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Salinity effects on species composition, productivity and decomposition of macrophytes in coastal peatlands

Salinitätseffekte auf die Artenzusammensetzung, Produktivität und Zersetzung von Makrophyten in küstennahen Moorgebieten

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Summary

Global warming causes global sea level rise, more intense and frequent extreme weather events and changed precipitation patterns, and is predicted to intensify in the future. These phenomena raised global concern since they will most likely cause coastal hazards such as submergence or flooding and erosion, which may significantly affect the low-lying coastal ecosystems. With this, the research training group “Baltic TRANSCOAST”, which aims to enhance our knowledge of the shallow coast ecocline, was conceptualized. The research aims to understand how the marine coastal zone is influenced by terrestrial processes and *vice versa*. As one of the components, this thesis investigates the impacts of changing salinity and flooding on coastal wetland vegetation.

To understand how the vegetation would react to future environmental changes (i.e. salinity increase, frequent flooding), a field survey of the macrophytes was initially done in four neighboring peatlands of slightly different salinity levels. These are the Schutower Moor (SM, freshwater), Diedrichshäger Moor (DM, 4.6 – 4.8, α-oligohaline), Hütelmoor1 (HM1, 4.1 – 4.3, α-oligohaline) and Hütelmoor2 (HM2, 6.5 – 6.8, ß-mesohaline) which are situated ≤ 15 km away from each other. The assessment aimed to determine the macrophyte species composition and dominance at each salinity level. A total of 51 macrophyte species, belonging to 20 families, was recorded across sites. Of these, 26 were found in SM, 21 in DM, 14 in HM1 and 12 in HM2. Poaceae (18 %) and Cyperaceae (12 %) are the two most represented families. *Phragmites australis* is the most dominant species and common to all sites while *Schoenoplectus tabernaemontani* and *Agrostis stolonifera* were found in three brackish sites. Of the four sites, the most diverse is SM (e^H = 9.84) while the more brackish peatlands, DM and HM2, have lower diversity indices. This resulted from low evenness in the more brackish sites due to the colonization of *P. australis* in most plots.

From these results, a salinity acclimation experiment was carried out to determine how *P. australis*, *Carex acutiformis*, *S. tabernaemontani* and *T. latifolia*, as habitat engineers, would respond to the predicted sea level rise which would most likely cause salinity increase and more frequent brackish water flooding. The emergent macrophytes were exposed to different salinity regimes, consisting of control (C+: permanently freshwater and C-: permanently brackish water) and alternating freshwater and brackish water with different exposure durations (A_{2b_2f}: 2 days brackish – 2 days fresh; A_{4b_4f}: 4 days brackish – 4 days fresh; A_{2b_4f}: 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*

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 (A_{2b_2f} and A_{2b_4f}) 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. Phragmites australis* showed signs of successful acclimation through decreased chlorophyll a:carotenoid ratio and high fluorescence yield at ≤ 20 mol m^{-2} and 40.1 – 60 mol m^{-2} irradiance. These 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.

If biomass production of *C. acutiformis* and *T. latifolia* would be negatively affected by salinity and frequent brackish water flooding, matter cycling may also be altered. Even though *P. australis* showed signs of successful acclimation and *S. tabernaemontani* showed no clear effects, changing salinity may influence the decay rates of these dominant emergent macrophytes. Hence, a decomposition study was conducted by deploying litter samples in SM and DM. Electrical conductivity difference of 1.2 – 8.0 mS cm^{-1} between the two sites did not significantly affect the decomposition of macrophyte litter. Between species, *S. tabernaemontani* lost a significantly higher mass in the first month of decomposition compared to *P. australis* and *Carex* sp. Litter decay rates for *S. tabernaemontani* was k = 0.0064 – 0.0078 d^{-1} while *P. australis and Carex* sp. both had k = 0.0017 – 0.0028 d^{-1}. After one year, *S. tabernaemontani* litter was completely decomposed while the other species had 40 – 60 % mass remaining relative to their initial dry mass confirming that *P. australis* and *Carex* sp. contribute to peat formation while *S. tabernaemontani* does not. Apparent differences in decomposition kinetics between *S. tabernaemontani* and the other species tested indicated that litter quality, especially C:P, C:N, N:P and C:Ca, is of great importance for microbial colonization (initial phase) as well as for sustaining decomposition after colonization. This study shows that litter quality controls litter decomposition more than narrow salinity range. Hence, we suggest that sea level rise, combined with increased precipitation, may not have significant impact on the decomposition of these macrophytes in the future. However, the future invasion of *P. australis* in areas currently inhabited by *T. latifolia* and *Carex* spp. in response to increasing salinity, peat formation would probably progress. In contrast, if *S. tabernaemontani* will spread in other areas due to increased water levels, carbon sequestration rates would most likely be affected since this species is non-peat-forming.

Zusammenfassung

Die globale Erwärmung führt zum Anstieg des Meeresspiegels, zu intensiveren und häufigeren Extremwetterereignissen und zu veränderten Niederschlagsmustern, die sich den Prognosen zufolge in Zukunft noch verstärken werden. Diese Phänomene sind weltweit besorgniserregend, da sie höchstwahrscheinlich Überschwemmungen oder Überflutungen und Erosionen an tief liegenden Küstenökosystemen verursachen werden, die diese erheblich beeinträchtigen können. Aus diesem Grund wurde das Forschungsprojekt Baltic TRANSCOAST ins Leben gerufen, um das Wissen über flache Küstenökosysteme zu erweitern. Ziel der Forschung ist es, zu verstehen, wie die Küstenzone durch terrestrische Prozesse beeinflusst wird und umgekehrt. Der Schwerpunkt dieser Arbeit liegt auf der Untersuchung der Auswirkungen des sich ändernden Salzgehalts und der Überschwemmung auf die Vegetation von Mooren an der Küste.

