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Floodplain Forest Foundation Species *Salix alba* L. Is Resilient to Seawater Pulses during Winter

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Abstract: (1) Background: Willow forests are well established as nature-based solutions contributing to flood protection in the riverine environment. With climate change, storm surges in winter may increasingly expose downstream floodplain forests to seawater pulses. The effects of seawater pulses on willows are unknown, as previous studies focused on long-term exposure effects. (2) Methods: We studied the resilience of the floodplain forest foundation species *Salix alba* L. to seawater pulses during winter. This corresponds to the effects of storm surges in the North Sea region on floodplain willow trees in downstream river stretches during their dormant stage. Seawater pulses were applied from November to May on vegetative propagules. The plants were placed on flooding stairways at three levels in a mesocosm experiment under ambient conditions in Zealand, NL. (3) Results: Twice-applied 48 h seawater pulses during winter led to increasing salinity in the soil where vegetative propagules were placed. Ninety-five percent of the plants developed leaves, shoots, and roots, and juvenile trees were established in the following spring. Although the aboveground and belowground dry masses decreased with increasing short-term seawater flooding, they increased from April to May. (4) Conclusions: The seawater pulse caused a growth-delaying effect in the young experimental propagation plants of *Salix alba*. Contrary to earlier findings on the growth-inhibiting effects on *S. alba* under long-term salinity treatments, we show that *S. alba* is resilient to short-term seawater pulses experienced during the dormant (winter) stage. This is good news for the inclusion of *S. alba* in nature-based flood defense schemes in downstream riverine stretches.

Keywords: *Salix alba*; downstream riverine reaches; seawater pulses; flooding risk; nature-based solution

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1. Introduction

The flooding of riverine and coastal ecosystems is a critical risk following climate change and sea level rise. Nature-based solutions (NbSs) like floodplain and watershed restoration can contribute to climate-resilient development with flood defense and enhance biodiversity [1]. Global biodiversity frameworks such as the Convention on Biological Diversity [2] and the Intergovernmental Platform on Biodiversity and Ecosystem Services [3] include the NbS concept as a component.

Floodplain forests in the temperate climate of the northern hemisphere are predominantly formed from tree species of the *Salicaceae* plant family. The genus *Salix* is adapted to floodplains through the flexibility and bending ability of its branches and its resilience to physical disturbance through its rapid resprouting capacity [4]. Floodplain riparian forests in Eurasia are characterized by the presence of *Salix alba* L., which reaches up to 20 m and higher in height [5]. *Salix alba*, or white willow, is a deciduous species and is native to Europe and western and central Asia. It is dioecious, with male and insect-pollinated female flowers appearing on different individual trees. A real-scale experiment on *S. alba* trees showed wave attenuation up to a 2.5 m wave height in its leaf-bearing and leafless seasons, suggesting that *S. alba* floodplain forests can play a significant role in year-round flood risk reduction [6]. This supports the findings of a flume study in which juvenile white and basket willows reduced the current velocity in summer and were leafless during winter when the willows lack leaves. Due to enhanced canopy permeability but maintained shoot length and diameter, the current velocity was particularly reduced during winter. This indicates that floodplain willow species with flexible twigs are suitable for inclusion and use in flood protection foreshore designs where storm surges during winter occur [7]. These experimental findings on living willows confirmed earlier modeling results of wave reduction due to a white willow belt in front of a dike in the Dutch delta. In this application project for nature-based flooding defense at the Nordwaard polder near the Nationalparc De Biesbosch, NL, *S. alba* stubs with a height of 0.3 m and 60 shoots each, with a height exceeding the maximum water level, were planted at a density of 4.3 m^{-2} to protect the dike and the polder against waves during storm conditions [8].

Salix alba defines the alluvial forest ecosystem *Salicion albae* and forms gallery riparian forests along medio-European lowland, hill, or submontane rivers. However, more than 99% of European *Salix* floodplain forests have been lost [9]. *Salix alba* floodplain forests are listed as a priority habitat type 91E0* and a good conservation status must be maintained or restored [10]. *Salix alba* is a foundation species of Eurasian floodplain forests, similar to tropical mangroves (especially *Rhizophora* species) in "mangrove forests", which both determine regional biodiversity and have a central place in an ecological network [11].

The potential of floodplain forest *Salix* species to protect riverbanks from hydrodynamic forces is well known. Riparian *Salix* buffer zones for streamside restoration have been established along streams in temperate climates [12]. However, the flood protection defense potential of *Salix alba* along downstream riverine stretches in temperate climates is unknown, whereas tropical mangroves are recognized as a natural defense against flooding. If mangrove forests were lost worldwide, then 15 million people would be flooded annually along coastlines. This estimate indicates the need for mangrove forest conservation and restoration for climate adaptation and disaster risk reduction [13]. Coastal wetland vegetation is highly valued due to its flooding defense contributions by decreasing storm surge effects and waves, by maintaining shallow water depths, and by absorbing flood waters caused by rain [14]. Wetland creation enhances sedimentation and flooding amelioration in downstream riverine stretches, estuaries, and deltas [15]. However, human impacts have accelerated over the past 150–300 years, transforming estuarine systems, which has led to the destruction of more than half of the tidal wetlands worldwide [16].

Salix forms the foundation of the riparian floodplain forests in the tidal freshwater wetlands of estuarine systems in Europe. In these *Salix*-dominated tidal wetland forests, *S. cinerea*, *S. caprea*, *S. triandra*, *S. fragilis*, *S. dasyclados*, and *S. viminalis* are the main co-occurring shrub species [17]. *Salix alba* maintains flexible twigs with a high bending capacity that provide year-round current reduction [7,18] and wave attenuation including during the winter storm surge season [6], but to our knowledge, studies on the current and wave reduction capacity of shrub species are lacking. Along downstream river stretches at the southwestern North Sea, extended *S. alba* floodplain forests were found at the upstream reaches of the Elbe, Ems, Dutch delta, and Scheldt estuary, whereas only small stands were confirmed in downstream tidal wetlands [19]. This seems to be a contradiction since these estuaries are dramatically altered. Particularly in the upstream tidal and freshwater reaches, port development and urbanization has taken place, e.g., at the Elbe (Hamburg port), Ems (cruise shipyard Papenburg), and Scheldt (port of Antwerp). At the Rhine–Meuse Delta, large-scale grey flood protection infrastructure has been constructed [17]. In the Rhine–Meuse estuaries, the Delta Works, consisting of large-scale grey flood protection infrastructure-like barriers, disrupts water and sediment flows. This has led to a movement toward working with nature to combine solutions for safety with solutions for environmental problems [20]. The Delta Programme of the Netherlands [21] aims to restore and strengthen natural processes to achieve a climate-resilient Dutch Delta. The Integrated Management Plan for the Elbe estuary [22] similarly aims to combine measures for restoration and flood protection by simultaneously maintaining the navigation function. Thus, the

Rhine–Meuse Delta and the Elbe estuary are model systems for our study and for creating new options for nature-based flood defense approaches in downstream riverine stretches.

