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Historic Human-Induced Species Shift Increases Climate Sensitivity of Today's Western European Floodplain Forests: Restoring Past Conditions for Future Resilience

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ABSTRACT

1. In many estuaries worldwide, climate change and human interventions are driving saltwater upstream. This increase in salinity can threaten temperate tidal floodplain forests, generally dominated by (cultivated) willow species, by reducing tree growth, increasing mortality and reducing key ecosystem services such as flood protection. Knowledge on how temperate tidal floodplain forests respond to saltwater intrusion is largely lacking.
2. This study analysed two common freshwater trees: *Salix alba* and *Alnus glutinosa*. *Salix alba* has been widely cultivated in tidal wetlands for centuries for harvesting its flexible twigs and branches, while *Alnus glutinosa* was historically dominant but is currently a minor inhabitant of many semi-natural tidal forests. We subjected both species to a combination of two flooding regimes, three different salt concentrations and two durations of salt stress.
3. Surprisingly, our results indicate that the historically dominant *Alnus glutinosa* exhibited a higher height growth and number of leaves in salt and tidal conditions compared to *Salix alba*. While tidal conditions enhanced the growth and survival of *Salix alba*, they had no significant effect on *Alnus glutinosa*, which consistently outperformed *Salix alba* regardless of tidal influence.
4. Our results underscore the adaptability of *Alnus glutinosa* to increasing salt intrusion and inundation expected with rising sea levels. They also highlight that conservation efforts aimed solely at preserving willow stands that became dominant due to historical horticultural practices may inadvertently diminish wetland resilience to climate change.

1 | Introduction

Worldwide, estuaries are increasingly affected by saltwater intrusion, driven by both climate change and human activities (Herbert et al. 2015). Climate change can lead to saltwater intrusion into the freshwater parts of estuaries as a result

of sea-level rise, more frequent storm surges and increased frequency and duration of extreme droughts, reducing freshwater input from the river and favouring the upstream movement of seawater. Meanwhile, direct human actions such as dredging to deepen navigation channels, groundwater extraction and river diversion can further exacerbate saltwater intrusion

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(Herbert et al. 2015; Tully et al. 2019). As a result, freshwater wetlands like tidal floodplain forests, which are globally rare and endangered (Havrdova et al. 2023), may face adverse consequences. Recognising the critical role these ecosystems play in biodiversity and ecosystem services, the European Union protects the remaining floodplain forests under the European Habitats Directive, which ensures their conservation and restoration (Council Directive 92/43/EEC 1992; Verhoeven 2014). However, regular habitat assessments conducted by Member States since 2001 reveal a trend towards 'unfavourable bad' for the majority of the floodplain forests (Article 17 web tool, n.d.), highlighting the vulnerability of these habitats and the need for continued conservation efforts.

In the tidal freshwater floodplain forests of the densely populated Rhine-Meuse estuary in NW-Europe, the originally dominant tree species have in the past been largely replaced by white willow (*Salix alba*) cultivations for use in basketry and land reclamation (Paalvast and van der Velde 2014; Struyf et al. 2009). In contrast, historic floodplain forests were dominated by black alder (*Alnus glutinosa*), with willow species like *Salix alba* and *Salix fragilis* and reed beds (*Phragmites australis*) co-occurring (Pierik et al. 2022; Vos 2015). The present dominant white willow stands are no longer economically profitable for basketry and land reclamation and have undergone a strong decline in biodiversity, with only a small fraction of them serving as man-made wetlands for conservation purposes and cultural heritage (Paalvast and van der Velde 2014; PDN/2010–108 2010; van den Bergh et al. 2009). As a consequence, these previously cultivated areas are now often left unmanaged, allowing the trees to grow unchecked, reaching heights of 10–15 m and increasing their vulnerability to storms (Struyf et al. 2009).

Negative impacts of salt intrusion can lead to tidal floodplain forests degradation, leading to a decline in ecosystem services such as flood defence by wave attenuation (van Wesenbeeck et al. 2022) and carbon sequestration (Herbert et al. 2015; Tully et al. 2019; White and Kaplan 2017). While floodplain forests and tidal wetlands have been proposed as nature-based solutions for flood protection (Borsje et al. 2011; Jakubínský et al. 2021; van Wesenbeeck et al. 2022), uncertainties in their susceptibility to saltwater have led some authors to suggest stimulating the establishment of more salt-resistant species in these areas (Van Coppenolle and Temmerman 2019). Additionally, studies on salt marsh species have demonstrated that flood protection capability depends on stem flexibility and breakability, highlighting species and wave exposure as influential factors rather than salinity, inundation or location (Silinski et al. 2018; Zhu et al. 2020). However, few studies have analysed the influence of salinity on these properties in freshwater species (but see Markus-Michalczyk et al. 2019). Given the significant variation in sensitivity to salt stress among species (Conner et al. 1997; Tolliver et al. 1997; White and Kaplan 2017), the dominance of a single species in these areas potentially increases vulnerability to saltwater intrusion compared to naturally diverse forests. Additionally, factors such as the intensity and duration of saltwater exposure, as well as altered hydrology (e.g., flooding and drought), play crucial roles in determining tree sensitivity to saltwater (Conner et al. 1997; Tolliver et al. 1997; White and Kaplan 2017),

although their precise role remains not fully understood (Herbert et al. 2015). For example, Li and Pennings (2018b) found that a longer duration of salinity exposure decreased aboveground biomass of herbaceous plants, but not for all species. Large differences between species are also found in response to flooding conditions (Conner et al. 1997), with a longer duration of tidal flooding leading to reduced plant growth (Markus-Michalczyk et al. 2019). How to manage current day, willow-dominated floodplain forests under increasing salinity stress is an ongoing concern. In-depth understanding of the response to both lethal and sub-lethal salt stress and its interaction with other stressors for various wetland tree species is thus essential for effectively protecting the last estuarine floodplain forests and determining their viability as a nature-based solution against salt intrusion.

The objective of this study is to determine the effect of different environmental variables (salinity concentration, salinity duration and the presence/absence of tidal inundation) on tree response to salt stress, comparing the two trees historically most common to European floodplain forests: *Salix alba* and *Alnus glutinosa*. We used a mesocosm study with a factorial setup to have full control over the test variables. We based the chosen salinity concentrations (2 and 5 PSU) on data we recorded as part of this study in tidal floodplain forests in the Rhine-Meuse estuary and on values found in literature. We varied the duration of the salt stress to understand how a storm surge (shorter salt stress, mimicked by 7 days per month exposure) affects trees differently than a drought (longer salt stress, mimicked by continuous exposure). Tides were added to understand how the fluctuating water levels found in tidal freshwater wetlands might help restore the system after a salt intrusion event and lead to higher vegetation survival. We hypothesised that (1) the duration of salt intrusion significantly affects plant response to salt stress, (2) tides can help alleviate salt stress, (3) salinity and tides might modify stem flexibility and consequently flood protection and (4) the human-selected and now dominant willow species (*S. alba*) may not be the most salt-tolerant species that can live in these areas, suggesting that human cultivation has made floodplain forests less climate-resilient by the gradual removal of *A. glutinosa*.

