ZONATION OF HALOPHYTIC VEGETATION ALONG A TIDE EXPOSURE GRADIENT AND ASSOCIATED PROCESSES

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RESUMEN

Zonación de la vegetación **halófila** a lo largo de un gradiente de exposición **mareal** y procesos asociados.

Se ha estudiado la zonación de la vegetación a lo largo de un gradiente topográfico a pequeña escala en la marisma de Mundaka-Gemika (Norte de España, Golfo de Vizcaya). La distribución de las especies aparece estrechamente ligada a los factores derivados de la topografía, como son la materia orgánica, el pH, la humedad y la conductividad. El potencial redox y la compactación del suelo varían independientemente, aumentando la heterogeneidad del hábitat. La altura media de las pleamares es el nivel a partir del cual los procesos de coexistencia dan paso a la dominancia de las especies competidoras. Se plantea un modelo de zonación. En este modelo, el grado de solapamiento disminuye hacia tierra adentro, donde se produce una competencia y una segregación de las especies inferiores hacia los lugares más expuestos. No se puede concluir que la marcada segregación de las especies a lo largo del gradiente sea debida exclusivamente a los requerimientos fisiológicos de las plantas. La dispersión mareal juega probablemente un importante papel en la distribución de las anuales *Salicornia* y *Suaeda,* pero escaso en las especies con crecimiento vegetativo, *Spartina maritima, Arthrocnemum perenne, Halimione portulacoides*, y *Arthrocnemum fruticosum.* La zonación de las plantas debe ser explicada teniendo en cuenta procesos asociados como la perturbación física y la competencia interespecífica, que deben ser considerados en relación con los factores edáficos, para explicar los mecanismos subyacentes de tal zonación. Es necesario el trabajo en el campo y en el laboratorio para determinar el nicho de estas especies en las marismas de esta parte de la Costa Atlántica.

Palabras clave: plantas de marisma, *Salicornia, Halimione,* competencia, exposición mareal, Golfo de Vizcaya, Costa del Atlántico.

ABSTRACT

The zonation of vegetation in the salt-marsh of Mundaka-Gemika (Bay of Biscay, N. Spain) is studied along a small scale topographic gradient. Species distribution appears closely linked to abiotic factors deriving from topographical level, such as organic matter, pH, moisture and conductivity. The redox potential and the compactness of the soil vary in other ways, thus increasing the heterogeneity of the habitat. There is a critical elevation, close to MHW level, after which coexistence processes give way to dominance by the best equipped species. A model of the zonation is given. In this model the degree of overlap decreases towards the top area, where there is competitive exclusion and segregation of interior species to the most exposed area. It can not be concluded that the marked segregation of the species along the gradient is exclusively due to physiological

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requirements of the plants. Tidal dispersal probably plays an important role on the distributional pattem of the annual species *Salicornia* and *Suaeda,* but a minor role on the species with vegetative expansion, *Spartina maritima, Arthrocnemum perenne, Halimione portulacoides,* and *Arthrocnemum fruticosum.* Plant zonation can only be explained bearing in mind associated processes such as physical disturbance and interspecific competition. As other authors found in higher latitudes, these processes will need to be considered in relation to edaphic factors in elucidating the underlying mechanisms of salt marsh plant zonation. Experimental work in field and laboratory is needed to determine the niche position of each species in the salt marshes in this part of the Atlantic Coast.

Key words: salt marsh plants, *Salicornia*, *Halimione*, competence, tidal exposure, Bay of Biscay, Atlantic Coast.

INTRODUCTION

The Mundaka-Gernika estuary is situated on the Bay of Biscay (43° 23' N, 2" 40' W) in Northern Spain (figure 1). It is arround 11 km. long, and 1 km. at its widest point. The tidal variation is approximately 4 m. Specific hydrological and geomorphological characteristics mean that this estuary has a strong marine influence (GOBIERNO VASCO, 1986). Human intervention is long-standing and intense, mainly through terracing and explotation for cultivation, though this has not prevented the formation of a salt-marsh on both sides of the tidal river. The vegetation of this salt-marsh has been studied from a phytosociological point of view (ONAINDIA & NAVARRO, 1986), and a series of plant associations have been described which are linked to the degree of tidal flooding. Other quantitative studies have detected ecological groups related to a set of environmental variables which can be summed up in an edaphogenesis produced by the altitudinal gradient (Benito *et al.,* 1988).

Vegetational variation occurring along broad "master" environmental gradients can mask significant trends occurring at finer scales, thus, these works give no information on the spatial exploitation of species on a small scale, which often forms real monospecific mosaics in the salt-marsh environment. Small transects with many contiguous quadrats allow one to analyse the distribution pattems on different scales, which are imperceptible in an overview. This method is satisfactory when demonstrating spatial exclusión of species and their relationship with edaphic factors (OTHMAN, 1980; GREIG-SMITH, 1983). The aims of this work is to identify the processes or mechanisms which

control de zonation of the salt marsh plánts and can be derived from the life strategies of the species involved.

METHODS

BIOTIC DATA

A typical zone with a representative vegetational variation was selected along the tidal gradient in the low marsh (between mean high water neap, MHWN, and mean high water spring level, MHWS). In the high marsh, above MHWS, other vegetation groups characterized by *Juncus rnaritirnus* and *Elymus pycnanthus* are present (BENITO *et al.,* 1988).

On the basis of the way some species grow (chamaephytes with clonal expansion), abundance was estimated as the cover of each species according to non-linear scale of 0 to 5 (0=0%, 1=0-5%, 2=5-25%, 3=26-50%, 4=51-75%, 5=76-100%) in grid squares along a transect of 34.5 m. taking in the altitudinal gradient and running between the low area, no provided of species, and the high area, which is homogeneous and dominated by *Hulirnione portulacoides.* The total number of quadrats was 138. Specific classification is based on TUTIN *et al.* (1964-1980).

