



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

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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, chlorophyll fluorescence, root:shoot ratio and photosynthetic pigments were measured. Salinity suppressed the growth of *T. latifolia* resulting in shorter height, smaller mean leaf area and higher root:shoot ratio. *Carex acutiformis* had smaller mean leaf area and higher root:shoot ratio. Photosynthetic pigment and chlorophyll fluorescence of both species were not affected. Shorter but frequent salinity pulses (alternate 2 days brackish – 2 days freshwater, and 2 days brackish – 4 days freshwater) decreased the leaf area 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*. *Phragmites australis* showed signs of successful acclimation through decreased chlorophyll a:carotenoid ratio and high fluorescence Δ yield at low and high 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.

Zusammenfassung

Bei einem Anstieg des Meeresspiegels verstärkt sich der Salzwassereinfluss in küstennahen Feuchtgebieten. Die Folge ist osmotischer Stress, der zu Veränderungen der Vegetationszusammensetzung führen kann. In der hier vorgestellten Arbeit stehen vor allem die Auswirkungen von kurzzeitigen Impulsen, wie sie bei Hochwasserereignissen zu erwarten sind, im Mittelpunkt. Dafür wurden *Typha latifolia*, *Carex acutiformis*, *Schoenoplectus tabernaemontani* und *Phragmites australis* verschiedenen osmotischen Stressregimes ausgesetzt (2 Tage Brackwasser—2 Tage Süßwasser; 4 Tage Brackwasser—4 Tage Süßwasser; 2 Tage Brackwasser—4 Tage Süßwasser sowie die entsprechenden Kontrollen mit permanenter Süß- bzw. Brackwasserexposition). Als Parameter wurden Pflanzenhöhe, Blattfläche, Photosyntheseyield, Wurzel:Spross-Verhältnis und Pigmentgehalte gemessen. Beobachtet wurden ein verringertes Wachstum von *T. latifolia* (Längenwachstum, mittlere Blattfläche und Spross:Wurzelverhältnis verringert) und *C. acutiformis* (mittlere Blattfläche und Wurzel:Sprossverhältnis verringert). Bei beiden Arten war allerdings weder der Photosyntheseyield beeinträchtigt noch traten Veränderungen in der Pigmentation auf. Das Wachstum von *P. australis* und *S. tabernaemontani* dagegen wurde weder durch den Salzgehalt noch

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durch die Frequenz des Salinitätswechsels beeinträchtigt. Bei diesen Arten konnten Anzeichen einer erfolgreichen Anpassung des Photosyntheseapparates (Chl.a/Car-Verhältnis sowie Photosyntheseyield) beobachtet werden. Die Ergebnisse deuten darauf hin, dass *T. latifolia* und *C. acutiformis* bei zunehmendem Salzeinfluss in Stresssituationen geraten können, die bis zur Verdrängung durch die besser angepassten Arten *S. tabernaemontani* und *P. australis* gehen können.

Keywords Salinity stress · Salinisation · Coastal wetlands · Peatland emergent macrophytes

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). 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). 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 from subtidal depths to the landward edge

(Wolanski 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, 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 (Bełdowska 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 peatlands. 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, Oldenburg, Germany). Water was taken from the Warnow River that traverses the state of Mecklenburg-Vorpommern, Northeast Germany specifically in Mühlendamm (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) × 49 cm (width) × 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.

