

Relationships between vegetation zonation and altitude in a salt-marsh system in northwest Spain

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Abstract. Vegetation zonation in salt marshes has traditionally been attributed largely to altitudinal differences, since altitude determines the temporal pattern of tidal flooding and is thus closely related to proximate determinants of the distribution of species and plant communities. We investigated the distribution of vascular plants and plant communities along a series of altitudinal transects in two salt marshes in the north-western Iberian Peninsula. Our results indicate that altitudinal range varies significantly both among species and among communities, and confirm that salt-marsh vegetation characteristics (species cover and composition) can be predicted on the basis of altitude, particularly at the lower levels of the profile.

Keywords: Coastal vegetation; Physical gradient; Tidal flooding.

Abbreviations: MHW = Mean High Water; MHWS = Mean High Water of Spring Tides; MLWS = Mean Low Water of Spring Tides.

Nomenclature: Castroviejo et al. (1986-1993) and Tutin et al. (1964-1980) for taxa; Izco et al. (1992) and Díaz & Fernández-Prieto (1994) for syntaxa.

Introduction

Vegetation zonation in intertidal environments has traditionally been largely attributed to differences in altitude, inundation duration and salinity. However, salinity and other proximate determinants seem to be closely correlated with elevation above sea level (Benito 1989), although the relationship between these factors and altitude is rarely simple; for example, Adam (1990) reported that minimum salinity showed an inverse linear relationship with altitude, while maximum salinity peaked just below MHWS, and de Leeuw et al. (1991) were able to detect a position along a salt-marsh altitudinal profile above which substrate salinity was affected by climatic variables, rather than tidal influence.

In the phytosociological literature, the importance of altitude in salt marshes is widely recognized, but there

have been few attempts to analyse its effects in detail, even in studies which deal specifically with the relationships between salt-marsh vegetation and altitude (e.g. Beeftink 1966; Hayon & Pelt 1969; Géhu-Frank & Géhu 1985; Vevle 1985). By contrast, the plant ecology literature includes many studies dealing with these relationships (e.g. Chapman 1938; Hinde 1954; Adams 1963; Pielou & Routledge 1976, Keddy 1983; Snow & Vince 1984; Zedler & Cox 1985; Lefor et al. 1987; and, in Europe, Gillham 1956; Russell et al. 1985; Olff et al. 1988). From the northern Iberian Peninsula the work of Benito (1989; Benito et al. 1990) can be mentioned.

In the work reported here, we aimed to investigate the relationships between altitude and the distribution of species and communities in two salt marshes in the northwest Iberian Peninsula.

Material and Methods

The study area

The study was carried out in the drowned river valleys of the Ría Ortigueira and Ría Ladrado (see e.g. Carter 1988), on the coast of Galicia (NW Spain; Fig. 1). These rias, both of which are bordered by extensive salt marshes, cover a total area of ca. 2900 ha (Anon. 1981), and both are included in the 'List of wetlands of international importance' from the Ramsar Convention. In both salt marshes the tidal range is mesotidal (3.6 m between MHWS and MLWS) and the periodicity is semidiurnal (Anon. 1993). However, fluvial freshwater input in the Mera is considerably more important than in the Ladrado. The climate in this region (humid mesothermic according to Thornthwaite's classification; Carballeira et al. 1983) is strongly oceanic, with monthly mean temperatures fluctuating little around the annual mean of 13 °C. Mean annual precipitation is ca. 1000 mm. Summer is the driest period, though drought conditions rarely occur in the area. The bedrock consists largely of gneisses and slates which give rise to a fine sediment after weathering.