Several samples of each species were taken along the length of the transect, in order to measure the water potential of the leaves in a pressure chamber (PMS, Inst. Co. Corvallis Oregon). This measurement gives information on the water stress on the plant in a saline medium. The samples were taken in late July 1988 (at noon in a typical summer day) at which time there was a good representation of annuals.
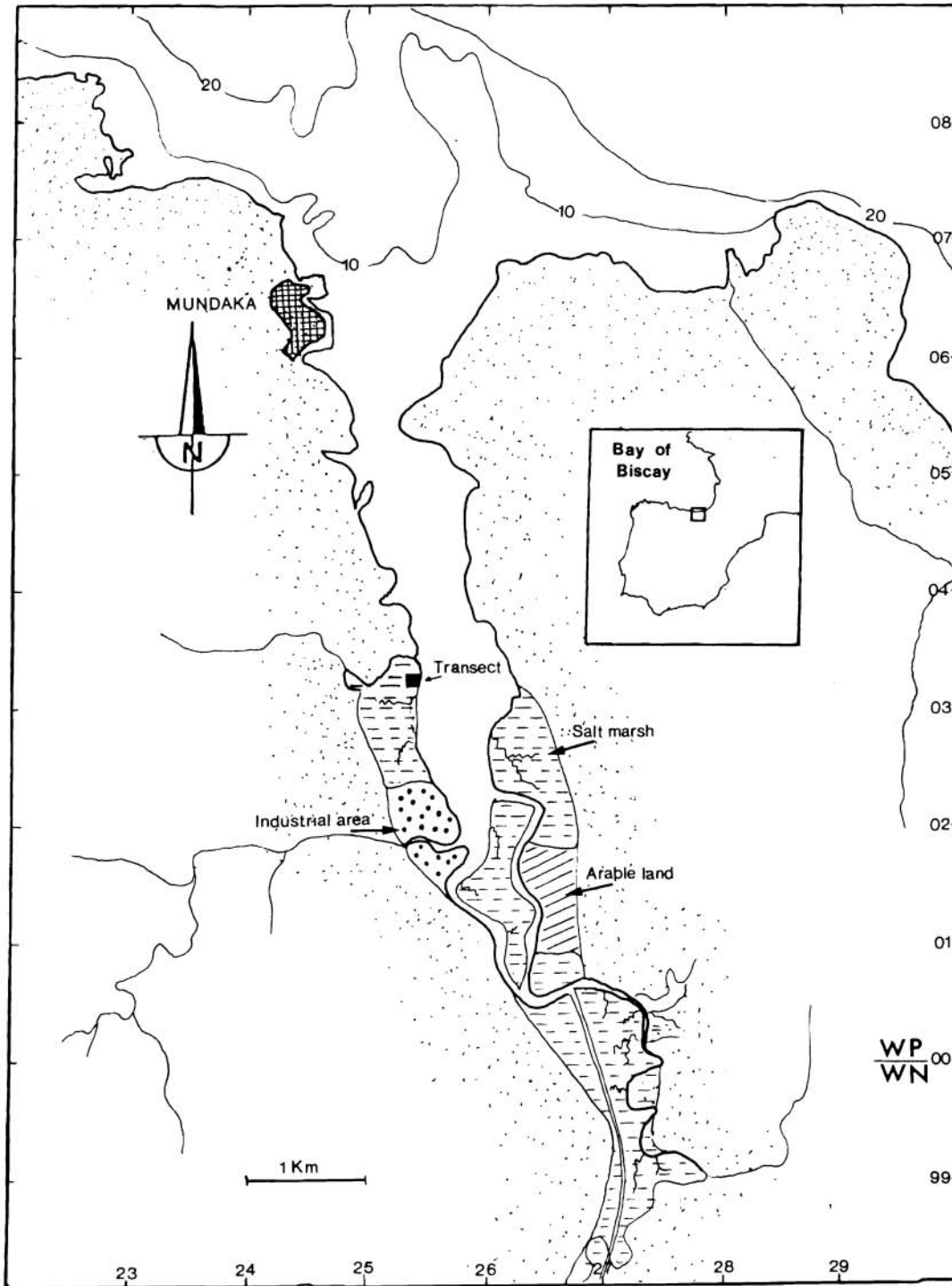
FIGURE 1.   Location of the Mundaka estuary and the transect.

Localización del estuario de Mundaka y del transecto estudiado.

ABIOTIC DATA

The physical-chemical factors chosen among those capable of determining the distribution of species were those which may be simply analysed, and which yield good information. The following measurements were taken in the field: elevation (in cm.) measured with a level for each quadrat with regard to the beginning of the transect and mean high water level (MHW), compactness using a Soiltest penetrometer, which gives an idea of the texture and degree of waterlogging of the soil. On alternate squares the redox potential (in mvolts) was measured at a depth of 5 cm. with a combined platinum electrode connected to an Orion monitor, which means that anoxia and anaerobiosis processes caused by tidal flooding could be detected. Furthermore, soil samples were taken at a depth of 5 cm. in alternate squares, for laboratory analysis. The variables measured were: pH in saturated paste, with a specific electrode connected to an Orion monitor; electrical conductivity (mS), with an INSTRAN 10 conductometer and an electrode with a cell constant of 0.99 on soil paste extracts; percentage of moisture, by drying at 105 °C for 48 hours; and percentage of organic matter, by ignition at 450 °C for 2 hours.

PROCESSING OF DATA

The matrix of abiotic data thus resulting was put through a Principal Component Analysis, PCA in order to determine the main principles of variation. For more efficient analysis, the data were normalized according to their density function. The transformations which brought kurtosis and skewness values of data distribution closest to 0 were log (1+x) log(x), $\sqrt{x}$ and $\sqrt[5]{x}$. Relations between the abundance of species and the factors analysed were established by Spearman rank correlation coefficients.

