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[Article begins on next page]

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Morphological and biomechanical responses of floodplain willows to tidal flooding and salinity

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Abstract

1. Willow floodplain plantations have been proposed as part of plans to create tidal wetlands for ecosystem-based flooding defence of estuaries. Softwood forests characterized by willows (genus *Salix*) are found in riparian floodplains in Europe up to the river mouth, e.g. up to tidal wetlands along the Scheldt and Elbe. However, sea level rise accompanied by accelerated tidal flooding and salt-water intrusion may limit the effectiveness of willows for flooding defence of floodplains located at estuaries near their junction with the sea.

2. We experimentally tested juvenile floodplain willows (*S. alba* and *S. viminalis*) in a combined tidal flooding and salinity treatment. Permanent flooding of roots and periodic flooding of shoots reduced shoot length, shoot biomass, bending capacity and breaking resistance. However, periodic submergence of both root and shoots did not affect shoot morphology or biomechanical traits. In *S. viminalis,* shoot diameter was generally larger and this increasing diameter resulted in a higher maximum breaking force. However, S. alba showed more consistent results in diameter size with lower variation than *S. viminalis*. The applied salinity treatments of up to 2 ppt did not have significant effects on willow shoot morphology or biomechanical traits.

3. We conclude that juveniles of both willow species are resilient to periodic tidal flooding and salinity values of up to 2 ppt with respect to shoot traits. *Salix alba* and *S. viminalis* may serve in innovative capacities as supplementary features for estuarine flooding defence in tidal wetlands and tools for ecological restoration. However, studies addressing whole ecosystems at a large scale are recommended before using *S. alba* and *S. viminalis* in floodplain plantations to protect river estuaries.

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1. Introduction

Tidal wetlands are highly desired as nursery grounds for fish, and for their capacities for biofiltration, carbon sequestration and coastal defense; however, they are threatened worldwide by global change processes and the impact of dense human populations (Kirwan & Megonigal, 2013). Ecosystem loss may be sudden, following a catastrophic shift when a critical threshold is exceeded. Theoretical research has suggested that early warning signals, like critical slowing down, may indicate the approach of a critical threshold (Scheffer *et al.*, 2009). For salt marshes, both time-series analyses by remote sensing and manipulative field experiments have revealed critical slowing down (i.e., reduced rates of disturbance recovery) in response to increasing submergence, which serves as a proxy for sea level rise (Van Belzen *et al.*, 2017). Similarly, native willow species that are widely used for river bank stabilization exhibited slow resprouting capacity after repeated disturbance of aboveground biomass by increasing tidal flooding levels (Markus-Michalczyk *et al.,* 2015). Despite the sensitivity of these ecosystems to increased flooding, coastal wetland creation has been proposed as a strategy for ecosystem-based coastal defense in estuaries, deltas and lagoons (Temmerman *et al.,* 2013). Salt marshes and mangroves have been identified as being highly effective in reducing the wave-loading on dikes in saline to brackish coastlines over a much wider tidal range than ecosystems located at lower elevations (Bouma *et al*., 2014). Floodplain willows that occur close to the mean high-water line in estuarine environments (e.g. Struyf *et al.,* 2009; Ellenberg & Leuschner, 2010) have been proposed as measures to reduce wave loading on levees and dikes in fresh and brackish (tidal) systems (Borsje *et al.,* 2011).

However, similar to salt marshes in coastal areas, softwood floodplain forests comprising willows in riparian environments have experienced dramatic declines over the last centuries, mainly resulting from deforestation for agriculture and changed hydrology due to dam and dike constructions (Tockner & Stanford, 2002). Floodplain inundation areas of large European rivers (e.g. the Danube, Elbe, Oder, and Rhine) have been reduced to 20% of their former extent (BMU & BfN, 2009), and most floodplain forests are no longer able to alleviate flood damage or foster biodiversity. Hence, remaining alluvial floodplain forests comprising willows are now protected as priority habitats (91E0) listed in Annex 1 of the European Habitats Directive. This means that their conservation status has to be fixed or restored (European Habitats Directive, 1992). The shrubby species *Salix viminalis* and the tree species *S. alba* are target species that are widely used in floodplain forest restoration of European river landscapes (Leyer *et al.*, 2012).

Softwood forests characterized by willows occur on floodplains along large European rivers up to the point of their entry into the North Sea (Ellenberg & Leuschner, 2010). Softwood floodplain forest productivity, structural and species diversity, maintenance of water quality, water retention, and riverbank stabilization are all regarded as highly desirable (Tockner & Stanford, 2002). In the estuarine environment, *Salix alba* and *S. viminalis* are keystone species of the tidal freshwater forested wetlands found, for example, along the Scheldt and the Elbe (Struyf *et al.*, 2009). Some studies have indicated that accelerated salt-water intrusion and sea level rise will change the vegetation in these tidal freshwater wetlands (Neubauer and Craft 2009). However, contrary to former assessments (e.g. Ellenberg *et al.,* 1992), *S. alba* and *S. viminalis* were found to be able to germinate and establish within four weeks in salinities of up to 2 parts per thousand (ppt) (Markus-Michalczyk *et al.,* 2016), thus able to tolerate

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oligohaline conditions as vegetative propagules in an experimental approach. Moreover, both species occur as mature individuals up to the mesohaline estuarine stretch with soil water salinities of at least up to 2 ppt during summer (Markus-Michalczyk *et al.,* 2014). Variable and fluctuating salinity is the principal stress confronting estuarine organisms (e.g. Odum, 1988; Mc Lusky & Elliott, 2004). In addition, estuarine flood plains may be severely affected by disturbances, such as flooding and storms (Mitsch & Gosselink, 2000). Moreover, the regional sea level rise along the North Sea coastline can be expected to range between 40 and 80 cm by the end of the twenty-first century (Gönnert *et al*., 2009) and may thus affect tidal wetland vegetation. An experimental tidal treatment of *S. alba* and *S. viminalis* showed that juvenile willows generated from cuttings were able to tolerate a tidal freshwater flooding of up to 0.6 m (Markus-Michalczyk *et al.,* 2016).

Borsje *et al.* (2011) have proposed *S. alba* for purposes of coastal ecological engineering because of its ability to cope with long inundation periods and attenuate waves during extreme storms. The goals of ecological engineering are to increase valuable ecosystem services *either* by restoring ecosystems that have been substantially disturbed by human activities *or* by developing new sustainable ecosystems that have value from both human and ecological perspectives (Mitsch & Jørgensen, 2004). *Salix alba* plantations along the coastline thus may represent innovative approaches to ecosystem creation, since softwood forests are less prevalent along the coast than in riverine and estuarine environments. *Salix alba* is adapted to highly disturbed amphibious floodplain sites (Karrenberg *et al.,* 2002). This species produces light wood with low density in combination with low transverse compressive strength, thus showing higher flexural rigidity in bending tests compared with terrestrial tree species (van Casteren *et al.,* 2012). Low tangential compressive strength may allow willow wood to buckle inwards in response to transverse compressive stresses being applied during bending. This may be the reason why willow twigs can so readily be woven, e.g. into baskets (Ennos & van Casteren, 2010), and used for purposes where high bending capacity is desired, such as wave attenuation for flood protection. Similar to *S. alba*, *S. viminalis* may also be useful in flooding protection since both *S. alba* and *S. viminalis* showed high flexural rigidity in a flume study (Wunder *et al.*, 2011).

