Ann. Bot. Fennici 36: 59–66
Helsinki 7 April 1999 ISSN 0003-3847

Natural regeneration in salt marshes of northern Spain

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Received 30 June 1998, accepted 12 January 1999

Onaindia, M. & Amezaga, I. 1999: Natural regeneration in salt marshes of northern Spain. — *Ann. Bot. Fennici* 36: 59–66.

The ecological range of the halophilous plants were studied in the salt marsh of Txipio (Butroi river) in northern Spain, with respect to some of the most influential edaphic parameters (moisture, conductivity, pH, organic matter) of the environment. This area has been undergoing a natural regeneration since 1965, when tide broke the water retaining walls and agricultural activities were stopped at the site. Thirteen plant species occurred and the most abundant ones were analysed according to different edaphic parameters. Conductivity was the primary factor explaining the distribution of halophilous plants. Texture was also a conditioning factor in species distribution in the marsh, while pH was not determinant. Despite the low regeneration time of the site, the species distribution and edaphic conditions showed a significant recovery of the area.

Key words: ecology, marsh plants, marsh soil, plant distribution, *Salicornia*, *Suaeda*

INTRODUCTION

Tidal salt marshes are highly productive coastal fringe ecosystems and the major contributors to this productivity are vascular plants (Hemminga *et al*. 1996). These areas are subject to periodic flooding as a result of fluctuations in the level of the adjacent water body (Adam 1993). Until recently, major salt marsh areas have been reclaimed for agriculture or development in all parts of the world (van Veen 1955, Wagret 1968, Gosselink & Baumann 1980, Doody 1984, Nichols *et al*. 1986, Esselink *et al*. 1998). However, nowadays there is a growing concern about the value of salt marshes and a lot of effort is going into conserving and restoring them (Brix 1994, Scatolini & Zedler 1996, Callaway *et al*. 1997, Kwak & Zedler 1997). Ecologists are trying to translate science into management action (Zedler *et al*. 1998), but many untested assumptions concerning the relationship between physical habitat structure and restoration ecology are being made in practical restoration efforts (Palmer *et al*. 1997).

Previous studies have shown that the range of some edaphic factors like conductivity, pH, organic matter, in which plants are found, can differ through different salt marshes (Valiela & Teal 1974, Chapman 1976, Othman 1980, Long & Mason 1983, Adam 1993, Van den Brink *et al.* 1995). It is also known that plant species in the salt marshes reflect the selection by the acting of environmental and biotic factors. Thus, the knowledge and comparison of the distribution of halophilous plants in different areas adds important information to the understanding of the ecological niche of these species.

In natural Cantabrian salt marshes, plant distribution in height gradients following tide levels has been modelled, describing gradients according to substratum flood levels (Onaindia & Navarro 1987). These height gradient distribution models, however, are not often fulfilled when edaphic factors that may be very important in explaining this zoning, are modified as happens in places affected by human activity. Any study of the distribution of halophilous flora requires, in this sense, a more detailed analysis dealing with factors that will not be detected through a global approach, and with the possibility of relating the presence of a species to a specific state of the abiotic variable under consideration (Piggott 1969, Long & Mason 1983, Rozema *et al.* 1985, Benito & Onaindia 1991, Van den Brink *et al.* 1995).

The objectives of this study are to evaluate the relationships between edaphic parameters (e.g., soil moisture, conductivity, pH, organic matter) and salt marsh vegetation in a salt marsh that has been undergoing natural restoration for three decades. This study will further our understanding of ecological preferences of salt marsh species, while also being applied toward predicting the response of degraded salt marshes to tidal reintroduction. Besides, knowledge of criteria for restoration in one region may help other regions avoid similar problems (Zedler 1996).

MATERIALS AND METHODS

Study area

The study site (Txipio) is located at the Butroi estuary 15 km away from Bilbao, in the Bay of Biscay (Cantabrian coast, northern Spain). It covers a total area of 5 ha (Gobierno Vasco 1998) and the tidal range is mesotidal (4.40 m between MHWS and MLWS) with a semidiurnal periodicity. The main meteorological feature is the almost total absence of dry months during the year, with maximum rainfall occurring in autumn–winter. The area has a temperate climate, registering an average annual temperature of around 13–15°C with a rainfall of more than 1 000 mm a year.

