Drivers of marsh plant zonation and diversity patterns along estuarine stress gradients

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Re: 'Drivers of marsh plant zonation and diversity patterns along estuarine stress gradients', by Jana Gesina Engels

To whom it may concern,

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ACKNOWLEDGEMENTS

1 General introduction

1.1 Environmental stress gradients

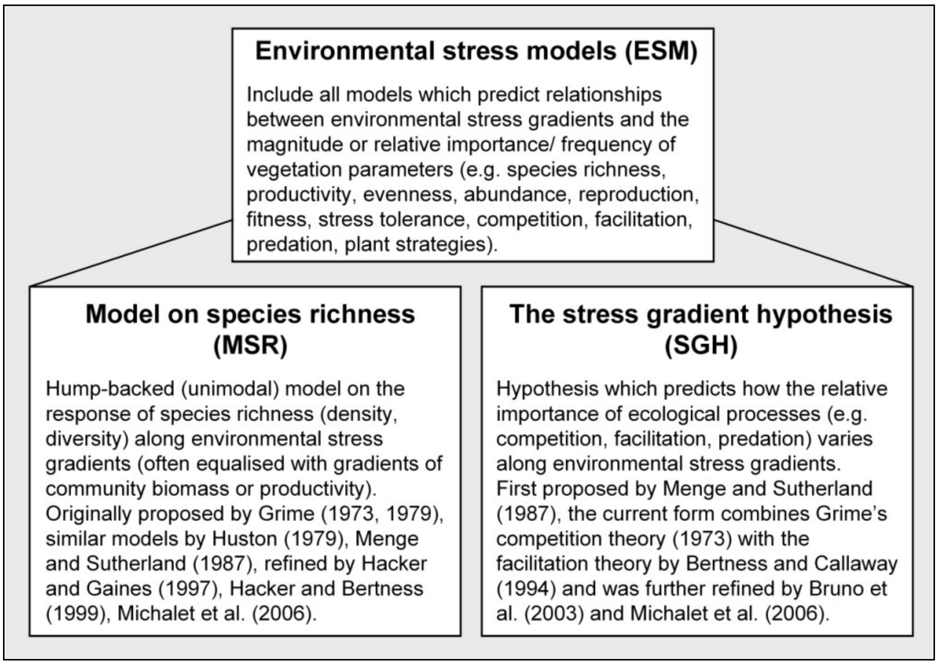
What is stress to a wetland plant? Trying to answer this question, a debate among ecologists emerged in the recent years concerning whether species adapted to living in a particular habitat are stressed or not (Otte 2001; Liancourt et al. 2005). It has even been questioned whether "stress" should be used at all in a biological context (Körner 2003). Actually, the term "stress" is used in many different ways and contexts in the field of biology depending on the discipline (e.g. physiology, ecology and evolutionary biology) and biological level of interest (molecular, physiological, organisms or population level; Bijlsma and Loeschcke 2005). Physiologists refer to stress as a factor affecting an individual and leading to an alteration in the metabolism (e.g. reduction of photosynthesis) that can be measured (Bohnert et al. 1995). In an evolutionary context, stress is defined as any environmental factor that causes environmental change and thereby reduces the fitness of organisms, finally leading to the evolution of adaptations (Bijlsma and Loeschcke 2005).

Plant ecologists mostly adopt the definition proposed by Grime (1979), who defined stress as "the external constraints which limit the rate of dry matter production of all or part of the vegetation". Most importantly, environmental stress and the level of stress imposed can only be defined in relation to the organism or population involved (Bijlsma and Loeschcke 2005). Thus, each species or each individual plant occurring in a specific environment (e.g. an estuarine marsh) may be differently affected by prevailing abiotic stress and react in a different way to the experienced stress (Ewing 1986). In this thesis, stress (or environmental severity) according to Grime (1979) is used and thus describes abiotic factors, i.e. edaphic factors (e.g. redox potential, salinity) and physical factors (e.g. flooding, tidal currents, wave action) which limit the performance of the occurring vegetation (measured e.g. as biomass production, plant height or species cover) and require specific adaptations of the occurring plants.

Environmental stress gradients are universal in all habitat types and result from spatial variation in one or multiple abiotic factors, which can correlate positively or negatively (Menge and Sutherland 1987). They have proved of great value in ecological research, since they allow a correlation of the response of a population or community to different levels of an environmental stress factor. The analysis of vegetation pattern across environmental gradients revealed the impact of biotic interactions (e.g. competition and facilitation) and physical factors on community dynamics and has led to substantial advances in ecological theory (Crain and Bertness 2006). In order to be able to predict the relative importance of abiotic factors and biotic processes in controlling community structure (i.e. plant distribution, abundance, trophic interactions and diversity, *sensu* Menge and Sutherland 1987), several environmental stress models (ESM; see box page 2), were developed and refined by various authors during the last 40 years.

1.2 Environmental stress models

Concerning the impact of biotic interactions along environmental stress gradients, the main focus of attention was initially on the role of competition in affecting plant species distribution (e.g. Grace and Wetzel 1981; Wilson and Keddy 1986; Bertness 1991a,b) and diversity (e.g. Grime 1973; Tilman 1982; Bertness and Ellison 1987). The competition theory of Grime (1973) predicts the importance of competition to be highest at low stress (and high biomass) conditions, whereas the importance of physical factors is highest at high stress (and low biomass) conditions. This theory is based on the idea that a trade-off exists between the ability of a plant to compete with other plant species and the ability to tolerate stress (Grime 1979; Liancourt et al. 2005). The so-called "humped-back" or unimodal model of Grime (1973), which in the following is referred to as "model on species richness" (MSR, Fig. 1.1), predicts that species diversity is low at the harsh end of an environmental stress gradient, because only few species exhibit the traits necessary to tolerate the harsh conditions, and at the benign end of a gradient due to competitive exclusion. A similar model was later proposed by Menge and Sutherland (1987) which additionally included the effect of predation on species diversity, which is thought to limit species diversity at very low stress levels. This model generally suggests that physical factors are most important at high, competition at intermediate and predation at low levels of environmental stress (assuming high rates of recruitment).



Environmental stress models (ESM)

Include all models which predict relationships between environmental stress gradients and the magnitude or relative importance/ frequency of vegetation parameters (e.g. species richness, productivity, evenness, abundance, reproduction, fitness, stress tolerance, competition, facilitation, predation, plant strategies).

Model on species richness (MSR)

Hump-backed (unimodal) model on the response of species richness (density, diversity) along environmental stress gradients (often equalised with gradients of community biomass or productivity). Originally proposed by Grime (1973, 1979), similar models by Huston (1979), Menge and Sutherland (1987), refined by Hacker and Gaines (1997), Hacker and Bertness (1999), Michalet et al. (2006).

The stress gradient hypothesis (SGH)

Hypothesis which predicts how the relative importance of ecological processes (e.g. competition, facilitation, predation) varies along environmental stress gradients. First proposed by Menge and Sutherland (1987), the current form combines Grime's competition theory (1973) with the facilitation theory by Bertness and Callaway (1994) and was further refined by Bruno et al. (2003) and Michalet et al. (2006).

In the 1990s, the significance of positive interactions (i.e. facilitation) for distribution patterns and vegetation dynamics was increasingly recognised. Several studies had indicated positive effects of facilitation, particularly under harsh habitat conditions, where stress-tolerant facilitator species ameliorate habitat conditions for less stress-tolerant species (Bertness and Callaway 1994). Facilitation was thus acclaimed to promote coexistence, enhance diversity and productivity and drive community dynamics (Callaway 1995; Bertness and Leonard

1997). Bertness and Callaway (1994) proposed a simple conceptual model which predicted the frequency of positive interactions to be high at high abiotic stress (due to habitat amelioration) and at high consumer pressure (due to associational defence), whereas the frequency of competition should be high at low abiotic stress and low consumer pressure (facilitation theory). Evidence for a shift in the predominant type of interaction from facilitation to competition as conditions become more benign, was provided by studies along vertical gradients in New England salt marshes, where stress-tolerant facilitator species lower soil evaporation by shading, which in turn reduces soil salinity and allows other species to colonise the otherwise too harsh habitats (Bertness and Shumway 1993; Bertness and Hacker 1994; Bertness and Leonard 1997). The model by Bertness and Callaway (1994) was since then often referred to as 'stress gradient hypothesis' (SGH, Fig. 1.1).

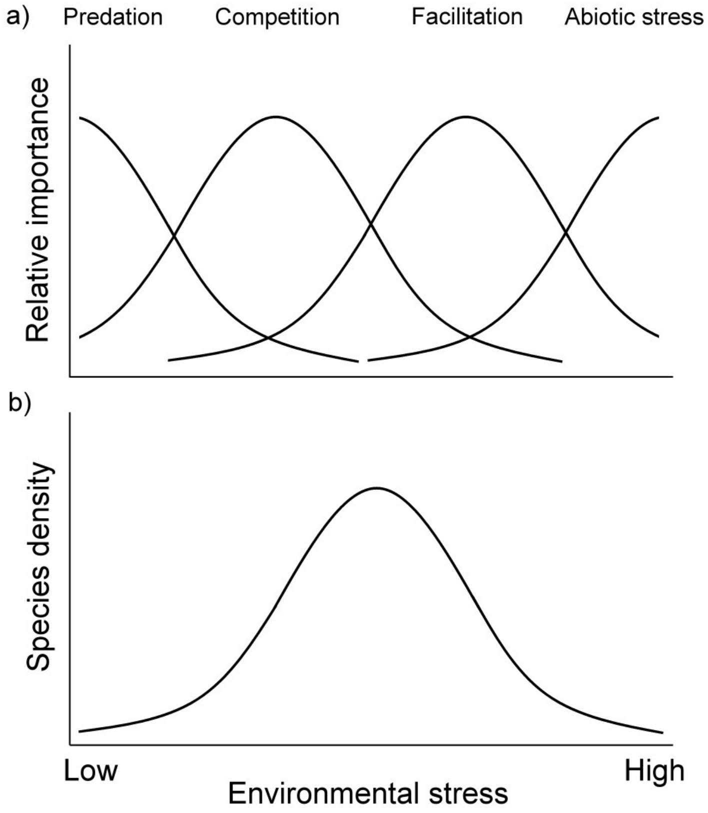


Figure 1.1 Illustration of environmental stress models (ESM). a) The stress gradient hypothesis (SGH), which predicts the relative importance of ecological processes (predation, competition, facilitation, abiotic stress) along a gradient of environmental stress (cf. Bruno et al. 2003); b) The hump-shaped model of species richness (MSR), which predicts the relationship between species density (SD) and environmental stress (cf. Michalet 2006).

Hacker and Gaines (1997) suggested that facilitation leads to an increase in species diversity at the harsh end of an environmental stress gradient, as facilitation may permit species to exist under high stress conditions which they normally would not be able to tolerate. The MSR was refined by Hacker and Bertness (1999) who point out the importance of facilitation for generating the peak of species diversity at intermediate levels of environmental stress, and Michalet et al. (2006) who suggest that the importance of facilitation decreases under extremely high environmental stress, thereby reconciling the MSR with the original hump-shaped model of species diversity. The MSR was recently supported by a study on species richness of alpine plant communities along a latitudinal gradient, where facilitation by cushion nurse plants led to an increase in species richness at the entire community level (Cavieres and Badano 2009).

Generally, the updated SGH predicts that predation is important at low environmental stress, competition at medium and facilitation at medium to high abiotic stress (Bruno et al. 2003, Michalet et al. 2006). However, the SGH is often merely applied to the inverse relationship between the importance of competition and facilitation along (shorter) environmental stress gradients. During recent years, the SGH has been tested along several environmental stress gradients in different ecosystems, and was supported e.g. along elevation and topography gradients in subalpine and alpine plant communities (Choler et al. 2001; Callaway et al. 2002), water stress gradients in semi-arid environments (Pugnaire and Luque 2001) and estuarine salinity gradients (Crain 2008). However, the SGH was also frequently rejected, e.g. along a water stress gradient in semi-arid steppe (Maestre and Cortina 2004) and under temporal varying rainfall conditions in deserts (Tielbörger and Kadmon 2000; for more examples see Callaway 2007 and Brooker et al. 2008), resulting in a debate on the general validity of the model (see Maestre et al. 2005; Lortie and Callaway 2006; Maestre et al. 2006) and a recent suggestion of refinement (Maestre et al. 2009).

1.3 Stress gradients in estuarine marshes

Throughout the history of ecological theory, the steep environmental gradients in salt marshes have been serving as model systems for the analysis of vegetation pattern (zonation, diversity) its relation to environmental gradients, and the drivers causing this pattern (e.g. Chapman 1940; Adams 1963; Snow and Vince 1984; Pennings et al. 2005). In the meantime, tidal freshwater marshes located further up the estuary have been largely ignored (Odum 1988; Meire et al. 2005). However, there was growing interest in vegetation patterns and community dynamics of tidal freshwater and brackish marshes in the 1990s, concerning plant zonation patterns (Coops et al. 1999) as well as the influence of abiotic stress (Baldwin et al. 1996) and disturbance (McKee and Mendelssohn 1989; Flynn et al. 1995; Baldwin and Mendelssohn 1998). Studies encompassing the whole estuarine salinity gradient were still rare at that time (but see Odum 1988; Abrams et al. 1992; Latham et al. 1994; Gough et al. 1994; Perry and Atkinson 1997). Recently, estuarine marshes have more and more moved into focus of current ecological research and the value of estuarine salinity gradients as model systems for landscape-scale gradients in physical stress has been recognised (Judd and Lonard 2002; Wetzel et al. 2004; Crain et al. 2004; Crain and Bertness 2006; Crain 2007; Crain 2008; Crain et al. 2008; Ji et al. 2009; Sharpe and Baldwin 2009; Więski et al. 2010; this work).

Estuaries are transition zones between riverine and marine habitats and comprise all areas of a river which are subjected to tidal influence. They are geomorphologically very dynamic systems shaped by both sea and land changes and form a complex mixture of many different habitat types (e.g. intertidal mudflats, marshes, lagoons, sand dunes). Estuarine marshes are affected by tidal currents, sedimentation and erosion processes and by varying salinities due to the intrusion of marine salt water (Odum 1988; Meire et al. 2005). In this thesis I define estuarine (or tidal) marshes as the areas of a river shore, which are regularly or irregularly impacted by tidal flooding and inhabited by herbaceous plants. The main environmental stressors for estuarine marsh vegetation are salinity and tidal flooding, which form horizontal (salinity) and vertical (tidal flooding) stress gradients (Odum 1988). The intertidal shoreline along the estuarine salinity gradient is inhabited by tidal freshwater, brackish and salt marshes, each of which exhibit specific vertical plant zonation patterns that form according to differences in tidal flooding frequency and duration (Kötter 1961; Bakker et al. 1993). Species occurring in brackish and salt marshes exhibit specific adaptations to increased soil salinities, while species growing at low marsh elevations require adaptations to waterlogged, anoxic soils and wave action. In addition to salinity and tidal flooding other edaphic factors such as soil temperature, organic matter content, nutrient availability, redox potential and sulphide concentrations may vary in estuarine marshes in a complex environmental pattern (Ewing 1986; Odum 1988; Crain 2007). Species distribution ranges along vertical and horizontal estuarine gradients are supposed to be controlled by both biotic interactions and individual species tolerances towards abiotic stress (e.g. Snow and Vince 1984; Bertness 1991a,b; Crain et al. 2004).

1.4 Aim of the thesis and hypotheses

The aim of this thesis is to analyse patterns of plant species diversity and plant zonation in tidal marshes along flooding and salinity gradients in the Elbe estuary and to elucidate the underlying abiotic and biotic processes driving the generation of these patterns. While the analysis of vegetation pattern along vertical gradients in estuarine marshes, particularly in salt marshes, has received considerable attention, experimental studies on the drivers of vegetation pattern along horizontal estuarine salinity gradients are still rare (but see Crain et al. 2004; Wetzel et al. 2004) and completely lacking for European estuaries.

I conducted three studies within the framework of this thesis which were mainly carried out in the Elbe estuary (see Chapter 2 for a description of the study system). In the first study, I analysed plant diversity patterns along vertical and horizontal stress gradients in the Elbe estuary and compared them with plant diversity patterns along estuarine gradients in the Connecticut River, USA. Additionally, I describe patterns of plant zonations in the two estuaries. In the second study, I carried out field transplant experiments with four dominant marsh plants along the estuarine salinity gradient in the Elbe River, in order to reveal the mechanisms leading to the generation of plant distribution patterns across this gradient. The third study, finally, was a mesocosm experiment in which I was interested in the role of seedling dynamics in generating the observed plant distribution patterns. I investigated effects of different tidal flooding and salinity regimes on seedling emergence and early establishment of tidal freshwater and salt marsh species.

According to ESM, I put forward the general hypothesis that abiotic factors limit plant performance, distribution and diversity at high levels of salinity or tidal flooding stress, particularly when both stresses are combined. On the other hand, I hypothesise competition to limit plant performance, distribution and diversity at low to medium salinity or tidal flooding stress. Overall, I hypothesise facilitation to be important at medium to high salinity or flooding stress and competition to be important at low to medium abiotic stress as suggested by the SGH.

This thesis contributes to our understanding of vegetation dynamics in estuarine marshes. Knowledge of factors limiting plant diversity and driving spatial distributions of plant species along estuarine marsh gradients is particularly important in the face of climate change (Callaway et al. 2007). The results of this thesis may help in predicting the response of estuarine marsh species to consequences of climate change, e.g. accelerated sea level rise and reduced freshwater input. Sea level rise and reduced freshwater run-off may lead to shifts in plant zonation patterns and alteration of vegetation composition of estuarine marshes due to increased water levels and an extension of the brackish water zone (Meire et al. 2005; Watson and Byrne 2009).

2 Patterns of wetland plant diversity along estuarine stress gradients of the Elbe (Germany) and Connecticut (USA) Rivers

J. Gesina Engels and Kai Jensen

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2.1 Abstract

Background: Estuaries are characterised by salinity gradients and regular flooding events. These environmental factors form stress gradients, along which species composition changes.

Aims: Analyse and compare patterns of plant species diversity along the estuarine salinity and flooding gradients of the Elbe and Connecticut Rivers.

Methods: Vegetation was sampled at three elevations (low, mid, high) in five sites of each marsh type (fresh, brackish, salt) in both estuaries. Patterns of species density (SD) and evenness (E) along the gradients were analysed and compared between the two estuaries with three-factor ANOVAs.

Results: The regional species pool was 33% higher for the Connecticut than for the Elbe. SD of fresh marshes (19 ± 2.2) was more than twice in the Connecticut than in the Elbe. We found an overall increase in SD from low to high elevation and from salt to freshwater marshes in both estuaries. However, SD and E were strongly depressed at intermediate elevations in the Elbe fresh and brackish marshes.

Conclusions: Although diversity patterns in the two estuaries show overall similarities, patterns of SD and E differ, when particular elevational zones and marsh types are compared. We hypothesise this to be due to evolutionary and historical influences on the regional species pools, shaping the impact of local biotic and abiotic processes.

2.2 Introduction

Species diversity of communities is one of the most often studied and at the same time most intensely discussed issues in vegetation ecology. However, the quantitative effects of abiotic stress, biotic interactions and of evolutionary processes on species diversity in local communities are still far from being generally incorporated into ecological theory (Ricklefs 2006; Harrison and Cornell 2008). In general, the more extreme a habitat, the fewer species will be found in a given plant community and the higher will be the abundance of the occurring species (Thienemann 1956). This old hypothesis on species diversity is based on the fact that only few species are adapted to extreme conditions and thus are capable of existing under stressful environmental conditions. In other words, only a small proportion of species from the regional species pool (Pärtel et al. 1996) is able to pass the filters that are constituted by the prevailing abiotic (and biotic) conditions in a certain habitat (Zobel 1997).

Estuaries contain at least two gradients of environmental stress for vascular plants in the intertidal zone: a horizontal (salinity) gradient on the landscape scale and a vertical (flooding) gradient at each shoreline location. Along the salinity gradient and the tidal inundation gradient, abiotic filters on the species pool become more severe with increasing salinity from fresh to saline conditions, and with increasing flooding frequency and duration from high to low elevation. In salt marshes of the North Sea coast, soil salinity increases along with increasing flooding frequency and duration from high to low marsh (Bockelmann and Neuhaus 1999) as an additional factor. Vegetation of estuarine marshes shows distinct plant distribution patterns along the salinity gradient with halophytic species in salt marshes and non salt tolerant wetland species in tidal freshwater marshes (Odum 1988; Latham et al. 1994; Crain et al. 2004).Similarly, distinct vegetation zonations have been observed along elevation gradients in salt marshes (Bertness 1991a,b; Bakker et al. 1993), brackish marshes (Kötter 1961; Hackney et al. 1996) and tidal freshwater marshes (Kötter 1961; Coops et al. 1999). This zonation has been attributed to both abiotic and biotic factors (Bertness and Ellison 1987; Crain et al. 2004).

Along with changing vegetation composition, plant species richness in estuarine marshes has been shown to decrease with increasing environmental severity, or stress (salinity, flooding frequency and/or duration) in marshes along estuarine salinity and elevation gradients in Louisiana (Gough et al. 1994) and New England (Brewer et al. 1997; Crain et al. 2004, but see Sharpe and Baldwin 2009 for another view). However, local species richness is not only determined by local processes, including abiotic and biotic factors, but also by the size of the regional species pool. The species pool hypothesis implies that richness on a smaller scale is primarily determined by the number of available species on the next larger scale and that the regional species pool is determined by large-scale processes such as speciation, migration and dispersal (Zobel 1997). Due to the late separation of the North American and the Eurasian landmasses, American and European marshes are characterised by a number of shared genera (Chapman 1977). However, generally, the regional species pools in temperate North America are thought to be comprised of more plant species than those in temperate Europe. This difference has been shown for temperate forest species (see Reid 1935) and is mainly accounted for by lower extinction rates during the course of glaciations in North America.

These lower extinction rates might have been caused by the north-south orientation of mountain ranges in North America as opposed to the east–west orientation of mountain ranges in Europe and by the presence of large areas in America with suitable climatic conditions for the survival of the temperate flora during periods of glaciation (Huntley 1993). To our knowledge, until now no study has analysed possible differences in wetland species pools between temperate North America and Europe. The aim of our study was to compare patterns of species diversity along horizontal and vertical gradients along estuaries of two major river systems in North America and north-west Europe. We asked whether the regional species pool for temperate marshes is larger in North America than in Europe (using the Elbe and Connecticut estuaries as examples) and whether these differences are also reflected in local species density in estuarine wetlands. We further asked how species diversity shifts along horizontal and vertical estuarine stress gradients. We hypothesised that species diversity decreases with increasing abiotic stress from higher salinities or longer tidal inundation, i.e.

from tidal freshwater to salt marshes and from high to low elevations. We used species density and evenness as measures of diversity. Although evenness is an important component of species diversity (Krebs 1999), only few studies have looked at evenness patterns along environmental gradients to date (Scrosati and Heaven 2007).

2.3 The study areas

The Elbe estuary

The Elbe estuary (53°43′ N; 9°27′ E) is the largest estuary on the German coast of the North Sea and an important waterway connecting the port of Hamburg with the sea (Kappenberg and Grabemann 2001). Tidal effects extend about 150 km, from Geesthacht (where a dam restricts tidal current, about 30 km east of Hamburg) to the North Sea at Cuxhaven, where the Elbe opens into the Wadden Sea (Garniel and Mierwald 1996; Fig. 2.1). Dikes have been constructed along the Elbe estuary for almost 1000 years. After a severe storm surge event in 1962, however, additional extensive embankments of marsh forelands and tributaries took place (Garniel and Mierwald 1996). As a result, in the freshwater part of the estuary about 70% of the marshes have recently been lost due to flood protection measurements and the construction of artificial bank reinforcements (Preisinger 1991; Kausch 1996). In addition, the river downstream from Hamburg has been subjected to canalisation and repeated river deepening since the middle of the nineteenth century (from 3 m to 14.4 m in 1996; Kerner 2007). During the same time, the tidal amplitude increased from 1.8 m in 1840 to 3.6 m in Hamburg in 1996 (Kausch 1996).