2 | Methods

2.1 | Field Observations to Obtain Reference Values

To obtain insight into the stress levels occurring during saltwater intrusion in freshwater wetlands, we selected a tidal floodplain forest along the Rhine-Meuse estuary close to the brackish-freshwater boundary (Visserijgriend 51°51'22.4" N 4°20'49.9" E). This forest is a former site of willow cultivation and has typical freshwater vegetation with *S. alba* as the dominant species. Here we installed a saltwater conductivity logger (HOBO U24-002-C, Onset, Bourne, MA, USA) close to the main channel entering the forest to record conductivity in mS/cm. The instrument was deployed from 21 July 2022 to 23 June 2023. Subsequently, the data was calibrated using HOBOWare software (Onset, Bourne, MA, USA) and converted to PSU using the gsw package in Python (McDougall and Barker 2011).

The observations of salt levels in the Visserijgriend floodplain forest were found to vary between 0 and 11 PSU, the latter value being equivalent to 1/3 of seawater. Salinities in the wetland remained below 2 PSU for 81% of the recorded days, between 2 and 5 for 14% and above 5 for 5% of the recorded days (Figure S1). Therefore, while this field site predominantly maintains freshwater conditions, during saltwater intrusion events it encounters salinity levels comparable to those used in this experiment: that is, 2 and 5 PSU.

2.2 | Manipulative Salt Stress Experimental Design

From April 2022 to September 2022, we conducted a mesocosm experiment at the Royal Netherlands Institute for Sea Research (NIOZ) in Yerseke, the Netherlands (51°29'17.8" N 4°03'25.9" E), to test the sensitivity of *Salix alba* L. and *Alnus glutinosa* (L.) Gaertn. to salt stress. These species were selected due to their current and historically widespread presence in European floodplain forests: *S. alba* is the dominant species in current day willow plantations while *A. glutinosa* was historically prevalent before the rise of willow cultivation (Struyf et al. 2009; Vos 2015). Both species are well adapted to wetland environments, thriving along river margins where periodic flooding facilitates seedling establishment and forest regeneration. They share similar water and light demands (Claessens et al. 2010; Karrenberg et al. 2002), but *A. glutinosa* has the unique ability to fix nitrogen through a symbiotic relationship with *Frankia* bacteria (Claessens et al. 2010). Since both species are deciduous, we conducted the experiment during the growing season, completing it before leaf fall. Despite their prevalence, there is little consensus on their salt tolerance; while some studies suggest that *S. alba* is not salt tolerant (Markus-Michalczyk et al. 2019), there are conflicting reports for *A. glutinosa*, describing it as either not tolerant or mildly tolerant (Buschbom 1968; Deptuła et al. 2020; Dirr 1976). We bought juvenile trees at a local tree nursery (Boomkwekerij De Bruyn bv, Begijnendijk, Belgium), to assure comparable morphological characteristics within species. These trees were around 2–3 years old and ranged in height between 70–90 cm for *A. glutinosa* and 110–125 cm for *S. alba*. While there is no consensus on salt tolerance during germination, research has shown that salt tolerance increases with tree age, with juvenile trees being more sensitive than mature trees (Kozłowski 1997; Niknam and McComb 2000). By using juvenile trees rather than adult trees, we can obtain a conservative estimate for the salt tolerance of the species studied. We planted the trees—one tree per pot—in pots (20×20×24 cm) with potting soil containing 10% organic carbon and total Nitrogen-Phosphate-Potassium as 3.7, 1.61 and 4.5 g/kg respectively (Terraflin BV, Grijpskerke, Netherlands). This substrate has a similar organic carbon and nutrient content to floodplain forest soils, but a larger grain size. A larger grain size is needed when growing trees in pots, as the clay soils found in floodplain forests would suffocate roots in mesocosm experiments due to their small grain size and increased soil compaction when used in pots.

We exposed the trees to a combination of two tidal regimes (tidal and non-tidal), three different salt concentrations (freshwater, 2 PSU and 5 PSU) and two durations of salt stress (continuously exposed to saltwater versus periodically 1 week each month, Figure 1). For the treatments, we used filtered seawater from the

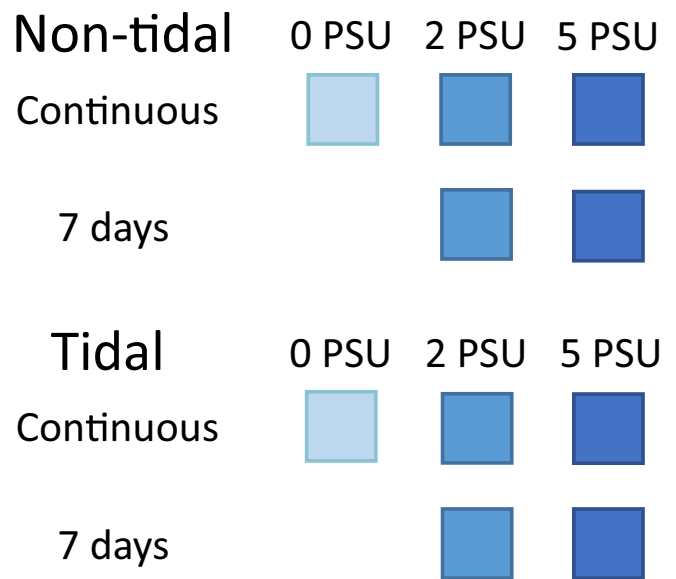


FIGURE 1 | Experimental setup. Each square indicates a different treatment; rows indicate the duration of the salt stress (continuous or 7 days each month) for both tidal and non-tidal conditions, while columns indicate salinity (0 PSU indicating freshwater, 2 PSU and 5 PSU).

nearby Eastern Scheldt estuary and mixed it with tap water to achieve the correct salinity. The periodical exposure to salt stress of 7 days per month was to simulate occasional and temporary salt intrusion, occurring during exceptional high tides or storm surges. The highest salt concentration employed was 5 PSU, which was previously observed as a survival threshold for freshwater trees (Markus-Michalczyk et al. 2014; Tolliver et al. 1997). The 2 PSU was used as an intermediate salinity and often occurs in the field (Figure S1). Finally, freshwater was used as the control treatment. The experimental design was full factorial, meaning that all possible treatment combinations were present. We randomly placed four trees of each species in mesocosms, resulting in 8 trees per mesocosm. For logistical reasons, we had to place more than one plant in the same mesocosm. To overcome this problem, we used two mesocosms to replicate each treatment and reduced interactions between individuals by planting one plant per pot.

