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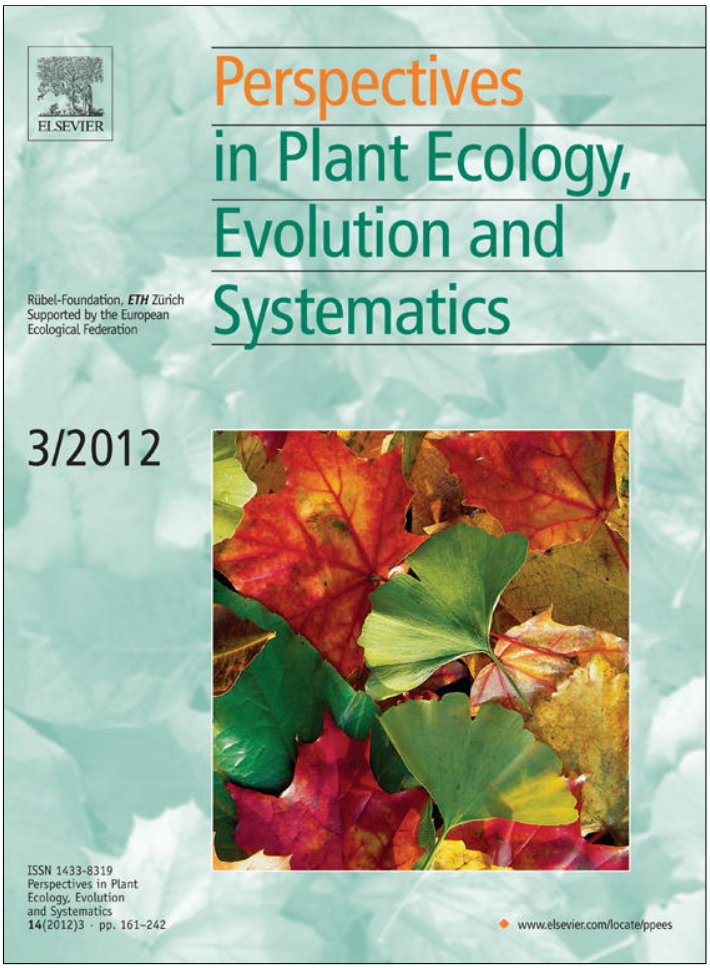

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Perspectives in Plant Ecology, Evolution and Systematics 14 (2012) 183–192

Contents lists available at SciVerse ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

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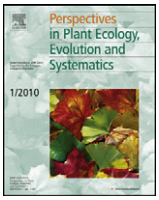

Research article

Plant trait–environment relationships in salt marshes: Deviations from predictions by ecological concepts

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ARTICLE INFO

Article history:
Received 28 June 2011
Received in revised form 25 October 2011
Accepted 4 January 2012

Keywords:
Allocation
Plant functional traits
Plant ecology strategy schemes
RLQ analysis

ABSTRACT

Salt marshes are exposed to high groundwater levels and salinity due to periodical inundation and are under constant influence of physical disturbance. Plants inhabiting salt marshes need to pursue different strategies to colonize this environment and hence, trait expressions should vary along the elevation gradient from pioneer zone to upper salt marsh. We verified various trait–environment concepts for their applicability to different salt marshes zones, and found some are opposite to that of other terrestrial plants.

We used RLQ to analyse the joint structure between environmental conditions (R-table) and species traits (Q-table) by use of a species abundance table (L-table). RLQ analyses the inertia of scores of R- and Q-table linked by species scores of L-table. Then we clustered species according to their position along the RLQ axes to form functional groups.

The 'physiological–ecological–amplitude' concept could not be confirmed from the trait perspective, as the species of the 'stressful' lower marsh show trait values indicating higher competitive ability (canopy height and stem mass fraction) than those of the 'benign' upper parts. Also, specific leaf area (SLA) and leaf dry matter content (LDMC) of salt marsh plants were more constrained by a salt–waterlogging gradient than by a nutrient gradient. This is opposite to the leaf economics spectrum, which describes a trade-off from fast growing species with the potential of quick return of investments of nutrients to species with long leaf lifetime and low rates of photosynthesis. Our results are consistent with the theory of functional equilibrium and Tilman's allocation model, which is a shift in allocation to plant organs responsible for capturing limiting resources resulting in higher fractions of that organ relative to the whole plant body.

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Introduction

Salt marsh plants are subject to constant changes of their habitat conditions. They are strongly controlled by geomorphological, physical and biological processes, such as sedimentation, tidal regime and wind-wave pattern (Bakker et al., 2005). Both biotic and abiotic factors play a major role in determining the distribution of species along the elevation gradient (Bockelmann and Neuhaus, 1999). Duration of tidal flooding, soil aeration (Armstrong et al., 1985), soil salinity and waterlogging (Adam, 1990) are the main determinants of the seaward limit of salt marsh species, whereas the boundary towards the more benign, physically less stressful upper part of the salt marsh, is supposed to be the result of competition (Pielou and Routledge, 1976). Species with high competitive ability monopolize benign habitats, and relegate inferior species to stressful habitats (Bertness, 1991). These interactions in salt marshes are represented in the 'physiological–ecological–amplitude' concept (Scholten et al., 1987), which has been discussed from species position on the elevation gradient or from experiments involving limited species numbers (Pennings and Callaway, 1992; Bockelmann and Neuhaus, 1999). According to Austin (1999), species niches in general are limited by physiological tolerances at the extremes of environmental gradients whereas competition controls the limits towards the centre of the gradient.

However, environmental stress in salt marshes can result from (i) a water related gradient where stressful refers to high inundation frequency, which influences groundwater level and salinity, soil waterlogging, temperature and desiccation stress (Adam, 1990), or (ii) a nutrient gradient where stress refers to low levels of soil nutrients which are more often found on sandy marshes compared to clayey marshes. It is not clear how these two gradients interact in distributing competitors and stress-tolerators on salt marshes.

In our study we ask whether the physiological–ecological–amplitude concept is supported by the functional trait composition of salt marsh plant communities, i.e. whether

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doi:10.1016/j.ppees.2012.01.002

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Table 1
Responses of plants and their related traits along gradients of stress and disturbance following different concepts of plant ecology strategy schemes.

Type of gradient	Response/*related traits*		Concept
Salt stress, waterlogging	Competitive ability/*canopy height*	Physiological adaptations/*exclusion, succulence, helomorphic tissue*	Physiological–ecological–amplitude-concept[a]
Nutrient availability	Fast growth, high turnover of biomass and resources/*SLA*	Slow growth, long leaf lifetime, nutrient retention/*LDMC, SDMC*	Leaf and whole plant economics spectrum[b]
Nutrient, light, CO_2 and/or water availability	Shoot:root ratio balanced	Shoot:root ratio imbalanced/*high/low mass fractions of leaf, stem, root, rhizome*	Theory of functional equilibrium[c]
Low stress/disturbance			High stress/disturbance

[a] Scholten et al. (1987).
[b] Wright et al. (2004) and Freschet et al. (2010).
[c] Brouwer (1962).

species occurring at the lower end of the elevation gradient show better adaptation to stress whereas species at the upper end invest more in traits conferring competitive effect. Furthermore, we ask if the trait–environment relationships of salt marshes are consistent with those found in other terrestrial habitats (Table 1).