The salt marsh has two main central channels and many side channels. The proximity of the water-bearing stratum has produced a central saline depression. This situation means that plants do not follow a gradient distribution model from the sea inland. Besides, the previous introduction of organic matter from agricultural activity may have modified the general distribution pattern for halophilous plants described for other Cantabrian marshes.

Study designs and methods

Twenty-seven randomly selected 2 × 2 m quadrants were sampled in the studied area at low tide (Benito & Onaindia 1991) in July 1997. Sampling was done in the summer to coincide with the optimum vegetative development of halophilous species. The abundance of each species present in the quadrant was assessed by visual estimate of coverage in terms of occupied surface (with a cover estimated to the nearest 10%). The species were identified in the laboratory using the keys to identification of Flora Europaea (Tutin *et al.* 1964–1980) and Aseginolaza *et al.* (1984). At the same time, 10 random samples of the marsh soil (depth of 10–15 cm and 7 cm diameter) were taken in each quadrant and pooled for the analysis.

The edaphic parameters measured were: texture, moisture, pH, conductivity, organic matter, total nitrogen and the C:N ratio. Analytical methods used were those presented in the *Official Methods for Soil and Water Analysis* (Anonymous 1981).

Possible relationships between edaphic parameters and the relative abundance of plant species, were estimated with Spearman's rank correlation coefficient and a Principal Components Analysis (PCA, employing the correlation coefficient), using the StatView program package (Abacus Concepts 1986).

RESULTS

Plant species and edaphic parameters

Overall thirteen halophilous species were found in the Txipio marshes (Table 1). The distribution of the species in relation to the most important edaphic factors is presented below.

Moisture

Moisture values varied from a maximum of 72.5% for the species *Aster tripolium* to a minimum of

41.9% for *Elymus pycnanthus* and *Phragmites australis*. Mean moisture levels over which species are distributed are shown in Fig. 1. The distribution gradient is fairly well defined.

The distribution of *Aster tripolium*, *Puccinellia maritima* and *Salicornia ramosissima* was positively correlated with moisture ($p < 0.05$; Table 2). *Aster tripolium* appeared in a moisture-range of 72.5% to 59.5%, *P. maritima* from 71.8% to 63.5% and *S. ramosissima* from 72.5% to 61.6% (Table 1). These species occupy the zones with the maximum moisture values found in the marsh and they should be considered species that cannot tolerate wide variation in moisture.

The distribution of *Phragmites australis*, which had a wider range (from 57% to 41.9%), was negatively correlated with moisture ($p < 0.01$). However, *Elymus pycnanthus,* the species with the widest range from 71.7% to 41.9%, together with *Halimione portulacoides* and *Juncus maritimus* (range from 72.5% to 57.9%, and from 67.3% to 57.9%, respectively), showed distributions that did not significantly correlate with moisture.

Table 1. Maximum and minimum values of the edaphic parameters for each species. (*Aster tripolium, Spartina maritima, S. ramosissima, Puccinellia maritima, Arthrocnemum perennis, A. fruticosum, Halimione portulacoides, Frankenia laevis, Juncus maritimus, Elymus pycnanthus, Polygonum maritimum, Festuca rubra, Phragmites australis*).

		Moisture content of soil (%)	pH of soil	Conductivity of soil (mS cm)	Organic matter of soil (%)
A. tripolium	max.	72.46	7.3	21.41	11.87
	min.	59.44	6.6	14.66	8.42
S. maritima	max.	71.68	7.1	19.66	11.87
	min.	61.92	7.0	14.87	8.48
S. ramosissima	max.	72.46	7.3	21.41	11.87
	min.	61.56	6.6	15.00	8.48
P. maritima	max.	71.75	7.1	21.41	11.87
	min.	63.45	6.6	16.83	9.86
A. perennis	max.	67.34	7.3	21.02	13.04
	min.	59.44	6.7	14.66	8.42
A. fruticosum	max.	71.17	7.3	21.02	13.04
	min.	59.44	6.7	14.66	8.42
H. portulacoides	max.	72.46	7.3	21.41	13.04
	min.	57.86	6.6	14.07	8.42
F. laevis	max.	66.38	7.05	16.97	9.76
	min.	57.86	6.75	14.07	8.48
J. maritimus	max.	67.34	6.9	21.02	13.04
	min.	57.86	6.6	13.60	7.92
E. pycnanthus	max.	71.68	7.7	19.66	11.87
	min.	41.89	6.7	2.85	7.19
P. maritimum	max.	71.68	7.1	19.66	11.87
	min.	43.68	6.7	7.01	9.86
F. rubra	max.	71.17	7.1	14.87	9.34
	min.	57.86	6.8	14.07	9.00
P. australis	max.	57.05	7.7	10.78	10.44
	min.	41.89	7.0	2.85	7.19

