

Above-ground biomass and species richness in a Mediterranean salt marsh

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Abstract. Species composition, above-ground biomass and diversity of herbaceous communities were recorded in 50 sites on the upper salt marsh of the Guadalquivir delta (SW Spain). Through Canonical Correspondence Analysis relationships were shown between plant-species characteristics abundance and environmental variables. Seven community types were distinguished and related to hydrological regime and physical and chemical soil parameters.

The higher species richness was associated with moderate values of above-ground biomass (Biomass at maximum diversity, BMD = 302 g/m²). Salinity was negatively correlated with species richness. There was no significant correlation with total above-ground biomass. Water regime and soil nutrient (Ca, Mg) content were significant predictors of the community above-ground biomass.

Keywords: Canonical Correspondence Analysis; Diversity; Doñana National Park; Marismas; Salinity; Standing crop; Water regime.

Nomenclature: Valdés, Talavera & Galiano (1987).

Introduction

Plant-species distribution and abundance in salt-marsh communities are strongly affected by the physical environment: soil oxygen level, inundation regime, nutrient availability, sulphur accumulation, drainage, and salinity of water and soil (Vince & Snow 1984; Bertness & Ellison 1987; Adam 1990). Biotic factors, such as interspecific competition, symbiont activity, and pressure by herbivores and parasites, may play additional important roles in shaping salt-marsh vegetation (Bertness & Ellison 1987; Rozema et al. 1988; Pennings & Callaway 1992).

Under the influence of a Mediterranean-type climate, the upper salt-marsh vegetation often comprises scattered chenopod shrubs and annual grassland. Only a few ecological studies have been focused on the species-rich transition zone between marsh and inland vegetation (Adam 1990; Callaway et al. 1990).

The objectives of this study are: (1) to analyse the relationships between environmental factors (salinity, water regime) and the distribution and abundance of herbaceous species; (2) to test the general model relating standing crop and species richness, and to analyse how both these community variables are affected by salinity and water regime.

Methods

Study area

The Guadalquivir River delta (SW of Spain) was formed by fluvio-marine sediments filling up the river estuary during the late Holocene. The resulting floodplain (ca. 1500 km²), at an average height of 3.6 m above mean sea level, is bounded by a coastal sand-dune system that prevents direct flooding by sea water. During the wet season (October-May), lower areas are flooded to a depth of < 70 cm, mainly by direct rainfall. The western part is additionally flooded by a temporary fresh-water flow draining from stabilised dune systems. A narrow fringe along the river banks is periodically flooded by the brackish water of the estuarine tides (about 2 m range).

The climate is Mediterranean, with cool and wet winters and warm and dry summers; average annual rainfall is 600 mm and average annual temperature is 18 °C. The soils are predominantly silty-clayey, calcareous and saline, with sodium, chloride and magnesium as major ions. The water and salt regimes of the soil are highly seasonal and strongly determined by the micro-relief (García unpubl.).

The area has been phytosociologically described by Rivas-Martínez et al. (1980). The vegetational variation in the ecotone between the marsh and the stabilized sand dunes has been related to soil pH, conductivity, sodium content, and to water flooding by González-Bernáldez et al. (1976) and Torres et al. (1977). Salt-marsh grassland productivity and nutritive values have been studied

by Murillo et al. (1986), and their protection was recommended for 'in situ' conservation of salt-tolerant plant-genetic resources (cf. Dijkema 1987; Marañón, García & Troncoso 1989; Marañón et al. 1989).

Plant and soil measurements

50 sampling sites were selected, representing the most common habitats and herbaceous communities in the delta. Above-ground biomass inside a 50 cm × 50 cm square was clipped at the time of peak biomass (April-June), sorted per plant species, oven-dried (> 48 h at 70 °C) and weighed. Samples were taken every year for three years (1989-1991) and thus covered inter-year variability in ecologically similar sites.

In each sampling site, a bulked sample (collected from three points) of the superficial soil horizon (10 cm depth) was taken. Field soil moisture (MOISTURE) was determined gravimetrically and expressed as % dry soil weight.