We use three sets of plant traits to indicate stress tolerance and competitive ability:

1. *Adaptation to waterlogging and salt stress*. This set of traits accounts for the ability of salt marsh species to cope with waterlogging and salt stress. These are the (i) ability of plants to form aerenchyma, (ii) exclusion of salt ions, (iii) succulent growth and (iv) morphological adaptations to osmotic stress. Plants growing in waterlogged soils potentially face a lack of oxygen and accumulation of phytotoxins (like sulphides), which might adversely affect plant growth (Adam, 1990). Some helomorphic species (sensu Ellenberg, 1979) form a network of intercellular spaces (aerenchyma), which connect the root tissue to the aboveground parts ensuring oxygen supply to the root in times of waterlogged soils (Adam, 1990). Salt marsh plants show various strategies to adapt to high levels of salt in the environment. One strategy all species of this study have in common is the accumulation of salt in their vacuoles and the synthesis of compatible osmotic solutes (see Rozema et al., 1982, 1985; Moghaieb et al., 2004; Geissler et al., 2009). By this the water potential in the metabolically active compartments (cytoplasm/organelles) is balanced, which would otherwise be subject to toxic concentrations of salt. Plants synthesising compatible osmotic solutes are able to keep up the turgor pressure of the cells and maintain their metabolism. The amount and sort of solutes synthesised differs between species and site conditions (i.e. salt concentrations in the soil, Flowers and Yeo, 1988; Flowers and Colmer, 2008). Another strategy limited to a distinct set of salt marsh species (see Table 2) is the exclusion of salt either by structural and functional adaptations that reduce salt uptake through the root or by active excretion of ions via glands and bladders and/or by constant renewal of the

Table 2
Species names of pioneer zone, lower and upper salt marsh following Pott (1995), with abbreviation in brackets, used for RLQ-table L. Species names follow Flora Europaea (*Triglochin maritimum* and *Elymus athericus* follow German Turboveg flora) in SynBioSys Species Checklist (SynBioSys Species Checklist, 2010). Trait samples were taken (x) or not taken (–) for species of the mainland and the island, depending on their occurrences in the plots. Number of measured individuals given in brackets. Different adaptations to waterlogging and salt stress are expressed by 'Yes' and 'No'. MAOS: morphological adaptation to osmotic stress. Source for MAOS, Suc, Exc and Helo: Ellenberg (1979), Kinzel (1982), Schirmer and Breckle (1982), Rozema et al. (1985), van Diggelen et al. (1986).

Species name (abbreviation)	Sampled for		Adaptation to salt and water stress			
	Mainland	Island	Exclusion	Succulence	MAOS	Helomorphic
Pioneer zone						
Salicornia europaea gr. (Sal.eur)	x (8)	x (10)	No	Yes	No	No
Suaeda maritima (Sua.mar)	x (8)	x (10)	No	Yes	No	Yes
Spartina anglica (Spa.ang)	x (8)	x (10)	Yes	No	No	Yes
Number of measured individuals	*24*	*30*				
Lower salt marsh						
Aster tripolium (Ast.tri)	x (8)	x (10)	Yes	Yes	No	Yes
Atriplex portulacoides (Atr.port)	x (8)	x (10)	Yes	No	No	No
Glaux maritima (Gla.mar)	–	x (10)	Yes	Yes	No	Yes
Limonium vulgare (Lim.vul)	x (8)	x (10)	Yes	No	No	No
Plantago maritima (Pla.mar)	x (8)	x (10)	Yes	No	No	Yes
Puccinellia maritima (Puc.mar)	x (8)	x (10)	Yes	No	No	Yes
Spergularia media (Spe.mar)	–	x (10)	No	Yes	No	No
Triglochin maritimum (Tri.mar)	x (8)	x (10)	Yes	Yes	No	Yes
Number of measured individuals	*48*	*80*				
Upper salt marsh						
Artemisia maritima (Atr.mar)	x (8)	–	No	No	Yes	No
Atriplex littoralis (Atr.lit)	x (8)	–	Yes	No	No	No
Atriplex prostrata (Atr.pro)	x (8)	–	Yes	No	No	No
Elymus athericus (Ely.ath)	x (8)	x (10)	No	No	Yes	No
Festuca rubra (Fes.rub)	x (8)	x (10)	No	No	Yes	No
Number of measured individuals	*40*	*20*				

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basal leaves (Schirmer and Breckle, 1982; van Diggelen et al., 1986). Other species produce enlarged mesophyll cells, which results in succulent growth (Kinzel, 1982). The fourth strategy 'morphological adaptation to osmotic stress' refers primarily to species of the upper salt marsh (see Table 2), which adapt to osmotic stress-induced water deficits by rolling in their leaves or sheathe their leaves with hair in order to reduce solar radiation (Rozema et al., 1985).

2. *Leaf economics spectrum*. This set, known as components of the leaf economics spectrum (Wright et al., 2004 and its expansion into the 'whole plant economics spectrum' by Freschet et al., 2010), consists of traits relating the investment of biomass to the area of the photosynthetic active surface (e.g. specific leaf area) and the vertical extension of the structural tissue necessary to support carbon gain (e.g. canopy height and stem mass fraction). These traits describe a gradient from slow growing species, retention of nutrients and biomass and stress tolerance to potentially fast growing species, high acquisition of resources, as well as strong light interception and shading (Wright et al., 2004).
3. *Plant allocation pattern*. This set of traits describes the plant allocation pattern in response to the resources supplied by the environment. Resource allocation patterns have usually been represented in terms of ratios of biomass of plant organs. The theory of functional equilibrium of Brouwer (1962) states that plants shift their allocation towards shoots when the carbon gain of the shoot is abated by low levels of aboveground resources, such as light and CO_2. On the other hand, when levels of belowground resources are impaired, such as nutrient availability and water, plants shift their allocation towards roots. This creates a trade-off between below- and aboveground plant organs involved in capturing different resources and may also determine investment in reproduction (Obeso, 2002). Rather than using root:shoot ratios, we follow the proposal of Poorter and Nagel (2000) to express the biomass of leaves, stems, roots and rhizomes as fractions of the total plant biomass because the combination of stems and leaves into shoots, as well as of roots and rhizomes into belowground biomass neglects the different functions of the plant organs. Additionally, we use reproductive effort (RE) which is diaspore mass as fraction of the total plant biomass.