Estuarine organisms cope with variable and fluctuating salinity as a principal stressor [23]. Estuarine floodplains are periodically and episodically affected by disturbances like floods and storm surges [24]. Seawater can either stress or facilitate biota; e.g., mangroves are established in the east of the Amazon mouth in the upper river reaches due to saltwater intrusion [25]. In the genus *Salix*, tolerance to salinity depends on the species and hybrid, and on the level and duration of saltwater influence [26]. Numerous authors found a resilience of *S. alba* hybrids to moderate salinity but not to long-term high-salinity treatments in hydroponics, e.g., [26–28], or in experiments with plants placed in soil, e.g., [29–31].

Salix alba L. was recently found in fragmented stands along the lower river reaches of the Elbe, Ems, Rhine–Meuse, and Scheldt [19]. It was confirmed for the brackish stretch of the Elbe with oligohaline soil water conditions during summer [32]. *Salix alba* can colonize tidal freshwater wetlands in the supratidal [17] and might be affected by seawater in downstream stretches only during storm surges in winter. However, the effect of such seawater pulses is unknown. We aim to answer the question of whether *S. alba* is resilient to seawater pulses during winter storm surges when *S. alba* is in the dormant, leafless condition. Since juvenile *S. alba* specimens have flexible twigs with high bending capacity and provide year-round current reduction [7,18], vegetative propagules, which develop into juvenile trees, were used as plant material in the experiment.

We hypothesize that the floodplain forest foundation species *S. alba* is resilient to seawater pulses corresponding to the effects of storm surges in winter while the tree species is in its dormant stage. We aim to answer the following questions: (i) How do seawater pulses affect the growth and the biomass of juvenile *S. alba*? (ii) Do the effects of seawater pulses during winter differ between populations with origins from tidal wetlands in the upstream and the downstream freshwater reaches?

2. Materials and Methods

A mesocosm experiment to elucidate the effects of seawater pulses on juvenile *Salix alba* during its winter dormant stage was conducted at the Royal Netherlands Institute for Sea Research NIOZ Department Estuarine and Delta Systems, Yerseke, from November 2022 to April 2023. Vegetative propagules of *S. alba* specimens (i) were exposed to short-term seawater treatments at three flooding levels (no flooding; soil flooding; complete flooding), whereas the cuttings were collected at two downstream river locations (ii) of two different origins (tidal freshwater stretch of the Elbe estuary versus the tidal polyhaline conditions of the Eastern Scheldt).

2.1. Plant Material

Both male and female *Salix alba* trees in tidal wetlands served as sources for cuttings, which act like vegetative propagules and from which juvenile trees develop. These cuttings were collected from a total of 10 trees at 2 sites: a tidal freshwater wetland at the upper stretch of the Elbe estuary (N 53°23′46.93″, E 10°13′50.88″) and a revetment at the polyhaline Eastern Scheldt (N 51°31′04.67″, E 4°00′23.95″). Five *Salix alba* trees with straight shoots of similar size and diameter were selected as sources for the cuttings at both sites. On 27 October 2022, 200 rods 30 cm in length were collected from each of the selected trees at the Elbe estuary, and on 31 October 2022, 200 rods 30 cm in length were taken from each of the selected specimens at the Eastern Scheldt. These cuttings were shortened to 25 cm in length and stored in water in plastic boxes at 4 °C in a cooling room until the start of the experiment. A planting substrate consisting of half river sand and half planting soil containing 10% organic matter (Terrafin BV) was mixed and filled in square pots (13 cm × 13 cm; 14 cm-high).

On 10 November, each cutting was trimmed to 20 cm in length to enhance water absorption via capillary forces. Afterwards, the cutting's initial mass was determined with a digital balance. Cuttings with similar weights were selected for utilization in the experiment. These cuttings were placed in pots with half of their lengths buried in the planting soil. The pots were watered until the soil was saturated and stored at the experimental site at NIOZ Yerseke under ambient conditions until the start of the experiment on 15 November 2022.

2.2. Seawater Treatment

The seawater treatment was conducted in ambient conditions at NIOZ Yerseke, Zeeland (1991–2020; mean max. temperature, 14 °C; mean min. temperature, 8.7 °C; precipitation, 759 mm/year; "URL https://www.wetterkontor.de/de/klima/" (assessed on 12 May 2022). The treatment was applied in four mesocosms (110 cm × 90 cm; 60 cm height). "Flooding stairways" containing three steps were installed to represent increasing flooding in the seawater treatment in each of these mesocosms: 1 (highest step), control with no flooding with seawater; 2 (middle step), seawater flooding of only belowground biomass (soil flooding); 3 (lowest step), seawater flooding of both aboveground and belowground biomass (complete flooding). Seven pots containing cuttings from the Elbe estuary and seven from the Eastern Scheldt were arranged randomly on each of the three flooding steps, resulting in 42 pots per mesocosm and 168 pots containing 168 *S. alba* cuttings in total, spread over the four mesocosms (N = 4) (Figure 1).

Figure 1. Effects of seawater pulses on *Salix alba* cuttings were tested during the dormant stage; twice with two-day lasting seawater flooding of three flooding levels: no flooding (control), flooding of belowground biomass (soil flooding), flooding of aboveground and belowground biomass (complete flooding); N = 4.

Seawater pulses were applied from November 2022 to May 2023 corresponding to the storm surge frequency in the southern North Sea. Detailed reports on North Sea storm surges from 2009 to 2022 were analyzed regarding their occurrence (Table 1).

According to the Federal Maritime and Hydrographic Agency [33], 64 severe storm surges (>2.5 m above MThw) occurred over the last 55 years (1967–2022), including 13 very severe storm surges (>3.5 above MThw) along the North Sea coastline in Germany. Two storm surges occurred on average per season, predominantly from December to February, lasting two days in average. Accordingly, two seawater pulses, lasting two days each, were applied in the experiment. On 5–6 December 2022 and 2–3 February 2023, seawater from the Eastern Scheldt was discharged into the mesocosms up to the described flooding levels to simulate storm surges with seawater pulses on *Salix alba* in tidal wetlands. The seawater was discharged out of the mesocosms after the applied pulse.