Soil samples were air-dried, crushed and sieved (< 2 mm). Electrical conductivity (EC_s), pH and soluble ions were measured in soil saturation extracts. Na and K were measured by flame emission spectroscopy; Ca and Mg by atomic absorption spectroscopy; Cl and SO₄ by visible spectrophotometry; and alkalinity (ALK) by acid neutralization. Before extraction, saturation percentage (SP) of the saturate paste was measured as an indicator of soil texture. Organic matter (OM) was determined using a modified Walkley & Black method and total inorganic carbonates (TIC) using a pressure-calimeter (Page, Miller & Keeney 1982).

Description of the physical environment in each sampling site included an estimation of the soil-water regime, associated with water availability and plant-root oxygen shortage stress. Two semi-quantitative variables were defined, based on site elevation (available from detailed microtopographic maps), climatic and tidal records for the sampling period, and field observations. The estuarine tidal flooding variable (TFLOOD) ranges from 5 (flooded daily during high tides) to 2 (flooded only by equinoctial spring tides) - value 1 means no tidal influence. Inundation from rainfall and fresh water (RFLOOD) can take one of the following assigned values: 1: non-flooded, well-drained soils; 2: non-flooded, moderately drained soils; 3: flooded yearly, <1 month and very shallow (<5 cm deep); 4: flooded yearly, 1-3 months, 5-15 cm deep; 5: waterlogged yearly, >3 months, >15 cm.

Data analysis

To examine the relationships between plant-species distribution and environmental variables, Canonical

Correspondence Analysis (CCA, ter Braak 1988) was applied, with the following options selected (1) plant species recorded only once were excluded; (2) species biomass data were log-transformed; (3) five samples appearing as outliers were made passive; (4) five soil chemical variables (Na, Mg, Ca, Cl and SO₄), largely multi-collinear and strongly correlated with electrical conductivity, were excluded. The definitive CCA was applied to 87 plant species, 50 sites and 12 environmental variables. The significance of the relations was tested using the Monte Carlo permutation test.

Site groups were defined in the ordination space obtained while using discriminant analysis to site coordinates in an iterative procedure. Species coordinate values were then assigned to groups.

Stepwise multiple regression (Anon. 1989) was used to analyse the relationships between the community parameters measured, species richness and standing crop, and the environmental variables. The above-ground biomass value at maximum diversity (BMD) was calculated analytically from the fitted regression equation.

Results

Environmental factors and species distribution

The first four CCA axes explain 56% of the species-environment variance (Table 1). Both the trace and the first eigenvalue were significant ($P < 0.01$). Rainfall flooding persistence and soil salinity are the environmental variables best correlated with axis 1, whereas tidal flooding frequency, total inorganic carbonates and pH best correlate with axis 2 (Table 1).

The ordination diagram of sites and environmental variables in the plane defined by the first and second CCA axes is shown in Fig. 1. The first ordination axis reflects a main environmental gradient closely linked to variation in microtopography in the non-tidal marsh. Depressed, saline, waterlogged and heavy-textured sites of temporary lagoons have high positive scores. Associated plant species are *Scirpus littoralis*, *Juncus subulatus*, *Aeluropus littoralis* and *Polypogon monspeliensis*. Elevated sites, with low EC_s values and which are not flooded, have the lowest scores. These sites are remnants of old, fragmented river-banks where ruderal species occur, such as *Carduus pycnocephalus*, *Beta vulgaris*, *Torilis nodosa* and *Capsella rubella*.

Tidal influence is the main environmental factor correlated with the second CCA axis. Daily tide-flooded sites in the estuary, having saline soils with high carbonate content and neutral pH, have the highest positive scores. Associated plant species are *Phragmites australis*,

Paspalum vaginatum, *Polygonum equisetiforme* and *Senecio aquaticus*.

