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Effects of Tidal Flooding on Juvenile Willows

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Abstract Tidal wetlands are affected by sea level rise. In the tidal freshwater stretches of estuaries in the temperate zone, willows (*Salix* spp.) form tidal freshwater forests above the mean high water level. Willows tolerance to prolonged periodic flooding in riverine systems is well documented, whereas effects of tidal flooding on willows are largely unknown. Flooding stress may play a major role in regeneration failure of willows in tidal forest stands along estuarine shores, and juvenile willows might be specifically affected by partial or total submergence. To assess the tolerance of juvenile willows to tidal flooding, we conducted a mesocosm experiment with cuttings from *Salix alba* and *Salix viminalis*, which are both characteristic species for tidal freshwater forests in Europe. Cuttings originating from either fresh or brackish tidal forest stands were grown under four tidal treatments with up to a tidal flooding of 60 cm. A general tolerance to a tidal flooding of 60 cm was observed in chlorophyll fluorescence, growth rates, and biomass production in both willow species. Overall, *S. alba* showed higher leaf and shoot growth, whereas *S. viminalis* produced more biomass. *S. alba* with brackish origin performed worst with increasing tidal flooding, suggesting a possible pre-weakening due to stressful site conditions in tidal wetlands at the estuarine brackish stretch. This study demonstrates that juvenile willows of *S. alba* and *S. viminalis* tolerate tidal flooding of up to 60 cm. It is concluded that tidal inundation acts as a stress by causing submergence and soil anaerobiosis, but may also act as a subsidy by reestablishing aerobic conditions and thus maintaining willows performance. Therefore, we suggest investigations on *Salix* tidal flooding tolerance and possible effects of willows on tidal wetland accretion under estuarine field conditions.

Keywords Tidal freshwater forested wetlands · Tidal flooding tolerance · Willows · Sea level rise

Introduction

Coastal wetlands are becoming increasingly stressed by various natural and human-induced factors such as storms, sea level rise and coastal engineering. Globally, about 35 % of the area of mangroves has disappeared since 1980 and the current global annual loss of tidal marshes is estimated to be between 1 and 2 % (Pendleton et al. 2012). Especially, estuaries with their steep gradients in energy and physicochemical properties are (in addition to direct human alterations; Ganju and Schoellhamer 2010) highly vulnerable to climate change (Jennerjahn and Mitchell 2013). For tidal freshwater wetlands, a rising sea level might both contribute to a rapid loss of area, of biodiversity (Baldwin and Mendelssohn 1998) and to vegetation changes caused by increased tidal flooding and concurrent saltwater intrusion (Neubauer and Craft 2009). However, in upstream tidal freshwater wetlands, river discharge largely prevents intrusion of saline water (Baldwin et al. 2009), and thus salt water intrusion is not expected to influence the upper reaches of today's tidal freshwater stretches. In North American tidal freshwater wetlands, diverse forest types occur, while European tidal freshwater forests at low-lying sites (e.g., at the

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microtidal Rhine-Meuse, at the macrotidal Scheldt, and the Elbe) are dominated by willows (Struyf et al. 2009).

Diverse floodplain willow species (genus *Salix*) benefit from their adaptations to the floodplain stressors like flooding (Karrenberg et al. 2002) and disturbance (Timoney and Argus 2006) by their high regeneration capacity (Ellenberg and Leuschner 2010). Moreover, floodplain willows contribute to ecosystem services like attenuating river currents and stabilizing river bank sediments (Radtke et al. 2012). Temmerman et al. (2004) found varying sediment deposition rates along the Scheldt estuary depending on the age of the tidal wetlands and controlled by mean high water level (MHWL) rise and suspended sediment concentration. At the Elbe estuary, accretion rates in low-lying tidal wetlands were found to be higher (5.8–20.3 mm year^{-1}) than current sea level rise indicating that these ecosystems may keep pace with sea level rise. By contrast, lower accretion rates were found at high elevations (1.1–3.1 mm year^{-1}) with less inundation (Butzeck et al. 2014): These tidal wetlands may become more inundated in the future, leading again to increasing accretion rates here. However, in the upper reaches of temperate estuaries, tidal freshwater wetlands at high elevations may be vulnerable to sea level rise due to insufficient sediment deposition rates (Butzeck et al. 2014). Here, the ability of tidal wetlands to keep pace with rising sea level might be also limited as the watershed sediment delivery is often largely reduced (Weston 2014). Although Kirwan et al. (2010) generally assess tidal wetlands in macrotidal estuaries with high sediment loads to likely remain stable, tidal wetlands which developed during periods of high sediment deposition in the past might submerge as sediment supplies decreases, e.g., due to dam construction. The future location of tidal freshwater forests might be expected to shift to more elevated landward sites with sea level rise. However, coastal engineering with dike construction largely prevents the landward movement of floodplain vegetation and restricts the extension of tidal wetlands in Europe (Doody 2004). Thus, today's willow habitat might be affected by a projected moderate sea level rise of up to 60 cm until 2081–2100 (IPCC 2013), and floodplain forest regeneration by small and juvenile willows might be specifically threatened by increasing tidal flooding and submergence.

