

Response of Four Peatland Emergent Macrophytes to Salinity and Short Salinity Pulses

Cheryl Batistel (✉ cheryl.batistel@uni-rostock.de)

University of Rostock <https://orcid.org/0000-0003-4029-9791>

Christian Porsche

University of Rostock: Universitat Rostock

Gerald Jurasinski

University of Rostock: Universitat Rostock

Hendrik Schubert

University of Rostock: Universitat Rostock

Research Article

Keywords: salinity stress, salinity pulses, coastal wetlands, peatland emergent macrophytes

Posted Date: March 18th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1442623/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Sea-level rise intensifies saltwater influx into coastal wetlands causing osmotic stress and probably changing vegetation composition. To determine especially the impact of salinity pulses that occur during flooding events, *Typha latifolia*, *Carex acutiformis*, *Schoenoplectus tabernaemontani* and *Phragmites australis* were exposed to different salinity regimes, consisting of control (permanently freshwater and permanently brackish water) and alternating freshwater and brackish water with different exposure durations (2 days brackish – 2 days fresh; 4 days brackish – 4 days fresh; 2 days brackish – 4 days fresh). Plant height, leaf area and chlorophyll fluorescence, root:shoot ratio and photosynthetic pigments were measured. Salinity suppressed the growth of *T. latifolia* and *C. acutiformis* resulting in shorter plants, smaller mean leaf area and higher root:shoot ratios whereas photosynthetic pigment ratios and chlorophyll fluorescence were not affected. Shorter but frequent salinity pulses (alternate 2 days brackish – 2 days freshwater, and 2 days brackish – 4 days freshwater) decreased the height of *T. latifolia* while *C. acutiformis* was not affected. Salinity and salinity pulses did not affect the height and root:shoot ratio of *P. australis* and *S. tabernaemontani*. *P. australis* showed signs of successful acclimation through decreased chlorophyll a:carotenoid ratio and high fluorescence yield at $\leq 20 \text{ mol m}^{-2}$ irradiance. Our results imply that with increasing seawater influx into coastal peatlands, *T. latifolia* and *C. acutiformis* may experience growth retardation or may even be replaced by *S. tabernaemontani* or *P. australis* since they are more resilient against salinity and frequent salinity pulses.

Introduction

Salinity is one of the main ecological factors that limits plant growth and productivity (Allakhverdiev et al 2000; Orlovsky et al 2016; Acosta-Motos et al 2017) or even causes death at high salinity levels (Parida and Das 2005). Salt stress influences plant growth in two ways, osmotic and ionic stress, affecting most stages of plant development from germination to vegetative growth and reproductive development (Munns 2002; Zhu 2007; Newell 2013). The most common symptoms of salt stress include a decrease in photosynthesis capacity, reduction in leaf surface expansion rate, high leaf abscission rate, chlorosis and growth suppression (Sudhir and Murthy 2004; Munns and Tester 2008).

Growth suppression due to salinization occurs in all plants, however, their tolerance levels and rates of growth reduction at lethal concentrations of salt vary widely among different plant species (Sudhir and Murthy 2004; Parida and Das 2005). Glycophytes, having low salt tolerance with an upper limit usually at 4‰ (Nielsen et al 2003), exhibit growth inhibition or even death at high salinity levels (Munns and Termaat 1986; Newell 2013). Halophytes, in contrast, representing 1% of the world flora, can survive at high NaCl concentrations (18–30‰) because they established better salt tolerance mechanisms (Flowers and Colmer 2015). Physiological mechanisms that mitigate salt stress come at a cost of reduced growth, reproduction, and competitive ability (Munns and Tester 2008). These include extrusion, elimination and redistribution of salt as well as succulence (Acosta-Motos et al 2017), with the latter allowing to keep concentrations constant by dilution in water.

Salinization can also exert ecological impacts in other indirect or non-lethal ways, including changes in species distribution, behavior, reproduction, and feeding (Xi et al 2016). Increased salinity results in changes in community composition and ecosystem structure by altering both the fitness of individuals and the strength of interspecific interactions as different biological groups show different salinity tolerances. Ultimately, this phenomenon shifts wetland communities towards species with greater salinity tolerance (Herbert et al 2015).

Coastal wetland ecosystems are found within an elevation gradient ranging between subtidal depths to the landward edge (Hopkinson et al 2009). These are special types of wetlands due to the influence of fluctuating water and salinity levels. They are vegetated by species that are uniquely adapted to the degree of inundation, hydrology and soil conditions (Tiner 2018). Due to the waterlogged conditions that hamper decomposition resulting in peat formation, they store more carbon than most other ecosystems on earth (Stagg et al 2018). Coastal peatlands at low-lying coastal areas of the southern Baltic Sea were mostly formed by the accumulation of organic material over millennia due to the episodic flooding (weekly to monthly) with flooded periods being generally shorter than non-flooded periods (Jurasinski et al 2018).

Globally, 15% of the total peatland area (4 million km²) was drained for anthropogenic purposes (Joosten 2015). However, in recent decades, rewetting and restoration of peatlands are on the rise (Tanneberger and Wichtmann 2011). Peatland rewetting is a top priority to address peatland degradation and biodiversity loss and to mitigate CO₂ emissions from peat oxidation and peatland fires (Parish et al 2008). With this, a Mire Conservation Program was established in the federal state of Mecklenburg-Vorpommern, Germany in 2000 under which more than 200 km² of degraded peatlands was already rewetted (Zerbe et al 2013). Recently, coastal wetlands were also rewetted by removing coastal protection structures such as dykes and levees allowing for regular water exchange between the land and the sea.

The global mean sea level has risen since the beginning of the last century with rates between 1 and 4 mm yr⁻¹, depending on the period and region (Baur et al 2013; IPCC 2014; IPCC 2019; Oppenheimer and Glavovic 2019). In the southwestern parts of the Baltic Sea, the rates of absolute mean sea level rise varied between 2 and 3 mm yr⁻¹ for the period 1995 to 2019 (Passaro et al 2021). Others (Richter et al 2012; Groh et al 2017) report an increase of about 1 mm yr⁻¹ in the region. Climate changes in recent years also brought more frequent, extreme natural phenomena such as storms and floods (Beldowska et al 2016) and increased precipitation in winter in the southern Baltic Sea region (BACC II Author Team 2015). In addition, the southern Baltic Sea that is characterized by flat, low-lying areas is subsiding in contrast to the uplifting Fennoscandian Shield in the north (Harff et al 2007). With all of these factors, discrete or combined, a more frequent influx of seawater may be expected in the future. This, in turn, suggests increased erosion, flooding and salinization of the adjacent coastal ecosystems.

Several studies examined the effects of varying salinity levels (Rasmuson and Anderson 2002; Stofberg et al 2015; Orlovsky et al 2016; Hadad et al 2017) on plant growth and development with much focus on crops. However, there is limited research that investigates the productivity and growth of vegetation in

irregularly salt-influenced peatland. Here, we determine the effects of salinity and different salinity change regimes on the growth of the most dominant emergent macrophytes in the coastal peatlands on the Southern Baltic Sea coast in Northern Germany through an acclimation experiment. Specifically, this consisted of control groups (permanently freshwater and brackish water, respectively) and groups treated with different durations of exposure to brackish water before returning to freshwater conditions. We hypothesized that 1) salinity reduces primary productivity due to the reduction of water potential, which limits water and nutrient transport; and 2) salinization regime is modulating the salinity tolerance response of emergent peatland macrophytes.

Materials And Methods

Preparation and Planting

Planting materials were bought from commercial suppliers to ensure uniformity of sources, handling and preparation. Seedlings of *Carex acutiformis* Ehrh. (pond-sedge), *Typha latifolia* L. (common cattail), *Phragmites australis* (Cav.) Trin. ex Steud. (common reed) and *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla (softstem bulrush) were bought from re-natur GmbH (Ruhwinkel, Germany). The soil used was an aquatic plant soil which is largely composed of peat (Floragard Wasserpflanzen). Water was taken from the Warnow River that traverses the state of Mecklenburg-Vorpommern, Northeast Germany specifically in Mührendamm (54°5'1.50"N and 12°9'5.09"E) for the freshwater and close to the river mouth (Schmarl Dorf, 54°8'11.72"N and 12°5'20.17"E) for the brackish water. The freshwater used had a salinity of 0.31‰ (EC 0.60 mS cm⁻¹) while the brackish water had a salinity of 9.58‰ (EC=15.36 mS cm⁻¹) and a pH of 8.65 and 9.01, respectively.