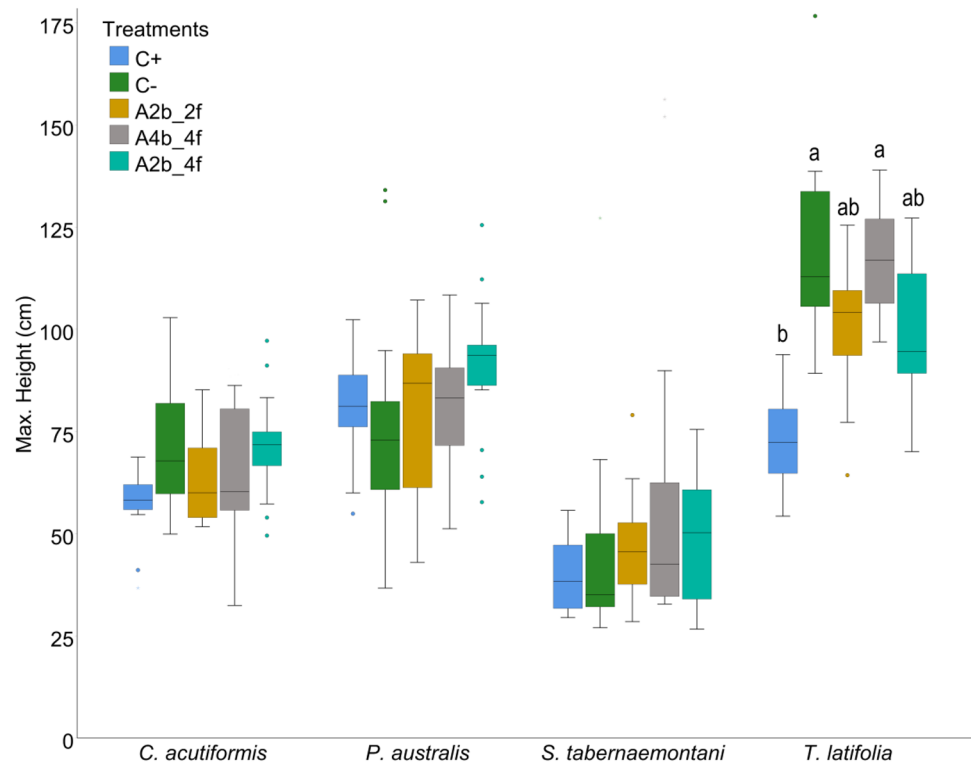
Six pots of seedlings for each species, *P. australis*, *T. latifolia*, *C. acutiformis* and *S. tabernaemontani*, were transplanted in a row, arranged randomly, per box. Treatments were applied for 10 weeks to each designated box after the 3-week establishment period wherein plants were exposed to freshwater under waterlogged conditions. Water was changed 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 water according to treatment into each box daily to replenish water loss due to evapotranspiration.

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

Fig. 1 Maximum height (cm; $n=15$) of the four emergent macrophytes under different treatments. Different letters above the boxes represent significant differences between treatments of the same species ($p\text{-value} \leq 0.05$) using Tukey's HSD multiple comparisons; absence of letters above the boxes means no significant difference found between treatments



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 Eq. 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, cm^2) was calculated

by multiplying the leaf length and width, assuming a nearly rectangular shape. The sum of all leaf area per individual plant was taken and the mean LA (MLA) is the average of all individuals 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 h 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 h 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*, the middle part of the stem was measured 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):

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

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

F_m' = 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 packages BB (Varadhan and Gilbert 2009). For the linear mixed models, we used the lme4 package for R (Bates et al. 2015). Resulting parameters of the growth model (i.e. maximum height and maximum growth rate) were analysed according to the experimental design to determine the effects of salinity regimes, species and its interactions under account of random effects. Therefore, a linear model with treatment (salinity regimes) and species as fixed factors and box as random factors. Additionally, chl a:b, chl a:car and root:shoot ratios were analysed, after checking for normality and variance homogeneity, using ANOVA with treatment (salinity regimes) as a factor. Post hoc pairwise multiple comparisons were carried out using Tukey's Honestly Significant Difference (HSD) against an alpha-level of 0.05 to identify difference between treatments. For the Δ Yield under certain light dose classes, Kruskal–Wallis test was used followed by Dunn's pairwise post hoc comparisons when results were significant at 0.05 alpha level since requirements for ANOVA were not met. For leaf area, a linear mixed model with repeated measurements was used to analyse the effects of salinity and species with respect to week number.

Results

Plant Height and Growth Rate

The maximum plant heights of the four emergent macrophytes relatively varied between treatments for each species (Fig. 1). However, statistically, the maximum heights of *Carex acutiformis*, *Phragmites australis* and *Schoenoplectus tabernaemontani* were not significantly affected by any of the treatments. In contrast, *Typha latifolia* showed significant growth suppression in response to both salinity and salinity pulses. Salinity stress (C+) resulted in 40% decrease in height of *T. latifolia* compared to those under freshwater (C-) condition (p -value = 0.004). The maximum height of *T. latifolia* exposed to A_{4b_4f} pulse was also significantly taller

than C+ (p -value = 0.006). Relatively more frequent salinization (A_{2b_2f} and A_{2b_4f}) also inhibited the plant height of *T. latifolia* by 17% although statistically not different.