Salt marshes differ in more than just elevation and inundation frequency. Nutrient regimes differ strongly depending on the amount of clay in the soil (Olff et al., 1997), groundwater tables determine soil aeration (Armstrong et al., 1985), whereas anthropogenic land use and natural sedimentation or erosion provide physical disturbance for the plants (van Eerdt, 1985). Rarely have trait–environment studies on salt marshes taken so many factors into account. In this study, we quantify the response of the functional composition of salt marsh species to inundation frequency, groundwater levels, salinity of the groundwater, soil nutrients and utilization (i.e. biomass removal via cattle grazing or mowing). To disentangle responses to nutrients, salt and stress by waterlogging, we sampled the inundation gradient and groundwater level and salinity on clay-rich salt marshes of the mainland coast and on sandy salt marshes of the island of Mellum in NW-Germany.

Using the three sets of traits from above we focus on the question if they respond to the salt marsh environment and if the combination of these traits is indicative of environmental stress and competition. We expect that (i) in areas with high inundation frequency and high groundwater levels and salinity plants should posses the ability to form aerenchyma (be helomorphic), exclude salt ions and grow succulent, respectively. Opposite to that, in infrequently inundated areas species should show morphological adaptations to osmotic stress by reducing the transpiration rate of the aboveground tissue (Rozema et al., 1985). We further assume that (ii) canopy height and SLA (specific leaf area) will increase with increasing nutrients and utilization as well as decreasing inundation frequency, ground water levels and salinity and accordingly we expect (iii) leaf and stem dry matter content to decrease; expectation (ii) and (iii) both refer to the physiological–ecological–amplitude concept by Scholten et al. (1987) and to the leaf economics spectrum by Wright et al. (2004). Revolving Brouwer's (1962) theory of functional equilibrium, we expect that (iv) high nutrient availability negatively affects root and rhizome biomass and positively affects stem biomass.

Materials and methods

Study area

The study took place in mainland salt marshes along the coast of Lower Saxony and in salt marshes on the island of Mellum, Germany. The study region has a mean annual temperature of about 9 °C and receives a precipitation from 770 mm to 830 mm per year (west to east, Deutscher Wetterdienst, 2009).

Mainland salt marshes often developed through land reclamation for agricultural use and seawall protection (Pott, 1995). Nowadays all salt marshes in the Wadden Sea are under national nature protection (Bakker et al., 2005). Clayey silt, loamy sand and loamy silt are predominant soil substrates in the study area. Along the mainland coast, elevation ranges from 0.2 m to 1.1 m above Mean High Tide (MHT). On the mainland, three different study areas were selected, these were Leybucht (53°32′N, 7°07′E, 8 survey plots), Norderland (53°40′N, 7°19′E, 32 plots) and Jade Bight (53°26′N, 8°09′E, 32 plots). Parts of the areas were subjected to cattle grazing and mowing, whereas the major part was not exploited.

The island of Mellum (53°43′N, 8°08′E, 42 plots) developed from barrier walls and consists predominantly of sandy substrate (Reineck, 1987). Today it is part of the National Park 'Niedersächsisches Wattenmeer' and is preserved from human interference. In the salt marshes of Mellum, elevation ranges from 0.0 m to 1.0 m above MHT. In contrast to the mainland, there are no grazing animals on Mellum, apart from staging geese.

Almost all abiotic factors differed significantly between mainland and island salt marshes: phosphorus, potassium, calcium carbonate ($CaCO_3$), sand content of the soil, salinity of the groundwater, and average groundwater level (one-way ANOVA, p-value 0.05, Fig. 1). Thus, these two types of salt marshes were considered different habitats for this study.

Literature distinguishes between three salt marsh zones, each of which is inhabited by a distinct set of species (Table 2, Pott, 1995): (a) the pioneer zone approximately 40–25 cm below mean high tide (MHT), (b) the lower marsh approximately 25 cm below to 30 cm above MHT and (c) the upper salt marsh positioned 30 cm above MHT and more. This classification served as an assistance to interpret our results, however, data on species were analysed unbiased of this categorization.

Sampling design

On the mainland, 72 plots were established and 42 plots on the island of Mellum (4 m × 4 m each). Plots were chosen by random stratified sampling. The strata were height above sea level (0.0–1.5 m above sea level, covering the elevation gradient) and disturbance (mowing, grazing and no exploitation, respectively). Random numbers were generated and provided distance measures from one corner of a plot to the corner of the next plot.

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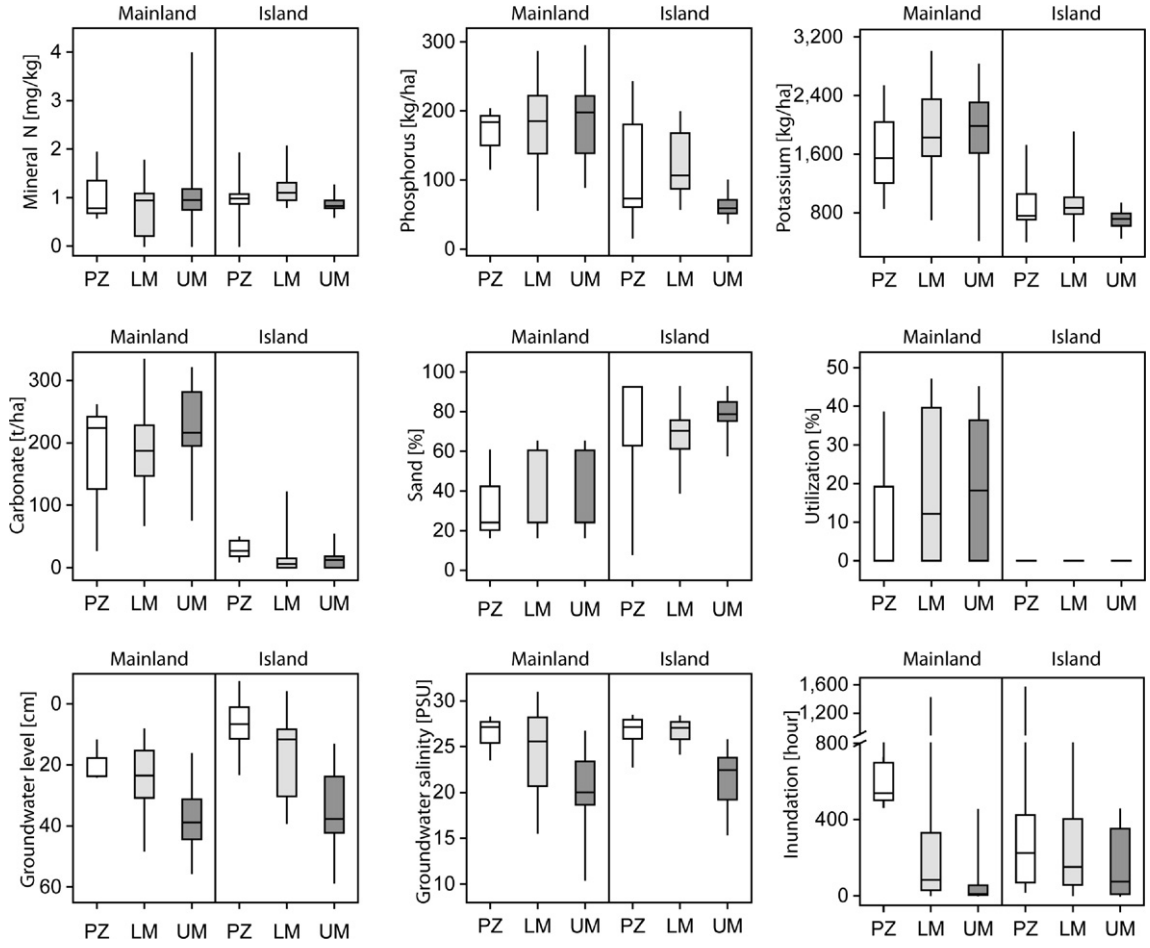

Fig. 1. Abiotic parameters of mainland and island marshes along the elevation gradient from pioneer zone (PZ) to lower and upper marsh (LM and UM). Significant differences between mainland and island marshes are not shown, but see text above.