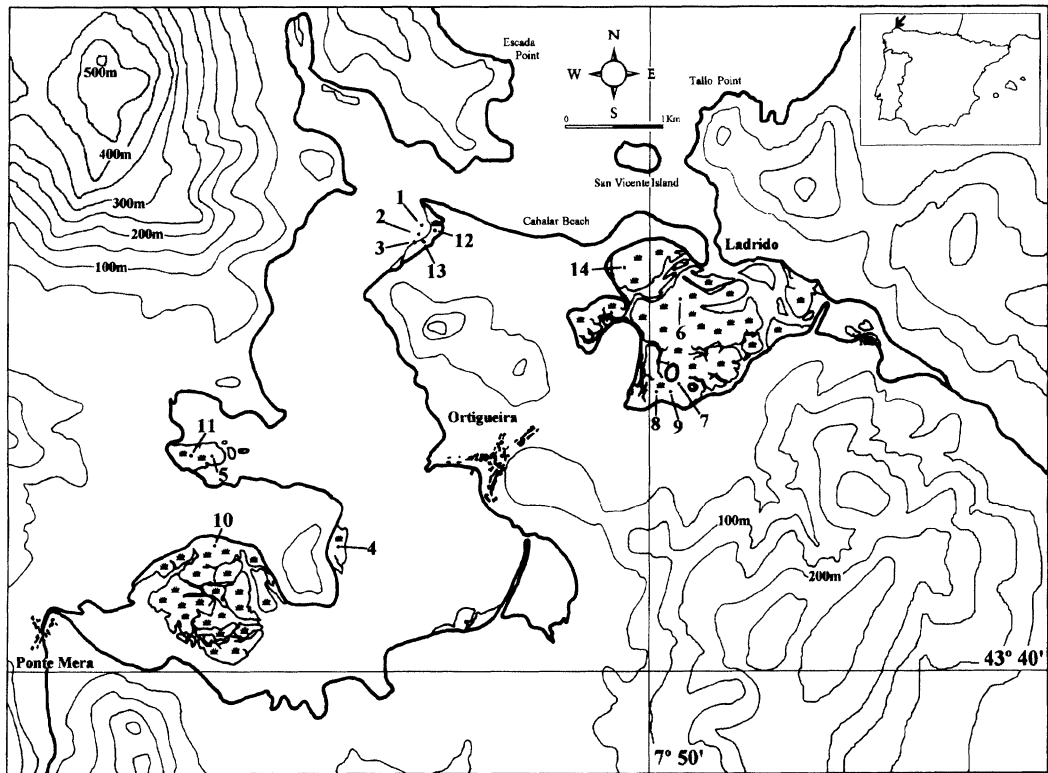


Fig. 1. Map of the study area with location of the transects in the salt marshes of Ladrido (Nos. 6 - 9 and 14) and Mera (Nos. 1 - 5, and 10 - 13). Transect characteristics are summarized in Table 1. Inset: location of the study area in the Iberian Peninsula.

Both salt marshes are little disturbed. Horse grazing occurs on a small area of the Ladrido salt marsh (excluded from our study). Mowing of *Juncus maritimus* was a frequent practice until the 1960s, but is now restricted to small areas of the upper salt marsh (those areas are also largely excluded).

Data collection

Vegetation was sampled between May and August 1993 along 14 belt transects in the Ladrido and Mera salt marshes (Fig. 1; Table 1). Vegetation was analyzed in 0.25 m² quadrats along the entire length of each transect. Quadrats of this size are considered representative for this vegetation type (cf. Hutchinson 1982). For each species the cover was estimated visually on a modified Braun-Blanquet scale (cf. Zedler & Cox 1985; Dawson & Bliss 1987): 1 = <10%; 2 = 10 - 25%; 3 = 25 - 50%; 4 = 50 - 75%; 5 = 75 - 100%. The altitude of each quadrat was determined (at the centre of the side closest to the sea) with the aid of a Fuji-Koh FL25M engineer's level and level rods and given in cm relative to mapped zero, i.e. zero elevation as appearing on Spanish nautical charts (in our study area, mean sea level is approximately 235 cm above mapped zero; Anon. 1993).

In addition, phytosociological relevés were made for

all communities crossed by each transect according to the conventional Zurich-Montpellier methodology.

Data analysis

We used a random nested ANOVA with the dependent variable *altitude of quadrat* and the factors *site* (Ladrido or Mera) and *species*, to investigate the importance of the relationship between altitude and species distribution. For each species, the relationship between altitude and cover index was explored by means of ecological profile analysis (Daget & Godron 1982); altitude class-intervals were determined on the basis of points of inflection in a plot of cumulative number of occurrences of all species against altitude, and the degree of association between each species and each altitude class was expressed as a weighted frequency, as recommended by Fraga et al. (1991).

All 1417 quadrats from all transects were classified by Average-Linkage Clustering (SPSS statistical package; Anon. 1988), with the reciprocal of square-root Euclidean distance as similarity index. Analysis of variance was used to investigate whether altitude of occurrence varied significantly among the resulting groups.