In estuarine environments, both tidal flooding and salinity may affect the morphological and biomechanical traits simultaneously for *S. alba* and *S. viminalis*. Changes in these properties may affect

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the wave-attenuating capacity of these woody species (e.g. Bouma *et al.*, 2005). In contrast to the many studies carried out on salt marshes, willows are still understudied in the context of tidal wetlands. We hence conducted an experiment applying a tidal treatment on willows characteristic of riverine and tidal wetlands in the transition zone between herbaceous and woody vegetation at mean high water levels. We asked whether tidal flooding and salinity affect the morphological and biomechanical parameters of willows. In particular, we addressed whether these factors interact and if the two studied *Salix* species (*S. alba* and *S. viminalis*) differ in their morphological and biomechanical responses to flooding and salinity in a factorial experiment using tidal treatment.

2. Material and Methods

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A climate chamber experiment applying tidal treatments to juvenile willows was conducted at the Royal Netherlands Institute for Sea Research (NIOZ) from January to April 2017. Plants grown from cuttings of (i) two *Salix* species (*S. alba* and *S. viminalis*) were exposed to (ii) three tidal flooding regimes (from partial up to permanent flooding) and (iii) four salinity levels (0–2 ppt). Since *S. alba* is a tree growing up to 30 m with trunk diameter up to 1m and more, and *S. viminalis* is a multi-stemmed shrub growing up to 6–8m (Dickmann & Kuzkovkina, 2014), we decided to use willow twigs of similar size in order to ensure comparability between results on these species.

2.1 Plant material

Since floodplain willows are able to resprout vigorously from vegetative propagules, we used these willow cuttings as sources for the juvenile willows in the experiment. Willow cuttings were collected from a tidal wetland along the Elbe estuary. The collection site was located along the upper freshwater stretch of the estuary (N53.283, E10.219). Specimens of *S. alba* and *S. viminalis* with straight shoots were selected and 10 specimens per species served as sources for cuttings. On January 3, 2017, 200 willow rods were harvested from each of the selected specimens. They were cut to 25 cm in length and kept wet in plastic boxes at 7 °C until the start of the experiment. The planting soil was prepared by mixing half river sand

and half planting soil containing 10% organic matter (Terrafin BV). After sieving, this mixture was used to fill square pots (13 cm x 13 cm, 14 cm high). Each cutting was freshly cut to 20 cm in length to enhance water absorption via capillary forces. Initial mass was determined to make sure that cuttings of similar weight were used in the treatments. The cuttings were then placed in the pots with half their lengths buried in the planting soil and half remaining aboveground. The pots were watered until the soil was saturated and stored at 18 °C in a climate chamber until the start of the experiment on January 23, 2017.

2.2 Study design

2.2.1 Tidal flooding treatment

We established tidal flooding treatments in eight mesocosms (110 cm length x 90 cm width x 60 cm height). In each of the mesocosms, “flooding stairways” containing three steps were installed to represent three flooding levels. On each of the three flooding steps, fourteen pots (7 each per *S. alba* and *S. viminalis*) were arranged randomly, resulting in 42 pots per mesocosm and 336 pots in total spread over the eight mesocosms. Sea level is expected to rise 20–80 cm by the end of the 21st century according to moderate climate change scenarios (IPCC, 2013). We installed flooding stairways in the mesocosm to create a corresponding range of increasing depth of tidal flooding in three steps. Plants on the uppermost step were exposed to hydrological conditions similar to those currently found at field sites with willows at the mean high-water line, and plants on the two lower steps of the stairways experienced increasing levels of tidal flooding.

Our study was conducted by stepwise application of daily tides with different flooding lengths: (1) the highest step corresponded to flooding of the root but not the shoot system (partial flooding), corresponding to sites at the current mean high water line; (2) on the middle step, the root and shoot system were fully submerged during high tide but not flooded during low tide (semi-permanent flooding); and (3) shoots of plants on the lower-most step were flooded during high tide but the root system was flooded during both high and low tide (permanent flooding).

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2.2.2 Salinity treatment

We applied four levels of a salinity treatment in parallel to the tidal flooding treatment. Freshwater served as the tidal flooding treatment in four of the mesocosms. In the other four mesocosms, sea salt was added to freshwater until a salinity of 2 ppt was reached. We limited the salinity treatment to 2 ppt based on the results of earlier experimental findings on both *S. alba* and *S. viminalis* (Markus-Michalczyk *et al.*, 2014). Estuarine hydrology is characterized by pronounced river discharge in early spring and decreased discharge in late spring and summer (von Storch *et al.,* 2016) and biweekly reoccurring spring tide; thus, a periodic change of salinity occurs and may affect willows in tidal wetlands. Accordingly, we applied a periodic change of salinity to the potted willows on the steps based on a biweekly schedule. One quarter of the willows was translocated from a mesocosm with a salinity of 0 ppt to another mesocosm with a salinity of 2 ppt, and vice versa, i.e. another quarter of the willows was translocated from a salinity of 2 ppt to a salinity of 0 ppt. The translocation of willows from a salinity of 2 ppt to a salinity of 0 ppt was used to mimic episodic increases in freshwater due to high precipitation rates and river discharge. The translocated plants were returned to their initial places after five days. This treatment of periodic change in salinity was applied biweekly to correspond with spring tide cycles. The remaining third and fourth quarters of the willows were maintained during the whole experiment under the same salinity: one quarter under 0 and the other under 2 ppt.

2.2.3 Tidal simulation system in the climate chamber

A tidal simulation system was installed that consisted of the eight aforementioned mesocosms with the flooding stairways and eight additional mesocosms of the same size. Each of the eight additional mesocosms was placed beneath a mesocosm with a stairway, serving as a water storage tank. Each water storage tank was equipped with a timer-controlled electronic pump (SuperFish Pond-Flow eco) and plastic tubes that enabled transfer of water between the storage tanks and the mesocosms. Mimicking a semidiurnal tidal cycle, 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 simulations of flood tide. During ebb tide, water was drained from the uppermost mesocosms via the

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tubes into the water storage tanks until the water level was level with the top of the pots on the lowest step. To approximate natural estuarine conditions, both the duration of the flood tide and the ebb tide were set to six hours.

Artificial light was provided for the willows in the climate chamber by fluorescent tubes. Ten tubes were installed above each mesocosm, creating on average 60-70 µE/m-2 s-1 of illumination. Note that this is only a third of the light measured in the shade under ambient daylight conditions at the field site. To approximate ambient conditions within the climate room, the timers were set to provide 12 hours of light for the willows. Temperature in the climate chamber was maintained at 18 °C during both simulated day and night. The willows were grown under experimental conditions with the tidal simulation system in the climate chamber from January 23 to April 7, 2017.

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2.3 Data collection

At the end of the experiment, all the willows were harvested from the mesocosms. First, the length of each grown shoot from each juvenile willow individual was recorded. Second, all willow leaves were removed and stored in paper bags. Then the diameter of each grown shoot from each juvenile willow individual was measured before testing the biomechanical parameters. We used an Instron® electromechanical universal testing machine (Instron® 5900 Universal Testing System) that performs tensile, compression, bend, peel, tear, puncture, friction, and many more tests to study the biomechanical properties of the *Salix* shoots. To fasten the *Salix* shoots on the “table” of the measurement device, the brackets were adjusted to a certain span length (15 x shoot diameter) in order to reach the required minimum span length to measure an object. Since the shoot diameters varied, we categorized them into short span lengths (diameter 0–2 mm) and long span lengths (>2mm). Each willow shoot was placed on the measurement table and fastened according to the measured diameter with the brackets. The testing software (Bluehill 3) was connected to Instron® to make measurements on the biomechanical properties of the willow shoots. We applied Instron® and Bluehill 3 to record (a) the bending capacity (Young´s Bending Modulus (N/mm^2) and flexural rigidity (flexural rigidity has SI units of Pa·m^4 which equals N*m²) defined as the capacity of a material to resist deformation; (b) the breaking resistance (Maximum breaking force (N)), defined as the force needed to break a material. After these measurements, the willow shoot biomass was harvested and cleaned. All harvested biomass was dried separately at 60 °C to constant weight and dry mass was recorded.