RESULTS

BIOTIC FACTORS

Figure 2 shows the cover values for the species registered, except for those only scarcely represented *(Puccinellia mar-itima, Limonium*

vulgare and *Triglochlin maritima).* The species found are well known in salty environments on the coasts of Europe (BEEFTINK, 1977). Except for *Spartina,* the species described are all *Chenopodiaceae. Salicornia ramosissima* J. Woods *(S. europea* L. group) and *Suaeda maritima* (L.) Dumort are short annual pioneering species widely distributed along the coasts of Europe. The remaining species are perennials, with a mainly vegetative growth. *Spartina maritima* (Curtis) Femald is a grass widespread around the coasts of Europe, normally occupying the lowest areas of salt-marshes. *Arthrocnemum perenne* (Miller) Moss is a short, perennial species with a mediterranean optimun, associated with places of high salinity and obstructed drainage. *Halimione portulacoides (L.)* Aellen a woody chamaephyte approximately 40 cm. in height, is one of the species which dominates this and many other European salt-marshes. It occupies mainly the edges of channels where soil aeration is high. *Arthrocnemum fruticosum* (L.) Moq is another tall, woody species with a Mediterranean distribution which has a slight presence in this salt-marsh.

EDAPHIC FACTORS

Figure 3 shows the evolution of the factors along the transect. The parallel variation of elevation, pH, moisture, organic matter and conductivity variables is worthy of note.

The greatest effect of pH variation is probably the availability of nutrients: N and P, which, contrary to other metallic cations, are limiting to primary production of salt-marshes (JEFFERIES, 1977). The range of values found in our study is great for such a small area, which indicates a high gradient in a the processes linked to the development of salt-marshes. The values found in the lower areas close to those of marine sediments (WAISEL, 1972), while the decrease as we approach the higher areas of the transect is linked to the accumulation of roots and dead organic matter, and the subsequent formation of humic acids, which means that the cation exchange points in the clay are saturated with H^+ ions (RANWELL, 1972; GRAY & BUNCE, 1972; BASSET, 1978).

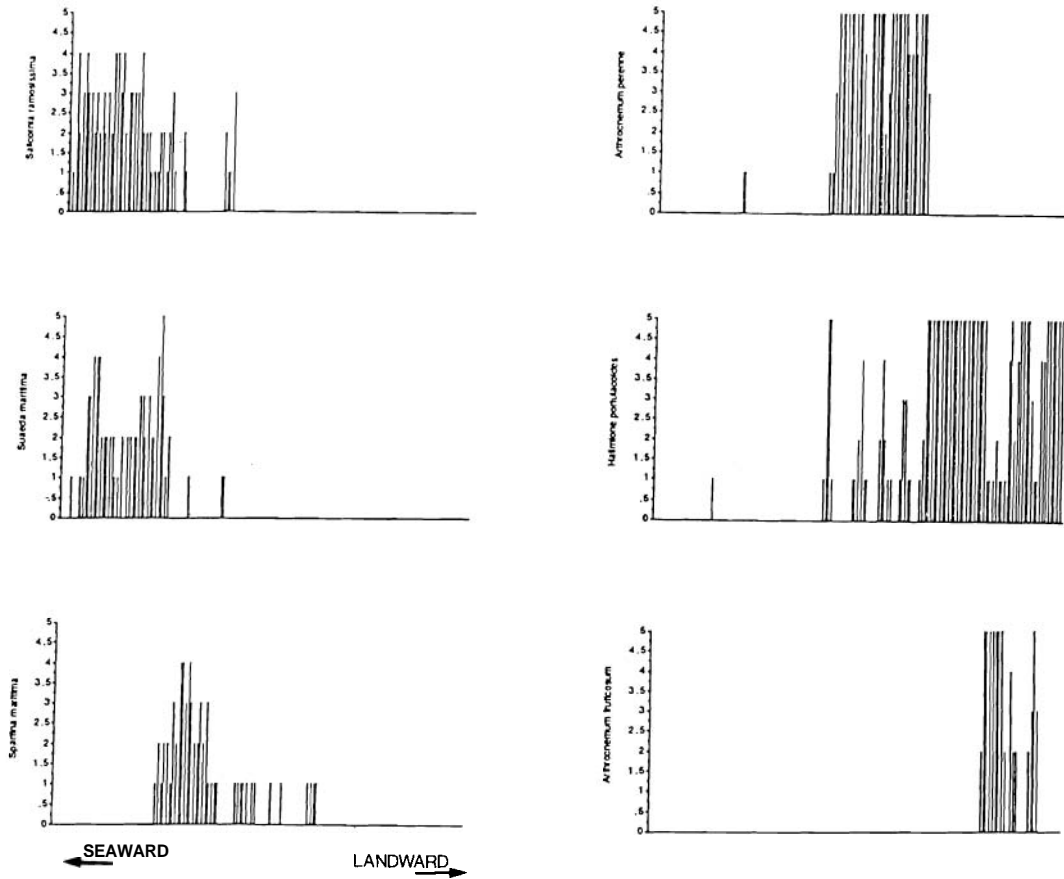The amount of organic matter seems to depend on the plant biomass, as it increases

FIGURE 2.   Species composition and cover values of the tansect.

Composición y cobertura de las especies a lo largo del transecto

towards the areas occupied by the woody species *Halimione portulaciodes* and *Al-throcnrmum fruticosum*. This increase of organic matter with topography and in relation to plant development seems logical, and has been found before in other studies, including the one carried out in this same salt-marsh during a previous work on the general distribution of halophytic species (BENITO *et al.,* 1988). Also, close relationships have been detected between organic matter and P, and specially with the total N (organic plus inorganic) (GRAY & BUNCE, 1972; BASSET, 1978, BRADY, 1974). The data collected are too limited for us to venture an opinion as to the amount of N or P which can be assimilated in the different parts of the transect, though, as some authors point out (WILSON & KEDDY,

1986) fertility may be expected to be greater in the less disturbed (higher) areas.

