

Seedling stability in waterlogged sediments: an experiment with saltmarsh plants

Regine Redelstein^{1,*}, Gerhard Zotz², Thorsten Balke^{2,3}

¹Plant Ecology and Ecosystems Research, University of Göttingen, 37077 Göttingen, Germany

²Institute of Biology and Environmental Sciences, University of Oldenburg, 26111 Oldenburg, Germany

³School of Geographical and Earth Sciences, University of Glasgow, Glasgow G12 8QQ, UK

ABSTRACT: Saltmarsh seedlings are exposed to extreme soil conditions in combination with mechanical disturbance by waves and tides, especially at the seaward fringe. We tested whether soil waterlogging affects resistance of seedlings to physical disturbance, thereby potentially influencing the distribution of saltmarsh species. A mesocosm experiment was conducted to investigate effects of waterlogging on plant traits, in particular root growth, and tolerance of seedlings to sediment erosion. Three species, each dominating different elevations in NW European salt marshes (*Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica*), were selected for the experiments. Individual seedlings were grown under different waterlogging treatments and finally subjected to an erosion treatment. The depth of erosion at which the seedlings toppled (E_{crit}) was determined and related to above- and below-ground morphological traits of the seedlings. Resistance to erosion decreased in all 3 species from drained to completely waterlogged soil conditions, with the strongest negative impact of waterlogging on the upper marsh species *E. atherica*. Root length and biomass, shoot biomass and the root:shoot biomass ratio were the most important traits positively affecting E_{crit} . The experiment demonstrates that rapid root growth is essential for the stability of seedlings, and is presumably of great importance for their successful establishment on tidal flats where sediment erosion may be a limiting factor. Root growth is in turn affected by a species-specific response to waterlogging. Our study suggests that this species-specific effect of waterlogging on seedling stability contributes to species sorting along the inundation gradient of coastal ecosystems.

KEY WORDS: Coastal ecosystems · Erosion · Root growth · Species distribution · Tidal inundation · Vegetation establishment

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INTRODUCTION

The establishment of seedlings is a crucial phase in plant ontogeny (Grubb 1977). Salt marshes are dynamic ecosystems with phases of lateral expansion, when new vegetation establishes on tidal flats, and phases of retreat due to lateral erosion or drowning (Balke et al. 2014, Bouma et al. 2016). Saltmarsh seedlings generally establish above mean high water of neap tides (MHWN; Balke et al. 2016) and are exposed to extreme abiotic conditions, particularly during immersion. Vascular saltmarsh plants require

a high degree of adaptation to their physically and physiologically stressful habitat (Bertness & Ellison 1987, van Diggelen 1991, Noe & Zedler 2000). Regular inundation by seawater leads to high salinity of saltmarsh soils and to waterlogged soil conditions accompanied by soil anoxia, increased concentrations of toxic compounds and decreased availability of nutrients (Armstrong et al. 1985, Pennings & Callaway 1992). High concentrations of soluble sulfide in waterlogged soils are directly toxic to plants and also reduce availability of essential elements such as Fe, Mn, Cu and Zn (Havill et al. 1985, Lamers et al.

*Corresponding author:
regine.redelstein@biologie.uni-goettingen.de

2013). Apart from waterlogged soil conditions, seedling establishment in salt marshes is strongly impacted by physical disturbance by waves and tidal currents. Resuspension of sediment from the tidal flat can lead to short-term erosion of several centimeters (Hu et al. 2015, Hu et al. 2017) and hence to toppling or excavation of seedlings.

With increasing distance from the sea (i.e. increasing elevation and less frequent inundation) there is a gradual change in abiotic conditions, leading to a zonation of saltmarsh vegetation with distinct species compositions (Fig. 1; Armstrong et al. 1985, Bockelmann et al. 2002). Salinity and flooding are the main abiotic factors controlling the establishment and species distribution in saltmarsh plant communities (Cooper 1982, Armstrong et al. 1985, Rozema et al. 1985, Ungar 1998). The local determinants of plant zonation in salt marshes may also include herbivory and facilitation (Ungar 1998, Noe & Zedler 2001, Ewanchuk & Bertness 2004, Pennings et al. 2005, Davy et al. 2011, He et al. 2015). In general, the seaward edge of the salt marsh is only inhabited by a few species, which are able to tolerate stressful abiotic conditions, whereas at higher elevations more competitive and less stress-tolerant species prevail (Levine et al. 1998, Rand 2000, Pennings & Moore 2001, Crain et al. 2004, Fariña et al. 2009).

Waterlogged soil conditions are common, especially in the lower salt marsh zones, and may directly affect saltmarsh vegetation through reduced germination of seeds (Clarke & Hannon 1970), the inhibition of root emergence at the seedling stage (Wijte & Gallagher 1996), or through growth inhibition in general (Cooper 1982). These effects vary among species from different saltmarsh zones, which leads to the characteristic vegetation pattern (Clarke & Hannon 1970). However, there has been no assess-

ment of how the tolerance of different saltmarsh species to erosion is affected by waterlogging, and how this influences the observed zonation. In general, seedlings are less tolerant to stressful environmental conditions than adult plants (Ungar 1978), while their establishment is crucial for vegetation formation. The first step of successful establishment of a seedling on the tidal flat is rapid anchoring during a disturbance-free period, the so-called 'window of opportunity' (Balke et al. 2014). After anchoring, seedling survival depends on resistance to dislodgement by hydrodynamic forces as well as on physiological abilities to cope with abiotic stress in tidally inundated soils (Balke et al. 2011, Davy et al. 2011, Friess et al. 2012).

Waterlogged soils in combination with physical disturbance affect a number of ecosystems besides salt marshes. In riparian floodplains, seedling survival is strongly dependent on the hydrological regime, sediment erosion and deposition, and the ability to root quickly (Segelquist et al. 1993, Mahoney & Rood 1998, Corenblit et al. 2007). Seagrass beds have been found to die off during events of extreme soil anoxia (Moore et al. 1993). However, populations of *Zostera marina* are able to recolonize quickly after such anoxic crises despite continuous sediment resuspension and strong hydrodynamic forces. This is due to rapid vegetative expansion after initial seedling recolonization (Plus et al. 2003). Waterlogging and associated anoxic soil reduce root growth and rooting depth across different wetland ecosystems (Visser et al. 1996, Bouma et al. 2001). This reduced development of plant roots should in turn make plants more susceptible to physical disturbance and thus play an essential role in the distribution of vascular plants along inundation and disturbance gradients. The interactive effects of seedling trait plasticity due to waterlogging and physical disturbance leading to plant