The maximum growth rates of the four emergent macrophytes were neither significantly affected by salinity nor the different frequency of salinity pulses (Fig. 2).

Leaf Area

The development of the mean leaf area of all three species (excluding *S. tabernaemontani*) relatively differed between treatment and species over time (weeks; Fig. 3; Table 1). In the first few weeks of brackish water exposure, both salinity and salinity pulses did not significantly affect the mean leaf area of all species. In *C. acutiformis*, the mean leaf area under treatment C+ started to differ significantly (p -value < 0.05) from the other treatments, except A_{4b_4f} , in week seven (Table 1). In week nine, treatment C+ was only different from C- and A_{2b_2f} but in week 10, the mean leaf area of those under salinity pulses A_{4b_4f} and A_{2b_4f} were significantly larger than C+. For *T. latifolia*, the mean leaf area of C- was consistently the largest among the treatments from week five. The mean leaf area of treatment A_{2b_4f} was smaller than C- and A_{2b_2f} (p -value < 0.05). In week six, the mean leaf area of C+ started to decline relative to the other treatments resulting in smaller leaves compared to C- (p -value < 0.01) from week six until termination. The mean leaf area under salinity pulse A_{2b_4f} was also smaller

than C- (p -value < 0.001) from week five until ten. Treatment A_{2b_2f} also started to decrease from week seven. This resulted in significantly smaller leaf area than C- in week ten (p -value < 0.01). Salinity and salinity pulses did not cause significant effect on the mean leaf area (p -value > 0.05) of *P. australis* although A_{2b_4f} was generally larger than the other treatments.

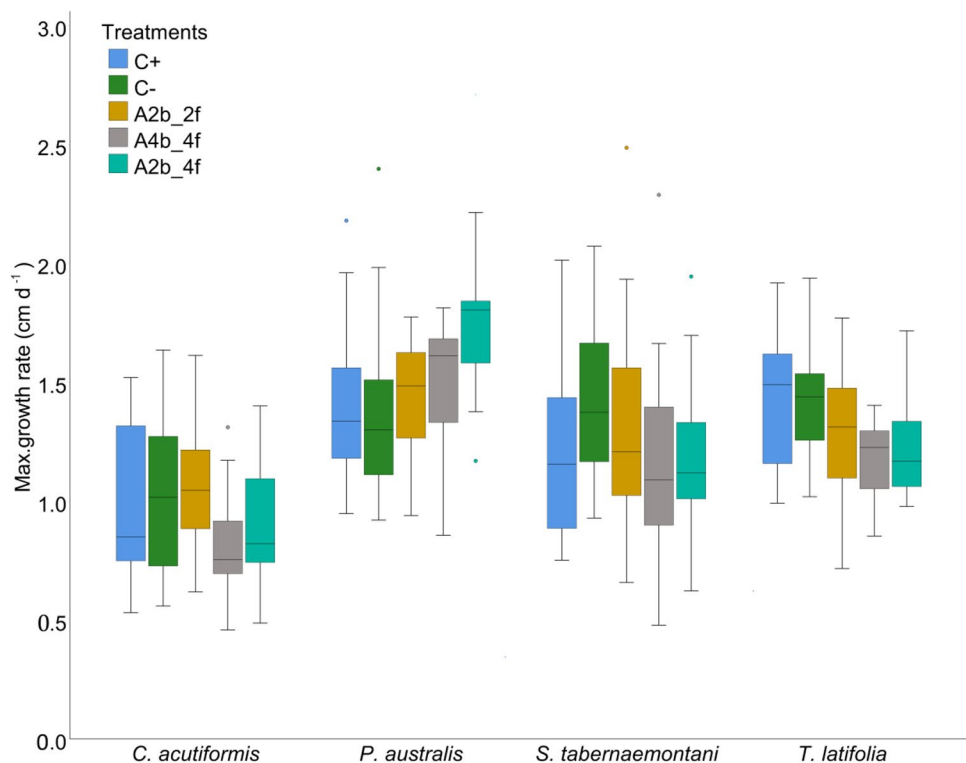
Photosynthetic Pigments

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).