Field and laboratory measurements

Species composition and abundance was recorded by frequency analysis at each plot in summer 2007. In a subplot facing southwest a 1 m × 1 m frame was laid out, which was subdivided into 100 gridcells of 0.1 m × 0.1 m. In each of the gridcells presence or absence of each species was recorded and summed up, i.e. a species which occurred in each gridcell was attributed the number 100.

To measure soil fertility, soil samples were taken at each plot. Upwelling groundwater allowed sample collection to a depth of 30 cm, which accorded to the zone with highest root densities. Bulk density was evaluated from 200 cm^3 of soil, see Schlichting et al. (1995). Soil samples were air dried, sieved through a 2 mm sieve and analysed for sand content (Table 3, Ad-Hoc-AG Boden, 2005). Calcium carbonate ($CaCO_3$) was determined by adding 10 ml hydrochloric acid (dilution 1:3) to a 10 g soil sample and by measuring the carbon dioxide produced (gasometric technique, according to Scheibler in Schlichting et al., 1995). Plant available potassium and phosphorus were extracted with ammoniumlactate-acetic acid at pH 3 following Egnér et al. (1960) and analysed by AAS (Atomic Adsorption Spectroscopy) and CFA (Continous Flow Analyser, Murphy and Riley, 1962), respectively. Synthetic ion-exchanger ('resin bags') were placed underneath the main roots from May to September 2007 (Skogley and Dobermann, 1996). Plant available ammonium and nitrate were extracted from the ion-exchangers with potassium chloride and analysed at 660 and 540 nm by CFA, respectively. Mineral N (approximately total mineral N) is the sum of ammonium and nitrate, expressed in mg/kg.

At each plot, a drainage pipe (6.5 cm diameter, 114 in total) was installed 80 cm vertically in the ground. In these pipes the groundwater level was recorded biweekly from May to September 2007 at ebb tide, as well as the salinity content of the groundwater via a conductivity measurement device ('pH/Cond 340i' with measuring electrode 'Tetracon 325'). Drainage pipes overtopped marsh surface and were covered with plastic bags during times of no measurement to ensure only vertical inflow of water. Variation due to the tidal variation was adjusted by regression analysis, as described below.

To record inundation frequencies data loggers ('diver', ecoTech, Pegel-Datenlogger PDLA, calibrated for temperature fluctuations and salt water density) recorded the water column in 18 drainage pipes each hour from May to September 2007. In each of the study areas (Leybucht, Norderland, Jade Bight and Mellum) one additional data logger was placed nearby the study plots to record the pressure of the surrounding air, with which the relative pressure of water accumulating in the pipes was calculated. Inundation frequency was calculated from the elevation of all plots relative to the water level measured by the data loggers. Elevation of plots was determined by combining plot locations recorded by GPS with a 1 × 1 resolution elevation map (via LIDAR, Light Detection and Ranging, NLWK, 2004).

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Table 3
Environmental variables recorded on study plot, used for RLQ-table R and correlation with first two RLQ axes; trait information for each species (mean), used for RLQ-table Q and correlation with first two RLQ axes.

Environmental variable	Abbreviation	Unit	RLQ axis 1	RLQ axis 2	RLQ axis 3
Phosphorus	P	kg/ha	−0.65	−0.44	−0.21
Potassium	K	kg/ha	−0.59	−0.59	−0.08
Calcium carbonate	$CaCO_3$	t/ha	−0.90	−0.35	−0.01
Utilization	Util	% biomass loss	−0.70	−0.39	0.53
Sand content	Sand	%	0.65	0.35	0.36
Mean level of groundwater	GW.mean	cm	0.66	−0.45	−0.30
Mean salinity of groundwater	GW.sal	PSU	0.53	−0.56	−0.11
Inundation frequency[a]	Inun	h	0.32	−0.59	0.48
Mineral N	N	mg/kg	0.15	0.15	−0.33

Trait	Abbreviation	Unit, attributes	RLQ axis 1	RLQ axis 2	RLQ axis 3
Canopy height	Cano	cm	−0.77	−0.51	0.09
Stem mass fraction	Stem MF	$g_{(stem)}/g_{(all)}$	−0.77	−0.17	−0.40
Reproductive effort	RE	$g_{(diaspore)}/g_{(all)}$	−0.67	−0.28	0.41
Leaf mass fraction	Leaf MF	$g_{(leaf)}/g_{(all)}$	0.63	0.35	−0.65
Root mass fraction[a]	Root MF	$g_{(root)}/g_{(all)}$	0.67	−0.02	0.55
Rhizome mass fraction	Rhiz MF	$g_{(rhizome)}/g_{(all)}$	0.53	−0.23	0.56
Exclusion of salt ions	Exc	1 – Yes/0 – No	0.16	−0.58	0.12
Succulence	Suc	1 – Yes/0 – No	0.31	−0.67	−0.63
Helomorphic plant	Helo	1 – Yes/0 – No	−0.08	−0.97	0.44
Morphological adaptations to osmotic stress	MAOS	1 – Yes/0 – No	0.33	0.63	0.32
Leaf dry matter content	LDMC	$mg\,g^{-1}$	−0.42	0.72	0.07
Stem dry matter content	SDMC	$mg\,g^{-1}$	0.02	0.84	0.14
Specific leaf area	SLA	$mm^2\,mg^{-1}$	−0.26	−0.60	0.46
Monocarpic plant	Mon	1 – Yes/0 – No	−0.20	−0.62	−0.02
Clonal growth organ	CGO	1 – Yes/0 – No	0.08	0.24	0.39
Diaspore mass[a]	Dia	g	−0.27	−0.07	0.16

[a] lg – transformation prior to analysis.

Some mainland marshes were mown or grazed by cattle. To assess the influence of management on the vegetation, a utilization factor was calculated. In the cattle grazed areas, plots were fenced to prevent grazing. Aboveground biomass was cut on an area of 0.5 m^2 on each plot, inside and outside the fence, respectively. Sampling was conducted in August 2007, which equals peak biomass (De Leeuw et al., 1990). Offset of the values gave the influence of cattle grazing in percent. The utilization factor represents the sum of (i) the herbage consumed by the cattle, and (ii) losses of herbage due to trampling, as a percentage of maximum standing biomass at each plot. For mown areas we used a utilization value of 45%, i.e. percentage of removed biomass by mowing. It was assumed that belowground plant organs were not affected by mowing or cattle grazing. Aboveground cutting left short stubbles of the vegetation which added up to 55% of intact vegetation after mowing.