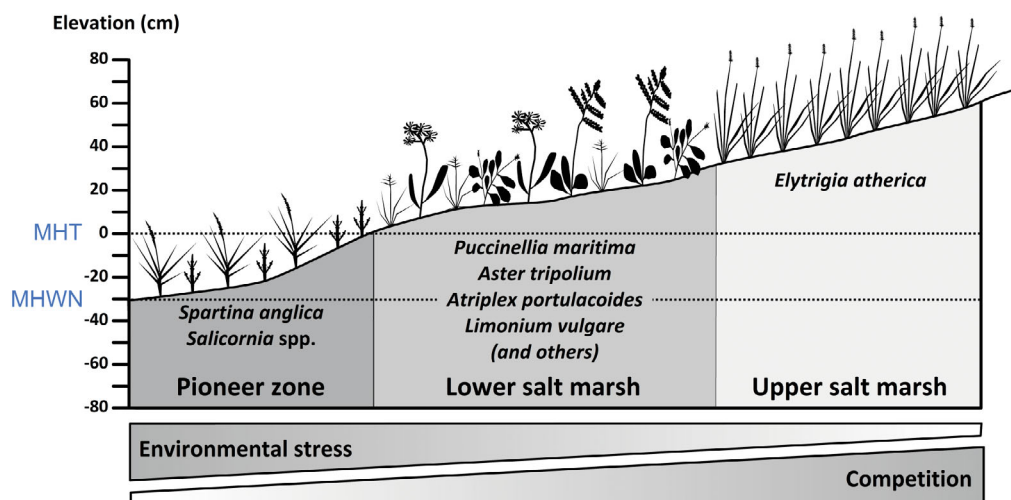


Fig. 1. The 3 zones of a NW European salt marsh with their elevations relative to the mean high tide (MHT) level and characteristic species. Mean high water of neap tides (MHWN) marks the transition from the bare tidal flat to the pioneer zone. Figure modified from Redelstein et al. (2018)

toppling are currently poorly understood, despite their potential relevance across biogeomorphic ecosystems (Corenblit et al. 2015).

Our study addresses the effect of waterlogged soil conditions on the stability of newly establishing seedlings in physically disturbed ecosystems such as salt marshes. We conducted a mesocosm experiment using seedlings of 3 species dominating the 3 saltmarsh zones in NW European salt marshes: the annual pioneer species *Salicornia europaea* (Chenopodiaceae), which dominates the lowest margin of the salt marsh (i.e. the 'pioneer zone', Fig. 1), the dwarf shrub *Atriplex portulacoides* (Chenopodiaceae) from the lower salt marsh, and *Elytrigia atherica* (Poaceae), which occupies well-aerated soils in the upper salt marsh. The pioneer zone just above MHWN is inundated during almost every high tide throughout the year (Balke et al. 2017) and species are subjected to permanently waterlogged and reduced soil conditions. The lower salt marsh lies just above the mean high tide (MHT) level and is inundated only during high water of spring tides, and the upper salt marsh is only inundated during very high spring tides and storm events. The lower and upper saltmarsh soils are generally well-drained and aerated during most of the summer (Armstrong et al. 1985, Veeneklaas et al. 2013).

Considering the lack of data on early root growth in the context of intertidal wetland succession (Friess et al. 2012), our study focuses on below-ground growth of seedlings in relation to shoot growth under the given experimental conditions. We hypothesize that (1) root growth plays an important role for the ability of seedlings to resist physical disturbances; (2) waterlogged soil conditions negatively affect root growth of developing saltmarsh seedlings, leading to reduced resistance against physical disturbance; (3) seedlings of pioneer zone species cope more successfully with waterlogged soil conditions and are more resistant to physical disturbances (i.e. erosion) under these conditions than lower and upper saltmarsh species; and (4) environmental stress (i.e. waterlogged soil) affects root morphology and leads to an increase in specific root length and a decrease in root tissue density, thus increasing the efficiency of soil exploitation at lower construction costs (Eissenstat et al. 2000).

Understanding the combined effects of soil waterlogging and disturbance on species distribution across the elevational gradient of the saltmarsh environment is an important step towards a better understanding of marsh zonation and improving the design of conservation and restoration measures. This is especially important in light of accelerated sea level

rise and changing wave climates. Furthermore, linking soil anoxia and seedling stability to key plant traits allows conclusions to be drawn that are also relevant for vegetation establishment in other frequently flooded and physically disturbed ecosystems (e.g. mangroves, riparian forests or seagrass beds).

MATERIALS AND METHODS

Three experimental tanks (1 m × 1 m × 0.5 m, length × width × height) were set up in a greenhouse at the Institute for Chemistry and Biology of the Marine Environment (ICBM) Terramare Wilhelmshaven (University of Oldenburg, Germany). A fourth tank that served as water reservoir was placed beneath the 3 experimental tanks. Tidal inundation was simulated by pumping water from the reservoir into the experimental tanks (EHEIM universal pump 1048, 600 l h⁻¹). Seawater was mixed with freshwater to obtain a salinity of 6.5, which corresponded to the salinity of the natural sediment collected from Jade Bay, Germany (53° 29' 9" N, 8° 10' 50" E). A timer on the pumps was used to fill the experimental tanks automatically, while switching off the pumps resulted in drainage of the upper tank through the pump back into the reservoir. An overflow return pipe inside the experimental tanks maintained the water depth at approximately 80 mm above the top of the plant pots. Each experimental tank was flooded twice daily for 1.5 h, once during daytime and once at night. Salinity in the mesocosms was measured every 2 to 3 d and maintained at 6.5 by the addition of fresh water to compensate for evaporation.

Seeds of *Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica* were collected in the salt marsh at the south side of the East Frisian Island Spiekeroog (Germany; 53° 45' 44" N, 7° 43' 23" E) in autumn 2014, air dried and stored dry at 7°C until the start of the experiment in early summer 2015.

Experimental pots were made from PVC pipes of 12 cm diameter and 15 cm length. The pots were prepared in order to obtain 3 different levels of waterlogging within the pots: (1) drained, (2) partly waterlogged and (3) waterlogged. Treatments were chosen to simulate permanently waterlogged soils on the tidal flats (i.e. initial location of pioneer establishment) and better drained soils in the lower and upper saltmarsh zones. For the drained treatment, slits were cut into the sides of the pots and pots were lined with a water permeable fleece to allow complete drainage. For the partly waterlogged treatment, holes with a diameter of 3 mm were drilled into the

Table 1. Sediment redox potential (mean \pm SE) measured at different sediment depths in experimental pots under 3 waterlogging treatments (mesocosm experiment) and in 3 saltmarsh zones and on a tidal mudflat (field measurement) at Spiekeroog Island (Germany). Measurements at the field site were taken during the growing period (August). Measured values were corrected by adding the potential of the reference electrode (210 mV) with respect to the standard hydrogen electrode