Effects of increasing water levels on floodplain willows of the intertidal zone are not well studied yet. *Salix alba* L. and *Salix viminalis* L. (hereafter referred to as *S. alba* and *S. viminalis*) are the most widespread willows in the floodplains of the Elbe estuary (Raabe 1986) and characteristic willow species in floodplains in temperate zones in Europe (Struyf et al. 2009) and thus served as our study species. *S. alba* forms floodplain forests above mean high water level, whereas *S. viminalis* forms shrubby belts at the floodplain forest edge at lower elevations above the reed zone (Ellenberg and Leuschner 2010). It is thus expected that the species differ in their flooding tolerance with S. *viminalis* being more flooding tolerant. Moreover, the phenotype of plants as the result of the interaction between the genotype and the environment may lead to locally adapted populations in heterogeneous environments (Schmid 1992), and Markus-Michalczyk et al. (2014) demonstrated that *S. alba* and *S. viminalis* cuttings originating from tidal freshwater and from brackish water wetlands differ in their salt tolerance. As *S. viminalis* specimens with a brackish origin have a higher stress tolerance to salinity and this may have physiological costs, it is expected that specimens with brackish origin have lower flooding tolerance than those with freshwater origin. We state that the floodplain willow species *S. alba* L. and *S. viminalis* L. are able to tolerate tidal freshwater flooding of a magnitude projected in moderate climate change scenarios. Specifically, we aimed to answer the questions (i) if juvenile willows tolerate tidal flooding until a critical value of total submergence is reached, (ii) if *S. viminalis* shows a higher flooding tolerance than *S. alba* plants, and (iii) if plants with brackish origin show lower flooding tolerance compared to freshwater origin due to physiological costs of pre-adaptation to salinity.

Material and Methods

From May to October 2012, a mesocosm experiment was conducted with four tidal freshwater treatments in the common garden at the University of Hamburg (N53.561, E9.858; 15 °C mean air temperature and 200 mm precipitation June–October 2012): Hamburg is located in the temperate zone with 9 °C mean annual air temperature and a mean of 793 mm precipitation per year (DWD 1981-2010; http://www.dwd.de/). Juvenile willow plants of (i) two *Salix* species (*S. alba* and *S. viminalis*), (ii) from two origins (freshwater and brackish water site) were exposed to (iii) four tidal freshwater flooding regimes (0m, 20, 40, 60 cm).

Plant Material

Plant material was collected from two tidal wetland sites along the Elbe estuary differing in salinity. The first site was located at the lower mesohaline stretch (N53.533, E9.152; hereafter referred to as brackish site) and the other site at the upper limnic stretch of the estuary (N53.283, E10.219; hereafter referred to as freshwater site). At each site, *S. alba* and *S. viminalis* specimens with straight shoots were selected. Twelve specimens per species—six of both origins—were used as sources for cuttings. We harvested 24 cuttings on March 28 and 29, 2012, from each of the selected specimen (576 in total) and kept the plant material in plastic bags in a climate chamber at 5 °C until March 30. The planting substrate used in the experiment was composed by half river sand and half compost as organic component. Both components were mixed and sieved, and pots (18-cm diameter, 14-cm high) were filled with the planting substrate. The cuttings were equalized to 20-cm length, and the initial mass was determined on March 30. In each filled pot, two cuttings of one species and a single origin were placed into the planting substrate and watered with spring water. In order to protect them from frost and damaging UV radiation, the cuttings were at first stored in a greenhouse for 4 weeks and then exposed to field conditions in the open. After that time period, the cutting with fewer developed leaves was removed from each of the pots. The remaining cuttings were grown to juvenile willows and served as plant material in the experiment.

Tidal Treatments

We established tidal freshwater flooding treatments in mesocosms (3 m × 1.5 m; 1.5-m high). Each of the four mesocosms contained flooding stairways of four steps, representing four flooding levels. According to Gönnert et al. (2009), the regional water level increase at the German Bight can be expected to range between 40 and 80 cm by the end of the twenty-first century. The setup of the tidal treatments corresponded to this expectation in the flooding depth on flooding stairways. Plants on the uppermost step were exposed to hydrological conditions similar to the lower field sites of both *Salix* species at the mean high water line, and plants on lower steps of the stairways experienced increasing flooding. The pot height was 14 cm and the differences between steps were 20 cm. The lowest flooding level of 0 cm reached the pots soil surface at the uppermost step and the highest flooding level of 80 cm reached 6 cm under the pot's bottom at the undermost step of the flooding stairways.