Each mesocosm (dimensions 110×90×60 cm) consisted of either a single tank or two tanks placed on top of each other in order to simulate the tidal regimes (cf. Cao et al. 2017). The upper tank contained the plants and the lower one served as water storage. The two tanks were connected by tubes, and the high and low water levels were controlled by the position of the tubes in the upper tanks. Pumps in the lower tank transferred the water from the lower compartment to the upper one, and a timer allowed control of the inundation time: 6 h high water alternated by 6 h low water. During low tide, the water submerged only the lower half of the pot (i.e., 12 cm deep), while during high tide, the water completely submerged the pots (i.e., 24 cm deep), covering the soil surface. In the non-tidal treatment, the pots were continuously partly submerged at a fixed water level (i.e., 12 cm deep) reaching half the pot height (i.e., 24 cm tall).

Salt concentrations were weekly checked with a salinity meter (HI98319 Hanna Marine Salinity Tester, Nieuwegein,

Netherlands) to control the treatment salinity in case of rain or evaporation. In the periodic treatment, saltwater was added to the mesocosm around the first week of the month. At the end of the week, the saltwater was pumped out, the mesocosms rinsed until the water became fresh and then filled up again with freshwater.

2.3 | Data Collection on Plant Growth and Salinity Treatments

A series of measures were taken monthly: tree height and diameter, number of leaves, soil and water salinity. As soil level varied between pots and over time due to compaction and plant growth, we measured the height of the trees relative to the rim of the pot to the highest point. In this way, all measures would start from a level common to all plants. For the same reason, tree diameter was measured at the height of the rim of the pot. To account for possible variability in leaf number between branches, we counted the number of leaves in two areas along the trunk, both of which included several branches. Both areas were 10 cm in size, the first between 10 and 20 cm from the highest point of the plant and the second between 10 and 20 cm from the edge of the pot. To estimate the health of the plants throughout the experiment, we counted the leaves categorised in three levels: completely healthy if without any visible damage, damaged if any signs of damage or colour alteration were present and dead if no green parts were present. This method did not take into account any dead leaves that may have fallen. Soil salinity and water salinity were measured with an EC-meter (EC1200, Nieuwkoop BV, Aalsmeer, Netherlands). As the tidal and non-tidal treatments could have resulted in different soil salinities in the upper part of the pot compared to the lower part of the pot, we took two measurements in each pot: one in the first few cm of topsoil and the second at the bottom of the pot.

In October, three quarters of the plants were harvested and the above- and belowground biomass retrieved. To investigate the influence of salt stress on stem flexibility, we collected the upper 20 cm and the lower 20 cm of each harvested plant and tested them for biomechanical parameters with an Instron electro-mechanical universal testing machine (Instron 5900 Universal Testing System, Norwood, MA, USA) and the manufacturer software (Bluehill Universal for Universal Testing Systems, Norwood, MA, USA). The maximum stem stress and strain were calculated with a three-point bending test, in a setup similar to Markus-Michalczyk et al. (2019) and Zhu et al. (2020). The distance between support points was set as 15 times the stem diameter. While harvesting the belowground biomass, the upper 12 cm of the root system was collected separately from the lower 12 cm to consider differences in water level during the treatment. The roots were washed to remove the soil, both above- and belowground biomass were weighed, dried at 60°C to constant mass and weighed again to get fresh and dry weight.

2.4 | Data Analysis

To assess how different treatment combinations affected tree growth during the growing season, we calculated the difference in diameter and height between the first measure (April) and the last measure (September). Since species varied greatly in the number of leaves present, direct comparisons were not feasible.

Therefore, we designed an index, the Leaf Health Index, to normalise the number of leaves and enable comparisons. This index assigns weights to the number of leaves based on their health: 1 for healthy leaves, 0.5 for damaged and -1 for dead leaves. The weighted leaves are then summed, and the total divided by the total number of leaves (Equation 1). If no leaves were present on the plant, we assigned an index value of -1. This ensured the index varied between 1 (all healthy leaves) and -1 (no leaves present or all dead). All weights are nonzero to ensure all counted leaves are considered in the calculation. These values were chosen to rank each leaf's contribution to plant health. In particular, healthy plants have a weight of 1 because their entire surface can still photosynthesise and contribute to plant health, while damaged leaves have a value of 0.5 because they contribute less to plant health than healthy leaves. Dead leaves have a weight of -1 because they are a symptom of stress; thus, a decrease in the index value indicates the impact of environmental stress on plants. By comparing the index values of the salinity treatments with the freshwater conditions, we can understand the effect of salt stress on the plants and exclude damage from other sources, such as insects. If the increased stress caused by the salinity treatments resulted in increased insect damage, we considered this damage to be part of the indirect effects of salt stress and therefore suitable for inclusion in the index calculation.

Leaf Health Index

$$= \frac{1 * \text{healthy leaves} + 0.5 * \text{damaged leaves} - 1 * \text{dead leaves}}{\text{total number of leaves}} \quad (1)$$

The slope-extension plots produced by the bending test were used to calculate key parameters: modulus of rupture (MOR, N/mm), modulus of elasticity (MOE, N/mm) and flexural stiffness (EI, N mm³). MOE was calculated as the slope of the linear part of the stress-strain curve. MOR and EI were calculated as follows, (Santini et al. 2013)

$$\text{MOR} = \frac{F_{\max} L}{\pi R^3} \quad (2)$$

$$\text{EI} = \frac{\text{MOE} \pi R^4}{4} \quad (3)$$

where $F_{\max}$ is the maximum load (N), L is the distance between support points (mm) and R is the specimen diameter (mm). MOR indicates the force necessary to plastically deform the stems (resulting in permanent deformation), whereas MOE reflects the force required to elastically deform the stems (resulting in temporary deformation).

All statistical analyses were performed with R Statistical Software (v4.2.2; R Core Team 2022). A linear mixed model was applied to all parameters (tree growth in height, Leaf Health Index, soil salinity in both layers, aboveground biomass and belowground biomass in both soil layers, MOE, MOR and EI) to compare differences between treatments, with species, salinity, tidal regime and their interactions as fixed variables and the mesocosm as a random variable. The biomass, MOE, MOR and EI values were first log transformed to achieve normality and homoscedasticity. An additional linear mixed model was performed for each single species, with tidal regime, salinity and their interaction as fixed variables and the mesocosm as a random variable.

3 | Results

3.1 | Salinity Levels by Treatment

The soil salinity showed significant differences between salinity treatments, with soil salinity in both soil layers increasing in the sequence: freshwater (mean 0.8 mS/cm), temporary salinity treatment (mean 1.1 mS/cm for the 2 PSU 7 days/month treatment and 1.32 mS/cm for the 5 PSU 7 days/month treatment), and continuous salinity treatment (mean 1.46 mS/cm for the 2 PSU treatment and 2.51 mS/cm for the 5 PSU treatment, Figure 2A for the upper layer and Figure S2A for the lower layer). Tides were found to have a significant effect only on the upper layer (Table 1), with higher salinities recorded in the non-tidal

treatments. Species had no significant effect on soil salinity in either layer. The mesocosms did not influence the observed values, as shown by the random intercept variance of 0. Overall, these measurements show that the treatments we applied created clear differences in soil salinity.