Um zu verstehen, wie die Vegetation auf künftige Umweltveränderungen (d. h. Erhöhung des Salzgehalts, häufigere Überschwemmungen) reagieren wird, wurden in vier benachbarten Mooren, welche ≤ 15 km voneinander entfernt liegen, zunächst Felduntersuchungen der Makrophyten mit leicht unterschiedlichem Salzgehalt durchgeführt: Schutower Moor (Süßwasser), Diedrichshäger Moor (4,6 – 4,8, α-oligohalin), Hütelmoor1 (4,1 – 4,3, α-oligohalin) und Hütelmoor2 (6,5 – 6,8, ß-mesohalin). Das Ziel der Studie war es, die Zusammensetzung und Dominanz der Makrophyten in den einzelnen Salzgehaltsstufen zu bestimmen. An allen Standorten wurden insgesamt 51 Makrophytenarten, die zu 20 Familien gehören, erfasst. Davon wurden 26 im Schutower Moor, 21 im Diedrichshäger Moor (DM), 14 im Hütelmoor1 (HM1) und 12 im Hütelmoor2 (HM2) gefunden. Poaceae (18 %) und Cyperaceae (12 %) sind die beiden am stärksten vertretenen Familien. *Phragmites australis* ist die dominanteste Art und kommen an allen Standorten vor, während *Schoenoplectus tabernaemontani* und *Agrostis stolonifera* an drei Brackwassermooren gefunden wurden. Von den vier Standorten ist SM der vielfältigste (e^H = 9,84), während die brackigeren Sümpfe DM und HM2 niedrigere Diversitätsindizes aufweisen. Dies ist auf die geringe Gleichmäßigkeit in den brackigeren Gebieten aufgrund der Besiedlung der meisten Parzellen mit *P. australis* zurückzuführen.

Auf der Grundlage der oben genannten Ergebnisse wurde ein Experiment zur Akklimatisierung an den Salzgehalt durchgeführt, um festzustellen, wie *P. australis*, *Carex acutiformis*, *S. tabernaemontani* und *T. latifolia* als Ökosystemingenieure auf den prognostizierten Anstieg des Meeresspiegels reagieren würden, welcher

höchstwahrscheinlich zu einem höheren Salzgehalt und häufigeren Brackwasserüberschwemmungen führen würde. Die gewählten Makrophyten wurden verschiedenen Salzgehaltsregimen ausgesetzt, bestehend aus einer Kontrolle (C+: permanentes Süßwasser und C-: permanentes Brackwasser) und einem Wechsel von Süß- und Brackwasser mit unterschiedlichen Expositionsdauern (A_{2b_2f}: 2 Tage Brackwasser – 2 Tage Süßwasser; A_{4b_4f}: 4 Tage Brackwasser – 4 Tage Süßwasser; A_{2b_4f}: 2 Tage Brackwasser – 4 Tage Süßwasser). Gemessen wurden die Pflanzenhöhe, die Blattfläche, die Chlorophyllfluoreszenz, das Verhältnis von Wurzel zu Spross und die photosynthetisch relevanten Pigmente. Der Salzgehalt unterdrückte das Wachstum von *T. latifolia* und *C. acutiformis*, was zu kürzeren Pflanzen, einer kleineren mittleren Blattfläche und einem höheren Verhältnis von Wurzel zu Spross führte, während das Verhältnis der photosynthetischen Pigmente und die Chlorophyllfluoreszenz unbeeinflusst blieben. Kürzere, aber häufigere Salzimpulse (A_{2b_2f} und A_{2b_4f}) verringerten die Höhe von *T. latifolia*, während *C. acutiformis* nicht betroffen war. Salzgehalt und Salzimpulse hatten keinen Einfluss auf die Höhe und das Wurzel-Spross-Verhältnis von *P. australis* und *S. tabernaemontani*. *Phragmites australis* zeigte Anzeichen einer erfolgreichen Akklimatisierung durch ein verringertes Chlorophyll-a zu Carotinoid Verhältnis und einen hohen Fluoreszenzertrag bei niedriger und hoher Bestrahlungsstärke. Diese Ergebnisse deuten darauf hin, dass *T. latifolia* und *C. acutiformis* bei zunehmender Brackwasserexposition im Küstenmarschland eine Wachstumsverzögerung erleiden oder sogar durch *S. tabernaemontani* oder *P. australis* ersetzt werden könnten, da letztere Arten resistenter gegenüber dem Salzgehalt und häufigen Salinitätsimpulsen sind.

Wenn die Biomasseproduktion von *C. acutiformis* und *T. latifolia* durch den Salzgehalt und häufige Brackwasserüberschwemmungen negativ beeinflusst wird, könnte sich auch der Stoffkreislauf verändern. Obwohl *P. australis* Anzeichen einer erfolgreichen Akklimatisierung zeigte und *S. tabernaemontani* keine eindeutigen Auswirkungen aufwies, könnten sich Änderungen des Salzgehalts auf die Zersetzungsraten dieser dominanten Makrophyten auswirken. Daher wurde eine Zersetzungsstudie mit Streuproben aus dem SM und dem DM durchgeführt. Der Unterschied in der elektrischen Leitfähigkeit von 1,2 – 8,0 mS cm^{-1} zwischen den beiden Standorten hatte keine signifikanten Auswirkungen auf die Zersetzung der Makrophytenstreu. Von den untersuchten Arten verlor *S. tabernaemontani* im ersten Monat der Zersetzung deutlich mehr Masse als *P. australis* und *Carex* sp. Insgesamt betrug die Zersetzungsrate der *S. tabernaemontani*-Streu k = 0,0064 – 0,0078 d^{-1}, während *P. australis* und *Carex* sp. beide eine Zersetzungsrate von

k = 0,0017 – 0,0028 d^{-1} aufwiesen. Nach einem Jahr war die Streu von *S. tabernaemontani* vollständig zersetzt, während bei den anderen Arten noch 40 – 60 % der ursprünglichen Trockenmasse vorhanden waren. Dies bestätigt, dass *P. australis* und *Carex* sp. zur Torfbildung beitragen, *S. tabernaemontani* hingegen nicht. Die offensichtlichen Unterschiede in der Zersetzungskinetik zwischen *S. tabernaemontani* und den anderen getesteten Arten lassen darauf schließen, dass die Streuqualität, insbesondere die Verhältnisse von C:P, C:N, N:P und C:Ca, sowohl für die mikrobielle Besiedlung (Anfangsphase) als auch für die Aufrechterhaltung der Zersetzung nach der Besiedlung von Bedeutung ist. Diese Studie zeigt, dass die Streuqualität die Streuzersetzung stärker beeinflusst als der niedrige Salzgehalt. Daher gehen wir nicht davon aus, dass der Anstieg des Meeresspiegels in Verbindung mit vermehrten Niederschlägen in Zukunft einen signifikanten Einfluss auf die Zersetzung dieser Makrophyten haben wird. Allerdings würde eine künftige Invasion von *P. australis* in Gebieten, die derzeit von *T. latifolia* und *Carex* spp. besiedelt werden, als Reaktion auf den steigenden Salzgehalt wahrscheinlich zu einer verstärkten Torfbildung führen. Sollte sich dagegen *S. tabernaemontani* aufgrund eines erhöhten Wasserstandes in anderen Gebieten ausbreiten, würde sich dies höchstwahrscheinlich auf die Kohlenstoffspeicherung auswirken, da diese Art keinen Torf bildet.