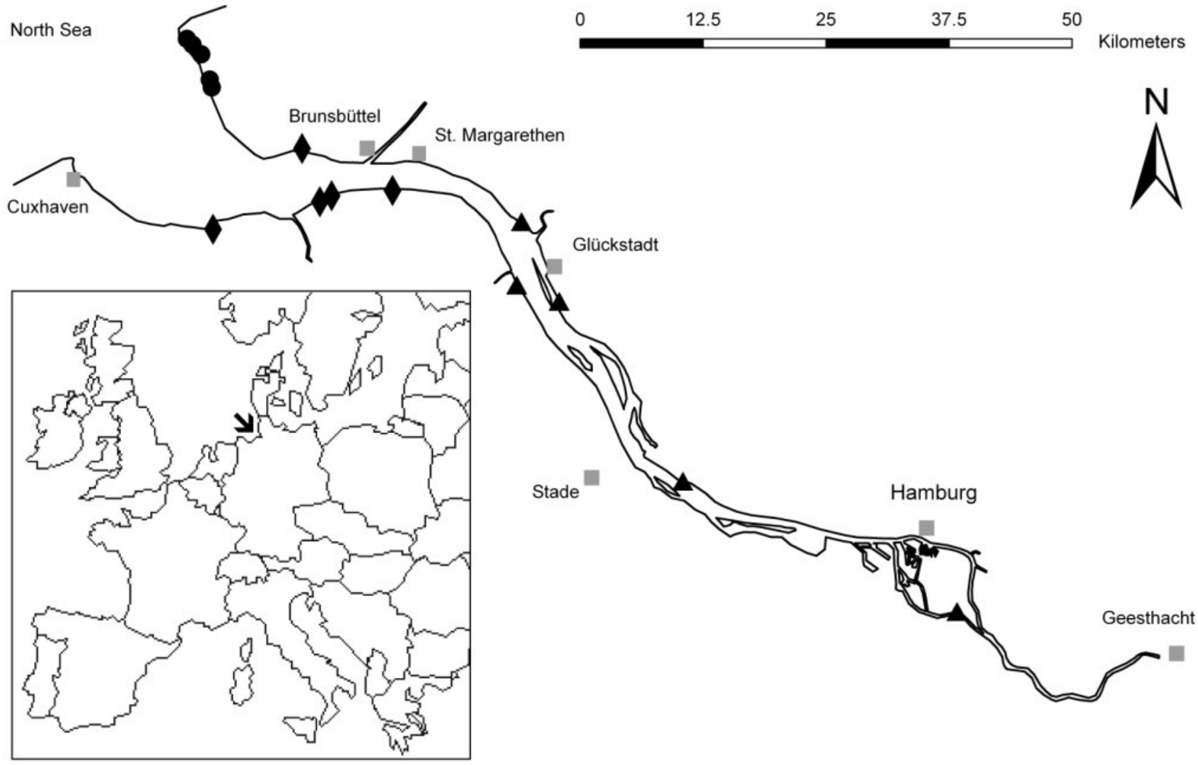

Figure 2.1 Map showing the Elbe estuary with the study sites marked – black circles, salt marshes; black diamonds, brackish marshes; black triangles, tidal freshwater marshes.

The mean tidal amplitude is 3 m at the mouth of the estuary, then slightly decreases up-estuary and rises again towards its maximum at Hamburg. At the upstream end of the estuary (Geesthacht/weir), the tidal amplitude is 2 m (Kappenberg and Grabemann 2001). Water salinities undergo strong spatio-temporal fluctuations depending on river discharge (Caspers 1959). Nevertheless, in terms of the salinity of the surface water, the estuary can be divided into a mesohaline zone (18 to 5 practical salinity units, psu) from the mouth of the estuary to St. Margarethen; an oligohaline zone (5 to 0.5 psu) from St Margarethen to Glückstadt; and a tidal freshwater zone (< 0.5 psu) from Glückstadt to Geesthacht (Caspers 1959). Estuarine marsh vegetation is more affected by soil salinity (Kötter 1961) than by the salinity of the surface water. Soil salinity might vary temporally depending on e.g. precipitation and evaporation (Mitsch and Gosselink 2000). The marshes along the Elbe estuary show a distinct differentiation with salt marshes at the mouth, brackish marshes in the middle reaches and tidal freshwater marshes at the head of the estuary. Tidal marshes show also a distinct vertical zonation that corresponds to tidal inundation frequency and duration. Each of three elevational zones can be distinguished in freshwater, brackish and salt marshes. A low marsh is inundated twice a day, a mid marsh located in the range of mean high tide becomes inundated at least twice a month during spring tides and a high marsh is inundated only during storm tides (Kötter 1961; Raabe 1986).

The Connecticut estuary

The Connecticut estuary (41°23′ N; 72°25′ W) is one of the major estuaries in north-east America. It has been less altered by human activities than the Elbe estuary. Tidal influence reaches more than 100 km upriver to the first dam just south of the border of the states Connecticut and Massachusetts. The mouth of the estuary opens into Long Island Sound and is marked by Griswold Point on the eastern and Lynde Point on the western side (Horne and Patton 1989; Fig. 2.2). The estuary can be divided into two distinct reaches: a northern reach that is occupied by fresh and brackish marshes from the head of the estuary to the Amtrak railroad/Interstate highway bridges, c. 5 km landwards of the mouth, and a southern reach which is mostly flanked by salt marshes downriver from the bridges to Long Island Sound (Patton and Horne 1992). The Connecticut estuary can be described as ‘microtidal’ with a mean tidal amplitude of 1.1 m. Tidal amplitudes are usually less than 2 m in Long Island Sound (Horne and Patton 1989) and the amplitude of tidal flooding is greatest at the mouth of the river and diminishes upriver (Barrett 1989). Hydrologic conditions and salinity distribution in the Connecticut estuary depend on freshwater discharge. Generally, water salinities in the mouth of the Connecticut are higher than in the Elbe estuary. Salt water from Long Island Sound (31 psu) intrudes about 5 km (at high freshwater discharges) to 15 km (at low freshwater discharges) up the estuary (Horne and Patton 1989). As in the Elbe estuary, the estuarine marshes of the Connecticut show distinct vegetation zonations along the salinity and the elevational gradient.

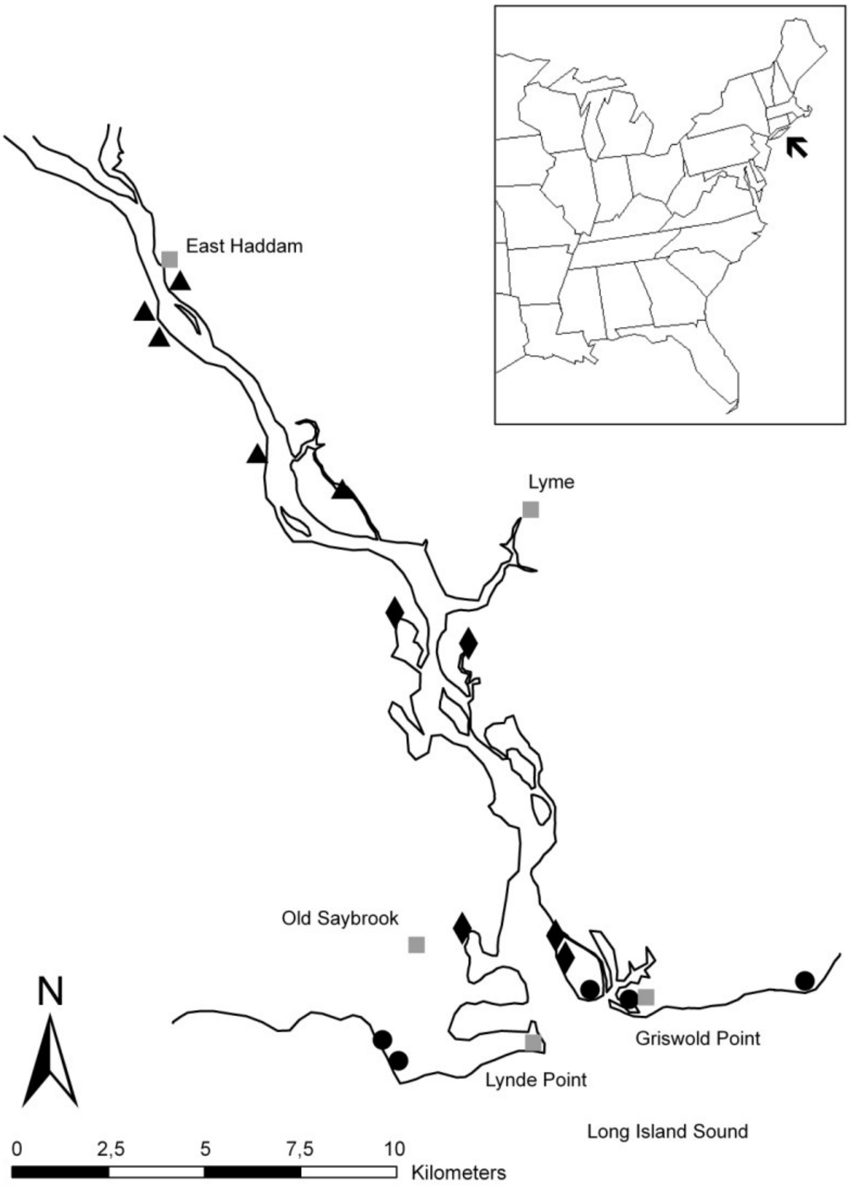

Figure 2.2 Map showing the Connecticut estuary with study sites marked – black circles, salt marshes; black diamonds, brackish marshes; black triangles, tidal freshwater marshes.

2.4 Methods

Study sites

The study was conducted in five sites, each of salt, brackish and freshwater marshes in the estuaries of the Elbe and the Connecticut (15 sites for each river in total, Figs 2.1, 2.2). The sites selected met several criteria: they were physically unaltered by humans (i.e. no structures such as embankments or wave breakers were present); they were not in agricultural use; they were accessible to us for research; they contained three vegetation zones along a vertical gradient (low marsh, mid marsh, and high marsh) and they were not dominated by non-native species. Salinity zones were differentiated using descriptions in the literature (Raabe 1986; Oertling 1992 for the Elbe, Barrett 1989 for the Connecticut estuary) and according to occurring species.

In the Elbe estuary, marshes were defined as ‘fresh’ if *Caltha palustris*, *Nasturtium officinale* or *Ranunculus ficaria* occurred in mid or high marshes. These species have a very low salinity tolerance and are characteristic of freshwater marshes (Berghausen 1992). Marshes were defined as ‘brackish’ if brackish species (e.g. *Cotula coronopifolia*) and/or halophytes (e.g. *Aster tripolium*) were observed in the vegetation. Marshes were defined as salt marshes, if their vegetation was exclusively composed of species typical for European salt marshes (Ellenberg 1996). Because the vertical zonation in the Elbe estuary is usually very distinct, the elevational vegetation zones could be differentiated according to species and position relative to mean high tide. The following species were used as indicators for the different elevational zones: fresh and brackish low marshes, *Bolboschoenus maritimus*; mid marshes, *Phragmites australis*; high marshes, *Phragmites* and tall forbs (e.g. *Angelica archangelica*, *Urtica dioica*). In salt marshes *Salicornia europaea* (low marsh), *Aster tripolium/Puccinellia maritima* (mid marsh) and *Elymus athericus/Festuca rubra* (high marsh) were used as indicators.

In the Connecticut, the vegetation zones were less distinctive. In freshwater marshes *Pontederia cordata* (low), *Peltandra virginica/Impatiens capensis* (mid) and *Thelypteris palustris* (high) were used as indicator species. *Zizania aquatica* (low), *Typha angustifolia* (mid) and *Thelypteris palustris* (high) indicated zones in the brackish marshes. In the salt marshes we used *Spartina alterniflora* (low), *Spartina patens* and *Distichlis spicata* (mid) and *Iva frutescens* (high).

Sampling

To examine species composition and plant species diversity, vegetation surveys were conducted in August 2006. In each study site, five 1-m^2-plots were sampled along a 50 m-line (shorter where the extent of a vegetation zone was smaller), parallel to the river shore in each of the three elevational vegetation zones. The plots were located evenly along the lines. The five plots from each transect representing one elevational vegetation zone were pooled and used as one replicate (resulting in 5 replicates of each vegetation zone in each marsh type). On each plot, percent cover of all occurring species was recorded according to 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 on the plot. Nomenclature of species follows Wisskirchen and Haeupler (1998) for the Elbe estuary and the USDA plant database (USDA NRCS 2009) for the Connecticut estuary. Soil salinity of each site in the Elbe and the Connecticut estuary was measured in the mid marsh by digging a hole in the sediment and measuring the salinity of the emerging water using a conductivity meter.

Data analyses

For measuring species diversity we used species density (SD = total number of species in five 1 m^2-plots along a transect). Additionally, we calculated the evenness (E), based on the Shannon Index, which is the degree of similarity in abundance among species (Krebs 1999). Evenness can be used as a measure of dominance, since a low E value indicates that one species is dominant over others (Scrosati and Heaven 2007). For calculation of E, the Londo-cover values of each species were converted to percent values using the midpoints of the cover classes (e.g. 0.1 was converted to 0.5%, 0.2 was converted to 1.5%). Evenness was then calculated based on the cover values of each species expressed as a proportion of the total plant cover along a transect. As an estimate for the size of the community species pools for salt, brackish and freshwater marshes, we used the total number of different species we found on the five study sites of the respective marsh type. For estimating the regional species pools for the two estuaries, we extracted species lists from comprehensive vegetation surveys. For the Connecticut estuary, we used Barrett (1978), a study with 227 plots in total (plot size 10 to 100 m^2). Since there was no all-encompassing study available for the Elbe estuary, we combined several studies, each including at least the same number of plots in each marsh type as the study we used for the Connecticut estuary. We used Kötter (1961) for the freshwater marshes (174 plots, plot size 100 m^2), Immeyer (1996) for the brackish marshes (75 plots, plot size 9-400 m^2), and unpublished data by S. Suchrow for the salt water marshes (489 plots, plot size 1 m^2) in the Elbe estuary. All studies sampled the whole elevational gradient from the lowest reaches of vascular plants to the marsh border.

Three-factor ANOVAs (analyses of variance) were performed to test the effects of region (Elbe, Connecticut), marsh type (fresh, brackish, salt), and elevation (low, mid, high marsh) and all possible interactions on SD and E (Table 2.1). SD values were square-root-transformed to approximate the assumptions of ANOVA. Evenness values were normally distributed, but the homogeneity of variances was violated. However, transformations of E values did not improve homogeneity of variances. As ANOVA is known to be robust against moderate violations of assumptions (Sokal and Rohlf 2005), and no appropriate nonparametric alternative is available for our three-factorial design, we decided to calculate an ANOVA with the untransformed data. To detect significant differences between groups, 'planned comparisons' were conducted for SD and E separately on the data of the two estuaries. We compared SD and E at the three elevations within the same marsh type and between the three marsh types on the same elevation (18 tests per estuary). The level of significance was adjusted using the Bonferroni-procedure, resulting in a P-level of 0.0028.

Detrended Correspondence Analysis (DCA) was used to analyse differences in species composition among marsh types and elevations. Londo-cover values were converted to percent values using the midpoints of the cover classes. Species that were observed in only one location were excluded from the dataset to reduce heterogeneity and improve the clarity of the ordination pattern. Additionally, the option 'downweight rare species' was selected, because otherwise the assumptions of the DCA were violated (residual was bigger than tolerance using Oksanen and Minchin's super strict criteria of tolerance = 0.0000001 and maximum number of iterations = 999; McCune and Mefford 1999). Data analyses were carried out using STATISTICA 8.0 (StatSoft, Tulsa, OK) for ANOVAs and PC-ORD 4.25 (McCune and Mefford 1999) for multivariate analyses. Evenness was calculated with PAST 1.86b (Hammer et al. 2001).

2.5 Results

Soil salinity

The mean ± SE salinity of the brackish marshes sampled in the Connecticut estuary was higher and more variable (9.3 ± 6.7 psu) than in the Elbe estuary (4.6 ± 1.1 psu). The mean salinity of the salt marshes was also higher (26.0 ± 2.3 psu) than in the Elbe estuary (18.0 ± 0.3 psu), whereas the mean salinity of the tidal freshwater marshes was slightly lower (0.1 ± 0.0) than in the Elbe estuary (0.5 ± 0.1).

Table 2.1 Results of the 3-factorial ANOVA testing the effects of region (Elbe, Connecticut), marsh type (fresh, brackish, salt), elevation (low, mid, high marsh) and their interactions on species density (values square-root-transformed) and evenness (values not transformed). Significant differences are indicated by asterisks (*** = p < 0.001; ** = p < 0.01; * = p < 0.05; n.s. = not significant).

	Species density					Evenness				
Source of variance	SS	DF	MS	F	*P*	SS	DF	MS	F	*P*
Region	10.75	1	10.75	38.57	***	0.17	1	0.17	3.88	n.s.
Marsh type	25.40	2	12.70	45.56	***	0.47	1	0.23	5.45	**
Elevation	33.15	2	16.58	59.45	***	0.67	2	0.34	7.82	***
Region* Marsh type	13.40	2	6.70	24.04	***	2.03	2	1.02	23.64	***
Region*Elevation	2.00	2	1.00	3.59	*	0.20	2	0.10	2.28	n.s.
Marsh type *Elevation	5.40	4	1.35	4.85	**	0.20	2	0.05	1.18	n.s.
Region*Marshtype*Elevation	3.10	4	0.78	2.78	*	0.82	4	0.21	4.78	**
Error	20.07	72	0.28			3.09	72	0.04		.

Species pools and species density

The community species pools increased from salt via brackish to tidal freshwater marshes in both the Elbe and the Connecticut estuary. The number of species found in the community species pools in the Elbe estuary was 17 in salt marshes, 33 in brackish marshes and 46 in tidal freshwater marshes. In the Connecticut, the community species pools were considerably larger than in the Elbe for brackish (54) and tidal freshwater marshes (75), but not in salt marshes (15). The total number of species we found in the estuaries on the 45 transects of our study was 68 species for the Elbe estuary and 114 species for the Connecticut estuary. The size of the regional species pool calculated for the Connecticut estuary (156 species) was 33% larger than the size of the species pool calculated for Elbe estuary (117 species). Regarding SD, all factors and interactions tested in the ANOVA were significant (Table 2.1). The three-way interaction among region, marsh type and elevation indicated that the effect of elevation on SD differed among the different marsh types and between the two regions. Because of this three-way interaction it is not possible to draw any conclusions concerning the main effects on SD in the two estuaries.

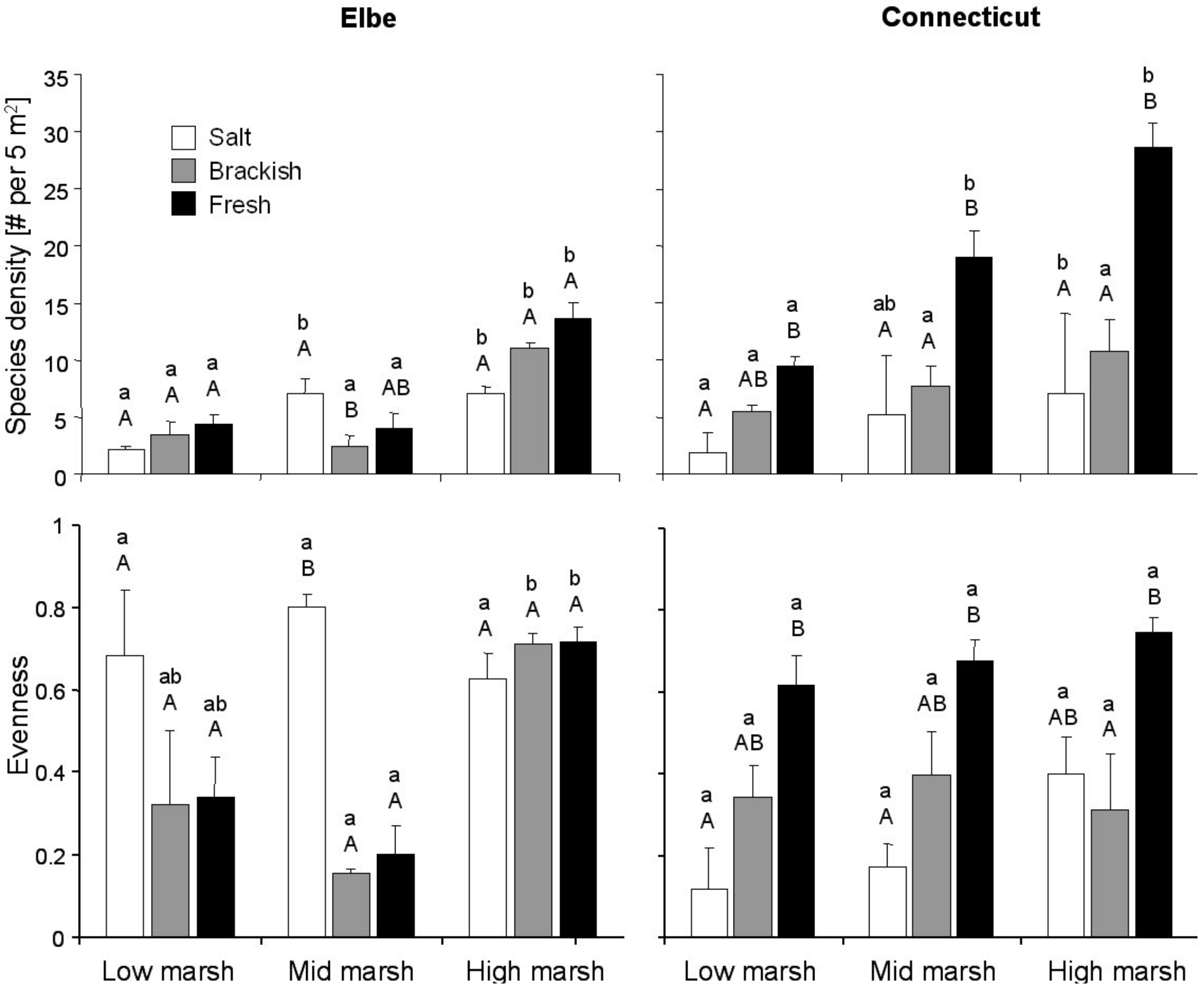

Figure 2.3. Observed species density and evenness of the vegetation in the Elbe and Connecticut estuaries. Values for low, mid and high elevations in fresh, brackish and salt marshes. Data are means ± SE. Significant differences of planned comparisons are indicated by different letters above bars: between elevations within the same marsh type lower case letters (e.g. a, ab, b) were used; between different marsh types at the same elevation upper case letters (e.g. A, AB, B) were used.

According to the planned comparisons, we observed a general increase in SD from low to high elevations in both estuaries ($P < 0.001$), except for the Connecticut brackish marshes (Table 2.1; Fig. 2.3). However, as indicated by the significant interaction between region and elevation, the response of SD was not identical in the two estuaries: SD increased from low to mid elevations in fresh ($P < 0.001$) and brackish marshes in the Connecticut, but not in the Elbe estuary. In the Elbe estuary, SD was similar at low and mid elevations in fresh and brackish marshes and significantly increased only from low and mid marsh to high marsh ($P < 0.001$). In the salt marshes, we found a significant increase in SD from low to mid marsh ($P < 0.0028$). SD showed a similar response to the salinity gradient in the Connecticut and Elbe estuaries at low and high elevations. Yet, we found differences in SD in relation to salinity at mid elevations: in the Connecticut estuary, SD generally increased from salt via brackish to fresh marshes on each elevation. Planned comparisons showed that at low elevations, SD significantly increased from salt to fresh, while there was no significant increase in SD from salt to brackish or from brackish to fresh respectively. At mid and high elevations there was a significant increase in SD from salt to fresh and from brackish to fresh ($P < 0.001$), but not from salt to brackish ($P > 0.05$). In the Elbe estuary, SD did slightly (although not significantly) increase from salt to fresh marshes at low and high elevations, whereas at mid elevations SD had its maximum in salt marshes and was significantly higher there than in brackish marshes ($P < 0.001$).

Evenness

According to the three-factor ANOVA, E was significantly affected by 'marsh type' and 'elevation'. However, the significant interaction among all of the three tested factors indicated different patterns of E along the elevational and salinity gradients in the two estuaries (Table 2.1). In the Connecticut estuary, E increased from salt to freshwater marshes (significantly at low and mid elevations) and predominantly from low to high elevations (not significantly) providing a relatively consistent picture (Fig. 2.3). In contrast, in the Elbe estuary, E did not increase consistently from low to high elevations in any of the three marsh types, and decreased from salt to freshwater marshes (except for high marshes). In more detail, E decreased (although not significantly) from low to mid marsh along the elevational gradient in fresh and brackish marshes. Additionally, E was significantly higher in salt marshes than in fresh or brackish marshes at mid elevations. In the Connecticut estuary, E was significantly higher in fresh than in salt marshes (low and mid elevations). There were no significant differences in E along the salinity gradient at high elevations in either of the estuaries ($P > 0.0028$).

Species composition

The ordination of the vegetation of the Elbe estuary produced well-defined groups allowing a visual estimation of similarity between the different vegetation zones (Fig. 2.4a). Whereas the salt marsh vegetation from the different elevation zones split up very clearly along the first coordinate axis, the vegetation of brackish and freshwater marsh formed a joint group which slightly differentiated corresponding to elevational vegetation zone (low marsh, mid marsh and high marsh). Fresh and brackish marshes were more similar to each other than brackish and salt marshes in the Elbe estuary and there were comparably small differences between fresh and brackish mid and high marshes. The length of the axis was 10.0, which corresponds to a more than two-fold species turnover. The length of axis 2 was 3.6 thereby indicating this axis to be less important. Low elevations in the Elbe salt marshes were dominated by *Salicornia europaea* agg. and *Spartina anglica*, mid marshes were composed of *Puccinellia maritima, Spartina anglica, Aster tripolium, Atriplex portulacoides* and others, while the high marsh was dominated by *Festuca rubra* and *Elymus athericus*. Brackish and fresh low marshes were generally dominated by *Bolboschoenus maritimus* and/or *Schoenoplectus tabernaemontani* accompanied by *Cotula coronopifolia* in brackish and glycophytes such as *Nasturtium officinale* in freshwater marshes. Brackish and fresh mid marshes were composed of monotypic *Phragmites australis* belts (in freshwater marshes associated with scattered *Caltha palustris, Nasturtium officinale* and other glycophytes). Brackish and fresh high marshes were dominated by tall forbs (e.g. *Angelica archangelica, Urtica dioica, Calystegia sepium, Anthriscus sylvestris*), intermixed with *Phragmites australis* and other grasses such as *Phalaris arundinacea*.