Soil moisture remains high, though its evolution' is the reverse of what was expected, and it increases towards the high area. This may be interpreted as being due to a lesser incidence of tides (neap tides during the sampling period, in mid summer), which failed to flood the gradient, even the lower part of the area, and to the greater retention of water in soils in the higher area on the basis of the higher organic matter and clay content. Also, the greater plant biomass in the higher area means less evapotranspiration and greater retention of water.

It is interesting to see how there is a rise in the amount of salts towards the high area, with values always well above those tolerable for
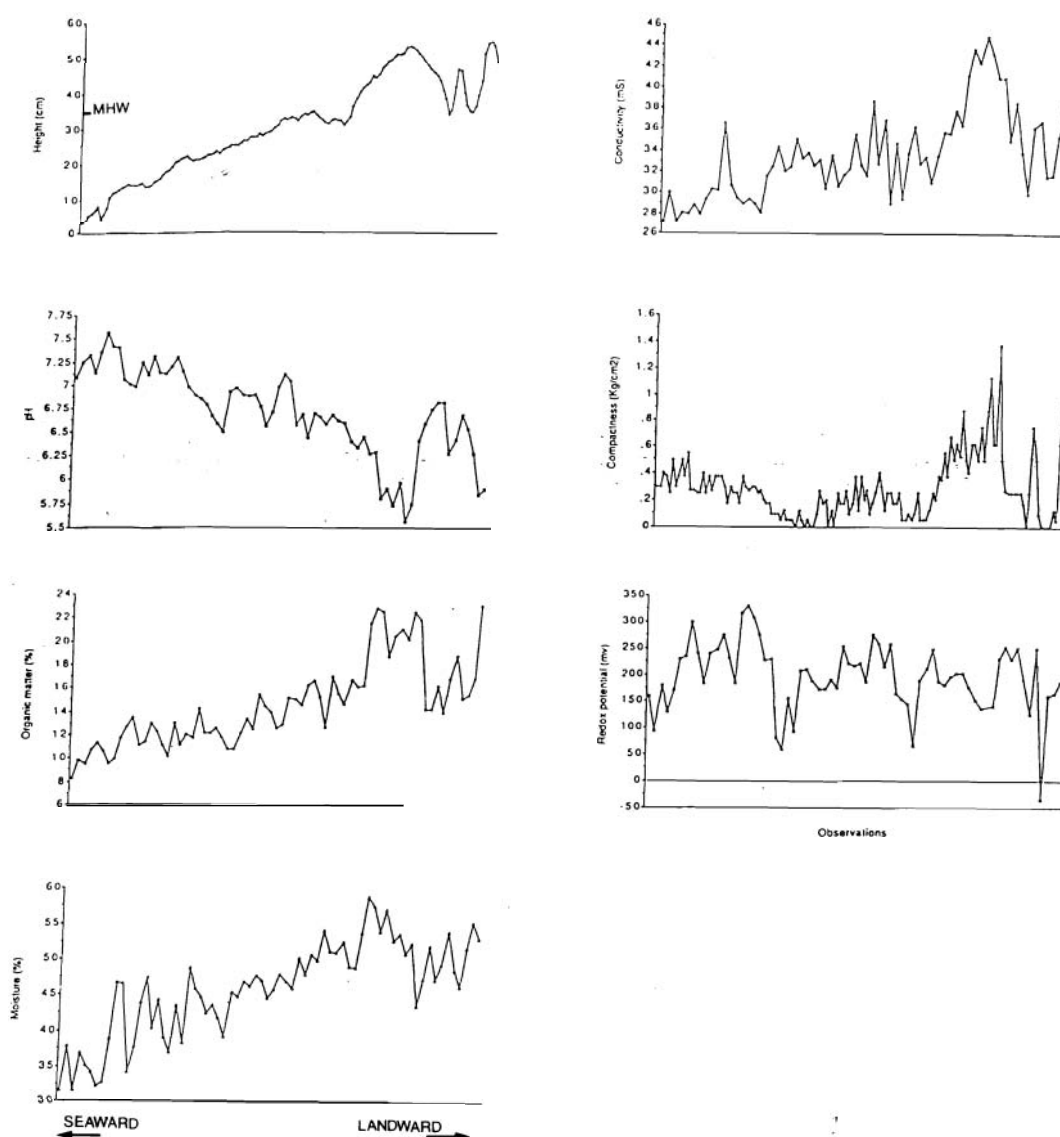
FIGURE 3. Edaphic factors in relation to position along the transect. The transectc locates above mean high water neap level (MHWN) and below mean high water spring level (MHWS). Mean high water level (MHW) is marked.

Variación de los factores edáficos a lo largo del transecto. El transecto se sitúa por encima del nivel medio de las pleamares muertas y por debajo del nivel medio de las pleamares vivas. Se ha señalado el nivel medio de la pleamar.

non-halophytes. This may have the same causes as the moisture: Na^+ is more easily retained in soils with a high organic matter content and in clay (BASSET, 1978). If the Na^+ concentration is calculated on the basis of the conductivity (RICHARDS, 1982), and it is taken into account that NaCl is the commonest salt in sea-water, values of between 270 meq NaCl/L and 410 meq NaCl/L are obtained. This is below the given value for hipersalinity: this is to be

expected, bearing in mind that the transect runs below MHWS level, where sea-water washing is foreseeable. In the same way, (RICHARDS, 1982), the values for the osmotic potential of the soil vary from -11 to -18 atmospheres.

The water potential of the species studied (Salicornia, Suaeda, A. perenne, Spartina, Halimione, A. fruticosum), whatever their position on the transect, is in all cases lower than -30 atmospheres, and is in fact on the limits of detection for the apparatus used (up to -40 atm.). These values are lower (more negative) than those calculated for the osmotic potential of the soil, and may indicate an accumulation of NaCl and osmotically active inert solutes (proline, betaine, polyhydric alcohols, etc.) in the cells (ROZEMA et al., 1985).

