide, water-table depth (i.e., a negative value) was taken as flooding depth for the purposes of data analysis. Electrical conductivity was measured with a 33 SCT conductivity meter (YSI model, Simpson Electric, Elgin, Ill.). For each site and each sampling day, redox potential (Eh) was determined as the mean of five readings taken directly from the soil close to each borehole; each reading was taken at a depth of about 10 cm (i.e., in the root zone) with an ORP platinum electrode (Hanna Instruments, Woonsocket, Ri.), after fluctuations in the reading had dropped below  $2 \text{ mV min}^{-1}$ ; the final value was corrected by adding the potential of a calomel reference electrode (244 mV); Eh was not corrected for pH, since



Figure 1. Map showing the location of the study area.

this is consistently close to 6.5 in all communities of the study area (Sánchez 1995).

### Data analysis

Data normality was confirmed by Kolmogorov–Smirnov tests. The data on water-table depth proved to be non-normal and were thus subjected to a logarithmic transformation before analysis. Whether the different variables were affected by *location* (Ortigueira or Ladrido) or *syntaxon* (plant community) (6 levels; the syntaxon PH was excluded from this analysis because it is present at only one of the two locations) was investigated by repeated-measures analysis of variance (15 repeated measures between March 1992 and April 1993). To investigate in greater detail the effects of the different variables on vegetation zonation, a step-wise discriminant analysis was performed with the four

environmental characteristics as independent variables and the seven syntaxa as groups to be discriminated; the analysis was performed as per Norusis (1994), with variable selection on the basis of minimization of Wilks' lambda. All statistical analyses were performed with the SPSS package (Anon. 1989–1995). Unless otherwise stated, statistical significance is taken to be indicated by probability levels below 0.05.

### Results

Repeated measures analysis of variance indicated that there was significant variation between locations only in high-tide flooding depth, whereas all four variables considered varied significantly among syntaxa (Table 1). Subsequent analyses were thus performed considering only the factor *syntaxon*.

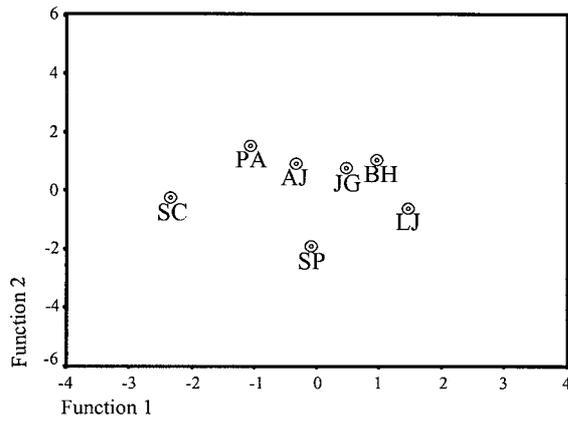


Figure 2. Mean scores of the different vegetation communities on the two canonical discriminant functions obtained by stepwise discriminant analysis (variables selected: electrical conductivity and redox potential).

Stepwise discriminant analysis selected electrical conductivity and redox potential as the variables explaining the majority of variation among groups (syntaxa). Conductivity loaded heavily on the first discriminant function, while redox potential loaded heavily on the second; both functions explained about 50% of total variance (Figure 2, Table 2). Group means in all cases differed significantly, except for the pair BH and JG ( $F = 2.15$ ,  $p = 0.12$ ).

Electrical conductivity declined from the lower- to the higher-altitude parts of the marsh (Figure 3). This indicates the existence of a gradient perpendicular to the coastline, and broadly coincides with vegetation zonation along the topographic profile (Sánchez et al. 1996). Note however that mean salinity was highest not at the SP sites but at the LJ sites; this is discussed below.

Redox potentials were consistently less than 300 mV, indicating anaerobic conditions (see Faulkner & Patrick 1992). However, both analysis of variance (see Table 1) and discriminant analysis indicated significant among-taxon differences. In the *Spartina maritima* and *Scirpus maritimus* communities (SP and SC), redox potentials were very low and indeed in many cases negative (Figure 4), indicating strongly reducing conditions. In the LJ, JG, AJ and PA communities, mean redox potentials were in the 100–200 mV range, while the highest values (mean >200 mV) were those recorded in the BH community (Figure 4).