Plant functional traits

Traits were collected for different species of the mainland and the island (Tables 2 and 3). Trait information was based on measurements of 242 individuals (8 and 10 individuals for every mainland and island species, respectively). For RLQ-analysis the mean trait values for each species were used.

Plants were collected at the peak of their generative stage, i.e. when seeds were ripened but not yet shed. Plants were dug out, roots and rhizomes were cleaned of soil material by rinsing off the soil substrate and roots of different individuals were carefully separated using tweezers. Roots were separated from rhizomes by inspecting the vascular bundles in the cross-sections of the various plant parts. Plant material was subsequently oven dried at 70 °C for 72 h. Leaves, stems, diaspores, roots and rhizomes were weighted after drying. Leaf mass fraction (Leaf MF) was calculated as proportion of leaves relative to the biomass of the whole plant ($g_{(leaf)}/g_{(all)}$), as were stem mass fraction (Stem MF), root mass fraction (Root MF), rhizome mass fraction (Rhiz MF) and reproductive effort (RE). Canopy height is defined as the distance between the highest photosynthetic tissue and the base of the plant (Weiher et al., 1999). LDMC (leaf dry matter content) is the ratio of dry leaf mass to fresh leaf mass ($mg\,g^{-1}$), the same counts for SDMC (stem dry matter content). SLA (specific leaf area) was calculated as the ratio of fresh leaf area to leaf dry mass ($mm^2\,mg^{-1}$). Leaf area was determined by scanning the leaf in a flatbed scanner and area was measured from the computer image. For species like *Salicornia europaea* the top 2 cm of a twig was used as leaf analogue, as recommended by Knevel et al. (2005). Calculation of LDMC, SDMC and SLA followed Knevel et al. (2005).

Exclusion (Exc) of salt ions, succulence (Suc) and morphological adaptations to osmotic stress (MAOS) and were literature derived plant traits, see Table 2. Information about the ability of a plant to form aerenchyma as an adaptation to waterlogging was derived from Ellenberg (1979), who called those plants 'helomorphic'. The resulting classification (Table 2) was confirmed by actual measurements of root porosity by Justin and Armstrong (1987) for most plant species of this study and by the findings of Hajibagheri et al. (1985) for *Suaeda maritima*. The plant traits monocarpic life span (Mon) and clonal growth organs (CGO) were observed in the field. For the latter the formations of CGOs like tuber splitters and/or hypogeogenous stems were checked directly at the plant.

Statistical analysis

Groundwater level

Groundwater level was recorded during low tide and thus lacked information about tidal variation. To adjust this, a regression was conducted with paired values of the hourly data produced by the 18 loggers and the biweekly data of the groundwater levels of all plots. First, a regression was conducted with the mean values of the biweekly groundwater levels and the mean water levels measured by the loggers for the 18 plots for which this information

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was available. Subsequently, the regression function was used to adjust values of mean groundwater level of all other plots to include information about high tide.

RLQ analysis and cluster analysis

Aim of our analysis was to relate species traits to environmental conditions, considering the abundances of species in the plots, for which RLQ-analysis is an adequate method (Dolédec et al., 1996; Dray et al., 2003).

The analysis investigates the joint structure among three tables, i.e. R-table (containing environmental variables), Q-table (species traits), and species abundance table (L-table, Dolédec et al., 1996; Dray et al., 2002). Table L serves as a link between R and Q, and measures the intensity of the relationship between them. Before the actual analysis, three separate analyses were accomplished. A correspondence analysis (CA) is applied on the L-table. The CA gives the optimal correlations between the study sites and the species scores. Ordination of table R and L was done by principal component analysis (PCA). Column weights of table L were used for ordination of table Q, also by PCA. Inundation (environmental variable), Root mass fraction and diaspore mass (traits) were transformed (log 10) prior to the analysis to achieve normal distribution. Subsequently, RLQ performed a co-inertia analysis on the cross-matrix of R, L, and Q. This analysis maximizes the covariance between the study site scores constrained by the environmental variables of table R and the species scores constrained by the traits of table Q. As a result, the best joint combination of the ordination of sites by their environmental characteristics, the ordination of species by their attributes (traits), and the simultaneous ordination of species and sites is calculated (Thuiller et al., 2006). Thus, the RLQ analysis combines the three separate ordinations to maximize the co-variance between the trait and environmental data via the use of co-interia analysis (Bernhardt-Römermann et al., 2008). Also of advantage is the possibility to incorporate both quantitative and qualitative data sets.

Following RLQ, hierarchical clustering of species scores on the first two RLQ axes yielded functional groups (Ward's method). The optimal number of groups was determined using Calinski criteria (Calinski and Harabasz, 1974). These clusters show the distribution of functional groups in the trait–environment space. Analyses were done using ade4 package of R (The R Foundation for Statistical Computing, 2010). Significance of RLQ was tested using the procedure randtest.rlq.

Results

Abiotic conditions on mainland and island marshes

All environmental parameters (except mineral N) resulted in significant differences between mainland and island marshes (one-way ANOVA, $p < 0.05$). Soils of mainland marshes were richer in phosphorus, potassium and carbonate, whereas those of island marshes contained more sand (Fig. 1). Groundwater level and groundwater salinity, as well as inundation frequency were higher in the island marshes. The utilization factor on Mellum was zero, as agricultural land use is prohibited in the island.

Along the elevation gradient (from pioneer zone to upper marsh), phosphorus, potassium and carbonate increased slightly in mainland marshes, whereas it remained similar in the island marshes. The water-related parameters, groundwater level, salinity of groundwater and inundation frequency decreased towards the upper marsh.

RLQ analysis

98.4% of the total variation (total inertia) were explained by the first three axes (76.5%, 20.2%, 1.7%, respectively). The randtest proofed that the RLQ-analysis was significant at $p < 0.001$.

Although the first RLQ axis showed high correlations to almost all environmental variables (Table 3), Fig. 2a and e reveals an orthogonal arrangement of the major sets of environmental variables which are rotated diagonally to the RLQ axes.

The first set of variables, i.e. potassium, phosphorus, $CaCO_3$, sand content and utilization, spanned a 'nutrient' gradient from nutrient rich sites on the mainland to nutrient poor sites found on the island (Fig. 3c). A second 'salt–waterlogging' gradient, uncorrelated to the first gradient, was determined by groundwater level and groundwater salinity and inundation frequency. It separated highly inundated sites with high levels of salty groundwater from infrequently inundated sites with low groundwater levels. Highly inundated sites were found in the lower parts of the mainland and the island marshes, whereas the upper marsh areas of both mainland and island were only infrequently inundated. Although the third axis only explained a small part of the total variation, it separated inundation frequency from groundwater level and groundwater salinity, and showed the strongest correlation to nitrogen availability, which otherwise correlated poorly with the first and the second axes. This 'nitrogen–inundation' gradient separated sites with high inundation frequency and high sand content of the soil (island) and which were utilised (mainland) from sites, which were richer in nitrogen (both island and mainland, Table 2, Fig. 3e and g).