Thus, the stairways were flooded by daily tides with different flooding height stepwise: (i) step one: 0 cm—flooded up to the pot's soil surface (corresponds to sites at mean high water line); (ii) step two: 20 cm—flooded up to 20 cm above the pot's soil surface; (iii) step three: flooded up to 40 cm above the pot's soil surface; (iv) step four: flooded up to 60 cm above the pot's soil surface. Sixteen pots (4 per both *S. alba* and *S. viminalis* and 4 per both freshwater and brackish origin) were arranged randomly on each of the 4 flooding steps resulting in 64 pots per mesocosms, applied in each of the 4 mesocosms adding up to 256 pots. The tidal treatments were applied from May 11 to October 17, 2012.

Tidal Simulation System

The tidal simulation system consisted of two water storage tanks and four mesocosms. The mesocosms were equipped with timer-controlled electronic pumps (Grundfos Typ Unilift CC7-A1—model 96280968) and connected to the water storage tanks. Tides were produced by water transfer between the water storage tanks and the mesocoms. During flood tide, well water was pumped from the water storage tanks via tubes into the mesocosms until the water level reached the soil surface of the pots on the uppermost step. During ebb tide, water was pumped from the mesocosms via tubes into the water storage tanks until the water level was below the bottom of the pots on the lowest step. To mimic natural conditions of the Elbe estuary, with a stronger and faster running flood tide compared to the ebb tide, the flood tide lasted 5 h and the ebb tide duration was 7 h. We set up the timer control of the electronic pump in a way that the turnaround of the tide occurred each day approximately 1 h later, similar to the daily inequality of semi-diurnal tides in natural systems, in order to adjust our tidal simulation system with the tide at the Elbe estuary.

Data Collection

Before the start of the experiment, cuttings were placed in pots and grew to juvenile willow plants from March 30 to May 11. After this period, the initial number of leaves, number of shoots and shoot length of the juvenile willow plants were determined. Then, the plants were placed on the flooding stairways in the mesocosms and the tidal treatments started. During the course of the tidal treatments, chlorophyll fluorescence and number of leaves, and number of shoots and shoot length were recorded every 2 weeks. Chlorophyll fluorescence was recorded as maximum quantum yield with a portable chlorophyll fluorometer (PAM-2100, Walz, Germany). The ratio of variable to maximal fluorescence (Fv/Fm) of dark adapted leaves was calculated as an indicator for the photosynthetic efficiency, based on the principle described by Schreiber et al. (1986).

To perform the measurements, the pots with the plants were removed from the flooding steps during simulated low tide and placed beside the mesocosms on a desk. After performing the measurements, the pots were rearranged randomly on the same flooding step they were placed before. On August 24, the aboveground biomass was harvested from each of the plants in the four mesocosms. In one of the four mesocosms, belowground biomass was also harvested. All harvested biomass was cleaned and dried separately at 60 °C to constant weight and weighed.

In order to analyze the ability of the plants to resprout under flooding conditions, the tidal treatments continued in those three mesocosms where only aboveground biomass was harvested. The number of resprouted leaves and the shoot length were recorded on October 17.

As growth could be limited by light availability during flooding, photon flux density was recorded during flooding biweekly at high noon (week 0: June 26, week 2: July 9, week 4: July 24, week 6: Aug. 7, 2013). For each flooding level in each of the four mesocosms, photon flux density was measured once in the water beside the soil surface of the pot and also in the air above the water column above the pot soil surface (LiCOR Data Logger; LI 192 UW quantum sensor), and calculated as relative irradiance in water (percentage of photon flux density in water in relation to photon flux density in air). The photon flux densities in the water decreased substantially with increasing flooding depth at each of the four biweekly measuring dates. In week 0, with overall lowest irradiance, values at 20 to 60 cm flooding dropped below 200 μmol $m^{-2}s^{-1}$. In week 4, with the second lowest irradiance, values at 60 cm flooding dropped below 200 μmol $m^{-2}s^{-1}$. In week 2 and week 6 with high irradiances, values remained above 200 μmol $m^{-2}s^{-1}$ at flooding 0 to 60 cm at noon. Relative irradiance in water generally decreased with increasing flooding depth in week 0 ($F = 25.02$; $p < 0.001$), week 2 ($F = 196.99$; $p < 0.0001$), week 4 ($F = 53.71$; $p < 0.0001$), and week 6 ($F = 69.92$; $p < 0.0001$). Here, relative irradiance in water dropped below 50 % at 40 cm flooding at each measuring date compared to irradiance on the surface. Moreover, at week 4 and week 6, values decreased below 25 % at 60 cm flooding.