Measurements taken for compactness show the soils studied to be of soft consistency. The low values are linked to the entry of water (waterlogging) in the low area principally occupied by Spartina and A. perenne, whereas the highest values, with the greatest rooting and soil consolidation are in Halimione's high area, though this factor is shown to develop independently of the rest.

The redox potential is again the opposite of what might be expected, since more waterlogged areas usually show lower values (ARMSTRONG et al., 1985). This appears to be caused by the better drainage of the lower area, while the greater water retention in the higher area hinders the spread of atmospheric O, to the extent where a blackish, anoxic profile is observed, due to accumulation of SFe below a depth of 10 cm. Positive values were obtained all along the transect, corresponding to the summer period of greater aeration, except for a rear area with entry and accumulation of water, which showed negative (-35 mvolt. pH 6.53). The maximum value (330 mv, pH 7.20) was found in the low area with Salicornia and Suaeda. The four minima found on the transect were at the beginning, in the Spartina area, in the A. perenne area and in the drainage channel at the top end. The results found in this study indicate edaphic conditions of moderate reduction (PATRICK & MAHAPATRA, 1968). The values found in the adjacent channel, which is flooded daily, show, on the other hand, a strong reduction ($x= -285.4\pm51.9$ s.e. mvolts; $n=5$). The results obtained for this factor must be taken cautiously, bearing in mind the great seasonal and short term variability, with the consequent ecological implications.

ABIOTIC CAUSAL FACTORS OF ZONATION

The most important of the factors whic have received special attention due to their physiological affect on plants, and subsecuently to the zonation observed in the field, are: salinity (ionic toxicity and osmotic disorders) (ROZEMA et al., 1985), waterlogging (deficiency in the spread of O, in the rizosphere, and toxic products derived from anoxia, interference in photosynthesis due to interruption of the CO, exchange in the leaves, etc.) (ARMSTRONG et al., 1985) and the availability of nutrients (principally N and P) (JEFFERIES, 1977; JEFFERIES & PERKINS, 1977). The results of different controlled physiological experiments (ROZEMA et al, 1985; ZAHRAN, 1987, GROENENDIJK, 1985) lead us to thing that distribution depends on a series of variables which act sigergically, rather that on the influence of any one single limiting factor: in this sense, ele-vation or degree of flooding act .as the main dimension of the niche of the species in a salt-marsh (RUSSEL et al., 1985), which sums up the general variation tendencies of the limiting factors.

In the multivariant descriptions made, there are numerous points of evidence which emphasize de decisive role of elevation or topography. (EWING, 1983; HUTCHINSON, 1982; GRAY & BUNCE, 1972; BENITO et al., 1988). With the matrix of 64 abiotic data and the 7 factors analysed, a PCA was made up. The percentage of variace absorbed by axis I was considerable (64.77%) and, as was to be expected, this depended upon variables related to topography. The factors which intervene most on axis (on the basis of the correlation between abiotic data and the axis) are, from highest to lowest, (0.946) organic matter > (-0.938) pH > (0.910) elevation > (0.901) moisture > (0.857) conductivity, closely related to each other ($p<0.001$). The model of edaphogenesis seen here on a small scale is a verification of what was observed on this salt-marsh on a larger scale (BENITO et al., 1988). The sencond axis ((0.766) compactness > (0.761) redox potential (18.19% of variance), discriminates, on the basis of aeration, between areas which do not coincide with the ends of the

transect, but which are modifications in the general pattern of axis I, due to microtopogaphy and secondary water inflow which reduces compactness and redox potential. Ecological value of the third axis (11.78% of the variance) is not high.

Due to the non linear response of the species to the environmental factors, the **PCA** method was not used. Instead, the most abundant species of each quadrat is plotted on the scatter diagram of the **PCA** (axis I and II) on the basis of the soil scores. The result obtained is an almost accurate representation of the zonation found in the salt marsh (figure 4). The correlation between the best represented species and the variables analysed in axes I and II of the **PCA** is shown in Table 1. The greatest correlations occur with topography related variables. The species studied in the lower area (Salicornia and Suaeda) show positive correlations with pH and negative ones

with organic matter, conductivity and moisture, which is contrary to those in the higher area (Halimione and A.fruticosum). Suaeda maritima appears positively related to redox potential, as it is situated in areas with good drainage. While Spartina and A. perenne are found on soft soils, Halimione prefers more consolidated soils, in which rooting plays an important part.

DISCUSSION

From the results is may be deduced that the species gradient observed is closely linked to physical-chemical changes, summed up in variable elevation or topography. Factors such as compactness and redox potential give minor deviations from the unidimensional model increasing the heterogeneity of the habitat. Redox potential measures remain between the limits of
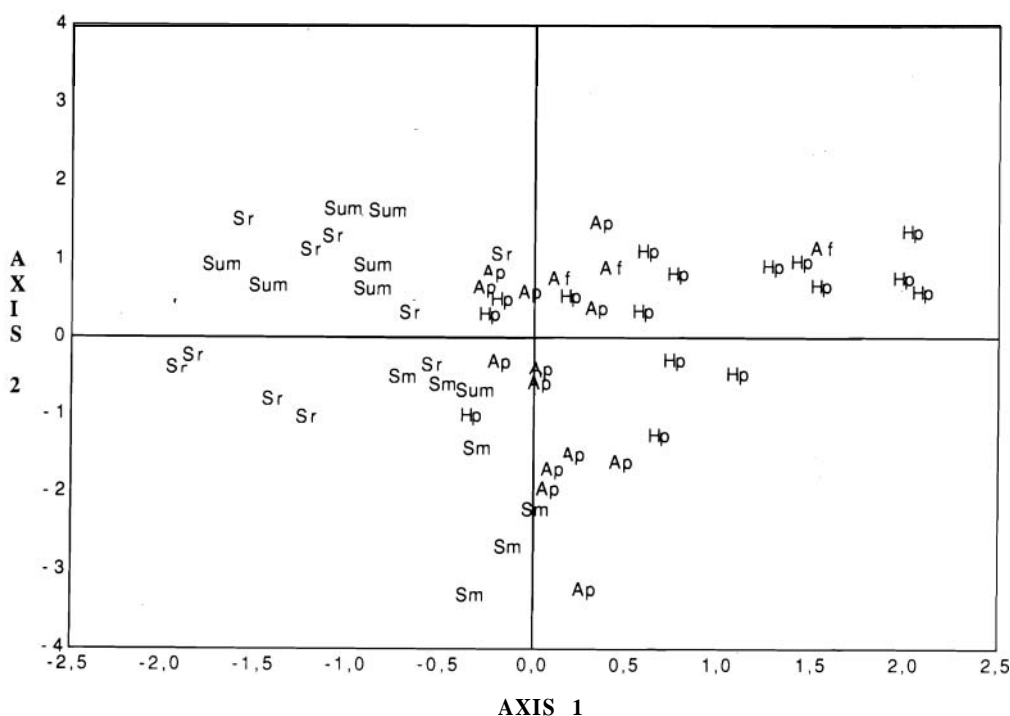