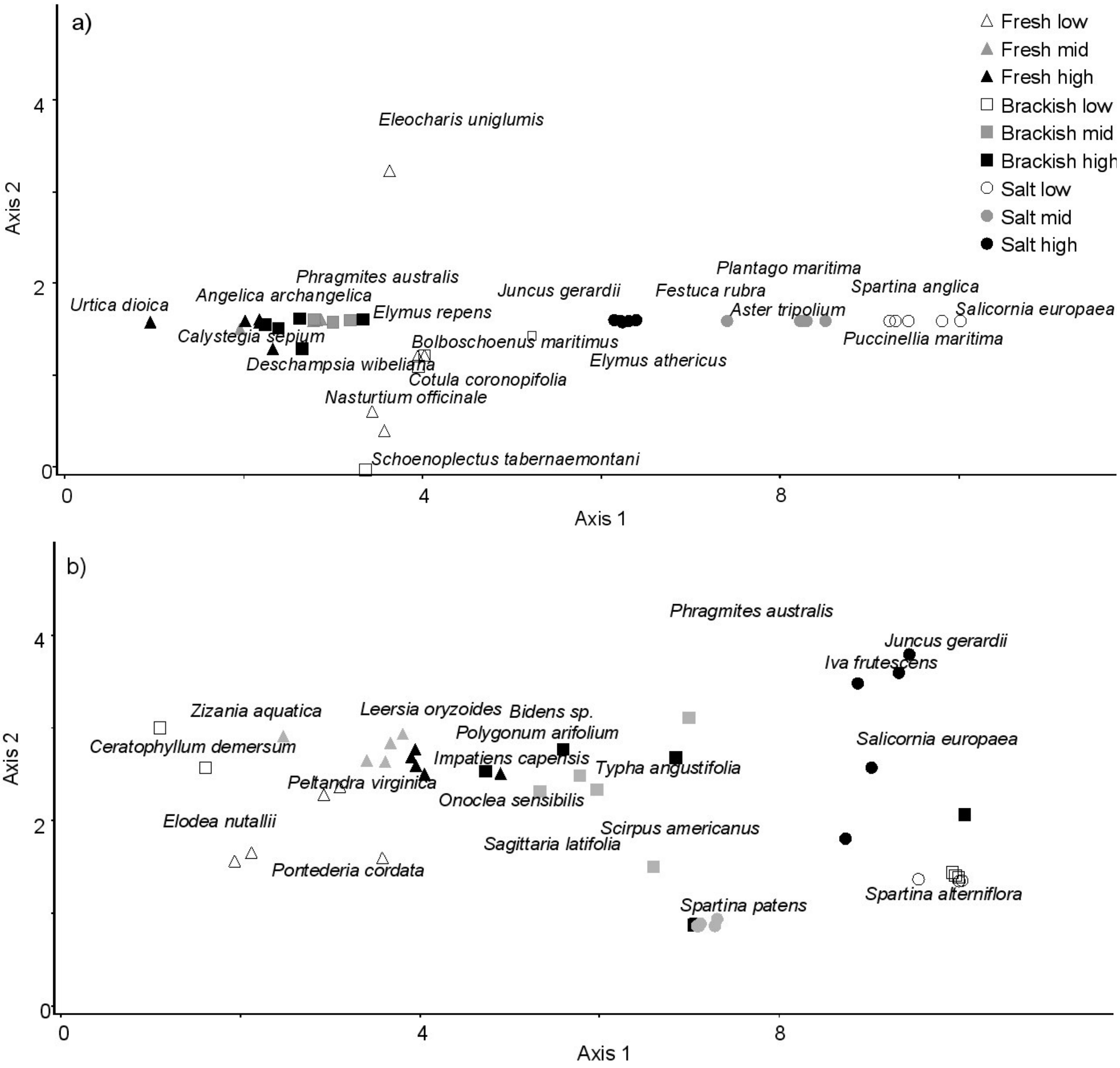

Figure 2.4 Ordination diagram of the sampled vegetation based on percent cover values of species derived from the recorded Londo-scale data (see Materials and methods for details) by using DCA (Detrended Component Analysis) for Elbe (a) and Connecticut estuarine marshes (b). The different marsh types and elevations are illustrated by circles (salt marshes); diamonds (brackish marshes) and triangles (tidal freshwater marshes). Species names are displayed without symbols.

The vegetation of the Connecticut estuary was generally more variable in species composition (Fig. 2.4b). All salt marsh sites separated out clearly on the right hand side of the plot. The brackish marshes were spread more widely. Some brackish low marshes appear to be more similar in species composition to freshwater marshes, while others grouped together with low salt marshes. There was also some variability within the brackish high marshes. The freshwater marsh vegetation separated from that of the other two marsh types forming more distinct groups in mid and high marshes and less distinct groups in low marshes. As in the Elbe estuary, fresh mid and high marshes appeared to be similar to each other with respect to vegetation composition. The length of axis 1 was similar to the one for the Elbe (9.6) indicating a similar species turnover. The length of axis 2 was 3.1. In the Connecticut estuary, salt and brackish low marshes contained more or less monotypic *Spartina alterniflora* stands. *Zizania aquatica* was also present in some brackish low marshes. Salt mid marshes were dominated by *Spartina patens*. Brackish mid marshes were mostly dominated by *Typha angustifolia* and *Scirpus americanus*. Salt high marshes had a mixed vegetation of *Juncus gerardii*, *Iva frutescens* and other halophytes, whereas brackish high marshes were either dominated by *Spartina patens* or *Typha angustifolia* mixed with *Thelypteris palustris* or *Polygonum arifolium*. The lowest elevations in freshwater marshes were composed of *Zizania aquatica, Pontederia cordata* and *Elodea nutallii*. Fresh mid and high marshes were primarily composed of forbs such as *Peltandra virginica*, *Impatiens capensis* and *Polygonum* species with *Onoclea sensiblis* and *Thelypteris palustris* in the high marsh.[1]

2.6 Discussion

The search for general relationships between environmental severity gradients and diversity patterns has long been an important issue in community ecology (e.g. Keddy 2007). Beside local processes (abiotic habitat conditions and biotic interactions), regional-scale influences, including evolutionary and biogeographic processes, are suggested to shape species diversity patterns via the size of the regional species pool (Harrison and Cornell 2008). Although the regional species pools of the Elbe estuary in Europe and the Connecticut estuary in North America share the majority of the occurring genera, our literature survey showed that beside the different composition of the regional species pools, the regional species pool for marsh vegetation of the Connecticut estuary was much (33%) larger than the regional species pool for the Elbe estuary. This is consistent with findings on the species pools of temperate forests in North America and Europe and is very likely due to differences concerning the evolutionary history of the continents leading to higher extinction rates in Europe (Reid 1935; see Introduction). The larger regional species pool for the Connecticut estuary was reflected in the higher SD we found in Connecticut freshwater marshes compared to the Elbe freshwater marshes (twice as many species on each elevation, Fig. 2.3). Surprisingly, we did not find a higher SD in Connecticut brackish or salt marshes compared to the Elbe marshes. However, this may be a consequence of local conditions, i.e. the higher salinity of the Connecticut brackish and salt marshes compared to the Elbe marshes, leading to a smaller number of species, which were able to pass this abiotic filter.

Regarding our hypothesis on species diversity patterns along the estuarine stress gradients, we found general similarities among the estuaries, but also some striking differences looking at the patterns in detail. In the Connecticut estuary, the pattern of species diversity almost perfectly supported our hypothesis of increasing SD and E with decreasing salinity or flooding stress. In the Elbe estuary, we found an overall increase of SD from low to high elevation in all marsh types, however, SD and E showed a strong depression in fresh and brackish mid marshes, i.e. the vegetation zones typically dominated by *Phragmites australis* (e.g. Kötter 1961). As a consequence, while our hypothesis was supported on low and high elevations along the salinity gradient in the Elbe estuary, SD and E were higher in salt marshes than in fresh or brackish marshes at mid elevations. The divergence of SD and E from the expected pattern along the estuarine gradients in the Elbe is striking, because we assume the most important abiotic filters along the estuarine stress gradients (salinity and tidal

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[1] For a list of mean species covers observed in the study plots in the different vegetation zones of Elbe and Connecticut estuarine marshes see Table A and B in the appendix.

inundation) to have a similar impact on the occurring marsh vegetation in the two estuaries. Overall, the salinity gradient was found to be a negative forcing factor on the regional and community species pools in both estuaries. Because of the non-continuous pattern of SD, the results for the Elbe estuary do partly contrast with other studies along estuarine gradients, which found SD to generally increase from salt to freshwater marshes (Barrett 1989; Garcia et al. 1993; Gough et al. 1994; Grace and Pugesek 1997; Crain et al. 2004) and from low to high elevation (Gough et al. 1994; Grace and Pugesek 1997; Khedr 1998). The pattern of E we found along the salinity gradient in the Elbe estuary does deviate from results by Crain et al. (2004), who found that lower salinity was related to a higher E in tidal marshes along an estuarine salinity gradient in New England, similar to our results from the Connecticut. In contrast, Scrosati and Heaven (2007) found highest E in seaweeds and invertebrates in rocky shore habitats at the most wave-exposed (stressful) sites.

The question is, why do the patterns of species diversity (species density and evenness) differ between the Elbe and the Connecticut estuary, or, more precisely, what is the reason for the depression in species diversity in mid marshes of the Elbe estuary? Although the design of our study is not sufficient to draw conclusions on mechanisms leading to the observed plant diversity patterns in the Elbe and Connecticut estuaries, we discuss some hypotheses on the factors, which may have caused these deviating patterns. First of all, abiotic factors beside salinity (e.g. other soil parameters, tidal amplitude, water quality) are likely to have differed between the Elbe and the Connecticut estuary (e.g. due to the long history of human alterations in the Elbe estuary) and may have directly affected species diversity of the marsh vegetation. It is unfortunate that we are not able to compare additional abiotic parameters between the estuaries. Beside abiotic factors, biotic interactions might also act as filters affecting diversity patterns. Thus, species which are not filtered out by habitat conditions may be excluded from the community by competition (Grace and Pugesek 1997; Zobel 1997), which may result in a reduction of SD and E. It seems likely that competition may have played a role for species diversity patterns in the Elbe estuary.

On the other hand, positive interactions between plants (facilitation) might enhance species diversity by ameliorating habitat conditions and thus promoting survival of species, which normally (i.e. without facilitation) would not be able to survive under the given conditions (Hacker and Gaines 1997; Michalet et al. 2006). Facilitation has been shown to be important predominantly under medium to harsh environmental conditions, where facilitator species allow more competitive but less stress-tolerant species to coexist (Hacker and Bertness 1999). In addition, a model proposed by Hacker and Gaines (1997) suggests that an observed peak in species richness at intermediate stress levels in New England salt marshes is the outcome of reduced interspecific competition, coupled with the presence of a facilitator species and conditions of intermediate environmental stress. They predict that in the absence of facilitation, species richness would be low at all tidal elevations. Our vegetation surveys showed that fresh and brackish mid marshes of the Elbe estuary were dominated by the highly competitive species *Phragmites australis*. We speculate that the low species diversity in fresh and brackish mid marshes in the Elbe estuary might be either due to high competition by the dominant *P. australis* or a lack of facilitation in this marsh zone (or a combination of both factors). This is supported by the low E values we observed in the *P. australis*-dominated zones. The important role of *P. australis* in affecting SD was stated by Lenssen et al. (2000) for riparian wetlands, in which SD decreased with an increasing standing crop of *P. australis*. In a transplant experiment along the salinity gradient in the Elbe estuary, halophytes being planted in dense *Phragmites* stands died due to competition with *P. australis* (Engels and Jensen, in press). In contrast, the high SD and E on mid elevations in Elbe salt marshes might indicate predominance of facilitation at intermediate stress levels. E is supposed to directly reflect effects of biotic interactions in plant communities (Stirling and Wilsey 2001).

In addition to local (abiotic and biotic) factors, regional and historical factors may influence diversity patterns (Pärtel et al. 1996). We suggest that the evolutionary history of the investigated regions may have affected the composition of the regional species pools and thus the availability of species with specific traits (e.g. high competitive ability). Moreover, the long history of human alterations in the Elbe estuary compared to the Connecticut estuary, may have altered the abiotic environment (e.g. higher tidal amplitude) in such a way, that individual species (e.g. *P. australis*) were stimulated. Recent studies suggest that shoreline development facilitates the spread of the non-native (European) genotype of *P. australis* in North American coastal marshes (e.g. Bertness et al. 2002). However *P. australis* is native to Europe and a natural component of fresh and brackish marshes in the Elbe estuary. Core analyses of marsh sediments have shown that *P. australis* has been a natural and formative component of tidal freshwater and brackish marshes at least since 600 BC in north-western Germany (Behre 1996; Gerdes 2003). In fact, we suspect that we might eventually have found a similar diversity pattern as in the Elbe in the Connecticut marshes, if we had included Connecticut marshes dominated by the non-native *P. australis*.

2.7 Conclusions and perspectives

The results of our study indicate that plant species diversity along horizontal and vertical estuarine stress gradients in a European (Elbe) and a North American (Connecticut) river system shows similar overall increases in SD from tidal salt to fresh marshes and from low to high elevations. However, patterns of SD and E differ, when particular elevational vegetation zones and marsh types are compared, even though abiotic filters are supposed to be largely similar. We hypothesise that this may be due to differences in the influence of biotic interactions (competition and facilitation) along environmental gradients in the two estuaries, altering the direct effects of abiotic stress on species diversity patterns. What controls the strength of biotic filters remains to be investigated by experimental studies. It is likely that the impact of biotic interactions on species diversity is at least partly driven by the evolutionary history of the regions leading to a particular size and composition of the regional species pools and by historical and recent human impacts on a local scale, which may directly (via alteration of abiotic conditions) or indirectly (via facilitating particular species or species traits) affect the species pool and species diversity.

2.8 Acknowledgements

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3 Role of biotic interactions and physical factors in determining the distribution of marsh species along an estuarine salinity gradient

Jana Gesina Engels and Kai Jensen

Oikos, in press (DOI: 10.111/j.1600-1706.2009.17940.x)

3.1 Abstract

Understanding the mechanisms that shape plant distribution patterns is a major goal in ecology. We investigated the role of biotic interactions (competition and facilitation) and abiotic factors in creating horizontal plant zonation along salinity gradients in the Elbe estuary.

We conducted reciprocal transplant experiments with four dominant species from salt and tidal freshwater marshes at two tidal elevations. Ten individuals of each species were transplanted as sods to the opposing marsh type and within their native marsh (two sites each). Transplants were placed at the centre of 9-m^2 plots along a line parallel to the river bank. In order to disentangle abiotic and biotic influences, we set up plots with and without neighbouring vegetation, resulting in five replicates per site.

Freshwater species (*Bolboschoenus maritimus* and *Phragmites australis*) transplanted to salt marshes performed poorly regardless of whether neighbouring vegetation was present or not, although 50-70% of the transplants did survive. Growth of *Phragmites* transplants was impaired also by competition in freshwater marshes. Salt marsh species (*Spartina anglica* and *Puccinellia maritima*) had extremely low biomass when transplanted to freshwater marshes and 80-100% died in the presence of neighbours. Without neighbours, biomass of salt marsh species in freshwater marshes was similar to or higher than that in salt marshes.

Our results indicate that salt marsh species are precluded from freshwater marshes by competition, whereas freshwater species are excluded from salt marshes by physical stress. Thus, our study provides the first experimental evidence from a European estuary for the general theory that species boundaries along environmental gradients are determined by physical factors towards the harsh end and by competitive ability towards the benign end of the gradient. We generally found no significant impact of competition in salt marshes, indicating a shift in the importance of competition along the estuarine gradient.

3.2 Introduction

Why do plants grow, where they grow? Finding answers to such a fundamental question is at the core of ecology. The mechanisms responsible for the formation of plant distribution patterns along environmental gradients have already been the subject of numerous studies and are still a burning issue today. While early works on plant zonation in salt marshes focused exclusively on abiotic factors such as tidal inundation and salinity (Adams 1963; Cooper 1982), Snow and Vince (1984) were the first to provide experimental evidence that the distribution of salt marsh species along the tidal flooding gradient was not solely due to physiological restrictions of the species but was also affected by interspecific competition. They generally concluded that species distributions are limited by species' physical tolerances toward one end of the gradient, and by competitive ability towards the other. Similar mechanisms were found to be responsible for species zonations in freshwater wetlands (Grace and Wetzel 1981; Wilson and Keddy 1985) and have since then been reinforced by numerous studies along salt marsh gradients (Bertness and Ellison 1987; Bertness 1991a,b; Pennings and Callaway 1992; Pennings et al. 2005). Inferred from these studies, marsh plant zonation has been agreed to be the outcome of competitively dominant plants monopolising physically benign habitats and displacing competitively subordinate plants to physically harsh habitats, where edaphic conditions preclude the persistence of the competitive dominants (Bertness and Leonard 1997). Recently, this hypothesis has been supported also by plant distribution patterns along estuarine salinity gradients in southern New England. Crain et al. (2004) found evidence that species of tidal freshwater marshes are restricted from salt marshes by physical factors, and that salt marsh species are precluded from tidal freshwater marshes due to competitive displacement by freshwater species.

Other studies suggest that while competition limits the distribution boundaries of salt marsh species towards benign habitats, positive plant interactions such as facilitation may amplify a species' distribution range towards physically harsh habitats by amelioration of stressful edaphic conditions, i.e. buffering soil salinity (Bertness and Hacker 1994; Bertness and Leonard 1997). A more general hypothesis is that the dominant type of biotic interaction between neighbouring plants shifts with the magnitude of abiotic stress; low-stress habitats would be characterised by intense competition, whereas in physically stressful habitats facilitation would become more important (Bertness and Shumway 1993; Bertness and Hacker 1994; Bertness and Leonard 1997). Besides vertical gradients in salt marshes, this shift in the relative importance of biotic interactions was also detected on a larger scale along estuarine salinity gradients (Crain 2008).

To date, most research on the interplay between physical and biotic factors affecting plant distribution in estuarine and coastal marshes has been conducted in North America. However, comparable studies dealing with plant zonations along environmental gradients in European marshes with different evolutionary history and different plant species composition (Engels and Jensen 2009) are almost completely lacking. In this study, we seek to elucidate the role of biotic interactions (competition, facilitation) and abiotic factors in creating horizontal plant zonation along salinity gradients in the Elbe estuary (Germany). Tidal freshwater and brackish marsh communities in the Elbe River are threatened by increased salinity levels and changes in tidal regime due to human alteration of river morphology and hydrology as well as sea level rise. Our study contributes to the general knowledge of community dynamics in estuarine marshes and may thus facilitate predictions on possible consequences of increased salt water intrusions in tidal freshwater marshes enforced by climate change and/or other human alterations such as channel deepening.

We hypothesised that the upper distribution boundary of salt marsh species in the Elbe estuary is determined by competition, whereas the lower distribution boundary of freshwater species is set by the species' tolerances to abiotic stress (i.e. salinity). To test this hypothesis, we conducted reciprocal transplant experiments with four dominant species of salt and tidal freshwater marshes at two tidal elevations along the estuarine gradient. In order to disentangle abiotic and biotic influences on transplant performance, we set up treatments with and without neighbouring vegetation. We predicted that (i) salt marsh species will grow as well as or better in freshwater marshes than in salt marshes in the absence of plant neighbours, but will not be able to survive in freshwater marshes with neighbouring plants present, and that (ii) freshwater species will perform poorly or die in salt marshes, particularly without neighbouring vegetation present, while in the presence of neighbouring plants their survival may be positively affected by facilitation.

3.3 Methods

The study system

The experiment was conducted in estuarine salt and freshwater marshes of the Elbe River. The Elbe estuary is the largest estuary on the German coast (150 km in length), extending from about 30 km east from Hamburg (weir restricts tidal surge) to the North Sea. The mean tidal range is 3 m at the inlet, 3.5 m at the port of Hamburg and 2 m at the upstream end of the estuary (Kappenberg and Grabemann 2001). For the last 1000 years, the Elbe estuary has been subjected to a multitude of human interventions such as land reclamation and dike construction as well as embankments of marsh forelands and tributaries, resulting in a considerable loss of natural habitats (Garniel and Mierwald 1996). Nevertheless, marshes of the Elbe estuary still exhibit a distinct differentiation of salt, brackish and tidal freshwater marshes. Salt marshes are mainly found on the northern shore of the river mouth, where water salinity is about 10 to 18 depending on river discharge (Caspers 1959, measured soil salinity with a refractometer in August 2007: 22-24). Tidal freshwater (oligohaline) marshes are found from the Stör tributary upriver to the weir with a water salinity between 0.5 and 3 (Caspers 1959; measured soil salinity with a refractometer in August 2007: 0.5-2). All tidal marshes show a distinct vertical zonation that corresponds to tidal inundation frequency and duration with a low marsh (inundated twice a day), a mid marsh located in the range of mean high tide (inundated at least twice a month during spring tides) and a high marsh (inundated only during storm tides; Engels and Jensen 2009).

Two salt marshes at Dieksanderkoog (site 1: 53°57’39.56”N, 8°52’47.32”W, site 2: 53°57’19.47”N, 8°53’13.75”W) and two tidal freshwater marshes (Hollerwettern: 53°49’59.98”N, 9°22’13.61”W and Krautsand: 53°46’34.96”N, 9°21’58.4”W) in the Elbe estuary were selected for this study. All sites can be considered as having close to natural conditions (i.e. no artificial bank reinforcements; no agricultural use) and show the vertical plant zonation typical for the respective marsh type.

Experimental design

Four dominant and typical species of salt and tidal freshwater marshes of the Elbe estuary were transplanted reciprocally within their elevation level: *Spartina anglica* (low salt marsh; henceforth referred to as *Spartina*) was exchanged with *Bolboschoenus maritimus* (low freshwater marsh; henceforth referred to as *Bolboschoenus*), and *Puccinellia maritima* (mid salt marsh; henceforth referred to as *Puccinellia*) was exchanged with *Phragmites australis* (mid freshwater marsh; henceforth referred to as *Phragmites*). Additionally, all species were transplanted to the marsh they derived from as a transplantation control. In order to test for neighbour effects, we established plots (3 x 3 x 3 m) with natural neighbouring vegetation and without neighbouring vegetation (aboveground vegetation removed) for each species in each marsh. Each treatment for each species was replicated five times within each study site and in two sites per marsh type to enhance the generality of the results. Thus we used a factorial design with the factors marsh type, ‘neighbour treatment’ and ‘study site nested in marsh type’.

The plots were set up at low (*Bolboschoenus*/*Spartina*) and mid elevations (*Phragmites*/ *Puccinellia*) of the selected salt and freshwater sites along two lines parallel to the river bank. The transplant sods were planted in the beginning of April 2007 and placed at the centre of 9-m^2 plots. One week before the start of the experiment, transplant sods containing intact shoots and rhizomes (20 x 20 x 25 cm) were cut and kept at the site in perforated plastic bags to prevent them from adhering to the substrate. Just before the start of the experiment, the transplant sods of each species were collected and randomly assigned to the sites and treatments. Aboveground biomass on the no-neighbour-treatments was cut to 5–10 cm height with hedge shears. This procedure was repeated every 2–4 weeks during the course of the experiment to keep the vegetation low. The experiment was terminated in September 2007.

Data collection

Once a month (in May, June, July and August), transplants were checked for survival, living shoots were counted, and shoot length and shoot diameter of eight randomly selected shoots per sod were recorded. Shoots were defined as alive as long as part of the shoot was green (for shoot length only the green part was measured). Transplants were described as dead if all shoots had died. At the end of the experiment in September 2007, live aboveground biomass of the transplant sods was harvested, dried at 60°C to a constant weight and weighed.

Biomass estimation

In order to follow biomass development during the course of the experiment, allometric biomass estimations were applied. This allowed calculating biomass values from the measured growth parameters (shoot length and diameter) of the transplants with non-destructive methods via a calibration curve. On the basis of 60 shoot samples per species that were taken in summer 2007 in close vicinity to the study plots, dry weight was related to shoot length and diameter (for *Puccinellia* only shoot length). We found a 2nd order polynomial regression to best represent the relationship between the measured growth parameters and the shoot dry weight of the transplants (extreme outliers removed). The regression models used shoot length x diameter as the predictor variate (x) and explained 85% of the variance in the data for *Spartina* ($y = 0.0002x^2 + 0.0412x$), 77% for *Bolboschoenus* ($y = 0.00004x^2 + 0.03757x$) and *Phragmites* ($y = 0.0001x^2 + 0.0585x$, and 58% for *Puccinellia* ($y = 0.0001x^2 + 0.0011x$).

For estimating the aboveground biomass per transplant sod, the mean biomass of one shoot was calculated on the basis of measured growth parameters of eight shoot samples per sod via the calibration curve and multiplied by the number of shoots on the sod. Unfortunately, it was not possible to determine the shoot number on *Puccinellia* sods. Therefore, shoot number was estimated via cover of green *Puccinellia* shoots on the sod. To relate percent cover to shoot density, we calculated a ‘shoot density index’ (i.e. mean number of shoots per 1 cm^2) estimated on the basis of 20 counts on plots of 3 x 3 x 3 cm with dense (100%) *Puccinellia* cover on an adjacent intact *Puccinellia* sward. Based on this index, biomass of each *Puccinellia* sod could be estimated via percent cover and sod size.