1 Introduction

Global warming in the last century brought global sea-level rise, extreme weather events and changed precipitation patterns (IPCC, 2019; Karl et al., 1995; Neubauer and Craft, 2009), which are projected to intensify in the future. Such phenomena raised global concern since they will most likely cause coastal hazards such as submergence or flooding and erosion, which may significantly affect the biogeochemical processes of adjacent low-lying coastal ecosystems. The lack of information about this matter stimulated the conceptualization of the research training group "Baltic TRANSCOAST" – under which this research is a component – to enhance our knowledge of the shallow coast ecocline. The research aims to understand how the marine coastal zone is influenced by terrestrial processes and *vice versa*. This thesis focuses on investigating the impacts of changing salinity and flooding on coastal wetland vegetation.

1.1 Wetlands and their importance

Wetlands are "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters at low tide, as well as human-made wetlands such as waste-water treatment ponds and reservoirs" (Ramsar Convention Secretariat, 2010). These ecosystems encompass a broad range of wet environments ranging from submerged coastal grass beds to salt marshes, swamp forests and boggy meadows (Kadlec and Wallace, 2008; Vymazal et al., 2006). They are ecotonal in nature since most wetlands lie at the interface between deep open water and the uplands (Gopal and Ghosh, 2008). Due to its landscape position, excess water occurs seasonally for a few weeks in most years when temperatures are warm enough to support plant growth, giving rise to wetlands (Tiner, 2018).

Based on the main source of water that enters the ecosystem, wetlands are classified into two main hydrological types. One is the rheotrophic wetland, the more common type that is fed by the flow of water derived from a watershed or catchment. The other, ombrotrophic wetlands, derive their water supply solely from rainfall (Moore, 2006). In terms of their global distribution, the warmer, drier regions only have rheotrophic wetlands since a larger catchment is required to support a wetland. Moreover, these ecosystems have either mineral or organic soils which are commonly acidic, although some communities have a generally neutral pH (Mitsch and Gosselink,

2016). Wetlands also occupy a range of trophic states and may be nutrient-rich (eutrophic) or nutrient-poor (oligotrophic) (Rich, 2015).

Wetland hydrology is characterized by prolonged flooding and/or saturation, typically creating anaerobic soil conditions (Reddy and DeLaune, 2008). These anaerobic processes in the soil force the biota, particularly rooted plants, to adapt to flooding (Keddy, 2010). The degree of wetness separates these ecosystems from terrestrial habitats, with unique properties and accompanying functions, making them highly valued natural resources (Tiner, 2018).

Wetlands are considered the modulator of processes between land and water because they are found at the interface of terrestrial and aquatic ecosystems and possess features of both (Keddy, 2010). They play an important function in water purification, flood protection, shoreline stabilization, groundwater recharge and stream flow maintenance. In addition, several important biogeochemical processes are favored in wetlands due to shallow water, which maximizes the sediment-to-water interface, high primary productivity, the presence of both aerobic and anaerobic sediments, and the accumulation of litter (Mitsch and Gosselink, 2016).

Climate regulation is another essential function of wetlands since they capture and store greenhouse gases (Joosten, 2015; Schumann and Joosten, 2008). The water-saturated soil almost throughout the year support dense vegetation and algal growth, capturing carbon dioxide for photosynthesis. Once dead, the organic material decomposes slowly due to the anaerobic condition hence, storing an enormous amount of carbon (Reddy & DeLaune, 2008). Therefore, wetlands are significant global carbon sinks (Brinson et al., 1981) storing about 45-70% of all terrestrial carbon (Mitra et al., 2005). This makes them important targets for conservation and major players in the global carbon cycle (McLeod et al., 2011). However, the magnitude of carbon sequestration by these ecosystems had been rapidly declining in the last century due to the loss of wetlands through human activity. Yet, their carbon burial rate remains one of the highest of all ecosystems on Earth (Hopkinson et al., 2012).

Peatland is a type of wetland that occupy 3% of the total global land area and contains around 600 Gt of carbon sequestered since the last Ice Age, making them a major terrestrial carbon stock and persistent natural carbon sink (Charman et al., 2013; Yu et al., 2011). They contain more carbon than the entire forest biomass of the world (Joosten, 2015). The majority of the peatland area is located north of 45°N latitude (Yu et al., 2011). In Europe, peatlands cover a total area of about 594 000 km^2, 54% of which are natural peatlands (European Union, 2000; Tanneberger et al., 2017). In Germany, peatlands cover an aggregate area of 12 800 km^2, which is 3.6% of the

country's total land area (Tanneberger et al., 2017).

In the past decades, about 15% of the global total peatland area (4 million km^2), and almost half of the peatland area in the Nordic and Baltic States, was drained for anthropogenic reasons which emitted a significantly higher amount of CO_2 (Joosten, 2015). Human-induced changes include about 50% for agriculture, 30% for forestry and 10% for peat extraction (Vasander et al., 2003). However, recently, there has been increasing recognition of its importance in policy-making, especially concerning climate change, biodiversity and ecosystem services. Therefore, rewetting and restoration of peatlands are on the rise (Tanneberger and Wichtmann, 2011). It is considered a top priority to address peatland degradation and biodiversity loss and to mitigate CO_2 emissions from peat oxidation and peatland fires (Parish et al., 2008). In the federal state of Mecklenburg-Vorpommern, Germany, a Mire Conservation Program was established in 2000 under which more than 200 km^2 of degraded peatlands was already rewetted (Zerbe et al., 2013).

1.2 Wetland Vegetation

Wetland plants, known as hydrophytes, macrophytes, or aquatic plants, are often the most conspicuous component of wetland ecosystems. These plants are uniquely adapted to the degree of inundation, hydrology and soil conditions (Tiner, 2018). They grow in water or on a substrate that is periodically oxygen-deficient because of excessive water content (Cowardin et al., 1979). Most of them are angiosperms although only about 3–5% of the known 250 000 species are adapted to the wetland environment (Cronk and Fennessy, 2009). Since they are primary producers, they are at the base of herbivorous and detritivorous food chains, as well as providing dissolved and suspended organic matter for decomposition by osmotrophic microorganisms (Moore, 2006; Rejmánková, 2011).

