Stress tolerance and biotic interactions determine plant zonation patterns in estuarine marshes during seedling emergence and early establishment

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Summary

1. Transplant experiments with adult plants showed that marsh plant zonation along estuarine salinity gradients develops according to species tolerances of abiotic factors and biotic interactions. Thus, glycophytes are restricted from salt marshes by abiotic stress, whereas halophytes are excluded from freshwater marshes by competition. We hypothesized that adult plant zonations along estuarine stress gradients are predefined by processes affecting plants during their seedling phase. In an experimental glasshouse study, we tested how a mixed community of glycophytes and halophytes developed during the first months of early establishment affected by different flooding and salinity regimes.

2. We set up two factorial mesocosm experiments that tested the effects of three tidal regimes (daily tide, spring tide, no tide) and three salinity levels (fresh, brackish, salt) on the emergence and early establishment of glycophyte and halophyte seedlings. In the Emergence Experiment seedlings were identified and removed once per week. In the Establishment Experiment species cover was estimated every 2 weeks, and after 15 weeks final above-ground biomass of each species was determined.

3. Both glycophytes and halophytes showed highest seedling emergence under freshwater conditions. Emergence of halophytes was less impaired by increased salinities than that of glycophytes. Emergence and establishment of glycophytes were extremely reduced under brackish and salt conditions, whereas under freshwater conditions, glycophytes showed a consistent increase in cover over time. Cover of halophytes showed a similar increase in brackish and salt treatments; however, in freshwater treatments it significantly decreased after week 9. While daily tides predominantly decreased seedling emergence and establishment, spring tides had no significant effects on seedlings in freshwater and negative effects in saltwater treatments.

4. *Synthesis.* The ability of a species to germinate and emerge under conditions representing a particular position along an environmental gradient is necessary but not solely responsible for determining plant zonation patterns along estuarine marsh gradients. Our results show that competitive exclusion of halophytes by glycophytes as an important driver of marsh plant zonations along estuarine salinity gradients takes effect already during the early seedling establishment phase of the co-occurring plants.

Key-words: brackish marsh, competition, flooding gradient, mesocosm experiment, plant population and community dynamics, salinity gradient, salt marsh, seedling recruitment, tidal freshwater marsh, wetlands

Introduction

Explaining patterns of species distributions along environmental gradients has been a dominant subject in ecological research for decades. Effects of abiotic habitat conditions (e.g. Adams 1963; Vince & Snow 1984), interspecific competition (e.g. Snow & Vince 1984; Wilson & Keddy 1985), facilitation (e.g. Bertness & Hacker 1994), as well as the impact of herbivores (e.g. Crain 2008) have been discussed as important drivers of the spatial variation in wetland plant distribution. However, abiotic and biotic impacts on early life stages of plants including

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factors such as dispersal (Rand 2000; Chang, Veeneklaas & Bakker 2007), germination and seedling survival and establishment (Coops & van der Velde 1995; Lenssen, ten Dolle & Blom 1998) have generally received less attention regarding their role in generating plant distribution patterns.

Marshes in estuaries exhibit distinct plant zonation patterns along horizontal and vertical stress gradients. These gradients are characterized by (i) decreasing salinity from coast to inland, leading to the formation of salt, brackish and tidal freshwater marshes, and (ii) decreasing tidal flooding frequency and duration at each marsh site, subdividing the marsh into a low, a mid and a high marsh zone along the elevation gradient (e.g. Odum 1988; Engels & Jensen 2009). These plant zonations have been found to be the outcome of the interplay between biotic interactions and the stress tolerance of species under harsh environmental conditions. Similar to the drivers of vertical zonations in salt marshes (e.g. Snow & Vince 1984; Bertness & Ellison 1987; Huckle, Marrs & Potter 2002; Pennings, Grant & Bertness 2005) and freshwater wetlands (Grace & Wetzel 1981; Wilson & Keddy 1985), transplant studies along estuarine gradients showed that salt marsh species are precluded from tidal freshwater marshes by competition, whereas freshwater species are excluded from salt marshes by physical stress (Crain *et al.* 2004; Engels & Jensen 2010).

All of these studies are based on the responses of adult plants, although mechanisms leading to spatial patterns of tidal marsh plants are likely to take effect already during the seedling phase. For instance, there is evidence that seedling dynamics are crucial for species ranges along vertical gradients in non-tidal wetlands (Coops & van der Velde 1995; Lenssen, ten Dolle & Blom 1998) and salt marshes (Bakker *et al.* 2007). In estuarine marshes, the majority of marsh species are perennials that predominantly rely on clonal reproduction (Shumway & Bertness 1992; Huiskes *et al.* 1995; Capers 2003). However, seedling recruitment was shown to be particularly important during secondary succession after large-scale disturbances, when bare patches serve as competitor-free refuges for seedlings and other fugitive plants (Bertness, Gough & Shumway 1992; Baldwin & Mendelssohn 1998). Physical conditions in bare patches can strongly differ between tidal freshwater and salt marshes: while bare patches in tidal freshwater marshes have benign conditions and are typically heavily colonized by seedlings (Parker & Leck 1985), bare patches in salt marshes often become hypersaline thereby strongly limiting seedling recruitment (Bertness, Gough & Shumway 1992; Crain, Albertson & Bertness 2008). Since disturbance (e.g. by tidal currents, wrack deposition or ice abrasion) is a common feature of estuarine marshes it is likely that seedling recruitment also plays an important role in generating plant zonation patterns along larger-scale gradients in estuaries. This is the first experimental study which examines the early establishment of marsh species in the light of marsh zonation development along estuarine salinity gradients.

Generally, seed survival, germination and early seedling establishment are considered to be the most critical life stages of a plant (Schupp 1995; Fenner & Thompson 2006). Besides a sufficient seed supply, successful establishment of a species

in an estuarine marsh habitat is constrained by its germination requirements, the seedling's tolerance towards environmental conditions, and its ability to compete with the established vegetation (Hopfensperger & Engelhardt 2008). The availability of propagules is mainly dependent on the local seed rain (Chang, Veeneklaas & Bakker 2007) and on hydrochorous dispersal of propagules (Noe & Zedler 2001; Neff & Baldwin 2005). In estuaries, where (unlike in riparian systems) water flow is bi-directional, tidal currents provide an efficient dispersal mechanism for plant propagules within and between marshes (Neff & Baldwin 2005; Chang, Veeneklaas & Bakker 2007) with the opportunity for long-distance dispersal by storm surges (Koutstaal, Markusse & Munck 1987; Huiskes *et al.* 1995; Chang, Veeneklaas & Bakker 2007). However, seed-barrier experiments in estuarine marshes suggest that seed dispersal predominantly takes place locally (Crain, Albertson & Bertness 2008).