Photosynthetic Yield

The difference in yield (Δ Yield) between morning (AM) and noon (NN) under light dose classes varies between treatment for each species (Fig. 4A–D). The mean Δ Yield in *C. acutiformis* from A_{4b_4f} was lower than in the other treatments

Fig. 2 Maximum growth rate (cm d^{-1} ; $n = 15$) of the four emergent macrophytes under different treatments. Different letters above the boxes represent significant differences between treatments of the same species (p -value ≤ 0.05) using Tukey's HSD multiple comparisons; absence of letters above the boxes means no significant difference found between treatments



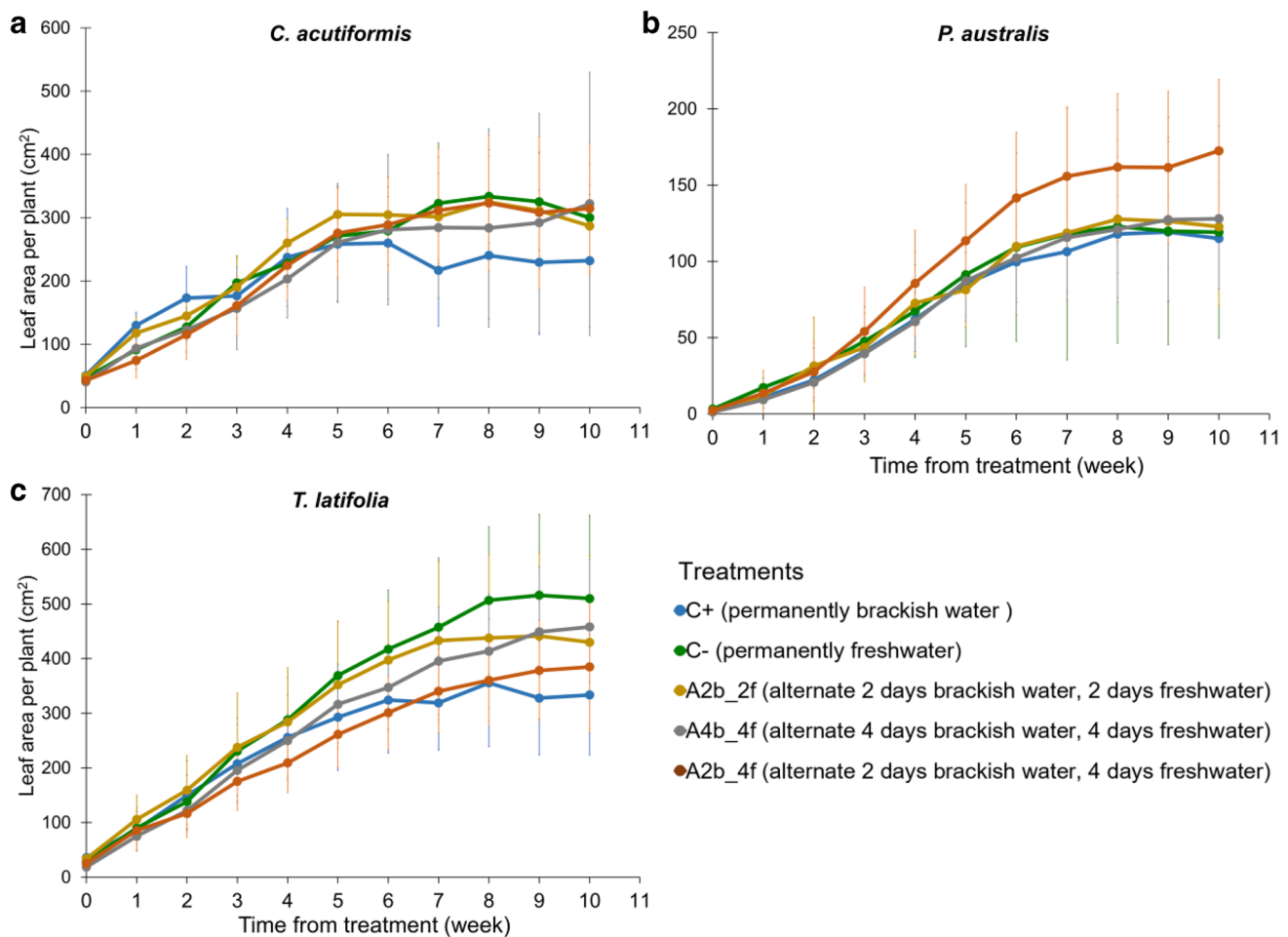


Fig. 3 Mean leaf area ($n=15$) per individual of **a)** *C. acutiformis*, **b)** *P. australis* and **c)** *T. latifolia* under different salinity regimes over time (weeks). Vertical lines represent standard deviation