3.2 | Salinity and Inundation Stress on Morphological Properties

Salix alba exhibited greater height growth compared to *A. glutinosa* across treatments (Figure 2B, $F=7.21$, $p<0.01$, Table 1). Generally, freshwater conditions resulted in higher growth rates, followed by the temporary 2 PSU treatment and the other

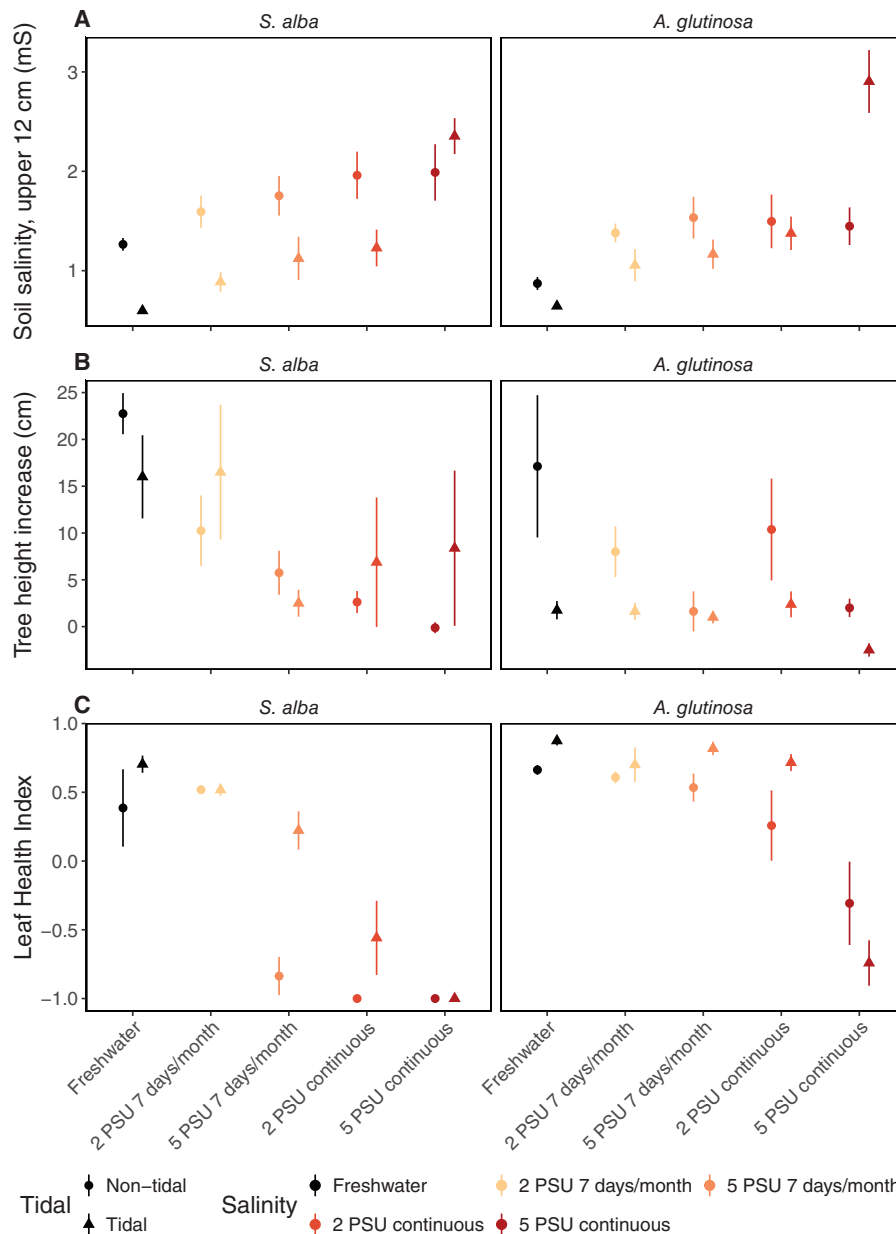


FIGURE 2 | (A) soil salinity in mS/cm normalised at 25°C taken in the upper layer of the pots on 21/09/2022. (B) the difference in tree height between the first (April) and last measure (September); (mean $\pm$ SE). (C) Leaf Health Index based on the leaves counted on 21/09/2022; (mean $\pm$ SE). In each plot, the left figure shows data for *Salix alba*, and the right figure shows data for *Alnus glutinosa*. Different colours indicate the salinity treatment; the freshwater control is in black, while a gradient from yellow to red indicates the increasing salinity treatment. Different shapes indicate the tidal regime, a circle for non-tidal water and a triangle for tidal regime.

TABLE 1 | Results of the linear mixed model (F -statistic and p -value) on the tree growth in height (difference between the last and the first measure), the September measures of Leaf Health Index and soil salinity in both soil layers, aboveground biomass, upper and lower half of the belowground biomass, Modulus of Rupture (MOR).

	Tree growth in height	Leaf Health Index	Soil salinity upper layer	Soil salinity lower layer	Aboveground biomass	Belowground biomass, upper layer	Belowground biomass, lower layer	MOR
Salinity	6.53***	51.55***	28.02***	41.26***	16.79***	26.2***	8.06**	2.14
Tidal	2.08	11.56**	5.67*	1.46	7.03**	10.66**	12.3**	0.05
Species	7.21**	102.68***	1.14	0	1.66	0.35	16.69***	128.96***
Salinity:Tidal	1.56	4.55*	11.38***	3.04*	0.25	0.48	1.25	1.97
Salinity:Species	1.34	13.06***	0.19	0.55	2.63*	8.36***	5.01**	7.11***
Tidal:Species	5.99*	3.76	11.52***	2.44	0.25	0.34	2.24	0.07
Salinity:Tidal:Species	0.68	1.8	0.78	0.39	1.42	0.97	3.71**	4.06**

Note: Significance codes: ***0.001, **0.01, *0.05.

treatments. The mesocosm did not have a significant effect on the observed values (Table S1). The observed differences in tree height growth appeared to be most strongly influenced by salinity treatment in *S. alba* and by both tidal regime and salinity treatment in *A. glutinosa* (Table S4), suggesting the presence of differential responses between species.

The Leaf Health Index revealed significant differences between species, with *A. glutinosa* maintaining higher leaf health than *S. alba* with increasing salinity (Figure 2C, Table 1). The most significant differences were between salinity treatments, while tidal regime and species had a lesser effect (Table 1). Mesocosm had only a small effect (variance = 0.01, Table S1). In general, the index values followed a consistent pattern for all species: highest leaf health in freshwater, followed by the temporary salinity treatments and finally the continuous treatments. In both temporary and continuous treatments, the 2 PSU treatment showed higher index values than the 5 PSU treatment (Figure 2C). With the exception of some *A. glutinosa* trees, all plants were severely damaged in the highest salinity treatment (Leaf Health Index < 0 at 5 PSU continuous). While *S. alba* was significantly affected by salinity, *A. glutinosa* was relatively salt-resistant, with only the highest salinity treatment of 5 PSU continuous having an effect (Figure 2C, Table S4).