Germination is generally triggered by abiotic factors. In estuarine marshes, seedling emergence may be impeded or hampered by high salinity (Ungar 1987; Baldwin, McKee & Mendelssohn 1996; Noe & Zedler 2001) or flooding (Coops & van der Velde 1995). Salinity and flooding are considered as stress factors, since increased soil salinity lowers soil water potential by the osmotic effect of ions, thereby making water absorption by germinating seeds and seedlings more difficult (Facelli 2008). Flooding can lead to substrate instability and reduces oxygen concentration in the soil (Titus & Hoover 1991). Following germination, successful seedling recruitment involves seedling survival and establishment in the given abiotic and biotic environment. Tolerance towards physical factors such as salinity and flooding are known to vary among adult marsh species (Snow & Vince 1984; Bakker, Dijkstra & Russchen 1985). However, seedling tolerances towards these factors may differ from the response of adult plants of the same species (Ungar 1978; Beare & Zedler 1987; Bakker *et al.* 2007). Seedlings may be more susceptible to abiotic stress (e.g. flooding) because of their small size (Facelli 2008). Since leaves of small seedlings do not emerge above the water, O_2 and CO_2 exchange may be impeded, leading to a reduction of photosynthesis and respiration (Ernst 1990; Bakker *et al.* 2007). During the phase of early establishment, seedling abundance and composition may be further modified by competition (Bakker, Dijkstra & Russchen 1985; Scholten *et al.* 1987; Noe & Zedler 2001; Hopfensperger & Engelhardt 2008). Differences in germination success as well as seedling tolerances and biotic interactions during the emergence and establishment stage may therefore be crucial for generating plant zonation patterns along estuarine gradients (cf. Coops & van der Velde 1995; Kellogg, Bridgham & Leicht 2003; Bakker *et al.* 2007; Facelli 2008).

In our study, we tested how salinity and tidal flooding as important physical factors in tidal marshes affect not only initial patterns of seedling emergence but also subsequent seedling survival and performance during the early establishment phase of tidal marsh species (Emergence and Establishment Experiment, respectively). We developed a novel tidal simulation system that allowed us to apply different inundation

frequencies and durations in combination with different salinity levels to a set of mesocosms. We set up two experiments with three salinity levels (fresh, brackish, salt) and three tidal regimes (without tidal flooding, tidal flooding twice per month, tidal flooding twice per day). In order to differentiate between responses of glycophyte and halophyte species, driftline material was added to the mesocosms containing seeds of both tidal freshwater and salt marsh species. Drift litter has been shown to contain high amounts of plant propagules and catch the majority of species dispersing via water in a wetland (Neff & Baldwin 2005; Vogt, Rasran & Jensen 2007).

We hypothesized (i) seedling emergence of both glycophytes and halophytes to be highest under freshwater conditions. However, we expected emergence of glycophytes to be strongly impeded in brackish or salt treatments, whereas emergence of halophytes should be less affected by increased salinities. We further hypothesized (ii) that during the early establishment phase, glycophytes should reach higher biomass and cover in freshwater treatments (fw) than halophytes over time, whereas halophytes should reach higher biomass and cover in brackish and salt treatments. Concerning the effect of tidal flooding, we hypothesized (iii) that seedling emergence and establishment of both glycophytes and halophytes are reduced with increasing tidal inundation frequency.

Materials and methods

TIDAL AND SALINITY TREATMENTS

The two experiments had a full-factorial design and were conducted in mesocosms that were set up in a glasshouse. We established three tidal regimes and three salinity levels, which were adjusted to the conditions in the different marsh vegetation zones along the vertical and horizontal gradients in the Elbe estuary (Caspers 1959; Engels & Jensen 2009). Each treatment combination (tidal regime × salinity level) was applied to five mesocosms, which were divided into two experimental chambers: one for the Emergence Experiment and one for the Establishment Experiment. Thus we had five replicates (experimental chambers) per treatment combination in each experiment, resulting in 45 mesocosms in total.

The tidal treatments were: (i) flooded by daily tides (daily tide, flooded twice in 24 h; corresponds to estuarine low marshes); (ii) flooded by spring tides (spring tide, flooded every 2 weeks; corresponds to estuarine mid marshes); and (iii) no tidal inundation (no tide; corresponds to estuarine high marshes). Flooding duration was 4 h from the beginning of the flood tide to the end of the ebb tide.

The three salinity treatments were (i) a fresh to oligohaline treatment (0.4–0.5 practical salinity units (psu); in the Elbe estuary occupied by typical freshwater marsh vegetation; in the following referred to as fw); (ii) an oligo- to mesohaline treatment (5–7.5 psu; in the Elbe estuary occupied by the typical brackish marsh vegetation; in the following referred to as brackish water treatment, bw); and (iii) a meso- to polyhaline treatment (13.7–19.3 psu; in the Elbe estuary occupied by the typical salt marsh vegetation; in the following referred to as salt water treatment, sw). The bw and sw treatments were produced by mixing spring water (used for the fw) with commercial additive-free sea salt. The no-tide treatments were saturated with water of the respective salinity before the start of the experiment and thereafter only watered with spring water from above.

EXPERIMENTAL MESOCOSMS

We used transparent plastic boxes (external dimension: 28 × 50 × 25 cm; W × L × H) as experimental mesocosms. These were divided into two experimental chambers (internal dimension: 26 × 21 × 25 cm) by a wall made of professional filter foam used in aquarium technology (width 5 cm, fine pores). This foam wall was water permeable, but impermeable to substrate and seeds. The two chambers were filled with 5 L of sand collected at a freshwater site of the Elbe estuary, resulting in a substrate height of 8–9 cm. One of the chambers was used for the Emergence Experiment and the other one for the Establishment Experiment.