Data Analyses

We applied ANOVAs to test for the effects of tidal treatments with four flooding levels (0, 20, 40, and 60 cm flooding depth) on juvenile plants of two species (*S. alba* and *S. viminalis*) from two origins (freshwater and brackish site). Repeated measurement ANOVA was applied on chlorophyll fluorescence and pairwise differences were tested with Tukey's post hoc tests. ANCOVAs were applied on aboveground dry mass (leaf mass and shoot mass) and on belowground dry mass (root mass) as well as on total dry mass and on the shoot-root ratio. Here, initial mass served as covariate. Growth as relative growth rate of leaf number (%), and increase in shoot length compared to initial values was analyzed with repeated measurement ANOVAs. Pairwise differences were tested by applying Tukey's post hoc tests.

Resprouting capacity was analyzed by applying repeated measurement ANOVAs on the number of resprouted leaves and the length of resprouted shoots and pairwise differences were tested with Tukey's post hoc tests.

Prior to all analyses, Levene's tests were applied to test for variance homogeneity. Change in total shoot length showed heteroscedasticity of variances and thus were log-transformed in order to approximate the assumptions of ANOVA. All data analyses were carried out with STATISTICA 9.0 (StatSoft 2009).

Results

Chlorophyll Fluorescence

Repeated measurement ANOVAs did not show a significant effect of tidal flooding on photosynthetic efficiency; moreover, photoinhibition of photosynthesis was not detected. Differences in chlorophyll fluorescence between *S. alba* and *S. viminalis* and between the origins were not significant. At none of the measurement dates, effects of flooding, species, or origin on photosynthetic performance were found (Appendix Table 3).

Dry Mass

Overall, dry mass of juvenile *Salix* plants decreased with increasing flooding level (Fig. 1; Table 1). Tukey's HSD tests confirmed significant differences between 0 and 20 cm tidal flooding ($p < 0.05$), 0 and 40 cm ($p < 0.01$), 0 and 60 cm ($p < 0.001$), and between 20 and 60 cm ($p < 0.001$) and 40

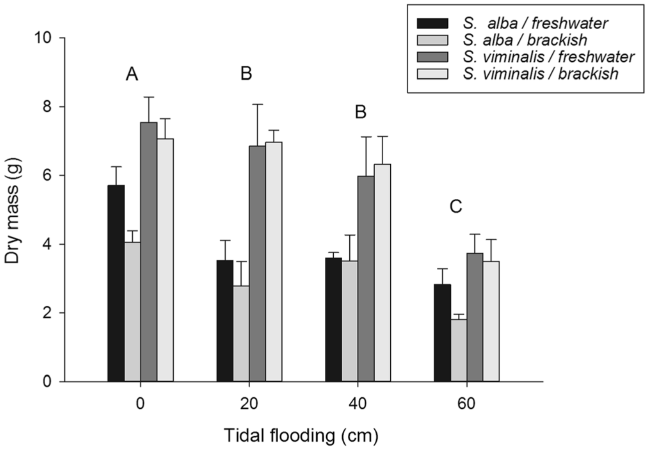

Fig. 1 The effect of tidal flooding on dry mass of juvenile willows (genus *Salix*) in a mesocosm experiment (mean ± SD, $N = 4$). *Salix* plants grown from cuttings were exposed for 15 weeks to a tidal regime according to moderate sea level rise scenarios (0, 20, 40, and 60 cm flooding depth). Different shades of *gray* indicate two *Salix* species and origins from two tidal wetland sites at the European Elbe estuary (*S. alba*/freshwater; *S. alba*/brackish; *S. viminalis*/freshwater; *S. viminalis*/brackish). Significant differences in dry mass between flooding levels are indicated by *different capital letters*

Table 1 Results of a three-factorial ANCOVA on the effects of tidal flooding depth (0, 20, 40, and 60 cm), species (*Salix alba* and *S. viminalis*), and origin (freshwater vs. brackish site) on dry mass and shoot-root ratio in tidal treatments ($N = 4$)

	Dry mass		Shoot-root ratio	
	F	*p*	F	*p*
Flooding	20.54	<0.001	8.53	<0.001
Species	70.72	<0.001	1.64	Not significant
Origin	0.81	Not significant	1.06	Not significant
Flooding*species	1.69	Not significant	0.06	Not significant
Flooding*origin	0.13	Not significant	0.29	Not significant
Species*origin	2.19	Not significant	5.38	<0.05
Flooding*species*origin	0.86	Not significant	0.36	Not significant

and 60 cm tidal flooding ($p < 0.001$). *S. viminalis* produced significantly more dry mass than *S. alba* ($p < 0.001$).