3.3 | Salinity and Inundation Stress on Biomass and Mechanical Properties

We observed significant differences in biomass between trees depending on salinity and tidal regime (Table 1, Table S4), while the mesocosm influenced only the belowground biomass (Tables S1 and S2). Similar to tree height, trees in the freshwater treatment had statistically significantly higher aboveground biomass values than all other treatments ($F = 16.79$, $p < 0.001$, Table 1, Figure 3A), while there is no statistically significant difference between the two species ($F = 1.66$, $p > 0.05$, Table 1). Similar statistically significant trends, although less pronounced, can be seen for the belowground biomass (Table 1, Figure S2B,C). The lower part of the root system consistently showed lower biomass than the upper layer, for example, *S. alba* root biomass in freshwater conditions ranged from 150 to 250g in the upper layer and 0 to 100g in the lower layer. Overall, both the salinity and the tidal treatment had a statistically significant effect on aboveground and belowground biomass (Table 1, Table S4).

Except for the Modulus of Rupture (MOR) of *S. alba*, which increased with increasing salinity treatment (Figure 3B, Table S4), there were no significant differences in mechanical properties (MOE, EI) between salinity or tidal treatments (Tables S3 and S4). The MOR values of *S. alba* were affected by salinity treatment, with increasing values at higher salinity treatments (ranging from 4N/mm to 12, Table S4). The MOR of *A. glutinosa* remained lower than that of *S. alba* (< 4N/mm) regardless of treatment.

4 | Discussion

Saltwater intrusion into estuaries will be an important determinant of the fate of tidal floodplain forests in a future dominated

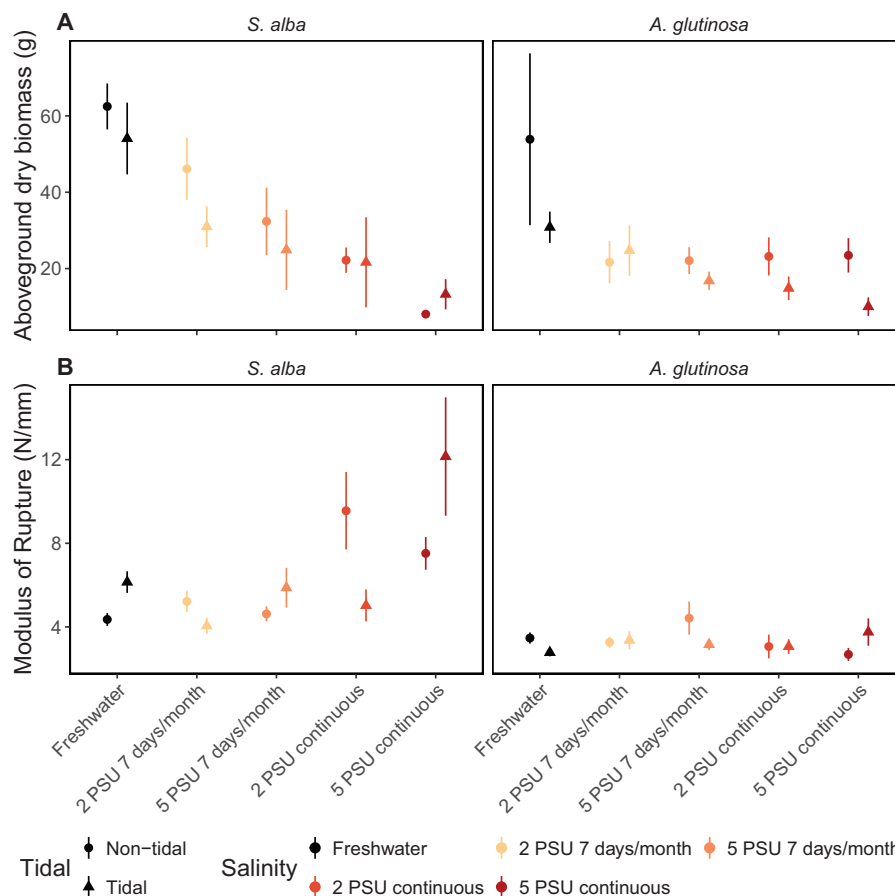


FIGURE 3 | (A) aboveground biomass; (mean ± SE). (B) Modulus of rupture (N/mm); (mean ± SE). In each plot, the left figure shows data for *Salix alba*, and the right figure shows data for *Alnus glutinosa*. Different colours indicate the salinity treatment; the freshwater control is in black, while a gradient from yellow to red indicates the increasing salinity treatment. Different shapes indicate the tidal regime: a circle for non-tidal water and a triangle for tidal regime.

by climate change and sea-level rise. Human exploitation of these floodplain forests has led to the dominance of willow species at the expense of the historically dominant black alder *A. glutinosa* (Pierik et al. 2022; Vos 2015). Our research highlights that *A. glutinosa* has generally higher salt tolerance than white willow *S. alba*, the currently dominant species in contemporary floodplain forests (Karrenberg et al. 2002). *Alnus glutinosa* was able to grow under both tidal and non-tidal exposure to salt water up to 5 PSU. Hence, our research highlights that *A. glutinosa* is generally well adapted to both tidal conditions and episodic salt intrusion. This emphasises that floodplain forests dominated by *A. glutinosa* are likely to be more resilient to future salt intrusion imposed by a changing climate than floodplain forests dominated by willow *S. alba*.

Our results have important implications for the management of tidal floodplain forest, a habitat that is currently endangered (Havrdova et al. 2023; Verhoeven 2014), and for which EU directives are imposing restoration obligations (Council Directive 92/43/EEC 1992). These tidal floodplain forests are protected within the Natura 2000 framework, with the goal to maintain the surface and quality of the habitat (PDN/2010–108 2010). However, these forests are often dominated by pollard willows of *Salix* species, which were planted as part of the willow cultivation that has occupied many freshwater intertidal areas until halfway through the 20th century, and do

not necessarily characterise a natural floodplain forest. Due to a drop in demand for willows as building material, many of the cultivation lots have been abandoned, allowing the pollard willows to grow to full height and to reach maturity (Bijlsma et al. 2009; Struyf et al. 2009). Despite extensive protection measures, many of these aging willow stands have gradually collapsed, with little rejuvenation of willows or other tree species, as the thick understory prevents the establishment of tree seedlings (Bijlsma et al. 2009). Our research highlights that in current day conditions, *S. alba* is no longer the optimal tree species, as conditions may increasingly favour *A. glutinosa*, which is better able to resist both the tidal regime as well as the salt intrusion events that are intrinsic to tidal conditions and will become more important under climate change. This has important implications for the conservation of current day tidal floodplain forest: management policies that aim to maintain the current species composition, which has resulted from human economic exploitation, may actually reduce the resilience of freshwater tidal floodplain forest to climate change-induced environmental stresses, therefore hampering their long-term nature-based flood defence ability.