TIDAL PUMPING SYSTEM

In order to simulate tidal inundation, we used a tidal pumping system consisting of two water storage tanks equipped with timer-controlled electronic pumps and connected to a set of five experimental mesocosms by 'communicating tubes' (Fig. 1). When the tide should rise, water was pumped from the main storage tank (2 × 90 L, 'main tank') via a 10 mm flexible tube into the 'intermediate tank' (50 L) by a centrifugal pump (Eheim Universalpumpe 1046; 5 Watt, Deizisau, Germany). The end of the tube was fixed to the wall of the tank with a clip, preventing it from touching the water surface. The intermediate tank was connected to the experimental mesocosms by several flexible 12 mm tubes, forming a communicating tube system. This system allows the generation of directional water flows between several tanks without the need of an additional energy source. As the water table rose in the intermediate tank, this also led to an influx of water into the experimental mesocosms via communicating tubes until water levels were balanced. When the tide should fall, another pump, which was installed in the intermediate tank, pumped the water back into the main tank, leading to a falling water level in the intermediate tank and therefore also in the experimental mesocosms. A precondition for the working of the communicating tube system was a permanent interconnected water body between the mesocosms and the intermediate tank, which was achieved by keeping a permanent water level of 3 cm in the intermediate tank and the mesocosms. The end of
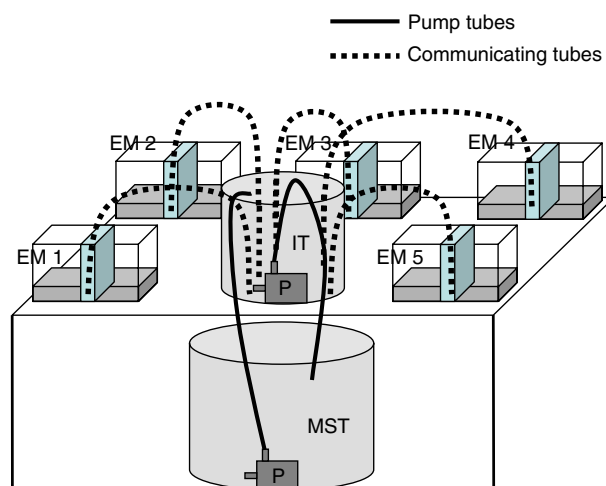

Fig. 1. Set-up of tidal simulation system with five experimental mesocosms (EM 1-5), main storage tank (MST) and intermediate tank (IT). Tides are produced by water transfer between the IT and MST via electronic pumps (P). EMs are connected to the IT by communicating tubes.

the tubes were fixed in the foam wall of the mesocosms. In order to prevent algae from growing in the tubes, the tubes were wrapped with aluminium foil and the intermediate tanks were covered with a piece of cloth. The no-tide treatments were not connected by communicating tubes.

Water levels in the main tanks were checked every few days and replenished with spring water when necessary allowing water salinities to slightly fluctuate. Because mean water salinities were rather stable during the course of the experiment, we only had to add salt once during the second half of the experiment in the brackish and salt treatments. All mesocosms were regularly watered from above with spring water imitating natural precipitation. The quantity of water supplied was determined by the water loss in the no-tide treatments, where we aimed at maintaining a water table of 3–4 cm relative to the bottom of the mesocosms. Because the substrate was nutrient-poor and seedlings showed signs of nutrient deficiency, we regularly added liquid NPK-fertilizer (Wuxal Top N: 12% N, 4% P_2O_5, 6% K_2O, 0.01% B, 0.004% Cu, 0.02% Fe, 0.012% Mn, 0.001% Mo, 0.004% Zn) to all treatments from week 5 onwards (3 mL per week and experimental chamber).

Due to logistical reasons, the five replicates for the daily-tide and spring-tide treatments were connected to one single pump system and placed adjacent to each other in the glasshouse. In order to prevent biases by possible gradients along the glasshouse (e.g. light, temperature), the mesocosms of the no-tide treatments were distributed all along the glasshouse.

DRIFTLINE MATERIAL

We used driftline material as a seed source for estuarine marsh species, which was collected along three fresh, brackish and salt marshes along the Elbe estuary after a storm surge in November 2007. The driftline material was kept at 4 °C until April 2008. Seed viability was tested and seed density was determined in a pilot study in December 2007–March 2008. After 2 weeks of cold stratification, driftline material was spread into plant pots using 0.125 L driftline material per 9 cm pot (38 pots per marsh type). The pots were filled with commercial garden soil and watered with spring water. Seed density present in the driftline sample of each marsh type was determined by calculating the mean number of germinated seedlings per pot. The average seed density was about 10 times higher in the salt marsh driftline sample (1488 seedlings L^{-1}) than in the freshwater (112 seedlings L^{-1}) and brackish driftline samples (144 seedlings L^{-1}), which was probably due to the greater width of salt marshes relative to tidal fresh and brackish marshes and to large numbers of seeds of *Atriplex prostrata* in the samples.

For the two experiments, we used a pooled driftline sample of fresh, brackish and salt marshes to have a sample containing seeds of species presenting the whole estuarine salinity gradient. To gain similar seed densities of fresh, brackish and salt driftline samples, we used a 10:10:1 mixture of fresh:brackish:salt driftline material (15 L fresh, 15 L brackish and 1.5 L salt marsh driftline material). The material was thoroughly mixed by hand to make the sample as homogeneous as possible. When the experiments were started, 0.35 L driftline material was added to each experimental chamber during high water in the daily-tide and spring-tide treatments to allow the material to soak with water. In the no-tide treatments, the driftline material was spread on the substrate and moistened with 0.1 L water of the respective salinity in each experimental chamber. Generally, seeds in the driftline material were representative for the species pool of estuarine marshes of the Elbe (Engels & Jensen 2009); however, seed abundances may have somewhat differed from species abundances in the

field dependent on the seed production of the occurring species and sampling time and local conditions. The driftline material was thoroughly mixed in a big (90 L) tub by hand for about 30 min. However, it is not possible for us to prove that seed abundances were equivalent across the mesocosms or replicates in retrospect.