Plant communities

Based on preliminary CCA biplots and previous descriptive studies of the Guadalquivir salt-marsh vegetation (González-Bernáldez et al. 1976; Allier & Bresset 1977; Torres et al. 1977; Rivas-Martínez et al. 1980), the 50 samples were grouped in six vegetation-environment groups. The classification procedure described above was then applied to the four-dimensional CCA ordination space. After one iteration, the overall test of means and the comparison tests among all possible pairwise group means gave significant differences at the $p < 0.01$ level.

A brief description of the herbaceous plant communities and habitat characteristics follows.

1. Ruderal communities. On small promontories, with well-drained non-saline soils ($EC_s < 2dS/m$) with Ca prevailing over Na. During the wet season, these emerged areas are refuges for large herbivores, which

Table 1. Results of the Canonical Correspondence Analysis: Eigenvalues, percentage of variance of species-environment relations, weighted correlations between species and environmental axes (S/E correlation), and weighted correlations between environmental variables and species-canonical axes (only significant values at $p < 0.01$ level).

Axis	1	2	3	4
Eigenvalue	0.68	0.58	0.44	0.38
Variance (%)	19	15	12	10
S/E correlation	0.96	0.94	0.96	0.87
Variables				
RFLOOD	0.92	-	-	-
EC _s	0.76	-	-	-
K	0.58	-	-	-
SP	0.55	-	-	-
MOISTURE	0.45	-	-	-
SO ₄ /Cl	-0.43	-	-	-
TFLOOD	-	0.82	-	-
TIC	-	0.66	-	-
pH	-	-0.64	-	-
Ca/Na	-	-0.44	0.70	-
ALK	-	-	-	0.64

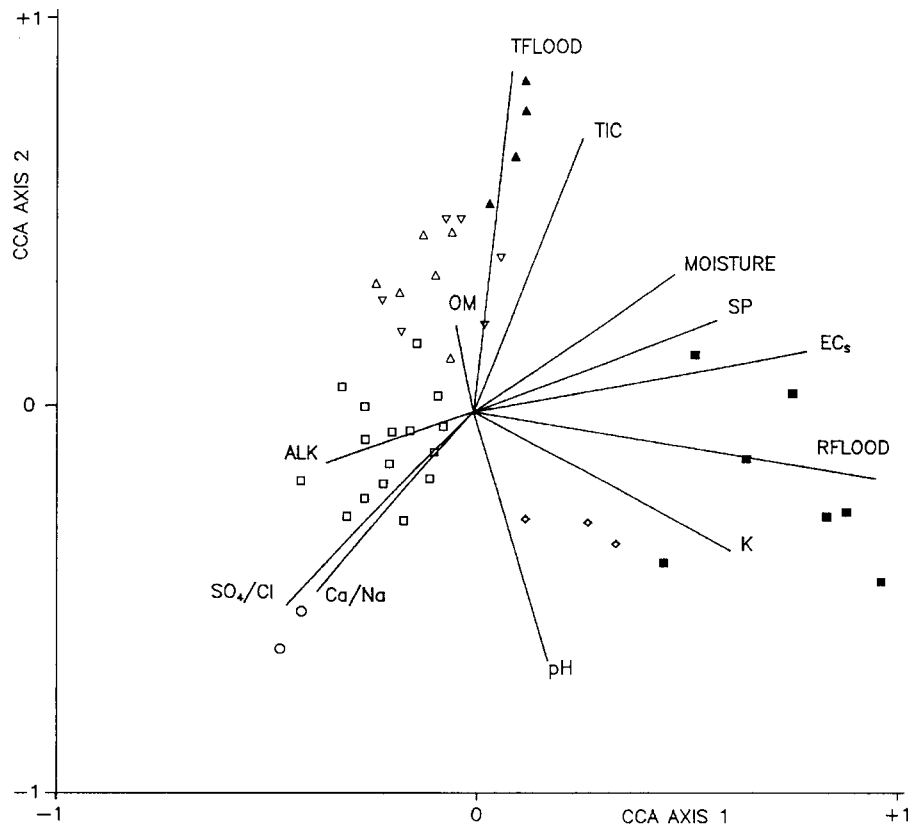


Fig. 1. Diagram of the first two ordination axes of the Canonical Correspondence Analysis. Symbols represent plant communities: 1 (○), 2 (□), 3 (◇), 4 (■), 5 (△), 5b (▽), and 6 (▲). Arrows represent environmental variables.