Data analysis

We used GLMs (generalised linear models) within the PASW Statistics 17 Advanced models procedure as data did not meet assumptions of ANOVA (data did not show homogeneity of variances). Since many of the transplants died during the course of the experiment, we first tested with a log-linear model how the factors ‘marsh type’, ‘neighbour treatment’ and ‘study site nested in marsh type’ affected the survival time (months survived) of the transplants assuming poisson errors. We then excluded all dead individuals (biomass = 0) from the dataset. We used another GLM assuming normal errors for testing effects of the same factors on the aboveground biomass of the surviving plants. We used the log-link function to compensate for the heteroscedasticity of the response variable.

Data were analysed separately for each species testing all main factors and their interactions. The biomass analyses were additionally conducted for all sampling dates. For May to August, we used biomass values based on the allometric estimation described above, and for September the actual biomass values. Following the GLM tests, we applied pairwise comparisons using the Bonferroni-procedure to determine treatment differences in terms of transplant survival and biomass.

Since the response of the transplants was most pronounced in July and August, when maximum biomass was reached, we decided to present the July (estimated) biomass values in comparison to the (measured) September values. In September, the biomass of all transplants had decreased, particularly in the freshwater marshes, probably due to the beginning of natural decay.

3.4 Results

Transplant survival

In general, the freshwater species survived when transplanted to salt marshes better than we expected. Half of the *Bolboschoenus* sods were dead by the end of the experiment, regardless of whether neighbouring vegetation was present or not (Table 3.1). Thirty percent of the *Phragmites* transplants died in the salt marshes in the plots without neighbours, while all transplants survived on the plots with neighbours present. In contrast to *Bolboschoenus*, many *Phragmites* transplants (80%) died in plots with neighbours in the freshwater marshes. These contrasting neighbour effects on *Phragmites* survival were reflected in a significant interaction between ‘marsh type’ and ‘neighbour treatment’ affecting the survival time of the species (Fig. 3.1; LR χ^2 (likelihood ratio χ^2) = 15.652; $p < 0.001$). Pairwise comparisons showed that *Phragmites* transplants survived significantly longer in freshwater marshes without neighbours than with neighbours present. Surprisingly, *Phragmites* transplants survived significantly longer in salt marshes than in freshwater marshes if neighbouring vegetation was present. Unlike *Phragmites*, the survival time of *Bolboschoenus* was only significantly affected by marsh type (LR χ^2 = 15.205; $p < 0.001$); *Bolboschoenus* survived generally better in freshwater marshes than in salt marshes with neighbour effects being less important.

Table 3.1 Survival (%) and final dry shoot biomass (g sod^{-1}, means ± SE) of transplants of *Bolboschoenus maritimus*, *Phragmites australis*, *Spartina anglica* and *Puccinellia maritima* in tidal freshwater and salt marshes on experimental plots with (+NV) and without (-NV) neighbouring vegetation in September.

	Survival (%)				Biomass (g/sod)			
	Fresh		Salt		Fresh		Salt	
	+NV	-NV	+ NV	-NV	+NV	-NV	+NV	-NV
Bolboschoenus	100	100	50	50	21.5 ± 5.2	37.7 ± 5.5	3.9 ± 2.7	0.7 ± 0.1
Phragmites	20	100	100	70	6.4 ± 1.9	24.2 ± 4.5	7.2 ± 1.8	3.9 ± 1.2
Spartina	0	100	100	100	0.0 ± 0.0	26.2 ± 2.9	23.2 ± 4.2	20.9 ± 2.2
Puccinellia	20	100	100	100	0.6 ± 0.3	9.3 ± 3.5	22.1 ± 4.2	28.1 ± 2.8

Salt marsh species all survived in the salt marshes, and also in the freshwater marshes, provided that neighbours were removed. With neighbouring vegetation present in the freshwater marshes all of *Spartina* and 80% of *Puccinellia* transplants were dead by the end of the experiment (Table 3.1). Survival time of both salt marsh species was significantly affected by both marsh type (*Puccinellia*: LR χ^2 = 104.5; $p < 0.001$; *Spartina*: LR χ^2 = 83.7; $p < 0.001$) and neighbouring vegetation (*Puccinellia*: LR χ^2 = 114.1; $p < 0.001$; *Spartina*: LR χ^2 = 83.7; $p < 0.001$) as well as by the interaction between marsh type and neighbouring vegetation (*Puccinellia*: LR χ^2 = 104.5; $p < 0.001$; *Spartina*: LR χ^2 =5 83.7; $p < 0.001$) illustrating the contrasting effect of neighbour presence in salt and freshwater marshes. Both species survived significantly longer without neighbours in freshwater marshes or with neighbours in salt marshes than with neighbours in freshwater marshes ($p < 0.001$). Additionally, survival time of *Puccinellia* was significantly, although less severely, affected by the site (nested in salinity) it was transplanted to (LR $\chi^2 = 70.4$; $p < 0.001$) and by the interaction between neighbouring vegetation and site (LR $\chi^2 = 70.4$; $p < 0.001$).

Transplant biomass

Surviving transplants of *Bolboschoenus* reached a significantly higher biomass (more than 20 times higher) in the freshwater marshes than in the salt marshes regardless of neighbour treatment in July (significant effect of 'marsh type'; LR $\chi^2 = 51.3$; $p < 0.001$; Fig. 3.2). Besides we found a small, but significant effect of "study site nested in marsh type" (LR $\chi^2 = 7.8$; $p < 0.05$). The significant difference in *Bolboschoenus* biomass between the marsh types was still visible as a trend in September (LR $\chi^2 = 3.8$; $p < 0.1$; Table 3.1), however, the effect of 'site' gained more importance and became highly significant at the end of the experiment (LR $\chi^2 = 16.535$; $p < 0.001$).

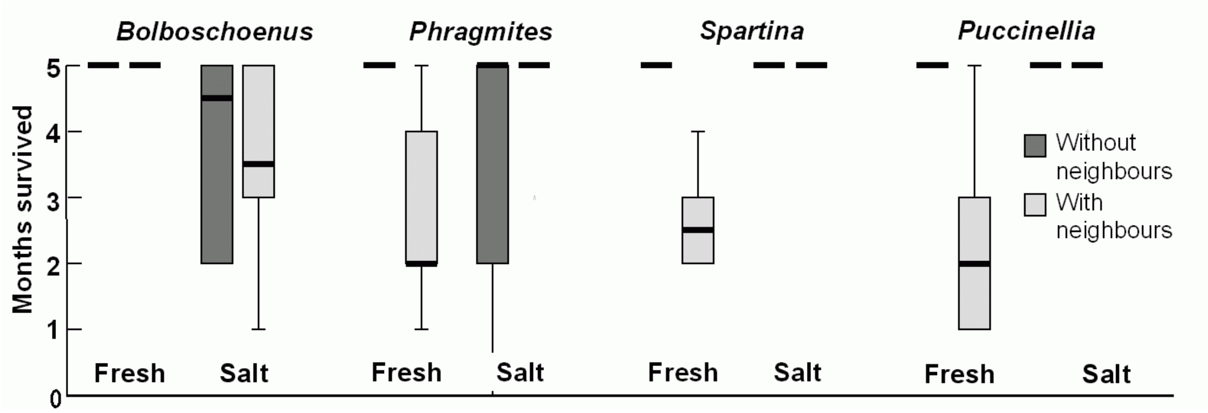

Figure 3.1 Survival time (months) for transplants of *Bolboschoenus maritimus*, *Phragmites australis*, *Spartina anglica* and *Puccinellia maritima* on experimental plots with and without neighbouring vegetation in freshwater and salt marshes (study sites pooled in graphic, n = 2 x 5). Medians lines, outliers (boxes) and extremes (whiskers) are shown.

Phragmites reached its maximum biomass in July/August, when biomass was more than 10 times higher in the freshwater than in the salt marshes in plots without neighbours. However, we could not detect any significant treatment effects on the biomass of surviving *Phragmites* transplants in July or September ($p < 0.1$; Fig. 3.2; Table 3.1), probably due to high variation in biomass of surviving plants in the freshwater marsh and the small sample size of surviving *Phragmites* individuals in total. That said, *Phragmites* growth did appear to be strongly limited upon transplantation to salt marshes, particularly in plots without neighbours (Fig. 3.2), but also if transplanted within its own vegetation type.

Biomass of *Spartina* transplants was significantly affected by the presence of neighbours (LR $\chi^2 = 15.0$; $p < 0.001$; Fig. 3.2) and by the 'marsh type' by 'neighbouring vegetation' interaction (LR $\chi^2 = 9.3$; $p < 0.01$) in July. Pairwise comparisons showed that biomass of surviving transplants was significantly higher in freshwater marshes compared to salt marshes, when neighbouring vegetation was excluded ($p < 0.001$). However, when neighbours were not excluded, *Spartina* biomass was higher in salt marshes ($p < 0.05$). We did not find any significant differences between plots with and without neighbours in the salt marshes. The results were the same for August, when peak biomass was reached and *Spartina* biomass in the freshwater without neighbours was doubling biomass of the salt marsh plots (data not shown). We could not carry out any statistics for September biomass (Table 3.1), as all transplants had died in the freshwater plots with neighbours at that time.

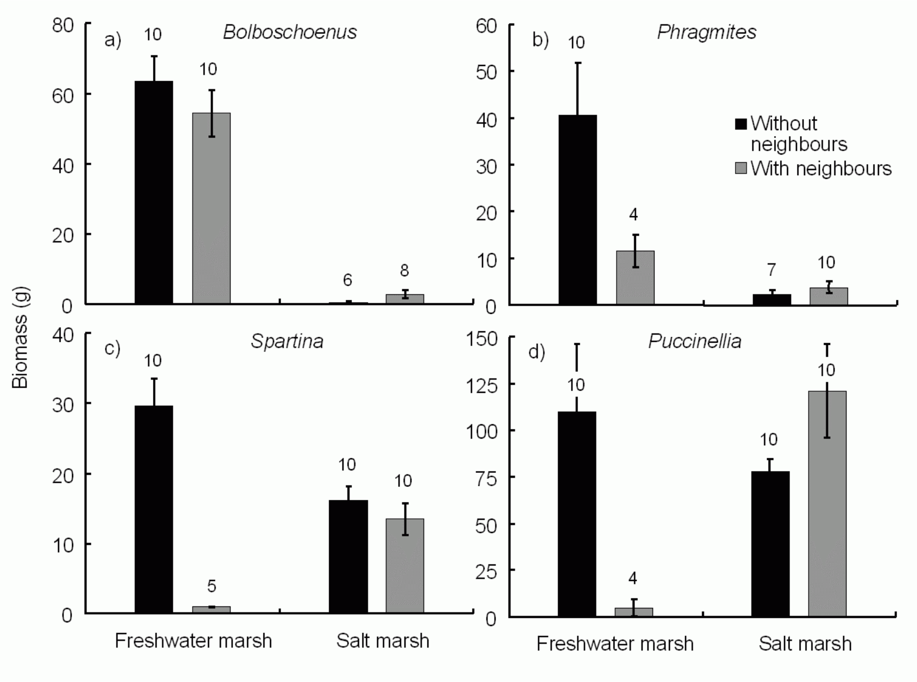

Figure 3.2 Estimated dry shoot biomass per sod of surviving transplants of *Bolboschoenus maritimus*, *Phragmites australis*, *Spartina anglica* and *Puccinellia* maritima on experimental plots with and without neighbouring vegetation in freshwater and salt marshes (study sites pooled) for sampling date July. Sample sizes (number of surviving transplants) are shown above bars. Means ± SE.

Similar to *Spartina*, surviving *Puccinellia* transplants were significantly affected by an interaction between 'marsh type' and 'neighbour treatment' (LR $\chi^2 = 5.7$; $p < 0.05$) in July, indicating contrasting effects of neighbours on the growth of *Puccinellia* in freshwater and salt marshes (Fig. 3.2). Thus, biomass of *Puccinellia* transplants was significantly higher in freshwater marshes without neighbouring vegetation than with neighbours present ($p < 0.05$), while there was no significant difference in biomass between neighbour treatments in the salt marshes. Without neighbouring vegetation present, biomass of *Puccinellia* was similar in salt marshes and tidal freshwater marshes. In September, the biomass of surviving transplants was very low also in plots without neighbours in the freshwater marshes, and the biomass of the transplants was significantly higher in the salt marshes (LR $\chi^2 = 8.4$; $p < 0.01$; Table 3.1). A significant effect of 'study site' was also found in September (LR $\chi^2 = 13.5$; $p < 0.01$).

3.5 Discussion

Understanding the forces driving the distribution of plants in nature is of crucial importance, particularly in the face of climate change. In our study, we show that horizontal plant zonation along the estuarine salinity gradient in the Elbe River is affected by both abiotic and biotic factors. To our knowledge, this is the first experimental study that investigated the drivers of plant distribution patterns along estuarine gradients in Europe.

Reciprocal transplant experiments constitute an appropriate method for distinguishing abiotic from biotic influences on plant zonation (Snow and Vince 1984). In our study, *Phragmites* controls with neighbouring vegetation present, performed poorly compared to adjacent established *Phragmites* stands. These results point out the overwhelming effect of competition exerted by established *Phragmites* stands in tidal freshwater marshes of the Elbe estuary. Additionally, *Phragmites* seemed to be impaired by transplantation. Since *Phragmites* is a clonal plant with an extensive underground rhizome system, it may be particularly sensitive to being cut from its physiologically integrated rhizomatous network (Hara et al. 1993). Another problem was encountered with the biomass estimation of *Puccinellia*: Estimated biomass in July/August was about four-fold the biomass measured in September, which cannot be solely explained by natural decay and is likely to involve a methodological error in the biomass estimation procedure (conversion of plant cover to abundance of shoots on the transplant sods). The estimated biomass values for *Puccinellia* can therefore only be used for comparison among treatments.

Nevertheless, our results did support our hypothesis on the performance of tidal freshwater species transplanted to salt marshes. The two studied freshwater species, *Bolboschoenus* and *Phragmites*, had a significantly reduced survival time when transplanted to salt marshes (for *Phragmites* only compared to no-neighbour-treatments in freshwater marshes). Besides, the surviving plants had extremely reduced biomass in salt marshes compared to freshwater marshes (not significant for *Phragmites*). This response was independent of whether neighbouring vegetation was present or not, indicating deterioration of the transplants by the prevailing physical conditions.

However, the majority of the freshwater transplants survived in the salt marshes, as 50% of *Bolboschoenus* transplants and 70% of the *Phragmites* transplants were still alive there by the end of the experiment. Here, our results deviate from those of Crain et al. (2004), who reported that the transplanted freshwater species *Typha angustifolia* and *Scirpus robustus* were almost entirely dead within the first summer in the salt marshes. Although we are not able to specify the underlying abiotic factor inhibiting the freshwater species from growing in salt marshes, it is likely that non-halophytes were not able to cope with the increased salinity in salt marshes. Soil salinity has been shown to be of major importance for plant performance in salt marshes, although other stressors (e.g. high sulphide concentration) may also play a role (Odum 1988). The reason for the high survival rate of the freshwater transplants in the salt marshes in our study may be that the salinity of the estuarine salt marshes in the Elbe is rather low (22–24 psu) compared to salt marshes in New England (27–33 psu, Crain et al. 2004). Additionally, the atypical high precipitation in June/July 2007 may have ameliorated local soil salinity stress (DWD 2009).

As hypothesised, the salt marsh species *Spartina* and *Puccinellia* performed well when transplanted to freshwater marshes as neighbouring plants were removed. Their biomass production in the freshwater marshes was then similar to or even higher than the biomass production in salt marshes. With neighbouring vegetation present, however, the survival time of the species was extremely reduced. The observed decrease in biomass of *Puccinellia* on plots without neighbouring vegetation in freshwater marshes in August/September was probably caused by the atypical extreme weather conditions in the summer (DWD 2009) leading to persistent standing water and wrack accumulation in the open plots (pers. obs.). In addition to waterlogging, burial by wrack has been shown to significantly reduce biomass of salt marsh species (Tolley and Christian 1999).

Our results do show that salt marsh species of the Elbe estuary are capable of living in freshwater marshes. The reason for the absence of salt marsh species from freshwater marshes must therefore be biotic interactions with the freshwater vegetation, which apparently suppress the salt marsh species under natural conditions. As we did not remove belowground biomass and thus competition for nutrients was not excluded, the type of competition operating on the plots with neighbours present was probably competition for light. This implies that the overall effect of interspecific competition may have been even underestimated in this study.

Our results suggest that the predominant type of biotic interaction shifts from tidal freshwater to salt marshes. While the presence of neighbouring plants heavily reduced growth of *Spartina*, *Puccinellia* and *Phragmites* transplants in the freshwater marshes (indicating competition), we did not find any negative impacts of neighbours on transplant biomass in the salt marshes. This shift in the impact of neighbours was reflected in a significant interaction between marsh type and neighbour treatment. For *Phragmites* the presence of neighbours in the salt marshes seemed to enhance transplant survival and biomass production, but we did not find any significant evidence of facilitation on any of the transplant species coming from the freshwater marsh. In contrast to our study, Crain (2008) reported a shift from negative to positive interactions between the same plant species along a gradient from oligohaline via brackish to estuarine salt marshes (salinity > 28 psu). Since effects of facilitation in salt marshes are most likely due to amelioration of physical stress (salinity, low redox potential) (Bertness and Hacker 1994), it is possible that the physical conditions in the salt marshes studied here were not harsh enough for facilitation to have a net significant effect, i.e. soil salinity was lower than in the salt marshes studied by Crain (2008).

3.6 Conclusions

Overall, the results of our study did support our hypothesis on the determinants of plant distribution boundaries along the horizontal salinity gradient in the Elbe estuary. Our results are also consistent with studies on vertical plant zonations in salt marshes (Bertness 1991a,b; Pennings et al. 2005). However, there are some studies, in which determinants of vertical salt marsh zonation deviate from commonly observed assumptions, indicating that competition does also shape lower species boundaries in salt marshes under specific conditions (Pennings and Callaway 1992; Bockelmann and Neuhaus 1999; Fariña et al. 2009). Overall, our study contributes to building up the general theory that species boundaries are determined by physical factors towards the harsh end of the environmental gradient and by a species' competitive ability towards the benign end of the gradient. This theory seems to be valid both for steep physical gradients on a local scale (e.g. elevational gradients in salt marshes), and also for gradients on a landscape scale (e.g. estuarine salinity gradients). Moreover, the hypothesis holds true for estuaries from different geographical regions (Europe and eastern North America, Crain et al. 2004) suggesting that the same mechanisms are working in similar habitats, even though plant species composition may be completely different (Engels and Jensen 2009). However, the fact that we only tested two species of each marsh community may be considered a limitation of our study design. We therefore emphasise the need for more experimental evidence on the mechanisms creating plant zonations along European estuarine gradients.

Based on our results, we conjecture that a shift of the upstream border of the brackish zone, along with a potentially rising high water level in the Elbe estuary due to sea level rise and human alterations of the river, may lead to an extension of salt and brackish marshes towards the upstream end of the estuary and a decline of tidal freshwater marshes, which are (due to a weir) not able to retreat further up-estuary (Neubauer and Craft 2009). This development would diminish available habitat for endemic species of tidal freshwater marshes in the Elbe estuary, threatening their long-term persistence. Similar trends are likely to be observed in other (dammed) estuaries as a consequence of sea level rise, and may implicate a threat to tidal freshwater habitats worldwide (Neubauer and Craft 2009). More generally, knowledge of the drivers of plant distributions along stress gradients is essential for successful conservation plans in the face of ongoing environmental change.

3.7 Acknowledgements

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

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4.1 Summary

1. Transplant experiments showed that vegetation zonation along estuarine marsh gradients generate according to the interaction of species tolerances towards 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 test for the first time, how seedling recruitment of marsh species is affected by tidal flooding and salinity. We generally hypothesise that species distribution patterns along estuarine stress gradients are predefined by processes affecting seedling emergence and early establishment.

2. We set up two factorial mesocosm experiments which 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 two weeks and after 15 weeks final aboveground 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 at 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 nine. Biomass of halophytes was higher than that of glycophytes and peaked under brackish conditions. While daily tides predominantly decreased seedling emergence and establishment, spring tides had rather positive 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 a necessary but not solely sufficient condition for determining species distribution patterns along estuarine marsh gradients. Thus, the absence of halophytes in freshwater marshes is controlled by constraints taking effect during the early establishment phase, while glycophytes are precluded from salt marshes due to highly reduced seedling emergence.

4.2 Introduction

Explaining patterns of species distributions along environmental gradients has been a dominating subject in ecological research for decades. Direct effects of abiotic habitat conditions (e.g. Adams 1963; Vince and Snow 1984), interspecific competition (e.g. Snow and Vince 1984; Wilson and Keddy 1985), facilitation (e.g. Bertness and 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 factors such as dispersal (Rand 2000; Chang et al. 2007), germination and seedling survival and establishment (Coops and van der Velde 1995; Lenssen et al. 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 characterised 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 and 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 along estuarine gradients. Similar to the drivers of vertical zonations in salt marshes (e.g. Snow and Vince 1984; Bertness and Ellison 1987; Huckle et al. 2000; Pennings et al. 2005) and freshwater wetlands (Grace and Wetzel 1981; Wilson and 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 and Jensen *in press*).

However, 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. Thus, although the majority of marsh species are perennials that predominantly rely on clonal reproduction (Huiskes et al. 1995; Shumway and Bertness 1992, Capers 2003), there is evidence that seedling dynamics are crucial for defining species ranges along vertical gradients in non-tidal wetlands (Coops and van der Velde 1995; Lenssen et al. 1998) and salt marshes (Bakker et al. 2007). Similarly, it is likely that seedling recruitment plays an important role in generating plant zonation patterns along larger scale estuarine salinity gradients, which has not been tested so far.

Generally, seed survival, germination and early seedling establishment are considered to be the most critical life stages of a plant (Schupp 1995; Fenner and 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 and Engelhardt 2008).

The availability of propagules is mainly dependent on the local seed rain (Chang et al. 2007) and on hydrochorous dispersal of propagules (Noe and Zedler 2001; Neff and 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 and Baldwin 2005; Chang et al. 2007) with the opportunity for long distance dispersal by storm surges (Koutstaal et al. 1987; Huiskes et al. 1995; Chang et al. 2007). Germination is generally triggered by abiotic factors. In estuarine marshes, seedling emergence may be impeded or hampered by high salinity (Ungar 1987; Baldwin et al. 1996; Noe and Zedler 2001) or flooding (Coops and 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 and 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 and Vince 1984; Bakker et al. 1985). However, seedling tolerances towards these factors may differ to the response of adult plants of the same species (Ungar 1978; Beare and 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 et al. 1985; Scholten et al. 1987; Noe and Zedler 2001; Hopfensperger and 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 and van der Velde 1995; Kellog et al. 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 initial patterns of seedling emergence and 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 which 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, the mesocosms were equipped with samples of driftline material which contained 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 and Baldwin 2005, Vogt et al. 2007).

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

4.3 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 greenhouse (Fig. 4.1). 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 and Jensen 2009). Each treatment combination (tidal regime x salinity level) was applied to five mesocosms, which were divided into two experimental chambers: one for the Emergence 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 two times in 24 hours; corresponds to estuarine low marshes); (ii) flooded by spring tides (spring tide, flooded every two weeks; corresponds to estuarine mid marshes); and (iii) no tidal inundation (no tide, control; corresponds to estuarine high marshes). Flooding duration was four hours 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 freshwater treatment, 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 freshwater treatment) 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.

Experimental mesocosms

We used transparent plastic boxes (external dimension: 28 x 50 x 25 cm; W x L x H) as experimental mesocosms. These were divided into two experimental chambers (internal dimension: 26 x 21 x 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.

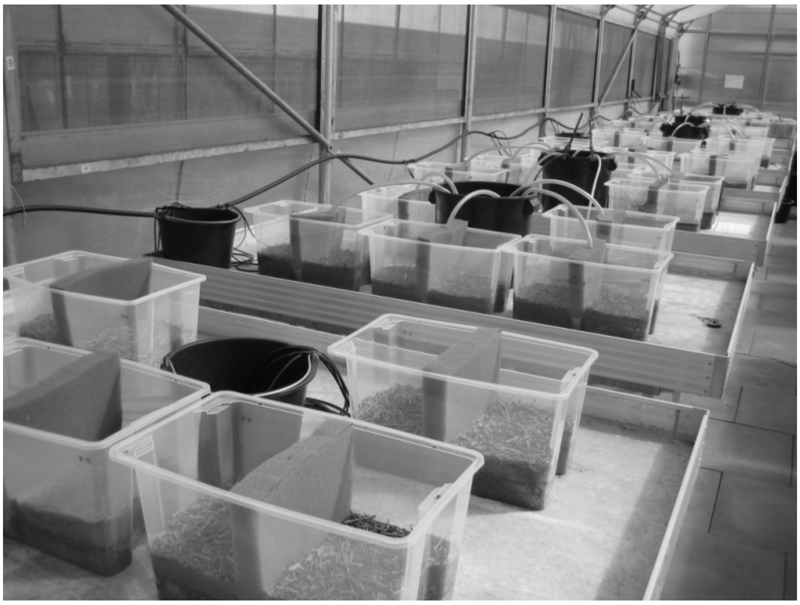

Figure 4.1 Set-up of the experiment in the greenhouse.