Wetland plants are classified based on their growth forms, namely free-floating, floating-leaved, submergent and emergent species (Chambers et al., 2008; Cronk and Fennessy, 2009; Moore, 2006) which are differentiated below. These groups are found in marshes and shallow water wetlands, such as ponds and prairie potholes, peatlands, and floodplains in a typical zonation pattern. Free-floating macrophytes are plants that typically float on or under the water surface. They move on the water surface with winds and water current and may be found throughout all wetlands. Floating-leaved plants have their leaves floating on the water surface while their roots are anchored in the substrate. They usually thrive at slightly greater depths, although

usually less than 1 m. Submersed macrophytes typically spend their entire life cycle beneath the surface of the water and are distributed in coastal, estuarine, and freshwater habitats. Most of them are rooted in the substrate although there are rootless species that float free in the water column. They grow throughout the water column often at greater depths than the emergent species as long as light penetration is adequate.

This thesis focuses on the emergent macrophytes. These are plants that are rooted in soils that are periodically inundated, with foliage extending into the air (Chambers et al., 2008). This group is dominated by herbaceous species, the most common of which are found in the large families of monocotyledons that tend to dominate both in freshwater and saltwater marshes. Among all the types of wetland plants, emergents are perhaps the most comparable to terrestrial species, relying on aerial reproduction and the soil as their exclusive source of nutrients. These plants often inhabit shallow waters in marshes, along lakeshores or tidal creeks, and because of their ability to intercept sunlight before it reaches the water's surface, they often dominate and outcompete floating-leaved and submerged plants in these habitats (Cronk and Fennessy, 2009).

The high primary productivity in wetlands makes them similar to rainforests and coral reefs (Keddy, 2010; Mitsch and Gosselink, 2016), which support vast life forms resulting in a highly diverse ecosystem (Moore, 2006). They commonly have rare species, which tend to have highly specific requirements, persisting only under a narrow set of wetland conditions. So, they are necessary for the survival of a disproportionately high percentage of endangered and threatened species that are restricted to these particular habitats (Mitsch and Gosselink, 2016). As a consequence, the decline in wetland areas has led to a decrease in wetland plant species diversity (Cronk and Fennessy, 2009; Davis, 1993; Lentz and Dunson, 1999), which, in turn, resulted in the diminishing population of their associated fauna.

1.3 Salinity as a factor shaping wetland vegetation

Salinity is one of the main environmental factors that limit plant growth and productivity (Allakhverdiev et al., 2000; Orlovsky et al., 2016) or even causes death at high salinity levels (Parida et al., 2003). Salt stress influences plant growth in two ways namely, osmotic and ionic stress, which affect most stages of plant development from germination to vegetative growth and reproductive development (Munns, 2002; Newell, 2013; Zhu, 2007). Osmotic stress is the initial phase that is caused by the

decrease in the water absorption capacity of plant roots and the increased transpiration rate resulting in excessive water loss. Ionic stress, on the other hand, occurs in cells due to excessive accumulation of sodium and chloride, which reduces the uptake of other mineral nutrients including potassium, calcium and manganese (Acosta-Motos et al., 2017; Munns and Tester, 2008; Sudhir and Murthy, 2004). Plants under salt stress possess the most common symptoms such as a decrease in photosynthesis capacity, reduction in leaf surface expansion rate, high leaf abscission rate, chlorosis and growth suppression (Munns and Tester, 2008; Sudhir and Murthy, 2004).

Macrophytes in coastal wetlands are vulnerable to inundation and saltwater intrusion associated with sea level rise although the effects vary widely among different species. Growth suppression due to salinization occurs in all plants, however, their tolerance levels and rates of growth reduction at lethal concentrations of salt differ between species (Parida and Das, 2005; Sudhir and Murthy, 2004). 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, 2008). 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.

Sea-level rise and/or subsidence of coastal habitats increase salinity levels, making salinity a critical factor that could change the composition and distribution of wetland plant communities (Brock et al., 2005; Spalding and Hester, 2007). Aside from these, other indirect or non-lethal impacts of salinization include changes in species behavior, reproduction, and feeding (Xi et al., 2016). Shifting in community composition and ecosystem structure occurs by altering both the fitness of individuals and the strength of interspecific interactions as different biological groups show different salinity tolerances. Ultimately, this phenomenon causes the replacement of freshwater plant communities with species with greater salinity tolerance (Herbert et al., 2015), and/or even biodiversity loss (Gerdol et al., 2018).

Changing salinity levels in coastal wetlands may also influence matter cycling, especially in terms of litter decomposition. This process is mainly controlled by climate, litter quality and the nature and abundance of decomposers (Stagg et al., 2018). Indirectly, salinity influences decomposition by altering microbial activities resulting in

changing patterns and rates of carbon cycling in wetlands (Sardinha et al., 2003). Qu et al. (2018) suggested that increased salinity may slow down the decomposition of dissolved organic carbon. However, knowledge of the impact of salinity on the decomposition rates of peatland macrophytes is still scarce. Burdick and Konisky (2003) recommended conducting studies examining the decomposition of *Phragmites* spp. across different salinity regimes to enhance the knowledge of wetland responses to salt intrusion. They added that the analysis of nutrient contents of plant litter should be determined to provide a better understanding of the decomposition process.

1.4 Coastal wetlands and global climate change

Coastal wetlands are wetlands occurring along the shorelines of the world's oceans, estuaries, and tidal rivers, including salt marshes, mangroves, tidal flats, and seagrasses. They are found on all continents and at all but extreme polar latitudes (Wolanski et al., 2009). They form the interface between aquatic and terrestrial ecosystems (Jurasinski et al., 2018) and are found within an elevation gradient ranging from subtidal depths to the landward edge (Wolanski et al., 2009). Thereby, their hydrology is largely influenced by tides, local weather conditions, and river discharge.

Salinity is an environmental factor in coastal wetlands that varies with distance from the source of saltwater as well as over elevational gradients. Salinity regimes can also fluctuate regularly with daily tides and irregularly during storms and flooding events (Howard and Mendelssohn, 1999a). These fluctuating water and salinity levels make coastal wetlands distinct from other types of wetlands. However, their position in the landscape also causes them to be highly vulnerable to seawater intrusion, erosion, and submergence (Kreuzburg et al., 2018; Neubauer and Craft, 2009).