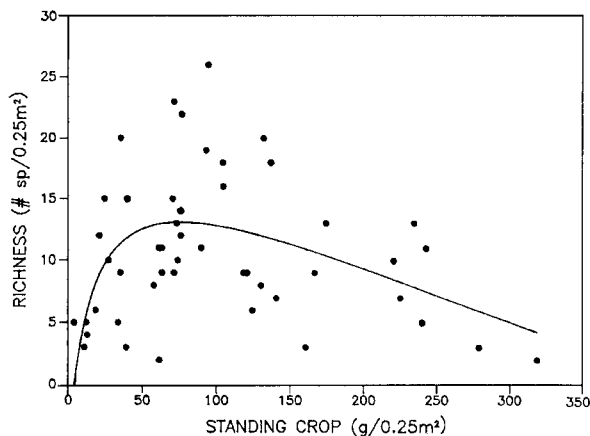


Fig. 2. Species richness versus standing crop for 50 sites from the Marismas in the Guadalquivir delta. The solid line corresponds to a significant (multiple $r = 0.54$, $r^2 = 0.29$, $p < 0.001$) third order polynomial regression equation.

graze heavily and deposit dung. Widespread, nitrophilous plants (e.g. several thistle species) are dominant.

2. Upper salt-marsh grasslands. Mostly found in areas rarely flooded, where soils are slightly to moderately saline (EC_s up to 11 dS/m, mean EC_s 4 dS/m) and with a silty-clayey loam texture. Rainfall leaches salts from the superficial horizons which are dry during the summer. Annuals dominate the grassland, which are mixed with scattered stands of chenopod shrubs (*Arthrocnemum macrostachyum*, *Sarcocornia perennis* ssp. *alpini* and *Suaeda vera*).

3. Lower salt-marsh grasslands. Transition zone, shallowly flooded for 1 - 3 months, with saline silty-clayey soils (EC_s up to 14 dS/m, mean EC_s 9 dS/m), with salt-tolerant annuals (*Frankenia pulverulenta*, *Spergularia nicaensis*, *Coronopus squamatus*) growing sparsely among chenopod stands (*Arthrocnemum macrostachyum*).

4. Lagoon sedge communities. On the banks of the saline lagoons (EC_s up to 38 dS/m, mean EC_s 21 dS/m), flooded > 3 months/year, with salt-tolerant helophytes (*Scirpus litoralis*, *S. maritimus*, *Juncus subulatus*) dominating. During the dry season, the creeping halophyte grass *Aeluropus litoralis* spreads on the desiccated mud.

5. Upper tidal grasslands. On the upper part of the estuarine banks, only occasionally flooded by the highest spring tides, kept moist by capillarity. Salinity is moderately high (EC_s up to 13 dS/m, mean EC_s 8 dS/m), but because of the persistent moisture, extreme salt concentrations in the soil solution do not occur. Perennial grasses (*Cynodon dactylon*, *Paspalum vaginatum*)

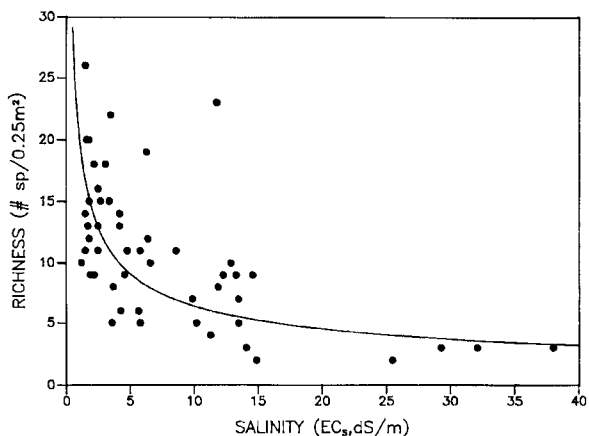


Fig. 3. Species richness versus electrical conductivity of the soil saturation extract for 50 salt-marsh samples. Solid line corresponds to a significant regression model ($r = -0.74$, $r^2 = 0.55$, $p < 0.001$). The fitted hyperbolic regression equation is $Y = K / X$, where $X = \sqrt{EC_s}$ and $K = 20.5$.

coexist with numerous annuals.