The shoot-root ratio significantly increased with increasing flooding (Fig. 2; Table 1). Here, Tukey's post hoc tests confirmed significant differences between 0 and 40 cm tidal flooding ($p < 0.01$) and 60 cm ($p < 0.001$) whereas ratios remained similar in 20 cm compared to 40 cm tidal flooding. Additionally, *S. alba* plants with brackish origin developed higher shoot-root ratios than with freshwater origin ($p < 0.05$). With regard to plants originating from the brackish site, *S. alba* showed higher shoot-root ratio than *S. viminalis* ($p < 0.05$).

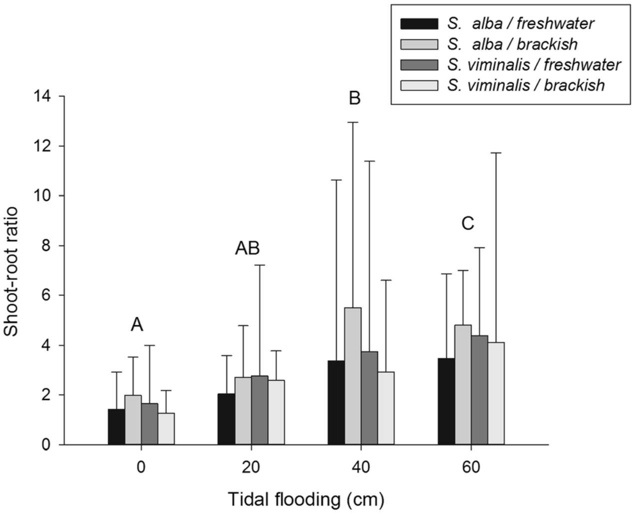

Fig. 2 Shoot-root ratio of juvenile willows after 15 weeks exposure to tidal flooding treatment (mean ± SD, $N = 4$) according to moderate sea level rise scenarios (0, 20, 40, and 60 cm flooding depth). The plants in the experiment were grown from *Salix* cuttings which served as vegetative propagules. Different shades of *gray* indicate two *Salix* species and origins from two tidal wetland sites at the European Elbe estuary (*S. alba*/freshwater; *S. alba*/brackish; *S. viminalis*/freshwater; *S. viminalis*/brackish). Significant differences in shoot-root ratio between flooding levels are indicated by *different capital letters*

Growth

Relative growth rate of leaf number was similar in each of the four flooding levels and no significant effect of tidal flooding was found. ANOVAs proved, however, significant differences between species and singular way interactions between time and flooding, time and species, time and origin, and time, flooding and species (Table 2). After 15 weeks of tidal treatments on juvenile willows, leaf number of *S. alba* was significantly higher than of *S. viminalis* ($p < 001$), and plants with a tidal freshwater wetland origin showed higher leaf numbers than those from the tidal wetland at the brackish stretch.

No significant effect of flooding on increase in shoot length was found after 15 weeks of tidal treatments. Significant differences in increase in shoot length were found between species (Table 2). *S. alba* shoot length after 15 weeks was significantly higher compared to initial values than *S. viminalis* shoot length. The interaction of time and species was found to be significant. Here, *S. alba* performed better at each time point except in May ($p < 0.001$).

Resprouting Rates in Juvenile Willows After Shoot Removal

Resprouting rates after shoot removal were 93 % in *S. alba* and 99 % in *S. viminalis* at the end of the tidal treatment. The number of resprouted leaves (Fig. 3) decreased with increasing flooding ($p < 0.001$). However, no significant differences in resprouted number of leaves were found between 20 and 40 cm tidal flooding treatments. Furthermore, we detected significant effects of species on the number of resprouted leaves ($p < 0.001$). Here, resprouted number of leaves was substantial higher in *S. viminalis* than in *S. alba* (Appendix Table 4).

Repeated measurement ANOVAs showed a temporal increasing length of resprouted shoots between three dates ($p < 0.001$) and decreasing shoot length with increasing flooding ($p < 0.001$). No significant differences in shoot length were found between 20 cm compared to 40 cm tidal flooding at all measurement dates (Fig. 4). Temporal shoot length development differed between species ($p < 0.001$). Resprouted shoots were substantially longer in *S. viminalis* than in *S. alba* (Appendix Table 4).