SAMPLING

The Emergence Experiment and the Establishment Experiment were conducted in a glasshouse. They ran for 16 weeks from April to the end of July 2008. For the Emergence Experiment, seedlings were continuously identified and removed from the mesocosms to prevent seedlings from impeding each other. Seedlings which could not be identified at this stage were transplanted to pots and allowed to grow until identification was possible. For the Establishment Experiment, the cover of the seedlings was estimated every 2 weeks starting in week 3 (30 April 2008). Cover was estimated for each species using the cover classes of Londo (1976; '0.1' = < 1%, '0.2' = 1–2%, '0.4' = 3–5%, '1' = 6–15%, '2' = 16–25%, '3' = 26–35%, '4' = 36–45%, '5' = 46–55%, '6' = 56–65%, '7' = 66–75%, '8' = 76–85%, '9' = 86–95%, '10' = > 96% cover of a species in the experimental chamber). Because seedlings grew in several layers, total plant cover could sum up to values higher than 100%. After week 15, both experiments were terminated and above-ground biomass of each species in the Establishment Experiment was determined (dry mass, dried at 60 °C to constant weight). Seedlings that could not be identified to species level were assigned to a genus (e.g. *Poa* sp., *Rumex* sp., *Sonchus* sp.).

DATA HANDLING AND STATISTICAL ANALYSES

In order to compare seedling emergence and establishment of species naturally occurring in freshwater and salt marshes, respectively, the occurring species were classified as halophytes (16 species) and glycophytes (41 species) using Ellenberg indicator values (Ellenberg *et al.* 1992). Ellenberg indicator values describe the ecological response of a plant species towards abiotic habitat conditions (e.g. salinity) by values between zero and nine. In our study, species with a salinity value from zero (no salt tolerance) to two (on soils with salinity up to 3 psu) were classified as glycophytes, while species with a salinity value from six (on soils with salinities between 9 and 12 psu) to nine (on soils with salinities of more than 23 psu) were classified as halophytes. Salinity values between three and five very rarely occurred, since there are very few 'true' brackish species (i.e. predominantly occurring in brackish marshes). Exceptions were *Cotula coronopifolia*, a generally brackish species (salinity value = five), which was classified as a halophyte species in our study and *Phragmites australis* (salinity value = zero or up to three for the ecotype occurring in coastal areas), which was assigned to the glycophyte group, because it commonly is restricted to fresh and brackish marshes of the Elbe estuary. Generally, if there were different salinity values for different ecotypes or sub-species for a certain species, we decided on the value best representing the distribution of species along the Elbe estuary (Kötter 1961, Raabe 1986, Engels & Jensen 2009). *Potentilla anserina* could not be clearly assigned to one group and seedlings were very few, so this species was excluded from the analysis. For a full list of species found in the driftline samples, Ellenberg salinity values and assigned groups see Table 1.

In the Emergence Experiment, we tested how different tidal regimes (no tide, spring tide, daily tide) and different salinity levels (fresh, brackish, salt) affected the number of emerged glycophyte and halophyte seedlings. We used GLMs (Generalized Linear Models) as

Table 1. List of species emerging from drift material collected in fresh, brackish and salt marshes of the Elbe estuary with life-forms, Ellenberg indicator values (Ellenberg *et al.* 1992) and assigned species groups. Nomenclature follows Wisskirchen & Haeupler (1998)

Species	Abbreviation	Life-form	Ellenberg salinity value	Assigned species group
Agrostis stolonifera	Agr-sto	Perennial	0	Glycophyte
Angelica archangelica	Ang-arc	Perennial	1	Glycophyte
Artemisia maritima	Art-mar	Perennial	5	Halophyte
Aster tripolium	Ast-tri	Biennial	8	Halophyte
Atriplex littoralis	Atr-lit	Annual	7	Halophyte
Atriplex portulacoides	Atr-por	Perennial	8	Halophyte
Atriplex prostrata	Atr-pro	Annual	7	Halophyte
Bellis perennis	Bel-per	Perennial	0	Glycophyte
Betula sp.	Bet-sp	Perennial	0	Glycophyte
Bidens sp.	Bid-sp	Annual	0	Glycophyte
Bolboschoenus maritimus	Bol-mar	Perennial	2	Glycophyte
Calystegia sepium	Cal-sep	Perennial	0	Glycophyte
Cardamine pratense	Car-pra	Perennial	0	Glycophyte
Carex sp.	Car-sp	Perennial	0	Glycophyte
Cerastium sp.	Cer-sp	Perennial	0	Glycophyte
Cotula coronopifolia	Cot-cor	Annual	5	Halophyte
Dactylis glomerata	Dac-glo	Perennial	0	Glycophyte
Elymus athericus	Ely-ath	Perennial	6	Halophyte
Elymus repens	Ely-rep	Perennial	0	Glycophyte
Epilobium hirsutum	Epi-hir	Perennial	1	Glycophyte
Festuca arundinacea	Fes-aru	Perennial	2	Glycophyte
Festuca rubra (littoralis)	Fes-rub	Perennial	7	Halophyte
Galium palustre	Gal-pal	Perennial	0	Glycophyte
Glaux maritima	Gla-mar	Perennial	7	Halophyte
Glyceria maxima	Gly-max	Perennial	0	Glycophyte
Juncus bufonius	Jun-buf	Annual	0–2	Glycophyte
Lolium perenne	Lol-per	Perennial	0	Glycophyte
Lycopus europaeus	Lyc-eur	Perennial	0	Glycophyte
Phalaris arundinacea	Pha-aru	Perennial	0	Glycophyte
Phleum pratense	Phl-pra	Perennial	0	Glycophyte
Phragmites australis	Phr-aus	Perennial	0/3*	Glycophyte
Plantago lanceolata	Pla-lan	Perennial	0	Glycophyte
Plantago major	Pla-maj	Perennial	0	Glycophyte
Plantago maritima	Pla-mar	Perennial	7	Halophyte
Poa sp.	Poa-sp	Annual/Perennial	1	Glycophyte
Poa trivialis	Poa-tr	Perennial	1	Glycophyte
Polygonum aviculare	Pol-avi	Annual	1	Glycophyte
Polygonum hydropiper	Pol-hyd	Annual	0	Glycophyte
Potentilla anserina	Pot-ans	Perennial	1	Glycophyte
Puccinellia maritima	Puc-mar	Perennial	8	Halophyte
Ranunculus repens	Ran-rep	Perennial	1	Glycophyte
Ranunculus sceleratus	Rab-sce	Annual	2	Glycophyte
Rorippa sp.	Ror-sp	Annual/Perennial	0	Glycophyte
Rumex sp.	Rum-sp	Annual/Perennial	0	Glycophyte
Salicornia europaea	Sal-eur	Annual	9	Halophyte
Scutellaria galericulata	Scu-gal	Perennial	0	Glycophyte
Sonchus sp.	Son-sp	Annual/Perennial	0–1	Glycophyte
Spartina anglica	Spa-ang	Perennial	8	Halophyte
Spergularia salina (marina)	Spe-sal	Annual	9	Halophyte
Stachys palustris	Sta-pal	Perennial	0	Glycophyte
Suaeda maritima	Sua-mar	Annual	8	Halophyte
Taraxacum officinale	Tar-off	Perennial	1	Glycophyte
Triglochin maritima	Tri-mar	Perennial	8	Halophyte
Trifolium repens	Tri-rep	Perennial	1	Glycophyte
Trifolium sp.	Tri-sp	Annual/Perennial	0–4†	Glycophyte
Urtica dioica	Urt-dio	Perennial	0	Glycophyte
Valeriana officinalis	Val-off	Perennial	0	Glycophyte