FIGURE 4.   Projection of the most abundant species onto the first two principal components of the soil data. Sr, Salicornia ramosissima; Sum, Suaeda *maritima*; Sm, Spartina mal-itima: Ap, *Arcthrocnemum* perenne; Hm, Halimione portulacoides; Af, Arcthrocnemumfruticosum.

Proyección de las especies más abundantes de cada cuadrícula en el plano formado por los dos primeros ejes del ACP de los datos edáficos. Sr, *Salicornia ramosissima*; Sum, *Suarda maritima;* Sm, *Sparrina maritima;* Ap, *Arthrocnemum perenne;* Hp, *Halimione portulacoides*; Af, *Arthrocnemum fruticosum.*

TABLE 1.　Spearrnan rank correlation coeficients of the species and the measured variables.
(**) p < 0,01; (*) p < 0,05.

Coeficientes de correlación de Spearman de las especies con respecto a las variables medidas. (**) p < 0,01; (*) **p** < 0,05

	ELEVATION	O. M.	COMPAC.	CONDUC.	MOIST	PH	REDOX P.	PCA 1	PCA 2
Salicornia	-0,775**	-0,695**	0,119	-0,601**	-0,692**	0,755**	0,212	-0,785**	0,256*
Suaeda	-0,64**	-0,554**	0,102	-0,516**	-0,564**	0,695**	0,411**	-0,656**	0,484**
Spartina	-0,219	-0,219	-0,527**	0,129	-0,208	0,084	-0,149	-0,122	-0,386**
A. *perenne*	0,042	0,129	-0,379**	-0,061	Q162	-0,013	-0,02	0,12	-0,309**
Halimione	0,849**	0,747**	0,328**	0,477**	0,741**	-0,74**	-0,186	0,776**	0,047
A. *fruticosum*	0,346	0,218	0,129	0,145	0,088	-0,189	0,155	0,175	0,167

moderate reduction. Only in the *Spartina* zone these values fall below 100 mvolts.

Soil salinity values measured in this study are well below the tolerance ranges of the accumulating type of halophytes i.e. *Halimione, Salicornia, Suaeda* (ROZEMA et al., 1985) and also probably A. *perenne* and A. *fruticosum*, and they do not reach hipersaline concentrations. To determine the role of this limiting factor in the zonation pattern, seasonal sampling would be neccesary. However, the inverse variation of conductivity found in this study and the high (negative) water potential of all the species involved, indicate the broad degree of adaptation of the species to periodical salinity fluctuations. Thus, salinity solely does not account for the zonation observed.

Progressive increase or decrease of the edaphic factor values are followed by a clear plant zonation, however, this response of the species is not linear, but, sharp boundaries between almost monospecific stands are found.

It might be thought that the space occupied by the species constitutes their physiological optimum, however, many studies show that the altitudinal range of halophytic species is very wide. Species such as *Salicornia, Suaeda, Limonium, Triglochin, Aster tripolium, Puccinellia maritima*, etc. show great fenotypic plasticity, and can be found in both high and low salt marshes (JEFFERIES, 1977; JEFFERIES et al., 1979; GRAY & SCOTT, 1977). Thus, it can

not be concluded that the marked segregation of the species along the gradient is exclusively due to physiological requirements of the plants.

If each species is not physiologically restricted to a different portion of the gradient, other factors, such as presence of herbivores, inadequate dispersal of the propagules, interspecific competition, tidal disturbance, or a combination of all these, should determine this zonation (SNOW & VINCE, 1984; ELLISON, 1987).

Intensive grazing may influence plant distribution, succesion and production in salt marshes (GRAY & SCOTT, 1977). The salt marsh of Mundaka is not grazed by cows or sheeps. Waders use Mundaka tidal flats as a feeding area mainly in autumn but consecuences for plant zonation do not appear to be significant.

The studied zone locates below MHWS level, thus flooding tides almost certainly disperse the rhizomes and seeds of salt marsh plants over the area. Seedlings of *Salicornia* and *Suaeda* can be seen in gaps of the upper part salt marsh produced by trampling and spring tides i. e. accumulation of debris and destruction of biomass. Furthermore, after the catastrophic storms in August 1983 and break of the protection wall of the cultivated marsh, extensive areas of the upper marsh were occupied by these annual species (BENITO, AGIRRE & ONAINDIA, personal observations). However, no propagules of A. *fruticosum* survive in the *Salicornia* zone, whilst seedlings of species with a mainly lateral

spread, as Halimione and A. perenne, grow very scarcely in the lower part of the area. Thus, the dispersion of propagules all along the gradient seems to be assured, but in areas other than the *Salicornia* tidal flat, the rates of vegetative expansion are probably more important than seedling establishment in producing and maintaining zonation patterns.

Recent studies emphasize the importance of dominance processes in the distribution of plants. To understand the zonation found, the role of interspecies competition interactions (OTHMAN 1980; SNOW & VINCE, 1984; SILANDER & ANTONOVICS, 1982; BERTNES & ELLISON, 1987; ELLISON 1987; RUSELL et al., 1985; WILSON & KEDDY, 1986) must be superimposed on the effects deriving from gradients of salinity, flooding or nutrients.