Tidal pumping system

In order to simulate tidal inundation, we used a tidal pump 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. 4.2). When tide should rise, water was pumped from the main storage tank (2 x 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). 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 tubes- 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 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 tanks and therefore also in the experimental mesocosms. A precondition for the working of the communicating tubes 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 the tube was 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.

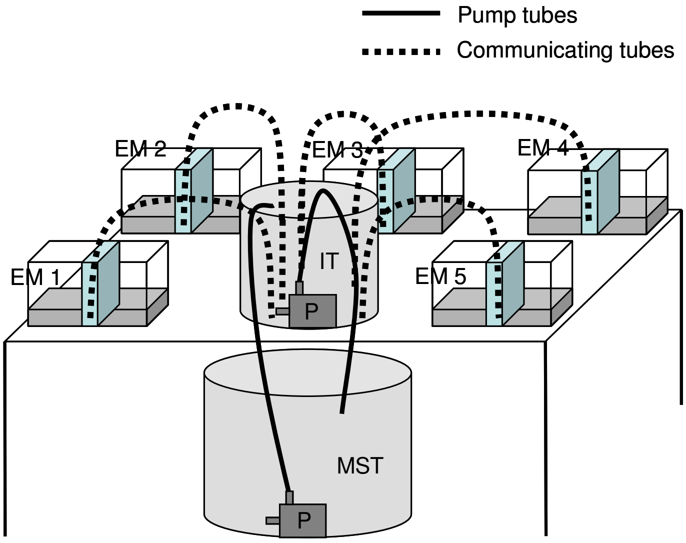

Figure 4.2 Set-up of tidal simulation system with five experimental mesocosms (EM 1-5), main storage tank (MST) and intermediate tank (IT). Tides are produced by water transfer between the IT and MST via electronic pumps (P). EMs are connected to the IT by communicating tubes.

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 mesocosm. Because the substrate was nutrient-poor and seedlings showed signs of nutrient deficiency, we regularly added liquid NPK-fertiliser (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 of the treatments from week five onwards (3 ml per week and experimental chamber).

Driftline material

We used driftline material as a seed source for estuarine marsh species, which was collected along three fresh/oligohaline, 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 two weeks of cold stratification, driftline material was spread on 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.

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 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 moisturised with 0.1 L water of the respective salinity in each experimental chamber.

Sampling

The Emergence and the Establishment Experiment were conducted in a greenhouse and 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 two weeks starting in week 3 (30 April 2008). Cover was estimated for each species using the cover classes of Londo (1976; “.1” = < 1%, “.2” = 1-2%, “.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 aboveground biomass of each species in the Establishment Experiment was determined (dry mass, dried at 60° C to constant weight). Seedlings, which 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 subspecies for a certain species, we decided for the value best representing the distribution of species along the Elbe estuary (Kötter 1961, Raabe 1986, Engels and Jensen 2009). *Potentilla anserina* could not be clearly assigned to one group and seedlings were very few, so this species was therefore excluded from the analysis. For a full list of species found in the driftline samples, with Ellenberg salinity values and assigned groups see Table C in the appendix.

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 (Generalised Linear Models) as 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 loglinear 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 (Fig. 4.3). 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. In order to follow the development of glycophytes and halophytes in the fresh treatment during the course of the experiment, we used Repeated Measurement Analyses of Variance (RM-ANOVAs). We tested how glycophyte and halophyte cover change during 15 weeks of the experiment was affected by different tidal regimes with "tidal regime" as between-treatments-factor and "time" as within-treatments-factor. 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 percent 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 into the analysis (for glycophytes week three was excluded because cover was zero). All ANOVAs were followed by Tukey post hoc comparisons to detect significant differences between treatments. Detrended Correspondence Analysis (DCA, implemented in PC-Ord; McCune and 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 dataset to reduce heterogeneity and improve the clarity of the ordination pattern. Additionally, the option 'downweight rare species' was selected.

4.4 Results

Emergence Experiment

Both glycophytes and halophytes seedlings emerged in high numbers under fw conditions Fig. 4.3). The GLM analysis showed that both glycophyte and halophyte seedling emergence was significantly affected by salinity (glycophytes: $LR\ \chi^2$ (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 at bw conditions (70% in no tide, 90% in spring tide and 98% in daily tide treatment compared to the fw control; 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 the fw control. In the other bw or sw treatments, seedling emergence usually never decreased more than 60%.

In fw, inundation by daily tides significantly reduced seedling emergence of glycophytes compared to the no-tide control ($P < 0.05$), while it did not for halophyte seedlings. Inundation by spring tides had a contrasting effect on the emergence of glycophyte and halophyte seedlings on different salinity levels: Fw combined with spring tide inundation produced the highest seedling emergence for both species groups (8% higher emergence of glycophytes and 22% higher emergence of halophytes than in the fw control, 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; $P < 0.05$). For glycophytes, a more frequent tidal inundation generally significantly decreased seedling emergence at bw ($P < 0.001$).

Establishment Experiment

Surprisingly, halophytes had higher biomass than glycophytes in all treatments (e.g. three times the biomass of glycophytes in the fw control) except for the fw treatment with daily tides (Fig. 4.3). Biomass of glycophytes was not affected by hydrologic regimes in the fw treatment (One-way-ANOVA, $F = 0.6$, $P > 0.05$). 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 (2-way-ANOVA, tidal regime: $F = 181.8$, salinity: $F = 139.7$, tidal regime x 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 at 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 ($P < 0.05$).

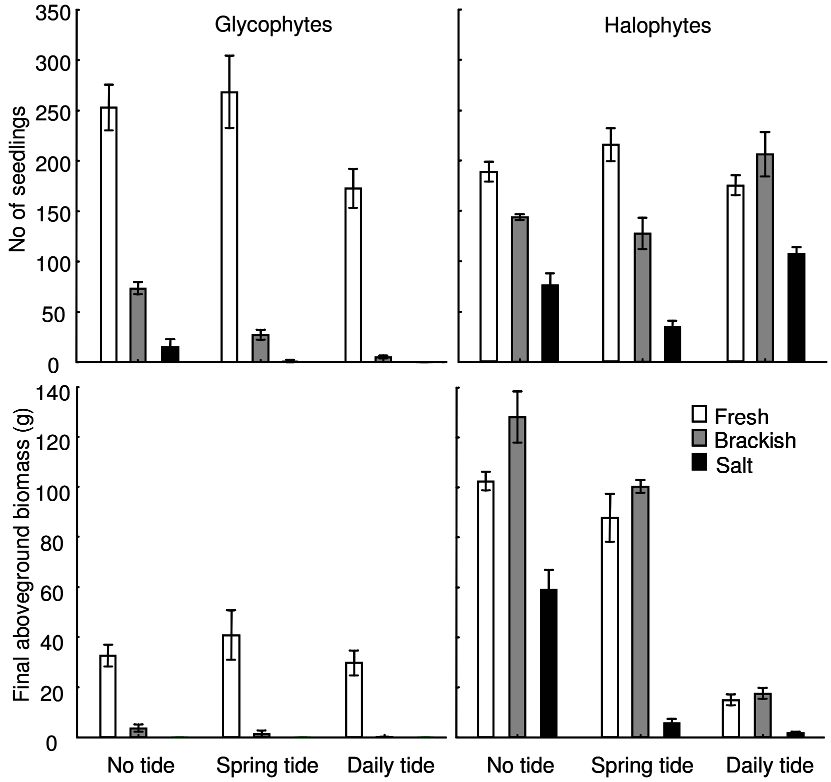

Figure 4.3 Numbers of emerged glycophyte and halophyte seedlings in the Emergence Experiment and final biomass (after 15 weeks) in the Establishment Experiment, each with three tidal regimes: no tide, with spring tide (flooded every two weeks), with daily tide (flooded twice per day) in fresh, brackish and salt treatments. Means ± SE for five replicates.

Cover of glycophytes and halophytes in the fw mesocosms changed significantly during the 15 weeks of the experiment (RM-ANOVA, glycophytes: $F = 121.2$; $P < 0.001$; halophytes: $F = 107.6$; $P < 0.001$). Generally, cover was significantly affected by tidal regime (RM-ANOVA, glycophytes: $F = 8.7$; $P < 0.01$; halophytes: $F = 47.1$; $P < 0.001$). Glycophytes and halophytes developed differently in terms of their cover during the course of the study (Fig. 4.4): The impact of the tidal regime on cover of both groups changed over time (RM-ANOVA, glycophytes: $F = 4.1$; $P < 0.001$; halophytes: $F = 8.9$; $P < 0.001$).

In the fw treatment, both species groups significantly increased in cover ($P < 0.001$) from the start of the measurements to week nine (week 11 in treatments with daily tide and with spring tide for glycophytes). After week nine, cover of glycophytes continued to slightly increase or started levelling off at high values, while cover of halophytes significantly decreased in the no-tide ($P < 0.01$) and spring-tide treatments ($P < 0.001$). In bw and sw treatments, where cover of glycophytes was zero or extremely low (no-tide treatment, maximum cover 14%), cover of halophytes was significantly affected by tidal regime, time, and their interaction (bw: RM-ANOVA, tidal regime: $F = 50.0$, time: $F = 109.4$, tidal regime x time: $F = 5.4$, $P < 0.001$; sw: RM-ANOVA, tidal regime: $F = 69.5$, time: $F = 132.9$, tidal regime x time: $F = 55.3$, $P < 0.001$). In bw, halophyte cover showed a more or less continuous increase from week three to week nine in all tidal regimes ($P < 0.001$; for spring tide: week eleven) and then levelled off.

In sw, however, halophyte cover showed a longer, more constant increase from the beginning of the experiment to week 13 in the treatment without tidal inundation ($P < 0.001$) and then started levelling off. With spring tide or daily tide, cover of halophytes was generally very low (maximum: 28% / 22.8%) and increased only slightly, but significantly, until week 15 ($P < 0.05$).

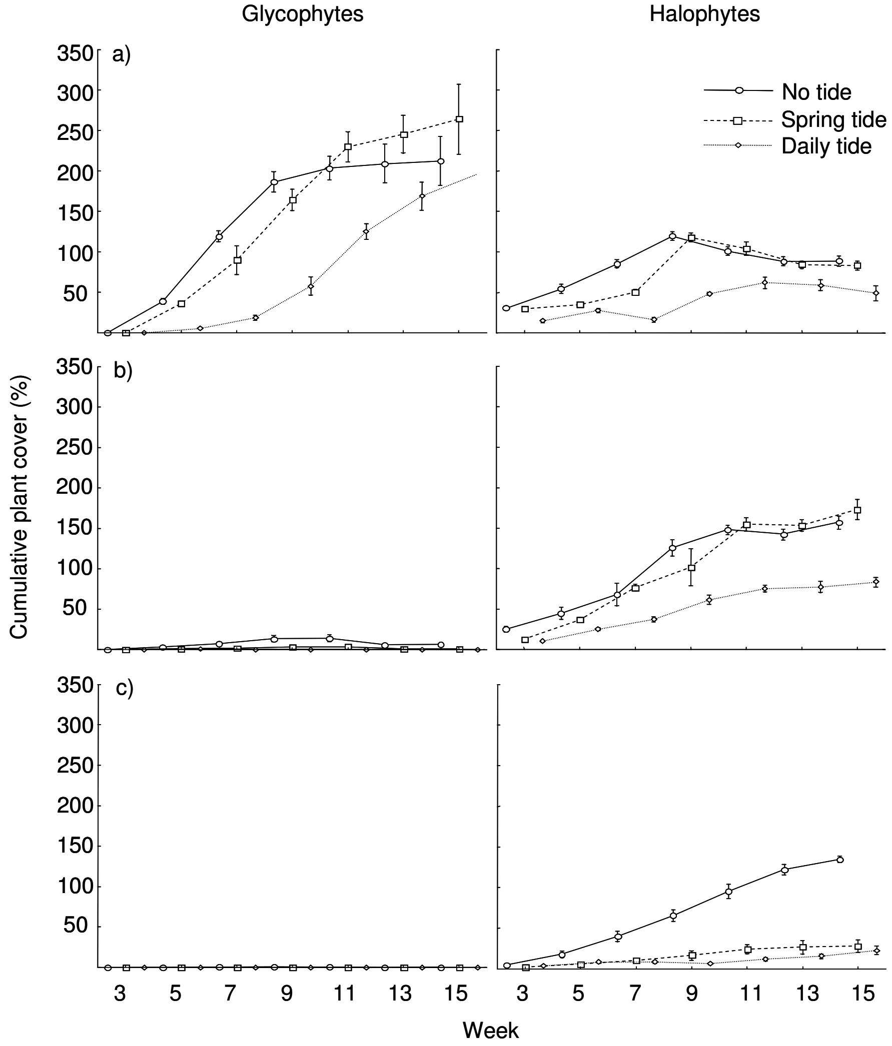

Figure 4.4 Change of cumulative plant cover (%) of glycophytes and halophytes in mesocosms during the course of the Establishment Experiment (15 weeks) for three tidal regimes: no tide, spring tide (flooded every two weeks), daily tide (flooded twice per day) in fresh (a), brackish (b) and salt (c) treatments. Cover of more than 100 % result from multiple vegetation layers in the mesocosms. Means ± SE for five replicates.

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. 4.5). 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.

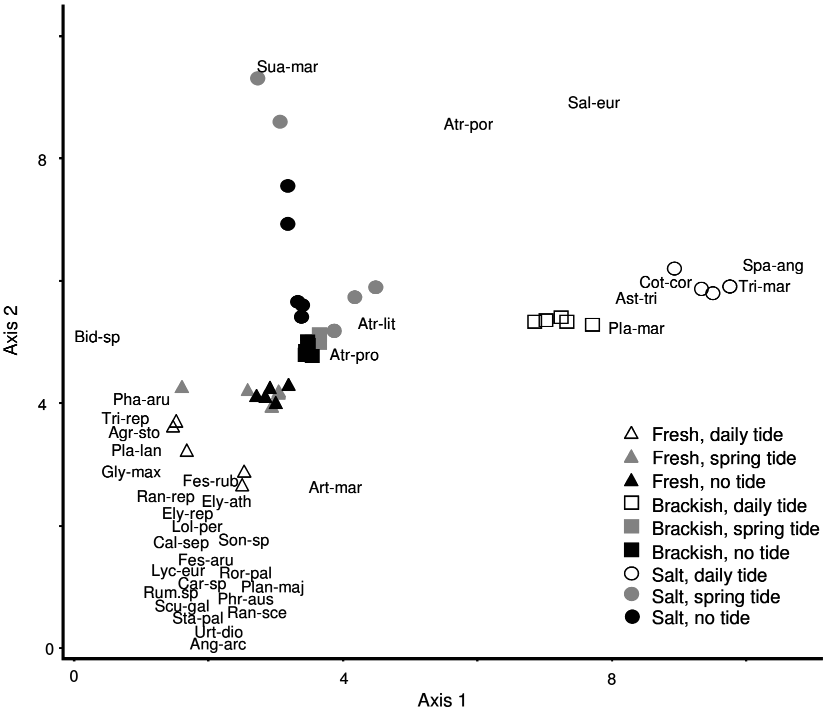

Figure 4.5 Ordination diagram of the species which established in the different treatments based on the final biomass values (after 15 weeks). The salinity treatments are illustrated by triangles (freshwater), diamonds (brackish) and circles (salt) and the hydrologic regimes are illustrated by white (daily tide), grey (spring tide) and black (no tide) symbols. Species names are displayed without symbols (see Table C in the appendix for abbreviations).

4.5 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 et al. 1985). However, our results show additionally 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, supporting our hypothesis. These results are consistent with studies of Bakker (1985) and Baldwin et al. (1996) who found germination or seedling emergence of glycophytes to be significantly reduced at 4 psu and impeded at conditions exceeding 10 psu. Salinity is generally known to constrain germination and seedling emergence in coastal marsh habitats (Ungar 1978; Shumway and Bertness 1992; Rand 2000).

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 hypothesis that tidal inundation generally decreases seedling emergence.

This might indicate that halophyte seeds or seedlings are more tolerant to 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 and 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 and van der Valk 1986; Baldwin et al. 1996; Baldwin et al. 2001). However, all of these studies tested the impact of permanent (long-term) flooding on seedling emergence, 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 and no experimental studies which investigated the effect of tidal flooding on seedling emergence of estuarine marsh species. Both Parker and Leck (1985) and Hopfensperger and Engelhardt (2008) found increasing seedling densities with decreasing tidal flooding frequency (increasing elevation) in tidal freshwater marshes, which is consistent with our mesocosm study.

Our results show that infrequent short-time flooding has substantially different effects on seedling emergence than daily tidal flooding and converse effects in fw compared to bw or sw conditions. The higher number of seedlings of glycophytes and halophytes in the spring-tide treatment compared to the no-tide control at fw conditions may be due to higher moisture levels stimulating germination (Noe and Zedler 2000; Elsey-Quirk et al. 2009). However, the decrease in seedling emergence at spring-tide flooding under bw and sw conditions is probably caused by an accumulation of salt in these treatments (salt crystals visible on substrate surface, own observation; see also Allison 1996).

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. Processes affecting seedling development and survival include physical factors, which can affect seedlings in a different way than seeds of the same species (Beare and Zedler 1987; Schupp 1995), and biotic interactions (Bakker et al. 1985; Scholten et al. 1987; Noe and Zedler 2001; Hopfensperger and Engelhardt 2008).

Although salt marsh plants are generally more tolerant towards increased salinity than freshwater plants (Crain et al. 2004), salinity does generally reduce survival and/or growth of both glycophyte (Beare and Zedler 1987) and halophyte seedlings (Ungar 1987; Shumway and Bertness 1992). In a study on the plant species zonation along an elevational salt marsh gradient, biomass of glycophytes seedlings decreased sharply at salinities higher than 5 psu while halophyte seedlings grew at a salinity of 10 psu without considerable biomass losses (Bakker et al. 1985). The extremely low biomass and cover proportions of glycophytes in our bw and sw treatments are in accordance with these results. Survival and growth of halophytes, however, were less affected at high salinities and even positively affected at medium salinities in our study.

Under fw conditions, seedlings of both species groups showed rapid growth within the first weeks of our experiment. However, the development of glycophytes and halophytes started to deviate from each other after two months. Here, glycophytes started to overgrow halophytes, thereby successively reducing their cover proportion. Cover development of glycophytes 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 at bw (particularly no-tide and spring-tide regimes) and sw conditions (no-tide regime), where glycophytic competitors were strongly inhibited. In contrast to this, an approximate saturation curve was not apparent at high stress conditions (for glycophytes at bw and for halophytes at sw conditions combined with daily tidal flooding). This is probably because growth is controlled here by high abiotic stress rather than by resource availability (e.g. space, light, nutrients).

The deviation of the cover response curve of halophytes from a saturation curve at fw conditions might be caused by competitive displacement. High competition can lead to a strong reduction of seedling density within a few months, particularly under low-stress conditions (Parker and Leck 1985). Accordingly, higher cover proportions and final biomass of halophytes at bw conditions compared to fw conditions may be the result of competitive release, since glycophytes were inhibited here by higher salinity. The ability of glycophytes to suppress halophytes at low salinity conditions has been shown before (e.g. Ungar 1998; Crain et al. 2004; Engels and Jensen *in press*). In the absence of competitors, halophyte species grow usually better at low salinity than under their natural habitat conditions (Snow and Vince 1984; Crain et al. 2004). On the contrary, there is also evidence that moderate salinity can stimulate the growth of some halophytes (Flowers 1977; Bakker 1985; Drake and Ungar 1989).

We were surprised to find that 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 aboveground biomass is relatively low.

Regarding the effect of tidal flooding on the establishment of glycophytes and halophytes, our results indicate that daily tidal inundation generally had negative effects on seedling growth, particularly on halophytes. In contrast, infrequent flooding by spring tides with fresh or brackish water had no or even positive effects on seedling establishment, rejecting our hypothesis on a generally detrimental effect of tidal flooding. Flooding may affect seedling growth in a different way than seedling germination and emergence (Lenssen et al. 1998; Bakker et al. 2007). Lenssen et al. (1998) found that although reed marsh and tall forb species both needed a drawdown for germination, their responses towards flooding differed during the phase of early establishment.

Generally, flooding tolerance seems to be species-specific (Coops and van der Velde 1995; Kellog et al. 2003). In our study, *Atriplex prostrata*, a species sensitive to flooding due to the lack of aerenchyma (Olff and Bakker 1988), constituted the majority of the halophyte seedlings, which explains the negative response of halophytes to daily tidal inundation. The extremely low biomass in the spring tide regime at sw conditions is likely to be explained by salt accumulation.

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 and Mendelssohn 1989; Willis and Hester 2004). These extreme conditions correspond to low elevations in salt marshes that are generally colonised by few species with specific adaptations (e.g. *Salicornia europaea* and *Spartina anglica* in European salt marshes; Odum 1988). Overall our experimental results indicate that species density in low elevation salt marshes is rather restricted by a bottleneck during seedling establishment than 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 three months of early establishment and that a typical estuarine marsh zonation is already developing in early stages of the corresponding plants life cycle. However, our results concerning the performance of halophyte seedlings are ambiguous and we are not able to exactly identify the mechanisms underlying the seedlings responses to the different treatments with the current study design. Therefore, more experimental studies are needed to confirm this assumption, e.g. studies with a fixed number of glycophyte and halophyte seedlings that allow the disentanglement of the effects of both abiotic factors and biotic interactions.

4.6 Acknowledgements

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5 General discussion

It is in the nature of transitional ecosystems that the inhabiting plant species are distributed along physico-chemical gradients in more or less distinct spatial patterns. Since the range a species covers along an environmental gradient is determined by its physiological tolerance mediated by biotic interactions, community attributes such as species density or evenness also vary along the gradient.

5.1 Relative importance of ecological processes in estuarine marshes

The results of this thesis suggest that the relative importance of physical factors as well as of positive and negative species interactions in limiting estuarine marsh vegetation varies along estuarine stress gradients as predicted by environmental stress models (ESM; e.g. Bertness and Callaway 1994; Bruno et al. 2003). We have clearly demonstrated in our transplant and seedling experiments that physical factors (e.g. tidal flooding, salinity) restrict plant survival and performance at high abiotic stress conditions in estuarine marshes (e.g. at low marsh elevations and/or in salt marshes). In contrast, at relatively benign conditions (e.g. at high marsh elevations and/or in tidal freshwater marshes), plant survival and performance are limited by competition. Extremely low seedling establishment and low species diversity at conditions with high soil salinity combined with frequent tidal inundation (low elevations in salt marshes) indicate that the cumulative stress of salinity and tidal flooding constitute the strongest constraint on marsh vegetation. Our results are consistent with Crain et al. (2004) and do support our general hypothesis on the relative importance of abiotic stress and competition along estuarine stress gradients.

The stress gradient hypothesis (SGH) predicts a shift from negative to positive interactions as abiotic stress increases along an environmental stress gradient (Bertness and Callaway 1994), which was supported by Crain (2008) along an estuarine salinity gradient. Since species interactions are always comprised of positive and negative components, this refers to the net-outcome of interaction, which may be either positive or negative (Bruno et al. 2003; Gross 2008). In our transplant study, we observed a shift in the net-outcome of biotic interactions along the estuarine stress gradient, with a net-negative interaction between neighbour vegetation and transplants in tidal freshwater marshes and a net-neutral interaction between neighbour vegetation and transplants in salt marshes. We further detected indications of facilitation at high to medium stress conditions in low and mid salt marshes, where transplanted freshwater species accumulated more biomass being planted within intact *Spartina anglica* or *Puccinellia maritima* stands than without neighbour vegetation (not statistically significant).

ESM predict herbivory (predation) to be important in low stress habitats. However, since we never observed any impact of herbivory in any of the marshes in the Elbe estuary, we did not include predation in our studies. Literature on predation in estuarine marshes is comparably rare (Dormann et al. 2000), but some studies suggest that herbivory and animal activity affect vegetation of both low salinity estuarine (Baldwin and Pendleton 2003; Crain 2008; Gedan et al. 2009) and salt marshes (Dormann et al. 2000; Costa et al. 2003; Crain 2008). Kuijper and Bakker (2003) showed that grazing by hares has substantial impact on vegetation development in salt marshes at the North Sea coast leading to a delay in salt marsh succession. To our knowledge, there are no studies which test the effects of herbivory on vegetation of tidal freshwater marshes in Europe so far.

5.2 Drivers of plant zonation patterns in estuarine marshes

Species ranges along environmental stress gradients were often proved to be determined by a species' tolerance towards abiotic habitat conditions at the severe and by its competitive ability towards the benign end of an environmental stress gradient (see Crain and Bertness 2006). This theory is in accordance with the SGH and is based on the assumption that although the physiological response curves of species occurring along an environmental stress gradient may be similar towards an environmental factor, competitively superior (and less stress-tolerant) species outcompete stress tolerant (and less competitive) species in physically benign habitats replacing them to physically stressful habitats (Grime 1979; Wilson and Keddy 1986). However, this theory assumes that abiotic stress continuously increases or decreases along an environmental stress gradient, i.e. from low via mid to high and from salt via brackish to tidal freshwater marshes along the estuarine gradients.