Seedlings were planted in 78 cm (length) x 49 cm (width) x 32 cm (height) black storage boxes with 10 cm high cobblestone bed covered with geotextile to allow water permeability. One rubber pipe, with a height and diameter of 24.0 cm and 5.5 cm, respectively, was inserted vertically in one corner of each box for easy water changing during treatment application. Then, the boxes were filled up with 25 kg soil on top of the geotextile.

Experimental set-up and treatment application

The experiment was conducted from April to July 2020 in an open area outside the Institute of Biology, University of Rostock. Fifteen boxes were set up in a Randomized Complete Block Design (RCBD), equally distributed in three rows as replicates. In each row, one box was designated per treatment as follows:

C+ : positive (+) control: permanently brackish water

C- : negative (-) control: permanently freshwater

A_{2b_2f} : alternating 2 days brackish water then 2 days freshwater

A_{4b_4f} : alternating 4 days brackish water then 4 days freshwater

A_{2b_4f} : alternating 2 days brackish water then 4 days freshwater

Henceforth, C+ and C- are referred to as salinity levels while A_{2b_2f}, A_{4b_4f} and A_{2b_4f} are salinity pulses.

Six pots of seedlings for each species, *P. australis*, *T. latifolia*, *C. acutiformis* and *S. tabernaemontani*, were transplanted in a row, arranged randomly, per box. Treatments were applied for 10 weeks to each designated box after the 3-week establishment period wherein plants were exposed to freshwater under waterlogged conditions. We changed the water by sucking the water out from each box using a rubber hose that was inserted into the pipe. Then, depending on the treatment, either freshwater or brackish water was poured into each box through the pipe up to the surface level to mimic peatlands which are normally water-saturated all year round. Water level was maintained by pouring appropriate water into each box daily.

Light (lux) and air temperature (°C) were monitored during the entire study period using HOBO UA-002-64 pendant temperature/light data loggers (HOBO Pendant® Temp/Light, Onset, Cape Cod, Massachusetts, USA). Salinity (‰), water conductivity (mS cm⁻¹), pH and water temperature (°C) were also monitored daily using HQ40D portable multimeter (Hach Lange GmbH, Berlin, Germany) to ensure similarity among treatment replicates. When salinity differed between treatment replications, e.g. due to heavy rainfall, water was replaced accordingly as soon as possible.

Growth measurement

Five individuals per species per treatment from each of the three replicate boxes were marked for weekly measurement of growth variables including plant height, number of leaves, and leaf length and width. Plant height (cm) was measured from the root collar to the tip of the tallest part of the shoot system using a meter stick. The potential maximum height and maximum growth rates were estimated using the Richards growth model (Richards 1959) following equation 1:

$$Y(t) = A + \frac{K-A}{(C+e^{-B(t-M)})^{\frac{1}{V}}} \quad (1)$$

Where, Y = height and t = time, and the 5 parameters are:

A: lower asymptote

K: upper asymptote when c=1: If A=0 & c=1, the K is the carrying capacity

B: growth rate

M: maximum growth rate

V > 0: affects near which asymptote maximum growth occurs

C: typically takes a value of 1, otherwise, the upper asymptote is

$$A + \frac{K-A}{C^{1/v}} \quad (2)$$

Leaf length (cm) of all leaves of each marked plant was measured from the base to the tip of each leaf while the leaf width (cm) was measured at the middle to determine maximum width using a ruler. Leaf area (LA, cm²) was calculated by multiplying the leaf length and width, assuming a nearly rectangular shape. The LA per individual plant was taken as the mean of all leaves while the mean LA (MLA) is the average of all LA per treatment per species.

All plants were harvested after 10 weeks, sorted into species per box, and then the aboveground biomass (stem and leaves) and belowground biomass (BGB, roots) parts were separated. Roots were thoroughly cleaned with tap water. AGB and BGB were determined by oven-drying harvested materials at 70 °C for 48 hours or until constant weight and weighed. Root:shoot ratio (RSR) was calculated by dividing the BGB and AGB dry weights.

Photosynthetic pigments

At the end of the experiment, leaf samples were taken from each leaf spot where photosynthesis measurement was done (see explanation below). These were individually weighed (mg) and placed in a 5 ml tube. Then, 3 ml of N,N-Dimethylformamide (DMF) was added. Samples were stored at 4 °C for 24 hours to extract the photosynthetic pigments. Absorption spectra of the extracts were measured with wavelengths ranging from 350 to 750 nm using the spectrophotometer (UV/VIS spectrometer Lambda 2, PerkinElmer, Waltham, Massachusetts, USA). Chlorophyll a and b, as well as carotenoid contents, were calculated using the following formula (Porra et al 1989) to determine ratios between Chlorophyll a and b (Chl a:b) and Chlorophyll a and carotenoid (Chl a:car).

$$\text{Chl a } (\mu\text{g} \cdot \text{g FM}^{-1}) = (A_{663.8} - A_{750}) \cdot 12 - (A_{646.8} - A_{750}) \cdot 3.11 \quad (3)$$

$$\text{Chl b } (\mu\text{g} \cdot \text{g FM}^{-1}) = (A_{646.8} - A_{750}) \cdot 20.78 - (A_{663.8} - A_{750}) \cdot 4.88 \quad (4)$$

$$\text{Car } (\mu\text{g} \cdot \text{g FM}^{-1}) = ((A_{480}-A_{470}) \cdot 1000 - \text{Chl a} \cdot 1.12 - \text{Chl b} \cdot 34.07) / 245 \quad (5)$$

where, A_x is the extinction coefficient at a specific wavelength x (nm)

Chlorophyll fluorescence yield

Three of the marked individuals per species and treatment were selected for the weekly measurement of Chlorophyll fluorescence. A JUNIOR Pulse Amplitude Modulated Chlorophyll Fluorometer (JUNIOR-PAM, Heinz Walz GmbH, Effeltrich, Germany) was used to estimate the quantum yield of photochemical energy conversion in photosystem II (PS II) of the acclimated macrophytes. Measurements were done weekly in the morning (AM, between 4:00-8:00) after dark acclimation at night and under high irradiance at noon

(NN, between 11:00-14:00). Time of measurement differed due to the increasing day length from spring to summer. Chlorophyll fluorescence yield was measured by connecting the middle part of the youngest fully developed leaf (3rd or 4th from the youngest leaf) to a magnetic leaf clip, with a 0.5 m long, 1.5 mm diameter light guide with the opposite end connected to the JUNIOR-PAM. For *S. tabernaemontani*, we measured at the middle part of the stem since it is basically leafless and the stem is its photosynthetic organ. The potential photosynthetic rate, measured as the quantum yield of photochemical energy conversion in photosystem II, was calculated as (Genty et al 1989):

$$Yield = \frac{Fm' - F}{Fm'} \quad (6)$$

where, Yield = quantum yield of photochemical energy conversion in PS II

Fm' = maximal fluorescence yield of illuminated sample with all PS II centers closed

F = fluorescence yield measured briefly before application of a saturation pulse

The coefficients of the linear regression analysis of the AM yield measurements (Supplemental Fig. 1) were used to correct the AM yield, eliminating the influence of light and representing the yield of dark acclimated samples. Yield difference (Δ Yield) was calculated by subtracting the NN from AM yield of the same measurement day per plant. These Δ Yield values were used to determine the photosynthetic efficiency of the plants under the combined effects of salinity and light intensity as abiotic stressors. Light intensity (lux) data was taken as the average of the recorded light intensity from two pendant HOBO-data loggers which was then converted into $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ using a conversion factor of 1.41 that was derived based on (Walsby 1997). Light dose was then taken as the total irradiance received by the plant from morning until the specific time of measurement at noon.

Statistical analysis

We fitted models of individual plant heights based on Richards growth model (Eq. 1) with R statistical software Version 4 (R Core Team 2020) and the package BB (Varadhan and Gilbert 2009). Statistical analyses were done using SPSS Version 27 (IBM SPSS Inc., Chicago, Illinois, USA). One-way analysis of variance (ANOVA) was used to determine significant differences in maximum height, maximum growth rate, leaf area, root:shoot ratio and pigment ratios between treatments of the same species. Post hoc pairwise multiple comparisons were carried out using Tukey's Honestly Significant Difference (HSD) against an alpha-level of 0.05. For some datasets (e.g. Δ Yield) where requirements for ANOVA could not be met, Kruskal-Wallis test was used followed by Dunn's pairwise post hoc comparisons when results were significant at 0.05 alpha level.