Since both the studied *Salix* species are light-demanding plants (Ellenberg and Leuschner 2010), the reduced light availability in the climate chamber may have had confounding effects on growth. Additionally, the radiation may have been even more reduced for willows on the lowermost steps on the flooding stairways. During the final week of the experiment, we thus recorded the photon flux density during the simulated low tide during a single sampling time since radiation remained the same during the whole course of the experiment. We used a LI-COR data logger (LI 1000 quantum sensor) to measure the radiation three times among each of the 14 willows on each of the steps in each of the eight mesocosms. The photon flux densities on the upper two steps were similar but reduced on the lowermost step: on the uppermost flooding step (partial flooding), the mean radiation was 73 µE/m-2 s-1 ± 15 SD; on the middle step (semi-permanent flooding), it was 74 µE/m-2 s-1± 10 SD; on the lowermost step (permanent flooding), mean radiation was 58 µE/m-2 s-1 ± 6 SD.

2.4 Data analyses

First, the data on morphological features (shoot length) and shoot biomass were analysed. Initially, the mean, maximum and total length of the *Salix* shoots from each willow individual were calculated. Then the data on shoot length (mean, maximum, total) and shoot biomass were analysed using three-way ANOVAs to test for the effects of tidal treatments with (i) three flooding levels (partial, semi-permanent and permanent tidal flooding), (ii) four salinity treatments (0 ppt, 2 ppt, periodic increase in salinity from 0 to 2 ppt; periodic decrease in salinity from 2 to 0 ppt) on (iii) two species (*S. alba* and *S. viminalis*). These tests were followed by Tukey HAS tests. Second, shoot diameter data were analysed and the data on plant biomechanical properties were prepared for statistical analyses by a script that calculated the slope (elasticity) of the linear part from each specimen. We applied three-way ANOVAs to test for the effects of tidal treatments (flooding, salinity) and species on Young´s bending Module, flexural rigidity, and maximum breaking force. In addition, we calculated the relation between diameter and maximum

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breaking force. The ANOVAs were followed by Tukey HAS tests. The statistical tests were conducted with the free software R.

3. Results

3.1 Morphological response to tidal flooding and salinity

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The three-factorial ANOVAs did show a highly significant reduction of the mean juvenile willow shoot length for both *S. alba* and *S. viminalis* showed highly significant reductions in mean shoot length in response to increased levels of flooding (Table 1a); however, mean shoot length was only significantly lower under permanent compared with partial flooding conditions (Tukey HAS test). The main effect of species was also highly significant (Table 1a), with shrubby *S. viminalis* generally being taller than the tree species *S. alba*. However, Tukey HAS test showed similar performance of both species within each flooding among all salinities. In addition, an interaction between flooding and species was found (Fig. 1a, Table 1a).

Maximum shoot length decreased significantly with increasing levels of flooding and salinity (Table 1b). The maximal shoot length decreased significantly in both *S. alba* and *S. viminalis* from partial to permanent flooding levels, and from partial and semi-permanent flooding levels at all salinity levels (Tukey HAS test). However, maximum shoot length was similar between semi-permanent and permanent flooding levels among all salinities except for *S. viminalis* at 0 ppt. A small species-flooding interaction was found with *S. viminalis* having a larger maximum shoot length (Table 1b). Also *S. viminalis* performed better under increasing salinity conditions (Fig. 1b; Table 1b).

Figure 1a

Figure 1b

Table 1

The total shoot length decreased with increasing levels of flooding and salinity (Table 1c). Highly significant differences were found between partial and permanent levels of flooding, and significant differences were found between partial and semi-permanent levels of flooding at all salinities (Tukey HAS test). Small interaction effects were found between salinity and flooding, and flooding and species, and highly significant interaction effects between salinity and species (Table 1c). Under the partial flooding level, *S. alba* and *S. viminalis* developed similar total shoot lengths, and no significant differences were found among the salinity treatments. Generally, both species performed similarly under semi-permanent flooding conditions. However, results for *S. alba* under semi-permanent and permanent flooding levels showed that total shoot length remained similar between salinity 0 ppt and under periodically changing salinity (0–2, 2–0), whereas length decreased significantly between 0 and 2 ppt under the semi-permanent flooding level. For *S. viminalis*, total shoot length remained similar among all salinity treatments under the semi-permanent flooding level (Fig. 2a, Table 1c).

The final shoot dry mass generally decreased with both increasing flooding and salinity (Table 1d). Also, *S. viminalis* generally developed significantly higher shoot dry mass than *S. alba*, but a highly significant interaction between flooding and species was found (Table 1d). At the partial and semi-permanent flooding levels, neither *S. alba* nor *S. viminalis* showed significant differences among salinity treatments (Tukey tests). At the partial flooding level, *S. viminalis* developed significantly higher shoot dry mass under periodically increasing salinity (0–2 ppt) than *S. alba*. At the permanent and semi-permanent flooding levels, however, no significant differences in shoot dry mass were found within species or between species (Fig. 2b, Table 1d).

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Figure 2a

Figure 2b

Significant effects of tidal flooding were found on the shoot diameter of both *S. alba* and *S. viminalis* (Table 2a), with shoot diameter decreasing with increasing flooding depth. Also, *S. viminalis* developed shoots with larger diameters compared with *S. alba*. However, variation in shoot diameter under the partial flooding level in *S. viminalis* was almost double (sal 0, mean 2.68mm, SD **±1.28**; sal 0–2, 2.63mm, **±1.07**; sal 2–0, 2.69mm, **±0.90**; sal 2, 2.40mm, **±0.75**) that of *S. alba* shoots (sal 0, 2.31mm, **±0,71**; sal 0–2, 2.28mm, **±0.57**; sal 2–0, 2.16mm, **±0.56**; sal 2, 2.20mm, **±0.49**).

Comparing partial and permanent flooding levels, there was a significant decrease in diameter for *S. alba* (salinity 0) but not for *S. viminalis* (Tukey tests). No significant differences in diameter were found for both species between partial and semi-permanent and between semi-permanent and permanent flooding levels. Diameter was not significantly affected by salinity nor were any significant interactions found (Fig. 3, Table 2a).

Figure 3

3.2 Biomechanical response to tidal flooding and salinity

3.3.1 Bending capacity

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Overall, the bending capacity of both *Salix* species shoots decreased strongly with increasing levels of flooding and slightly with salinity treatment (Fig. 4; (a) the bending capacity (Young´s Bending Modulus (N/mm^2)) and (b) flexural rigidity (flexural rigidity has SI units of $Pa·m^4$ which equals $N*m^2$); Table 2b; Table 2c). This is demonstrated by the highly significant p-values of increasing tidal flooding on Young´s Bending Modulus (F = 54.50, $p < 0.001$) and flexural rigidity (F = 68.38, p < 0.00.1), and the less significant p-values for the effect of salinity on Young´s Bending Modulus (F = 4.02, $p < 0.01$) and flexural rigidity (F = 3.27, $p < 0.05$).

Species differed in performance with respect to both Young´s Bending Modulus (Table 2b) and flexural rigidity (Table 2c). Regarding values of Young´s Bending Modulus for *S. alba*, no significant differences were found between partial and semi-permanent, and between semi-permanent and permanent flooding levels; however, values of Young`s bending Modulus were significantly lower under permanent than under partial flooding levels at low salinity (0 ppt). In contrast, values of Young`s bending Modulus for *S. viminalis* were significantly lower under permanent than under partial flooding levels only under the periodically increasing salinity treatment (0–2). No significant interactive effects were found.