Vegetated coastal ecosystems protect the coastline from storms and erosion and help buffer the impacts of sea level rise. However, with the rising global mean sea level that is happening since the last century, coastal wetland vegetation and their associated species are confronted with various adversities. Several literatures reported rates of sea-level rise ranging between 1 and 4 mm yr^{-1}, depending on the period and region (Baur et al., 2013; IPCC, 2014, 2019; Oppenheimer and Glavovic, 2019). Irrespective of these uncertainties, sea level rise raises global concern as this could result in coastal hazards such as submergence of low-lying areas or more and frequent coastal flooding and erosion (IPCC, 2019). The panel also reported that over the last 100 years, almost 50% of coastal wetlands have been lost because of the combined effects of localized human pressures, sea level rise, warming and extreme climate events. With sea level rise alone, up to 22% of the global coastal wetland area

might be lost by 2080 or up to 70% if combined with other losses due to direct human action (Nicholls et al., 1999).

The higher precipitation rates and increased storm-water runoff from upstream environments may also bring more freshwater input to coastal wetlands in the future (Mulholland et al., 1997). Together with the increased saltwater inflow during storm events, salinity levels of brackish wetlands may raise while causing saltwater intrusion into coastal freshwater wetlands. These altered flooding and salinity regimes may lead to landward transgression of coastal wetlands (Neubauer, 2013) and shifting of vegetation community composition, particularly replacing the dominant non-halophytes with salt-tolerant species and/or decreasing species richness (Neubauer and Craft, 2009). Consequently, these changes may influence ecosystem functions like photosynthetic activity, biomass production, litter decomposition (Herbert et al., 2015; Stagg et al., 2018), and ultimately nutrient cycling (Neubauer and Craft, 2009). However, knowledge about the influence of intermittent flooding in coastal wetlands on these processes is still limited hence, the pressing need to study.

1.5 Baltic Sea and environmental impacts of climate change

Baltic Sea is an intracontinental, semi-enclosed sea that is surrounded by nine countries and separates the Scandinavian Peninsula from the rest of continental Europe (Figure 1). It is connected to the Atlantic Ocean *via* the Danish straits and receives outflows from more than 200 rivers. Consequently, Baltic Sea is one of the largest brackish water bodies in the world with surface-water salinity ranging between 1.8-11.3 (Snoeijs-Leijonmalm et al., 2017).

In comparison to other seas, the Baltic Sea is atypical since it lacks an intertidal zone due to the absence of regular daily high and low water level fluctuations. In most parts, the tidal amplitude ranges only from 2 to 5 cm, about 10 cm in the Belt Sea and over 10 cm from the eastern Gulf of Finland (Leppäranta and Myrberg, 2009). Air-pressure changes and winds mainly drive the fluctuating seawater level (Novotny et al., 2006) while two long-term factors influence the changing Baltic Sea water level. First, the land uplift in the northern part decreases the water level by up to 1 cm yr^{-1}. Second, the global sea level increases due to the melting of the Earth's glaciers and expansion of the seawater volume by global warming (BACC II Author Team, 2015). The latter trend has caused an increase in the water level of the Baltic Sea by 19.5 cm since 1870 (SMHI, http://www.smhi.se).

Figure 1. Map showing the Baltic Sea (Source: worldatlas.com)

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 (Groh et al., 2017; Richter et al., 2012) 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.

A significant portion of the European peatlands (25% or 240 000 km^2) are located in the Baltic Sea basin (Seppä, 2002). In the southern Baltic Sea, the low-lying coastal areas are characterized as fen peatlands which were mostly formed by the accumulation of organic material over millennia due to episodic, weekly to monthly, flooding with much shorter flooded periods than non-flooded periods (Jurasinski et al., 2018). Recently, these 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. However, regardless of wetting-rewetting status, during severe weather, these brackish wetlands would be subjected to sudden influxes of relatively high salinity water that inundate an area for relatively short periods. Although such events may not permanently alter the physicochemical characteristics of a site, the community structure and composition may change, depending on the responses of individual plant species to the stressors and on species interactions (Howard and Mendelssohn, 1999; McKee and Mendelssohn, 1989).

The biodiversity of the Baltic Sea is particularly sensitive to changes in salinity, which can have a cascading effect on ecological processes in the land-sea interface (BACC II Author Team, 2015). Despite potential impacts on primary productivity, the effects of short-term changes in salinity regime on brackish peatland plant community dynamics are still not clear. In the past, several studies examined the effects of varying salinity levels (Hadad et al., 2017; Orlovsky et al., 2016; Rasmuson and Anderson, 2002; Stofberg et al., 2015) 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.

Therefore, there is a need to assess the macrophyte composition and dominance pattern in coastal peatlands under different salinity levels on the Southern Baltic Sea coast. It is also necessary to determine the effects of saline-water flooding on the growth of the most dominant emergent macrophytes since they are considered as ecosystem engineers – species that physically modifies a habitat (Wright et al., 2002). For these, an *in situ* assessment combined with a laboratory experiment was carried out wherein the latter was done by having control groups (permanently freshwater and brackish water, respectively) and groups treated with different durations of exposure to brackish water before returning to freshwater conditions. Moreover, to investigate the effects of salinity on litter decomposition, a two-site comparison approach was used to evaluate the litter decomposition rates of the most dominant emergent macrophytes in two neighboring coastal peatlands, freshwater and brackish. These two sites have similar characteristics, i.e. the same geologic origin and climatic conditions, except that one is influenced by brackish water while the other is not. This setting allowed us to examine the effects of narrow salinity ranges on litter decomposition *in situ*.

To address these knowledge gaps and to determine the future development of emergent macrophytes in the Baltic Sea coastal wetlands as influenced by salinity, the following hypotheses are formulated:

Hypothesis 1

The composition and dominance pattern of macrophytes in coastal wetlands change as influenced by brackish water flooding regime.

Hypothesis 2

The dominant emergent macrophytes of the coastal wetlands are impacted by salinity to different degrees through the following mechanisms:

a. Salinity affects primary productivity due to the reduction of water potential, which limits water and nutrient transport; and
b. The frequency of flooding events with brackish water is modulating the salinity tolerance response of emergent peatland macrophytes.

Hypothesis 3

Salinity changes impact matter cycling through altered litter decomposition patterns of the dominant emergent macrophytes even at low salinity levels. Specifically,

a. Increasing salinity decreases the decomposition rate of litter from dominant wetland macrophytes; and
b. Salinity-driven changes will be similar for all macrophytes.

To prove the validity of these hypotheses, a combination of field observations as well as field and laboratory experiments were conducted, which will be outlined and discussed in the following sections.