Results

Plant height and growth rate

The highest maximum plant heights of the four emergent macrophytes relatively varied between treatments for each species (Fig. 1). However, statistically, the maximum heights of *Phragmites australis* and *Schoenoplectus tabernaemontani* were not significantly affected by any of the treatments. In contrast, *Carex acutiformis* and *Typha latifolia* showed significant growth suppression in response to both salinity and salinity pulses. The maximum height of *C. acutiformis* under brackish water (C+) was 20% shorter (p-value = 0.042) relative to those in freshwater (C-). The maximum height of C+ was also shorter than A_{2b_4f} by 25% (p-value = 0.033). For *T. latifolia*, salinity stress (C+) resulted in 40% decrease in height compared to those under freshwater condition. Relatively more frequent salinization (A_{2b_2f} and A_{2b_4f}) also inhibited the plant height of *T. latifolia* by 17%.

The maximum growth rates of *C. acutiformis* and *S. tabernaemontani* were neither affected by salinity nor by the different frequency of salinity pulses (Fig. 2). However, in *T. latifolia* under treatments A_{4b_4f} and A_{2b_4f}, the maximum growth rates were up to 15% lower than C- (p-value < 0.05) while the other treatments did not significantly vary. In *P. australis*, the maximum growth rates of A_{2b_4f} were significantly higher than C+, C- and A_{2b_2f}.

Leaf area

The development of the mean leaf area (MLA) of all three species (excluding *S. tabernaemontani*) relatively differed between treatment and species over time (weeks; Fig. 3; Table 1). Between treatments, MLA of *C. acutiformis* differed with C+ producing significantly larger leaves than in the other treatments (p-value < 0.05), except A_{2b_2f}, in the first two weeks (Table 1). In week three, salinity pulses caused a decrease in MLA of A_{4b_4f} and A_{2b_4f} relative to both C+ and C- (p-value < 0.05). Thereafter, the MLA of the five treatments did not differ significantly. *P. australis* reacted differently towards salinity and salinity pulses during the study period. In week one, MLA of C- was up to 46% larger than A_{4b_4f}, with the former significantly larger than the other treatments (p-value < 0.05). Treatment A_{2b_4f} produced larger leaves from week three, and become significantly different from the rest of the treatments in week six (p-value < 0.05). In week seven, only C+ differed from A_{2b_4f} (p-value < 0.05). There was no more difference in MLA between treatments (p-value > 0.05) from week eight until ten. In *T. latifolia*, initially, both salinity and salinity pulses did not show significant effects on the species. In week three, treatment C- and A_{2b_2f} had significantly larger leaves than A_{2b_4f} but after a week, C- did not differ anymore. In week 6, both C- and A_{2b_2f} differed once again from A_{2b_4f}. From week seven until week 10, the MLA of C+ was significantly smaller than C-. The MLA of A_{2b_4f} also differed significantly from C+ from week eight to nine.

Photosynthetic pigments

The chlorophyll a:b ratio across species and treatments on week ten ranged from 2.1 to 4.0 (Table 2). Salinity and salinity pulses did not alter the Chl a:b ratios of *C. acutiformis*, *P. australis* and *T. latifolia*. For *S. tabernaemontani*, pigment ratios of A_{4b_4f} reacted to the relatively longer (4 days) exposure to freshwater and then brackish water, resulting in a significantly lower Chl a:b ratio compared to the other

treatments. Chl a:car ratio of the macrophytes ranged from 1.7 to 5.0. ANOVA shows no treatment effects on all species (p-value > 0.05), except *P. australis* wherein Chl a:car of A_{4b_4f} was significantly lower than C- (p-value = 0.039).

Table 1. Results of ANOVA post hoc multiple comparisons using Tukey's HSD of the mean leaf area between treatment per species. Different letters represent significant differences between treatments of the same species (p-value ≤ 0.05); ☐ represents weeks with p-value > 0.05

Species	Time	Treatments				
	(Week)	C+	C-	A _{2b_2f}	A _{4b_4f}	A _{2b_4f}
<i>Carex acutiformis</i>	1	a	bc	ab	bc	c
	2	a	b	b	b	b
	3	a	a	ab	b	b
	☐					
<i>Phragmites australis</i>	1	ab	a	ab	b	ab
	☐					
	6	b	ab	b	b	a
	7	b	ab	ab	ab	a
	☐					
<i>Typha latifolia</i>	☐					
	3	ab	a	a	ab	b
	4	ab	ab	a	ab	b
	5	ab	a	ab	ab	b
	6	ab	a	a	ab	b
	7	b	a	ab	ab	b
	8	b	a	ab	ab	b
	9	b	a	ab	ab	b
	10	b	a	ab	ab	b

Table 2. Mean Chl a:b and Chl a:car ratios (± SD; n=3) of the four macrophytes after ten weeks of treatment application. Different letter superscripts represent significant differences between treatments of

the same species ($p\text{-value} \leq 0.05$) calculated with ANOVA post hoc multiple comparisons using Tukey's HSD

	Treatments	<i>C. acutiformis</i>	<i>S. tabernaemontani</i>	<i>P. australis</i>	<i>T. latifolia</i>
Chl a:b	C+	2.13 ± 0.97	3.25 ± 0.06ab	3.47 ± 0.17	3.19 ± 0.06
	C-	3.32 ± 0.13	3.06 ± 0.10ab	3.98 ± 0.31	3.11 ± 0.12
	A2b-2f	3.31 ± 0.13	3.29 ± 0.15a	3.36 ± 0.32	3.14 ± 0.01
	A4b-4f	2.98 ± 0.01	2.99 ± 0.03c	2.74 ± 0.83	3.07 ± 0.03
	A2b-4f	2.68 ± 0.61	3.03 ± 0.03bc	3.33 ± 0.27	3.35 ± 0.39
Chl a:Car	C+	3.22 ± 0.58	4.39 ± 0.12	3.90 ± 0.40ab	4.08 ± 0.19
	C-	3.97 ± 0.40	4.31 ± 0.64	4.34 ± 0.60a	3.61 ± 0.26
	A2b-2f	4.24 ± 0.34	4.63 ± 0.12	3.35 ± 0.14ab	3.90 ± 0.17
	A4b-4f	4.17 ± 0.22	4.83 ± 0.07	2.53 ± 0.68b	3.84 ± 0.12
	A2b-4f	3.73 ± 0.58	4.01 ± 0.33	2.91 ± 1.05ab	3.71 ± 0.12

Photosynthetic yield

The difference in yield (ΔYield) between morning (AM) and noon (NN) under light dose classes varies between treatment for each species (Fig. 4A–D). The mean ΔYield in *C. acutiformis* from A_{4b_4f} was lower than in the other treatments ($p < 0.05$) when the leaves received up to 40 mol m⁻² of light dose from dawn until noontime measurement. The mean ΔYield of *T. latifolia* from A_{4b_4f} was also significantly lower than other treatments at 20.1–40 mol m⁻² light dose. There was no difference between treatments at 40.1–60 mol m⁻² light dose in both species. For *P. australis*, the ΔYield of C+ was significantly lower than most of the other treatments at < 20 mol m⁻² light dose. At 40.1–60 mol m⁻² light dose, C+ differed significantly from C- and A_{2b_4f}. Both salinity and salinity pulses showed no treatment effects on the ΔYield of *S. tabernaemontani*, regardless of the light dose received.

Root:shoot ratio

The root:shoot ratio of all macrophytes after ten weeks differed between treatments for each species with values ranging from 0.63 to 2.60 (Fig. 5). All species, except *P. australis*, generally showed an increased root:shoot ratio when permanently exposed to brackish water relative to freshwater condition. The root:shoot ratio of *C. acutiformis*, *S. tabernaemontani* and *T. latifolia* increased by 32%, 36% and 53%, respectively, but ANOVA revealed that these differences are statistically insignificant ($p\text{-value} > 0.05$; $n=3$).

However, a significantly lower root:shoot ratio (p -value < 0.05) of *T. latifolia* was observed under relatively frequent salinity pulses (A_{2b_2f} and A_{2b_4f}) compared to C+.