A subgroup (5b) of moist grasslands was split off, with two highly productive annual legumes, *Trifolium isthmocarpum* and *T. resupinatum*, occurring on the margins of the delta, on non-saline ($EC_s < 4$ dS/m), sandy, wet soils near freshwater sources with high Ca/Na and SO_4/Cl ratios.

6. Lower tidal grasslands. On sites exposed daily to estuarine tides (having EC_s up to 15 dS/m, mean EC_s 12 dS/m), a salt-tolerant perennial grass (*Paspalum vaginatum*) dominates in a dense wet grassland. At the lower level, reeds (*Phragmites australis*) grow on the channel slopes, occasionally spreading into the wet grassland.

Salinity, species richness and standing crop

Species richness ranged from 2 to 26 species per 0.25-m² plot, and standing crop varied from 3.2 to 317 g/0.25 m². The relationship between the two parameters shows a unimodal trend (Fig. 2), fitting a third-order polynomial regression (multiple $r^2 = 0.29$, $p < 0.001$); this seems to support Grime's (1979) model.

Using mean values calculated on a logarithmic scale as regression variables (Moore & Keddy 1989), a better fit of the polynomial equation was obtained ($r^2 = 0.72$, $p < 0.005$, $n = 14$). The Shannon index of diversity, which is strongly linearly correlated to species richness ($r = 0.82$, $p < 0.0001$), also fits a third-order polynomial regression with standing crop ($r^2 = 0.32$, $p < 0.001$). On the other hand, no significant relationship between even-

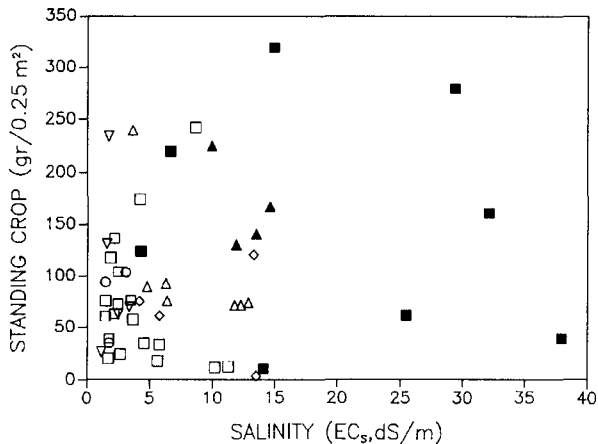


Fig. 4. Standing crop plotted against electrical conductivity of the soil-saturation extract for 50 salt-marsh samples. Symbols represent plant community types as shown in Fig. 1.

ness and standing crop was found.

Species richness is conversely related to salinity, fitting a hyperbolic curve (Fig. 3, $r = -0.74$, $r^2 = 0.55$, $p < 0.001$). Increasing soil salinity is associated with a steep drop in species richness.

Stepwise regression analysis selected soil salinity, flooding persistence and salt quality (Ca/Na) as the best set of predictor variables of species richness (multiple $r = 0.71$, $p < 0.005$). The relationship is significantly negative for salinity (as shown above) and flooding persistence, and significantly positive for salt quality. Salinity level, sodium toxicity (inverse of Ca/Na) and water-logging seem to be the main environmental factors limiting species richness in the salt marsh.

Salinity, as a separate factor, does not explain the variations in standing crop (Fig. 4). Nevertheless, the elements calcium and magnesium and the water-regime variables TFLOOD, RFLOOD and MOISTURE, were selected as significant predictor variables of standing crop (multiple $r = 0.64$, $p < 0.005$). Total above-ground biomass seems to depend mainly on water availability during the growing season and content of bivalent cations (Ca, Mg) in the soil solution.