Figure 4a

Figure 4b

3.2.2 Breaking Resistance

Breaking resistance (Maximum breaking force (N)) decreased with increased flooding and salinity treatment in a similar fashion to bending capacity. Flooding had a strong effect, whereas the effect of salinity on both *Salix* species was much weaker but still statistically significant (Table 2d). However, Tukey tests neither confirmed significant differences within species and salinity among flooding levels nor within species and flooding level among salinity levels except for a significant decrease in breaking

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resistance in *S. viminalis* between high and low flooding level in the periodic increase of salinity treatment (0–2). Species were not significantly different in terms of their breaking resistance. However, both flooding*species and salinity*species interacted significantly (Fig. 5a, Table 2d).

The relation between maximum breaking force (N) and shoot diameter (mm) was not significant in *S. alba*. However, maximum breaking force was found to increase with increasing shoot diameter in *S. viminalis* (p < 0.001, Fig. 5b).

Figure 5a

Figure 5b

Table 2

4. Discussion

The morphological and biomechanical response of juvenile willows of two floodplain species (*S. alba* and *S. viminalis*) were tested after exposure to flooding and salinity embedded within tidal treatments in a climate chamber. Permanent flooding of the roots caused reduced shoot length and decreased diameter in both species, but final biomass was reduced only in *S. alba*. Mean shoot diameter was higher in *S. viminalis*, and maximum breaking force increased with increasing diameter. However, variation in diameter was also higher in *S. viminalis*. Permanent flooding of the roots reduced both shoot bending capacity and breaking force. Growth and biomass production remained similar under all the applied salinity treatments (up to 2 ppt). Shoot bending capacity and breaking force did not differ among the salinity treatments.

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4.1 Morphological properties

4.1.1. Response to tidal flooding

Juvenile willows that had been exposed to contrasting tidal treatments during their early establishment phase differed in their shoot biomass among the applied flooding and salinity treatment levels. Permanent flooding of the belowground biomass reduced the mean, maximum and total shoot length of both species. The filling of soil pores with water lowers oxygen supply (e.g. Blom & Voesenek, 1996) and may have caused root cease, thus reducing nutrient uptake and growth in willows that were exposed to permanent flooding of the roots in our experiment. Submergence of the below- and aboveground biomass only during the high tide phase, however, did not affect mean shoot length, but this did reduce the maximum and total shoot length shoot length of both species. Narrow-leaved floodplain *Salicaceae* species are adapted to highly disturbed environments where they are subject to flooding and disturbance. Floodwaters even act as dispersal agents for plant fragments resulting from physical disturbance of willows along the water edge and enhance regeneration of vegetative propagules in moist soil (Karrenberg *et al.,* 2002). However, flooding has also been shown to adversely affect the performance of willow cuttings. Permanent flooding led to biomass loss and reduced root porosity in *Salix nigra.* However, willow cuttings also developed pronounced aerenchyma tissue in response to periodic flooding, which commonly occurs in riparian systems (Li *et al*., 2005).

Salix nigra is a native willow tree species of the floodplains of south-eastern United States (Mitsch & Gosselink, 1993), where cuttings are planted along eroded streambanks for soil stabilization, erosion control, and habitat rehabilitation (Schaff *et al.,* 2003). Similarly, the shrub species *S. viminalis* and tree species *S. alba* are widely-used target species in floodplain forest restoration in European river landscapes. At sites with greater water-level fluctuation and flooding, the probability of occurrence was found to be higher for young shrubby *Salicaceae* compared with tree *Salix* species in a hydrological model on the suitability of floodplain vegetation types (Leyer *et al.,* 2012). Similarly, higher mean and maximum shoot length of *S. viminalis* were found under increased flooding conditions compared with *S. alba* in our experiment. In an earlier tidal field experiment on *S. alba* and *S. viminalis*, more than 90% of

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both willow species cuttings resprouted, and the increase in shoot length was similar up to a flooding depth of 60 cm. However, *S. viminalis* produced significantly more biomass compared with *S. alba* overall (Markus-Michalczyk *et al.,* 2016). In the present study, *S. viminalis* was also found to produce more shoot dry mass compared with *S. alba*. Shrubby vegetation was found to have higher resprouting capacity from flood-damaged stumps and therefore dominated flood-prone sites (Bendix & Hupp, 2000), whereas *Salicaceae* tree species like *S. alba* generally show a higher probability of occurrence at sites with higher average water level but lower water level fluctuations (Leyer *et al.,* 2012).

4.1.2 Response to salinity

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The ability of the white willow to cope with long inundation periods was highlighted by Borsje *et al.* (2011) as a criterion for selecting *S. alba* to use in large-scale applications as an ecosystem engineering species in coastal protection measurements. Intertidal ecosystems can contribute to coastal defence (Koch *et al.*, 2009) e.g. clearly demonstrated for salt marshes (e.g. Möller *et al.*, 2014). Ecosystems can contribute most effectively to coastal protection by wave attenuation in areas with relatively small tidal amplitudes and/or where intertidal areas are wide (Bouma *et al.,* 2014). Accordingly, our results on willow flooding tolerance show that both *S. alba* and *S. viminalis* may be useful as measures in flooding protection up to the river mouth. Both *Salix* species occur in European riverine habitats (e.g. Leyer *et al.,* 2012) and tidal freshwater wetlands (Struyf *et al.*, 2009), and thus a sensitivity to higher salinities can be assumed. However, *S. alba* and *S. viminalis* also occur in floodplains up to the river mouth at the North Sea (Ellenberg & Leuschner, 2010) and recently, the presence of both *Salix* species was confirmed along the brackish stretch of the Elbe estuary in tidal wetlands up to a soil water salinity of 2 ppt (Markus-Michalczyk *et al.,* 2014). This corresponds to our present experimental findings: the applied salinity treatments of up to 2 ppt had no effects on the mean shoot length of both *Salix* species. However, total shoot length for *S. alba* was reduced by a salinity of 2 ppt under the semi-permanent flooding level, whereas shoot length for *S. viminalis* remained similar among all salinity treatments. Low vegetation height accompanied by high flexural strength and flexibility contributed to the stability of herbaceous salt-marsh plants (Vuik *et al.,* 2017). This finding may be also applicable to the shorter shoots found in *S. alba* compared with *S. viminalis*. *Salix viminalis* developed more shoot dry mass under the periodically increasing salinity treatment (0–2) at the partial flooding level compared with *S. alba*, and thus a slightly higher sensitivity to salinity can be confirmed for *S. alba*. Our results are supported by the similar growth rates and biomass production that were found up to a salinity of 2 in a hydroponic greenhouse experiment on *S. alba* and *S. viminalis* cuttings; indeed, *S. viminalis* cuttings with origin from brackish wetlands even showed an enhanced performance and slight acclimation to oligohaline conditions (Markus-Michalczyk *et al.*, 2014). Closely related *Salix* species were found to have settled at sites with a soil water salinity of 7.35 ppt in a field survey on the flood plains of the river Murray, Australia, and cuttings were found to tolerate oligohaline conditions (Kennedy *et al.,* 2003). Generally, the negative effect of increasing flooding was much stronger than the effect of increasing salinity in our experiment, and significant differences in shoot dry mass were not found either within species or between species at semi-permanent and permanent flooding levels under salinities up to 2 ppt. We thus assume that our studied willow species may be used for flooding protection at sites with periodically higher salinities, since the effects of salinity were nearly negligible in our experiment.