Another important finding is the ability of *A. glutinosa* to thrive under tidal conditions typically associated with *S. alba*. While *A. glutinosa* is commonly found in waterlogged soils and flooded areas, indications of its coexistence with *S. alba*

in tidal conditions are scarce (Barendregt et al. 2006; Struyf et al. 2009; Waller and Kirby 2021). We suggest that although *A. glutinosa* can thrive in tidal conditions, other factors such as the presence of *S. alba* and other species during early establishment may hinder its establishment in freshwater tidal wetlands and favour *S. alba* as the dominant species. However, the dominance of *S. alba* in present-day floodplain forests may also be the result of centuries of willow cultivation for basketry and land reclamation (Paalvast and van der Velde 2014; Struyf et al. 2009), given the historical dominance of *A. glutinosa* (Vos 2015). In a future with increased salt intrusion, *A. glutinosa* may outcompete *S. alba*, as confirmed by the greater reduction in Leaf Health Index in *S. alba* compared to *A. glutinosa*. Our results indicate that, in the face of sea-level rise and concurrent salt intrusion, efforts to restore and conserve tidal freshwater wetlands to preserve remnant willow stands from historic human horticultural practices may inadvertently reduce wetland resilience to climate change. To ensure the preservation of forested wetlands in a salinised environment, diversifying species and allowing for natural succession dynamics is strongly recommended (Messier et al. 2019). Introducing multiple species with varying stress tolerances can prevent mass mortality, enhance resilience against saltwater intrusion and additionally ensure constant soil cover, reduced erosion and increased flood protection (Berendse et al. 2015; Quijas et al. 2010).

Aside from the current study, there have been few direct comparisons of salinity tolerance among tree species native to European tidal freshwater forests, and existing studies sometimes yield contrasting results. Our findings align with the Ellenberg-type indicator values proposed by Tichý et al. (2023), which describe the abiotic conditions in which each plant species thrives. On a scale from 0 (salt sensitive) to 10 (salt tolerant), *S. alba* scores 0.1, while *A. glutinosa* scores 0.6 (Tichý et al. 2023), indicating that *A. glutinosa* is more salt tolerant than *S. alba*. In contrast, observational data from the Netherlands suggest higher survival rates for *S. alba* than *A. glutinosa* after the exceptional flooding and salt intrusion event of 1953 (Hayward and Bernstein 1958; van der Linde and van der Meiden 1954). Nevertheless, the authors highlighted the limitations of these observations, noting that data collected in such an exceptional storm may lack conclusive value with regard to salt sensitivity. Studies investigating the salt tolerance of other species typical of floodplain forests also show inconsistencies. For example, *Betula pendula*, *Salix cinerea*, *Salix viminalis*, *Populus alba* and *Populus nigra* are considered in the literature to be either not tolerant or moderately tolerant to salt stress (Buschbom 1968; Deptuła et al. 2020; Markus-Michalczyk et al. 2014; Tichý et al. 2023). These mixed results highlight the difficulty of studying salt tolerance, as many factors and environmental conditions influence the salt tolerance of trees.

There are uncertainties in our study as well: in contrast with the results from the Leaf Health Index, *S. alba* showed higher height growth (and consequently higher biomass values) in the 2 PSU 7 days/month treatment compared to *A. glutinosa*, while all higher salinity treatments showed an equal reduction in height and biomass. The reason for this may be twofold: the Leaf Health Index may be more sensitive to salt stress relative

to height growth, or alternatively the higher initial height of *S. alba* individuals than those of *A. glutinosa* may have had an effect on the results. However, this was exactly the reason for developing the Leaf Health Index: by normalising for the number of leaves, we were able to compare species with very different growth characteristics. The comparable results with tree height and biomass, despite some discrepancies, highlight that this index can effectively represent the health of the plants and their response to stress and is more sensitive to the effect of salinity treatments on the plants relative to biomass or height. Additionally, this study used juvenile trees rather than adult trees, which previous research has shown to be more sensitive to salinity (Kozłowski 1997; Niknam and McComb 2000). As a result, the findings may overestimate the long-term negative impacts of salinity on mature trees. By focusing on juvenile trees, this study provides valuable insights into seedling recruitment and thus forest regeneration. It also provides conservative estimates for managers to determine salinity levels that can be accepted without causing problems. Nevertheless, these uncertainties and the contrasting results within the literature underline the complexity of salinity tolerance in tidal freshwater species and highlight the need to study multiple species and their interactions within these naturally diverse environments.

While we observed clear signs of vegetation stress under continuous 5 PSU exposure, temporary exposure to the same salt concentration was less detrimental, suggesting that trees may withstand repeated short-term saltwater exposure at potentially lethal concentrations. Studies on other species and for test salinities up to 18 PSU showed similar results (Hootsmans and Wiegman 1998; Li and Pennings 2018a, 2018b). We deduce that plants can withstand temporary saltwater intrusion at low salinities (up to 5 PSU in this study) without visible damage. To protect the remaining floodplain forest, the complete exclusion of saltwater is most likely impossible and also unnecessary to maintain biodiversity and natural value. Instead, it could be more effective to allow some level of saltwater to enter the system and reduce the duration of salt stress by ensuring the area is rapidly refreshed afterwards. That is, rather than attempting to completely exclude saltwater from floodplain forests, employing strategies to warrant quick refreshment after such salt intrusion events might be more cost-effective and feasible. The development of such strategies should be the focus of further research to preserve and restore climate-proof and tree species diverse tidal floodplain forests.

4.1 | Concluding Management Recommendations

To protect Europe's remaining tidal floodplain forests against climate change and increased salt intrusion, it is essential to reassess our current management strategies. Current practices, which tend to favour the maintenance of willow-dominated forests with the species composition inherited from historic plantations, may render these forests more vulnerable to saltwater intrusion. Our results, by revealing the differences in salt tolerance between species, provide further proof of the importance of species diversity to increase the resilience of ecosystems to new stressors induced by climate change (Isbell et al. 2015; Messier et al. 2019; Mori et al. 2013). Moreover, the species examined

in our study demonstrated resistance to temporary salt stress, suggesting that complete exclusion of saltwater from wetlands may not be necessary. Instead, reducing the duration of salt exposure could prove effective. Consequently, we recommend that further research focus on strategies to ensure the refreshing of floodplain forests after a saltwater intrusion event. This approach could enhance the resilience and ecological functionality of these ecosystems.