Discussion

Response of macrophytes to salinity

Our results reveal that the four emergent macrophytes respond differently to salinity and short salinity pulses. The shorter maximum height of *C. acutiformis* and *T. latifolia* under constant brackish water (C+, salinity = 9.58‰; EC = 15.36 mS cm⁻¹) than those in freshwater (C-; Fig. 1) suggests that these species are more sensitive to salinity. Height shortening indicates salinity stress confirming that both *C. acutiformis* and *T. latifolia* has an Ellenberg indicator value, an index given to each plant species of a certain region to express its environmental preferences, for salt tolerance of zero – absent from saline sites (Ellenberg 1974; Hill et al 2004). Although *T. latifolia* can grow in brackish environments, its growth significantly decreases at salinities 3–5‰ and death occurs at 25‰ (Shay and Shay 1986; Glenn et al 1995; Macek and Rejmánková 2007). Both *C. acutiformis* and *T. latifolia* had consistently lower relative growth rates under brackish water than in freshwater from week one until week ten (please see Supplemental Table 1). This could be the effect of inhibition of lateral shoot development due to moderate salinity stress (Munns and Tester 2008). The maximum growth rates of the two species under treatments C + and C- did not differ (Fig. 2) implying that at some point of development they were both growing fast but the accumulated effect of salinity stress in C + still resulted in height reduction.

The difference in leaf area between treatments may explain their height variation since the leaf provides the photosynthetic material required for carbon fixation and growth (Goodman et al 2010). Thus, *T. latifolia* under C- possessing the highest mean leaf area also had the highest maximum height. In contrast, shorter height under C + could be explained by the smaller leaf area that is due to the lower leaf elongation rate starting week one from exposure (please see Supplemental Table 2). The reduction in leaf surface expansion rate is the earliest response of non-halophytes when exposed to an elevated salinity that consequently reduces the photosynthetic area (Wang and Nii 2000; Cramer 2003; Munns and Tester 2008). This can be related to a reduction in turgor pressure (Sucre and Suárez 2011) as leaf expansion can be limited by water fluxes as the leaf develops (Pantin et al 2011). This reflects the adaptation of plants to salinity and water deficiency to cut water losses by minimizing transpiration and delaying the onset of more severe stress (Chaves et al 2009; Sucre and Suárez 2011). Also, this may result from the reduction of intercellular spaces in leaves (Delphine et al 1999).

For *C. acutiformis*, the higher mean leaf area recorded under C + compared to those under C- in the first two weeks of exposure is caused by the slightly higher number of leaves albeit statistically insignificant (C + = 5.93 ± 1.1 ; C- = 5.87 ± 0.9) which may be caused by other factors but salinity. However, in the succeeding weeks, under C + less leaves were produced and these had a lower expansion rate thus, the lowest mean leaf area among the treatments from week six until ten (Fig. 3A). This conforms with Munns and Tester (2008) and Munns (2002) who state that cell elongation and cell division rates reduce over

days, due to the osmotic effect of the salt around the roots, resulting in slower leaf initiation and smaller final size.

Despite the generally smaller mean leaf area of *T. latifolia* and *C. acutiformis* under C+ compared to C-, the concentration of their photosynthetic pigments as well as the ratios did not differ. This is contrary to other studies which reported that chlorophyll content in chloroplasts significantly decreases in salt-sensitive plants when exposed to saline environments (Hernández et al 1995). However, Munns and Tester (2008) stated that in some species, salinity can result in smaller and thicker leaves resulting in a higher chloroplast density per unit leaf area, which may be the case for *T. latifolia* and *C. acutiformis*. With this, photosynthetic yield, as well as Δ Yield, were also similar even under high light doses (Fig. 4). Reportedly, salt stress can suppress photosynthesis (Kao et al 2001; Romero-Aranda et al 2001) but others report that the rates of photosynthesis per unit leaf area in salt-treated plants did not change (Rajesh et al 1998; Kurban et al 1999; James et al 2002). Our findings for these two emergent macrophytes are consistent with the latter.

Generally, our findings suggest that salinity stress does not greatly affect the pigment contents and photosynthetic activity of *C. acutiformis* and *T. latifolia* but rather changes the shoot elongation rates and biomass allocation patterns. The relatively higher root:shoot ratios of *C. acutiformis* ($\leq 32\%$) and *T. latifolia* ($\leq 53\%$) under brackish water compared to the other treatments supports this notion, although the difference was not significant due to the low number of replication ($n = 3$; Fig. 5). The relatively higher root:shoot ratios in both species under C+ than in C- is due to the lower dry weight of stem and leaves and higher dry weight of the roots. This entails that root growth is less affected than shoot growth, or root growth may not even decrease at all while shoot growth declines (Munns and Termaat 1986). Increased root:shoot ratio is a common response of non-halophytes to salinity stress to retain toxic ions in the root system and control their translocation to the aerial parts (Hsiao and Xu 2000; Acosta-Motos et al 2017).

Phragmites australis and *Schoenoplectus tabernaemontani* are both less sensitive to salinity. This is shown by the similar response pattern of those plants under freshwater and brackish water with a salinity of 9.58‰ in terms of maximum height, maximum growth rate, leaf area (for *P. australis* only) and root:shoot ratios, as well as photosynthetic pigment ratios. All of these indicators support the claim of Howard et al (2020) that salinity of less than 10‰ is within the normal range of these two wetland species. *P. australis* thrive in areas with conductivities $< 20 \text{ mS cm}^{-1}$ (Burdick et al 2001), and growth deficiency occurs at salinities up to 30‰ (Sinicrope et al 1990). *S. tabernaemontani*, on the other hand, is primarily found in areas with salinities $< 5\%$ although it can withstand up to 10‰ for a short period (Hutchinson 1988; Latham et al 1991).

The significantly lower Δ Yield of *P. australis* under constant brackish water (C+) than in freshwater (C-) at light dose classes $< 20 \text{ mol m}^{-2}$ and $40.1\text{--}60 \text{ mol m}^{-2}$ shows that this species acclimated in a peculiar way to increased salinity. Salt stress is shown to inhibit photosystem II (PS II) activity in some higher plants (Parida et al 2003; Mishra and Tanna 2017) whereas others observed no effect on PS II (Morales et al 1992). However, a decreased Δ Yield at increased salinity for low irradiances compared to freshwater

conditions was not observed yet. As a hypothesis, this could be explained by a shift in photosynthesis-irradiance (P/I)-characteristics towards high-light characteristics after salinity acclimation. It must be considered that water deficiency, which is a major factor for terrestrial plants exposed to saline soils, is not effective for swamp plants. Consequently, the observed effects can be expected to be caused by salinity effects on photosynthesis only and may be compared to results obtained from Cyanobacteria that are often used as model systems for chloroplasts. In salt-adapted cells of the cyanobacterium *Synechocystis* sp., a diminished energy transfer from phycobilisomes to the photosystem II accompanied by increased energy transfer towards PS I has been observed (Schoor et al; Schubert and Hagemann 1990; Schubert et al 1993), resulting in a shift of P/I-characteristics as suggested here. The reason for this was seen in an increased energy demand for osmoregulation, which was fulfilled by cyclic electron transfer driven by PS I and indicated by both increased energy transfer towards photosystem I as well as decreased PS II/PS I ratio (Schubert and Hagemann 1990). However, this is still speculative and requires further investigation. Still, the significant effect seen here demonstrated the capability of *P. australis* for successful adaptation to salinity by physiological mechanisms, namely photosynthesis.

Response Of Macrophytes To Short Salinity Pulses

Our results suggest that the four emergent macrophytes differ in tolerance to frequent brackish water exposure. *T. latifolia* is relatively sensitive to frequent changes in water salinity as shown by the lower maximum heights of *T. latifolia* under treatments A_{2b_2f} and A_{2b_4f} compared to those constantly under freshwater (C-). This could mean that the plants were not able to compensate for the reduced growth rate during the recovery period after being exposed to brackish water for two days. This can be supported further by the lower maximum growth rates under treatment A_{2b_2f}. Under treatment A_{4b_4f}, however, plants may have been stressed during the early stage of development resulting in lower maximum growth rate but they seemed to recover eventually ending their growth with comparable maximum heights like those of treatment C-. Under the latter, the lower mean leaf area in the first few weeks of treatment followed by increased growth as the plant developed could have contributed to this result. *C. acutiformis* showed relative tolerance to the changing salinity pulses as the maximum height, maximum growth rates, root:shoot ratio and pigment ratios did not deviate from those constantly under freshwater.