1.2. Biomechanical responses to tidal flooding and salinity

Ecosystems that contribute to flooding defence by wave attenuation should provide either high standing biomass that directly attenuates waves year-round or a biogeomorphic effect that creates a stable and persistent alteration of the fore-shore bathymetry (Bouma *et al.,* 2014). Contrary to herbaceous salt-marsh vegetation, which exhibits seasonal loss of aboveground biomass during winter (Koch *et al.,* 2009), the aboveground stems and shoot biomass of woody willows persist during the stormy winter season and may soften the impacts of waves and currents. A flume study on the willow identified the significance of the projected plant area on flexural rigidity (Wunder *et al.,* 2011). Thus, our results on shoot diameter are important. Shoot diameter responded with a similar reduction to increased flooding as shoot length and dry mass, but was not affected by salinity. However, increasing flooding treatment resulted in strong reduction of shoot diameter in *S. alba* but not in *S. viminalis*. This corresponds to findings on decreasing shoot diameter and dry mass in *S. alba* with increasing submergence in a permanent flooding experiment (Rodriguez *et al.*, 2018). Similar to our experiment, complete submergence had a stronger effect on growth reduction and caused more morphological changes than partial submergence of the belowground

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biomass. *Salix matsudana*, a related flood-tolerant willow tree species native to China, showed similar decreases in diameter and height with increasing submergence in a study on vegetation restoration of the hydro-fluctuation zone of the Three Gorges Dam Reservoir (Wang *et al.,* 2017). Comparable to *S. matsudana*, *S. alba* is a riparian willow species found in periodically flooded environments and may be less tolerant to stagnant water compared to willows that grow in wetlands (e.g. *S. nigra*) or directly along riverbanks like *S. viminalis*, which is one of the best species for consolidation of banks and dykes (Dickmann & Kuzovkina, 2014). Accordingly, *S. viminalis* produced larger shoot diameter in our experiment. However, its variation in diameter values was almost double, meaning that its behaviour under flooding may be inconsistent and thus should be tested in a flume study before this species is used for flooding protection at the mouth of rivers.

The extremely strong mechanical resistance of floodplain *Salicaceae* woody structures explain in part the propensity of biogeomorphic succession and landform construction (Corenblit *et al.*, 2009). Traits that contribute to the stability of herbaceous salt-marsh plants (large shoot diameter, high flexural strength, low vegetation height, high flexibility, and low drag coefficient and stem breakage) were found to be higher in *Spartina anglica* than in *Scirpus maritimus* (Vuik *et al.*, 2017). However, both *Spartina anglica* and *Schoenoplectus americanus* (syn. *Scirpus americanus*) showed a critical slowdown of recovery after disturbance (removal of aboveground biomass) with increasing inundation (van Belzen *et al.,* 2017). *Salix* cuttings resprouted vigorously in a tidal treatment under ambient light conditions (Markus-Michalczyk *et al.*, 2016), but growth strongly decreased with increased flooding in our climate chamber experiment. The bending capacity of *S. alba* and *S. viminalis* decreased with permanent flooding compared with periodic flooding of the belowground biomass, but no difference among salinities within flooding levels were found. Similarly, the breaking resistance decreased with increasing flooding but no difference was found between species. However, the maximum breaking force increased with increasing diameter in *S. viminalis*, whereas no relation was found for *S. alba*. The combination of larger shoot diameters and higher shoot biomass production in *S. viminalis* indicates better performance in estuarine environments. *Salix* performance in the field may be even better than performance in our experiment since floodplain willows are light-demanding pioneer species (Karrenberg *et al.*, 2002), as shown earlier in a tidal experiment on *S. alba* and *S. viminalis* under ambient light conditions (Markus-Michalczyk *et al.,* 2016).

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Conclusions

With our experimental results, we provide the first insights into the sensitivity of juvenile willow establishment in the intertidal zone based on combined flooding and salinity tidal treatments. Our findings clearly show that the willow has *i)* persistent shoots even during the dormant stage, *ii)* vigorous ability for vegetative resprouting, *iii)* fast growth and *iv)* biomechanical properties like high bending capacity and breaking resistance, all of which can be favourable under tidal conditions. These are important findings as the willow species studied may contribute to the protection of shorelines along tidal freshwater to brackish areas. However, before applying ecosystems in flood defence schemes, the protective value of ecosystems under extreme events and knowledge on long-term resilience should be gained (Bouma *et al.*, 2014). We thus strongly recommend studies on whole willow softwood floodplain forest ecosystem: *in situ* investigations at spatial and temporal scales that include most, if not all, of the ecosystem processes, including principles of self-design and ecological feedbacks key to the functioning of the whole system (Mitsch & Day, 2004), needed for the application and restoration of *S. alba* and *S. viminalis* under real world settings in the estuarine environments.

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Table 1. Results of three-way factorial ANOVAs on response of shoots of two willow species (*Salix alba* and *S. viminalis*) to three tidal flooding levels (partial, semi-permanent and permanent flooding) and four salinity treatments (0, 2, periodic increase of salinity from 0 to 2, periodic decrease of salinity from 2 to 0) in a tidal experiment on juvenile willows. The juvenile willows were grown from cuttings originating from tidal freshwater wetlands of the Elbe estuary. Four shoot parameters were measured: (a) mean shoot length, (b) maximum shoot length, (c) total shoot length, and (d) shoot dry mass (N= 4).

Shoot	(a) mean length		(b) max length		(c) total length		(d) dry mass	
	F	*p*	F	*p*	F	*p*	F	*p*
flooding	216.06	<0.001	285.22	<0.001	275.82	<0.001	157.85	<0.001
salinity		ns	10.37	<0.001	13.66	<0.001	6.54	<0.001
species	11.59	<0.001		ns		ns	8.51	<0.01
flooding*salinity		ns		ns	2.24	<0.05		ns
flooding*species	3.55	<0.05	3.08	<0.05	3.37	<0.05	8.32	<0.001
salinity*species		ns	2.77	<0.05	2.99	<0.05		ns
flooding*salinity*species		ns		ns		ns		ns

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Table 2. Results of three-way factorial ANOVAs (flooding level*salinity*species) on the response of biomechanical properties in the same experiment as described in Table 1. Four biomechanical parameters were measured: (a) shoot diameter (mm), (b) Young´s Bending Modulus (MPa), (c) Flexural rigidity (N/mm2), and (d) Maximum breaking force (N). (N = 4).

Biomechanical property of the *Salix* shoots	(a) Diameter (mm)		(b) Young´s Bending Modulus (MPa)		(c) Flexural rigidity (N/mm2)		(d) Maximum breaking force (N)	
	F	*p*	F	*p*	F	*p*	F	*p*
flooding	41.68	<0.001	54.50	<0.001	68.38	<0.001	20.62	<0.001
salinity		ns	4.02	<0.01	3.27	<0.05	3.63	<0.05
species	6.12	<0.05	5.92	<0.05	8.06	<0.01		ns
flooding*salinity		ns		ns		ns		ns
flooding*species		ns		ns		ns	4.39	<0.05
salinity*species		ns		ns		ns	4.02	<0.01
flooding*salinity*species		ns		ns		ns		ns

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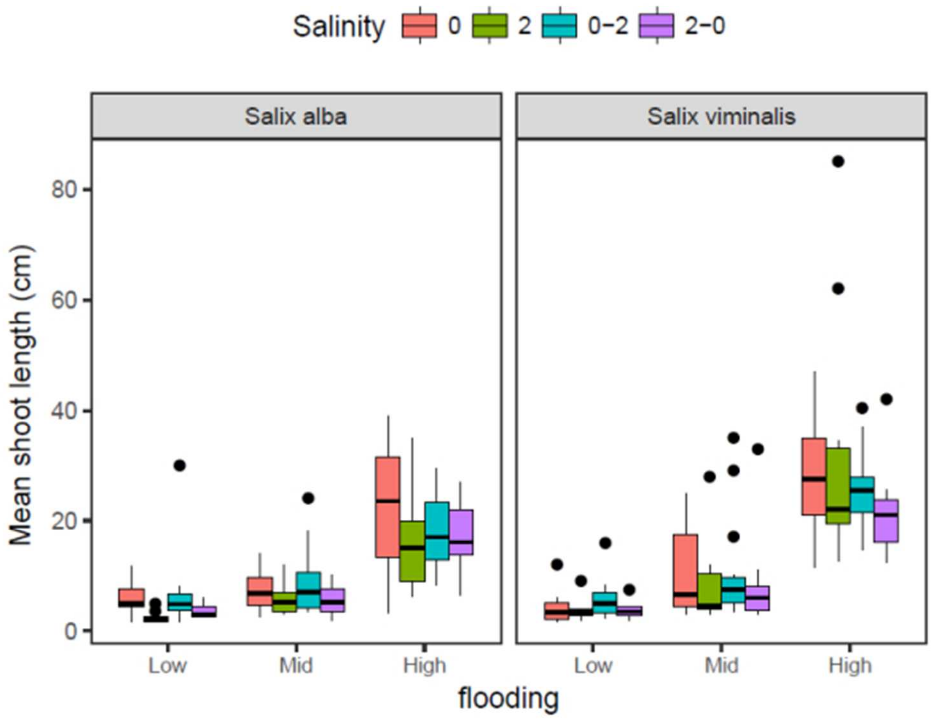
a