Author Contributions

E.S., T.J.B., J.V.D.K.: conceptualisation. E.S., T.J.B., J.K., W.B.: developing methods. E.S., W.B.: conducting the research. E.S.: data analysis, preparation of figures and tables. E.S., T.J.B., J.K., S.J.M.H.H., W.B.: data interpretation, writing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data is available upon reasonable request to the corresponding author.

References

- Article 17 web tool (n.d.). Retrieved April 16, 2024, from, <https://nature-art17.eionet.europa.eu/article17/habitat/summary/?period=5&group=Forests&subject=91E0®ion=>.
- Barendregt, A., D. F. Whigham, P. Meire, A. H. Baldwin, and S. Van Damme. 2006. "Wetlands in the Tidal Freshwater Zone." In *Wetlands: Functioning, Biodiversity Conservation, and Restoration*, edited by D. F. Whigham, 117–148. Springer. https://doi.org/10.1007/978-3-540-33189-6_6.
- Berendse, F., J. van Ruijven, E. Jongejans, and S. Keesstra. 2015. "Loss of Plant Species Diversity Reduces Soil Erosion Resistance." *Ecosystems* 18, no. 5: 881–888. <https://doi.org/10.1007/s10021-015-9869-6>.
- Bijlsma, R. J., E. J. Weeda, E. Verkaik, et al. 2009. "Wentelwilgen, Wortelkluitten en Wave Dieback: Diversiteit Door Natuurlijke Processen in Bosreservaten in de Biesbosch. [Rolling Willows, Root Balls and Wave Dieback. Diversity Through Natural Processes in Forest Reserves in the Biesbosch]." <https://edepot.wur.nl/14587>.
- Borsje, B. W., B. K. van Wesenbeeck, F. Dekker, et al. 2011. "How Ecological Engineering Can Serve in Coastal Protection." *Ecological Engineering* 37, no. 2: 113–122. <https://doi.org/10.1016/j.ecoleng.2010.11.027>.
- Buschbom, U. 1968. "Salzresistenz Oberirdischer Sproßteile von Holzgewächsen." *Flora Oder Allgemeine Botanische Zeitung. Abt. B. Morphologie und Geobotanik* 157, no. 4: 527–561. [https://doi.org/10.1016/s0367-1801\(17\)30096-0](https://doi.org/10.1016/s0367-1801(17)30096-0).
- Cao, H., Z. Zhu, T. Balke, L. Zhang, and T. J. Bouma. 2017. "Effects of Sediment Disturbance Regimes on Spartina Seedling Establishment: Implications for Salt Marsh Creation and Restoration." *Limnology and Oceanography* 63, no. 2: 647–659. <https://doi.org/10.1002/lno.10657>.
- Claessens, H., A. Oosterbaan, P. Savill, and J. Rondeux. 2010. "A Review of the Characteristics of Black Alder ((L.) Gaertn.) and Their Implications for Silvicultural Practices." *Forestry* 83, no. 2: 163–175. <https://doi.org/10.1093/forestry/cpp038>.
- Conner, W. H., K. W. McLeod, and J. K. McCarron. 1997. "Flooding and Salinity Effects on Growth and Survival of Four Common Forested Wetland Species." *Wetlands Ecology and Management* 5, no. 2: 99–109. <https://doi.org/10.1023/a:1008251127131>.
- Council Directive 92/43/EEC. 1992. "Of 21 May 1992 On the Conservation of Natural Habitats and of Wild Fauna and Flora., (92/43/EEC)." <http://data.europa.eu/eli/dir/1992/43/2013-07-01>.
- Deptuła, M., A. Piernik, A. Nienartowicz, P. Hulisz, and D. Kamiński. 2020. "A*lunus glutinosa* L. Gaertn. As Potential Tree for Brackish and Saline Habitats." *Global Ecology and Conservation* 22: e00977. <https://doi.org/10.1016/j.gecco.2020.e00977>.
- Dirr, M. 1976. "Selection of Trees for Tolerance to Salt Injury." *Arboriculture & Urban Forestry* 2, no. 11: 209–216. <https://doi.org/10.48044/jauf.1976.053>.
- Havrdova, A., J. Douda, and J. Doudova. 2023. "Threats, Biodiversity Drivers and Restoration in Temperate Floodplain Forests Related to Spatial Scales." *Science of the Total Environment* 854: 158743. <https://doi.org/10.1016/j.scitotenv.2022.158743>.
- Hayward, H. E., and L. Bernstein. 1958. "Plant-Growth Relationships on Salt-Affected Soils." *Botanical Review* 24, no. 8–10: 584–635. <https://doi.org/10.1007/Bf02872595>.
- Herbert, E. R., P. Boon, A. J. Burgin, et al. 2015. "A Global Perspective on Wetland Salinization: Ecological Consequences of a Growing Threat to Freshwater Wetlands." *Ecosphere* 6, no. 10: 1–43. <https://doi.org/10.1890/Es14-00534.1>.
- Hootsmans, M. J. M., and F. Wiegman. 1998. "Four Helophyte Species Growing Under Salt Stress: Their Salt of Life?" *Aquatic Botany* 62, no. 2: 81–94. [https://doi.org/10.1016/s0304-3770\(98\)00085-0](https://doi.org/10.1016/s0304-3770(98)00085-0).
- Isbell, F., D. Craven, J. Connolly, et al. 2015. "Biodiversity Increases the Resistance of Ecosystem Productivity to Climate Extremes." *Nature* 526, no. 7574: 574–577. <https://doi.org/10.1038/nature15374>.
- Jakubínský, J., M. Prokopová, P. Raška, et al. 2021. "Managing Floodplains Using Nature-Based Solutions to Support Multiple Ecosystem Functions and Services." *WIREs Water* 8, no. 5: e1545. <https://doi.org/10.1002/wat2.1545>.
- Karrenberg, S., P. J. Edwards, and J. Kollmann. 2002. "The Life History of Salicaceae Living in the Active Zone of Floodplains." *Freshwater Biology* 47, no. 4: 733–748. <https://doi.org/10.1046/j.1365-2427.2002.00894.x>.
- Kozłowski, T. T. 1997. "Responses of Woody Plants to Flooding and Salinity." *Tree Physiology* 17, no. 7: 490. <https://doi.org/10.1093/treephys/17.7.490>.
- Li, F., and S. C. Pennings. 2018a. "Response and Recovery of Low-Salinity Marsh Plant Communities to Presses and Pulses of Elevated Salinity." *Estuaries and Coasts* 42, no. 3: 708–718. <https://doi.org/10.1007/s12237-018-00490-1>.
- Li, F., and S. C. Pennings. 2018b. "Responses of Tidal Freshwater and Brackish Marsh Macrophytes to Pulses of Saline Water Simulating Sea Level Rise and Reduced Discharge." *Wetlands* 38, no. 5: 885–891. <https://doi.org/10.1007/s13157-018-1037-2>.
- Markus-Michalczyk, H., D. Hanelt, K. Ludewig, D. Müller, B. Schröter, and K. Jensen. 2014. "Salt Intrusion in Tidal Wetlands: European Willow Species Tolerate Oligohaline Conditions." *Estuarine, Coastal and Shelf Science* 136: 35–42. <https://doi.org/10.1016/j.ecss.2013.11.008>.
- Markus-Michalczyk, H., Z. C. Zhu, and T. J. Bouma. 2019. "Morphological and Biomechanical Responses of Floodplain Willows to Tidal Flooding and Salinity." *Freshwater Biology* 64, no. 5: 913–925. <https://doi.org/10.1111/fwb.13273>.
- McDougall, T. J., and P. M. Barker. 2011. "Getting Started With TEOS-10 and the Gibbs Seawater (GSW) Oceanographic Toolbox." SCOR/IAPSO WG127.