In addition, the vegetation types (syntaxa) recognized in the area were identified by comparing the

relevés made with phytosociological tables for salt-marsh vegetation in other areas of NW Spain (Onaindía & Navarro 1987; Guitián 1989; Herrera 1989; Izco et al. 1992; Díaz & Fernández-Prieto 1994). Analysis of variance was used to investigate whether the range of occurrence varied significantly among the syntaxa. All analyses of variance were carried out with the statistics package SYSTAT (Anon. 1992).

Results

Quadrat altitude ranged between 191 and 434 cm above mapped zero (Table 1). 30 species were recorded. 13 of the 30 species were present in more than 10 % of quadrats. Species richness increased with quadrat altitude; the lowest quadrats often contained only a single species.

Species distributions with respect to altitude

The mean altitudinal ranges of species (Fig. 2) shows close correspondence to the classic geomorphological profile of a salt marsh. The lowest level is occupied by *Zostera noltii* and this zone is clearly separated from the next higher level, occupied by *Spartina maritima*. These two levels constitute the tidal flat and the low marsh, abruptly separated from the mid-altitude level, which is largely occupied by communities dominated by *Juncus maritimus*. Between-species differences in mean altitude of occurrence are much less pronounced in this altitude range (Fig. 2). At higher levels in the profile, such differences again become more pronounced.

The factor *species* was a significant source of variance in *altitude-of-quadrat* ($F = 382.57, p < 0.01$). The

Table 1. Characteristics of the 14 transects.

| Transect | No. of spp. | Length (m) | Max. height (cm) | Min. height (cm) |
|----------|-------------|------------|------------------|------------------|
| 1 | 1 | 50 | 235 | 191 |
| 2 | 2 | 36 | 271 | 243 |
| 3 | 2 | 31 | 275 | 241 |
| 4 | 11 | 68 | 345 | 201 |
| 5 | 12 | 43 | 343 | 266 |
| 6 | 16 | 53 | 378 | 307 |
| 7 | 18 | 93 | 409 | 287 |
| 8 | 21 | 62 | 386 | 333 |
| 9 | 19 | 87 | 423 | 271 |
| 10 | 12 | 37.5 | 366 | 346 |
| 11 | 18 | 34 | 353 | 310 |
| 12 | 8 | 37 | 418 | 334 |
| 13 | 6 | 23 | 428 | 353 |
| 14 | 21 | 54 | 434 | 340 |

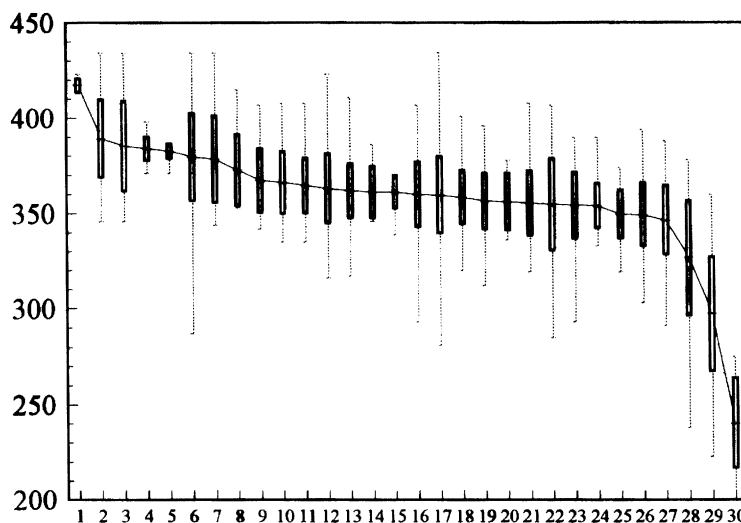
factor *site* was not a significant source of variance ($F = 1.88, p = 0.18$). These results indicate that there is significant among-species variability in altitude of occurrence, and that quadrat altitudes did not differ significantly between the two study sites.

When only species with > 25 % cover are included, five species – *Apium graveolens*, *Aster tripolium*, *Centaurium pulchellum*, *Sarcocornia perennis* and *Scirpus lacustris* – are omitted. The altitudinal profile for the remaining 25 species (not shown here) shows a steeper middle section of the curve. For the reduced data set, nested analysis of variance indicated that *species* was a significant source of variance in *altitude-of-quadrat* ($F = 474.94, p < 0.001$), but that the effect of *site* was not significant ($F = 0.81, p = 0.38$).