Phragmites australis is negatively influenced by saltwater at seedling stage (Chambers et al 2003) but it can recover rapidly when salt stress is removed (Mauchamp and Mesleard 2001). This could be confirmed by the similar maximum height and root:shoot ratios between C- and the other treatments. The higher maximum growth rate of *P. australis* under A_{4b_4f} and A_{2b_4f} compared to the other treatments may be caused by other factors (e.g. nutrient access) which were not so important when the plants developed. The similar maximum growth rates of the treatments C+, C- and A_{2b_2f} also suggests that the plants were still at the adaptation stage but were eventually able to keep pace with the other treatments resulting in similar final height and biomass. This would support previous findings that chronic exposure to low salinity and short-term exposure to elevated salinity does not inhibit seedling growth of *P. australis*, and that its tolerance to salinity even increases as it develops (Mauchamp and Mesleard 2001; Chambers et

al 2003). Also, Vasquez et al (2005) stated that European *P. australis* haplotype has higher salinity tolerance than the native variety which explains its rapid establishment and spread in tidal wetlands that experience saltwater intrusion.

Similar mean leaf area between C- and the different frequency of salinity pulses proves that *P. australis* is well-adapted to changing salinity levels making it thrive in tidal and non-tidal wetlands and marshes (Hickmann 1993; Welsh 2003). The relatively lower Chl a:car ratio under different frequencies of salinity pulses suggests salinity stress resulting in decreases in chlorophyll and carotenoid concentrations (Parida and Das 2005; Stepien and Johnson 2009). The increased carotenoid per unit of chlorophyll protects the chloroplast by acting as a photoprotective agent (Maoka 2020). This led to the successful acclimation of *P. australis* resulting in similar maximum height and root:shoot ratio. The significantly higher Δ Yield at light dose class 40.1–60 mol m⁻² under treatment A_{2b_4f} compared to C-, A_{2b_2f} and A_{4b_4f} implies that when there is no limitation in irradiance, photosynthetic efficiency of *P. australis* decreases. This resulted most probably from stomatal closure that decreased carbon assimilation rate (Parida and Das 2005; Sucre and Suárez 2011). Also, the decreased PSII efficiency may be caused by the increase in non-photochemical quenching as a mechanism to safely dissipate excess excitation energy within chlorophyll-containing complexes and prevents the formation of damaging free radicals (Maxwell 2000; Murchie and Lawson 2013; Acosta-Motos et al 2017). However, this higher Δ Yield under A_{2b_4f} seemed to be unrelated to salinity stress as the height and biomass upon termination are both comparable to C- indicating that their biomass production rate is the same. The higher maximum growth rate of A_{2b_4f} may also indicate that the lower photosynthetic efficiency at high irradiance was compensated by the higher MLA specifically from week six until seven.

Results for *S. tabernaemontani* also shows that it can thrive under unstable water regimes with salinities within its tolerance level (Shay and Shay 1986). This is shown by the similarity in the growth responses and photosynthetic yield between treatments of different salinity pulses and those permanently under freshwater (C-). The significantly lower Chl a:b ratio under treatment A_{4b_4f} (2.99 ± 0.03) than C+, C- and A_{2b_2f} is due to low Chl a ($267.2 \mu\text{g g}^{-1}$ FM) and Chl b ($89.3 \mu\text{g g}^{-1}$ FM) content. Reduction in photosynthetic pigments, including Chl a and b, can be interpreted as a sign of salt-induced stress which may have resulted in impaired biosynthesis or accelerated pigment degradation (Ashraf and Harris 2013). In *P. australis*, we also observed a significantly lower Chl a:car under similar treatment (A_{4b_4f}). However, we only had pigment data available for week 10 and, hence, cannot prove this idea here. We recommend further investigation of this aspect to gain better understanding of this phenomenon. Yet, in both species, this has not impaired biomass production.

Conclusions

Overall, our study reveals that all of the tested emergent macrophytes can survive under conditions of short but frequent salinity pulses. *T. latifolia*, however, exhibited more negative responses to salinity and salinity pulses than the other species. The other species, including the salt-sensitive *C. acutiformis*,

seemed to be more resilient towards this changing environmental factor. Moreover, both *T. latifolia* and *C. acutiformis* are more sensitive to salinity and, thus, will likely be affected resulting in growth retardation or may even be eventually replaced by the less salt-sensitive species, *S. tabernaemontani* and *P. australis*, with increased seawater influx into coastal wetlands. Additionally, when climate change-driven sea-level rise and increased precipitation will increase the water levels up to 1.5 m deep, the coverage of *S. tabernaemontani* in coastal wetlands may expand (Nicol et al 2015) while *P. australis* may die after being exposed to water deeper than one meter for at least three years (Shay and Shay 1986). If so, carbon cycling in coastal peatlands may be altered since *S. tabernaemontani* is a non-peat-forming species (Batistel et al 2021). It is noteworthy, however, that the salinity tested in this study is only classified as β -mesohaline (Schubert et al 2017) so results may vary for coastal wetlands which may acquire higher salinity levels hence, further study is necessary.

Declarations

Funding: This study was conducted within the framework of the Research Training Group 'Baltic TRANSCOAST' that is funded by the Deutsche Forschungsgemeinschaft (DFG) under grant number GRK 2000 (www.baltic-transcoast.uni-rostock.de).

Competing Interest: The authors have no relevant financial or non-financial interests to disclose.

Author Contributions: All authors contributed significantly to the study. **Cheryl Batistel:** conceptualization, methodology, data gathering, data analysis and visualization, and preparation of the first draft of the manuscript. **Christian Porsche:** data analysis, visualization and review and editing of the manuscript. **Gerald Jurasinski:** conceptualization, review and editing, supervision and funding acquisition. **Hendrik Schubert:** conceptualization, methodology, review and editing, supervision, and funding acquisition. All authors have read and agreed to the final version of the manuscript.

Data Availability Statement: Data is contained within the article and supplementary materials.

References

1. Acosta-Motos JR, Ortuño MF, Bernal-Vicente A, et al (2017) Plant responses to salt stress: Adaptive mechanisms. *Agronomy* 7:1–38. doi: 10.3390/agronomy7010018
2. Allakhverdiev SI, Sakamoto A, Nishiyama Y, et al (2000) Ionic and osmotic effects of NaCl-induced inactivation of photosystems I and II in *Synechococcus* sp. *Plant Physiology* 123:1047–1056. doi: 10.1104/pp.123.3.1047
3. Ashraf M, Harris PJC (2013) Photosynthesis under stressful environments: An overview. *Photosynthetica* 51:163–190. doi: 10.1007/s11099-013-0021-6
4. BACC II Author Team (2015) Assessment of Climate Change for the Baltic Sea Basin. Assessment of Climate Change for the Baltic Sea Basin. doi: 10.1007/978-3-540-72786-6

5. Batistel CC, Jurasinski G, Schubert H (2021) Salinity exerted little effect on decomposition of emergent macrophytes in coastal peatlands. *Aquatic Botany* 175:103446. doi: 10.1016/j.aquabot.2021.103446
6. Baur O, Kuhn M, Featherstone WE (2013) Continental mass change from GRACE over 2002-2011 and its impact on sea level. *Journal of Geodesy* 87:117–125. doi: 10.1007/s00190-012-0583-2
7. Bełdowska M, Jędruch A, Łęczyński L, et al (2016) Coastal erosion as a source of mercury into the marine environment along the Polish Baltic shore. *Environmental Science and Pollution Research* 23:16372–16382. doi: 10.1007/s11356-016-6753-7
8. Burdick DM, Buchsbaum R, Holt E (2001) Variation in soil salinity associated with expansion of *Phragmites australis* in salt marshes. *Environmental and Experimental Botany* 46:247–261. doi: 10.1016/S0098-8472(01)00099-5
9. Chambers RM, Osgood DT, Bart DJ, Montalto F (2003) *Phragmites australis* invasion and expansion in tidal wetlands: Interactions among salinity, sulfide, and hydrology. *Estuaries* 26:398–406. doi: 10.1007/BF02823716
10. Chaves MM, Flexas J, Pinheiro C (2009) Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. *Annals of Botany* 103:551–560. doi: 10.1093/aob/mcn125
11. Cramer GR (2003) Differential effects of salinity on leaf elongation kinetics of three grass species. *Plant and Soil* 253:233–244. doi: 10.1023/A:1024527401033
12. Delphine S, Alvino A, Zacchini M, Loreto F (1999) Consequences of salt stress on conductance to CO₂ diffusion, Rubisco characteristics and anatomy of spinach leaves. *Aust. J. Plant Physiol.* 25:395–402.
13. Ellenberg H (1974) Zeigerwerte der Gefäßpflanzen Mitteleuropas. *Scripta Geobotanica*
14. Flowers TJ, Colmer TD (2015) Plant salt tolerance: Adaptations in halophytes. *Annals of Botany* 115:327–331. doi: 10.1093/aob/mcu267
15. Genty B, Briantais JM, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta - General Subjects* 990:87–92. doi: 10.1016/S0304-4165(89)80016-9
16. Glenn E, Thompson TL, Frye R, Riley J (1995) Effects of salinity on growth and evapotranspiration. *Water* 52:75–91.
17. Goodman AM, Ganf GG, Dandy GC, et al (2010) The response of freshwater plants to salinity pulses. *Aquatic Botany* 93:59–67. doi: 10.1016/j.aquabot.2010.03.004
18. Groh A, Richter A, Dietrich R (2017) Recent baltic sea level changes induced by past and present ice masses. *Coastal Research Library* 19:55–68. doi: 10.1007/978-3-319-49894-2_4
19. Hadad HR, Mufarrege MM, Di Luca GAD, Maine MA (2017) Salinity and pH effects on floating and emergent macrophytes in a constructed wetland. *Water Science and Technology* 270–275. doi: 10.2166/wst.2018.110