Table 1. Storm surges in the southern North Sea 2009–2022 [33].

Storm Surge Season	Date	Number of Storm Surges per Season	Total Number of Days with Storm Surges per Season
2009/2010	4. Oct.	1	1
2010/2011	4.–5. Feb.	1	2
2011/2012	5.–6. Jan.	1	2
2012/2013	31. Jan.	1	1
2013/2014	28. Oct.; 5.–6. Dec.	2	3
2014/2015	22. Oct.; 9.–11. Jan.	2	4
2015/2016	-	-	-
2016/2017	26.–27. Dec.; 3.–4. and 11.–14. Jan.	3	8
2017/2018	13. Sept.; 29. Oct.	2	2
2018/2019	8. Jan.	1	1
2019/2020	15. Dec.; 15. Jan.; 10.–12. Feb.	3	5
2020/2021	-	-	-
2021/2022	21. Oct.; 7. Nov.; 1. Dec.; 5. and 29.–30. Jan.; 1.–7. and 17.–22. Feb.	7	18

The soil water salinity was recorded two times: after the first seawater pulse (5–6 December) on 9 December 2022 and on 11 April 2023 before the growing season. A digital EC-METER for soil EC1210 (Nieuwkoop, Aalsmeer, The Netherlands; NL) was used to record the data in each of the 168 pots at a soil depth of 5 cm.

2.3. Morphological Parameters and Biomass

We collected the data on morphological parameters twice, once in mid-April and a second time in mid-May at the end of the experiment. On 12 April, the plants were carefully removed from the mesocosms. The shoot numbers and the leaves per shoot of each plant were recorded. The length of each shoot that developed per vegetative propagule was measured. Maximum shoot length, mean shoot length, and total shoot length were calculated. Afterwards, the plants were returned to the mesocosms. On 9 May, the experiment was terminated and the numbers of shoots and leaves per shoot of each plant were recorded. The length of each shoot that developed from the vegetative propagule was measured again. Maximum shoot length, mean shoot length, and total shoot length were calculated. At the end of the experiment, to obtain shoot and root biomass, the cuttings were harvested, dried separately at 60 °C to a constant weight, and weighed (Satorius AC 2115; Satorius Lab Instruments GmbH & Co.KG, Goettingen, Germany).

2.4. Data Analyses

The mean was calculated for the electrical conductivity and for the morphological parameters (maximum shoot length; mean shoot length; total shoot length; shoot number; leaf number; leaf/shoot ratio), which were recorded on the juvenile *Salix alba* trees in the mesocosm experiment and are displayed in graphs.

Secondly, the data on electrical conductivity and morphological parameters of the juvenile *Salix alba* grown from vegetative propagules were analyzed statistically. One-way ANOVAs were applied to test the effects of seawater pulses on the electrical conductivity of the soil among the three flooding levels. The data on morphological parameters were analyzed by applying ANOVAs. To test the effects of both seawater pulses (at three flooding levels: no flooding; soil flooding; complete flooding) and origin (cuttings from tidal freshwater wetland at the Elbe estuary; cuttings from the revetment at the polyhaline

Eastern Scheldt), two-factorial ANOVAs were applied. To determine differences among groups, post-hoc tests were conducted as pairwise multiple comparison procedures.

Finally, the aboveground (leaf and shoot) and belowground (root) dry masses were analyzed. To account for possible differences in cuttings' initial weights, which might have affected dry mass, ANCOVAs were applied where the initially measured cutting biomass was included as a covariate.

3. Results

3.1. Electrical Conductivity

The electrical conductivity (EC) of the soil water of the pots in the mesocosm experiment rose with increasing flooding level. After the first seawater pulse (5–6 December), on 9 December 2022, the EC was significantly ($p < 0.05$) increased between the control (mean 0.29 mS/m) and that of the complete flooding level (mean 1.79 mS/m). After the second seawater pulse (2–3 February), when the EC was measured on 11 April 2023 before the beginning of the growth season, a significant difference ($p < 0.05$) between the ECs of the control (mean 0.11 mS/m) and complete flooding (mean 0.32 mS/m) was found.

3.2. Morphological Parameters

The results for the morphological parameters (maximum shoot length; mean shoot length; total shoot length; shoot number; leaf number; leaf/shoot ratio) recorded in the mesocosm experiment are presented in Table 2 and illustrated graphically in Figure 2.

The growth parameters (maximal shoot length; mean shoot length; total shoot length; shoot number; leaf number; shoot/leaf ratio) recorded in the experiment both in April and at the end of the experiment in May (Table 2; Figure 2) were analyzed with two-way ANOVAs followed by pairwise multiple comparison procedures to determine differences between groups.

Table 2. Morphological parameters of juvenile *Salix alba* trees (April and May 2023) in a mesocosm experiment on the effects of seawater pulses in the dormant season (November2022–May 2023) with (i) two 2-day treatments of seawater flooding at three flooding levels: no flooding (control—1), flooding of the belowground biomass (soil—2), flooding of aboveground and belowground biomass (complete—3), and (ii) cuttings originating from tidal freshwater wetlands of the Elbe estuary versus revetment at polyhaline site of the Eastern Scheldt. Seawater pulse treatments were applied twice, lasting for 2 days (5–6 December; 2–3 February) corresponding to the average occurrence of storm surges in the southern North Sea 2009–2022 recorded by the Federal Maritime and Hydrographic Agency; GER [33]. N = 4; mean ± SD.

	Measurement in April						**Measurement in May**					
Plant Origin	**Elbe Estuary**			**Eastern Scheldt**			**Elbe Estuary**			**Eastern Scheldt**		
Flooding Level	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Shoot (no)	5.0 ± 2.0	3.6 ± 1.1	3.8 ± 2.6	2.9 ± 1.2	3 ± 2.5	1.4 ± 1.1	5.5 ± 1.9	3.8 ± 1.3	4.6 ± 2.3	3.5 ± 1.3	4.2 ± 2.4	1.9 ± 1.4
Max shoot length (cm)	3.0 ± 1.2	5.2 ± 1.6	2.2 ± 1.3	3.1 ± 1.2	1.8 ± 1.3	2.6 ± 2.1	10.5 ± 3.4	14.3 ± 5	7.6 ± 3.6	6.7 ± 3	6.8 ± 3.6	5.4 ± 3.9
Shoot length average (cm)	2.2 ± 0.8	3.7 ± 1.3	1.6 ± 0.8	2.3 ± 0.9	1.3 ± 0.9	1.9 ± 1.5	5.5 ± 2	7.9 ± 2.9	4.6 ± 2.1	4.6 ± 1.8	3.8 ± 2.1	4.3 ± 3.4
Shoot length total (cm)	11 ± 5.3	12.8 ± 3.6	7.2 ± 5.3	6.9 ± 3.5	6.7 ± 3.8	4.9 ± 2.8	27.2 ± 8.1	27.3 ± 7.3	22 ± 12	15.4 ± 6.7	17.8 ± 11	8.6 ± 7.2
Leaves (no)	28 ± 11	29 ± 7.6	21 ± 14	17 ± 9.7	15 ± 13	6 ± 6.5	46 ± 15	34 ± 9	38 ± 20	28 ± 12	32 ± 21	13 ± 12
Leaf/shoot ratio	5.5 ± 1.3	8.3 ± 1.8	4.8 ± 2.3	5.5 ± 1.9	4.8 ± 1.6	4.2 ± 1.7	8.8 ± 2.1	9.1 ± 2	7.8 ± 3.5	8.2 ± 2.4	6.6 ± 3.4	5.8 ± 3.5