For the ecological profile analysis, seven altitude classes were defined on the basis of the changes in the slope of the curve expressing cumulative numbers of occurrences of all species against altitude (Daget &

Fig. 2. Altitudinal range of species along salt-marsh transects. Species ordered according to decreasing maximum height. Vertical bars represent standard deviations and dotted lines the species' complete range.

- 1 *Eleocharis uniglumis*
- 2 *Limonium binervosum*
- 3 *Paspalum vaginatum*
- 4 *Apium graveolens*
- 5 *Scirpus lacustris*
- 6 *Festuca litoralis*
- 7 *Agrostis stolonifera*
- 8 *Frankenia laevis*
- 9 *Carex extensa*
- 10 *Glaux maritima*
- 11 *Samolus valerandi*
- 12 *Juncus gerardi*
- 13 *Armeria maritima*
- 14 *Scirpus maritimus*
- 15 *Centaurium pulchellum*
- 16 *Plantago maritima*
- 17 *Juncus maritimus*
- 18 *Aster tripolium*
- 19 *Puccinellia maritima*
- 20 *Inula crithmoides*
- 21 *Suaeda maritima*
- 22 *Halimione portulacoides*
- 23 *Limonium narbonense*
- 24 *Sarcocornia perennis*
- 25 *Salicornia ramosissima*
- 26 *Spergularia media*
- 27 *Triglochin maritima*
- 28 *Bostrychia scorpioides*
- 29 *Spartina maritima*
- 30 *Zostera noltii*.



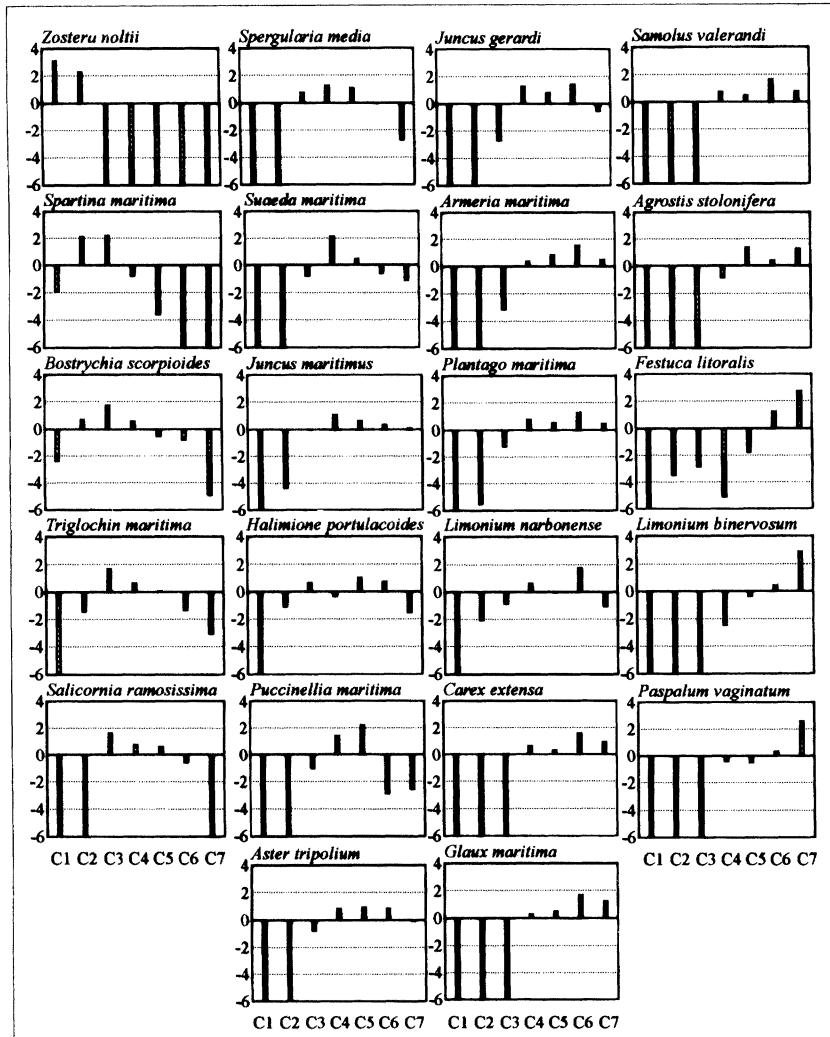


Fig. 3. Ecological profiles relative to altitude for the 22 species whose distribution among the seven altitude classes was non-uniform (χ^2 tests, $\alpha = 0.05$). The vertical axis represents the natural logarithm of weighted frequency. The 22 species are ordered from top to bottom and from left to right on the basis of the class in which weighted frequency is maximal. The altitude classes are < 250 cm (C1), 250 - 300 cm (C2), 300 - 330 cm (C3), 330 - 350 cm (C4), 350 - 360 cm (C5), 360 - 375 cm (C6) and > 375 cm (C7).