Sediment depth (cm)	Redox potential (mV)						
	Mesocosm experiment			Field measurement			
	Drained	Partly waterlogged	Waterlogged	Upper salt marsh	Lower salt marsh	Pioneer zone	Mudflat with initial colonization
2.5	+126.5 \pm 9.1	+107.5 \pm 7.9	+6.2 \pm 5.32	+412.7 \pm 10.8	+345.6 \pm 10.2	+236.0 \pm 33.2	+87.0 \pm 107.0
5	-2.5 \pm 5.2	+4.1 \pm 8.0	-18.2 \pm 3.4	+409.0 \pm 7.3	+355.7 \pm 30.0	+289.2 \pm 36.5	-26.6 \pm 92.2
10	-54.2 \pm 2.7	-39.9 \pm 3.1	-40.4 \pm 2.3	+424.0 \pm 11.5	+371.8 \pm 25.0	+254.9 \pm 55.0	-196.9 \pm 19.0

upper 3 centimeters of the pots. The lower part of the pots, which was not perforated, was lined with a plastic bag. In addition, fleece was inserted into the pots to avoid sediment loss through the holes. For the waterlogged treatment, pots were entirely lined with plastic bags. Sediment was collected from the tidal flats of Jade Bay. The grain size distribution of the sediment was: sand ($>63 \mu\text{m}$): 95.9%; silt ($<63 \mu\text{m}$): 4.1%; clay ($<2 \mu\text{m}$): 0%. After collection, the sediment was frozen at -18°C for 3 d in order to remove any live zoobenthos. Afterwards, the sediment was sieved (mesh size: 5 mm) and filled into the experimental pots. The pots were placed within the experimental tanks. Seven days after initiation of the tidal regime different redox potentials became established according to the treatments (Table 1) and seedlings were transferred to the experimental pots (see below). Redox potential was measured as an index for soil aeration and we expected waterlogged treatments to be associated with low redox potentials (Davy et al. 2011). Each experimental tank included 1 reference pot per treatment without a seedling to measure redox potential. This was done every 2 to 3 d throughout the experiment at 3 different sediment depths (2.5, 5 and 10 cm) at varying locations in each reference pot by means of a metal combination electrode with an Ag/AgCl reference system (3 M KCl) and a platinum sensor (Pt 61, SI Analytics). Measured values were corrected by adding the potential of the reference electrode (210 mV) with respect to the standard hydrogen electrode. In addition, the redox potential was measured in the field on Spiekeroog Island, in the 3 saltmarsh zones and on a tidal flat with initial seedling colonization (Table 1).

Seeds were sown in the same sediment outside of the mesocosms and seedlings were transferred 3 to 4 d after germination to the experimental pots. Each

pot was planted with 1 seedling with visible cotyledons and a size of a few millimeters (Fig. 2a). Seedlings were assigned to pots using a random number list whereby species and treatments were distributed evenly among the 3 experimental tanks. Per species and treatment, 18 (*E. atherica* and *S. europaea*) or 12 (*A. portulacoides*) replicate pots were used. The seedlings were grown in the experimental pots inside the mesocosms for a period of 47 to 55 d and monitored throughout the experiment for survival and height 3 times wk^{-1} . On the last day, all surviving seedlings were subjected to an erosion treatment. Following the methods of previous studies (see Han et al. 2012 for seagrass; Balke et al. 2013 for mangroves; Cao et al. 2017 for *Spartina* spp.), erosion was mimicked by inserting 3 mm thick discs into the experimental pots from the bottom and pushing the sediment above the edge of the pot. Protruding sediment was carefully removed by water spray without breaking seedlings or roots. Additional discs were inserted until the seedlings toppled under their own weight (Fig. 2b). The depth of sediment removed was defined as the critical erosion depth (E_{crit}). Toppled seedlings were removed from the sediment, washed and maximal root length (length of the longest root) and shoot height were determined. Fresh roots and shoots were separated from each other, the roots were scanned under a flatbed scanner and total root length, root surface area, root volume and root diameter were determined using the software WinRhizo (Regent Instruments). After scanning, roots and shoots were oven dried at 70°C for 72 h and weighed to determine dry mass. Specific root length (SRL) (root length/root dry weight), specific root area (SRA) (root surface area/root dry weight) and root tissue density (RTD) (root dry weight/root volume) were calculated from these measurements.

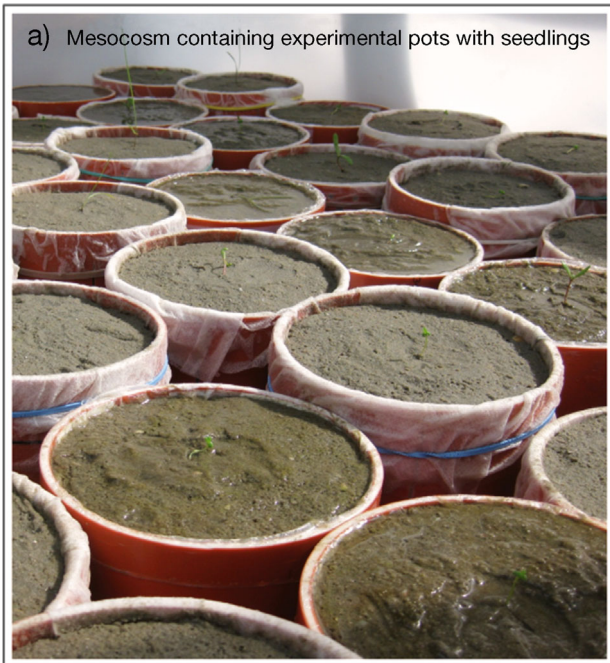
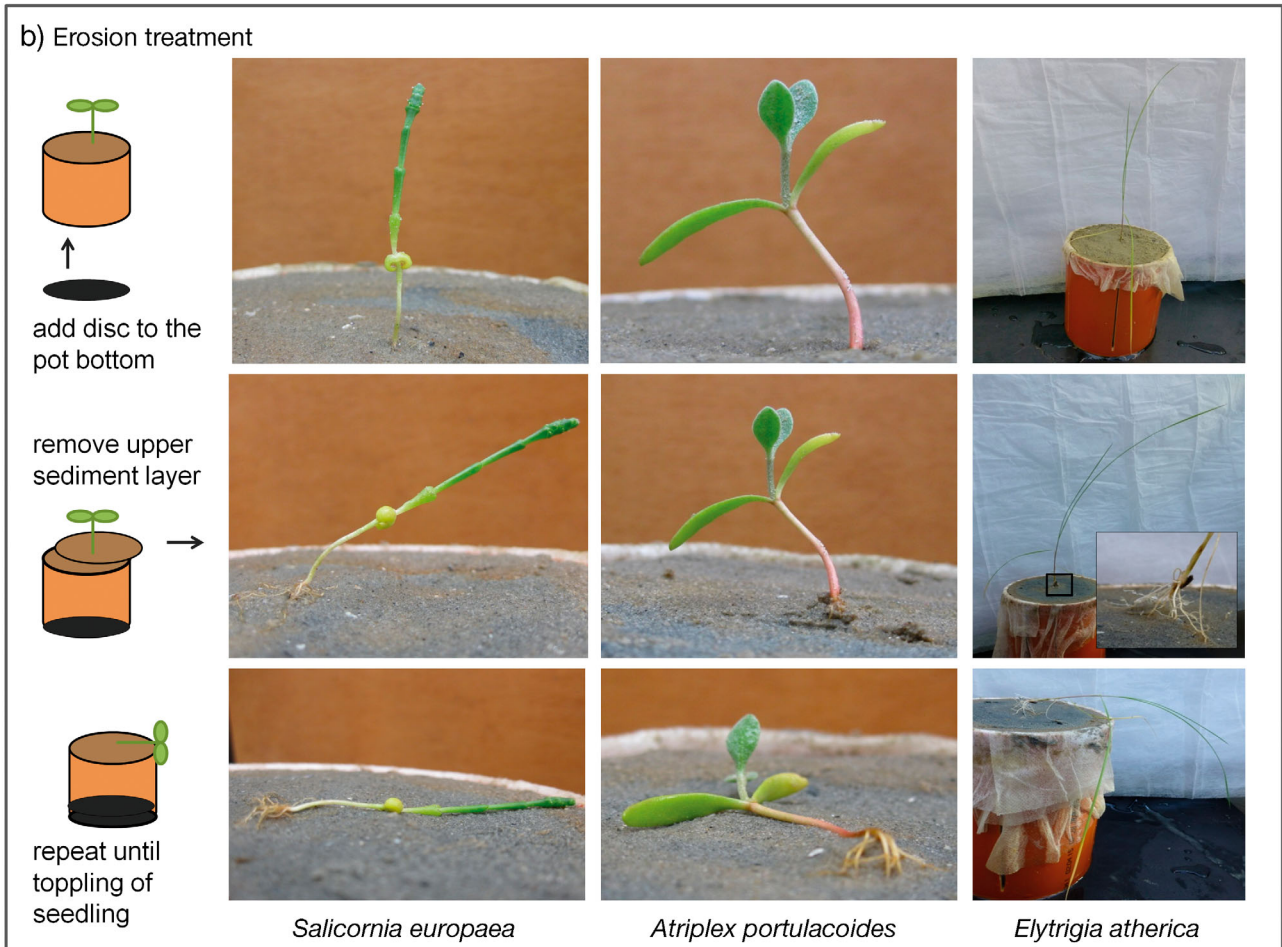