In the Northern-temperate zone, e.g. North-East-America and North-West-Europe, where summer precipitation is comparably high, salinity stress in salt marshes is supposed to consistently decrease from low to high elevations along with decreasing inundation frequency and duration (Bockelmann and Neuhaus 1999). Under such conditions, dominant marsh competitors typically occupy the more favourable higher marsh elevations, whereas less competitive species are replaced to high salinity and waterlogged low marsh elevations (e.g. Bertness 1991a,b; Thompson et al. 1991; Huckle et al. 2002). However, in warm and arid regions, e.g. in Californian salt marshes, vertical stress gradients are typically discontinuous. Here, high evaporation coupled with low tidal flooding frequency leads to salt accumulation in the upper soil layers at high marsh elevations (e.g. Pennings and Callaway 1992), as was also observed in spring-tide treatments in our greenhouse experiments. Under such conditions, mid marsh elevations are the least stressful habitats, compared to low and higher marsh elevations, which are subjected to intense flooding and high salinity stress, respectively. Anyway, plant zonation here is still driven by typical assumptions based on the trade-off between competitive ability and stress tolerance, i.e. dominant competitors excluding stress tolerant subordinates to more stressful conditions.

In Chilean salt marshes, which are affected by Mediterranean climate but are lacking regular tides and thus are only casually flooded due to winds and storms, salinity decreases significantly from low to high marsh. Nevertheless, plant zonation along vertical gradients in these marshes is solely determined by biotic interactions, predominantly competition, across all marsh elevations (Fariña et al. 2009). Moreover, Bockelmann and Neuhaus (1999) showed that the high marsh species *Elymus athericus* is competitively excluded from more stressful lower elevations by *Atriplex portulacoides* in a salt marsh at the German North Sea coast.

Unfortunately, studies elucidating the underlying processes of vertical plant zonations in tidal freshwater marshes are extremely rare. A study by Lenssen et al. (1999) supported typical assumptions in generating plant zonation patterns in a freshwater marsh with reduced tidal influence, where abiotic stress (flooding and waterlogging) is supposed to decrease with increasing elevation. However, they showed that in another freshwater marsh, the tall forb *Epilobium hirsutum* was competitively excluded from lower elevations by *Phragmites australis* in a freshwater marsh, while concurrently *P. australis* was excluded from higher elevations by competition with *E. hirsutum* (Lenssen et al. 2004).

While in salt marshes discontinuous vertical gradients are caused by an interaction between two physical stressors (salinity and tidal flooding), in tidal freshwater marshes the effect of tidal flooding itself may be inversed along the vertical gradient. Thus, although flooding is mainly considered as a stress factor (Jackson and Colmer 2005), results of our seedling experiments indicate rather positive than negative impacts of infrequent tidal flooding with freshwater on seedling emergence and biomass of estuarine marsh species. That high soil moisture or moderate flooding can increase seedling emergence and stimulate production of wetland plants has been shown before (Mitsch and Gosselink 2000; Willis and Hester 2004; Elsey-Quirk et al. 2009). Evidence on positive effects of tidal flooding can also be derived from the fact that tidal freshwater marshes are more productive than non-tidal freshwater marshes, which is attributed to tidal flooding providing nutrient rich sediments (Mitsch and Gosselink 2000). On the other hand, freshwater marshes not subjected to tidal inundation exhibit higher plant species richness than tidal freshwater marshes. The question, whether tidal flooding acts upon marsh vegetation as stress or subsidy was asked before ("subsidy-stress" hypothesis; e.g. Steever et al. 1976; Odum et al. 1979; Odum et al. 1983; Megonigal et al. 1997; Sims and Thoms 2002; Pratolongo et al. 2008). Since we did not test drivers of plant zonation along vertical estuarine gradients, we are not able to come to a conclusion here.

Our transplant experiment along the estuarine salinity gradient of the Elbe estuary showed that competitively subordinate salt marsh species are restricted to salt marshes by more competitive freshwater species, a result which was also found in New England estuarine marshes by Crain et al. (2004). Since we did only test the two extreme ends of the estuarine salinity gradient (salt and tidal freshwater marshes) and there are no other studies on this subject available, it is hard to say if the typical rules of marsh assembly apply along the entire estuarine salinity gradient (i.e. also for brackish marshes) and whether these results can be applied to other estuaries than the ones studied. Generally, results of our seedling experiments indicate that stress tolerance and competition predefine plant zonation patterns along estuarine salinity gradients already during the seedling phase. The importance of seedling dynamics for the generation of plant distribution patterns was also shown along vertical gradients in non-tidal (Coops and van der Velde 1995; Lenssen et al. 1998) and tidal freshwater marshes (Parker and Leck 1985) and salt marshes (Bakker et al. 1985; Rand 2000).

5.3 Drivers of plant diversity patterns in estuarine marshes

We originally hypothesised plant species diversity of estuarine marshes to gradually increase with decreasing abiotic stress, i.e. with increasing marsh elevation (decreasing flooding frequency and duration) and from coast to inland (decreasing soil salinity). Increasing plant species diversity with decreasing salinity (e.g. Odum 1988; Garcia et al. 1993; Crain et al. 2004, Więski et al. 2010) and tidal flooding (e.g. Gough et al. 1994; Brewer et al. 1997; Kunza and Pennings 2008) has been supported by the majority of previous studies on diversity along estuarine gradients (but see Sharpe and Baldwin 2009). Eventually, diversity patterns of estuarine marshes of the Connecticut River almost completely responded to this hypothesis, which on the whole also applied to patterns in the Elbe estuary.

Our results support our original hypothesis, however, they are contrary to the MSR, as we did not generally observe a decrease in species diversity at the benign end of salinity and flooding gradients (i.e. in tidal freshwater marshes or on high marsh elevations) caused by competitive exclusion. A possible explanation for this may be that the horizontal and vertical estuarine gradients that we studied did not encompass complete environmental stress gradients. Thus, tidal freshwater marshes representing the benign end of the estuarine salinity gradient in our study can still be regarded as stressful because of regular tidal flooding, and similarly, high marsh elevations as benign ends of vertical estuarine gradients can be seen as stressful, since they are subjected to storm surges. We therefore did probably only cover part of the unimodal MSR in our study (cf. Brewer et al. 1997; Scrosati and Heaven 2007).

We did not explicitly test the mechanisms leading to the observed diversity patterns along vertical and horizontal estuarine gradients in the Elbe and Connecticut Rivers. However, our experimental transplant study in the Elbe estuary allowed us to disentangle impacts of abiotic factors and biotic interactions on the performance of transplants by manipulating neighbour vegetation. Based on this we are to a certain extent able to assess the strength of the impact of abiotic factors and biotic interactions by which the plants in the respective communities in the Elbe estuary are constrained. Hence, the extremely high mortality of transplants planted within *P. australis* stands at mid elevations in tidal freshwater marshes of the Elbe estuary indicates that the vegetation in this marsh zone is strongly controlled by competition. Based on this, it seems obvious that competition may also be responsible for the low diversity in fresh and brackish mid marshes of the Elbe estuary. On the contrary, the comparably high species diversity on mid elevations in salt marshes may be due to facilitation (Hacker and Bertness 1999).

The observed depression in species diversity on mid elevations of fresh and brackish tidal marshes of the Elbe estuary is not consistent with the MSR, which predict species richness to peak at intermediate levels of environmental stress (e.g. Michalet 2006). However, dominant species like *P. australis* have been shown to play an important role regarding species richness and distribution patterns in wetlands (Lenssen et al. 2000), and there are cases when impacts of dominant competitors even conflict with established ecological theories. Thus, Prach and Pysek (1999) list species traits typical for dominant species giving them advantages over others, e.g. they are tall, wind-pollinated and often geophytes capable of intensive lateral spread, but on the other hand, require high nutrient supply and sufficient site moisture.

Actually, Grime's CSR-model forbids plant species to be both dominant competitors and good stress-tolerators at the same time (cf. Grime 1979). However, there are species which possess a combination of traits that does not follow expected correlations between traits and theoretical trade-offs and make them highly competitive. According to Prach and Pysek (1999), such species produce large numbers of easily dispersed seeds and are able to spread vegetatively as is the case for *P. australis*, which can be called a "super-species" (sensu Huston and Smith 1987). Elmendorf and Moore (2007) suggest that dominant competitors can strongly alter environmental conditions, e.g. by directly influencing soil environment, biogeochemical cycles or disturbance. We speculate that the importance of a dominant competitor as *P. australis* on the importance of biotic interactions and its influence on vegetation patterns may even surpass that of environmental conditions (Elmendorf and Moore 2007).

5.4 General applicability of environmental stress models

The general applicability of models, which have been suggested to predict vegetation responses (e.g. plant distribution, diversity, productivity) and the relative importance of ecological processes along environmental stress gradients, has been and still is intensely disputed (Maestre et al. 2009). The reason why such models are supported along some but not all environmental stress gradients may be due to differences concerning the type of environmental stress gradients i.e. resource or non-resource gradients (e.g. Maestre et al. 2009), different lengths of studied gradients (e.g. Scosati and Heaven 2007), variations among the occurring species (Wilson and Keddy 1988; Maestre et al. 2009), the existence of multiple environmental gradients (Elmendorf and Moore 2007), the equalisation of environmental stress gradients with productivity gradients (Austin and Gaywood 1994), and differences in the measurement of the studied processes (e.g. Greiner La Peyre et al. 2001; Maestre et al. 2009).

Several studies showed that facilitation can increase species richness in plant communities characterised by high competition (Gross 2008), interactions between stress-tolerators can be competitive (Choler et al. 2001) and that stress tolerant low marsh plants become competitive dominants under high nutrient availability (Emery et al. 2001). All these observations do not agree with the CSR-model of Grime (1977, 1979) which constitutes the basis of later developed ESM and assumes that species can either be competitive or stress tolerant. Grime's model was supported by numerous studies (e.g. Wilson and Keddy 1986; Bertness and Ellison 1987; Keddy 1990; Gough et al. 1994; Grace and Pugesek 1997; Liancourt et al. 2005); however, most studies analysed the relative importance of competition at the species level (e.g. Grace and Wetzel 1981; Wilson and Keddy 1986; Pennings and Callaway 1992), while the importance of competition was shown to respond differently to an environmental stress gradient at the community level (Greiner La Peyre et al. 2001).

Other authors have criticised Grime's model to be oversimplified, since it does not take into account effects of several environmental stress gradients and overlooks the importance of species-specific effects for the net-outcome of biotic interactions (Austin and Gaywood 1994; Liancourt et al. 2005; Elmendorf and Moore 2007). Overall, it appears that relationships between stress tolerance and biotic interactions and their importance along environmental stress gradients may be less predictable than previously assumed.

5.5 Conceptual model on species richness

Based on the species diversity patterns we observed along horizontal and vertical gradients of the Elbe and Connecticut estuaries, we propose a simple conceptual model illustrating how biotic interactions may affect species density (SD) along environmental stress gradients (Fig. 5.1). Our conceptual model suggests that the basically linear response of species density (SD) to an environmental stress gradient (decreasing SD with increasing abiotic stress) is modified by the impact of biotic interactions. Thus, we assume that competition generally decreases and facilitation generally increases SD at any position of the gradient, subsequently resulting in curved or hump-shaped relationships between environmental stress and species diversity. We visualise potential effects of biotic interactions on SD by focussing exemplarily on the effects of competition. However, the model can easily be applied to potential effects of facilitation on SD by reversing the direction of the effect (increasing or decreasing SD) and mirroring the respective response curve of SD.

Regarding effects of competition, the model is based on the assumptions (i) that species density will continuously increase with decreasing environmental stress in the absence of competition (null model; abiotic filters are stronger then biotic filters), and (ii) that competition leads to the dominance of a few species and to a reduction of diversity at any position along environmental stress gradients. If competition is high (effect of competition > effect of abiotic filters), SD will be depressed due to competitive exclusion and thus the (linear) relationship between environmental stress and SD of the null-model (Fig. 5.1a) will be impaired. How competition may affect the relation between environmental stress and SD is dependent on the position(s) at which competition is acting (shown in Figs 5.1b to 5.1h). Figure 5.1g shows the hump-shaped relation between environmental stress and SD resulting from competition under low stress conditions. This corresponds to Grime's traditional hump-shaped model (Grime 1973; Hacker and Gaines 1997; Hacker and Bertness 1999; Michalet et al. 2006). In the Connecticut River, we predominantly found the relationship which is presented in Figure 5.1a (abiotic stress seems to be more important than competition). This relation was also found for the Elbe estuary along the salinity gradient on low and high marshes. In contrast, Figure 5.1h reflects the relationship along the salinity gradient on mid marshes in the Elbe estuary. Figure 5.1e shows the relationship, which we observed along the vertical gradient of fresh and brackish marshes (competition reduces SD on mid elevations). Figure 5.1g largely resembles the SD pattern found in salt marshes of the Elbe estuary along the flooding gradient. Here, competition seems to reduce SD in high marshes.

Other deviating patterns of diversity along environmental stress gradients may result from the strength and the position at which competition or facilitation override abiotic filters. For example, Sharpe and Baldwin (2009) found that species richness was as high or higher in oligohaline marshes than in tidal freshwater marshes in an estuary of Chesapeake Bay. They explain this by increased coexistence of fresh and brackish marsh species due to competitive release under moderate disturbance (fluctuating salinities) in this marsh type. However, facilitation may also have played a role in creating this diversity peak. Generally, it is important to consider that facilitation and competition may operate at the same time thereby offsetting each other (Gross 2008). Therefore, effects of biotic interactions may often be masked by what seems to be the exclusive impact of abiotic stress. Further experimental studies investigating the pattern of species diversity along environmental gradients and testing our proposed model will lead to a better general understanding of the role of abiotic conditions and biotic interactions in shaping diversity patterns.

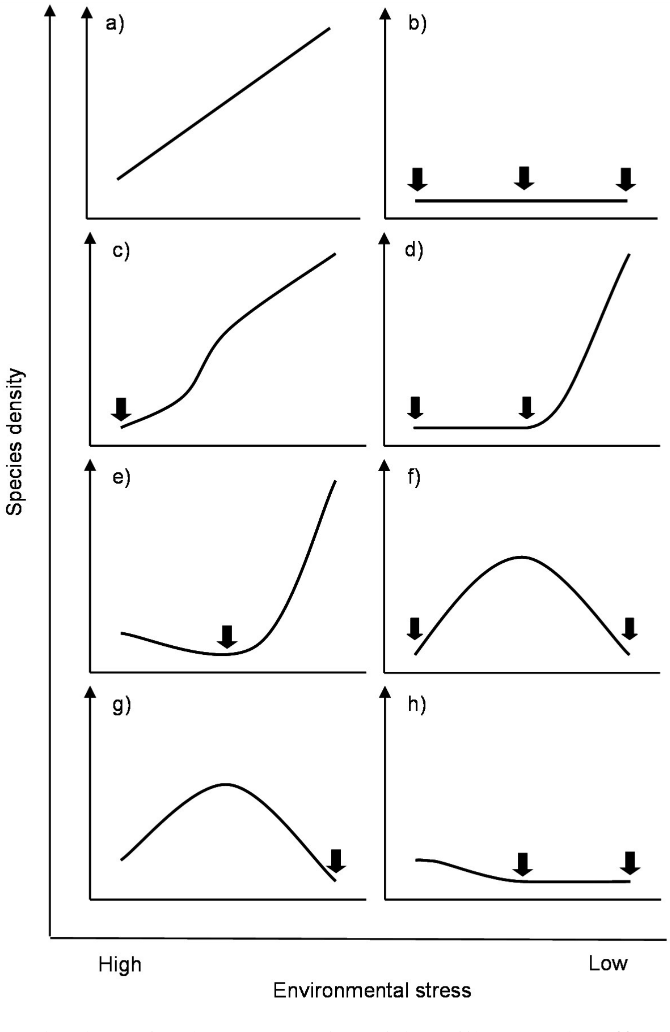

Figure 5.1 The graphs a) – h) show simple conceptual models to illustrate the effect of competition on species density (SD) along environmental stress gradients. The position of an effect of competition on SD is indicated by black arrows. Graph a) is a reference model, which shows the relationship between SD and environmental stress in the absence of competition, b) Competition of equal strength at each position along the stress gradient, c) Competition effect at position of high environmental stress, d) Competition effects at positions of high and medium environmental stress, e) Competition effect at position of medium environmental stress, f) Competition effects at positions of high and low environmental stress, g) Competition effect at position of low environmental stress, h) Competition effects at positions of medium and high environmental stress.

6 Conclusions and Perspectives

The results of this thesis indicate that abiotic and biotic processes interact in determining plant zonation and diversity patterns along estuarine stress gradients. Based on our three studies in which we looked at responses of species diversity, zonation and seedling recruitment of marsh vegetation to estuarine stress gradients, we show that plant performance and survival, as well as species diversity are limited by abiotic stress (e.g. flooding, salinity) under relatively harsh environmental conditions (e.g. at low marsh elevations and/or in salt marshes) and by competition under relatively benign conditions (e.g. at high marsh elevations and/or in tidal freshwater marshes). Our results therefore support our general hypothesis which we formulated in the introduction. In more detail, our findings indicate that halophytes are precluded from freshwater marshes by competition, whereas glycophytes are restricted from salt marshes due to physical stress. However, we found indication that facilitation by salt marsh vegetation may increase survival of glycophytes in salt marshes. Therefore, our results support the general hypothesis that the net outcome of biotic interactions shifts along the estuarine salinity gradient, i.e. from competition in tidal freshwater marshes to facilitation in salt marshes as predicted by the stress gradient hypothesis (SGH; Bertness and Callaway 1994).

Overall, our results support current environmental stress models (ESM; e.g. Bruno et al. 2003; Michalet et al. 2006), and results of previous studies on the processes driving plant zonation patterns and species diversity along horizontal salinity and vertical flooding gradients in estuarine marshes (e.g. Snow and Vince 1984; Bertness 1991a,b; Crain et al. 2004). Similar results were also found along environmental gradients in other ecosystems, e.g. alpine communities (Kikvidze et al. 2005) and arid environments (Pugnaire et al. 2004). Additionally, our mesocosm experiments provide evidence for the hypothesis that stress tolerance and biotic interactions determine plant zonation along estuarine salinity gradients already during seedling emergence and early establishment. The importance of seedling dynamics for the generation of plant zonation patterns was also found along vertical gradients in salt marshes (Rand 2000; Bakker et al. 2007) and non-tidal wetlands (Coops and van der Velde 1995; Lenssen et al. 1998). However, further studies, e.g. competition studies with a fixed number of glycophyte and halophyte seedlings, are needed to corroborate our findings on the impacts of seedling competition on plant distribution patterns along estuarine salinity gradients.

On the basis of the results of our transplant study, we provide for the first time evidence on drivers of plant zonation patterns along European estuarine salinity gradients. So far, we are only aware of very few experimental field studies on plant zonation along European estuarine gradients, which were exclusively conducted along vertical gradients in salt marshes (e.g. Thompson et al. 1991, Bockelmann and Neuhaus 1999; Huckle et al. 2002). The findings of our study on the determinants of zonation patterns along estuarine salinity gradients should be corroborated by transplanting more species along the estuarine salinity gradient.

More experimental studies, e.g. transplant experiments, on vertical zonations of estuarine freshwater and brackish marshes would be helpful in establishing generally applicable rules explaining the generation of plant zonation patterns and the relative importance of biotic interactions and physical factors as driving forces in shaping zonation patterns along estuarine stress gradients.

However, our results did contrast to some aspects of ESM, since we detected effects of intense competition at mid elevations in tidal freshwater and brackish marshes of the Elbe estuary which apparently led to a depression in diversity in this vegetation zone. Since there is growing evidence in the literature that ESM are not generally supported along environmental stress gradients (see e.g. Maestre et al. 2009), we suggest that biotic interactions may possibly affect vegetation composition and diversity at any position along an environmental stress gradient. Studies indicate that the importance of biotic interactions (e.g. of competition and facilitation) can depend on factors other than that predicted by a single environmental stress gradient, e.g. on multiple underlying stress gradients, the type of stress gradient involved or specific traits of the occurring species. Our proposed conceptual model illustrates how biotic interactions can potentially modify the relationship between abiotic stress and species diversity with competition generally decreasing and facilitation generally increasing species diversity. Further experimental studies investigating the pattern of species diversity along environmental gradients and testing our proposed model will lead to a better general understanding of the role of abiotic conditions and biotic interactions in shaping diversity patterns.

Studies on factors driving vegetation structure and dynamics of tidal marshes along estuarine salinity gradients of the Elbe and other European estuaries are still extremely limited. With this thesis, we hope to stimulate research on vegetation dynamics in estuarine marshes. Estuarine marshes provide the unique opportunity to analyse effects of two interacting environmental stress gradients (salinity and tidal flooding) on vegetation. Anyway, more studies are needed to test the general validity of our results and to assess whether vegetation in other European estuaries are driven by similar processes as we observed in marshes of the Elbe estuary. While we did address effects of plant-plant-interactions and abiotic factors on estuarine marshes in our studies, the impact of herbivory was only rarely addressed so far. Studies concerning the effect of herbivory on European tidal freshwater marshes are particularly lacking in current research.

In our mesocosm experiment, we also detected as of yet unknown differential effects of tidal flooding on seedling performance. The type of effect (detrimental or facilitating) of tidal flooding strongly depended on the frequency of tidal inundation. To our knowledge, our experiment is currently the only laboratory experiment analysing effects of tidal flooding on herbaceous plants (but see Sharpe and Baldwin, in prep) with a tidal simulation system. We aim to encourage further mesocosm-experiments on the effects of tidal flooding. Our study provides detailed information on the simple and cost-efficient set-up of such a system.

Generally, the results of this thesis provide knowledge on the principles controlling vegetation dynamics in estuarine marshes. Since estuarine marshes are predicted to be substantially affected by global change (Callaway et al. 2007), such knowledge is urgently needed to predict the response of estuarine marshes to e.g. sea level rise, reduced summer precipitation and increasing temperatures. It has been shown that a potential rise of the sea level may lead to shifts of vertical and horizontal vegetation zones along the estuarine shorelines (Watson and Byrne 2009).

Since in all of the large European estuaries dikes are commonly restricting upward movement of estuarine marshes, high marsh zones may decline, unless estuarine marshes are able to accrete as much sediment as is necessary to keep pace with sea level rise (Day et al. 2008; Watson and Byrne 2009). Additionally, increased salt water intrusion concurrent with sea level rise may lead to an upstream shift of salt and brackish marsh zones severely threatening tidal freshwater marshes, which due to restriction of the tidal influence by dams may not be able to move further up-estuary (Neubauer and Craft 2009).

Eventually, marshes of the Elbe estuary and other large estuaries in Europe (e.g. Rhine, Weser, Scheldt) are generally highly impacted by human alterations such as embankments as well as channeling and deepening of the river for shipping purposes or other economical reasons and flood protection (Meire et al. 2005). These measurements often result in accelerated flow velocities and may amplify effects of sea level rise by increasing high water levels and tidal amplitudes (Meire et al. 2005). This in turn gives rise to increased erosion on marsh edges, which may lead to additional marsh losses particularly in brackish and tidal freshwater parts of the estuary. A decline in the area of tidal freshwater marshes may in particular cause declines in ecosystem services, such as biomass production, waste treatment (e.g. nitrogen sequestration) and natural shoreline protection (Craft et al. 2009). Along with tidal freshwater marshes, also rare and endangered species are threatened by the consequences of sea level rise, e.g. the endemic species *Oenanthe conioides* and *Deschampsia wibeliana* which are globally restricted to low salinity marshes of the Elbe estuary. In order to estimate the threat of global change on European estuarine marshes, particularly tidal freshwater marshes, and to take measurements for protection of these unique habitats, detailed information on sedimentation and accretion of estuarine marshes is urgently needed.

7 Summary

The relative importance of abiotic factors and biotic interactions along gradients of environmental stress is a burning issue in current ecological research. In contrast to the well-studied vertical gradients in salt marshes, evidence on the structuring forces of marsh vegetation along estuarine gradients is still rare. Estuaries contain two main environmental stress gradients for vascular plants in the intertidal zone: a horizontal (salinity) gradient on the landscape scale and a vertical (flooding) gradient at each shoreline location.

In order to elucidate drivers of plant diversity and distribution patterns along estuarine stress gradients, I carried out three studies within the framework of this thesis. In the first study I investigated the alteration of plant species diversity and composition along the horizontal salinity and vertical tidal flooding gradients in a European (Elbe) and an American estuary (Connecticut). In the second study I experimentally tested the role of ecological processes in driving the observed plant zonation patterns in the Elbe estuary by transplanting tidal freshwater and salt marsh species reciprocally along the estuarine salinity gradient into plots with and without natural neighbour vegetation. In the third study, I analysed the impact of two estuarine stressors on seedling emergence and early establishment of marsh species in mesocosm experiments.