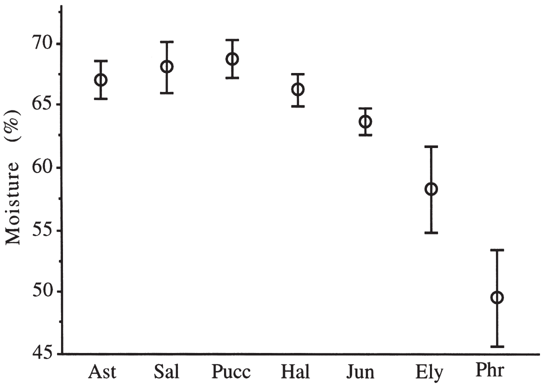

Fig. 1. Species distribution according to moisture (%). Mean and standard error bars. Ast = *Aster tripolium,* Sal = *Salicornia ramosissima,* Pucc = *Puccinellia maritima,* Hal = *Halimione portulacoides,* Jun = *Juncus maritimus*, Ely = *Elymus pycnanthus,* Phr = *Phragmites australis.*

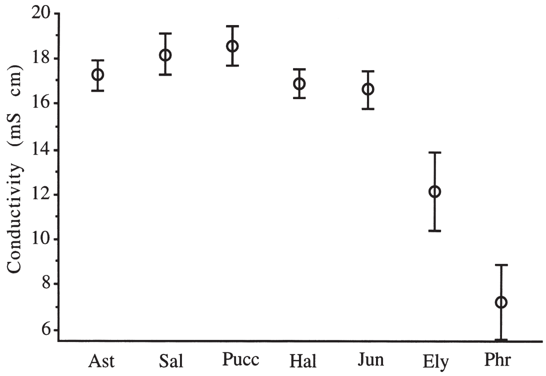

Fig. 2. Species distribution according to conductivity (mS cm). Mean and standard error bars. Ast = *Aster tripolium,* Sal = *Salicornia ramosissima,* Pucc = *Puccinellia maritima,* Hal = *Halimione portulacoides,* Jun = *Juncus maritimus,* Ely = *Elymus pycnanthus,* Phr = *Phragmites australis.*

Conductivity

Conductivity values ranged from 2.85 mS cm to 21.41 mS cm and the species showed a clear distribution along a conductivity gradient (Fig. 2).

The distribution of *Aster tripolium*, *Puccinellia maritima* and *Salicornia ramosissima* was positively correlated with conductivity ($p < 0.05$). The ranges of distribution of the species according to conductivity were: 21.41 mS cm to 14.66 mS cm for *A. tripolium*, 21.41 mS cm to 16.83 mS cm for *P. maritima* and 21.41 mS cm to 15 mS cm for *S. ramosissima.*

The distribution af *Elymus pycnanthus* (from 19.66 mS cm to 2.85 mS cm) and *Phragmites australis* (from 10.78 mS cm to 2.85 mS cm) was negatively correlated ($p < 0.05$) with conductivity.

pH and organic matter

Values of pH in the marsh soil varied between 6.6 and 7.7. Species gradation according to pH was not very pronounced (Fig. 3). However, the species found in beds with the highest mean pH values, *Phragmites australis*, coincided with a wide range of tolerance to this parameter (from 7.0 to 7.7), which means that it is a species adapted to different pH values. *Juncus maritimus*, whose distribution was negatively correlated with pH ($p < 0.05$), showed a range of pH from 6.6 to 6.9 (the lowest measured value).