- Messier, C., J. Bauhus, F. Doyon, et al. 2019. "The Functional Complex Network Approach to Foster Forest Resilience to Global Changes." *Forest Ecosystems* 6, no. 1: 21. <https://doi.org/10.1186/s40663-019-0166-2>.
- Mori, A. S., T. Furukawa, and T. Sasaki. 2013. "Response Diversity Determines the Resilience of Ecosystems to Environmental Change." *Biological Reviews* 88, no. 2: 349–364. <https://doi.org/10.1111/brv.12004>.
- Niknam, S. R., and J. McComb. 2000. "Salt Tolerance Screening of Selected Australian Woody Species — A Review." *Forest Ecology and Management* 139, no. 1–3: 1–19. [https://doi.org/10.1016/s0378-1127\(99\)00334-5](https://doi.org/10.1016/s0378-1127(99)00334-5).
- Paalvast, P., and G. van der Velde. 2014. "Long Term Anthropogenic Changes and Ecosystem Service Consequences in the Northern Part of the Complex Rhine-Meuse Estuarine System." *Ocean and Coastal Management* 92: 50–64. <https://doi.org/10.1016/j.ocecoaman.2014.02.005>.
- PDN/2010-108. 2010. "De Staatssecretaris van Economische Zaken, Landbouw en Innovatie. Besluit Natura 2000-Gebied Oude Maas." https://www.natura2000.nl/sites/default/files/documenten/gebieden/108/n2k108_db%20h%20oude%20maas.pdf.
- Pierik, H. J., J. I. M. Moree, K. M. van der Werf, et al. 2022. "Vegetation and Peat Accumulation Steer Holocene Tidal-Fluvial Basin Filling and Overbank Sedimentation Along the Old Rhine River, the Netherlands." *Sedimentology* 70, no. 1: 179–213. <https://doi.org/10.1111/sed.13038>.
- Quijas, S., B. Schmid, and P. Balvanera. 2010. "Plant Diversity Enhances Provision of Ecosystem Services: A New Synthesis." *Basic and Applied Ecology* 11, no. 7: 582–593. <https://doi.org/10.1016/j.baae.2010.06.009>.
- R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Santini, N. S., N. Schmitz, V. Bennion, and C. E. Lovelock. 2013. "The Anatomical Basis of the Link Between Density and Mechanical Strength in Mangrove Branches." *Functional Plant Biology* 40, no. 4: 400–408. <https://doi.org/10.1071/FP12204>.
- Silinski, A., K. Schoutens, S. Puijalon, et al. 2018. "Coping With Waves: Plasticity in Tidal Marsh Plants as Self-Adapting Coastal Ecosystem Engineers." *Limnology and Oceanography* 63, no. 2: 799–815. <https://doi.org/10.1002/lno.10671>.
- Struyf, E., S. Jacobs, P. Meire, K. Jensen, and A. Barendregt. 2009. "Plant Communities of European Tidal Freshwater Wetlands." In *Tidal Freshwater Wetlands*. Backhuys Publishers/Margraf Publishers.
- Tichý, L., I. Axmanová, J. Dengler, et al. 2023. "Ellenberg-Type Indicator Values for European Vascular Plant Species." *Journal of Vegetation Science* 34, no. 1: e13168. <https://doi.org/10.1111/jvs.13168>.
- Tolliver, K. S., D. W. Martin, and D. R. Young. 1997. "Freshwater and Saltwater Flooding Response for Woody Species Common to Barrier Island Swales." *Wetlands* 17, no. 1: 10–18. <https://doi.org/10.1007/bf03160714>.
- Tully, K., K. Gedan, R. Epanchin-Niell, et al. 2019. "The Invisible Flood: The Chemistry, Ecology, and Social Implications of Coastal Saltwater Intrusion." *Bioscience* 69, no. 9: 368–378. <https://doi.org/10.1093/biosci/biz027>.
- Van Coppenolle, R., and S. Temmerman. 2019. "A Global Exploration of Tidal Wetland Creation for Nature-Based Flood Risk Mitigation in Coastal Cities." *Estuarine, Coastal and Shelf Science* 226: 106262. <https://doi.org/10.1016/j.ecss.2019.106262>.
- van den Bergh, E., A. Garniel, R. K. A. Morris, and A. Barendregt. 2009. "Conservation of Tidal Freshwater Wetlands in Europe." In *Tidal Freshwater Wetlands*, edited by D. W. A. B. Aat Barendregt, 320. Margraf Publishers GmbH.
- van der Linde, R. J., and H. A. van der Meiden. 1954. "De Invloed Van de Inundatie 1953 [The Effect of the Inundation of 1953 on Woody Plants]." *Fruittelt*, 44.
- van Wesenbeeck, B. K., G. Wolters, J. A. A. Antolinez, et al. 2022. "Wave Attenuation Through Forests Under Extreme Conditions." *Scientific Reports* 12, no. 1: 1884. <https://doi.org/10.1038/s41598-022-05753-3>.
- Verhoeven, J. T. A. 2014. "Wetlands in Europe: Perspectives for Restoration of a Lost Paradise." *Ecological Engineering* 66: 6–9. <https://doi.org/10.1016/j.ecoleng.2013.03.006>.
- Vos, P. 2015. *Origin of the Dutch Coastal Landscape*. Barkhuis. <https://doi.org/10.2307/j.ctt2204s8d>.
- Waller, M., and J. Kirby. 2021. "Coastal Peat-Beds and Peatlands of the Southern North Sea: Their Past, Present and Future." *Biological Reviews of the Cambridge Philosophical Society* 96, no. 2: 408–432. <https://doi.org/10.1111/brv.12662>.
- White, E., and D. Kaplan. 2017. "Restore or Retreat? Saltwater Intrusion and Water Management in Coastal Wetlands." *Ecosystem Health and Sustainability* 3, no. 1: e01258. <https://doi.org/10.1002/ehs2.1258>.
- Zhu, Z., Z. Yang, and T. J. Bouma. 2020. "Biomechanical Properties of Marsh Vegetation in Space and Time: Effects of Salinity, Inundation and Seasonality." *Annals of Botany* 125, no. 2: 277–290. <https://doi.org/10.1093/aob/mcz063>.

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