In the first study, I tested the hypothesis that species diversity of estuarine marshes decreases with increasing abiotic stress. In more detail, I hypothesised diversity to decrease with increasing salinities or tidal inundation, i.e. from tidal freshwater to salt marshes and from high to low elevations. Additionally I asked whether patterns of species density (SD) and evenness (E) along estuarine gradients differ between two regions with different regional species pools. I analysed patterns of SD and E based on vegetation surveys at three marsh elevations (low, mid, high) in five sites of each estuarine marsh type (tidal freshwater, brackish, salt) in the Elbe and Connecticut estuaries, respectively. Additionally, I estimated the size of the regional species pools for the two estuaries from literature and analysed differences in species composition among marsh types and elevations.

The results showed that the regional species pool was 33% larger for the Connecticut than for the Elbe estuary, very likely due to differences in the evolutional history of the region. This difference between regions was reflected in SD of Connecticut tidal freshwater marshes, which was more than twice (19 ± 2.2) the SD of Elbe freshwater marshes (7 ± 1.4). We found an overall increase in SD from low to high elevation and from salt to freshwater marshes in both estuaries, supporting our hypotheses. However, SD and E were strongly depressed at intermediate elevations in tidal fresh and brackish marshes of the Elbe estuary, whereas they significantly increased from brackish to salt marshes at the same elevation. These deviations from the pattern observed in the Connecticut might be due to differences in the effect of biotic interactions (competition and facilitation) along environmental gradients in the two estuaries. These differences are likely to be driven by the evolutionary history of the regions and by historical and recent human impacts on a local scale leading to a particular size and composition of the regional species pools.

In contrast to my descriptive first study, I was able to draw conclusions on the underlying mechanisms of observed patterns in my transplant experiment. I hypothesised that the upper distribution boundary of salt marsh species in the Elbe estuary is determined by competition, whereas the lower distribution boundary of freshwater species is set by the species' tolerances to abiotic stress (i.e. salinity). In order to test this hypothesis, I transplanted four dominant and typical species of salt (*Spartina anglica* and *Puccinellia maritima*) and tidal freshwater marshes of the Elbe estuary (*Bolboschoenus maritimus* and *Phragmites australis*) reciprocally within their elevation level in two sites per marsh type (tidal freshwater and salt) and within their native marsh. In order to disentangle effects of abiotic and biotic factors, transplants were placed in plots with and without neighbouring vegetation.

The study showed, that freshwater species transplanted to salt marshes performed poorly regardless of whether neighbouring vegetation was present or not. This indicates that freshwater species are excluded from salt marshes because they are not able to tolerate the stressful abiotic conditions (i.e. high salinity). However, more transplants of *P. australis* survived on plots with rather than without neighbours which may indicate facilitation of salt marsh vegetation on *P. australis*. In the presence of neighbours, salt marsh species generally had extremely low biomass when transplanted to freshwater marshes and 80 to 100% died. However, without neighbours, biomass of salt marsh species in freshwater sites was similar to or higher than in salt marshes. This demonstrates that salt marsh species of the Elbe estuary are capable of living in freshwater marshes, but are precluded from freshwater marshes by competition. Overall, these results supported my initial hypothesis on the determinants of species distribution boundaries along the estuarine salinity gradient of the Elbe estuary.

Based on the findings of my transplant study, I tested in my third study whether the processes leading to plant zonation patterns (tolerance towards abiotic stress, competition, facilitation) already take effect during seedling emergence and early establishment of estuarine marsh species. Therefore, I set up two factorial mesocosm experiments (Emergence experiment and Establishment experiment) which tested effects of three tidal regimes (daily tide, spring tide, no tide) and three salinity levels (fresh, brackish, salt) on emergence and early establishment of glycophyte and halophyte seedlings. The levels of the hydrologic and salinity regimes were adjusted to conditions at low, mid and high elevation in tidal fresh, brackish and salt marshes of the Elbe estuary, respectively.

Both glycophytes and halophytes showed highest seedling emergence under freshwater conditions. However, while halophyte seedlings proved to be relatively salt tolerant, seedling emergence and establishment of glycophytes were extremely reduced under brackish and salt conditions. This suggests that the absence of glycophytes in salt marshes can be explained by intolerance to increased salinities during germination and seedling emergence. On the contrary, halophytes generally started to decrease in cover after two months in the freshwater treatments of the establishment experiment whereas glycophytes further increased. This result indicates that the absence of halophytes in tidal freshwater marshes is controlled by factors affecting the plants during their establishment phase, i.e. very likely by competition with glycophytes.

The impact of tidal flooding was strongly dependent on inundation frequency and water salinity. While (frequent) daily tides predominantly decreased seedling emergence and establishment, (infrequent) spring tides had rather positive effects on seedlings in freshwater and negative effects in saltwater treatments. Surprisingly, biomass of halophytes was higher than that of glycophytes in all experimental treatments. Nevertheless, results of this study suggest that the typical estuarine marsh zonation along the estuarine salinity gradient is already developing in early stages of the corresponding plants life cycle.

Overall, the results of this thesis indicate that the relative importance of physical factors as well as of positive and negative species interactions in limiting estuarine marsh vegetation varies along estuarine stress gradients as predicted by current environmental stress models. Thus, physical factors (e.g. tidal flooding, salinity) restrict plant survival, performance and diversity under high abiotic stress conditions in estuarine marshes (e.g. at low marsh elevations and/or in salt marshes), with indication of facilitation mitigating effects of abiotic stress. In contrast, at relatively benign conditions (e.g. at high marsh elevations and/or in tidal freshwater marshes), plant survival, performance and diversity are limited by competition. The zonation of marsh vegetation along estuarine salinity gradients develops according to the relative importance of these processes mediated by traits of individual species, which start to take effect already during early life stages of estuarine marsh plants. Knowledge of the principles controlling vegetation dynamics in estuarine marshes is essential for predicting potential impacts of global change or human alterations on marsh vegetation.

8 Zusammenfassung

Die Frage, wie sich die relative Bedeutung von abiotischen Faktoren und biotischen Interaktionen entlang abiotischer Stressgradienten ändert, wird in der ökologischen Forschung derzeit intensiv diskutiert. Während vertikale Gradienten in Salzmarschen gut untersucht sind, ist das Wissen über die ökologischen Prozesse, die die Vegetation von Marschen entlang ästuariner Gradienten bestimmen, vergleichsweise gering. Als Marschen werden die von krautigen Pflanzen besiedelten tide-beeinflussten Zonen in Ästuaren bezeichnet. Ästuarine Marschen sind durch zwei Haupt-Stressgradienten geprägt: einen horizontalen Salinitätsgradienten, der auf Landschaftsebene vom Binnenland bis zur Küste verläuft und einen vertikalen Überflutungsgradienten, der jede einzelne Marsch zusätzlich auf lokaler Ebene strukturiert. Entlang dieser ästuarinen Gradienten lässt sich die Ausbildung bestimmter Verteilungs- und Diversitätsmuster der Vegetation in den Marschen beobachten.

Das Ziel dieser Doktorarbeit war es, die entlang der ästuarinen Gradienten zu beobachtenden Verteilungs- und Diversitätsmuster zu beschreiben und die Prozesse, die die Ausbildung dieser Muster bedingen, aufzudecken. Dazu wurden drei Untersuchungen durchgeführt: In der ersten Untersuchung wurde die Veränderung der Artendiversität und -verteilung entlang des horizontalen Salinitäts- und des vertikalen Überflutungsgradienten in einem europäischen (Elbe) und einem nordamerikanischen Ästuar (Connecticut) analysiert. Die zweite Untersuchung stellte ein Verpflanzungsexperiment dar, in dem typische Arten der Süßwasser- und Salzmarschen reziprok entlang des Salinitätsgradienten des Elbeästuars in Flächen mit und ohne Nachbarvegetation verpflanzt wurden. In der dritten Untersuchung wurde der Einfluss der für ästuarine Marschen typischen Stressfaktoren Salinität und Tide-Überflutung auf das Keimlingsaufkommen und die frühe Etablierung von Arten der Marschenvegetation in zwei Gewächshaus-Experimenten untersucht.

In der ersten Untersuchung wurde die Hypothese überprüft, ob die Artendiversität von ästuarinen Marschen mit zunehmendem abiotischen Stress abnimmt, also mit zunehmender Salinität (von Süßwasser- zu Salzmarschen) und zunehmender Tide-Überflutung (von höher gelegenen Vegetationzonen zu niedriger gelegenen Vegetationszonen). Zusätzlich sollte die Frage beantwortet werden, ob sich die entlang der beiden ästuarinen Gradienten ausgebildeten Diversitätsmuster zwischen Elbe und Connecticut mit ihrem unterschiedlichen regionalen Artenpool unterscheiden. Dazu wurden Muster der Artendichte und der Gleichverteilung der Arten (Evenness) mit Hilfe von Vegetationsaufnahmen auf drei Höhenstufen (untere, mittlere, obere Marsch) an je fünf Lokalitäten eines jeden Marschtyps (Süßwasser-, Brackwasser- und Salzmarsch) in der Elbe und im Connecticut-Ästuar untersucht. Außerdem wurden die Artenpools der beiden Ästuare mit Hilfe von Literatur bestimmt und Unterschiede zwischen der Artenzusammensetzung der Marschen innerhalb der verschiedenen Marschtypen und Höhenstufen analysiert.

Es zeigte sich, dass der regionale Artenpool des Connecticut-Ästuars um 33% größer war als der des Elbeästuars, was vermutlich auf die unterschiedlichen evolutionären Hintergründe der beiden Regionen zurückzuführen ist. Der Unterschied im Artenpool spiegelte sich in ebenfalls deutlich höherer Artendiversität der Süßwassermarschen im Connecticut. So wiesen die Süßwassermarschen des Connecticut mehr als doppelt so viele Arten (19 ± 2.2) auf als die Süßwassermarschen des Elbeästuars (7 ± 1.4). Insgesamt nahm die Artendichte in beiden Ästuaren von der unteren bis zur oberen Marsch sowie von Salz- zu Süßwassermarschen zu, was die aufgestellte Hypothese bestätigte. Allerdings wies die mittlere Marschzone von Süß- und Brackwassermarschen des Elbeästuars eine deutlich niedrigere Artendichte und Evenness auf als erwartet, während Artendichte und Evenness entgegen der aufgestellten Hypothese in der mittleren Marsch von Brackwasser- zu Salzmarschen signifikant anstiegen. Die Unterschiede innerhalb der Diversitätsmuster der beiden Ästuare sind vermutlich auf eine unterschiedliche Intensität und Bedeutung biotischer Interaktionen (Konkurrenz, Facilitation) entlang der ästuarinen Gradienten in Elbe und Connecticut zurückzuführen. In welchem Ausmaß abiotische und biotische Prozesse eine Rolle entlang von ästuaren Stressgradienten spielen, kann durch Unterschiede in Größe und Zusammensetzung der regionalen Artenpools bedingt sein, die wiederum durch die individuelle evolutionäre Geschichte der Regionen sowie historische und aktuelle menschliche Eingriffe geprägt sind.

Im Gegensatz zu der deskriptiven ersten Untersuchung ermöglichte die zweite experimentelle Untersuchung, Schlüsse hinsichtlich der auf die Marschenvegetation wirkenden Prozesse zu ziehen. Es wurde die Hypothese untersucht, dass die obere (flussaufwärts gelegene) Verbreitungsgrenze von Halophyten in Ästuaren von Konkurrenz, die untere (flussabwärts gelegene) Verbreitungsgrenze von Glykophyten jedoch von der Salztoleranz der Arten bestimmt wird. Um diese Hypothese zu testen, wurden zwei dominante und typische Arten der Salzmarschen (*Spartina anglica* und *Puccinellia maritima*) und zwei dominante und typische Arten der Süßwassermarschen (*Bolboschoenus maritimus* and *Phragmites australis*) reziprok innerhalb ihrer Höhenstufe verpflanzt, d.h. in jeweils zwei Lokalitäten des entgegengesetzten Marschtyps und als Kontrolle zusätzlich in den Marschtyp, von dem sie stammten. Um zwischen der Wirkung abiotischer Faktoren und biotischer Interaktionen unterscheiden zu können, wurden die Pflanzen sowohl in Flächen mit natürlich vorhandener Nachbarvegetation verpflanzt als auch in Flächen, in denen die Nachbarvegetation oberirdisch entfernt worden war.

Das Experiment ergab, dass die Glykophyten, die in die Salzmarschen verpflanzt worden waren, nur eine geringe Biomasse aufwiesen und zwar unabhängig davon, ob in den Untersuchungsflächen die natürliche Nachbarvegetation vorhanden war oder nicht. Daraus lässt sich der Schluss ziehen, dass Glykophyten deshalb nicht in den Salzmarschen vorkommen, da sie die dort vorherrschenden abiotischen Bedingungen (z.B. hohe Salinität) nicht vertragen. Allerdings zeigte sich, dass das Überleben von *P. australis*-Individuen in Flächen mit natürlicher Nachbarvegetation höher war als in Flächen ohne Nachbarvegetation. Dies spricht für die Wirkung von Facilitation der Vegetation der Salzmarschen auf *P. australis*. Die in die Süßwassermarschen verpflanzten Halophyten wiesen eine extrem niedrige Biomasse auf, wenn sie direkt in die Vegetation der Süßwassermarschen verpflanzt wurden und 80 bis 100% waren am Ende des Experiments abgestorben. Wurden sie hingegen auf Flächen verpflanzt, auf denen die Vegetation der Süßwassermarschen entfernt worden war, so war ihre Biomasse mindestens ebenso groß wie an ihren natürlichen Standorten in den Salzmarschen.

Dies beweist, dass Arten der Salzmarschen des Elbeästuars durchaus in der Lage sind, in Süßwassermarschen zu gedeihen, jedoch durch Konkurrenz mit der dort vorhandenen Vegetation von diesen Standorten ausgeschlossen werden. Insgesamt bestätigen die Ergebnisse dieser Studie die zu Beginn aufgestellte Hypothese in Bezug auf die Verbreitungsgrenzen der Arten entlang des ästuarinen Salinitätsgradienten im Elbeästuar.

Auf Basis der Ergebnisse des Verpflanzungsexperiments wurde in der dritten Untersuchung getestet, ob die zur Ausbildung von Artenverteilungsmustern führenden Prozesse (Stresstoleranz, Konkurrenz, Facilitation) bereits während der Keimung und der frühen Etablierung der beteiligten Arten einsetzen. Dafür wurden zwei voll-faktorielle Mesokosmos-Experimente durchgeführt, in denen die Effekte von drei Tideregimen (tägliche Überflutung, Springtide-Überflutung, ohne Überflutung) und drei Salinitätsstufen (Süßwasser, Brackwasser, Salzwasser) auf die Keimung und Etablierung von Glykophyten und Halophyten untersucht wurde. Die Abstufung der beiden Behandlungen (Tide-Überflutung und Salinität) wurde an die jeweiligen Bedingungen in unterer, mittlerer und oberer Marsch bzw. in Süßwasser-, Brackwasser- und Salzmarschen des Elbeästuars angepasst.

Sowohl Glykophyten als auch Halophyten zeigten das höchste Keimlingsaufkommen unter Süßwasserbedingungen. Die Halophyten erwiesen sich jedoch im Hinblick auf das Keimlingsaufkommen als relativ salztolerant, während das Keimlingsaufkommen und die Etablierung der Glykophyten unter Brackwasser- und Salzwasser-Bedingungen extrem reduziert waren. Dies deutet darauf hin, dass die Abwesenheit von Glykophyten in den Salzmarschen auf Intoleranz gegenüber erhöhter Salinität während der Keimungsphase beruht. Im Gegensatz dazu wurde während der Etablierungsphase erkennbar, dass die Deckung der Halophyten unter Süßwasserbedingungen nach ca. zwei Monaten zurückging, während die Deckung der Glykophyten weiter zunahm. Dieses Ergebnis weist darauf hin, dass die Abwesenheit der Halophyten in Süßwassermarschen durch Faktoren bedingt ist, die die Keimlinge während ihrer Etablierungsphase negativ beeinflussen. Vermutlich handelt es sich dabei um Konkurrenzausschluss durch die konkurrenstärkeren Glykophyten. Die Effekte von Überflutung hingen stark von der Überflutungshäufigkeit sowie der Salinität des Überflutungswassers ab. So übte die 14-tägig stattfindende Springtide-Überflutung mit Süßwasser eher positive Effekte auf die Keimlinge aus, während die Springtide-Überflutung mit Salzwasser sich stark negativ auf die Keimlinge auswirkte. Häufige (zweimal tägliche) Überflutung führte generell vorwiegend zu einer Abnahme des Keimlingsaufkommens und der Keimlingsetablierung. Entgegen der Erwartungen war die Biomasse der Halophyten in allen experimentellen Varianten höher als die der Glykophyten. Die Ergebnisse dieser Untersuchung weisen darauf hin, dass sich die typische Marschenzonierung entlang des Salinitätsgradienten in Ästuaren bereits während der Keimlingsphase der beteiligten Arten zu entwickeln beginnt.

Insgesamt zeigen die Ergebnisse dieser Dissertation, dass sich die relative Bedeutung abiotischer Faktoren sowie positiver und negativer biotischer Interaktionen, welche die ästuarine Marschenvegetation beeinflussen, entlang von Stressgradienten verändert. Diese Ergebnisse sind in Übereinstimmung mit derzeit diskutierten Modellen (environmental stress models): Demnach steuern abiotische Faktoren (z.B. Tide-Überflutung und Salinität) das Überleben, die Biomasseproduktion und die Artendiversität der Arten bzw. der Vegetation von ästuarinen Marschen in Habitaten mit hohem abiotischem Stress (untere Marschstufe und/oder in Salzmarschen). Im Gegensatz dazu wird das Überleben, die Biomasseproduktion und Artendiversität der Arten bzw. der Vegetation von ästuarinen Marschen in Habitaten mit geringem abiotischen Stress in erster Linie durch Konkurrenz limitiert. In Habitaten, die durch hohen abiotischen Stress gekennzeichnet sind (z.B. Salzmarschen), wurden außerdem Anzeichen für Facilitation festgestellt, die den abiotischen Stress bis zu einem gewissen Grade vermindern und somit das Überleben, die Biomasseproduktion und Artendiversität der Arten bzw. der Vegetation erhöhen kann. Die Zonierung der Vegetation von Marschen entlang von ästuarinen Salinitätsgradienten wird durch die an der jeweiligen Position des Stressgradienten vorherrschenden ökologischen Prozesse (abiotische Faktoren, Konkurrenz, Facilitation) im Zusammenwirken mit den individuellen Eigenschaften der vorkommenden Arten bestimmt. Die Ergebnisse der Dissertation zeigen, dass die zur Ausbildung von Pflanzenzonierungen und Diversitätsmustern führenden Prozesse bereits während sehr früher Lebensphasen der Arten von ästuarinen Marschen einsetzen. Diese Dissertation trägt dazu bei, potentielle Auswirkungen des Klimawandels sowie menschlicher Eingriffe auf die Vegetation ästuariner Marschen zu beurteilen.

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Appendix

Table A Species covers (%) on five 1 m^2-plots at low marsh, mid marsh and high marsh elevations in tidal fresh, brackish and salt marshes of the Elbe estuary (recorded in August 2006). Heu = Heuckenlock, Het = Hetlingen, Glü = Glückstadt, Kraut = Krautsand, Holl = Hollerwettern, Hünck = Hünckenbüttel, Bal = Balje, Hör = Hörne, Neu = Neufeld, Ott = Otterndorf, DK 1-5 = Dieksanderkoog 1-5; Fresh = tidal freshwater marsh, Brack= brackish marsh, Salt = salt marsh

Name of site	Heu	Heu	Heu	Het	Het	Het	Glü	Glü	Glü	Kraut	Kraut	Kraut	Holl	Holl	Holl
Marsh type	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh
Elevation zone	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh
Acorus calamus	0	0	0	0	0	18,2	0	0	0	0	0	0	0	0	0
Agrostis stolonifera	0	2,9	0	0,4	0,2	0	0	0	0	0	0	0	0	0,4	0
Alisma plantago-aquatica	0	0	0	0	0	0	0	0	0	0	0	0	0	0,2	0
Angelica archangelica	0	0	0	0	0	30,7	0	0	12,4	0	0	0	0	0	41,2
Anthriscus sylvestris	0	0	0	0	0	2,3	0	0	0	0	0	0,1	0	0	0,7
Artemisia maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster salignus	0	0	0	0	0	0	0	0	8,1	0	0	2,4	0	0	0
Aster tripolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atriplex portulacoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atriplex prostrata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bolboschoenus maritimus	24,3	0	0	14,7	0,5	0,1	6,2	0	0	95	2,6	0	93	0	0
Caltha palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,1
Calystegia sepium	0	0	37,2	0	0	3	0	0	8,4	0	0	24,7	0	0	18,7
Carex hirta	0	0	0	0	0	0	0	0	0,8	0	0	0	0	0	0
Chaerophyllum bulbosum	0	0	0	0	0	0,1	0	0	0	0	0	0	0	0	0
Cirsium arvense	0	0	0	0	0,8	14,6	0	0	32,7	0	0	0	0	0	1,7
Cirsium oleraceum	0	0	0	0	0	0	0	0	0	0	0	20,3	0	0	0
Cotula coronopifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dactylis glomerata	0	0	0	0	0,1	2,5	0	0	0	0	0	0,1	0	0	2,9
Deschampsia wibeliana	0	0	0	1,1	0	0	0	9,2	0	0	0	0	0	0	0
Eleocharis uniglumis	0	0	0	0,1	0	0	68,9	0	0	0	0	0	0	0	0
Elymus athericus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elymus repens	0	0	0,3	0	0	0	0	0	0,1	0	0	0,3	0	0	0
Epilobium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epilobium hirsutum	0	0	6,1	0	0	0,8	0	0	0	0	0	0	0	0	0,3
Equisetum arvense	0	0	0	0	0	22,4	0	0	32,5	0	0	0	0	0	0
Festuca arundinacea	0	0	0	0	68,5	7	0	0	4,1	0	0	0	0	0	26,5
Festuca rubra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Filipendula ulmaria	0	0	0,3	0	0	0	0	0	0	0	0	0	0	0	0
Galium aparine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glaux maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glechoma hederacea	0	0	0,3	0	0	0	0	0	4,2	0	0	0	0	0	0
Heracleum sphondylium	0	0	0	0	0	0	0	0	0	0	0	0,1	0	0	0
Juncus gerardii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limonium vulgare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lythrum salicaria	0	0	0	0	0	0	0	0	0	0	0	12,4	12,1	0	0
Mentha aquatica	0	0	0	0	0	0	0	0	0	0	0	0	0	0,1	8,9
Nasturtium officinale	0,1	0	0	0	0,1	0	0	0	0	0	0	0	0	0	0
Phalaris arundinacea	18,1	0	0	0,4	4,7	6,3	0	0	5,3	0	0	24,5	0	0	3,3
Phleum pratense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phragmites australis	0	90	0,4	0	0	0	0	93	20,5	0	98	0,2	0	98	27,1
Plantago lanceolata	0	0	0	0	0,1	0	0	0	0	0	0	0	0	0	0
Plantago maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poa trivialis	0	0	0	0	0	0	0	6,2	0	0	0	0	0	0	0
Polygonum amphibium	0	0	0	0	0	0	0	0	0,1	0	0	0	0	0	0
Polygonum hydropiper	0,2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla anserina	0	0	0	0	0	0,1	0	0	0	0	0	0	0	0	0
Puccinellia maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus repens	0	0	0	0	0	0,3	0	0	0,1	0	0	0	0	0	0
Rorippa spec.	0,8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus caesius	0	0	40,3	0	0	0	0	0	0	0	0	0	0	0	0
Rumex obtusifolius	0	0	0	0	0	0,2	0	0	0	0	0	0	0	0	0
Salicornia europaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schoenoplectus tabernaemontani	34,4	0	0	31,4	0	0	0,1	0	0	0,2	0	0	0,1	0	0
Sonchus arvensis	0	0	0	0	0	0	0	0	0	0	0	0,3	0	0	6,1
Spartina anglica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spergularia maritima/salina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stachys palustris	0	0	0	0	0	0,1	0	0	0	0	0	0	0	0	0
Stellaria graminea	0	0	0	0	0,1	0	0	0	0	0	0	0	0	0	0
Suaeda maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Symphytum officinale	0	0	0	0	0	0	0	0	0	0	0	4,1	0	0	0
Tanacetum vulgare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triglochin maritimum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Typha angustifolia	0	0	0	0	0	0	0	0	0	0,8	0	0	0	0	0
Urtica dioica	0	0	48,6	0	0	0	0	0	0	0	0	1,3	0	0	0,6
Valeriana officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veronica catenata	1,4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vicia cracca	0	0	0	0	0	0,9	0	0	12,2	0	0	0,5	0	0	2,3