Fig. 2. (a) Mesocosm with experimental pots containing seedlings of *Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica* grown from seeds collected from a NW European salt marsh. The pots were prepared in order to simulate 3 different levels of waterlogging: (1) drained, (2) partly waterlogged and (3) waterlogged. (b) Design and implementation of a test to simulate erosion and determine the critical erosion depth (E_{crit}) of each species. Photographs: R. Redelstein



In addition, *Salicornia* spp. seedlings from a natural tidal flat close to a salt marsh near Westerhever (Schleswig-Holstein, Germany; 54°37'50" N, 8°63'52" E) were subjected to the same erosion treatment by inserting one of the experimental pots into the sediment around a seedling, digging out the pot containing the seedling and surrounding sediment, and performing the critical erosion test as described above. Seedlings were brought to the laboratory, washed, maximal root length and shoot height were determined and roots were scanned, dried and weighed for the determination of root morphological traits as described above. Seedlings were chosen with a similar shoot height as the seedlings grown in the mesocosm experiment. Due to difficult differentiation between taxa at the seedling stage and the challenging taxonomy of *Salicornia* in general (Kadereit et al. 2012), here we refer to the genus *Salicornia* spp.

Statistical analyses were conducted using R 3.3.2 software (R Development Core Team 2016). A growth curve for each species was fitted to a 3 parameter-logistic growth model in accordance with Paine et al. (2012) using the package 'nlme' as follows:

$$H_t = \frac{H_0 \times K}{H_0 + (K - H_0) \times e^{-r \times t}} \quad (1)$$

where H_t is seedling height at time t , H_0 is seedling height at start of experiment (when seedlings were transferred to experimental pots), K is seedling height at harvest, and r is relative growth rate. H_0 , K and r were treated as random effects on the individual level. To test for differences between treatments the restricted maximum likelihood method was used.

To account for species differences in initial seedling size and to compare shoot and root growth between species, absolute growth rates were calculated as the increase in seedling height or root length divided by the exposure period of the experiment (Paine et al. 2012). Absolute growth rates are appropriate to capture age- and size-dependent growth (i.e. initial seedling growth in our study) (Paine et al. 2012). Growth rates and seedling morphology data were log-transformed to achieve normality of residuals and homoscedasticity according to the Shapiro-Wilks test (Shapiro.test, package 'stats') and Levene's test (leveneTest, package 'car'), respectively. Two-way factorial ANOVAs were conducted to compare the main effects of species and treatments and the interaction between species and treatments on the different morphological traits and growth rates. Tukey's HSD tests allowed multiple comparisons between species and treatments (Anova and HSD.test, packages 'car' and 'agricolae', respectively). In cases

where there were significant interaction effects, 1-way ANOVAs with subsequent Tukey's HSD tests were conducted to investigate significant differences between levels within the variables (species, treatment) separately. Where normality of residuals could not be achieved (for values of E_{crit}), a Kruskal-Wallis test (kruskalmc, package 'pgirmess') was used for multiple comparisons of E_{crit} between treatments and species. Statistical significance was based on a 0.05 probability level. A principal components analysis (PCA) was used to assess how parameters of seedling size and stability interrelate between species and treatments, using the software CANOCO, version 5.02 (Biometris).

RESULTS

Growth of seedlings dependent on waterlogging treatment

Shoot growth rates differed between the 3 species in all treatments, with highest shoot growth rates for *Elytrigia atherica* and lowest shoot growth rates for *Atriplex portulacoides* ($p < 0.001$; Figs. 3 & 4a). This resulted in substantial differences in seedling size at the end of the experiment. Seedlings of *E. atherica* (252 mm shoot height in the drained treatment) were 4 times and 8 times taller than those of *Salicornia europaea* (75 mm) and *A. portulacoides* (34 mm), respectively (Table 2; see also Table S1 for measurements of seedling height and Table S2 for results of 2-way factorial ANOVAs, both in the Supplement at www.int-res.com/articles/suppl/m590p095_supp.pdf). Absolute root growth rates in the drained treatment differed between the 3 species ($p < 0.001$; Fig. 4a). Root growth rates of *E. atherica* were significantly higher than those of *S. europaea* and *A. portulacoides*. Under waterlogged conditions there were no significant inter-specific differences.