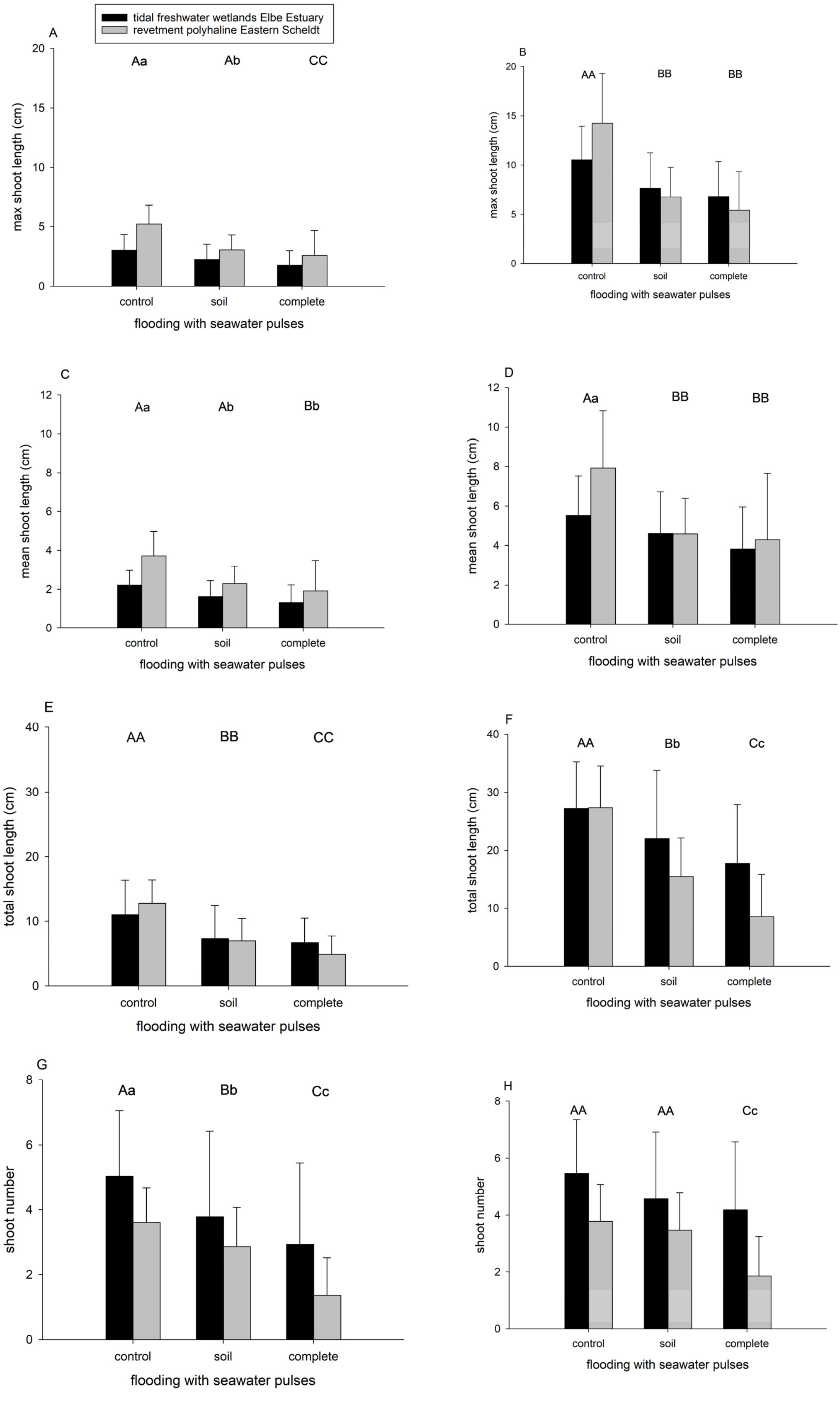

Figure 2. *Cont.*

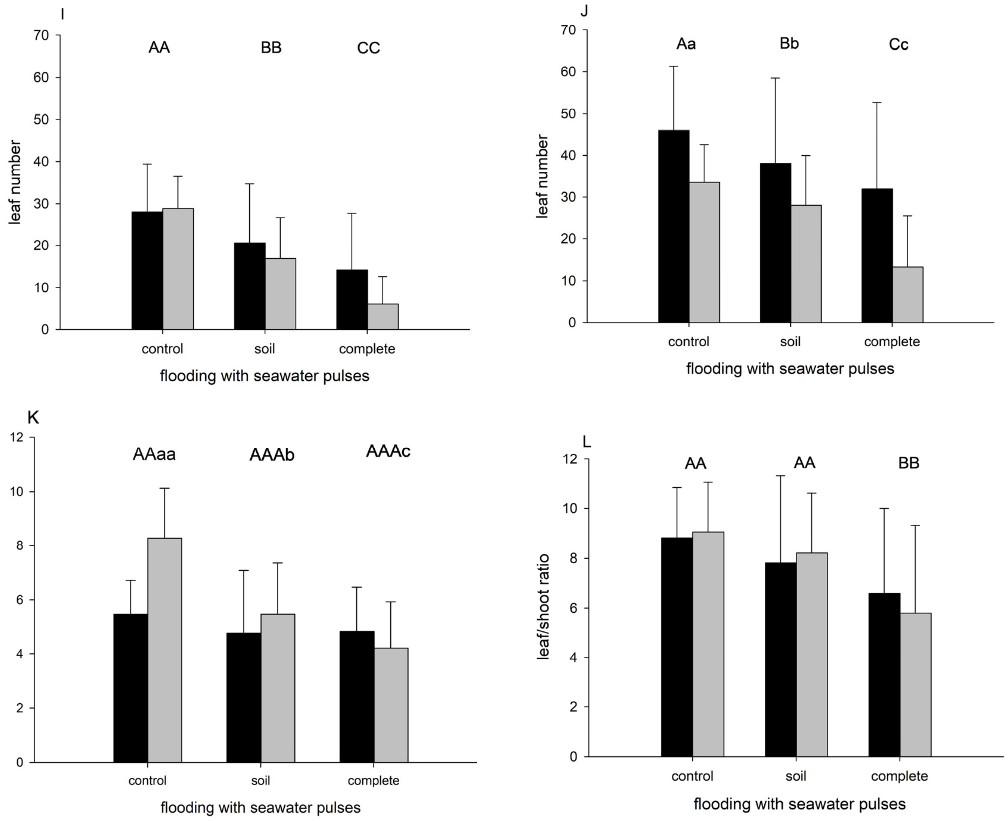

Figure 2. (**A**–**L**) Morphological parameters (maximal shoot length (mean shoot length; total shoot length; shoot number; leave number; leaf/shoot ratio) of juvenile *Salix alba* trees (April: graphs on the left hand side and May: graphs on the right hand side) in a mesocosm experiment on the effects of seawater pulses on vegetative propagules in the dormant stage (November 2022–May 2023); (i) two 2-day treatments of seawater flooding on three flooding levels: no flooding (control), flooding of the belowground biomass (soil), flooding of aboveground and belowground biomass (complete); (ii) cuttings origin from tidal freshwater wetlands of the Elbe estuary versus revetment at the polyhaline site of the Eastern Scheldt. Seawater pulse treatments were applied twice, lasting for 2 days (5–6 December; 2–3 February) and corresponding to the average occurrence of storm surges in the southern North Sea [33]. N = 4; mean ± SD.

3.2.1. Growth Parameters in April

The maximal shoot length of plants from the Eastern Scheldt was significantly larger than those from the Elbe estuary in the control ($p < 0.001$) and in soil flooding ($p < 0.05$). The maximal shoot length from plants originating from the Elbe estuary decreased significantly between the control and complete flooding ($p < 0.01$). The maximal shoot length from plants originating from the Eastern Scheldt decreased significantly between the control and soil flooding and complete flooding ($p < 0.001$) and between soil and complete flooding ($p < 0.05$) (Table 3; Figure 2A).

The mean shoot length was larger in plants from the Eastern Scheldt in the control ($p < 0.001$), soil flooding ($p < 0.05$), and complete flooding ($p < 0.05$). The mean shoot length from plants from the Elbe estuary decreased significantly between the control and complete flooding ($p < 0.01$), but the mean shoot length of plants from the Eastern Scheldt was significantly larger in the control compared to both soil flooding ($p < 0.001$) and complete flooding ($p < 0.001$) (Table 3; Figure 2B).

Table 3. Results of a two-factorial ANOVA on morphological parameters recorded in April in a mesocosm experiment on the effects of seawater pulses on juvenile *Salix alba* trees in the dormant stage (November 2022–May 2023); cuttings originating from tidal freshwater wetlands of the Elbe estuary versus revetment at the polyhaline site of the Eastern Scheldt. Seawater pulse treatments were applied twice, lasting for 2 days (5–6 December; 2–3 February) and corresponding to the average occurrence of storm surges in the southern North Sea [33]. N = 4.

	Seawater Pulse	Origin of Plants	Seawater × Origin
max shoot length	F = 34.228; $p < 0.001$	F = 27.787; $p < 0.001$	F = 5.864; $p < 0.05$
mean shoot length	F = 23.838; $p < 0.001$	F = 31.651; $p < 0.001$	F = 3.077; n.s.