Name of site	Hünk	Hünk	Hünk	Bal	Bal	Bal	Hör	Hör	Hör	Neu	Neu	Neu	Ott	Ott	Ott
Marsh type	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack
Elevation zone	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh
Acorus calamus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis stolonifera	0	6,5	3,3	0	0	0,3	0	9,6	0	0,5	0	0	21,2	0	0
Alisma plantago-aquatica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Angelica archangelica	0	0	0,8	0	0	11,2	0	0	14,2	0	0	0,5	0	0	26,4
Anthriscus sylvestris	0	0	0	0	0	0	0	0	0	0	0	0,3	0	0	0
Artemisia maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster salignus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster tripolium	0	0	0	0	0	0	0,1	0	0	0	0	0	22,5	0	0
Atriplex portulacoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atriplex prostrata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bolboschoenus maritimus	64,5	6,1	8,3	0	0	0	64,5	0	0	89,5	0	0	48,5	0	0
Caltha palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calystegia sepium	0	0	1,6	0	0	26,5	0	0	16,5	0	0	0	0	0	13,2
Carex hirta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaerophyllum bulbosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium arvense	0	0	0,3	0	0	7,9	0	5	2,1	0	0	13	0	0	4,8
Cirsium oleraceum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotula coronopifolia	34,5	0	0	0	0	0	0	0	0	1,5	0	0	0	0	0
Dactylis glomerata	0	0	0	0	0	0	0	0	12,3	0	0	0	0	0	0
Deschampsia wibeliana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eleocharis uniglumis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elymus athericus	0	0	0	0	0	0	0	0	0	0	0	14,5	0,1	0	6,2
Elymus repens	0	0	0	0	0	0	0	0,1	0	0	0	16,3	0	0	0,8
Epilobium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0,1	0	0	0
Epilobium hirsutum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Festuca arundinacea	0	0	26,3	0	0	4,3	0	0	0,1	0	0	2,1	0	0	1,1
Festuca rubra	0	0	0	0	0	0	0	7	0	0	0	0	6,2	0	0
Filipendula ulmaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium aparine	0	0	0	0	0	0	0	0	0	0	0	0,3	0	0	0
Glaux maritima	0	0	0	0	0	0	0	0	0	0	0	0	17,2	0	0
Glechoma hederacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heracleum sphondylium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus gerardii	0	0	0	0	0	0,4	0	0	0	0	0	0	6,3	0	0
Limonium vulgare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lythrum salicaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mentha aquatica	0	0	14,1	0	0	8,1	0	0	0	0	0	0	0	0	0
Nasturtium officinale	0	0	0	0	0	0,1	0	0	0	0	0	0	0	0	0
Phalaris arundinacea	0	0	39,3	0	0	16,3	0	0	10,2	0	0	0	0	0	0
Phleum pratense	0	0	0,3	0	0	0	0	0	0	0	0	0	0	0	0
Phragmites australis	0	98	0,1	0	98	42,4	0	98	46,4	0	93,5	45,9	0	98	66,5
Plantago lanceolata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poa trivialis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum amphibium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum hydropiper	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla anserina	0	0	0	0	0	0	0	0,8	0	0	0	1,2	0	0	0
Puccinellia maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus repens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rorippa spec.	0	0	0,1	0	0	0	0	0	0	0	0	0	0	0	0
Rubus caesius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex obtusifolius	0	0	8,1	0	0	0	0	0	0	0	0	0	0	0	0
Salicornia europaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schoenoplectus tabernaemontani	3,4	0	0	56,5	0	0	0	0	0	0	0	0	0	0	0
Sonchus arvensis	0	0	0	0	0	0	0	0	2,1	0	0	8,2	0	0	2,1
Spartina anglica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spergularia maritima/salina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stachys palustris	0	0	0	0	0	0	0	0	2,2	0	0	0	0	0	0
Stellaria graminea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Suaeda maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Symphytum officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanacetum vulgare	0	0	0	0	0	0	0	0	4,2	0	0	0	0	0	0
Triglochin maritimum	0	0	0	0	0	0	0	0	0	0	0	0	5,4	0	0
Typha angustifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Urtica dioica	0	0	0	0	0	0	0	0	11,2	0	0	0	0	0	0
Valeriana officinale	0	0	0	0	0	0,1	0	0	0	0	0	0	0	0	0
Veronica catenata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vicia cracca	0	0	0	0	0	0,3	0	0	0	0	0	0	0	0	6,5

Name of site	DK5	DK5	DK5	DK4	DK4	DK4	DK3	DK3	DK3	DK2	DK2	DK2	DK1	DK1	DK1
Marsh type	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt
Elevation zone	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh
Acorus calamus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis stolonifera	0	0	0	0	0	20,4	0	0	0,1	0	0	0	0	0	0
Alisma plantago-aquatica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Angelica archangelica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthriscus sylvestris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artemisia maritima	0	0	0	0	0	24,3	0	0	8,1	0	0	14,7	0	0	0,3
Aster salignus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster tripolium	0	1,7	12,2	0	28,7	0,9	0	36,5	14,1	0	26,5	0	0	28,5	2,3
Atriplex portulacoides	0	0	0	0	0	0	0	0	0,1	0	20,4	13	0	6,4	0,1
Atriplex prostrata	0	64,5	1,9	0	26,4	20,5	0	0	0,2	0	0	0	0	0	0
Bolboschoenus maritimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caltha palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calystegia sepium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex hirta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaerophyllum bulbosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium oleraceum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotula coronopifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dactylis glomerata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deschampsia wibeliana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eleocharis uniglumis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elymus athericus	0	0	67,5	0	0	37,9	0	0	70	0	0	42,6	0	0	66,5
Elymus repens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epilobium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epilobium hirsutum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Festuca arundinacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Festuca rubra	0	0	52,5	0	0	40,4	0	0	38,3	0	36,3	61,5	0	0	58,5
Filipendula ulmaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium aparine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glaux maritima	0	0	0	0	0	0,1	0	0	0,9	0	0,1	0	0	0	0
Glechoma hederacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heracleum sphondylium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus gerardii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limonium vulgare	0	0	0	0	0	0	0	0	0	0	0,8	0	0	0	0
Lythrum salicaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mentha aquatica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nasturtium officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalaris arundinacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phleum pratense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phragmites australis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago lanceolata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago maritima	0	0	0	0	0	0,3	0	0,3	0	0	0,3	0,3	0	0	0
Poa trivialis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum amphibium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum hydropiper	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla anserina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Puccinellia maritima	0	18,5	0,1	0	9,4	0	2,9	7,9	0	0	2,5	0	0	16,4	0
Ranunculus repens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rorippa spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus caesius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex obtusifolius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salicornia europaea	48,5	0	0	58,5	0	0	36,5	1,2	0	15,1	4,8	0	24,5	26,4	0
Schoenoplectus tabernaemontani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sonchus arvensis	0	0	0,1	0	0	2,1	0	0	0	0	0	0	0	0	0
Spartina anglica	10,7	38,5	8,4	0,8	54,7	0	52,5	34,4	0	28,5	20,6	0	23,2	16,6	0,1
Spergularia maritima/salina	0	0	0	0	0	0	0	0	0	0	0,1	0	0	0,3	0
Stachys palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stellaria graminea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Suaeda maritima	0	0	0	0	10,3	0	0	32,5	0	0	3,1	0	0	15,2	0
Symphytum officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanacetum vulgare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triglochin maritimum	0	0	0	0	0	0	0	0	0	0	6,3	0	0	2,3	0
Typha angustifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Urtica dioica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Valeriana officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veronica catenata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vicia cracca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table B Species covers (%) on five 1 m^2-plots at low marsh, mid marsh and high marsh elevations in tidal fresh, brackish and salt marshes of the Connecticut estuary (recorded in August 2006). CK = Chester Creek, DR = Deep River, PC = Post Cove, WC = Whalebone Creek, SC = Seldon Creek, LC = Lord Cove, GM = Great Meadow, RRC = Ragged Rock Creek, GI = Great Island, UI = Upper Island, GP = Griswold Point, RN = Rocky Neck State Park, OS1 = Old Saybrook 1, OS2 = Old Saybrook 2; Fresh = tidal freshwater marsh, Brack= brackish marsh, Salt = salt marsh.

Name of site	CK	CK	CK	DR	DR	DR	PC	PC	PC	WC	WC	WC	SC	SC	SC
Marsh type	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh
Elevation zone	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh
Acorus americanus	0,2	2,8	3	2	44	8,4	0,2	2,8	0,6	0	22,8	7	0	2	0,6
Agalinis maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis sp.	0	0	0	0	0	0	0	0,4	0	0	0	0	0	0	0
Agrostis stolonifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alnus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,8
Amaranthus cannabinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amorpha fruticosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphicarpa bracteata	0	0	0	0	0	0,4	0	0,6	1,4	0	0	0,6	0	1,2	1,2
Apios americana	0	0	2,2	0	0	3,6	0	0,8	0	0	0	0,4	0	0	0
Asclepias incarnata	0	0	0,2	0	0	0	0	0	0	0	0	0	0	0	0
Aster novi-belgii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster puniceus	0	0	0,4	0	0	1,2	0	0	1,2	0	0,2	0,4	0	0	1,4
Aster subulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster tenuifolius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atriplex hastata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atriplex subspicata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bidens laevis	0	0	0	0	0	0	0	0	0	0,4	0	0,2	0	0	0
Bidens sp.	0,4	1,8	0,8	0	0	0	0,2	0,4	0	0	1,6	0,2	0	1,8	0,4
Boehmeria cylindrica	0	0	0,6	0	0	4	0	0	0	0	0	1	0	0	2,8
Calamagrostis canadensis	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0
Calystegia sepium	0	0	0,6	0	0,4	1,2	0	0,4	1,2	0	0	0	0	0	0
Callitriche sp.	18,8	0,4	0	0	0	0	0	0,2	0	0,2	0	0	0	0	0
Carex lacustris	0	0	0	0	1	3,8	0	0,6	4,6	0	0	0,2	0	0,8	46
Carex stricta	0	14	4,4	0	0	9,2	0	15,2	5,2	0	0	10	0	4,4	12,8
Ceratophyllum demersum	0	0	0	0	0	0	6,4	0	0	0,8	0	0	0	0	0
Cicuta maculata	0	0,2	0,8	0	0	0	0	0	0	0	0	0	0	0,2	0
Cornus amonum	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cuscuta sp.	0	0	0,2	0	0	0	0	0	0	0	0	0,2	0	0	0,2
Distichlis spicata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elodea nutallii	0,2	0	0	0	0	0	12,4	0	0	14	0	0	1,4	0	0
Elymus virginicus	0	0,2	0	0	0,2	0,4	0	0,4	0	0	0	0	0	0	0
Epilobium coloratum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Equisetum arvense	0	0	0	0	0	0	0	0	0	0	0	0,6	0	0	0
Equisetum fluviatile	0	0	0,8	0,2	0	0	0	1,2	2,6	0	0	0	0	0	0
Eupatorium maculatum	0	0	4,2	0	5,6	2,4	0	0	0,2	0	0	1,2	0	0	0
Galium palustre	0	0	1	0	0	1	0	0,4	0,6	0	0	2	0	0	1,2
Galium tinctorium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Gerardia tenuifolia	0	0	0,6	0	0	0	0	0,4	0,2	0	0	0,4	0	0,2	0,6
Impatiens capensis	0	4,4	1,2	0	1	0,6	0	3,2	6,4	0	0	1,8	0	0,4	4,6
Iris sp.	0	0	1,2	0	0,8	0	0	0	0	0	0	0,4	0	0,2	0
Iva frutescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus gerardii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncuc sp.	0	0,6	4,2	0	3,2	0,8	0	0	0	0	9,6	0	0	0	0
Leersia oryzoides	0	1,2	1,8	0	0	0	0	0,8	0,6	0	1,2	0,8	0	2	0
Lemna minor	0	0	0	0	0	0	0	0	0	0,4	0	0	0	0	0
Limonium carolinianum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobelia cardinalis	0	0	0	0	0	0	0	0	0	0	0	0,4	0	0	0
Ludwigia palustris	0	0	0	0	0	0	0	0	0	0,2	0	0	0	0	0
Lycopus rubellus	0	0	0,8	0	0	0	0	0	0	0	0	0,2	0	0	1
Lysimachia lanceoloata	0	0	0	0	0,2	0,2	0	0	0	0	0	0,2	0	0	0
Lythrum salicaria	0	0	0	0	0	0	0	0	0,4	0	0	0,8	0	0	0
Mikania scandens	0	0	0	0	0	0	0	0	0	0	0	0,8	0	0	1,2
Myosotis scorpioides	0	0	0	0	0	0	0	0	0	0	0	0	0	0,2	1
Nuphar variegatum	68,0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onoclea sensibilis	0	0	0	0	0	36	0	0	10,2	0	0	0	0	0	0,2
Panicum virgatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peltandra virginica	12,6	24	22	50	8	10	0	44,8	4,4	0	2,4	4,2	0	26	2,8
Phragmites australis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pilea pumila	0	0	0	0	0,2	0,2	0	0,2	0,2	0	0	0,6	0	0,4	0
Plantago maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pluchea purpuascens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum arifolium	0	7	9,4	0	7	6,4	0	4,2	11,6	0	9,2	32	0	2	20
Polygonum hydropeperoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum punctatum	0,2	0,8	0	0,4	0,2	1,6	0	0,8	0	0	2,4	0	0	1,8	0
Polygonum sagittatum	0	0	1	0	0	0	0	0,4	0,6	0	0,2	1,4	0	0,4	1,8
Pontederia cordata	0,8	2,2	1	10,8	0	0	26,2	0,2	0	20,8	0,6	0	18	0	0
Potentilla anserina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Name of site	CK	CK	CK	DR	DR	DR	PC	PC	PC	WC	WC	WC	SC	SC	SC
Marsh type	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh
Elevation zone	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh
Potamogeton crispus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa palustris	0	0	0	0	0	0	0	0	0	0	0	0,4	0	0	0
Rumex orbiculatus	0	0	0	0	0	0	0	0	0	0	0	0,2	0	0	0
Sagittaria graminea	0,6	0	0	2,2	0	0	1,2	0	0	18,2	0	0	0	0	0
Sagittaria latifolia	0	0	0,4	1	4	0,2	0,4	0,8	0	0,2	3,4	0	10,8	0	1
Sagittaria montevidensis	0	0	0	0,4	0	0	5,2	0	2	0	0	0	7,2	0	0
Salicornia europaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix sp.	0	0	0	0	0	0	0	6,4	0	0	0	0	0	0	0
Samolus parviflorus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus americanus	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
Scirpus fluviatilis	0,2	0,4	0	0	0	0	0	0	0	0,8	8,6	18,4	0	0	1,2
Scirpus robustus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Scirpus tabernemontani	0	0	0	0	2,8	0	0	0	0	0	0	0	0	0	0
Scutellaria galericulata	0	0	0,4	0	0	0	0	0,2	0,2	0	0	0	0	0	0
Scutellaria latifolia	0	0	2,4	0	0	0	0	4	0	0	0	0	0	0,4	0,8
Solidago sempervirens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spartina alterniflora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spartina cynosuroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sparganium eurycarpum	0	3,6	2	0	0	0	0	0	0	0	0	0	0	0	0
Spartina patens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stachys tenuifolia	0	0	0,4	0	0	0	0	0	0	0	0	0	0	0	0
Suaeda maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalictrum polygamum	0	0,4	0,6	0	0	0,4	0	0	0,4	0	0	0	0	0	0
Thelypteris palustris	0	0,8	6	0	0,8	1,2	0	0	2,8	0	0	2,8	0	0	1
Toxicodendron rydbergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,2
Triadenum virginicum	0	0	0,2	0	0	0,6	0	0	0	0	0	0	0	0	0,2
Typha angustifolia	0	0	4,6	0	0,8	1,4	0	0	48	0	0	0	0	0	0
Viola sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,2
Vitis riparia	0	0	0	0	0	0	0	0	0	0	0	0,4	0	0	0
Zanichellia palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zizania aquatica	0	0,6	0	0	0	0	1,6	5,2	0	2,4	3	0	2,8	46	0

Name of site	LC	LC	LC	GM	GM	GM	RRC	RRC	RRC	GI	GI	GI	UI	UI	UI
Marsh type	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack	Brack
Elevation zone	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh
Acorus americanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agalinis maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis stolonifera	0	0	0	0	0	0	0	0,4	0	0	0	0	0	0	0
Alnus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amaranthus cannabinus	0	0	0,4	0	0	0	0,6	0,8	0	0,6	0	0	0,8	0	0
Amorpha fruticosa	0	0	0	0	0	0,6	0	0	0	0	0	0	0	0	0
Amphicarpa bracteata	0	0	0	0	0	0,4	0	0	0	0	0	0	0	0	0
Apios americana	0	0	0	0	0	0,6	0	0	0	0	0	0	0	0	0
Asclepias incarnata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster novi-belgii	0	0	0	0	0	0	0,4	0	1,6	0	0	0	0	0	0
Aster puniceus	0	0	0	0	0	0,6	0	0	0	0	0	0	0	0	0
Aster subulatus	0	0	0	0	0	0	0	0,2	0	2,4	0	0	0	0,4	0,2
Aster tenuifolius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atriplex hastata	0	0	0	0	0	0	0	0,4	0	0	0	0	0	0	0
Atriplex subspicata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bidens laevis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bidens sp.	0	0	1	0	0	0	0	0,6	0,2	0	0	0	0	0	0
Boehmeria cylindrica	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Calamagrostis canadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calystegia sepium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callitriche sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex lacustris	0	0	0	0	0,4	7,2	0	0	0	0	0	0	0	0	0
Carex stricta	0	0	0	0	0	15,2	0	0	0	0	0	0	0	0	0
Ceratophyllum demersum	26,8	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Cicuta maculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornus amonum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cuscuta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Distichlis spicata	0	0	0	0	0	0	0	0	0	0	0	0,8	0	0,4	0
Elodea nutallii	0,2	0	0	10	0	0	0	0	0	0	0	0	0	0	0
Elymus virginicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epilobium coloratum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum fluviatile	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eupatorium maculatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium palustre	0	0	0,4	0	0	0,6	0	0	0	0	0	0	0	0	0
Galium tinctorium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gerardia tenuifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Impatiens capensis	0	0	0	0	0	1,8	0	0	0	0	0	0	0	0	0
Iris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iva frutescens	0	0	0	0	0	0	0	0	0	0	0,8	0,2	0	0	0,2
Juncus gerardii	0	0	0	0	0	0	0	0	0	0	0,2	0,6	0	0,2	0
Juncuc sp.	0	0	5,2	0	0	0	0	0	0	0	0	0	0	0	0
Leersia oryzoides	0	0	0,2	0	0	0	0	0	0	0	0	0	0	0	0
Lemna minor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limonium carolinianum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobelia cardinalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ludwigia palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycopus rubellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lysimachia lanceoloata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lythrum salicaria	0	0	0	0	0,2	0,6	0	0	0	0	0	0	0	0	0
Mikania scandens	0	0	0	0	6,2	0,8	0	0	0	0	0	0	0	0	0
Myosotis scorpioides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuphar variegatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onoclea sensibilis	0	0	0	0	0	1,2	0	0	0	0	0	0	0	0	0
Panicum virgatum	0	0	0	0	0	0	0	0	1,2	0	0	0	0	0,2	0
Peltandra virginica	0	0	0	0	4,6	9,2	0	0	0	0	0	0	0	0	0
Phragmites australis	0	0	5,6	0	0	0	0	0,8	0,2	2	19,2	0,2	1	1	0,4
Pilea pumila	0	0	0	0	0	0,4	0	0	0	0	0	0	0	0	0
Plantago maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pluchea purpuascens	0	0	0	0	0	0	0	0	0	0	0,2	0	0	0,2	0,2
Polygonum arifolium	0	0	6,4	0	8,6	6,6	0	0	0	0	0	0	0	0	0
Polygonum hydropeperoides	0	0	0	0	0	0	0,2	0	0	0	0	0	0	0,2	0
Polygonum punctatum	0,2	0	1	0,2	0	0	0	1	0	0	0	0	0	0	0
Polygonum sagittatum	0	0	0	0	0	0,4	0	0	0	0	0	0	0	0	0
Pontederia cordata	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0
Potentilla anserina	0	0	0	0	0	0	0	0	0	0	0	0,4	0	0	0
Potamogeton crispus	2,8	0	0	0,4	0	0	0	0	0	0	0	0	0	0	0
Rosa palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex orbiculatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagittaria graminea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagittaria latifolia	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0
Sagittaria montevidensis	0	0	0	0,2	0	0	0	0	0	0	0	0	0	0	0
Salicornia europaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Name of site	LC	LC	LC	GM	GM	GM	RRC	RRC	RRC	GI	GI	GI	UI	UI	UI
Marsh type	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh
Elevation zone	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh
Samolus parviflorus	0	0	0,2	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus americanus	0	0	3,2	0	0	0	0	0	2,2	0	0,2	0	0	14,0	0
Scirpus fluviatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus robustus	0	0	0	0	0	0	12,4	0,6	0	2,4	0	0,2	0	0,2	0
Scirpus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus tabernemontani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scutellaria galericulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scutellaria latifolia	0	0	0	0	0	0,2	0	0	0	0	0	0	0	0	0
Solidago sempervirens	0	0	0	0	0	0	0	0	0	0	0	0,2	0	0	0
Spartina alterniflora	0	0	0	0	0	0	72,0	0	0,6	72,0	0	0	70	0	0
Spartina cynosuroides	0	0	0	0	0	0	0,2	0	0	0	46	0	0	0,8	0
Sparganium eurycarpum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spartina patens	0	0	0	0	0	0	0	8	82	0	23	90,0	0	42,0	86,0
Stachys tenuifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Suaeda maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalictrum polygamum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thelypteris palustris	0	0	0	0	0,2	26	0	0	0	0	0	0	0	0	0
Toxicodendron rydbergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triadenum virginicum	0	0	0	0	0	0,2	0	0	0	0	0	0	0	0	0
Typha angustifolia	0	52,0	32,0	0	52,0	34,0	0	66,0	0	0	0	0	0	20,0	0
Viola sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vitis riparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zanichellia palustris	1,6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zizania aquatica	54,0	0,2	0,2	40,0	0	0	0	0	0	0	0	0	0	0	0

Name of site	GP	GP	GP	GI	GI	GI	RN	RN	RN	OS1	OS1	OS1	OS2	OS2	OS2
Marsh type	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt	Salt
Elevation zone	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh
Acorus americanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agalinis maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0,2	0
Agrostis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis stolonifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alnus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amaranthus cannabinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amorpha fruticosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphicarpa bracteata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apios americana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asclepias incarnata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster novi-belgii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster puniceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster subulatus	0	0	0	0	0	0	0	0	0,8	0	0	0	0	0	0
Aster tenuifolius	0	1	0,4	0	0	0	0	0	0	0	0	0,8	0	2	0,2
Atriplex hastata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atriplex subspicata	0	0	0,4	0	0	0	0	0	0	0	0	0	0	0	0
Bidens laevis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bidens sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boehmeria cylindrica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calamagrostis canadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calystegia sepium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callitriche sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex lacustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex stricta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratophyllum demersum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cicuta maculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornus amonum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cuscuta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Distichlis spicata	0	1,2	6,6	0	0	0,2	0	0,2	58	0	11,2	5,4	0	8,8	32
Elodea nutallii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elymus virginicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epilobium coloratum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum fluviatile	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eupatorium maculatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium palustre	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium tinctorium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gerardia tenuifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Impatiens capensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iva frutescens	0	0	22,4	0	0	0	0	0	15	0	0	5,6	0	0,2	1,6
Juncus gerardii	0	0	46	0	0	90	0	0,4	18,6	0	0,2	78	0	0	46
Juncuc sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leersia oryzoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lemna minor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limonium carolinianum	0	0	4,2	0	0	0	2,8	0	1,2	0	0,6	0,6	0	7,2	0
Lobelia cardinalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ludwigia palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycopus rubellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lysimachia lanceoloata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lythrum salicaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mikania scandens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myosotis scorpioides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuphar variegatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onoclea sensibilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Panicum virgatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peltandra virginica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phragmites australis	0	0	10,0	0	0	0	0	0	0	0	0	0	0	0	0,2
Pilea pumila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0,4	0
Pluchea purpuascens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum arifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum hydropeperoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum punctatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum sagittatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pontederia cordata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla anserina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potamogeton crispus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex orbiculatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagittaria graminea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagittaria latifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagittaria montevidensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salicornia europaea	0	0,2	0,2	0	0,2	3	3,2	0,8	0,2	0	0,8	0,6	0	0,2	0,6
Salix sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Name of site	GP	GP	GP	GI	GI	GI	RN	RN	RN	OS1	OS1	OS1	OS2	OS2	OS2
Marsh type	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh
Elevation zone	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh	Low marsh	Mid marsh	High marsh
Samolus parviflorus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus americanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus fluviatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus robustus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scirpus tabernemontani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scutellaria galericulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scutellaria latifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solidago sempervirens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,4
Spartina alterniflora	72,0	0	0,2	96,0	1,4	0,4	62,0	0,8	0	82	0,8	0,8	84	0,4	0
Spartina cynosuroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sparganium eurycarpum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spartina patens	0	90	0,2	0	94,0	0,2	11	86	0	1	80	0	0	78	0
Stachys tenuifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Suaeda maritima	0	0	0,2	0	0	0	0	0	0	0	0	0	0	0	0
Thalictrum polygamum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thelypteris palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Toxicodendron rydbergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triadenum virginicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Typha angustifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vitis riparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zanichellia palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zizania aquatica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table C 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 Wisskirschen and 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[1]	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[2]	Glycophyte
Urtica dioica	Urt-dio	Perennial	0	Glycophyte
Valeriana officinalis	Val-off	Perennial	0	Glycophyte

[1] for ecotypes occurring in coastal areas

[2] for *T. fragiferum*

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