Neither water-table depth nor flooding depth were effective predictors of syntaxon. Flooding depth discriminated the *Spartina maritima* community, but did

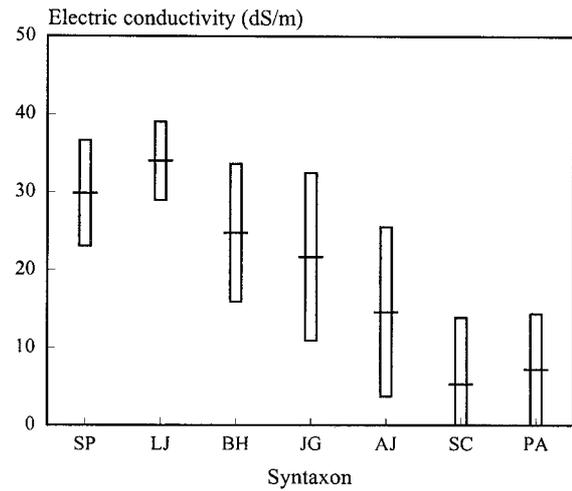


Figure 3. Electrical conductivity (means  $\pm$  standard deviation) in each community. The different communities are shown in order of distance from the sea, from seashore (left) to inland (right).

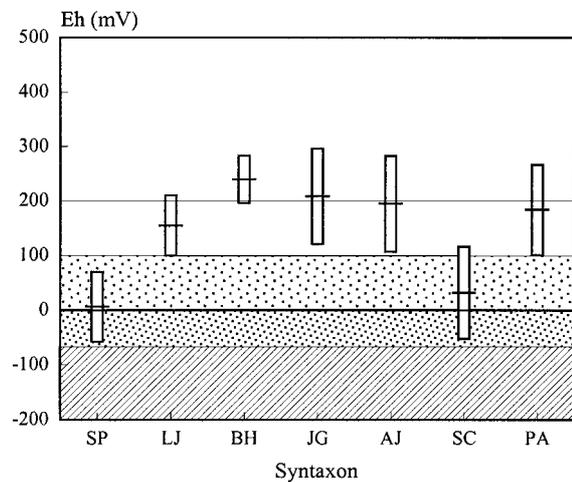


Figure 4. Redox potential (means  $\pm$  standard deviation) in each community. The different communities are shown in order of distance from the sea, from seashore (left) to inland (right). Reduction of  $Mn^{4+}$  to  $Mn^{2+}$  occurs below 200 mV, and reduction of  $Fe^{3+}$  to  $Fe^{2+}$  below 100 mV (Patrick & Jugsujinda 1992); reduction of  $SO_4^{2-}$  to  $S^{2-}$  occurs below 0 mV (Ingold & Havill 1984), while  $S^{2-}$  concentrations of about 1 mM are typically associated with redox potentials of about  $-70$  mV (Koch et al. 1990).

not discriminate among the remaining communities (Table 3). Mean water-table depth was highest in the *Spartina maritima* and *Scirpus maritimus* communities, and lowest (mean  $-16$  cm) in the *Bostrychio-Halimionetum* community (Table 3). As expected, water-table depth was negatively correlated with redox potential ( $r_s = -0.62$ ).

Table 2. Results of the stepwise discriminant analysis performed to identify the best set of discriminant functions for predicting the syntaxon present at a site given that site's environmental characteristics. The predictor variables selected were electrical conductivity (E.C.) and Eh. Percent of cases correctly classified by the model is 57.3%.

Variable	Unstandardized discriminant function coefficients		Standardized discriminant function coefficients		Correlation coefficients	
	Function 1	Function 2	Function 1	Function 2	Function 1	Function 2
Electric Cond.	0.10	-0.56	0.87	-0.49	0.86	-0.51
Eh	7.04E-3	0.01	0.51	0.86	0.49	0.87
Constant	-3.08	-0.44				

	Function 1	Function 2
Eigenvalue	1.35	1.31
Canonical correlation.	0.76	0.75
Variance explained (%)	50.80	49.17

Table 3. Water-table depth (cm below ground level) and high-tide flooding depth (cm above ground level) in each of the syntaxa. Values shown are means  $\pm$  standard deviations. If the high tide did not reach the site in question, flooding depth was recorded as water-table depth (i.e., a negative value).

Syntaxon	Water table depth	Flooding depth
SP	-0.2 $\pm$ 0.8	52.9 $\pm$ 40.9
LJ	-5.9 $\pm$ 12.1	18.9 $\pm$ 34.9
BH	-17.1 $\pm$ 7.6	8.7 $\pm$ 32.5
JG	-14.9 $\pm$ 19.4	-1.1 $\pm$ 32.9
AJ	-10.7 $\pm$ 13.4	3.7 $\pm$ 27.9
SC	-2.8 $\pm$ 4.1	8.4 $\pm$ 18.2
PA	-17.2 $\pm$ 6.2	-6.8 $\pm$ 25.3

## Discussion

In the present study we investigated variation in physicochemical conditions among areas of a salt-marsh occupied by different vegetation types. Though we did not specifically consider within-area variation, various previous studies have demonstrated that differences among areas occupied by different vegetation types are consistently significant (see for example Pennings & Callaway 1992; Hackney et al. 1996; Woerner & Hackney 1997), at least when consideration is of representative examples of the 'established vegetation' ('perennial turfs' *sensu* Bertness et al. 1992), as in the present study. The results of our analysis of variance, which show that most variation is due to differences among communities rather than among sites (Table 1), are consistent with this view.