2 Materials and Methods

2.1 Macrophyte assessment

2.1.1 Characteristics of Study sites

The study was conducted in three coastal peatlands within the city borders of Rostock, Northeastern Germany (Figure 2). These peatlands differ in salinity level; hence, they were selected to compare the species composition, dominance pattern and litter decomposition of macrophytes. Site selection was based on the proximity of the area (aerial distance ~ 8 km) and similarity in environmental characteristics except for salinity. Schutower Moor (SM; 54.1029°N / 12.0594°E) is a freshwater peatland predominantly vegetated with *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), with patches of *Carex* sp. (pond sedge) and a few stands of *Typha latifolia* L. (common cattail) occupying the edges of the peatland. The other site, Diedrichshäger Moor (DM; 54.1685°N / 12.0659°E), is a brackish peatland with salinity 4.6 – 4.8 that is classified as alpha-oligohaline based on the Modified Venice System for the Baltic Sea (Schubert et al., 2017). It receives brackish water *via* groundwater flow from the Baltic Sea and from the estuary of the Warnow River, both of which are about 800 m away. DM is dominated by *P. australis* with patches of *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla (softstem bulrush) occupying certain parts of the peatland margin.

Hütelmoor (HM) is about 8 km away from Diedrichshäger Moor and 15 km away from Schütower Moor. It is a natural reserve located in the northeast of Rostock, northeastern Germany. The landside is a partly degraded peatland, extending 1.59 km in the north-south direction and 1.38 km in the east-west direction (Koebsch et al., 2013). Its northern and western parts, on the other hand, connect to the Baltic Sea, receiving brackish waters periodically. A patchy mosaic of dominant stands of *Bolboschoenus maritimus* (L.) Palla, *S. tabernaemontani*, *Carex acutiformis* (Ehrh.) and *P. australis* characterize the area with the common reed being the most common vegetation. For the macrophyte assessment, two sampling stations were established at this site due to varying salinity levels and referred to here as HM1 (54.2131°N / 12.1849°E) which is oligohaline (4.10-4.30) and is relatively farther from the coast than HM2 (54.2149°N / 12.1773°N) which is mesohaline (6.45-6.75). However, for the decomposition, this site was excluded.

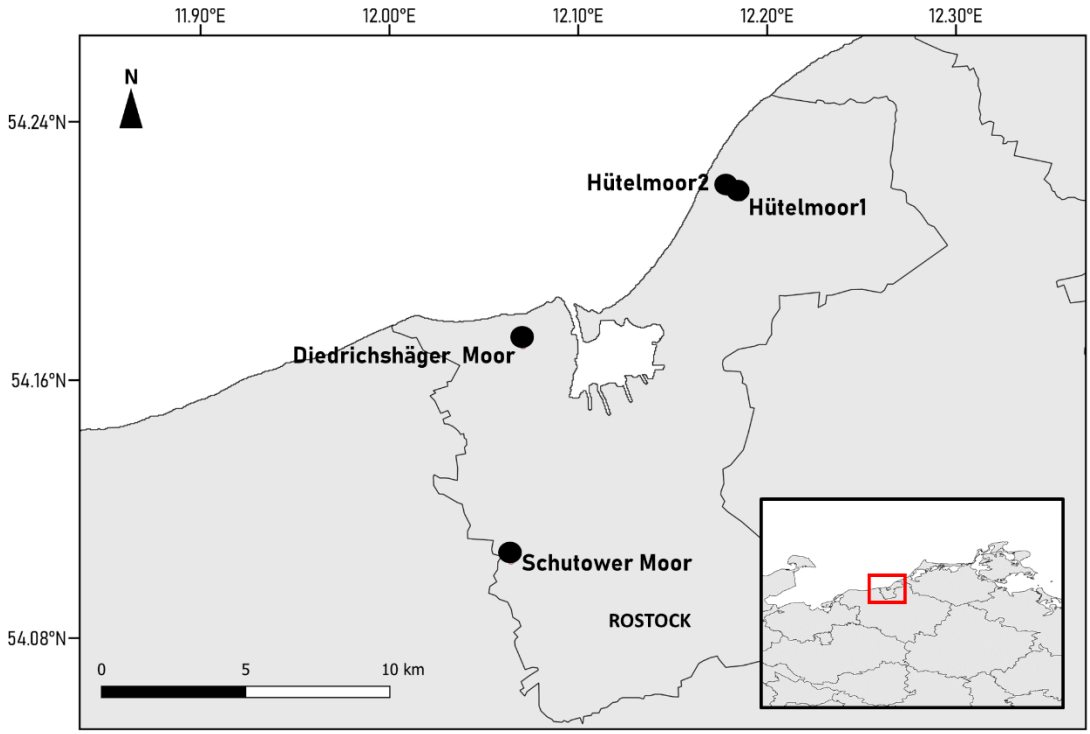

Figure 2. Map showing the location of the four study sites created with QGIS version 3.4 Madeira (QGIS Development Team). Map data source: GADM data version 4.1 (gadm.org)

2.1.2 Vegetation assessment

A total of 28 1 x 1 m plots were established at 10 m apart from the edge towards the middle of the peatlands for the assessment of species composition and monitoring of growth patterns of macrophytes. These plots were established in Schutower Moor (8), Diedrichshäger Moor (10) and another 10 in Hütelmoor which were equally divided into two sampling stations, HM1 and HM2. These plots served as permanent plots for the monitoring of growth and macrophyte composition within the growing season. Species-Area curve was initially plotted (Figure 3) to ensure that the minimum area required for sampling vegetation in the study sites is met.

During the first sampling, the geographic coordinates of each plot were recorded using the Geographic Positioning System (GPS). In each plot, species composition and abundance (% cover) were assessed from seedling until full-grown stage. Sampling was done for three seasons, spring (April/May), summer (June/July) and late summer (August/September) to represent early, middle and full-grown stages of development, respectively.

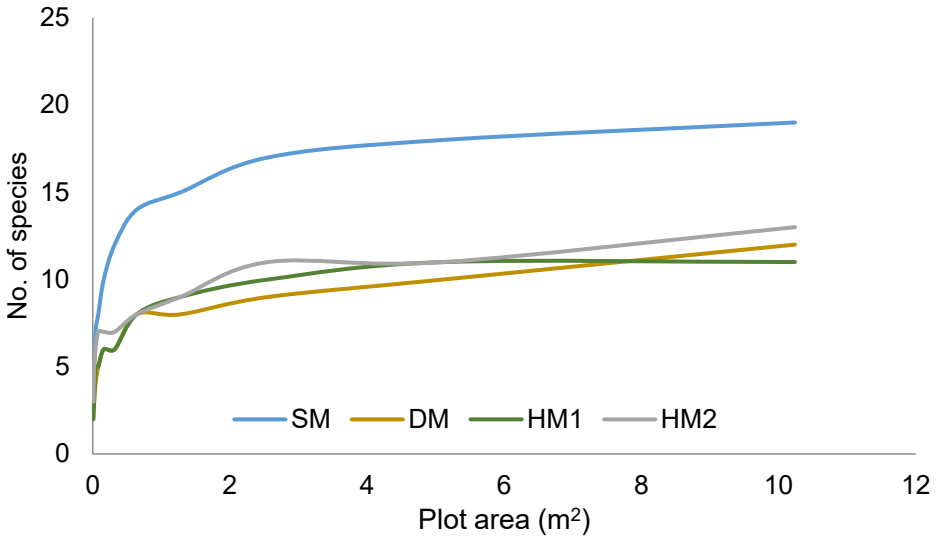

Figure 3. Species-area curve of the four study sites

The gathered data were used to calculate species diversity indices of each site including species richness (S), Shannon-Wiener diversity (H') and Shannon's evenness (also called Pielou's *J*). The following are the corresponding computing formula of each index.