total shoot length	F = 44.077; $p < 0.001$	F = 0.0137; n.s.	F = 2.110; n.s.
shoot number	F = 18.100; $p < 0.001$	F = 20.992; $p < 0.001$	F = 0.529; n.s.
leaf number	F = 39.138; $p < 0.001$	F = 5.147; $p < 0.05$	F = 2.665; n.s.
leaf/shoot ratio	F = 29.039; $p < 0.001$	F = 7.095; $p < 0.01$	F = 16.317 $p < 0.001$

Salix alba's total shoot length (Table 3; Figure 2E) decreased with increasing seawater flooding level. The level of seawater flooding was highly significant ($p < 0.001$) between all, including between the control and both soil and complete flooding as well as between soil and complete flooding.

The shoot number (Table 3; Figure 2G) was higher in the control compared to soil ($p < 0.05$) and complete flooding ($p < 0.001$). Plants in soil flooding developed more shoots compared to those in complete flooding ($p < 0.003$). *Salix alba* from the Elbe estuary developed more shoots compared to plants from the Eastern Scheldt ($p < 0.001$).

Plants in the control developed significantly ($p < 0.001$) more leaves than those in soil flooding and complete flooding with seawater, and plants in soil flooding performed better than those in complete flooding ($p < 0.001$) (Table 3; Figure 2I).

In the leaf/shoot ratio (Table 3; Figure 2K), the difference was highly significant ($p < 0.001$) between both the control and soil flooding and complete flooding. The leaf/shoot ratio was significantly ($p < 0.05$) higher in soil flooding compared to complete flooding. The origin of the plants had a significant effect on the leaf/shoot ratio in the control ($p < 0.001$), but not in soil flooding or complete flooding. The leaf/shoot ratio of *S. alba* from the Elbe estuary was not significantly different between any of the seawater flooding levels. However, the leaf/shoot ratio of *S. alba* plants from the Eastern Scheldt decreased significantly ($p < 0.001$) between the control, soil flooding, and complete flooding and between soil flooding and complete flooding with seawater.

3.2.2. Growth Parameters in May

The maximum shoot length (Table 4; Figure 2B) decreased between both the control and soil ($p < 0.001$) as well as complete flooding ($p < 0.001$). *S. alba* from both the Elbe estuary and the Eastern Scheldt performed better in the control compared to soil flooding and complete flooding with seawater ($p < 0.01$), but no differences in maximal shoot length between soil and complete flooding were observed.

The mean shoot length (Table 4; Figure 2D) decreased with increasing seawater flooding between the control, soil, and complete flooding ($p < 0.001$) and was significantly higher in the plants from the Eastern Scheldt ($p < 0.01$). This difference was valid for the control ($p < 0.001$) but not in soil or complete flooding. Highly significant ($p < 0.001$) differences in mean shoot length of *S. alba* from the Eastern Scheldt were found between the control, soil, and complete flooding.