*For ecotypes occurring in coastal areas.
†For *T. fragiferum*.

implemented in the spss 16.0 Advanced Models Procedure to analyse our factorial design, assuming Poisson errors as typical for count data combined with a log-linear model. Data were analysed separately for glycophytes and halophytes testing the two factors 'tidal regime' and 'salinity' and the interaction between the two factors. For the glycophytes, the salt treatment was excluded from the analysis because seedling numbers were extremely low. Bonferroni Pairwise Comparisons were applied *post hoc* to detect significant differences between the individual treatments.

In the Establishment Experiment, we tested how the final biomass of glycophytes and halophytes was affected by the different treatments. We applied a two-way analysis of variance (ANOVA) with the factors 'salinity' and 'tidal regime' on halophyte biomass and a one-way ANOVA with the factor 'tidal regime' on glycophyte biomass in the oligohaline salinity. Biomass values were $\log(x + 1)$-transformed to approximate ANOVA assumptions. We used repeated measurement analyses of variance (RM-ANOVAs) to test how glycophyte and halophyte cover changed during 15 weeks of the experiment. We additionally tested how cover of halophytes changed in the brackish and salt treatments. We did not test the development and final biomass of glycophytes in the brackish and salt treatments, because glycophyte cover and biomass were extremely low. For the analyses, the Londo cover values were converted to percentage values using the midpoints of the cover classes. Cover values of species were summed up per species group for each experimental chamber. All available sampling dates (weeks 3, 5, 7, 9, 11, 13, 15) were included in the analysis (for glycophytes week 3 was excluded because cover was zero). All ANOVAs were followed by Tukey *post hoc* comparisons to detect significant differences between treatments.

Detrended Correspondence Analysis (implemented in PC-ORD; McCune & Mefford 1999) based on biomass values after 15 weeks was used to analyse differences in species composition among treatments. Species occurring only as a single seedling were excluded from the data set to reduce heterogeneity and improve the clarity of the ordination pattern. Additionally, the option 'downweight rare species' was selected.

Results

EMERGENCE EXPERIMENT

Both glycophytes and halophytes seedlings emerged in high numbers under fw conditions (Fig. 2). The GLM analysis showed that both glycophyte and halophyte seedling emergence was significantly affected by salinity (glycophytes: LR χ^2 (Likelihood Ratio χ^2) = 289.0, $P < 0.001$; halophytes: LR $\chi^2 = 180.5$, $P < 0.001$), tidal regime (glycophytes: LR $\chi^2 = 48.5$, $P < 0.001$; halophytes: LR $\chi^2 = 16.2$, $P < 0.001$) and by their interaction (glycophytes: LR $\chi^2 = 27.5$, $P < 0.001$; halophytes: LR $\chi^2 = 45.5$, $P < 0.001$).

Seedling emergence of glycophytes was extremely reduced under bw conditions (71% in no-tide, 89% in spring-tide and 98% in daily-tide treatment compared to the fw no-tide treatment; Bonferroni pairwise comparisons: $P < 0.001$) and was almost zero under sw conditions. Seedling emergence of halophytes was in almost all cases also impaired by increased salinity ($P < 0.01$). However, bw in combination with daily tides had a similar seedling emergence as fw. In the other bw or sw treatments, seedling emergence usually never decreased by more than 60%.
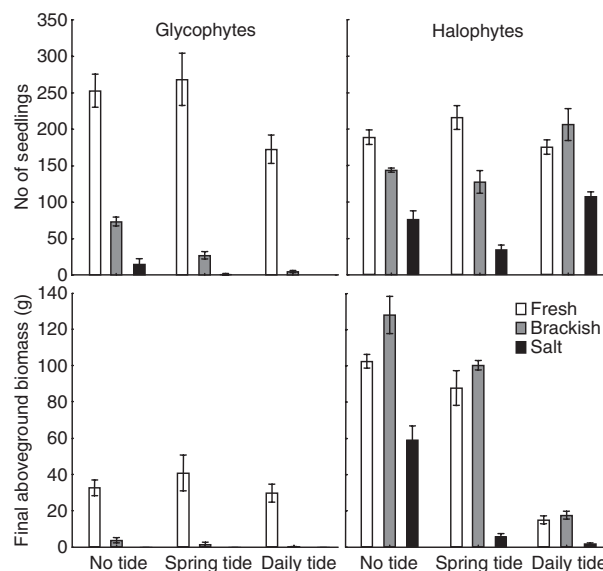

Fig. 2. Numbers of emerged glycophyte and halophyte seedlings in the Emergence Experiment and final biomass (after 15 weeks) in the Establishment Experiment, each with three tidal regimes: no tide, with spring tide (flooded every 2 weeks), with daily tide (flooded twice per day) in fresh, brackish and salt treatments. Mean ± SE for five replicates.