Salinity
0
2
0−2
2−0
Salix alba
Salix viminalis
Mean shoot length (cm)
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20
40
60
80
Low
Mid
High
Low
Mid
High
flooding

view

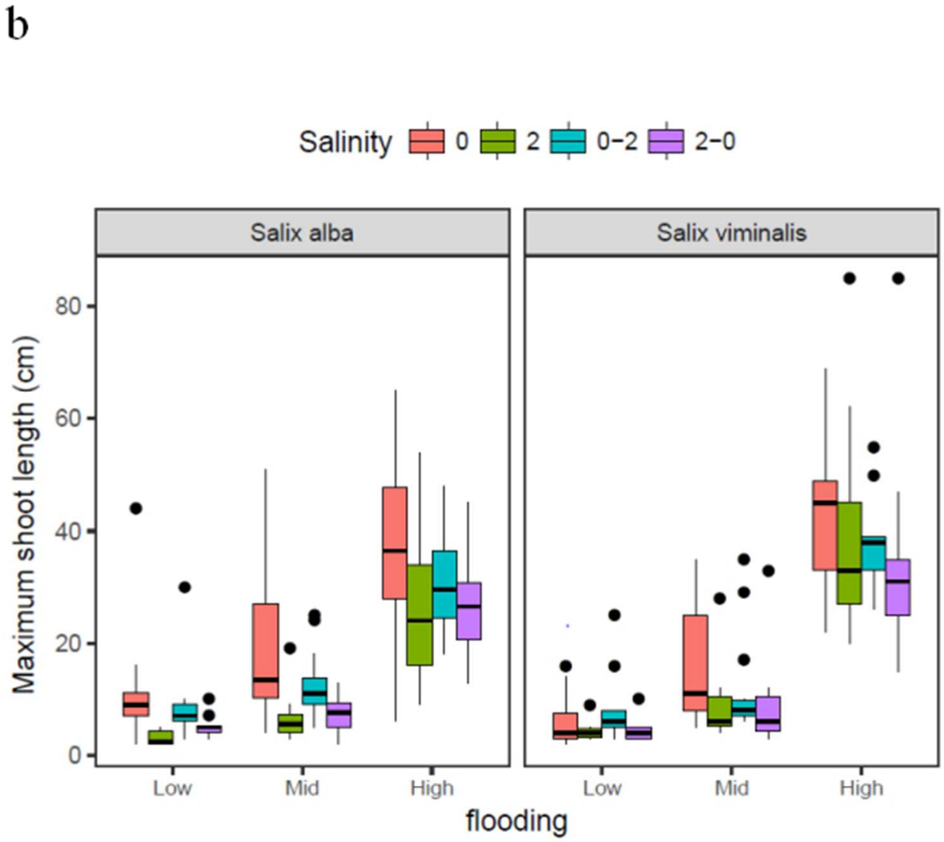
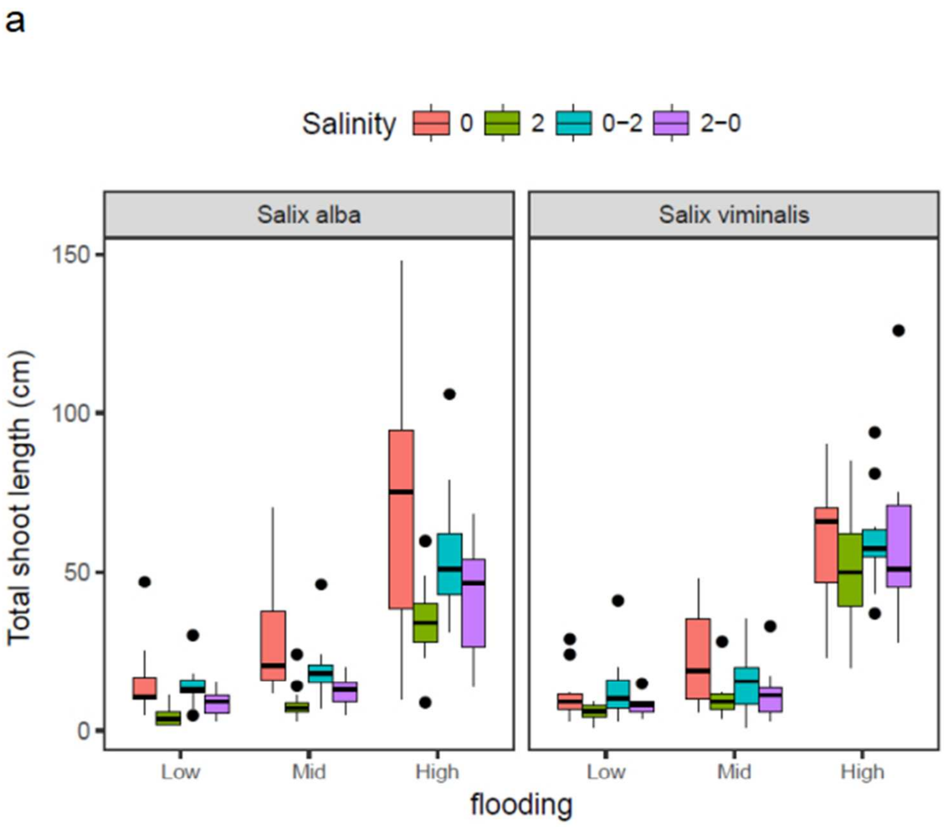


Fig. 1. Final shoot length of juvenile willows after ten weeks of tidal treatment (see table 1 for desciption of flooding and salinity levels and plants origin) on two Salix species (S. alba nd S. viminalis): (a) mean shoot length, (b) maximal shoot length) (N = 4).