Total shoot length (Table 4; Figure 2F) decreased highly significantly ($p < 0.001$) with increasing seawater flooding level between the control, soil, and complete flooding and between soil and complete flooding. Cuttings from the Elbe estuary developed larger total shoot length compared to plants from the Eastern Scheldt ($p < 0.001$) whereas the difference was significant in soil flooding ($p < 0.01$) and complete flooding ($p < 0.001$) but not in the control. Total shoot length of *S. alba* from the Elbe estuary was larger in the control compared to complete flooding ($p < 0.001$) whereas for those from the Eastern Scheldt the decrease in total shoot length was highly significant ($p < 0.001$) between the control, soil, and complete flooding and between soil flooding and complete flooding with seawater ($p < 0.01$).

Table 4. Results of a two-factorial ANOVA on morphological parameters recorded in May in a mesocosm experiment on the effects of seawater pulses on juvenile *Salix alba* trees in the dormant stage (November 2022–May 2023); cuttings originating from tidal freshwater wetlands of the Elbe estuary versus revetment at the polyhaline site of the Eastern Scheldt. Seawater pulse treatments were applied twice, lasting for 2 days (5–6 December; 2–3 February) and corresponding to the average occurrence of storm surges in the southern North Sea [33]. N = 4.

	Seawater Pulse	**Origin of Plants**	**Seawater × Origin**
max shoot length	F = 43.186; $p < 0.001$	F = 0.661; n.s.	F = 6.226; $p < 0.01$
mean shoot length	F = 17.617; $p < 0.001$	F = 7.319; $p < 0.01$	F = 4.798; $p < 0.01$
total shoot length	F = 38.543; $p < 0.001$	F = 16.117; $p < 0.001$	F = 4.766; $p < 0.01$
shoot number	F = 10.550; $p < 0.001$	F = 38.301; $p < 0.001$	F = 0.915; n.s.
leaf number	F = 17.309; $p < 0.001$	F = 35.838; $p < 0.001$	F = 0.801; n.s.
leaf/shoot ratio	F = 7.437; $p < 0.001$	F = 0.787; n.s.	F = 1.471; n.s.

The number of shoots (Table 4; Figure 2H) decreased with increasing flooding level between the control and complete flooding and between soil flooding and complete flooding ($p < 0.001$) but not between the control and soil flooding. Complete flooding ($p < 0.01$) caused higher shoot numbers in plants with origin from the Elbe estuary compared to those from the Eastern Scheldt ($p < 0.001$).

In the control, the number of leaves (Table 4; Figure 2J) was significantly higher in comparison to soil ($p < 0.03$) and complete flooding ($p < 0.001$) and between soil and complete flooding ($p < 0.001$). *Salix alba* from the Elbe estuary developed more leaves in the control ($p < 0.01$), in soil flooding ($p < 0.01$), and in complete flooding with seawater ($p < 0.001$) compared to plants from the Eastern Scheldt. The factor of seawater flooding led to significantly fewer leaves in *S. alba* from the Elbe estuary only in the control compared to complete flooding ($p < 0.01$). The leaf number was also reduced in *S. alba* from the Eastern Scheldt in the control compared to complete flooding ($p < 0.001$) and between soil and complete flooding ($p < 0.01$).

The leaf/shoot ratio (Table 4; Figure 2L) significantly decreased with increasing seawater flooding between the control and complete flooding ($p < 0.001$), but not between the control and soil flooding. However, between soil and complete flooding, a significant difference in leaf/shoot ratio was observed ($p < 0.05$).

3.3. Aboveground and Belowground Dry Mass

The aboveground (leaf; shoot) and belowground (roots) dry masses were measured and recorded (Figure 3). To account for possible differences in the cuttings' initial biomass, which might affect the dry mass, ANCOVAs were applied, whereas the initially measured cutting biomass was included as a covariate.

The effect of the different seawater flooding treatment levels on the leaf dry mass (Figure 3A) did not depend on the covariate initial biomass of the cutting. However, the leaf dry mass decreased significantly with increasing seawater flooding ($p < 0.001$). Compared to the control (mean 2.89), the leaf dry mass was lower in soil flooding (mean 1.77; $p < 0.001$) and further decreased in complete flooding (mean 0.89; $p < 0.001$); a significant difference was also detected between soil and complete flooding ($p < 0.01$). The effect of origin on leaf dry mass did not depend on the covariate initial biomass of the cutting, nor was a significant effect found between the leaf dry mass from the Elbe estuary (mean 2.17) and that from the Eastern Scheldt (mean 1.53).