WILSON & KEDDY (1986) pointed out the relevant role of wave action as an underlying factor of diffuse competition, suggested by the close correlation between the organic matter of the sediment and the biomass. The biomass (living plus dead) values found in this salt-marsh in August were 415 g/m² (Salicornia *ramosissima*), 617.5 g/m² (*Spartina* maritima) and 1251.2 g/m² (Halimione protulacoides). These values, extrapolated onto the transect, show a positive correlation between biomass and organic matter in the soil. In this sense, areas exposed to strong tidal action have a low organic matter content in the soil, and low biomass: this generates low intensities of diffuse competition, whilst, competition is increased in conditions of greater fertility i. e. the higher part of the transect (BAZZAZ & HARPER, 1976).

Diversity (Shannon index) spectrum by elevation class (fig. 5 a) (the sampling is tested by entropy parameters, and its quality is high $Q_1=0.967$) reveals a progressive increase up to class 5, which is interpreted as an improvement of the conditions of the medium through tidal independence. Class 6 (i. e. MHW level), dominated by Arthrocnemum perenne, breaks the H increase trend. Successive peaks are linked to the sporadic entry of rare species into areas dominated by a particular species.

Overlap (according to Pianka, 1973) with respect to the elevation of the species found along the transect (fig. 5 b) shows a decreasing profile, in proportion to the occurence of tidal independence. With this, compensatory mechanisms increase (resource partitioning). In the first

place, Salicornia ramosissima and Suaeda maritima, two short annuals, show great affinity, and colonize spaces cleared by tidal action: tolerance of unfavourable situations of habitat on the one hand, and the small competitive ability of these short lived plants on the other, mean that annuals colonize the highest risk environments, i. e. those which are permanently or regularly disturbed. Subsequently, overlap diminishes to a minimum, with the inclusion of perennial species, due to the segregation between A. perenne (a short perennial 10 cm. in height) and Halimione portulacoides (a woody perennial of greater height: 30-40 cm.) at a critical elevation where the slope sharpens considerably, thus giving rise to this break. The greater overlap between the competing species H. portulacoides and A. *fruticosum* is explained by the as yet slight development of the latter, a woody species of considerable growth which displaces H. portulacoides in the more favoured points of the area studied.

In conclusion. in the low areas. the absence of competitors permits a process of coexistence. Decline of stress and disturbance to the most landward edge favours the appearance of compeiing species which displace the others, generating low diversity mosaics.

SNOW & VINCE (1984) concluded that species occurring in zones along the tidal gradient in a Alaskan salt-marsh are limited by physiological tolerance toward one end of the gradient (extreme edaphic conditions), and by competitive ability towards the other, where many species could potentially survive and reproduce.

As an hypothesis for further research, the model in figure 6 illustrates the potential distribution of species in the low salt-marsh of Mundaka in relation to the exposure gradient, and the real distribution produced by segregation based on resource partitioning, due to which the least competitive species are displaced to the most unfavourable area of the transect, which serves them as spatial or temporal shelter. Clearly, to determine if (i) each species performs best in a different portion of the gradient (however, tolerance ranges are sufficiently broad that species would grow in other habitats were it not for competitively superior species) or (ii) all species prefer the same portion of the gradient (but species are displaced along the grandient according to their breadth of tolerance, com-
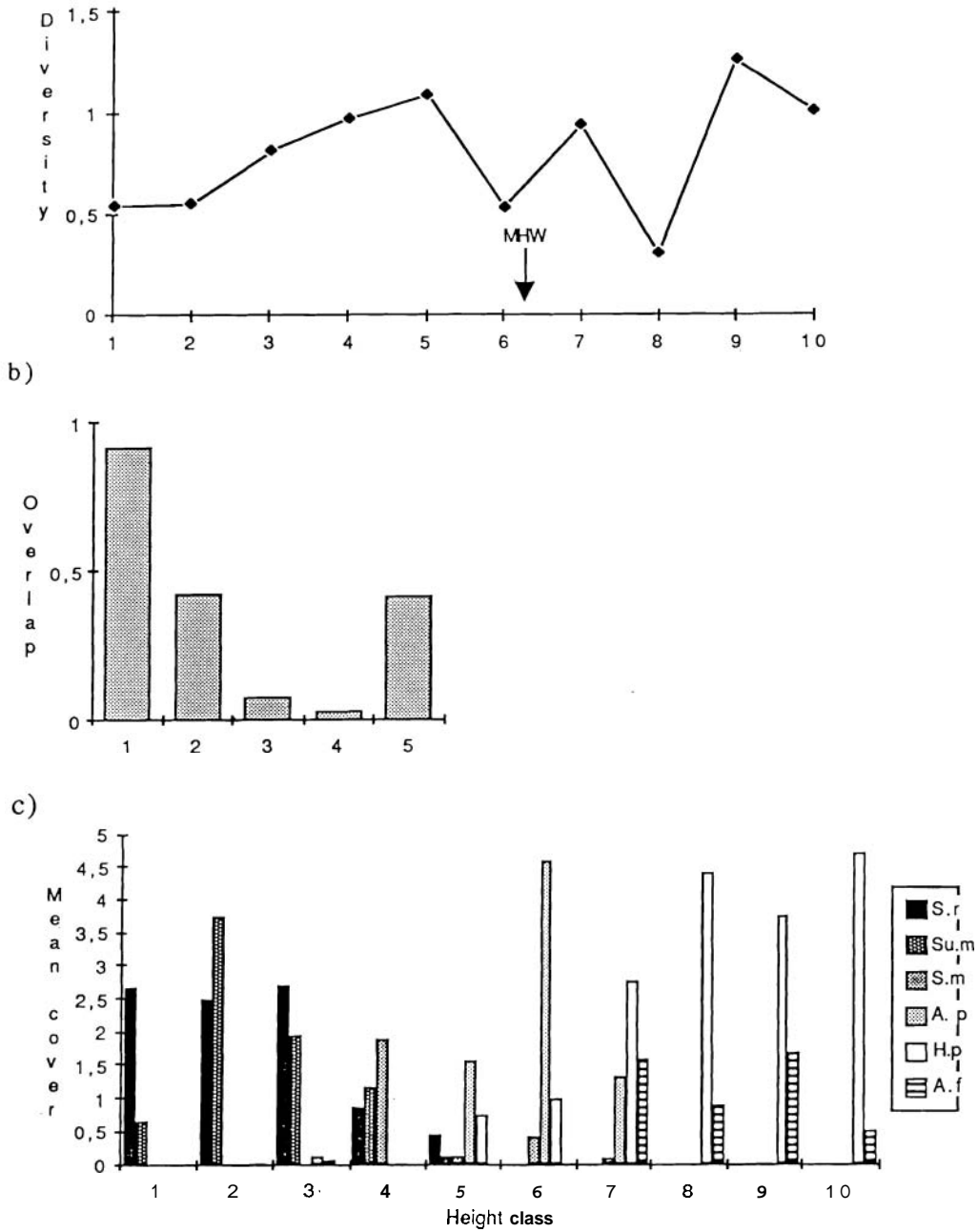
FIGURE 5. a)   Diversity (Shannon index) plotted against resource class along the elevation dimension. b) Mutual overlap values of each species with the inrnediately adjacent species along the transect, according to Pianka's formula. 1: Sr-Sum, 2: Sum-Sm, 3: Srn-Ap, 4: Ap-Hp, 5: Hp-Af. c) Mean species cover in each of the ten resource class on the elevation dimension.