Aster tripolium, *Salicornia ramosissima, Puccinellia maritima, Halimione portulacoides* and *Juncus maritimus*, which appeared in the lowest values of pH, occupied zones with the highest or-

Table 2. Spearman correlation coeficients for species showing the correlation with the edaphic parameters.

Species	Moisture content of soil (%)	Sand content of soil (%)	Silt content of soil (%)	pH of soil	Conductivity of soil (mS cm)	Organic matter of soil (%)
Aster tripolium	+0.58**	+0.10	–0.12	–0.70	+0.50**	+0.29
Elymus pycnanthus	–0.28	–0.09	+0.15	+0.19	–0.43*	–0.01
Halimione portulacoides	+0.50*	–0.30*	+0.25	–0.40*	+0.43*	+0.27
Juncus maritimus	+0.12	–0.45**	+0.35*	–0.53**	+0.25	+0.02
Puccinellia maritima	+0.49*	–0.14	+0.08	–0.30	+0.51**	+0.41*
Phragmites australis	–0.54**	+0.13	–0.11	+0.26	–0.58**	–0.01
Salicornia ramosissima	+0.44*	+0.20	–0.23	–0.06	+0.49*	+0.30

Levels of significance: * $p < 0.05$, ** $p < 0.01$

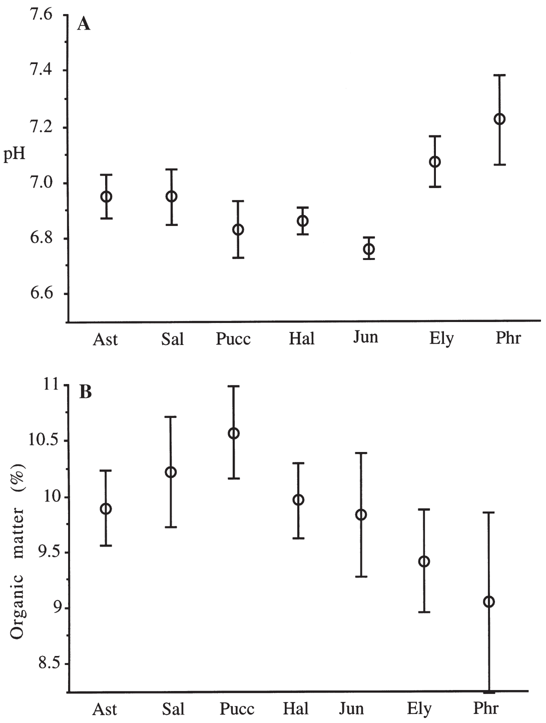

Fig. 3. Species distribution according to (A) pH and (B) Organic Matter (%). Mean and standard error bars. Ast = *Aster tripolium,* Sal = *Salicornia ramosissima,* Pucc = *Puccinellia maritima,* Hal = *Halimione portulacoides,* Jun = *Juncus maritimus,* Ely = *Elymus pycnanthus,* Phr = *Phragmites australis.*

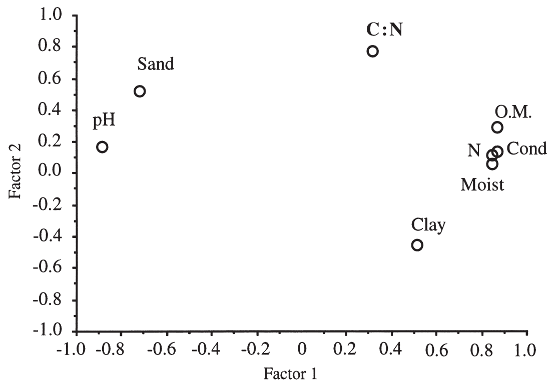

Fig. 4. Variables of the principal components analysis of the plant environment with the following loading factors: pH, conductivity (Cond), % of sand (Sand), % of clay (Clay), C:N ratio (C:N), organic matter (O.M.), total N (N) and moisture (Moist).

ganic matter content, although they showed high variances (Fig. 3). In general, organic matter content was high within the studied site.