Godron 1982). The limits of these classes broadly correspond to the changes in slope of the curve in Fig. 2. χ^2 tests ($\alpha = 0.05$) indicated that the distribution of 22 of the 30 species among these altitude-classes was non-uniform. The ecological profile plots for these species are shown in Fig. 3. Since species are ordered by the altitude class in which their weighted frequency is highest, the resulting order differs from that shown in Fig. 2 – which is due to the fact that the ecological profile analysis takes cover values into account.

Quadrat clusters and their relation to altitude

The result of quadrat clustering procedure is summarized in Table 2. Of the 30 groups obtained at the selected cut-off-point, nine are not considered further since they contained less than five quadrats.

Analysis of variance revealed that the factor *group* was a significant source of variance ($F = 173.38$, $p <$

0.01) in *altitude-of-quadrat*. A simple one-way analysis was used instead of a two-way nested analysis, since *site* had no significant effect on the altitudes of occurrence of species and can thus be expected to have no effect on the altitudes of occurrence of species groups.

The ranking plot of mean altitudes of occurrence of the clustering-derived groups is sigmoid (Fig. 4). Between-group differences are most marked at the extremes of the altitudinal gradient, as in the corresponding species plots (Figs. 2 and 3). However, the slope of the central part of the curve is steeper than in the corresponding species plots and the corresponding syntaxa plot (see below; Fig. 5).

Syntaxa and their distribution in relation to altitude

Based on the Braun-Blanquet approach, 11 syntaxa were identified in the areas covered by the transects (Fig. 5). Generally, they corresponded fairly closely

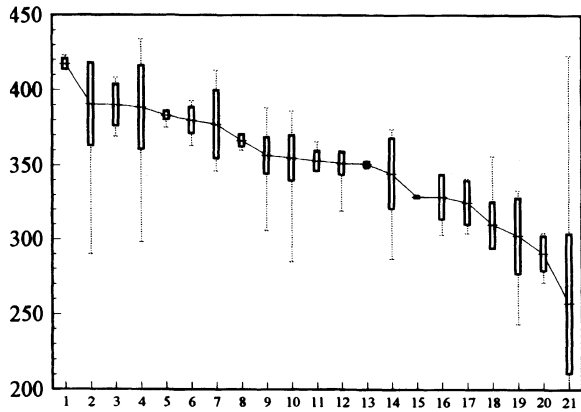


Fig. 4. Sequence of 21 quadrat clusters as to mean altitude range. Vertical bars represent standard deviations; dotted lines the groups' complete range. Group numbers as in Table 2.

to the quadrat clusters; however, the larger number of groups derived by clustering (21) reflected altitude-related variability more effectively. Of the 1417 quadrats, 1080 were readily assignable to one of the 11 syntaxa, allowing estimation of minimum, maximum and mean altitudes for each syntaxon. The ranked plot of mean altitudes of occurrence of syntaxa is again sigmoid (Fig. 5), though the central part of the curve is less steep than in the corresponding plot of clustering-derived groups (Fig. 4). Analysis of variance indicated that the factor *syntaxon* is a significant source of variance ($F = 623.84$, $p < 0.01$) in *altitude-of-quadrat*.

Discussion

General characteristics of the vegetation

The altitudinal range covered by the salt marshes of the Ortigueira and Ladrado rivers (191 - 434 cm above mapped zero, i.e. from ca. 185 cm below to 58 cm above MHW) is similar to that reported for salt marshes in other areas. Hutchinson (1982), for example, found that salt-marsh vegetation in Lulu Island (Canada), with a similar tidal range to that of the present study area, extended from about 142 cm below to about 56 cm above MHW. This author did not consider the tidal flat level, occupied by *Zostera noltii* in our study area.

The principal topographic features of the typical salt-marsh profile (e.g. Long & Mason 1983; Pethick 1984) are the 'steps' separating the tidal flat and the low, middle and upper marshes. In the present study, these steps were located at ca. 260, 350 and 400 cm above mapped zero, respectively.