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

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

($p < 0.05$) 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 $20.1\text{--}40 \text{ mol m}^{-2}$ light dose. There was no difference between treatments at $40.1\text{--}60 \text{ mol m}^{-2}$ light dose in both species. For *P. australis*, the ΔYield of

Table 2 Mean Chl a:b and Chl a:car ratios ($\pm$ SD; $n=3$) of the four emergent macrophytes after ten weeks of treatment application. Different letter superscripts represent significant differences between treatments of the same species (p -value ≤ 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 $\pm$ 0.97	3.25 $\pm$ 0.06 ^{ab}	3.47 $\pm$ 0.17	3.19 $\pm$ 0.06
	C-	3.32 $\pm$ 0.13	3.06 $\pm$ 0.10 ^{ab}	3.98 $\pm$ 0.31	3.11 $\pm$ 0.12
	A _{2b-2f}	3.31 $\pm$ 0.13	3.29 $\pm$ 0.15 ^a	3.36 $\pm$ 0.32	3.14 $\pm$ 0.01
	A _{4b-4f}	2.98 $\pm$ 0.01	2.99 $\pm$ 0.03 ^c	2.74 $\pm$ 0.83	3.07 $\pm$ 0.03
	A _{2b-4f}	2.68 $\pm$ 0.61	3.03 $\pm$ 0.03 ^{bc}	3.33 $\pm$ 0.27	3.35 $\pm$ 0.39
Chl a:Car	C+	3.22 $\pm$ 0.58	4.39 $\pm$ 0.12	3.90 $\pm$ 0.40 ^{ab}	4.08 $\pm$ 0.19
	C-	3.97 $\pm$ 0.40	4.31 $\pm$ 0.64	4.34 $\pm$ 0.60 ^a	3.61 $\pm$ 0.26
	A _{2b-2f}	4.24 $\pm$ 0.34	4.63 $\pm$ 0.12	3.35 $\pm$ 0.14 ^{ab}	3.90 $\pm$ 0.17
	A _{4b-4f}	4.17 $\pm$ 0.22	4.83 $\pm$ 0.07	2.53 $\pm$ 0.68 ^b	3.84 $\pm$ 0.12
	A _{2b-4f}	3.73 $\pm$ 0.58	4.01 $\pm$ 0.33	2.91 $\pm$ 1.05 ^{ab}	3.71 $\pm$ 0.12