20. Harff J, Lemke W, Lampe R, et al (2007) The Baltic Sea coast - A model of interrelations among geosphere, climate, and anthroposphere. *Special Paper of the Geological Society of America* 426:133–142. doi: 10.1130/2007.2426(09)
21. Herbert ER, Boon P, Burgin AJ, et al (2015) A global perspective on wetland salinization: Ecological consequences of a growing threat to freshwater wetlands. *Ecosphere* 6:1–43. doi: 10.1890/ES14-00534.1
22. Hernández JA, Olmos E, Corpas FJ, et al (1995) Salt-induced oxidative stress in chloroplasts of pea plants. *Plant Science* 105:151–167. doi: 10.1016/0168-9452(94)04047-8
23. Hickmann JC (1993) *The Jepson manual: higher plants of California*. University of California Press, Berkeley
24. Hill MO, Preston CD, Roy DB (2004) *Plant Attributes of British and Irish Plants: Status, Size, Life history, Geography and Habitats*. Centre for Ecology and Hydrology 80.
25. Hopkinson CS, Wolanski E, Cahoon DR, et al (2009) *Coastal wetlands: A synthesis*. Coastal Wetlands: An Integrated Ecosystem Approach, First edit. Elsevier B.V., pp 1–75
26. Howard RJ, Rafferty PS, Johnson DJ (2020) Plant Community Establishment in a Coastal Marsh Restored Using Sediment Additions. *Wetlands* 40:877–892. doi: 10.1007/s13157-019-01217-z
27. Hsiao TC, Xu LK (2000) Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport Theodore. *Journal of Experimental Botany* 51:1595–1616. doi: 10.1093/jexbot/51.350.1595
28. Hutchinson I (1988) Salinity tolerance of plants of estuarine wetlands and associated uplands. Washington State Shorelands and coastal zone management program: Wetlands Section 1–81.
29. IPCC (2014) Summary for policymakers. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects*. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In: Sutton MA, Howard CM, Erisman JW, et al (eds) Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp 1–32
30. IPCC 2019: Summary for Policymakers (2019) *IPCC The Ocean and Cryosphere in a Changing Climate Summary for Policymakers*.
31. James RA, Rivelli AR, Munns R, Von Caemmerer S (2002) Factors affecting CO₂ assimilation, leaf injury and growth in salt-stressed durum wheat. *Functional Plant Biology* 29:1393–1403. doi: 10.1071/FP02069
32. Joosten H (2015) *Peatlands, climate change mitigation and biodiversity conservation*. Peatlands, climate change mitigation and biodiversity conservation. Copenhagen, Denmark
33. Jurasinski G, Janssen M, Voss M, et al (2018) Understanding the coastal ecocline: Assessing sea-land interactions at non-tidal, low-lying coasts through interdisciplinary research. *Frontiers in Marine Science* 5:1–22. doi: 10.3389/fmars.2018.00342
34. Kao WY, Tsai HC, Tsai TT (2001) Effect of NaCl and nitrogen availability on growth and photosynthesis of seedlings of a mangrove species, *kandelia candel* (L.) Druce. *Journal of Plant*

- Physiology 158:841–846. doi: 10.1078/0176-1617-00248
35. Kurban H, Saneoka H, Nehira K, et al (1999) Effect of salinity on growth, photosynthesis and mineral composition in leguminous plant *Alhagi pseudoalhagi* (Bieb.). *Soil Science and Plant Nutrition* 45:851–862. doi: 10.1080/00380768.1999.10414334
 36. Latham PJ, Pearlstine LG, Kitchens WM (1991) Spatial distributions of the softstem bulrush, *Scirpus validus*, across a salinity gradient. *Estuaries* 14:192–198. doi: 10.2307/1351693
 37. Macek P, Rejmánková E (2007) Response of emergent macrophytes to experimental nutrient and salinity additions. *Functional Ecology* 21:478–488. doi: 10.1111/j.1365-2435.2007.01266.x
 38. Maoka T (2020) Carotenoids as natural functional pigments. *Journal of Natural Medicines* 74:1–16. doi: 10.1007/s11418-019-01364-x
 39. Mauchamp A, Mesleard F (2001) Salt tolerance in *Phragmites australis* populations from coastal Mediterranean marshes. *Aquatic Botany* 70:39–52. doi: 10.1016/S0304-3770(00)00140-6
 40. Maxwell K and JGN (2000) Chlorophyll fluorescence—a practical guide. *Journal of Experimental Botany* 51:659–668.
 41. Mishra A, Tanna B (2017) Halophytes: Potential resources for salt stress tolerance genes and promoters. *Frontiers in Plant Science* 8:1–10. doi: 10.3389/fpls.2017.00829
 42. Morales F, Abadía A, Gómez-Aparisi J, Abadía J (1992) Effects of combined NaCl and CaCl₂ salinity on photosynthetic parameters of barley grown in nutrient solution. *Physiologia Plantarum* 86:419–426. doi: 10.1111/j.1399-3054.1992.tb01338.x
 43. Munns R (2002) Comparative physiology of salt and water stress. *Plant, Cell and Environment* 25:239–250. doi: 10.1046/j.0016-8025.2001.00808.x
 44. Munns R, Termaat A (1986) Whole-plant responses to salinity. *Australian Journal of Plant Physiology* 13:143–160. doi: 10.1071/PP9860143
 45. Munns R, Tester M (2008) Mechanisms of salinity tolerance. *Annual Review of Plant Biology* 59:651–681. doi: 10.1146/annurev.arplant.59.032607.092911
 46. Murchie EH, Lawson T (2013) Chlorophyll fluorescence analysis: A guide to good practice and understanding some new applications. *Journal of Experimental Botany* 64:3983–3998. doi: 10.1093/jxb/ert208
 47. Newell N (2013) Review: Effects of Soil Salinity on Plant Growth. *Plant Physiology* 1–4.
 48. Nicol J, Gehrig S, Frahn K (2015) Establishment success and benefits to the aquatic plant community of planting *Schoenoplectus validus* around the shorelines of lakes Alexandrina and Albert-2014.
 49. Nielsen DL, Brock MA, Rees GN, Baldwin DS (2003) Effects of increasing salinity on freshwater ecosystems in Australia. *Australian Journal of Botany* 51:655–665. doi: 10.1071/BT02115
 50. Oppenheimer M, Glavovic B (2019) Chapter 4: Sea Level Rise and Implications for Low Lying Islands, Coasts and Communities. IPCC SR Ocean and Cryosphere.