Discussion

Tolerance of Juvenile Willow Plants to Tidal Flooding

The study clearly demonstrates that juvenile plants of the floodplain willow species *Salix alba* L. and *Salix viminalis*

Table 2 Results of a three-factorial repeated measurement ANOVA on the effects of tidal flooding depth (0, 20, 40, and 60 cm), species (*S. alba* and *S. viminalis*) and origin (freshwater vs. brackish site) on the relative growth rate of leaf number and the increase in shoot length in tidal treatment (N = 4)

	Relative growth rate of leaf number		Increase of shoot length	
	F	*p*	F	*p*
Flooding	0.87	0.45	0.19	0.13
Species	59.19	< 0.001	279	<0.001
Origin	0.004	0.95	0.06	0.80
Time*flooding	2.72	<0.001	4.10	<0.001
Time*species	17.97	<0.001	179.73	<0.001
Time*origin	4.17	<0.001	1.16	Not significant
Time*flooding*species	2.41	<0.001	5.43	<0.001
Time*flooding*origin	0.92	Not significant	1.45	Not significant
Time*species*origin	0.30	Not significant	0.26	Not significant
Time*flooding*species*origin	1.35	Not significant	0.60	Not significant

L. are able to tolerate tidal freshwater flooding at least to the maximum applied tidal flooding depth of 60 cm. Furthermore, both species were found to have a high resprouting capacity of more than 90 % after shoot removal even under submergence. These findings have to be viewed against the background of differences in the effects which changing water levels in tidal systems with alternating flooding and exposure may cause in comparison with stagnant water levels and long-term submergence.

In our tidal treatments, plants experienced alternating flooding and exposure to high-light conditions. Here, photosynthetic activity of juvenile willows was generally optimal (no decrease of *F*v/*F*m), although plants growing in low-light habitats are usually sensitive to high UV radiation (Hanelt and Roleda 2009). Intertidal zones, where plants are suddenly exposed to UV radiation after flooding during high water, are habitats with potential for induction of damage by high photosynthetically active radiation (PAR) or UV radiation (Hanelt et al. 1997). Post-submergence growth recovery requires also efficient photosynthetic acclimation to increased O_2 and irradiance to minimize photo-oxidative damage (Luo et al. 2009). This is in agreement with our results of photosynthetic activity (*F*v/*F*m) and plants growth which remained optimal after tidal flooding indicating an adaptation to the tidal floodplain habitat.

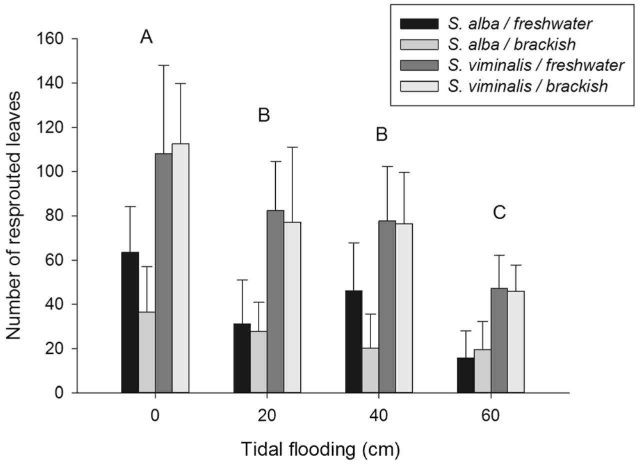

Fig. 3 Effect of tidal flooding on the number of resprouted leaves of juvenile willows in a mesocosm experiment (mean ± SD, *N* = 3). The tidal flooding regime simulated projected moderate sea level rise scenarios (tidal flooding depth 0, 20, 40, and 60 cm). Plants were grown from cuttings which serve as vegetative propagules. Different shades of gray indicate two *Salix* species and origins from two tidal wetland sites at the European Elbe estuary (*S. alba*/freshwater; *S. alba*/brackish; *S. viminalis*/freshwater; *S. viminalis*/brackish). Significant differences in number of resprouted leaves between flooding levels are indicated by different capital letters