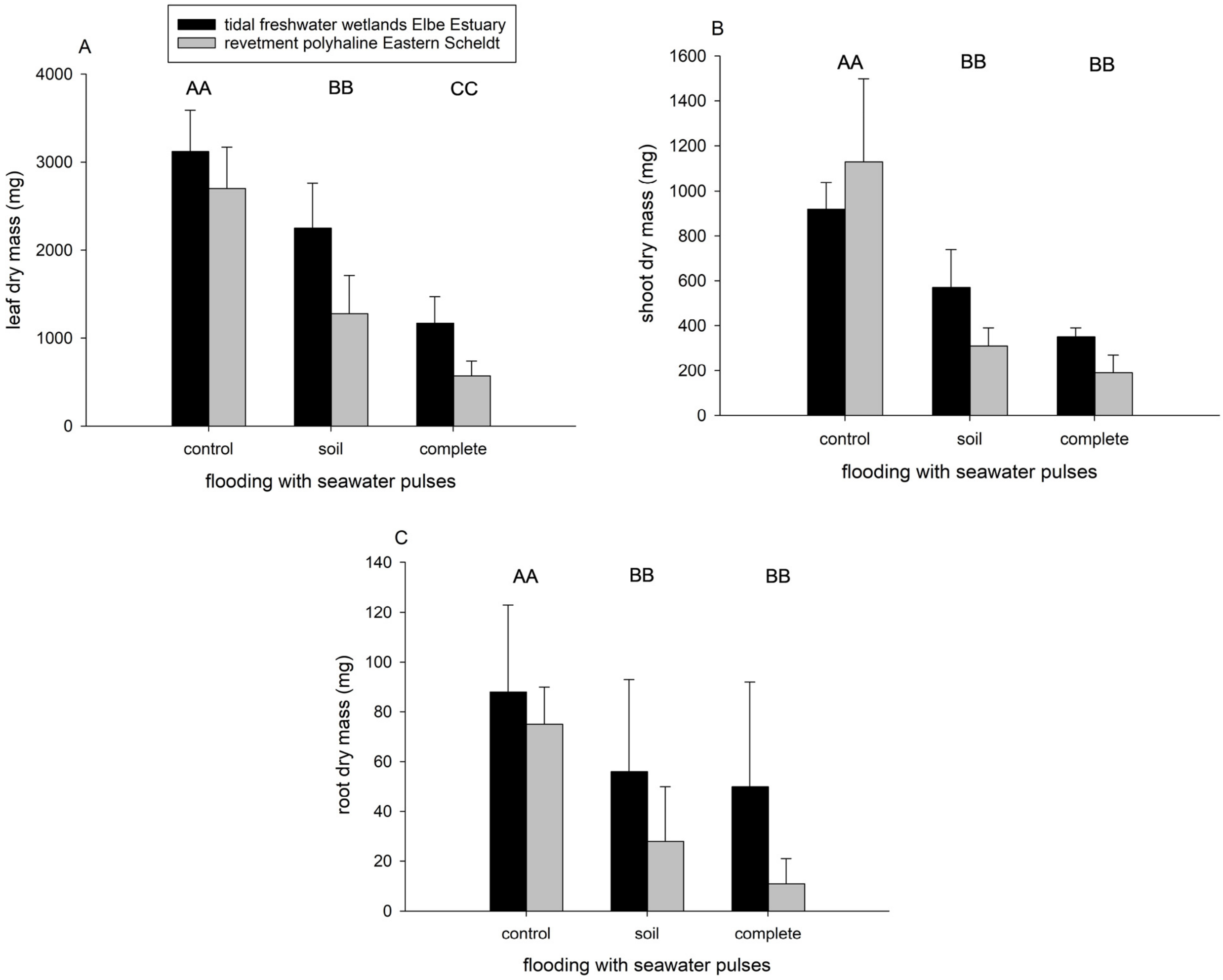

Figure 3. Dry mass of (**A**) leaf, (**B**) shoot, and (**C**) root of juvenile *Salix alba* specimens in a mesocosm experiment on the effects of seawater pulses in the dormant season (November 2022–May 2023); (i) two 2-day seawater flooding treatments at three flooding levels: no flooding (control), flooding of the belowground biomass (soil), and flooding of the aboveground and belowground biomass (complete); (ii) cuttings originating from tidal freshwater wetlands of the Elbe estuary versus revetment at the polyhaline site of the Eastern Scheldt. Seawater pulse was applied twice, lasting for two days (5–6 December; 2–3 February) and corresponding to the average annual occurrence of storm surges in the southern North Sea 2009–2022 recorded by the Federal Maritime and Hydrographic Agency; GER [33]; N = 4; mean ± SD.

The shoot dry mass at the different seawater flooding levels (Figure 3B) did not depend on the value of the covariate initial biomass of the cutting, nor on the plant origin. However, the effect of seawater flooding level on the shoot dry mass was significant ($p < 0.001$). In both soil flooding (mean 0.44; $p < 0.001$) and complete flooding (mean 0.33; $p < 0.001$), the shoot dry mass decreased significantly compared to the control (mean 1.02), but no effect between soil and complete flooding was detected. The origin of the cuttings from the Elbe estuary (mean 0.56) and the Eastern Scheldt (mean 0.64) did not affect the shoot dry mass significantly.

The effect of seawater flooding level on root dry mass (Figure 3C) did not depend on the value of the initial biomass of the cutting, and there was no significant effect between the flooding level and the covariate. However, a significant effect of flooding level on root dry mass was detected ($p < 0.01$). The root dry mass decreased significantly between the control (mean 78.94), soil flooding (mean 40.91; $p < 0.05$), and complete flooding (mean 34.50; $p < 0.05$). However, no significant effect on root dry mass was detected in the comparison of soil and complete flooding. Regarding the origins of the cuttings, neither a significant effect of covariate initial biomass nor a significant effect between the origins of Elbe estuary (mean 64.67) and Eastern Scheldt (mean 38.24) on root dry mass was detected.

4. Discussion

We studied the effects of seawater pulses corresponding to storm surges on the floodplain riparian forest foundation species *Salix alba* in the dormant winter stage with implications for conservation, restoration, and new options for flood defense. Our results showed that twice-applied two-day seawater pulses during winter lead to increasing salinity in the soil where vegetative propagules were placed in autumn. However, 95% of the juvenile *S. alba* trees in the pots placed in the seawater pulse treatment developed roots, shoots, and leaves in the following spring, indicating that *S. alba* is resilient to seawater pulses applied in winter. Corresponding to our results, salinity was determined as the main stress factor limiting the initial growth and biomass production of *S. alba* hybrids in a study that showed that the combination of waterlogging and salinity did not affect biomass production more than a sole salinity treatment, with differing results of resilience among different *Salix* hybrids [34]. This was confirmed by [26], whose results showed an inhibition of *S. alba* hybrid growth and root development at high salinity (10 dS/m) in a 120-day treatment in hydroponics.

4.1. Growth of the Juvenile S. alba Trees

Of the 168 juvenile *S. alba* trees that were treated with seawater in our experiment, 159 developed leaves and shoots, but 6 juvenile *S. alba* plants did not establish or develop shoots and roots. The shoot length decreased with increasing seawater flooding both in April and in May, but the maximal, mean, and total shoot length was generally higher in May compared to April, indicating that plants continuously grew after the seawater treatment in winter. In a three-month salt treatment on hybrid and native juvenile *Salix*, the shoot growth was not significantly affected by 7 dS/m, and the plants recovered from delayed growth in the early stage by the final stage at the end of the treatment [30]. Shoot growth rates were inhibited by high salinity (14 dS/m treatment), whereas hybrid willows did not recover; however, for native willows, the early height reduction was partially reversed by the final stage of the treatment, but still about 50% less compared to the control. This corresponds to our results, in which the decreased shoot length of the plants that were treated with seawater pulses can be interpreted as delayed but not inhibited shoot growth. However, the more often harsh salt pulses (16 dS/m) were applied to *Salix* hybrids, the more the shoot length decreased in ten experimentally studied clones [31], whereas *S. alba* and *S. alba* hybrids performed best, with *S. matsudana x S. alba* performing even better compared to *S. alba* and *S. babylonica x S. alba*. We also found effects of the origin of the studied *S. alba*, with differences between trees originating from the revetment at the polyhaline Eastern Scheldt and tidal freshwater wetlands of the Elbe estuary. Juvenile *S. alba* originating from the Eastern Scheldt showed a larger maximum and mean shoot length in the control compared to those from the Elbe estuary. However, the latter developed more shoots and a correspondingly larger total shoot length in both semi- and complete flooding at the final stage of the experiment. This may indicate a negative predisposition of the juvenile *S. alba* from the polyhaline Eastern Scheldt.