Trait expressions of salt marsh plants differed along the gradients (Table 3, Fig. 3b and f). Along the 'nutrient' gradient (from sites rich in phosphorus, potassium and carbonate to nutrient poor, sandy sites) canopy height, Stem MF and RE increased and Leaf MF, Root MF and Rhiz MF decreased.

On the other hand, traits associated with salt adaption and leaf economics followed the salt–waterlogging gradient. Exc and Suc, as well as the ability to form aerenchyma (Helo) and SLA (specific leaf area) increased with salt–waterlogging (negative correlation with RLQ axis 2) whereas MAOS, leaf and stem dry matter content (LDMC and SDMC) decreased (positive correlation with RLQ axis 2).

Along the 'nitrogen–inundation' gradient plants growing in the sandy sites with high inundation allocated proportionally more biomass to roots and rhizomes (high Root MF and Rhiz MF). At the opposite end of the gradient, in the nitrogen richer sites, plants showed higher allocation to aboveground biomass (i.e. high Stem MF and Leaf MF). The most interesting result regarding this gradient is the positive correlation of specific leaf area (SLA) with RLQ axis 3, which should be positively correlated with nitrogen following the leaf economics spectrum.

Monocarpic life span (Mon), clonal growth organs (CGO) and diaspore mass (Dia) only showed weak relationships to the environmental variables, probably because they are distributed more or less equally along the gradients, so that an assignment to a specific end of a gradient is not possible; these traits are omitted from further discussion.

Cluster analysis

The cluster analysis yielded six stable functional groups showing how multiple trait expressions combine in species groups (Fig. 3d and h, clusters A to F). All clusters were clearly separated in the trait–environment space. Clusters A and B were orientated along the increasing 'nutrient' gradient, whereas clusters C, D and E were arranged along the increasing 'salt–waterlogging' gradient. On the other hand, cluster B could also be viewed on the nutrient

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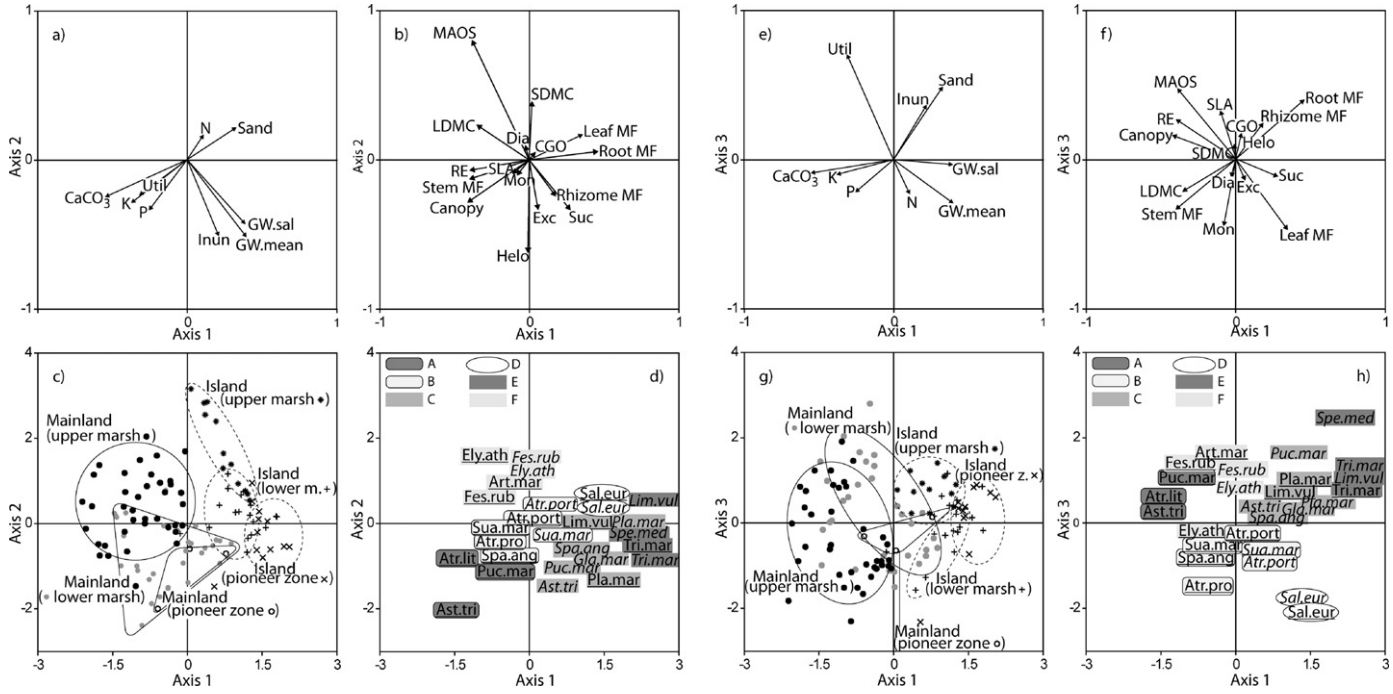

Fig. 2. Ordination diagrams of the first three axes of the RLQ-analysis displaying the environmental variables (a and e, first and second, and first and third axis, respectively), plant traits (b and f), distribution of plots along the elevation gradient (c and g) and distribution of species (results of cluster analysis, with *mainland* and *island* species, d and h, with clusters A to F). Abbreviations explained in Tables 2 and 3.

gradient, because it is positioned close to the centre of both gradients. Along the 'nitrogen–inundation' gradient, clusters C and E were positioned on the end showing high inundation whereas cluster B was found at the 'nitrogen-side' of the gradient.

Clusters A and B comprised only species from the mainland (despite *Atriplex portulacoides* from the island in cluster B), whereas their island counterparts were placed in clusters C, indicating that these species respond in a plastic way to the environmental constraints. Opposite to that, trait-plasticity of *S. europaea*, *Festuca rubra*, *Elymus athericus* and *Triglochin maritima* was low, because the respective species from mainland and island were grouped together in cluster D, E and F.

Cluster A included three mainland species, two of the lower and one of the upper salt marsh. Cluster B combined mainland (and one island) species of the pioneer zone and the lower marsh. Species of both clusters primarily exclude salt ions or grow succulent, produce helomorphic tissue, and showed high Stem MF, low Root MF and low Rhiz MF and intermediate LDMC and SDMC (Fig. 3). Moreover, species of cluster A showed the highest canopy height, the highest RE and the lowest Leaf MF, whereas species of cluster B produced the heaviest diaspores.

Species in cluster C were found in the lower parts of the marsh and were primarily characterised by high biomass allocation to rhizomes (Rhiz MF) and small stature. Cluster D comprised only *S. europaea*, both from mainland and island sites, which dilute salt ions (grow succulent) and showed high allocation to leaves and low SLA.