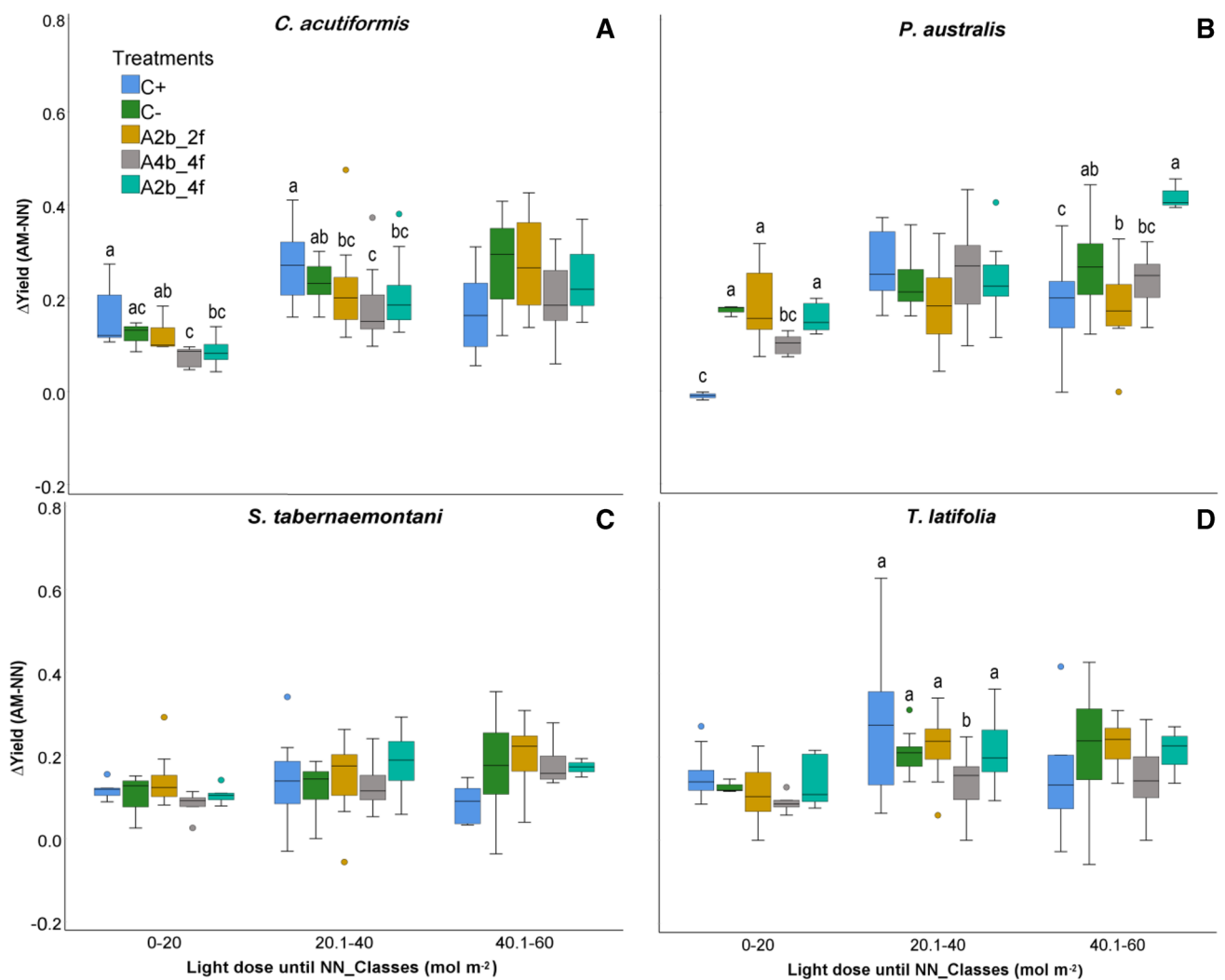


Fig. 4 Difference in photosynthetic yield (Δ Yield) between morning (AM) and noon (NN) measurements of the four emergent macrophytes under different treatments grouped into classes based on light dose received. Different letters above the boxes represent significant

differences between treatments of the same species (p -value ≤ 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

C+ was significantly lower than most of the other treatments at $< 20 \text{ mol m}^{-2}$ light dose. At $40.1\text{--}60 \text{ mol m}^{-2}$ light dose, C+ differed significantly from C- and A_{2b_4f}. Both salinity and salinity pulses showed no treatment effects on the Δ Yield of *S. tabernaemontani*, regardless of the light dose received.

Root:Shoot Ratio

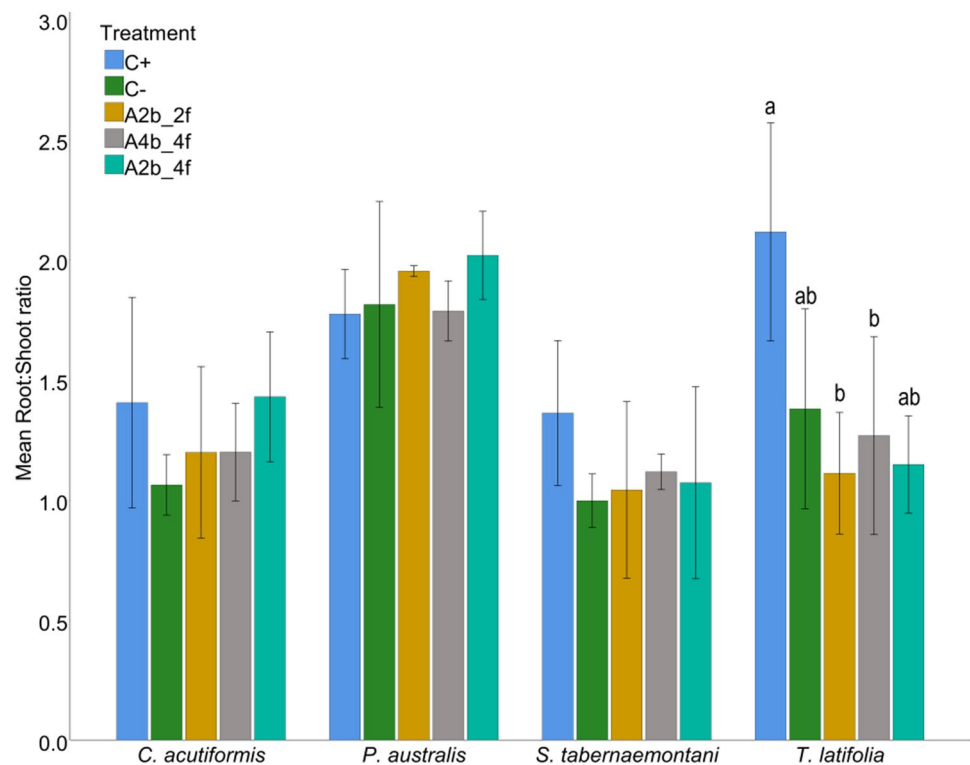
The root:shoot ratio of all macrophytes after ten weeks differed between treatments for each species with values ranging from 0.63 to 2.60 (Fig. 5). All species, except *P. australis*, generally showed an increased root:shoot ratio when permanently exposed to brackish water relative to freshwater condition. 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 ($p\text{-value} < 0.05$) of *T. latifolia* was observed under relatively frequent salinity pulses (A_{2b_2f} and A_{2b_4f}) compared to C+.