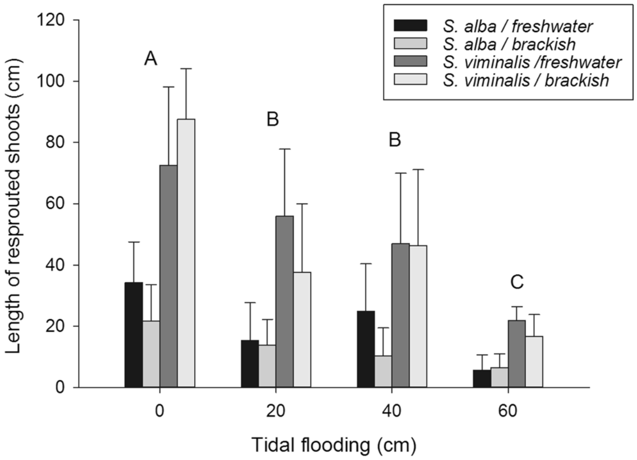

Fig. 4 Resprouting capacity of juvenile willows (genus *Salix*) after 6 weeks of tidal treatment with flooding depth (mean ± SD, *N* = 3) according to projected in moderate sea level rise scenarios (0, 20, 40, and 60 cm flooding depth). Resprouting capacity was measured as resprouted shoot length of plants grown from *Salix* cuttings. Different shades of *gray* indicate two *Salix* species and origins from two tidal wetland sites at the European Elbe estuary (*S. alba*/freshwater; *S. alba*/brackish; *S. viminalis*/freshwater; *S. viminalis*/brackish). Significant differences in length of resprouted shoots between flooding levels are indicated by *different capital letters*

At complete submergence, gas diffusion dramatically decreases and limits the entry of CO_2 for photosynthesis and of O_2 for respiration (Colmer and Pedersen 2008). Accordingly, the significant decrease in dry mass at increasing flooding depth might be viewed as an effect of short-term complete submergence. This finding might also be caused by the decreased light availability with increasing water depth, which might drop below the light compensation point (Sand-Jensen and Borum 1991). In our experiment, irradiance dropped several times below 200 μmol $m^{-2}s^{-1}$ so energy need for biomass production might have become light limited. Sufficient light supply underwater increases the survival of submerged terrestrial plants (Mommer and Visser 2005), and submerged plants usually require at least appr. 30 % of the incident light measured just below the water surface (Dennison et al. 1993). Thus, the decrease of the impinging light down to 50 % of surface irradiance observed at a flooding depth of 40 cm, and down to 25 % at 60 cm might have caused the significant reduction in dry mass in the juvenile willows in the tidal treatments.

In flooded soils, filling of soil pores with water lowers oxygen supply for roots (Blom and Voesenek 1996). The increasing shoot-root ratio at increasing flooding might thus indicate physiological stress on roots. In Amazonian *Salix martiana*, a high capacity to produce adventitious roots was found in the field during flooding and in an experiment under stagnant submergence (Parolin et al. 2002; De Simone et al. 2002). However, plants in our experiment with tidally changing water levels did not produce adventitious roots. The decreased root compared to shoot dry mass is typical for many wetland plants exhibiting reduced root mass with increased flooding (Mitsch and Gosselink 2000), In agreement with this, a North American floodplain willow (*Salix nigra*) showed decreased root biomass in a waterlogged soil compared to drained conditions (Li et al. 2006), and cuttings of mid European floodplain willows showed reduced root mass production in waterlogged compared to moist conditions (Radtke et al. 2012).

Interspecific Differences in Tidal Flooding Tolerance of Juvenile Willow Plants

Interspecific differences in tidal flooding tolerance of juvenile willows varied according to measured parameters in our experiment. In the first instance, higher dry mass and greater resprouting capacity in juvenile plants of the shrubby *S. viminalis* compared to the arboreal *S. alba* seem to support our hypothesis of a higher tolerance of *S. viminalis* to tidal flooding. A better growth performance of floodplain shrubs compared to floodplain trees under severe abiotic disturbance at the floodplain edge at low elevations was also reported earlier (e.g. Amlin and Rood 2001; Francis and Gurnell 2006). However, a large overlap of areas with suitable hydrologic conditions for both floodplain trees and shrubs was identified by modeling for the Elbe river floodplains (Mosner et al. 2011). Here, mechanical disturbance was differentiating species niches at low-lying sites. In general, shrubby vegetation with high resprouting capacity from flood-damaged stumps dominates at flood-prone sites (Bendix and Hupp 2000). Thus, the higher dry mass and higher resprouting capacity of juvenile *S. viminalis* in our experiment may be rather an outcome of adaptations to mechanical disturbance than of a higher tolerance to tidal flooding.