Mean and standard deviation of the diversity and biomass data for the six community types are shown in Fig. 5. Lagoon sedge communities (4) and lower tidal grasslands (6) show the highest mean standing crop and the lowest mean species richness. Ruderal communities (1) have the highest mean species richness and a low standing crop. Most common grassland types have intermediate species richness values. Salt-marsh grasslands (2, 3) have lower mean standing crop than upper tidal grasslands (5) and non-saline moist grasslands (5b).

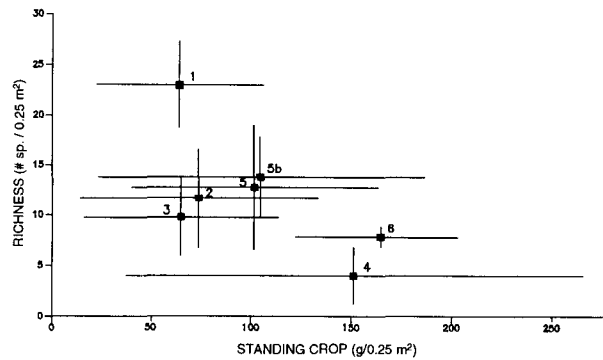


Fig. 5. Mean and standard deviation of species richness and standing crop for the six plant communities.

Discussion and Conclusions

A topographic gradient, associated with seasonal flooding and soil salinity variation, primarily determines herbaceous plant distribution and abundance in the Guadalquivir delta. Despite the continuous variation, a sequence of plant communities can be described for the sake of simplicity: ruderal communities (type 1) on drained, leached promontories; extensive annual grasslands (type 2) interspersed with chenopod shrubs; open vegetation with annuals (type 3), chenopod shrub communities in a transitional, seasonally flooded area; and halophilous sedges (type 4) around saline lagoons.

Along the estuarine banks, tidal flooding is a main factor determining a distinct vegetation, formed by perennial grassland (type 6), enriched with annual species on higher sites (type 5). These tidal grasslands (locally called playas), grow all year round and have a high productivity (up to 900 g/m^2 , mean 660 g/m^2). Despite their local occurrence, they represent an essential forage source for herbivore populations, especially during the dry season (Murillo et al. 1986; Marañón et al. 1989).

Plants with an annual life-form benefit from a reduction in soil salinity during the wet season. They set seed before the adverse summer condition, i.e. a dry, strongly saline soil, start to prevail. Communities dominated by annuals are well documented for upper salt marshes in a Mediterranean climate, particularly in the Mediterranean Basin (Molinier & Tallon 1970; Waisel 1972; Rivas-Martínez et al. 1980), but also in California (Callaway et al. 1990).

Maximum species richness values correspond to intermediate standing crop values; the biomass value at maximum diversity, $\text{BMD} = 302 \text{ g/m}^2$. A similar general

trend has been found in many herbaceous plant communities, but with different biomass values at maximum diversity levels: higher BMD values were found in data sets of herbaceous communities in temperate northern Europe (around 510 g/m², Grime 1979), wetlands (400-500 g/m², Vermeer & Berendse 1983), grasslands (ca. 600 g/m², Oomes 1992) and fens (1500 g/m², Wheeler & Giller 1983). Lower BMD values have been reported for lake-shore communities in Canada (80-260 g/m², Wisheu & Keddy 1989a, b). Similar BMD values are shown by chalk grasslands in temperate Europe (150-350 g/m², Willems 1980), Spanish pastures (200 g/m², Puerto et al. 1990) and riverine wetlands in Canada (300 g/m², Day et al. 1988). However, no significant relationship between species richness and standing crop was found in fens of temperate Europe (Vermeer & Verhoeven 1987). The general model, which is appropriate at the between-vegetation type scale, may not be optimal at the within-vegetation type scale where different processes may determine patterns of species richness (Moore & Keddy 1989).

We suggest an analytical approach to the estimation of above-ground biomass at maximum diversity (the BMD value) instead of the commonly applied approximate graphical method to estimate 'optimum' and high diversity corridors (Grime 1979; Vermeer & Berendse 1983; During & Willems 1984, Day et al. 1988). This approach would allow a more rigorous comparison between data sets (Table 2). More studies are needed to build a general model of BMD variation among ecological and biogeographical scenarios.