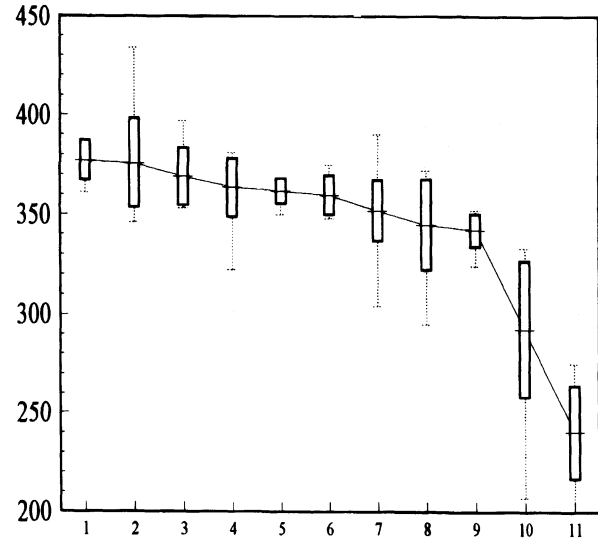


Fig. 5. Sequence of the 11 syntaxa identified in the present study as to mean altitude of occurrence. Vertical bars represent standard deviations and dotted lines the syntaxa's complete range. Syntaxa are numbered as follows: 1. *Scirpetum maritimae*; 2. *Agrostio stoloniferae-Juncetum maritimae*; 3. Comm. of *Frankenia laevis* and *Limonium ovalifolium*; 4. *Limonio serotini-Juncetum maritimi halimionetosum portulacoidis*; 5. Comm. of *Plantago* and *Limonium narbonne*; 6. *Limonio serotini-Juncetum maritimi juncetosum gerardii*; 7. *Limonio serotini-Juncetum maritimi typicum*; 8. *Bostrychio scorpioidis-Halimionetum portulacoidis*; 9. *Sarcocornio perennis-Salicornietum ramosissimae*; 10. *Spartinetum maritimae*; 11. *Zosteretum noltii*.

Distribution of species in relation to altitude

The species rank curve of species mean-altitude occurrence (Fig. 2) is sigmoid in form. This reflects the low species richness of the tidal flat and low marsh, and the relatively high species richness of the middle marsh.

The upper tidal flat and low marsh are typically occupied by single species, such as *Zostera noltii* or *Spartina maritima*, while the middle marsh is occupied by a relatively wide range of species. The upper marsh is characterized by mesohalophytes, of which *Eleocharis uniglumis* is a good example. The transition from middle to upper marsh is apparent in Figs. 2 and 3. However, the upper levels of some transects crossed areas of freshwater input, typically occupied just upstream by *Phragmites australis* stands; here the transition between middle and upper marsh was less well defined.

When cover values are considered, the ranking of species by mean altitude is similar to that obtained by ecological profile analysis (Fig. 3). Both methods are based on cover values; hence these rankings reflect species altitudinal optima more closely than the presence/absence-based ranking of Fig. 2.

Table 2. Summarized species composition of the 21 groups obtained by clustering. Roman numerals indicate percentage frequency of species in clusters quadrats: V: > 81 %; IV: 61 - 80 %; III: 41 - 60 %; II: 21 - 40%; I: 11 - 20%; +: 6 - 10%; r: < 6 %.