As with cluster C, species of cluster E also showed high Rhiz MF, but also high Root MF, low canopy height and Stem MF. These species also produced clonal growth organs, as did species of cluster F, which only contained upper marsh species. Cluster F was furthermore characterised by high RE, high SDMC and low Rhiz MF.

Altogether, the clusters varied most significantly in carbon allocation traits and canopy height. Clusters A and B comprised the largest plants with highest investments in stems and reproduction and occurred at nutrient rich sites. Species of clusters C and E were small with strong allocation to roots, rhizomes and leaves and were found on nutrient poor sites (compare with Fig. 3d), with cluster E on sites with higher salt–waterlogging stress. Species of cluster F took an intermediate position in allocation patterns but showed higher LDMC and SDMC than all other clusters. They occurred on sites with low salt–waterlogging stress and intermediate to high nutrient levels.

Discussion

Trait responses to the interaction of a resource gradient with a direct environmental factor that cannot be consumed (such as salt) have rarely been investigated so far. In our study, this interaction produced trait–environment linkages that only partly confirmed our hypotheses. In particular, traits of salt marsh plants associated with the leaf economics spectrum showed different responses than those of other terrestrial habitats, whereas vegetative biomass allocation ratios followed predictions by Brouwer (1962) or Tilman (1988).

Submergence due to inundation, waterlogging and salinity are considered major factors influencing the distribution of salt marsh species (Adam, 1990). Plants growing in waterlogged soils have to cope with lack of oxygen and accumulation of toxins (Adam, 1990). Stress induced by salt and waterlogging is usually highest in the lower parts of the salt marsh (Bockelmann and Neuhaus, 1999), whereas the upper parts experience decreased salt levels and longer periods of oxidation due to irregular inundation frequency and dilution by rain water (Armstrong et al., 1985). However, in periods of high insolation and temperature, the soil solution in the upper marsh may become hypersaline due to increased evapotranspiration (De Leeuw et al., 1990). The main environmental gradients (nutrient, salt–waterlogging and nitrogen–inundation) were arranged almost orthogonally to each other, indicating that

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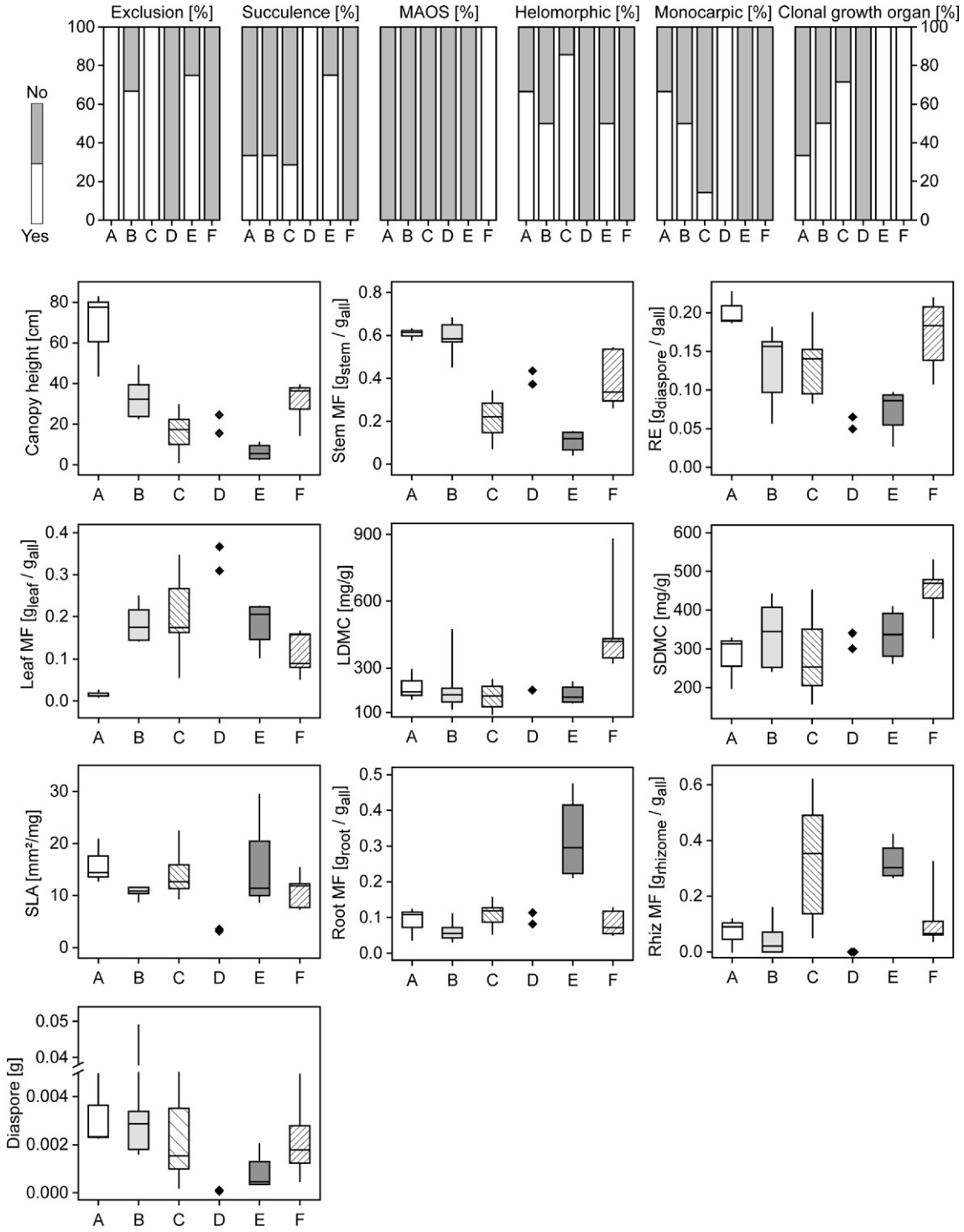

Fig. 3. Trait attributes of each cluster (A to F). The vertical bar graphs show the nominal variables with scaling 'Yes' or 'No' in percent for each cluster (MAOS: morphological adaptations to osmotic stress). Boxplots show quantitative variables with their ranges in each cluster.

they were uncorrelated. The main driver of the nutrient gradient was the sand content of the soil which was higher on the island than on the mainland. Mainland soils of the Frisian coast usually contain more silt, therefore have a higher sorption capacity and are thus richer in nutrients. They are shielded from the open sea water by barrier islands and mostly originate from land reclamation measures (Pott, 1995). Even the high marshes of the mainland were richer in phosphorus, potassium and carbonate than the lower marshes of the island. Although many of the mainland marshes were utilised without any fertilization, the nutrient levels of these sites were higher than the unused sites of corresponding elevation on the island.