Seedling size at the end of the exposure period was significantly affected by waterlogging treatments within species for *S. europaea* and *E. atherica*. Performance of *S. europaea* seedlings was slightly better under partly waterlogged and fully waterlogged conditions compared to the drained treatment. However, only the partly waterlogged treatment led to a significant increase in shoot height (21.5%) compared to the drained treatment ($p < 0.05$). *E. atherica* was affected negatively in its growth by waterlogging. Shoot height of seedlings was lower by 37% ($p < 0.001$) in the waterlogged treatment compared to the drained treatment (Fig. 3, Table 2). Absolute root

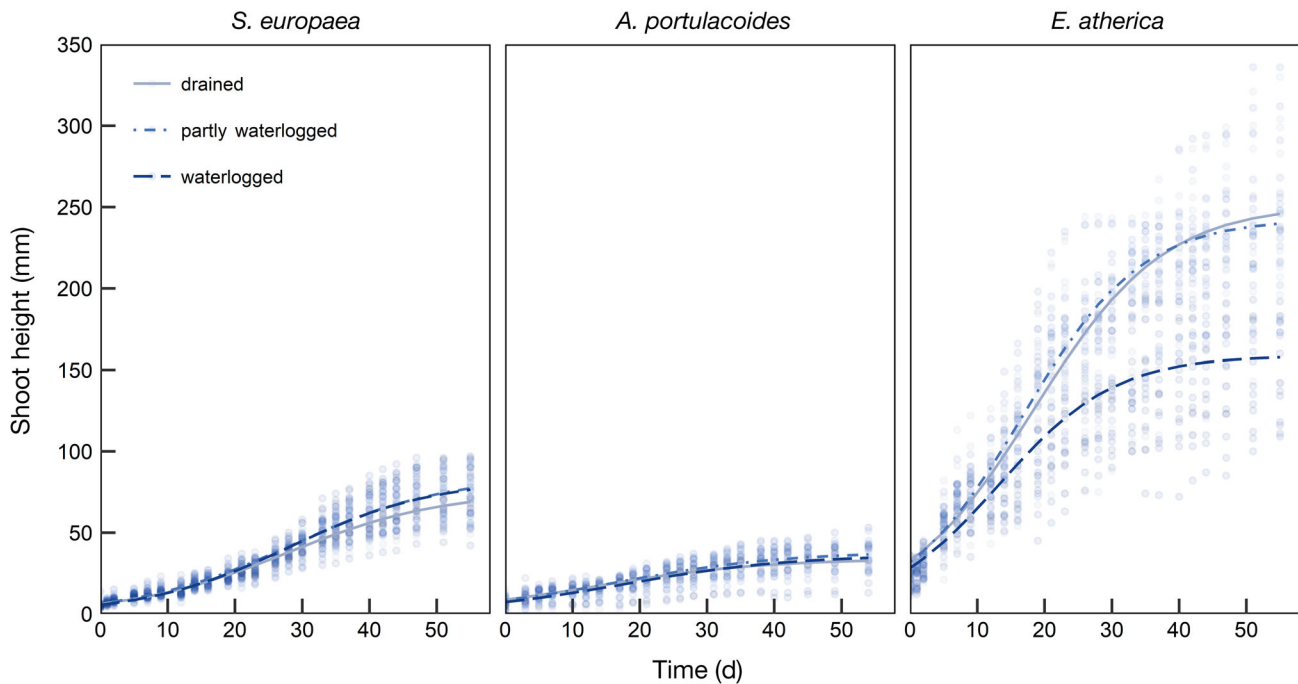


Fig. 3. Growth of *Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica* seedlings under 3 different waterlogging treatments (drained, partly waterlogged, and waterlogged). Dots represent measurements of individual seedlings; lines represent predictions of a 3-parameter logistic model for the different treatments. Note overlying lines under different treatments for *S. europaea* and *A. portulacoides*

growth rates of *A. portulacoides* and *E. atherica* were reduced by waterlogging treatments (Fig. 4b). Absolute root growth rate of *A. portulacoides* seedlings was reduced by 36% ($p < 0.05$) when waterlogged. This effect was also evident for *E. atherica* (70% reduction in absolute root growth rate; $p < 0.001$). Root and shoot biomass showed similar patterns as shoot height and root length (Table S1 in the Supplement).

Effects of waterlogging on seedling morphology

In the 3 species, root length:shoot length ratios tended to decrease from the drained to the waterlogged treatment, although this trend was only significant for *S. europaea* (33% decrease) and *E. atherica* (40% decrease, $p < 0.05$; Fig. 4c). Root length:shoot length ratios differed between all 3 species in all treatments ($p < 0.001$) and were highest in *A. portulacoides* seedlings and lowest in *E. atherica*. The root morphological traits SRL, SRA, RTD and root diameter were not affected by the treatments (Fig. 4d–f, Table S1 in the Supplement). *S. europaea* seedlings showed higher SRL and SRA and lower RTD under drained and partly waterlogged conditions compared to the other species ($p < 0.001$).

Effects of waterlogging on seedling stability

A significant decrease of E_{crit} from the drained to the waterlogged treatment was only found in *E. atherica* (80% decrease; Kruskal-Wallis test, $p < 0.05$; Fig. 5). Furthermore, *E. atherica* seedlings from the drained and partly waterlogged treatments showed a significantly higher E_{crit} compared to *S. europaea* and *A. portulacoides* within treatments. Under waterlogged conditions, E_{crit} of *E. atherica* was similar to that of *S. europaea* and *A. portulacoides*.

Comparison with *Salicornia* seedlings from the tidal flat

Salicornia spp. seedlings naturally established in the field showed significant differences compared to experimental plants. Although similar in shoot height (Table S1 in the Supplement), they had higher root biomass, shoot biomass, root length and root:shoot ratios of biomass and length (1-way ANOVA with Tukey's HSD tests, $p < 0.001$ in all cases; Table S1). SRL and SRA were lower ($p < 0.001$), whereas RTD ($p < 0.05$) and root diameter ($p < 0.001$) were higher compared to seedlings from the greenhouse. E_{crit} of naturally recruited seedlings was more than 5-fold