The comparison between the pH and organic matter values (Fig. 3) showed a negative correspondence between them. Thus, the highest pH values corresponded with low organic matter and *vice versa. Puccinellia maritima*, a species positively correlated with organic matter (Table 2) and found at the quadrants with the highest values for organic matter, could be used as a good indicator for higher values of organic matter at a site (from 9.9% to 11.9%).

Principal Component Analysis (PCA)

After analysing the species distribution with regard to the most important edaphic parameters, the species were ordered spatially using a PCA to provide an objective overview of distribution.

The analysis stored 51% of the variance on the first axis and 15% on the second. The remaining axes had less information, and have not been taken into account (Fig. 4).

The main loading factors in the first axis were moisture and conductivity in the positive zone, meaning that this axis followed a gradient from zones with greater water retention and conductivity to zones with lower moisture and conductivity. Organic matter followed the same gradient as conductivity, which is not characteristic of a natural gradient, but rather of an intense external influence (in the present case, due to the excess of organic matter in the soil from crops in the past). The pH followed an opposite behaviour in relation to conductivity, which is not so usual in salt marshes, but that could be due in this case to the former agricultural use of the site.

The main loading factor in the second axis was percentage of sand, reflecting a sandy texture, which permits a good "drainage" and a lower flooding. Texture was therefore, a conditioning factor in species distribution in the marsh.

The species distribution was as follows. In the lower part of the PCA (Fig. 5) appeared *Aster tripolium, Salicornia ramosissima, Puccinellia maritima, Spartina maritima* and *Polygonum maritimum*, species characteristics of areas with a high mud:sand ratio at low parts of the salt marsh. Above this group were *Phragmites australis* and *Elymus pycnanthus* (top of Fig. 5), characterized for colonizing sites of low level of moisture and

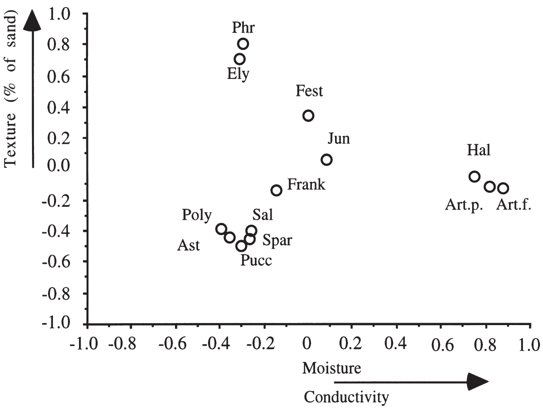

Fig. 5. Projection of the species onto the principal component analysis axes. Ast = *Aster tripolium,* Spar = *Spartina maritima,* Sal = *Salicornia ramosissima,* Pucc = *Puccinellia maritima,* Art.p. = *Arthrocnemum perenne,* Art.f. = *A. fruticosum,* Hal = *Halimione portulacoides,* Frank = *Frankenia laevis,* Jun = *Juncus maritimus,* Ely = *Elymus pycnanthus,* Poly = *Polygonum maritimum,* Fest = *Festuca rubra,* Phr = *Phragmites australis.*

conductivity and of a low mud/sand ratio. *Halimione portulacoides*, *Arthrocnemum perennis* and *A. fruticosum* appeared in a situation defining a different texture of soil (with medium percentage of sand). *Festuca rubra, Juncus maritimus* and *Frankenia laevis* (in the centre of Fig. 5) were in intermediate conditions and they were not high in relation with any measured factor.

DISCUSSION

The edaphic characteristics found in Txipio were similar to other natural salt marshes along the Cantabrian coast (Benito & Onaindia 1991), but they seem to correspond to the low part of the salt marshes, with high sea tide influence. Moisture varied from a maximum of 72.5% to a minimum of 41.9%, while in mature marshes has been defined between 84% and 14.5% (Benito & Onaindia 1991). Conductivity in natural Cantabrian salt marshes ranged from 0.3 mS cm to 54.8 mS cm (Benito & Onaindia 1991, Benito *et al.* 1988), this range being narrower at the studied site (from 2.85 mS cm to 21.41 mS cm). However, organic matter content followed the same gradient as conductivity as in other altered nearby marshes (Benito & Onaindia 1991), meaning that natural edaphic conditions have not been reached in Txipio.