In a long-term salt treatment [30], the leaf number decreased with increasing salinity, whereas hybrid willows developed more leaves at the low and high salinity levels, as well as the control compared to native willows. Similarly, our results showed a general increase in leaf number in May compared to April, but an overall decrease in leaf number with increasing seawater pulse flooding level. In the early stage of sprouting after winter, the origin did not affect the leaf number. However, at the final stage in May, juvenile *S. alba* originating from the tidal freshwater wetlands of the Elbe estuary developed more leaves in soil and complete flooding with seawater as well as in the control, again indicating a better performance. In terms of an application for flood defense, the contribution of leaves to the crucial frontal surface area is limited since under wave loads, *S. alba* leaves adopt a stream-wise position, with the smallest frontal area facing the stream [6]. Thus, the reduced leaf number of juvenile *S. alba* after seawater pulses does not indicate a reduced value for flood defense.

4.2. Aboveground and Belowground Dry Mass of the Juvenile Salix alba Trees

Although 95% of the juvenile *S. alba* trees developed leaves, the two 2-day seawater pulses reduced the leaf dry mass significantly in our experiment. This corresponds to another study [28] that showed a reduced photosynthetic capacity of *S. alba* leaves under the high salt stress of 342 mM NaCl and higher, which triggered photoinhibition and led to damage of the leaves, which was not true for the application of low salt concentrations like 171 mM NaCl. *Salix alba* showed moderate drought and salinity tolerance, indicating that this *Salix* species can withstand a salt concentration of at least up to 5 dS/m in the long term [27]. Other species like *Salix matsudana* Koidz are resilient to higher salinity levels of up to 13.8 dS/m [35], and the *S. matsudana x S. alba* hybrid was even resilient to a 45-day salinity treatment [29]. Regarding the aboveground shoot dry mass, salinity was considered as the primary factor for limited biomass production [28]. Shoot dry mass decreased by 50% in moderate (5 dS/m) treatments and by 70% in high-salinity (10 dS/m) treatments. The reduced biomass production differed among the studied *Salix* clones (*Salix matsudana* × *Salix alba*; *Salix babylonica x Salix alba*) in their long-term hydroponics experiment. In our experiment, more than 95% of the studied plants developed shoots, which may be due to the shorter duration of the seawater pulse during the dormant stage. However, the shoot dry mass was decreased due to seawater pulses, but there was no difference between the origins of the juvenile *S. alba* trees.

Salinity led to decreased root development in cuttings from different *Salix* hybrids. At higher salinity levels (10 dS/m), rooting was totally inhibited, and it was limited at a moderate salinity level (5 dS/m). However, waterlogging ameliorated this salinity effect in some genotypes in a 120-day hydroponics experiment [34]. This corresponds to the decreased root dry mass with increased flooding level between the control and both soil and complete flooding in our experiment. However, after the short-term seawater pulses in winter, in none of our juvenile *S. alba* trees was root development totally inhibited. All plants developed roots, indicating differing effects of short-term salt pulses in our seawater treatment compared to long-lasting salinity in other experiments. Treatment in hydroponics may have an additional negative effect on *Salix* root biomass development compared to root growth in the soil, which corresponds more closely to natural field conditions. Moreover, the root dry mass was generally low at all flooding levels in our experiment, ultimately due to the short time for establishment from winter to May 2022. Although the root development differed among treatments, another experiment [26] on *S. alba* showed the trend that low salinity even stimulated root growth, whereas under high salt-stress, root growth decreased but was still present. In that study, cuttings were treated with NaCl concentrations of 171 mmol, 342 mmol, 513 mmol, and 684 mmol for 20 days in hydroponics. To the contrary, we applied a full load of seawater to *S. alba* cuttings twice for a short time period of two days. The root growth ultimately decreased less due to the seawater pulse and more due to the remaining salinity in the soil water of the pots where the juvenile trees developed. In the field, seawater that intrudes in the soil during storm surges in winter will be more thoroughly washed out during heavy rainfalls and may have less of an effect on the sprouting of *S. alba* during spring.

Salix alba even shows an ability to self-regulate and adapt to salt stress by intercepting Na^+ in the roots, improving the selective absorption of K^+ and Ca^{2+} and the transport capacity to the aboveground plant parts [28]. Even leaf abscission would not affect *S. alba* negatively. Floodplain *Salix* are adapted to flooding disturbance and regenerate after the loss of plant parts [4]. Moreover, the biomass production of *Salix* hybrids was higher the shorter a salt treatment lasted [31], with even 100% survival of juvenile *S. alba* trees in the highest experimentally applied salinity. This corresponds to our results of 95% established juvenile trees, indicating a resilience of *S. alba* to brief seawater pulses corresponding to the effects of winter storm surges when the floodplain trees are in the dormant stage.

5. Conclusions

Salix alba is a floodplain riparian forest foundation species that is resilient to seawater-pulses affecting the trees during the dormant stage in winter when storm surges usually occur. More than 95% of juvenile *S. alba* were established after seawater pulses in the spring. The decrease in shoot growth and leaf and root development in our experiment may be due to the delayed development of seawater-affected trees rather than reduced sprouting capacity. In a large-scale wave channel experiment, *Salix alba* showed a high wave attenuation capacity even with reduced leaf and shoot canopy [20]. The ability of living juvenile willows to contribute to flood defense may have even been enhanced due to canopy permeability during winter, while shoot bending capacity remained active, which resulted in less turbulence and shear stress on the sediment [7]. Cuttings originating from the tidal freshwater wetlands of the Elbe estuary developed longer shoots and more leaves, resulting in a higher aboveground dry mass and indicating a better suitability to withstanding seawater pulses. However, caution should be taken before the application of *S. alba* as a NbS in foreshore riparian and estuarine habitats. It is not clear whether male or female individuals of *S. alba* are able to withstand seawater pulses differently or whether there is an advantage to planting both over individuals of one sex or the other. More investigations with upscaling experiments with respect to local conditions are needed to test the value of *S. alba* in riparian and estuarine systems as a new option for flood defense. Based on our results, we suggest the science-based restoration of *Salix alba* floodplain forests in upstream tidal freshwater wetlands and their establishment in downstream reaches where seawater pulses can affect the *Salix alba* floodplain forests during the dormant stage in winter. The enhancement of the lowest naturally occurring *Salix alba* floodplain forest habitats and the flood control potential should be accompanied by scientific research. As a nature-based solution, the restoration and establishment of *Salix alba* floodplain forests in tidal wetlands could also contribute to mitigating climate change and sea level rise influences and enhancing floodplain biodiversity.

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