51. Orlovsky N, Japakova U, Zhang H, Volis S (2016) Effect of salinity on seed germination, growth and ion content in dimorphic seeds of *Salicornia europaea* L. (Chenopodiaceae). *Plant Diversity* 38:183–189. doi: 10.1016/j.pld.2016.06.005
52. Pantin F, Simonneau T, Rolland G, et al (2011) Control of leaf expansion: A developmental switch from metabolics to hydraulics. *Plant Physiology* 156:803–815. doi: 10.1104/pp.111.176289
53. Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: A review. *Ecotoxicology and Environmental Safety* 60:324–349. doi: 10.1016/j.ecoenv.2004.06.010
54. Parida AK, Das AB, Mitra B (2003) Effects of NaCl stress on the structure, pigment complex composition, and photosynthetic activity of mangrove *Bruguiera parviflora* chloroplasts. *Photosynthetica* 41:191–200. doi: 10.1023/B:PHOT.0000011951.37231.69
55. Parish F, Sirin A, Charman D, et al (2008) Assessment on Peatlands, Biodiversity and Climate Change: Main Report. Global Environment Centre, Kuala Lumpur and Wetlands International, Wageningen.
56. Passaro M, Müller FL, Oelsmann J, et al (2021) Absolute Baltic Sea Level Trends in the Satellite Altimetry Era: A Revisit. *Frontiers in Marine Science* 8:1–16. doi: 10.3389/fmars.2021.647607
57. Porra RJ, Thompson WA, Kriedemann PE (1989) Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochimica et Biophysica Acta* 384–394.
58. R Core Team (2020) R: A language and environment for statistical computing. R Found. Stat. Comput.
59. Rajesh A, Arumugam R, Venkatesalu V (1998) Growth and photosynthetic characteristics of *Ceriops roxburghiana* under NaCl stress. *Photosynthetica* 35:285–287.
60. Rasmuson KE, Anderson JE (2002) Salinity affects development, growth, and photosynthesis in cheatgrass. *Journal of Range Management* 55:80–87. doi: 10.2307/4003267
61. Richards FJ (1959) A flexible growth function for empirical use. *Journal of Experimental Botany* 10:290–301. doi: 10.1093/jxb/10.2.290
62. Richter A, Groh A, Dietrich R (2012) Geodetic observation of sea-level change and crustal deformation in the Baltic Sea region. *Physics and Chemistry of the Earth* 53–54:43–53. doi: 10.1016/j.pce.2011.04.011
63. Romero-Aranda R, Soria T, Cuartero J (2001) Tomato plant-water uptake and plant-water relationships under saline growth conditions. *Plant Science* 160:265–272. doi: 10.1016/S0168-9452(00)00388-5
64. Schoor A, Schubert H, Hagemann M Immediate effects of a salt shock on energy distribution to the photosystem of *Synechocystis* sp. PCC 6803. International Photosynthesis congress; 10th, Photosynthesis: from light to biosphere. Kluwer Academic; , Dordrecht, Netherlands, Montpellier; France, pp 697–700
65. Schubert H, Fulda S, Hagemann M (1993) Effects of Adaptation to Different Salt Concentrations on Photosynthesis and Pigmentation of the Cyanobacterium *Synechocystis* sp. PCC 6803. *Journal of*

- Plant Physiology 142:291–295. doi: [https://doi.org/10.1016/S0176-1617\(11\)80425-6](https://doi.org/10.1016/S0176-1617(11)80425-6)
66. Schubert H, Hagemann M (1990) Salt effects on 77K fluorescence and photosynthesis in the cyanobacterium *Synechocystis* sp. PCC 6803. FEMS Microbiology Letters 71:169–172. doi: [10.1016/0378-1097\(90\)90051-Q](https://doi.org/10.1016/0378-1097(90)90051-Q)
67. Schubert H, Schories D, Schneider B, Selig U (2017) Brackish water as an environment. Biological Oceanography of the Baltic Sea. Springer, pp 3–21
68. Shay JM, Shay CT (1986) Prairie marshes in western Canada, with specific reference to the ecology of five emergent macrophytes. Canadian Journal of Botany 64:443–454. doi: [10.1139/b86-059](https://doi.org/10.1139/b86-059)
69. Sinicrope TL, Hine PG, Warren RS, Niering WA (1990) Restoration of an impounded salt marsh in New England. Estuaries 13:25–30. doi: [10.2307/1351429](https://doi.org/10.2307/1351429)
70. Stagg CL, Baustian MM, Perry CL, et al (2018) Direct and indirect controls on organic matter decomposition in four coastal wetland communities along a landscape salinity gradient. Journal of Ecology 106:655–670. doi: [10.1111/1365-2745.12901](https://doi.org/10.1111/1365-2745.12901)
71. Stepien P, Johnson GN (2009) Contrasting responses of photosynthesis to salt stress in the glycophyte *Arabidopsis* and the halophyte *Thellungiella*: Role of the plastid terminal oxidase as an alternative electron sink. Plant Physiology 149:1154–1165. doi: [10.1104/pp.108.132407](https://doi.org/10.1104/pp.108.132407)
72. Stofberg SF, Klimkowska A, Paulissen M, et al (2015) Effects of salinity on growth of plant species from terrestrializing fens. Aquatic Botany 121:83–90. doi: [10.1016/j.aquabot.2014.12.004](https://doi.org/10.1016/j.aquabot.2014.12.004)
73. Sucre B, Suárez N (2011) Effect of salinity and PEG-induced water stress on water status, gas exchange, solute accumulation, and leaf growth in *Ipomoea pes-caprae*. Environmental and Experimental Botany 70:192–203. doi: [10.1016/j.envexpbot.2010.09.004](https://doi.org/10.1016/j.envexpbot.2010.09.004)
74. Sudhir P, Murthy SDS (2004) Effects of salt stress on basic processes of photosynthesis. Photosynthetica 42:481–486. doi: [10.1007/S11099-005-0001-6](https://doi.org/10.1007/S11099-005-0001-6)
75. Tanneberger F, Wichtmann W (2011) Carbon credits from peatland rewetting Climate - biodiversity - land use. Schweizerbart Science Publishers, Stuttgart, Germany
76. Tiner RW (2018) Hydrology of coastal wetlands. The Wetland Book: I: Structure and Function, Management, and Methods 217–231. doi: [10.1007/978-90-481-9659-3_63](https://doi.org/10.1007/978-90-481-9659-3_63)
77. Varadhan R, Gilbert PD (2009) BB: An R package for solving a large system of nonlinear equations and for optimizing a high-dimensional nonlinear objective function. Journal of Statistical Software 32:1–26. doi: [10.18637/jss.v032.i04](https://doi.org/10.18637/jss.v032.i04)
78. Vasquez EA, Glenn EP, Brown JJ, et al (2005) Salt tolerance underlies the cryptic invasion of North American salt marshes by an introduced haplotype of the common reed *Phragmites australis* (Poaceae). Marine Ecology Progress Series 298:1–8. doi: [10.3354/meps298001](https://doi.org/10.3354/meps298001)
79. Walsby AE (1997) Modelling the daily integral of photosynthesis by phytoplankton: Its dependence on the mean depth of the population. Hydrobiologia 349:65–74. doi: [10.1023/a:1003045528581](https://doi.org/10.1023/a:1003045528581)
80. Wang Y, Nii N (2000) Changes in chlorophyll, ribulose biphosphate carboxylase-oxygenase, glycine betaine content, photosynthesis and transpiration in *Amaranthus tricolor* leaves during salt stress.

81. Welsh SL (2003) A Utah flora. Print Services, Brigham Young University, Provo, Utah, U.S.A.
82. Xi H, Feng Q, Zhang L, et al (2016) Effects of water and salinity on plant species composition and community succession in Ejina Desert Oasis, northwest China. *Environmental Earth Sciences* 75:1–16. doi: 10.1007/s12665-015-4823-7
83. Zerbe S, Steffenhagen P, Parakenings K, et al (2013) Ecosystem service restoration after 10 years of rewetting peatlands in NE Germany. *Environmental Management* 51:1194–1209. doi: 10.1007/s00267-013-0048-2
84. Zhu J (2007) Plant Salt Stress. *Encyclopedia of Life Sciences (ELS)*. doi: 10.1002/9780470015902.a0001300.pub2

Figures

Figure 1

Maximum height (cm; n=15) of the four macrophyte species under different treatments. Different letters above the boxes represent significant differences between treatments of the same species (p-value $\leq$ 0.05) calculated with ANOVA *post hoc* multiple comparisons using Tukey's HSD; absence of letters above the boxes means no significant difference found between treatments

Figure 2

Maximum growth rate (cm d⁻¹; n=15) of the four macrophytes under different treatments. Different letters above the boxes represent significant differences between treatments of the same species (p-value $\leq$ 0.05) calculated with ANOVA *post hoc* multiple comparisons using Tukey's HSD; absence of letters above the boxes means no significant difference found between treatments