In fw, inundation by daily tides significantly reduced seedling emergence of glycophytes compared to the no-tide treatment ($P < 0.05$), while it did not for halophyte seedlings. The effect of inundation by spring tides on the emergence of glycophyte and halophyte seedlings depended on water salinity: fw combined with spring tide inundation produced the highest seedling emergence in both species groups (6% higher emergence of glycophytes and 14% higher emergence of halophytes than in the fw no-tide treatment, not significant). However, under bw or sw conditions, inundation by spring tides had a significantly negative impact on seedling emergence of halophytes compared to inundation by daily-tide (bw) or to the no-tide treatments (sw; $P < 0.05$), very likely due to salt accumulation in these mesocosms (salt crystals visible on the soil surface). For glycophytes, more frequent tidal inundation generally significantly decreased seedling emergence in bw ($P < 0.001$).

ESTABLISHMENT EXPERIMENT

In bw, where cover of glycophytes was almost zero, halophyte cover showed more or less constant increases from week 3 to week 9 (week 11 in spring-tide treatment) of the experiment ($P < 0.001$, respectively) and then gradually levelled off (Fig. 3). However in fw, halophytes showed significant increases until week nine, similarly to the glycophytes ($P < 0.001$, respectively), but after week 9 significantly decreased in the fw no-tide ($P < 0.01$) and spring-tide treatments ($P < 0.001$), while glycophytes gradually levelled off.

Generally, cover of glycophytes in the fw treatments and cover of halophytes in all three salinity treatments were
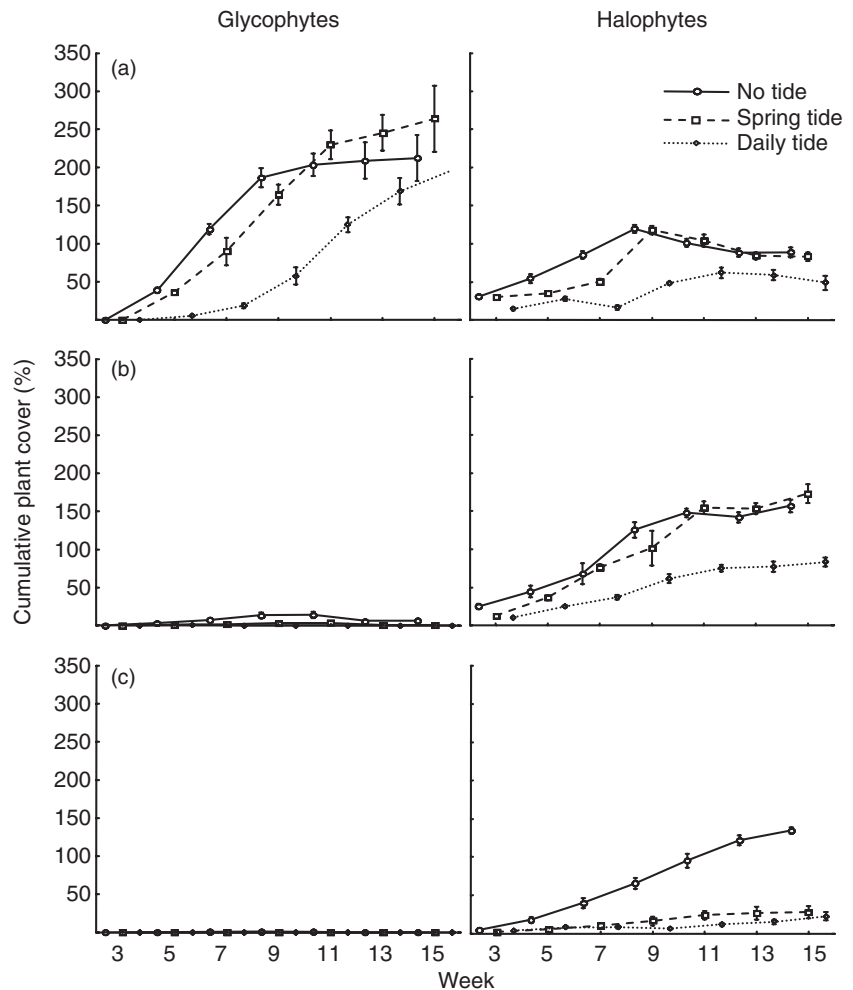
Fig. 3. Change of cumulative plant cover (%) of glycophytes and halophytes in mesocosms during the course of the Establishment Experiment (15 weeks) for three tidal regimes: no tide, spring tide (flooded every 2 weeks), daily tide (flooded twice per day) in fresh (a), brackish (b) and salt (c) treatments. Cover of more than 100% results from multiple vegetation layers in the mesocosms. Mean ± SE for five replicates.

significantly affected by time (fw glycophytes: $F = 121.2$; fw halophytes: $F = 107.6$; bw halophytes: $F = 109.4$; sw halophytes: $F = 132.9$; $P < 0.001$, respectively), tidal regime (fw glycophytes: $F = 8.7$, $P < 0.01$; fw halophytes: $F = 47.1$, $P < 0.001$; bw halophytes: $F = 50.0$, $P < 0.001$; sw halophytes: $F = 69.5$, $P < 0.001$) and the interaction between time and tidal regime (fw glycophytes: $F = 4.1$; fw halophytes: $F = 8.9$; bw halophytes: $F = 5.4$; sw halophytes: $F = 55.3$; $P < 0.001$, respectively). In sw no-tide treatments, where glycophytes did not survive, cover of halophytes showed constant increases until week 13 ($P < 0.001$, respectively), whereas in both tidal treatments, the significant increases in cover were prolonged to week 15 ($P < 0.05$), although plant cover was generally very low here.

Surprisingly, halophytes had higher biomass than glycophytes in all treatments (e.g. three times the biomass of glycophytes in fw) except for the fw treatment with daily tides (Fig. 2). Biomass of glycophytes was not affected by hydrologic regimes in the fw treatment ($F = 0.6$, $P > 0.05$). It was extremely reduced under bw and sw conditions. Tidal inundation seemed to have further reduced biomass of glycophytes in the bw treatments. Biomass of halophytes was significantly

affected by tidal regime and salinity, as well as by their interaction (tidal regime: $F = 181.8$, salinity: $F = 139.7$, tidal regime × salinity: $F = 16.3$, $P < 0.001$). Biomass of halophytes was highest in bw throughout all hydrologic regimes. Exposure to sw led to a significant decrease in biomass of halophytes compared to bw levels at all hydrologic regimes ($P < 0.05$). Daily tide significantly reduced biomass of halophytes at all salinities compared to the no-tide treatment of the same salinity ($P < 0.001$). While spring tide did not have an effect under fw or bw conditions, it significantly reduced biomass of halophytes ($P < 0.001$) in sw, and daily tide led to a further significant decrease compared to spring tide ($P < 0.05$).