Discussion

Response of Emergent Macrophytes to Salinity

Our results reveal that the four emergent macrophytes respond differently to salinity and short salinity pulses. The shorter maximum height of *T. latifolia* under constant brackish water than those in freshwater (C-; Fig. 1) suggests that this species is more sensitive to salinity. Height shortening indicates salinity stress confirming that *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). *Typha latifolia* under brackish water had consistently lower relative growth rate than in freshwater from week one until week ten (please see Supplementary 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 this 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.

Fig. 5 Mean root:shoot ratio of the emergent 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



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 brackish water exposure (please see Supplementary 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*, although the maximum height and maximum growth rates between freshwater and brackish water conditions did not differ significantly, the relative growth rate of C- is generally higher than C+ (Supplemental Table 1). More pronounced effect of salinity stress on the species is manifested in the leaf area (Fig. 3A). The smaller leaf area under treatment C+ from week seven resulted from the lower expansion rate starting week five (Supplementary Table 2). 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. This findings support Hill et al. (2004) that the Ellenberg indicator value of *C. acutiformis* for salt tolerance is also zero.

Despite the 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 support 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 salinity $< 20\%$ (Burdick et al. 2001), and growth deficiency occurs at salinities up to 30‰ (Sinicrope et al. 1990). *Schoenoplectus 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. 1995; 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 Emergent Macrophytes to Short Salinity Pulses

Our results suggest that the four emergent macrophytes respond differently to frequent brackish water exposure. *Typha latifolia* is relatively sensitive to frequent changes in water salinity as shown by the relatively shorter maximum heights under treatments A_{2b_2f} and A_{2b_4f} compared to those constantly under freshwater (C-) albeit statistically insignificant. A more distinct indicator of salinity stress is shown by the lower mean leaf area of those under frequent salinity pulses resulting from the lesser number of leaves produced by the plants under treatments A_{2b_2f} and A_{2b_4f}. This could mean that the plants were not able to compensate for the reduced leaf initiation rate during the recovery period after being exposed to brackish water for two days. As mentioned above, leaf growth reduction is the earliest response of glycophytes exposed to salinity stress. Additionally, reducing the leaf canopy area could be a mechanism to minimize water loss by transpiration (Munns and Termaat 1986; Acosta-Motos et al. 2017). In contrast, plants under treatment A_{4b_4f} may have been able to recover once they were exposed again to freshwater condition for four days resulting in comparable maximum growth rate, height and leaf area with those of treatment C-. *Carex 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 permanently under freshwater.

Phragmites australis may be 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 growth rate, maximum height and root:shoot ratios between C- and the other treatments. This would support previous findings that chronic exposure to low salinity and short-term exposure to elevated salinity does not inhibit the 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 and Johnson 2000; Murchie and Lawson 2013). 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 mean leaf area specifically from week six until seven.

Results for *S. tabernaemontani* also show 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. *Typha 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 frequent but short salinity exposure. Moreover, both *T. latifolia* and *C. acutiformis* are more sensitive to salinity and, thus, long exposure to brackish water will likely affect both species resulting in growth retardation or may even be eventually outcompeted 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.

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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.

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Data Availability All data is contained within the article and supplementary materials.

Declarations

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

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