a
Salinity
0
2
0−2
2−0
Salix alba
Salix viminalis
Total shoot length (cm)
0
50
100
150
Low
Mid
High
Low
Mid
High
flooding

iew

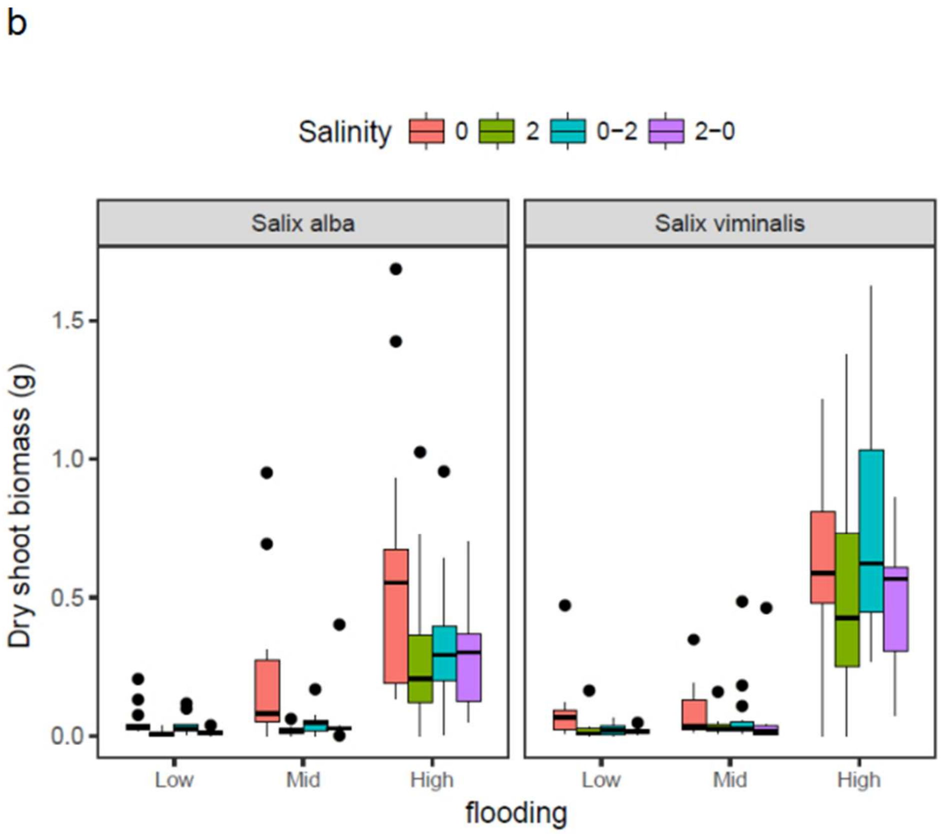


Fig. 2. (a) Total shoot length and (b) shoot dry mass of juvenile willows after ten weeks of tidal treatment (see table 1 for desciption of flooding and salinity treatments and plants origin) on two Salix species (S. alba nd S. viminalis) (N = 4) .

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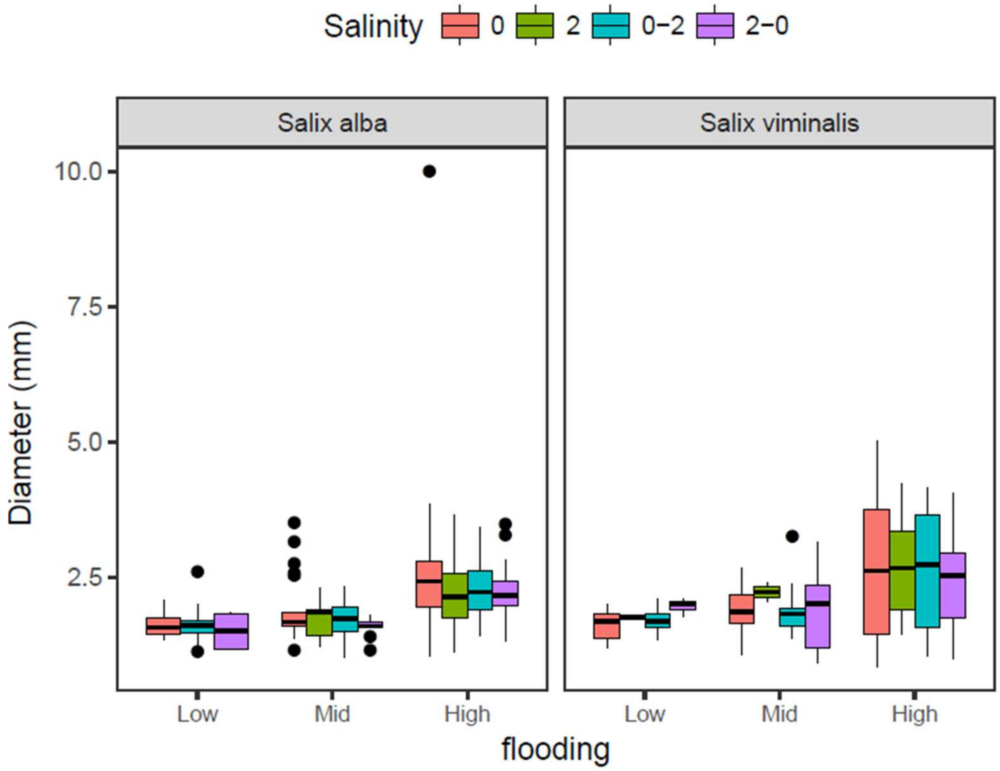

Fig. 3 Shoot diameter (mm) of juvenile willows after ten weeks of tidal treatment (see table 1 for desciption of flooding and salinity levels and plants origin) on two Salix species (S. alba nd S. viminalis)(N = 4).

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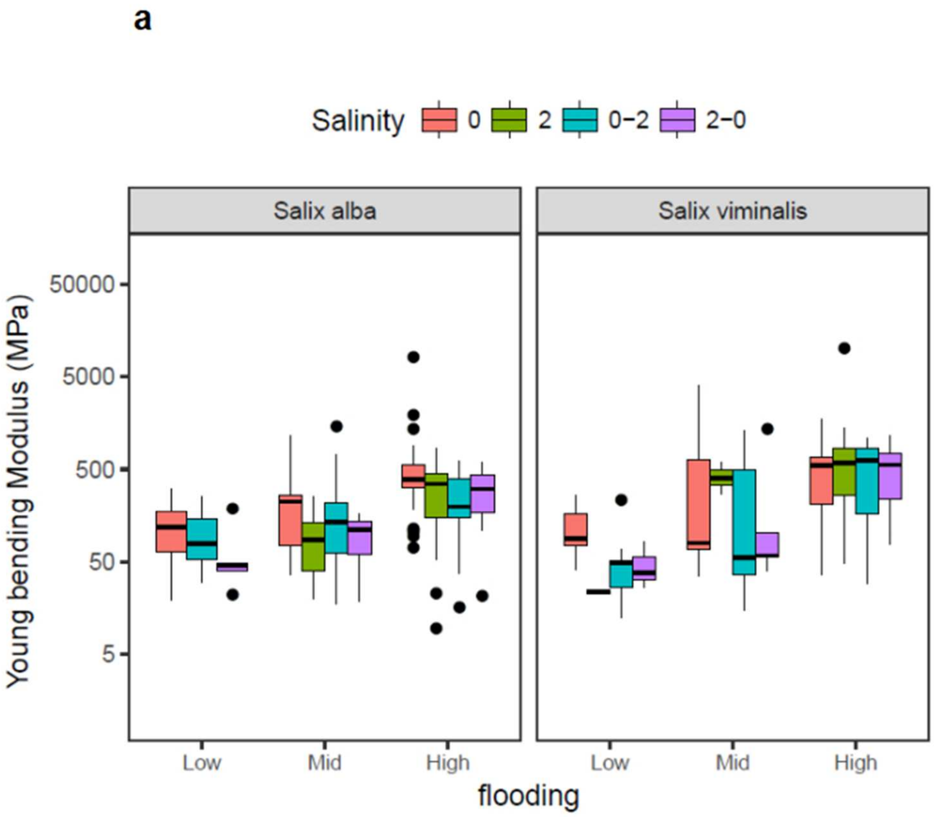
a
Salinity
0
2
0−2
2−0
Salix alba
Salix viminalis
Young bending Modulus (MPa)
50000
5000
500
50
5
Low
Mid
High
Low
Mid
High
flooding