| Cluster | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | |
|--------------------------------|-----|-----|----|-----|-----|-----|-----|----|-----|----|-----|-----|----|-----|----|----|-----|-----|-----|----|-----|---|
| Quadrats per clusters | 9 | 59 | 6 | 33 | 14 | 34 | 53 | 14 | 405 | 45 | 28 | 43 | 6 | 107 | 6 | 5 | 7 | 11 | 118 | 6 | 264 | |
| <i>Lychnis flos-cuculi</i> | III | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Galium palustris</i> | III | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Juncus obtusifolius</i> | II | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Parapholis strigosa</i> | . | r | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Eleocharis uniglumis</i> | V | . | . | . | . | . | r | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Festuca arundinacea</i> | V | . | . | . | . | . | r | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Hypochaeris radicata</i> | III | . | . | . | . | . | II | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Limonium binervosum</i> | . | V | V | IV | . | III | . | . | . | . | I | . | r | . | . | . | . | . | . | . | . | + |
| <i>Festuca litoralis</i> | . | . | V | V | . | V | r | . | . | r | . | . | . | r | . | . | . | . | . | . | . | . |
| <i>Agrostis stolonifera</i> | V | . | r | + | V | I | V | IV | r | + | III | . | I | . | . | . | . | . | . | . | . | . |
| <i>Paspalum vaginatum</i> | II | III | IV | IV | I | r | III | I | . | . | V | I | . | . | . | . | . | . | . | . | . | . |
| <i>Apium graveolens</i> | . | . | . | . | IV | . | r | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Scirpus lacustris</i> | . | . | . | . | V | . | II | . | . | . | V | . | . | . | . | . | . | . | . | . | . | . |
| <i>Juncus gerardi</i> | IV | . | . | I | II | r | IV | V | I | II | V | . | . | . | . | . | . | . | . | . | . | . |
| <i>Armeria maritima</i> | . | . | V | II | . | IV | . | I | IV | + | . | II | V | . | . | . | . | . | . | . | . | . |
| <i>Glaux maritima</i> | . | . | I | r | . | II | IV | V | I | + | IV | . | . | . | . | . | . | . | . | . | . | . |
| <i>Carex extensa</i> | . | . | V | II | . | V | I | V | I | I | I | . | I | . | . | . | . | . | . | . | . | . |
| <i>Samolus valerandi</i> | . | . | . | . | III | I | + | V | I | I | r | . | . | r | . | . | . | . | . | . | . | . |
| <i>Scirpus maritimus</i> | . | . | . | . | V | . | r | + | . | . | . | . | I | . | . | . | . | . | . | . | . | . |
| <i>Frankenia laevis</i> | . | II | . | . | . | . | . | . | . | . | r | . | . | + | . | . | . | . | . | . | . | r |
| <i>Centaurium pulchellum</i> | . | . | . | . | . | + | . | . | I | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Plantago maritima</i> | . | r | V | III | . | V | . | + | V | II | . | II | V | II | I | + | III | + | . | . | . | . |
| <i>Juncus maritimus</i> | II | . | V | V | V | V | V | V | V | V | V | V | V | III | V | V | V | + | . | . | . | r |
| <i>Aster tripolium</i> | . | . | V | r | . | r | r | + | + | II | . | III | . | I | . | . | . | . | . | . | . | r |
| <i>Puccinellia maritima</i> | . | II | V | . | . | . | . | . | r | . | . | V | V | + | . | . | . | I | . | . | . | + |
| <i>Inula crithmoides</i> | . | . | . | . | . | r | . | . | r | r | . | r | . | . | . | r | . | . | . | . | . | . |
| <i>Suaeda maritima</i> | . | II | . | . | . | . | . | . | . | . | III | I | I | . | . | . | . | . | . | . | . | r |
| <i>Phragmites australis</i> | . | . | . | . | . | . | . | . | + | . | . | . | . | . | V | . | . | I | . | . | . | . |
| <i>Halimione portulacoides</i> | . | II | II | I | . | II | + | . | r | II | . | r | r | V | . | + | II | IV | r | II | r | r |
| <i>Limonium narbonense</i> | . | . | I | r | . | IV | . | II | V | II | . | I | V | I | I | + | III | III | r | . | . | . |
| <i>Salicornia ramosissima</i> | . | + | V | . | . | . | . | . | r | r | . | III | . | r | . | . | . | . | . | . | . | r |
| <i>Spergularia media</i> | . | r | V | . | . | r | . | . | I | r | . | III | V | I | . | r | . | III | . | . | . | r |
| <i>Triglochin maritima</i> | . | . | II | . | . | II | III | + | III | II | V | II | V | + | V | V | IV | V | r | . | . | . |
| <i>Bostrychia scorpioides</i> | . | . | I | r | . | . | . | + | II | I | . | r | r | IV | r | V | V | + | V | IV | r | r |
| <i>Sarcocornia perennis</i> | . | . | . | . | . | r | . | . | r | r | . | r | V | r | . | . | . | + | . | . | . | . |
| <i>Spartina maritima</i> | . | . | . | . | . | . | . | . | . | . | . | r | . | + | . | . | V | + | V | V | + | + |
| <i>Zostera noltii</i> | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | V | V |

Our data indicate that the altitudinal ranges of the tidal-flat and low-marsh species *Zostera noltii* and *Spartina maritima* are wider than those of other salt-marsh species. Other authors have reported similar findings. Adams (1963) and Lefor et al. (1987), in studies of salt marshes with microtidal regimes (i.e. tidal range < 2 m), found that *Spartina alterniflora* occurs over altitudinal ranges of ca. 90 and 50 cm respectively. Such wide ranges may be attributable to the absence of competitors in the high-stress tidal flat environment. A number of previous studies of salt-marsh vegetation have suggested that intensity of competition increases with altitude. Snow & Vince (1984), for example, suggested that physiological tolerance was the limiting factor at lower levels, while competitive ability became more important at higher levels. Hutchings & Russell (1989) found that seed production and seedling loss were higher at higher levels.