In accordance with our first prediction, the three physiological traits conferring tolerance to salinity were most strongly correlated to the salt–waterlogging and the nitrogen–inundation gradient. The more 'active' traits, succulence and exclusion of salt, increased with increasing groundwater level and salinity and inundation frequency whereas the more 'passive' trait, morphological

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adaptations to osmotic stress, was prevalent at lower values of groundwater level and salinity. These opposite directions suggest that succulence and exclusion confer higher tolerance to salt than morphological responses.

Many authors have interpreted species distributions in salt marshes according to the physiological–ecological–amplitude concept by Scholten et al. (1987, see for example Bertness, 1991). According to their findings, abiotic factors control the boundary of a population towards the more extreme end of a gradient, whereas the boundary towards the more benign end is a result of competition. We expected the benign end of a salt marsh to be low in environmental stress and disturbance (low influence of salinity and inundation, high nutrient availability in the mainland sites), whereas the 'stressful' part of a salt marsh should be the seaward side with high influence of the tidal regime, and in the framework of this study, the island sites with low nutrient availability. High competitive effect is often attributed with high canopy height, high stem mass fraction, high SLA and low LDMC (see Cornelissen et al., 2003); thus we expected these traits to be strongly exhibited by the plants colonizing the upper marsh areas of the mainland sites. Whilst it was evident that the physiological tolerance to salt and waterlogging decreased landward, it was not evident that competitive ability increased landward. All traits commonly associated with strong competitive effect through shading either responded strongest to the nutrient gradient (biomass allocation to stems, canopy height) or showed an opposite pattern to that expected on the salt–waterlogging gradient (SLA, LDMC and SDMC). Consequently, the question arises whether the undoubtedly strong competitive effect of e.g. the upper marsh plant *E. athericus* (Kuijper et al., 2005) is produced by the living plant. Based on a strong relationship between LDMC, C:N-ratio and litter decomposition in salt marshes of northwest Germany (Minden and Kleyer, unpublished) we suggest that high LDMC, SDMC and C:N-ratio may lead to decreasing decomposition of dead biomass and thus to thick litter layers in *E. athericus* stands, which hamper the establishment of other species. We did not survey the influence of detritivores on litter decomposition, but we expect them to play a major role in litter accumulation and decomposition, respectively (see Buth and de Wolf, 1985). Many studies reported an adverse effect of litter on biodiversity in various communities (Xiong and Nilsson, 1999).

For terrestrial plants, the leaf economics spectrum describes a trade-off from long lifetime of leaves, and low rates of photosynthesis and respiration to leaf traits with the potential of quick return of investments of nutrients, which proofed strongly correlated with SLA (Wright et al., 2004). The leaf economics spectrum was recently extended to a whole plant economics spectrum, including stem and leaf dry matter content (SDMC and LDMC), and related to a soil nutrient gradient (Freschet et al., 2010). Contrary to these findings and our expectations, results for SLA, LDMC and SDMC support the idea that leaf trait expressions of salt marsh species show an inverse relationship to those featured by other terrestrial plants. These traits only showed weak correlations to the nutrient gradient, but were strongly correlated to the salt–waterlogging and inundation gradient. This means that leaf traits like LDMC and SLA of salt marsh species are more constrained by salt, waterlogging and inundation than by nutrients and utilization (see opposite position of SLA to nitrogen along RLQ axis 3, Fig. 3e and f). For instance, the species of the upper marsh experience physiological water deficits due to osmotic stress (*E. athericus* and *F. rubra*, Rozema et al., 1985) to which they respond by lignification of cell walls and increase in LDMC similar to plants experiencing frequent soil desiccation (Vendramini et al., 2002). In addition, high SDMC gives structural strength and supports upright position when turgor pressure is low. On the other hand, succulent growth leads to decreased LDMC- and increased SLA-values by extending surface without increasing dry weight. The increased water content in leaves of some succulent lower marsh species contributed to higher SLA values, which was also found by Vendramini et al. (2002). However, we still expected a stronger relationship towards the nutrient gradient, which for example better explained SLA than climate data (e.g. mean annual precipitation) in a study by Ordoñez et al. (2009).

Considering partitioning of biomass on the nutrient gradient, our expectations were confirmed. As in other terrestrial and freshwater habitats, species growing at the nutrient rich salt marsh sites showed high values of stem mass fractions and canopy height (Westoby et al., 2002). These species shift their allocation to the stem to maintain dominance by occupying space and with that, compete for light (Kuijper et al., 2005). In contrast, when nutrient availability is low, the species showed high root and rhizome mass fractions. Seasonal nutrient storage is essential for the success of species in more nutrient poor sites (Chapin, 1980), because it enables growth when temperatures and radiation are most favourable and prevents species from day-to-day dependence upon available nutrients. Likewise, species showed high leaf mass fraction which can be attributed to a concurrent reduction in allocation to stems. Additionally, some of the species were rosette plants (e.g. *Plantago maritima*, *Triglochin maritimum*). Leaves of rosette plants grow near to ground-level and run a high risk of being shaded by taller plants. This feature may lead to impaired competitive ability, which restricts these species to nutrient poor sites (see also van der Wal et al., 2000).

These results are consistent with Brouwer's (1962) theory and Tilman's allocation model (1988) of a shift in allocation to plant organs that are responsible for capturing the resource that is limiting at a certain time, resulting in higher fractions of that organ relative to the whole plant body. Additionally, they support the meta-analysis of Poorter and Nagel (2000) showing that variations in biomass partitioning respond mainly to the nutrient gradient but less so to other environmental gradients, in our case to the salt–waterlogging gradient.

Conclusions

This study verified three common trait-environmental concepts for their applicability on salt marshes. The physiological–ecological–amplitude concept by Scholten et al. (1987) could only be supported for the nutrient gradient but not for the salt–waterlogging gradient. Species growing in the 'stressful' zones of the lower marsh showed a higher competitive ability (canopy height, stem mass fraction) than the species of the upper marsh, although the latter were growing in the 'benign' landward parts of the salt marsh. Leaf traits such as SLA and LDMC were more constrained by the influence of salt and waterlogging than by nutrient availability, which is opposite to the concept of the leaf economics spectrum (Wright et al., 2004) for other terrestrial plants. As in semi-arid environments (Vendramini et al., 2002), succulence led to an opposed response of leaf traits to environmental stress. Our results support Brouwer's (1962) theory of functional equilibrium and Tilman's (1988) allocation model insofar as biomass fractions of belowground organs were high in nutrient poor sites, whereas species of nutrient rich sites showed high allocation to stem biomass to compete for light.

Acknowledgements

We thank the administration of the National park 'Niedersächsisches Wattenmeer' and 'Mellumrat e.V.' for their support during field work. Many thanks to G. Scheiffarth and M. Heckroth for

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supporting our work at Mellum and to J.P. Bakker for helpful comments on previous versions of the manuscript. We also thank Michal Hajek and another anonymous reviewer whose comments helped to improve the text. This study was conducted as part of the TREIBSEL project and was supported by the 'II. Oldenburgischer Deichband' and the 'Wasserverbandstag e.V.' (NWS 10/05).

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