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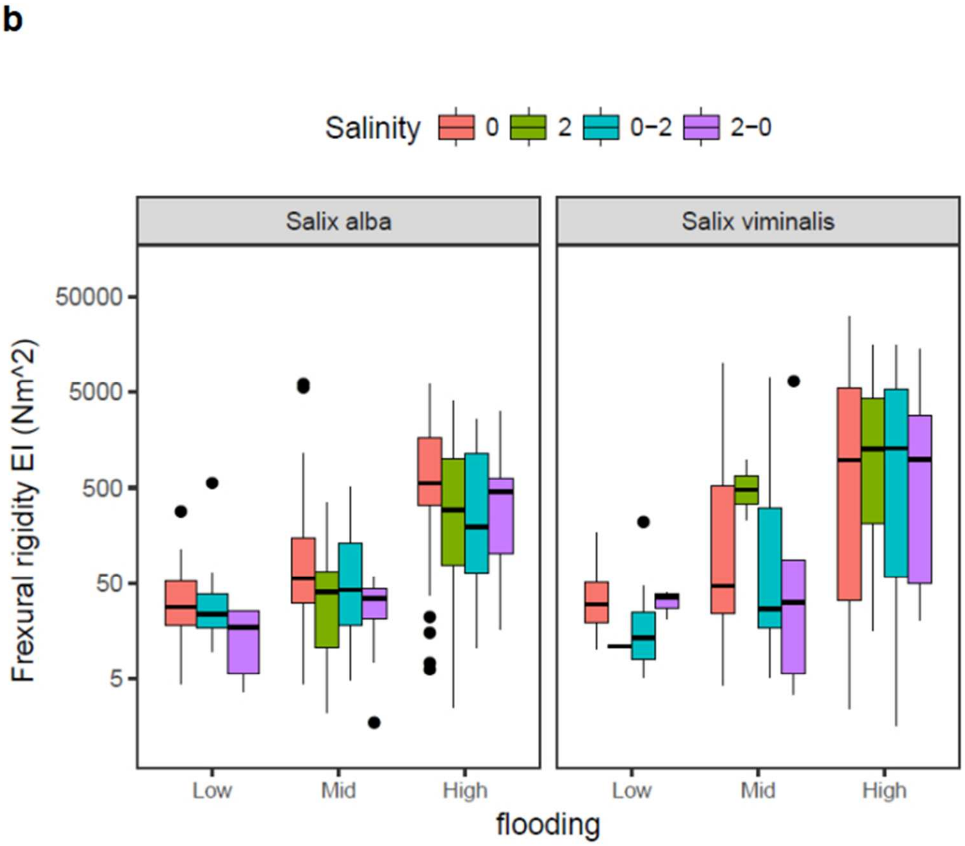
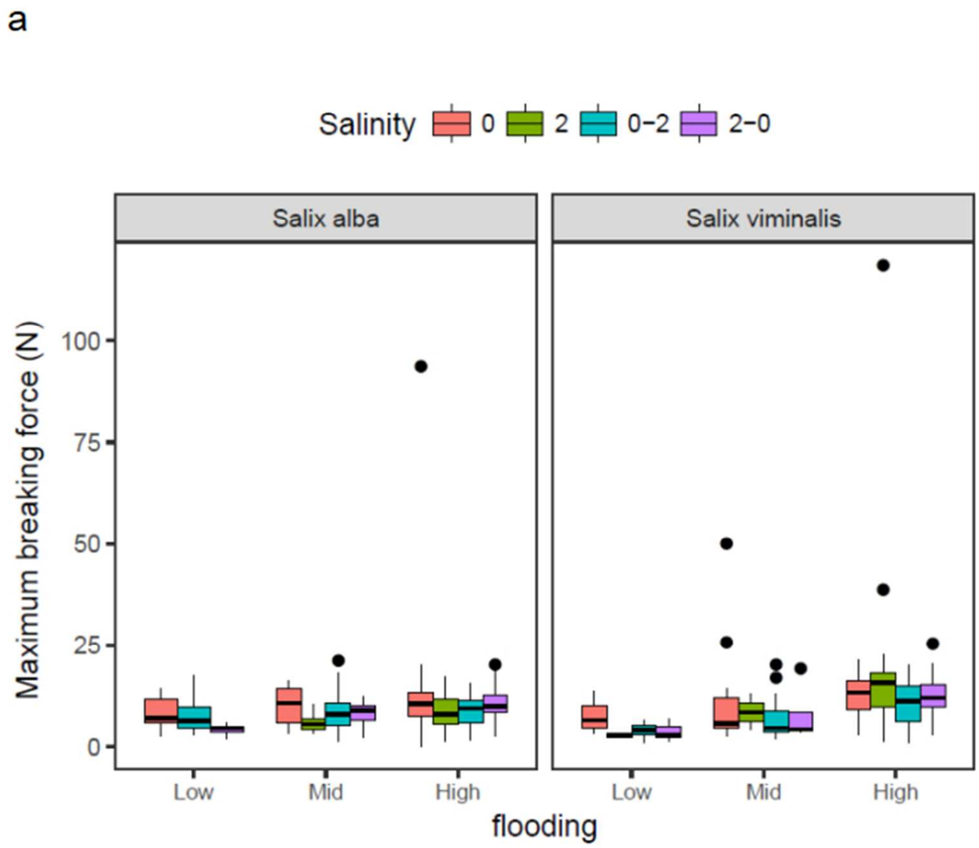


Fig. 4. Bending capacity expressed as (a) Young´s Bending Modulus (N/mm²) and (b) flexural rigidity (flexural rigidity has SI units of N*m²) of juvenile willows shoots after ten weeks of tidal treatment (see table 1 for description of flooding and salinity levels and plants origin) on two Salix species (S. alba nd S. viminalis) (N = 4).


a
Salinity
0
2
0−2
2−0
Salix alba
Salix viminalis
Maximum breaking force (N)
0
25
50
75
100
Low
Mid
High
Low
Mid
High
flooding

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b

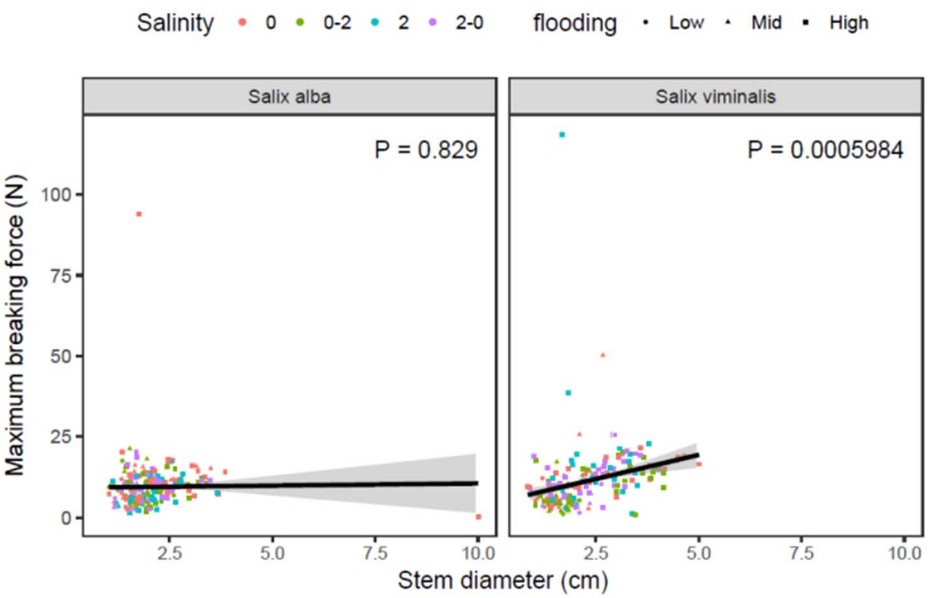

Fig. 5. Breaking resistance measured in terms of (a) Maximum breaking force (N), and (b) the relation between maximum breaking force (N) and shoot diameter (mm)) of juvenile willows shoots after ten weeks of tidal treatment (see table 1 for description of flooding and salinity levels and plants origin) on two Salix species (S. alba nd S. viminalis)(N = 4).

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