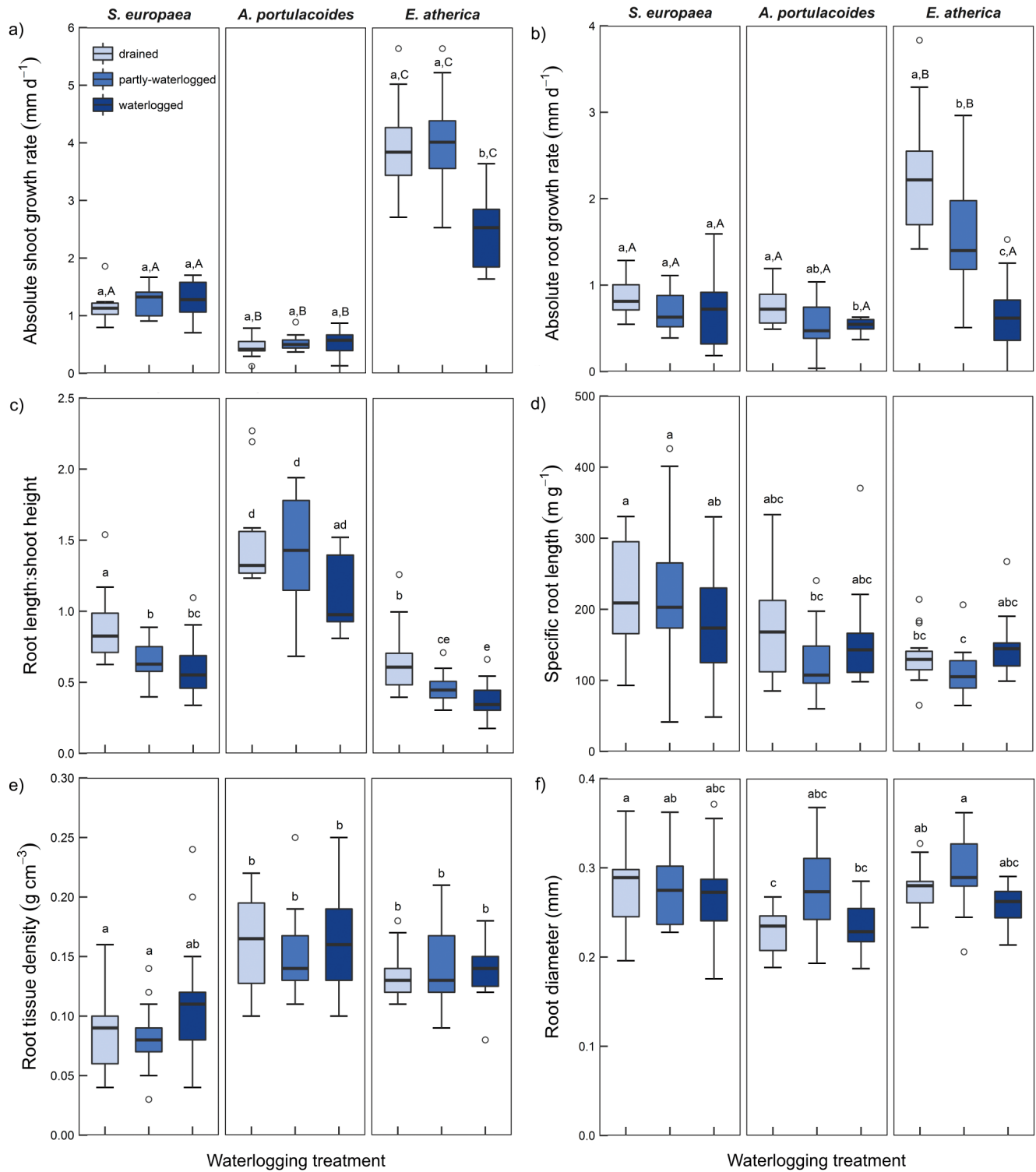


Fig. 4. Root and shoot growth rates, and measures of root morphology for *Salicornia europaea*, *Atriplex portulacoides* and *Elyt-rigia atherica* seedlings grown under different waterlogging treatments (drained, partly waterlogged, and waterlogged). Horizontal lines indicate median values, boxes the interquartile range, and error bars minimum and maximum values. Open circles represent outliers. Where the interaction effect was significant, different lower case letters indicate statistical differences between treatments within species, while different upper case letters mark significant differences between species within treatments according to 1-way ANOVA with Tukey's HSD tests ($p < 0.05$). Elsewhere, different lower case letters indicate significant differences comparing species and treatments by 2-way factorial ANOVA with Tukey's HSD tests ($p < 0.05$)

Table 2. Parameters of a 3-parameter logistic model for the growth of *Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica* seedlings exposed to 3 waterlogging treatments. H_0 : height at beginning of the experiment (mm), K : shoot height at harvest (mm); r : relative growth rate ($\text{mm mm}^{-1} \text{d}^{-1}$). Values for partly waterlogged and waterlogged treatments are given as deviation from the drained treatment. Deviations were non-significant (restricted maximum likelihood test) except where shown: * $p < 0.05$; *** $p < 0.001$

	$H_0 \pm \text{SE}$	$K \pm \text{SE}$	$r \pm \text{SE}$	Residuals
<i>S. europaea</i>				
Drained	6.2 ± 0.5	75.4 ± 3.4	0.0868 ± 0.0030	2.095
Partly waterlogged	0.3 ± 0.7	$9.7 \pm 4.9^*$	0.0003 ± 0.0041	2.095
Waterlogged	-0.6 ± 0.7	7.3 ± 4.8	0.0062 ± 0.0041	2.095
<i>A. portulacoides</i>				
Drained	8.7 ± 1.0	34.0 ± 3.0	0.0797 ± 0.0060	1.855
Partly waterlogged	-0.3 ± 1.3	4.4 ± 4.1	-0.0014 ± 0.0079	1.855
Waterlogged	-1.4 ± 1.3	2.3 ± 4.2	-0.0002 ± 0.0080	1.855
<i>E. atherica</i>				
Drained	32.8 ± 1.9	251.5 ± 10.3	0.1031 ± 0.0090	10.966
Partly waterlogged	-0.9 ± 2.6	-8.4 ± 14.4	0.0100 ± 0.0122	10.966
Waterlogged	-4.5 ± 2.8	$-92.5 \pm 15.1^{***}$	0.0127 ± 0.0132	10.966

higher compared to those grown in the experimental mesocosms (Fig. 5). Redox potentials measured at the tidal flat, where seedlings were collected, were intermediate between the values of partly waterlogged and waterlogged treatments in the experiment at shallow depth (+87 mV in upper 2.5 cm), but more negative compared to the experimental pots in deeper sediment (approx. -200 mV at 10 cm) (Table 1). Redox potential in the vegetated saltmarsh zones was positive in the pioneer zone (approx. +200 mV) and increased to highly oxidized conditions in the upper salt marsh (approx. +400 mV).

Linking seedling morphology to stability of seedlings against erosion

PCA revealed that E_{crit} was strongly positively associated with the first axis (eigenvalue 0.63) together with root length and biomass as well as shoot biomass and the ratio root biomass: shoot biomass (Fig. 6, Table S3 in the Supplement). Furthermore, shoot height was strongly negatively associated with the second axis (eigenvalue 0.33), while the ratio root length:shoot length was positively associated with this axis. The PCA plot in Fig. 6 indicates that *S. europaea* and *A. portulacoides* seedlings resembled each other

in terms of seedling size and stability in all 3 treatments, while the drained and the partly waterlogged treatments formed a cluster separated from the waterlogged treatment in the case of *E. atherica*. *Salicornia* spp. seedlings grown under natural field conditions did not group with any of the treatments of *S. europaea* in the greenhouse or with the other 2 species.