The results of the present study indicate that groundwater salinity (as estimated by electrical conductivity) and redox potential seem to be the two key factors related to vegetation zonation in the study area (Figure 2; Table 2), in accordance with previous reports (see for example Armstrong et al. 1985; Brandyopadhyay et al. 1993). The two other variables considered (water-table depth and high-tide flooding depth) are not effective predictors of vegetation type. That water-table depth was not an effective discriminant may simply reflect the difficulties involved in accurately measuring this variable (see Faulkner et al. 1989); waterlogging regime is almost certainly a key factor affecting vegetation zonation, as reflected in the effectiveness of redox potential for discriminating among communities. Flooding depth discriminated only the *Spartina maritima* community, in accordance with previous studies which have likewise shown that this variable is scarcely correlated with vegetation zonation in upper estuarine sites (see Adam 1990).

Resistance to NaCl appears to be the most important factor correlated with distribution of salt-marsh vegetation (Rozema et al. 1985a). Our data are in accordance with this finding, since electrical conductivity of groundwater was the variable loading most heavily on the first discriminant function in the discriminant analysis. Mean conductivity values declined with increasing distance from the sea and increasing altitude, in clear accordance with the principal pattern of vegetation zonation (Figure 3). However, mean conductivity was highest in the lower middle marsh (the LJ community in our study area), probably as a result of evapotranspiration (see Kadlec 1982). It is well

known that groundwater salinity is determined by tidal influences at low levels in the profile, but that climatic variables become increasingly important with increasing altitude (de Leeuw et al. 1990, 1991; Andreu et al. 1994).

The second most important factor, with a loading similar to that of conductivity in the discriminant analysis, was redox potential. Under anaerobic conditions, salt-marsh microorganisms use any of various inorganic ions as terminal electron acceptors in the process of mineralization of organic matter. Depending on soil redox potential, the electron acceptors used (from high redox potential to low) are  $\text{NO}_3^-$ ,  $\text{Mn}^{4+}$ ,  $\text{Fe}^{3+}$  or  $\text{SO}_4^{2-}$ , these being reduced to  $\text{NH}_4^+$ ,  $\text{Mn}^{2+}$ ,  $\text{Fe}^{2+}$  and  $\text{S}^{2-}$  respectively (Patrick & Jugsujinda 1992). The latter three ions ( $\text{Mn}^{2+}$ ,  $\text{Fe}^{2+}$  and  $\text{S}^{2-}$ ) are generally considered to be phytotoxic (see, for example, Ingold & Havill 1984; Rozema et al. 1985b; Koch & Mendelssohn 1989; Singer & Havill 1993), and may be growth-limiting. The reductions of  $\text{Mn}^{4+}$  to  $\text{Mn}^{2+}$ ,  $\text{Fe}^{3+}$  to  $\text{Fe}^{2+}$ , and  $\text{SO}_4^{2-}$  to  $\text{S}^{2-}$  occur at redox potentials below about 200, 100 and 0 mV respectively (according to Patrick & Jugsujinda 1992; for Mn and Fe, and to Ingold & Havill 1984, for S). The Eh values recorded in the present study show marked coincidence with these values (see Figure 4), suggesting that the observed vegetation zonation may be at least partially due to manganese, iron and/or sulphur toxicity.

The community dominated by *Halimione portulacoides* (BH) is that which occupied the most strongly oxidizing soils: mean Eh for this community was more than 200 mV (Figure 4), which is the point below which reduction of  $\text{Mn}^{4+}$  occurs. Note, however, that manganese toxicity has been ruled out as a factor affecting the distribution of this species in a previous study of a mesohaline marsh (Singer & Havill 1993). The redox potentials determined at sites occupied by this species (Figure 4) are probably not low enough to cause  $\text{Fe}^{2+}$  or  $\text{S}^{2-}$  toxicity. This community was also that least strongly correlated with water-table depth (Table 3). These results are in accordance with those of previous studies that have found *H. portulacoides* to be limited to well-aerated areas of salt-marshes and to be a poor competitor in flooded soils (Beefink 1977; Armstrong et al. 1985). In our study area, this species generally occurs along the edges of channels, where the high hydraulic conductivity permits rapid drainage and thus favours aeration (see Jordan 1985; Price et al. 1988).