By contrast, we assess *S. alba* to be more tolerant to tidal flooding. In the flooding treatments, leaf number increased substantially more over time in *S. alba* than in *S. viminalis*. Leaf surface characteristic might serve as a possible explanation for this interspecific difference. Leaves of *S. alba* are covered with hydrophobic hairs on the upper and lower leaf surface (Lautenschlager-Fleury 1994; Zander 2000), whereas leaves of *S. viminalis* are hairy beneath only. Leaf gas films on completely submerged rice facilitate gas exchange and thus, have been termed “plant plastrons” (Pedersen et al. 2009). Beneficial effects of leaf gas films on internal aeration during tidal submergence were shown for *Spartina anglica* (Winkel et al. 2011). Different capacities to develop leaf gas films of *S. alba* and *S. viminalis* may partly explain the higher leaf growth of *S. alba*. However, specific investigations on effects of gas films on *Salix* leaves and photosynthetic activity are needed to confirm this hypothesis. Generally, better leaf performance in *S. alba* juvenile plants and larger increase in shoot length might be due to overall better tolerance to prolonged flooding of this species (Chmelař and Meusel 1986; Lautenschlager-Fleury 1994). Borsje et al. (2011) highlight the ability of *S. alba* to cope with long inundation periods as a criteria for its use in flood protection measurements to trap sediment and damp waves.

Effects of Origin on Tidal Flooding Tolerance of Juvenile Willow Plants

Effects of different origins on tidal flooding tolerance in juvenile *S. alba* and *S. viminalis* plants were marginal in our experiment, although generally high within-population genetic variability in the genus *Salix* may be assumed due to disturbance-driven vegetation dynamics in floodplains (Karrenberg et al. 2002). Significant differences related to the plants origin were found only in *S. alba*. Here, a higher shoot-root ratio and lower dry mass were detected in plants with origin from the brackish site compared to freshwater origin. In addition, a pronounced decrease in performance of plants with origin from the brackish site was found with increasing tidal flooding, which might be caused by the pre-adaptation of the plants to higher salinity at these sites (Markus-Michalczyk et al. 2014).

Conclusion

For the first time, a tolerance to tidal flooding up to 60 cm was found for juvenile willows of *Salix alba* and *Salix viminalis*, both characteristic species in European forested tidal freshwater wetlands. We conclude that periodic tidal inundation acts as a stress by causing submergence and soil anaerobiosis but also as a subsidy by reestablishing aerobic conditions maintaining the functionality of the photosynthetic apparatus and willows performance in tidal wetlands.

However, vegetation was also found to play an important role in long-term development of tidal wetlands: In mangroves and salt marshes, vegetation increases sediment accretion and contributes to wave reduction (Krauss et al. 2014; Möller et al. 2014). The role of willows in tidal freshwater wetlands for surface accretion rates has not been investigated yet, but is of importance for the fate of this ecosystem under sea level rise, the conservation of willow softwood forests as priority habitats, and the protection of tidal wetlands as Ramsar cites (Ramsar 2014). We thus suggest investigations on *Salix* tidal flooding tolerance and possible effects of willows on tidal wetland accretion under estuarine field conditions.

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Appendix

Table 3 Chlorophyll fluorescence (*Fv*/*Fm*) of juvenile willows (genus *Salix*) in a mesocosm experiment (mean ± SD, $N = 4$). *Salix* plants grown from cuttings were exposed for 15 weeks to a tidal regime according to moderate sea level rise scenarios (0, 20, 40, and 60 cm flooding depth)

Tidal flooding (cm)	*S. alba*/ freshwater	*S. alba*/ brackish water	*S. viminalis*/ freshwater	*S. viminalis*/ brackish water
0	0.771 ± 0.025	0.782 ± 0.026	0.754 ± 0.025	0.765 ± 0.021
20	0.761 ± 0.030	0.747 ± 0.043	0.761 ± 0.017	0.773 ± 0.026
40	0.748 ± 0.032	0.765 ± 0.030	0.750 ± 0.024	0.760 ± 0.024
60	0.771 ± 0.036	0.774 ± 0.030	0.750 ± 0.039	0.773 ± 0.022

Table 4 Results of a three-factorial repeated measurement ANOVA on the effects of tidal flooding depth (0, 20, 40, and 60 cm), species (*S. alba* and *S. viminalis*) and origin (freshwater vs. brackish site) on the resprouting capacity (number of resprouted leaves, and length of resprouted shoots) in a tidal treatment ($N = 4$)

	Length of resprouted shoots		Number of resprouted leaves	
	F	*p*	*F*	*p*
Flooding	51.15	<0.000	35.88	<0.000
Species	194.87	<0.000	235.95	<0.000
Origin	3.64	0.058	2.66	0.104
Time*flooding	27.22	<0.000	11.89	<0.000
Time*species	88.74	<0.000	24.23	<0.000
Time*origin	1.47	0.231	5.59	<0.01
Time*flooding*species	4.03	<0.000	1.29	0.260
Time*flooding*origin	1.97	0.069	2.88	<0.01
Time*species*origin	1.45	0.235	1.91	0.150
Time*flooding*species*origin	4.29	<0.000	1.10	0.362

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