The ordination of the biomass values of the occurring species produced well-defined groups allowing a visual estimation of similarity between species composition of the different treatment combinations (Fig. 4). Fw treatments cluster in the lower-left corner (with a large number of glycophyte species), bw in the centre and sw in the right and upper part of the graph, where halophytes are also displayed. For all salinity levels, daily-tide treatments are clearly separated from spring and no-tide treatments, respectively.
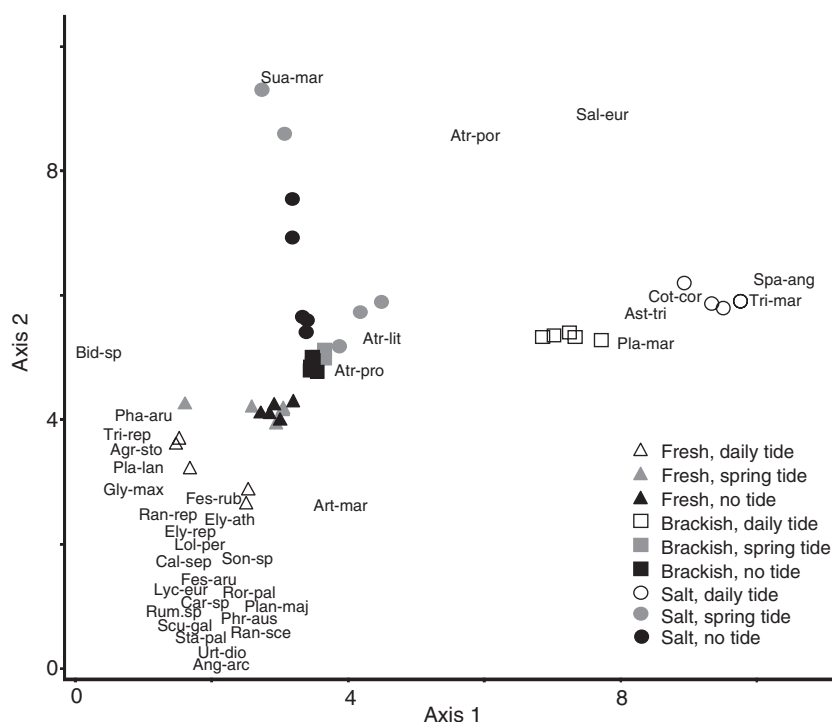
Fig. 4. Ordination diagram of the species which established in the different treatments based on the final biomass values (after 15 weeks). The salinity treatments are illustrated by triangles (freshwater), diamonds (brackish) and circles (salt) and the hydrologic regimes are illustrated by white (daily tide), grey (spring tide) and black (no tide) symbols. Species names are displayed without symbols (see Table 1 for abbreviations).

Discussion

GLYCOPHYTES AND HALOPHYTES: SEEDLING EMERGENCE PATTERNS

Despite their absence in tidal freshwater marshes, halophytes showed the highest seedling emergence at the lowest salinity treatment in our experiment (together with glycophytes). Thus, our experimental findings clearly demonstrate that plant distribution patterns along (estuarine) salinity gradients can not solely be explained by germination requirements (see also Ungar 1978; Bakker, Dijkstra & Russchen 1985). However, our results show that seedling emergence of halophytes has a pronounced tolerance towards salinities up to polyhaline conditions (19 psu), whereas emergence of glycophytes is strongly inhibited at bw and sw conditions, which is in accordance with other studies on emergence of glycophytes and halophytes (Bakker, Dijkstra & Russchen 1985; Baldwin, McKee & Mendelssohn 1996).

We found variable effects of tidal flooding on seedling emergence, depending strongly on inundation frequency, water salinity and species group. In contrast to the emergence of glycophytes, which was significantly reduced when subjected to daily tides, emergence of halophytes was hardly ever affected by daily tidal inundation. Seedling emergence in halophytes even seems to have benefited from daily tides in the bw treatments, rejecting our third hypothesis that tidal inundation generally decreases seedling emergence. This might indicate that halophyte seeds or seedlings are more tolerant of tidal inundation than glycophyte seeds or seedlings, or it might mirror effects of early competitive release taking place already at the seedling stage under high abiotic stress conditions (Parker & Leck 1985; Scholten *et al.* 1987).

Detrimental effects of flooding on seedling emergence have been reported by several studies on species of fresh and oligohaline tidal marshes (e.g. Galinato & van der Valk 1986; Baldwin, McKee & Mendelssohn 1996; Baldwin, Egnotovich & Clarke 2001). However, all of these studies tested the impact of permanent (long-term) flooding, which is likely to have different impacts on plant performance than tidal (short-term) flooding, because intermittent drainage between the tides may allow aeration of the soil (Armstrong *et al.* 1985). We are aware of only two observational studies which investigated the effect of tidal flooding on seedling emergence of estuarine marsh species. Both Parker & Leck (1985) and Hopfensperger & Engelhardt (2008) found increasing seedling densities with decreasing tidal flooding frequency (increasing elevation) in tidal freshwater marshes. This is partly consistent with our mesocosm study, since frequent (daily) flooding strongly reduced seedling emergence of glycophytes in our experiment. However, in contrast to these findings, infrequent short-time (spring-tide) flooding with fw did not have any detrimental effects on seedling emergence of estuarine marsh species in our study.

The decrease in seedling emergence of halophytes we observed in treatments with spring-tide flooding under bw and sw conditions might be explained by an accumulation of salt in these treatments caused by high temperatures in the glasshouse. Watering the mesocosms from above with fresh water was apparently not enough to compensate for the high evaporation. Salt accumulation in upper soil layers is a common phenomenon observed at higher (infrequently flooded) marsh elevations of Mediterranean climate salt marshes (Pennings & Callaway 1992; Allison 1996), and salt accumulation in bare patches was shown to decrease seedling emergence and recruitment in salt marshes of New England (Bertness, Gough &

Shumway 1992). Consequently, we assume that the negative effect of infrequent flooding with saline water on seedling emergence of halophytes was more severe (due to salt accumulation) than should be expected under field conditions with lower temperatures and a temperate climate. Since the bw and sw no-tide treatments were only saturated with saline water at the beginning of the experiment and after that watered with fresh water from above, salt accumulation may have been less of a problem here.