DISCUSSION

Seedling establishment is a critical phase in plant ontogeny, especially in frequently disturbed ecosystems such as salt marshes, mangroves and riparian forests. Short-term sediment erosion during inundation can excavate and dislodge seedlings; rapid root anchorage is thus crucial for seedling survival in these environments. Understanding bottlenecks for vegetation establishment is particularly important when attempting restoration of tidal wetlands, which are increasingly acknowledged for their ecosystem services. Our study demonstrates that waterlogged soil conditions may inhibit root growth of saltmarsh seedlings, leading to decreased resist-

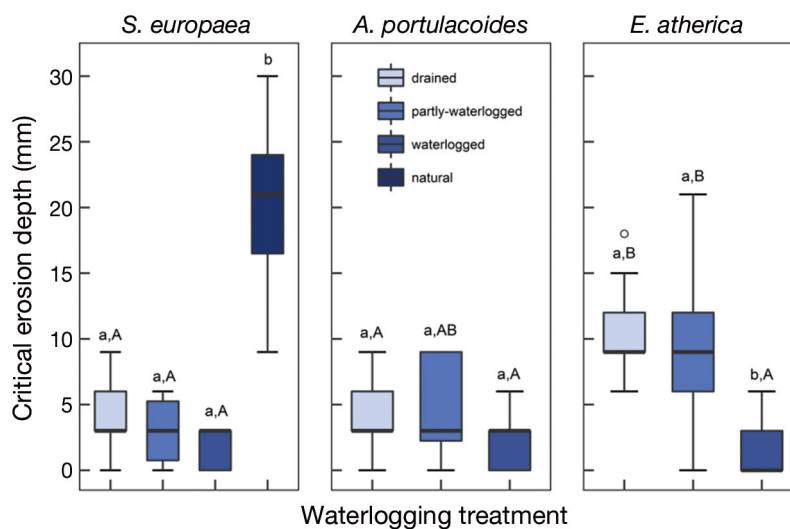


Fig. 5. Critical erosion depth (E_{crit}) of *Salicornia europaea*, *Atriplex portulacoides* and *Elytrigia atherica* seedlings under different waterlogging conditions in the mesocosm experiment and of *Salicornia* spp. seedlings grown under natural field conditions. Lower case letters mark statistically significant differences between treatments within species, while upper case letters mark statistically significant differences between species within treatments (Kruskal-Wallis multiple comparisons, significance level $p < 0.05$).

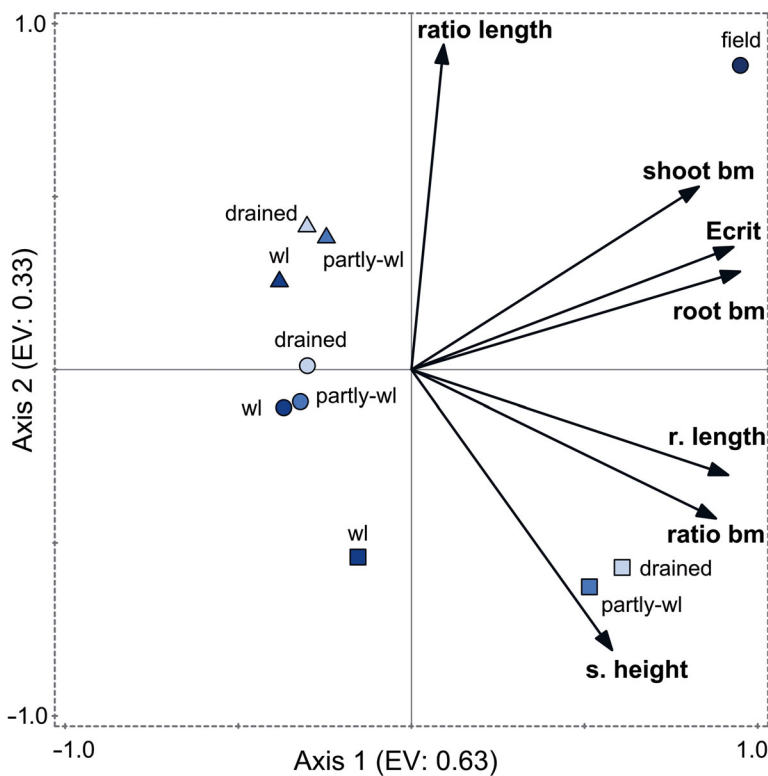


Fig. 6. Results of principal components analysis (PCA) of factors influencing seedling stability in response to erosion for *Atriplex portulacoides* (triangle), *Salicornia* spp. (circle), and *Elytrigia atherica* (square). Seedlings were subjected to 3 treatments: drained, partly waterlogged (partly-wl) and completely waterlogged (wl); in addition seedlings of *Salicornia* spp. were grown under natural field conditions. Factors considered in the analysis included measures of seedling size and the critical erosion depth (E_{crit}) determined for each species under different conditions (see Fig. 5). For detailed results of the PCA see Table S3 in the Supplement. Abbreviations: r. length: root length; s. height: shoot height; root bm: root biomass; shoot bm: shoot biomass; ratio length: ratio of root length to shoot length; ratio bm: ratio of root biomass to shoot biomass

ance of seedlings against physical disturbance. The strongest negative effect of waterlogging was found for the upper saltmarsh species *Elytrigia atherica*. While seedlings of *E. atherica* grew fastest throughout the experiment under drained conditions, they were most susceptible to waterlogging (Figs. 3–5). This result supports previous findings that *E. atherica* is a highly competitive species, but very sensitive to waterlogging (Armstrong et al. 1985, Schröder et al. 2002, Veeneklaas et al. 2013). Along the NW European North Sea coast, *E. atherica* spreads rapidly in many sites, frequently forming monospecific stands on the rarely inundated upper salt marsh (Bockelmann & Neuhaus 1999, Stock et al. 2005). Rhizomes of *E. atherica* can spread rapidly and locally outcompete other species, but successful seedling establishment is still necessary for reproduction over larger distances (Veeneklaas 2013). Our study indicates that success-

ful establishment of *E. atherica* seedlings on tidal flats may be limited by a strong inhibition of root growth and the resulting decreased stability of seedlings during erosion events. In the upper salt marsh however, *E. atherica* is able to outcompete *Salicornia* spp. and *Atriplex portulacoides* due to its rapid root and shoot growth under drained conditions.

Bockelmann & Neuhaus (1999) investigated competition between *E. atherica* and *A. portulacoides* and concluded that *E. atherica* is excluded from the lower salt marsh due to competition with *A. portulacoides* rather than by abiotic factors. Our study suggests that *E. atherica* may also be disadvantaged at frequently flooded sites in the absence of competition due to a higher sensitivity to waterlogging at the seedling stage. This may be especially important where newly available habitats are colonized by saltmarsh plants (Balke et al. 2017).

In contrast to the strong negative impact of waterlogging on *E. atherica*, *Salicornia europaea* and *A. portulacoides* were hardly affected in their growth by the waterlogging treatments. Shoot height of *S. europaea* was even higher under partly-waterlogged conditions compared to the drained treatment (Fig. 3, Table 2), indicating the good adaptation of this species to waterlogged conditions on tidal flats. Although root growth of *A. portulacoides* was reduced under waterlogged conditions, there was no difference between seedling stability of *S. europaea* and *A. portulacoides*. Thus, further abiotic and biotic components and their interactions need to be considered when explaining niche separation across the saltmarsh gradient, such as salinity tolerance (Cooper 1982, Rozema et al. 1983, Armstrong et al. 1985, Rozema et al. 1985, Redondo-Gómez et al. 2007, Katschnig et al. 2013), interspecific competition (Huckle et al. 2000, Balke et al. 2017), or herbivory (He et al. 2015).