Richness (S) – number of species

$$H = -\sum_{i=1}^{s} p_i \ln p_i \qquad \text{(Shannon, 1948)} \qquad (1)$$

where p_i is the proportion of individuals belonging to species *i, ln* is the natural logarithm while *s* is the total number of species. Then, the exponent of *H* (e^H) was calculated to convert the Shannon diversity index into effective number of species (ENS) as follows:

$$ENS = e^H \qquad \text{(MacArthur, 1965)} \qquad (2)$$

The equitability of species distribution within the sample is calculated using the Shannon's evenness index:

$$J = \frac{H}{\ln(S)} \qquad \text{(Shannon, 1948)} \qquad (3)$$

where *J* is the Shannon's evenness index, *H* is the Shannon's diversity index, *ln* is the natural logarithm and *S* is the number of species.

Based on the dominance of macrophytes on site, the top 4 emergent macrophytes across study sites were selected for the salinity acclimation (see section 2.2) and top 3 for the decomposition (see section 2.3) studies. Selection was based on the most and second dominant species per site so they are considered the ecosystem engineers therefore, they are expected to have more impact relative to the other species.

2.2 Salinity acclimation of dominant emergent macrophytes*

2.2.1 Preparation and Planting

Planting materials were bought from commercial suppliers to ensure uniformity of sources, handling and preparation. Seedlings of *Carex acutiformis*, *Typha latifolia*, *Phragmites australis* and *Schoenoplectus tabernaemontani* were bought from re-natur GmbH (Ruhwinkel, Germany, Oldenburg, 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 (54.0838ºN and 12.1514ºE) for the freshwater and close to the river mouth (Schmarl Dorf, 54.1366ºN and 12.0889ºE) 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.

2.2.2 Experimental set-up and treatment application

The experiment was conducted from April until June 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 (Figure 4). 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.

*This section is from Batistel et al. 2022. Response of four peatland emergent macrophytes to salinity and short salinity pulses. Wetlands 42:67. https://doi.org/10.1007/s13157-022-01592-0

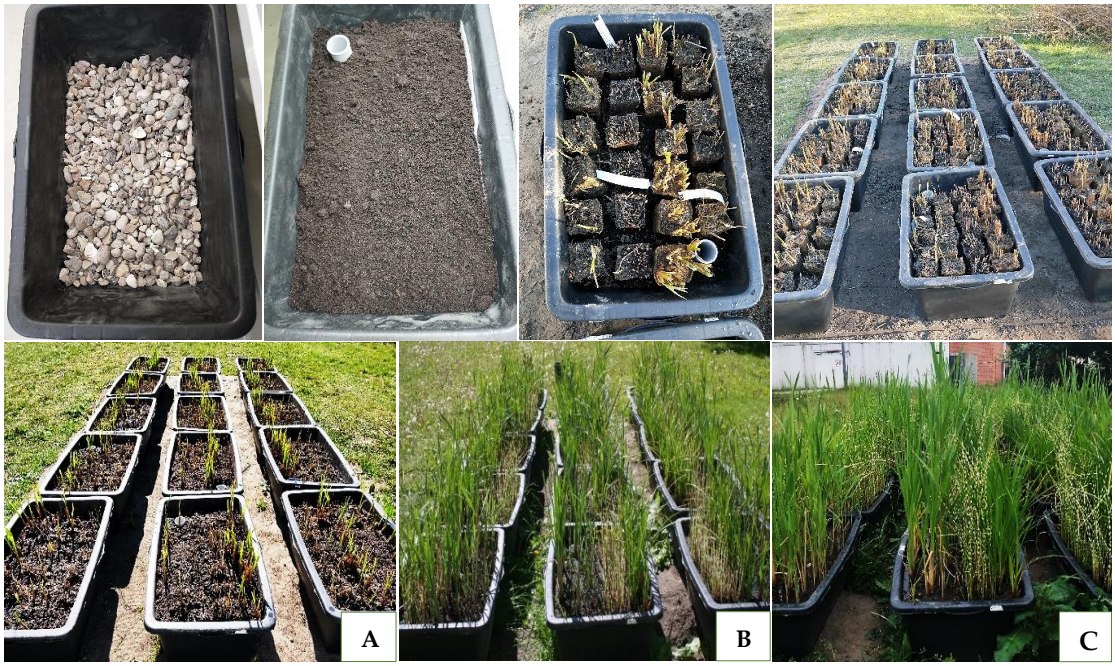

Figure 4. Preparation of experimental setup (upper), A) adaptation phase, B) 4 weeks and C) 10 weeks from treatment application

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. The water salinity per treatment throughout the study is shown in Figure 5. Points in the graph where salinity was not within the usual values (i.e. 5 & 20 June in treatments A_{2b_2f}, A_{2b_4f}) were during heavy rainfall. In such cases, water was replaced immediately to ensure that treatment effects are not changed.