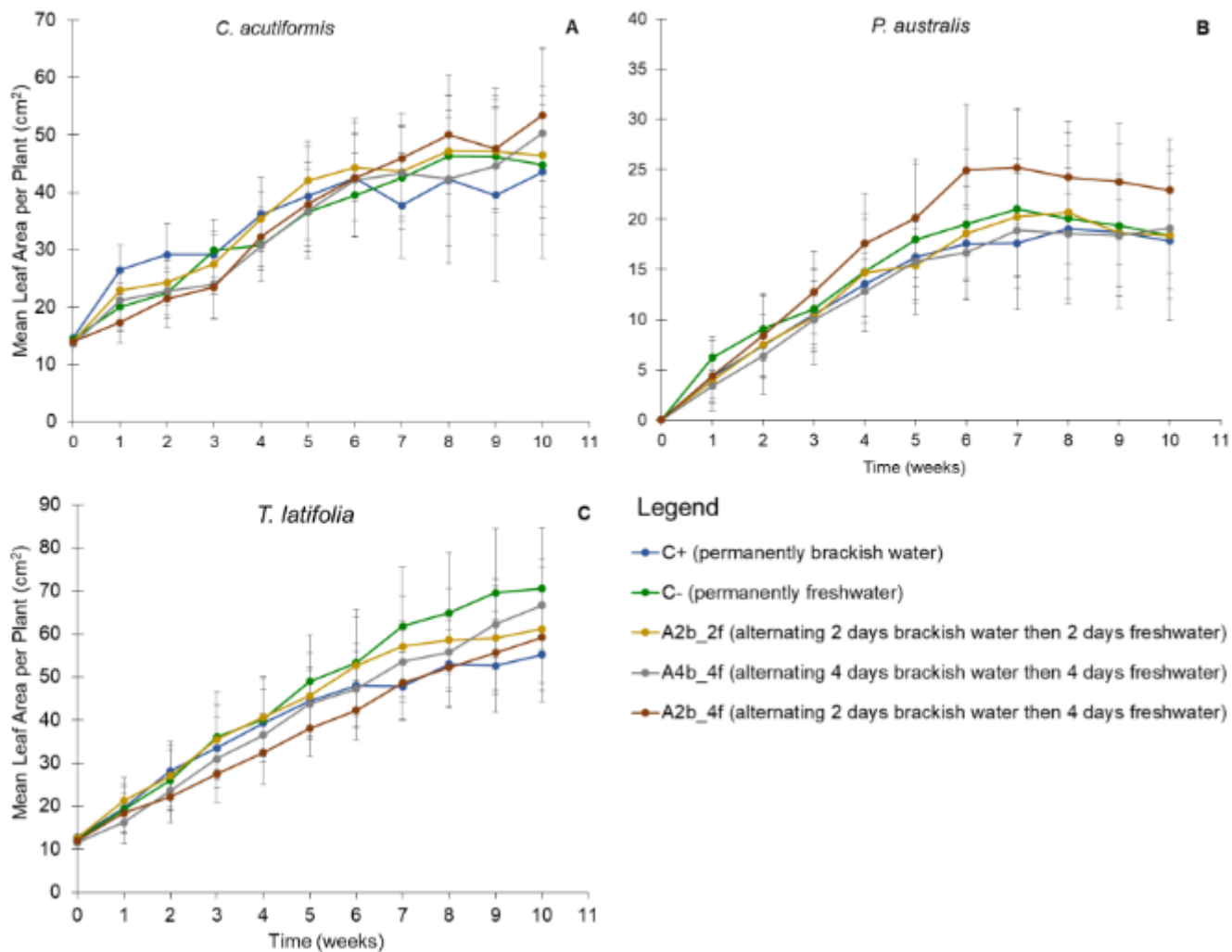


Figure 3

Mean leaf area (n=15) per individual of A) *C. acutiformis*, B) *P. australis* and C) *T. latifolia* under different treatments over time (weeks). Vertical lines represent standard deviation

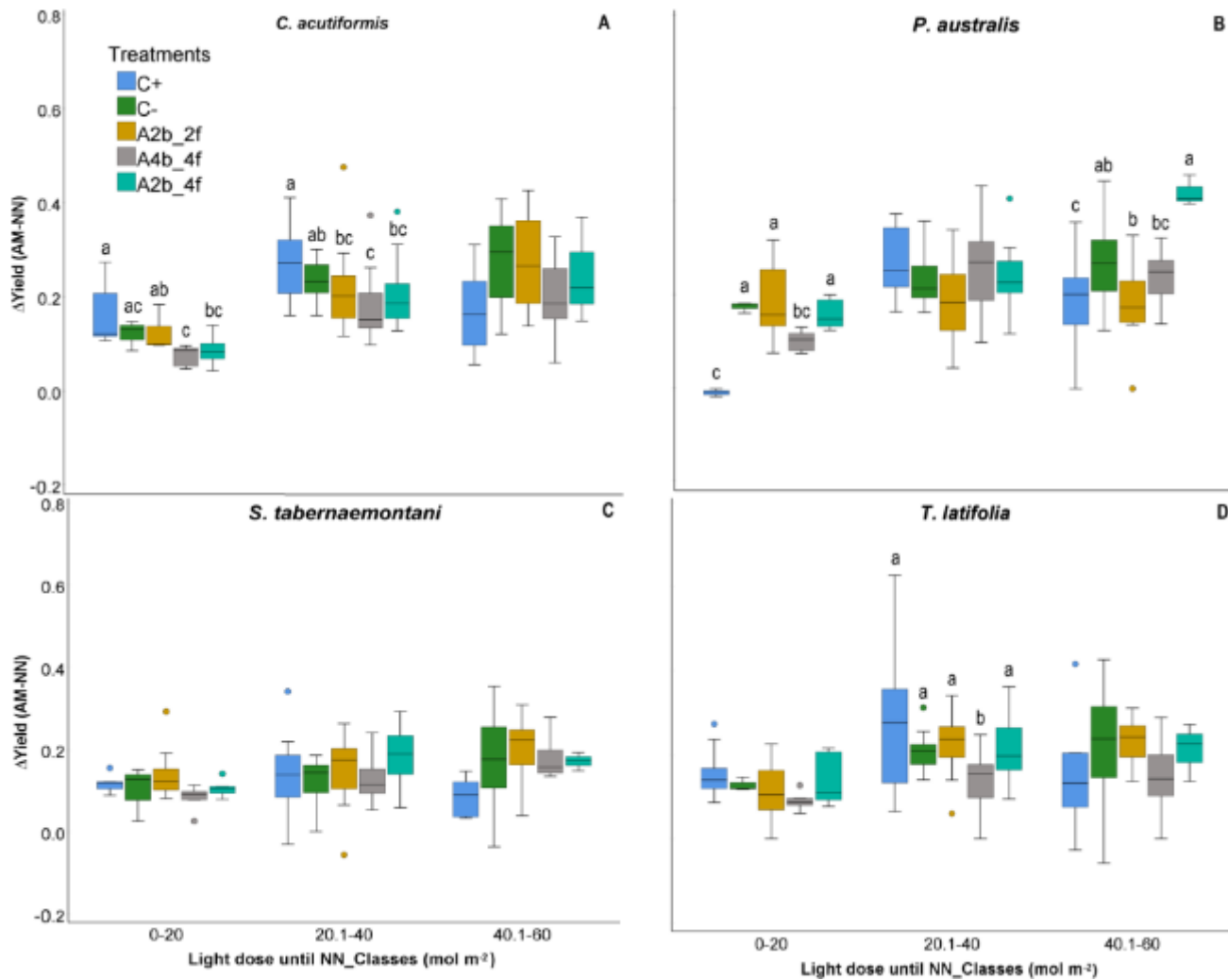


Figure 4

Difference in photosynthetic yield (ΔYield) between morning (AM) and noon (NN) measurements of the four macrophytes A) *C. acutiformis*; B) *P. australis*; C) *S. tabernaemontani*; D) *T. latifolia* under different treatments classified into classes based on light dose received. Different letters above the boxes represent significant differences between treatments of the same species ($p\text{-value} \leq 0.05$; $n \geq 25$) calculated with Kruskal-Wallis Test *post hoc* multiple comparisons using Dunn's pairwise; absence of letters above the boxes means no significant difference found between treatments

Figure 5

Mean root:shoot ratio of the macrophytes after 10 weeks of treatment application. Error bars represent standard deviation ($n=3$). Different letters above the boxes represent significant differences between treatments of the same species ($p\text{-value} \leq 0.05$; ANOVA *post hoc* multiple comparisons using Tukey's HSD); absence of letters above the boxes means no significant difference found between treatments

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryData.pdf](#)