In our study area, another species occurring over a wide altitudinal range is *Halimione portulacoides*

(Figs. 2 and 3). The wide altitudinal range of this species has been pointed out previously by Géhu-Frank & Géhu (1985) and Russell et al. (1985). According to Beefink (1966) it occurs on well aerated substrates ranging from euhaline to polyhaline.

Juncus maritimus is the dominant species throughout the middle marsh, particularly at higher levels. This species was present in almost all quadrats at these levels, generally with high cover and sometimes forming a monospecific community. In plots where *Juncus maritimus* occurs, other species are typically present with low cover, unless mowing has opened the way for their expansion.

As illustrated by the ecological profile plots (Fig. 3), some species are restricted to specific altitude classes. *Zostera noltii*, discussed above, is restricted to the first two classes (up to 300 cm), *Spartina maritima* occurs predominantly in the second two classes (250-330 cm), and is absent from the highest altitude classes. Several species occur predominantly in the central altitude classes

(e.g. *Puccinellia maritima* and *Suaeda maritima*). Most of the remaining middle-marsh species, however, show less clearly defined distribution patterns with respect to altitude. As mentioned above, *Halimione portucaloides* shows particular 'indifference' to altitude, and is absent only from the < 250 cm class. A few species, such as *Carex extensa* and *Festuca litoralis*, occur predominantly in the highest altitude classes.

Distribution of communities with respect to altitude

Generally, the distribution pattern of communities is similar to that described above for species. Most importantly, tidal-flat and low-marsh communities, which are almost invariably monospecific (Beefink 1977), tend to occur over a broader altitudinal range than middle- and upper-marsh communities. As is to be expected, the altitudinal range of communities is narrower than that of the constituent species; communities can thus be considered to be more reliable indicators of altitude than single species.

Possible causes of the observed patterns of distribution

The distribution patterns of species and communities identified in the present study are similar to those described by phytosociological methods in other Atlantic coastal regions of Europe (e.g. Beefink 1966; Hayon & Pelt 1969; Géhu-Frank & Géhu 1985; Onaindía & Navarro 1987; Guitián 1989; Herrera 1989) as well as by other methods in various regions of Europe and North America (e.g. Hinde 1954; Gillham 1956; Zedler & Cox 1985; Benito 1989; de Leeuw et al. 1991).

Our data reveal that species differ in their distributions with respect to altitude, but mean altitudes of occurrence did not differ significantly between the two study sites, despite the fact that the influence of river water input is different at each site. Similar results were reported by Adams (1963) in a study of North American salt marshes; he considered topography to be the principal factor affecting the distribution of vegetation in salt marshes – topography controls the temporal pattern of inundation by sea-water. For a given biogeographical region, it should thus be possible to predict vegetation type on the basis of altitude, as suggested long ago by Johnson & York (1915). The results of our study support this suggestion. However, other factors may also have a significant effect (Chapman 1940). Biotic factors, such as propagule availability and the time elapsed since propagule establishment (Hutchings & Russell 1989; Bertness & Shumway 1993), as well as between-species competition (Pielou & Routledge 1976), may be of particular importance. Furthermore, the plant itself

may have marked effects on the local environment, for instance by particle entrapment.

Unlike Benito (1989), we consider that, in relatively undisturbed salt marshes such as those studied here, species tend to show higher cover values in the most favourable sections of the gradient. Even those species which tend to occur over a wide altitudinal range often display altitude-dependent phenotypic variability (see also Mendelssohn & Seneca 1980; Linthurst & Seneca 1981; Huiskes et al. 1985; Seliskar 1985a, b). Moreover, seed germination and seedling survival rates of salt-marsh plants have been reported to be highest at sites where percentage cover and seed production are highest (Hutchings & Russell 1989).

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