Species distribution reflected a gradient pattern quite similar to natural salt marshes, but with fewer species (13 species). Benito and Onaindia (1991) observed at least 25 different halophilous species in the salt marsh of Mundaka-Urdaibai, just 10 km away from Txipio. Some of the species not found in the studied marsh are *Zostera noltii, Suaeda maritima* and *Spergularia media*. The low number of species and the composition of the communities in Txipio show a semi-natural situation of the area and that it may be in a process of plant re-colonization. Knowing that the transport of seeds between salt marshes is not easy (Adam 1993), more time will be needed in order to reach higher species richness in Txipio.

On the other hand, plant distribution reflected an underlying pattern of geomorphology, as in some other wetlands (Walbridge 1994). Moisture and conductivity were the primary factors explaining the distribution of halophilous plants. Texture (in relation to flooding) was the second explaining factor. The study of correlations between distribution and edaphic factors can be considered a first step towards understanding physical niches (Martínez-Taberner *et al.* 1992, Martínez-Taberner & Moyá 1993), and moreover, the distribution of halophilous species has already been recognised to follow environmental gradients (Hutchinson 1982, Boise 1985, Carnevale *et al.* 1987). Thus, in the salt marsh of Txipio species distribution was similar to that found in other salt marshes. *Phragmites australis* and *Elymus pycnanthus* appeared at low levels of moisture and conductivity (top of Fig. 5). The former halophyte is known to have a cosmopolitan distribution, adapting remarkably well to different conditions, and can be found over a wide latitudinal range. *Elymus pycnanthus*, in natural conditions, is found in coastal sands and at the external fringe of marshes (Aseguinolaza *et al.* 1984). Both species usually appear in the less flooded areas of salt marshes and they seem to be good species for recovering the high part of salt marshes.

Aster tripolium, Salicornia ramosissima, Puccinellia maritima, Spartina maritima and *Polygo-*

num maritimum were restricted to sites characteristic of the low parts of the salt marsh (Fig. 5). As salt marsh plant species are known to modify environmental conditions associated with their distribution (Nyman *et al*. 1995), these species could be used to accelerate the recolonization of the first stages of the low zones of degraded salt marshes. *Aster tripolium*, a biannual species, produces many, easily dispersed seeds that readily colonise openings produced by human intervention or accumulations of organic matter (Beeftink 1977). *Spartina maritima* communities can be found from the south of England and southwest Holland to the western coast of Morocco, and in the lagoons of the Bay of Venice (Beeftink 1977). It has also been described in South Africa (Pierce 1983). However, in the last century the spread of *S. anglica* has been altering the salt marsh ecology in northern Europe and also on the Cantabrian coast. Thus, the fact of not detecting the presence of this invasive *Spartina* species in Txipio gives a significant conservation value to the marsh, as *S. maritima* is now extremely rare in northern Europe (Adam 1993). *Salicornia* spp. in temperate latitudes produces a lot of ripe seeds (Jefferies *et al*. 1983) but does not usually build up a seed bank. However, there can be an import of seeds carried in by the tide, despite that most of the produced seeds are deposited close to the parent plants (Watkinson & Davy 1985, Ellison 1987).

Overall, it seems that 30 years has not been long enough for the restoration of the site, according to the conditions found in nearby salt marshes, e.g., species richness and organic matter gradient (Benito & Onaindia 1991). Salt marshes are not continuous ecosystems along the coast and successful transport of seeds from an area in one estuary to a developing marsh in another area is unlikely to be of frequent occurrence. Although seeds of halophytes may be imported by tide (Watkinson & Davy 1985) or dispersed by birds (Olney 1963, de Vlaming & Proctor 1968, Proctor 1968, Siira 1970, VivianSmith & Stiles 1994), it would be interesting to try an active replantation following natural succession patterns in order to favour the recolonization of missing species, as Txipio has only two sea-water entrances.

Acknowledgements: This work was supported by the UPV/EHU grant (UPV 118.310-EA201/96), the CICYT grant (AMB 96/0464) form the Spanish Ministry of Education and Culture, and the Basque Visiting Fellowship of Eusko Ikaskuntza/Sociedad de Estudios Vascos at St. Anthony's College in Oxford.

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