a) Valores de diversidad (índice de Shannon) frente a las clases en que se ha dividido la elevación. b) Valores de solapamiento de cada especie con la siguiente a lo largo del transecto, según la ecuación de Pianka. c) 1: Sr-Sum, 2: Sum-Sm, 3: Sm-Ap, 4: Ap-Hp, 5: Hp-Af. c) Valor medio de cobertura de las especies en cada una de las clases de elevación o nivel topográfico.
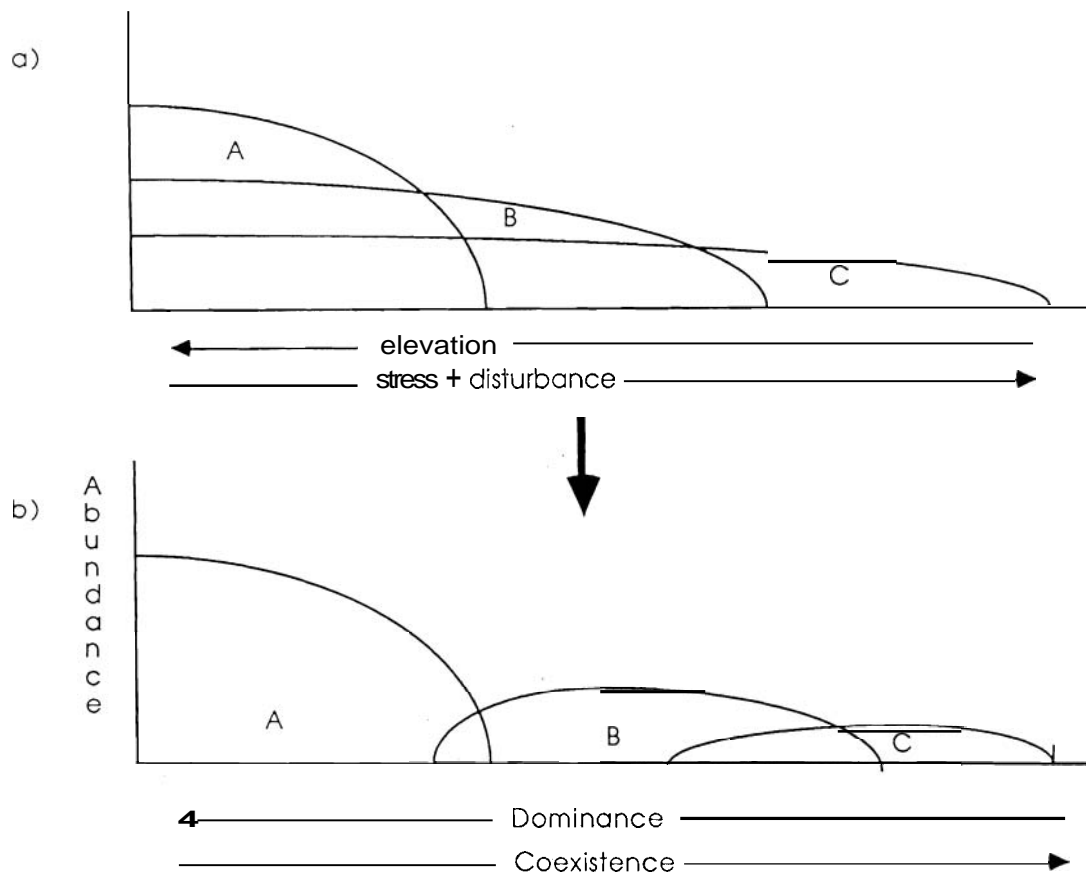
FIGURE 6.   a) Hypothetical and b) real distribution of the species along the gradient: tidal independence and improvement of the edaphic conditions give rise to segregation.

a) Distribución hipotética y b) real de las especies a lo largo del gradiente: la independencia mareal y la mejora de las condiciones edáficai dan lugar a la segregación encontrada.

petitive abilities), experimental work in the field and in the laboratory should be carried out in salt marshes of this part of the Atlantic Coast. Experiments with reciprocal transplanting of species at different points if the salt-marsh, and with the effects of physical disturbance and artificial fertilization could provide a great deal of information on this.

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