In the communities with high cover values of *Juncus maritimus* (LJ, AJ, JG) or *Phragmites australis* (PA), redox potentials were significantly lower than in

the BH community. In areas of salt-marsh not adjacent to channels, evapotranspiration is the main cause of water loss from the soil (Dacey & Howes 1984; Huiskes 1990). As a result, water-table depth at such sites declines much more slowly than at channel-side sites, and most rapidly during the summer (Howes & Goehrig 1994). In all of these communities, redox potentials were generally within the range at which  $\text{Mn}^{2+}$  exists stably, and indeed the species of these communities have been reported to tolerate this ion (Singer & Havill 1993). However, our data suggest that these communities are rarely present in sites at which redox potential is such that iron exists as  $\text{Fe}^{2+}$  (Figure 4). This result appears to contradict those of other authors (Rozema et al. 1985b; Snowden & Wheeler 1993), who have reported these communities to be  $\text{Fe}^{2+}$ -tolerant. Note that the three *Juncus* communities (LJ, AJ and JG) could be discriminated by conductivity but not by redox potential (see Figure 2).

The most strongly reducing conditions were recorded in the communities dominated by *Spartina maritima* (SP) and *Scirpus maritimus* (SC), as expected given the heavy waterlogging to which these communities are subject (Table 3). Redox potentials were well within the range at which iron exists as  $\text{Fe}^{2+}$ , and in many cases within the range at which sulphur exists as  $\text{S}^{2-}$  (Figure 4). The resistance of species of the genus *Spartina* to  $\text{Fe}^{2+}$  and  $\text{Mn}^{2+}$  toxicity has been well documented (Adams 1963; Rozema et al. 1985b), as has the resistance of *Scirpus maritimus* to  $\text{Fe}^{2+}$  (Clevering & van der Putten 1995). That redox potentials were in many cases within the  $\text{S}^{2-}$  range is of interest, since this ion is generally phytotoxic and is widely considered to be one of the major constraints on the distribution of macrophytes in coastal ecosystems (see, for example, Ingold & Havill 1984; Mendelssohn & Mckee 1988; Koch et al. 1990). In the present study we did not determine sulphide levels; however, the characteristic 'bad eggs' smell of  $\text{H}_2\text{S}$  was only noted at SP and SC sites.

Previous studies have likewise found *Spartina maritima* to occur at sites with strong reducing conditions (Castellanos et al. 1994), and similar results have been obtained for other species of this genus, such as *S. anglica* (Armstrong et al. 1985) and *S. alterniflora* (Bertness 1991b; Hackney et al. 1996). Under such conditions, *Spartina* species appear to escape competition from other macrophytes, which cannot tolerate sulphide. As a result, any increase in redox potential – due for example to sediment entrapment and thus increased altitude, or to a reduction in tidal flooding –

facilitates invasion by other species and displacement of *Spartina* (Bertnes 1991b; Castellanos et al. 1994; Adams & Bate 1995).

Greenhouse experiments performed by Koch & Mendelssohn (1989) have indicated that sulphide becomes toxic to *S. alterniflora* at levels above 1 mM, corresponding to redox potentials of  $-70$  mV or less (Koch et al. 1990). This result is in accordance with our findings in the present study, since redox potential at SP sites was rarely below this threshold (Figure 4). At such low redox potentials, sulphide appears to be toxic to *Spartina* species because it inhibits alcohol dehydrogenase, an essential enzyme in the anaerobic respiration pathway used by the plant under anoxic conditions (Koch et al. 1990; Pezeshki et al. 1993); this leads to reduced uptake of nitrogen, reduced energy availability and reduced growth (Koch & Mendelssohn 1989; Koch et al. 1990; Bandyopadhyay et al. 1993).

*Scirpus maritimus*, like other species of the same genus (see Hackney et al. 1996), is likewise able to withstand high sulphide levels. Its lower limit of distribution closely matched that of *Spartina maritima*, suggesting that the threshold level for sulphide toxicity is similar. Despite the similar distributions of the *Scirpus maritimus* and *Spartina maritima* communities with respect to redox potential, however, the latter was correlated with high salinity (Figure 3); this is in accordance with the results of Broome et al. (1995), who found *Spartina* (*S. patens*) to tolerate higher salinity than *Scirpus* (*S. olneyi*).

In conclusion, these results suggest that vegetation zonation in the rias of Ortigueira and Ladrado is largely governed by soil salinity and degree of waterlogging. However, generalized models of vegetation zonation in salt-marshes should take account of other possible effects, such as those due to biotic interactions.

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