GLYCOPHYTES AND HALOPHYTES: THE PHASE OF EARLY ESTABLISHMENT

A contrasting pattern of initial seedling emergence and final biomass of halophytes in our experiments suggests that early development of halophytes in our experimental marsh communities underlies other constraints than seedling emergence.

Generally, growth and survival of both halophyte and glycophyte seedlings were reduced by high salinities (sw), which is in accordance with other studies (Beare & Zedler 1987; Ungar 1987; Shumway & Bertness 1992). However, while exposition to moderate salinity (bw) significantly reduced cover and biomass of glycophyte seedlings, halophytes were not or even positively affected by moderate salinity. Under fw conditions, seedlings of both species groups showed rapid growth within the first weeks of our experiment. After 2 months, however, the glycophytes started to overgrow the halophytes, thereby successively reducing their cover proportion. Our results on cover development of glycophytes and halophytes during the early establishment phase therefore generally supported our second hypothesis, i.e. glycophytes reached higher cover in fw than halophytes over time, whereas halophytes reached higher cover in brackish water and sw.

Cover development of glycophytes in fw followed a saturation curve, which appeared to level off when the carrying capacity of the mesocosms was reached. A similar curve was observed for halophytes under bw (particularly no-tide and spring-tide regimes) and sw conditions (no-tide regime), where glycophytic competitors were strongly inhibited. The deviation of the cover response curve of halophytes from a saturation curve under fw conditions consequently seems to be caused by competitive displacement by glycophytes. Accordingly, higher cover proportions and final biomass of halophytes under bw conditions compared to fw conditions may be the result of competitive release. Thus our results give for the first time experimental evidence that interspecific competition as an important driver of the development of plant zonations starts to take effect already during the seedling phase of the occurring species.

The ability of (adult) glycophytes to suppress halophytes under low-salinity conditions has been shown before (e.g. Ungar 1998; Crain *et al.* 2004; Engels & Jensen 2010). Moreover, in the absence of competitors, halophyte species grow usually better at low salinity than under their natural habitat conditions (Snow & Vince 1984; Crain *et al.* 2004). On the contrary, there is also evidence that moderate salinity can stimulate the growth of some halophytes (Flowers, Troke & Yeo 1977; Bakker, Dijkstra & Russchen 1985; Drake & Ungar 1989).

We were surprised to find that the final biomass of halophytes was substantially higher than that of glycophytes in most treatments. This applies also to fw conditions, although we observed a higher canopy cover for glycophytes than for halophytes here (except for the daily-tide regime). Thus, results of the Establishment Experiment only partly support our hypothesis, in which we presumed biomass and cover to have a similar treatment response. An explanation for this may be that biomass predictions based on non-destructive estimations (e.g. cover) are dependent on plant architecture (Shaver *et al.* 2001): Plants with large leaves (e.g. *Rumex* sp.) may provide high canopy cover and consequently a high shading effect, although above-ground biomass is relatively low.

Daily tidal inundation generally had negative effects on seedling establishment, particularly on halophytes. In contrast, infrequent flooding by spring tides with fresh or brackish water had no significant effects on seedling establishment, rejecting our third hypothesis on a generally detrimental effect of tidal flooding. Flooding may affect seedling growth in a different way than seedling germination and emergence (Lenssen, ten Dolle & Blom 1998; Bakker *et al.* 2007). Generally, flooding tolerance seems to be species-specific (Coops & van der Velde 1995; Kellogg, Bridgham & Leicht 2003). In our study, *A. prostrata*, a species sensitive to flooding due to the lack of aerenchyma (Olff, Bakker & Fresco 1988), constituted the majority of the halophyte seedlings, which may explain the negative response of halophytes to daily tidal inundation. The extremely low biomass of halophytes in the spring tide regime under sw conditions is likely explained by salt accumulation (see above).

The low biomass and cover values in the sw treatments with daily tidal inundation indicate that most species in our study were not able to tolerate the cumulative stress exerted by high salinity combined with frequent tidal flooding during their early establishment phase (cf. McKee & Mendelssohn 1989; Willis & Hester 2004). These extreme conditions correspond to low elevations in salt marshes that are generally colonized by few species with specific adaptations (Odum 1988), e.g. *Salicornia europaea* and *Spartina anglica* in European salt marshes. Overall our experimental results indicate that species density in low-elevation salt marshes is rather restricted by a bottleneck during seedling establishment than by one during germination.

IMPACT OF SEEDLING DYNAMICS ON THE GENERATION OF PLANT ZONATION PATTERNS

Our results show that the ability of a species to germinate and emerge under certain habitat conditions representing a particular position along an environmental gradient is a necessary, but not solely sufficient, condition for determining the species distribution pattern along estuarine marsh gradients. While the inability of glycophytes to tolerate increased salinities during germination and seedling emergence coupled with high mortality during the early establishment phase seems to be the main reason for the absence of glycophytes in salt marshes, the

absence of halophytes in tidal freshwater marshes seems to be exclusively controlled by factors affecting the plants during their establishment phase. Our results suggest that competitive exclusion of halophytes by glycophytes at low salinities starts to take place in the first 3 months of early establishment.

However, our results also indicate that halophyte seeds which reach tidal freshwater marshes by dispersal are able to germinate and survive in these marshes up to several months. Thus, although the typical estuarine marsh zonation starts to develop already during early stages of the corresponding plant's life cycle, it may take months or years until halophytes disappear completely from disturbed sites during secondary succession and the 'disturbance community' mirrors mature vegetation.

Overall, we demonstrate that the mechanisms leading to the development of marsh zonation patterns along estuarine salinity gradients start taking effect already during a very early stage of development of the occurring plants, i.e. the early seedling establishment phase. So far, these mechanisms (competition, physical stress) have only been shown to affect the distribution of adult clonal marsh perennials along estuarine salinity gradients (Crain *et al.* 2004; Engels & Jensen 2010). Our study therefore enhances our overall understanding of plant distribution along estuarine gradients.

Acknowledgements

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