Simulations based on multi-species resource competition models have predicted hump-backed resource richness-species richness curves that match the general relationships between resource richness (or standing crop) and species richness (or diversity) found in many observational and experimental studies (Tilman 1982, 1983). This suggests that relationships between these community parameters could be explained while considering only species responses to limiting resources, some loss factors (which may be counteracted by higher resource availabilities) and habitat heterogeneity. However, data reported here as well as in other studies (e.g. Pennings & Callaway 1992; Austin 1990) seem to support the hypothesis that species richness and its relationships with standing crop and resource richness also depends on species tolerance to toxic conditions.

Experimental studies have demonstrated that plants tolerant of stress can grow vigorously in favourable habitats (Snow & Vince 1984; Bertness & Ellison 1987), but because of their low ability in terms of resource competition they are competitively displaced by non-tolerant plants (Rozema et al. 1988). Both tolerance and competition are relevant in environmental gradients with

Table 2. Analytically calculated values of biomass at maximum species diversity, BMD, from published significant polynomial equations, number of samples (*n*), polynomial coefficients in descending order of power, and BMD (g/m²).

<i>n</i>	Coefficients			BMD	Reference
224	- 5.8	16.5	- 0.9	101.6	Moore & Keddy 1989
15	- 5.2	15.5	- 1.1	118.4	Moore & Keddy 1989
121	- 4.6	17.5	- 2.9	315.3	Wisheu & Keddy 1989a
28	- 7.9	26.9	- 5.5	197.6	Wisheu & Keddy, 1989a
28	- 21.4	66.8	- 36.3	141.5	Wisheu & Keddy 1989a
29	- 3.1	9.1	0.6	113.4	Wisheu & Keddy 1989a
50	- 7.9	26.4	- 15.5	1.3	García et al. (this paper)
14	- 8.8	29.0	- 16.1	0.0	García et al. (this paper)

complex resource richness / severity conditions. The capacity to resist adverse conditions limits species richness at the 'harsh' end of the gradient, while resource competition mainly determines species composition at the species-richer 'favourable' end of the gradient (Snow & Vince 1984; Bertness & Ellison 1987; Adam 1990; Pennings & Callaway 1992).

Stress, disturbance and dominance are the three processes regulating species richness in Grime's model (Grime 1979). Salinity, sodium toxicity and low soil oxygen act as ecological filters that reduce species richness in the salt marsh. The perspectives for the evolution of a tolerant genotype for these harsh environmental factors seem to be limited (Grubb 1987). Only relatively few plant species are able to tolerate a high salt concentration in the soil solution (Flowers, Troke & Yeo 1977), or low soil redox potentials.

The ambiguous term stress, related to biomass reduction (Grime 1979), is confusing in this case, where harsh environmental factors clearly reduce species richness, but not necessarily biomass production (Grubb 1987). Plants which are able to cope with harsh conditions, benefit from a high availability of water, light and nutrients, compensate for the 'extra cost for tolerance' (Yeo 1983) and may produce a large amount of biomass. Growth of some halophytes can be stimulated with increasing salinity, up to about 200 mol/m³ (Greenway & Munns 1980). Primary production of salt marshes, especially where *Spartina* is dominant, may reach high levels - up to 1700 g/m² of live above-ground biomass - in comparison with non-saline inland grasslands (Long & Woolhouse 1979; Howes, Dacey & Goehring 1986; Groenendijk & Vink-Lievaart 1987).

The higher productivity, associated with light, water and nutrient availability, is paralleled in this case by a narrower ecological and evolutionary filter (salinity, water-logging) which seems primarily to reduce diversity. Mechanistic models based on resource competition, including only resource-counteracted mortality factors (Tilman 1982, 1983, 1988), cannot be used to predict species diversity and abundance along complex environmental gradients if species tolerances to harsh factors are not considered (Austin 1990).

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