Frequent inundation and accompanying strongly reduced soil conditions as simulated in our experiment are especially common on bare tidal flats suitable for new colonization, but also in the lowest elevations of the salt marsh. Anoxia persists in this zone throughout the growing season even in the upper centimeters of the sediment (Table 1; Armstrong et al. 1985). All treatments of our experiment had lower re-

dox potentials compared to field measurements in the salt marsh (including the pioneer zone), whereas sediment of the tidal flat was overall more reduced than the partly waterlogged and drained treatments. Davy et al. (2011) studied the relationship of species distributions and redox potential: *S. europaea* was found to tolerate redox potentials of less than -100 mV, *A. portulacoides* was absent in plots below a threshold of $+100$ mV and *E. atherica* was absent below $+200$ mV. Comparison of these thresholds to the values measured in our experimental treatments shows that seedlings in the experimental pots were subjected to extremely reduced conditions, below the limits found in their natural habitats (Table 1). However, seedlings of all 3 species not only were able to survive these extreme conditions but also showed treatment-dependent effects. This suggests an effect of anoxia on seedling development that may also depend on site (e.g. sediment type, salinity, wave exposure) and life stage (e.g. isolated seedling, adult plant in competition with other species). Relatively small differences in redox potential between treatments in deeper sediment layers, despite the differences in water level of the sediment, indicate that a less negative redox potential in the upper sediment layers is already sufficient for the seedlings to establish roots which are strong enough to withstand erosion.

Unexpectedly, waterlogging treatments had no within-species effects on root morphology. This indicates that these herbaceous and grass species do not adjust their root morphology under changing environmental conditions as found for example for tree species (Eissenstat et al. 2000, Ostonen et al. 2007, Vanguelova et al. 2007). *S. europaea* had significantly higher SRL and SRA and lower RTD compared to *E. atherica* and *A. portulacoides* in the drained and the partly waterlogged treatments. This is consistent with findings that roots with a shorter lifespan have lower RTD (Ryser 1996) and higher SRL and therefore make relatively small investments in structural carbon (Eissenstat et al. 2000). Annual plants, such as *S. europaea*, are typical examples. Moreover, the taproot system of *S. europaea* and *A. portulacoides* may have advantages for plant stability compared to the fibrous root system of *E. atherica*, as is common in monocotyledons. The fibrous root system may also explain the strong competitive abilities of *E. atherica*, since it provides better opportunities for resource exploitation. However, from the roots at the seedling stage (i.e. time of harvest in our experiment) differences in root structure could not be observed between species (as evidenced by the WinRhizo images, not shown). We therefore conclude that

these differences in root structure do not yet play a role at the early seedling phase and may only become important during later development stages.

We found substantial differences between naturally recruited seedlings and those grown in the greenhouse experiment. Although similar shoot heights were chosen, seedlings from the tidal flat showed significantly higher stability. This may be related to a higher root length (Figs. 5 & 6, Tables S1 & S3 in the Supplement) and possibly also to the already well-developed taproot (WinRhizo images), which was still lacking in the experimental seedlings. Field material was harvested in late June and hence approximately 2 to 3 mo after germination in March to April (i.e. they were approximately of same age as the experimental seedlings). Differences between field- and greenhouse-grown plants have been observed in various ecosystems e.g. for germination rates (Elberse & Breman 1990), photosynthetic induction (Zotz & Mikona 2003) or salt tolerance in *Salicornia* spp. (Riehl & Ungar 1982). This indicates the need for caution when interpreting data from laboratory studies. In our study, differences between field and experimental seedlings indicate that permanently acting mechanical stress from wind and waves, which was not simulated in the greenhouse, may lead to important plastic morphological responses (i.e. thigmomorphogenesis; Jaffe 1973, Chehab et al. 2009). Increased root allocation of field-grown seedlings by thigmomorphogenesis increases their resistance to mechanical perturbation ('tolerance strategy'; Puijalon et al. 2011) and has been observed by other authors in aquatic (Puijalon & Borrette 2006) and terrestrial (Crook & Ennos 1996, Goodman & Ennos 1996) plants as a response to mechanical stimulation. In addition, lower light levels in the greenhouse may have affected growth rates and seedling morphology in relation to surveyed seedlings in the field. Pennings et al. (2005) conducted field and greenhouse experiments with *Juncus roemerianus* and made similar observations: biomass was much higher in individuals grown in the field than in those grown in the greenhouse, but the response of seedlings to various flooding and salinity treatments was highly correlated between field and glasshouse. Thus, we conclude that the results of our mesocosm experiment are of ecological relevance, especially comparisons among the 3 species grown under same, controlled conditions in the greenhouse. However, this study highlights that the effects of thigmomorphogenesis on seedling stability may also play a role in seedling establishment on tidal flats; this requires further experimental investigation.

The close relationship between E_{crit} of seedlings grown in the experimental mesocosms and seedling traits such as root and shoot biomass and length (Fig. 6, Table S3) may also be relevant to other plant species in biogeomorphic ecosystems (i.e. mangroves, riparian vegetation or seagrass beds). Rapid root growth of seedlings in their first weeks of development is crucial for their tolerance to physical disturbance in these habitats. It is known that several intertidal wetland pioneer species (i.e. *Salicornia* spp., *Spartina* spp. and *Avicennia* spp.) show rapid root emergence and development (Friess et al. 2012). With rapid root growth, saltmarsh and mangrove pioneers are able to utilize disturbance-free windows of opportunity to acquire tolerance to subsequent disturbance by inundation, wave action and short-term sediment erosion (Balke et al. 2011, 2014, Cao et al. 2017). The present study showed that seedling stability within the first weeks after emergence can be severely limited by soil waterlogging through reduced root growth.

CONCLUSIONS

Our study showed that waterlogged and anoxic soil conditions can eliminate species-specific differences in root growth and tolerance of seedlings against erosion that otherwise exist in drained conditions. Niche separation in salt marshes may thus not only be attributed to tolerance of salt and inundation stress or competitive strength, since tolerance against physical disturbance at the seedling stage may be strongly influenced by soil waterlogging. This interaction could be demonstrated for the upper saltmarsh species *Elytrigia atherica* in our study and may be one determinant for the distribution of this species across the elevational saltmarsh gradient. Further studies are suggested across frequently disturbed and inundated ecosystems (mangroves, riparian forests, seagrass beds) to investigate the effects of soil anoxia on plant traits and stability, and the spatial relationship between exposure to disturbance and soil anoxia in habitats suitable for colonization. This is especially important to improve restoration success in coastal wetland ecosystems.

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