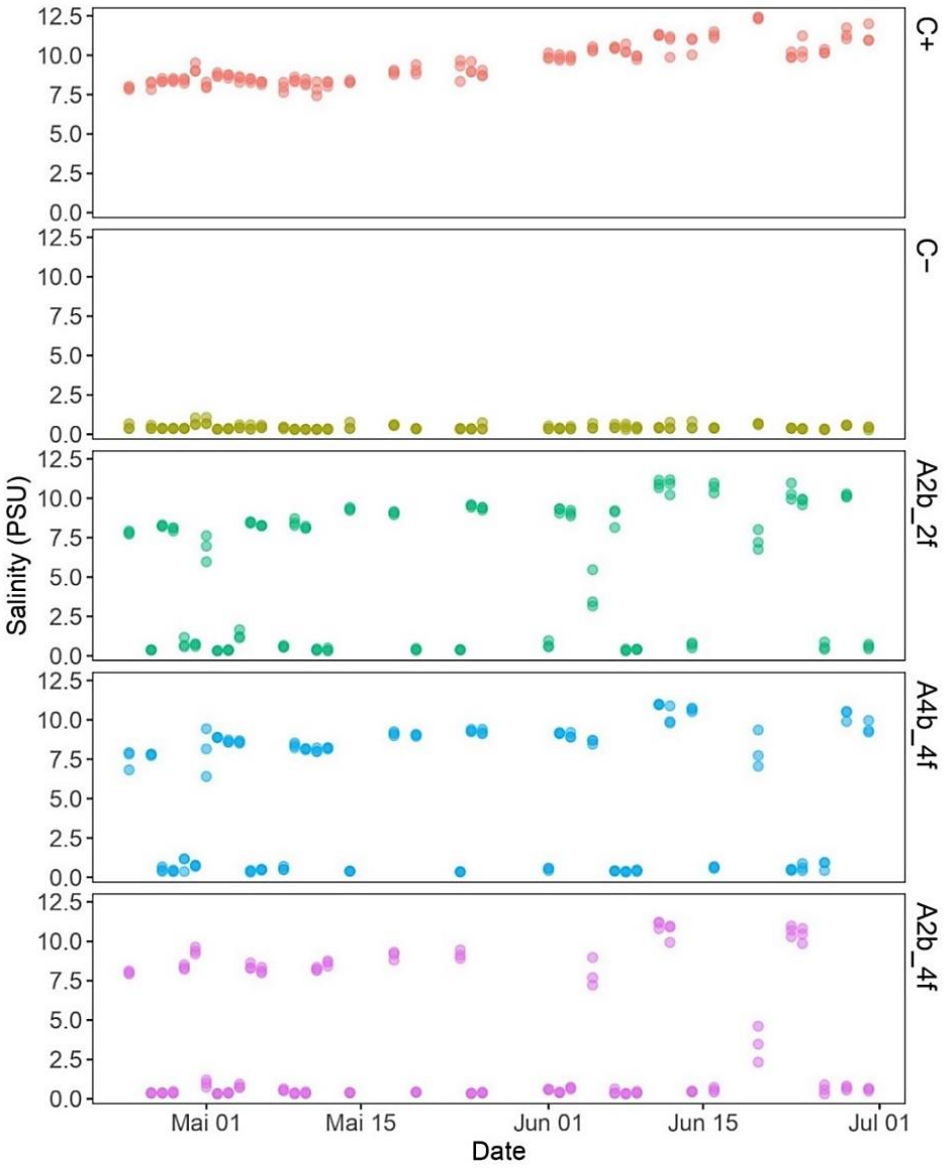

Figure 5. Salinity in the aqueous phase under different treatments (C+ : permanently brackish water; C-: permanently freshwater; A_{2b_2f}: alternating 2 days brackish water then 2 days freshwater; A_{4b_4f}: alternating 4 days brackish water then 4 days freshwater; A_{2b_4f} : alternating 2 days brackish water then 4 days freshwater) throughout the acclimation study

2.2.3 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 4. A sample graph showing the growth curve and the different parameters is shown in Figure 6.

$$Y(t) = A + \frac{K-A}{(C+e^{-B(t-M)})^{\frac{1}{v}}} \quad (4)$$

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

$$A + \frac{K-A}{C^{1/v}} \quad (5)$$

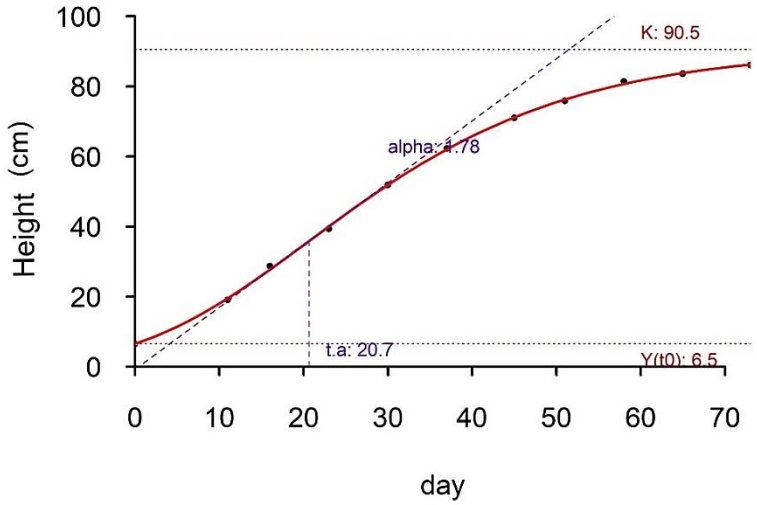

Figure 6. Growth curve of *P. australis* under treatment A_{2b_2f} (alternating 2 days brackish water then 2 days freshwater), replicate 1, plant sample 4 derived using the Richard's growth curve model. K is the maximum height; alpha is the maximum growth rate; t.a. is time when alpha occurs; Y(t0) is the height at day 0

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 the 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 areas per individual plant was taken and the mean leaf area (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 hours or until

constant weight and weighed. Root:shoot ratio (RSR) was calculated by dividing the BGB and AGB dry weights.

2.2.4 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 by Porra et al. (1989) to determine ratios between Chlorophyll a and b (Chl a:b) and Chlorophyll a and carotenoid (Chl a:car).

$$\text{Chl a } (\mu g \cdot g\ FM^{-1}) = (A663.8 - A750)\ 12 - (A646.8 - A750) \cdot 3.11 \quad (6)$$

$$\text{Chl b } (\mu g \cdot g\ FM^{-1}) = (A646.8 - A\ 750) \cdot 20.78 - (A663.8 - A750) \cdot 4.88 \quad (7)$$

$$\text{Car } (\mu g \cdot g\ FM^{-1}) = ((A480\text{-}A470) \cdot 1000 - \text{Chl a} \cdot 1.12 - \text{Chl b} \cdot 34.07) / 245 \quad (8)$$

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

2.2.5 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 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):

$$\text{Yield} = \frac{Fm'-F}{Fm'} \quad (9)$$

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 (Figure 7) were used to correct the AM yield, eliminating the influence of light and representing the yield of dark acclimated samples. Yield difference (ΔYield) was calculated by subtracting the NN from AM yield of the same measurement day per plant. These ΔYield 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 µmol photons $m^{-2}s^{-1}$ 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.

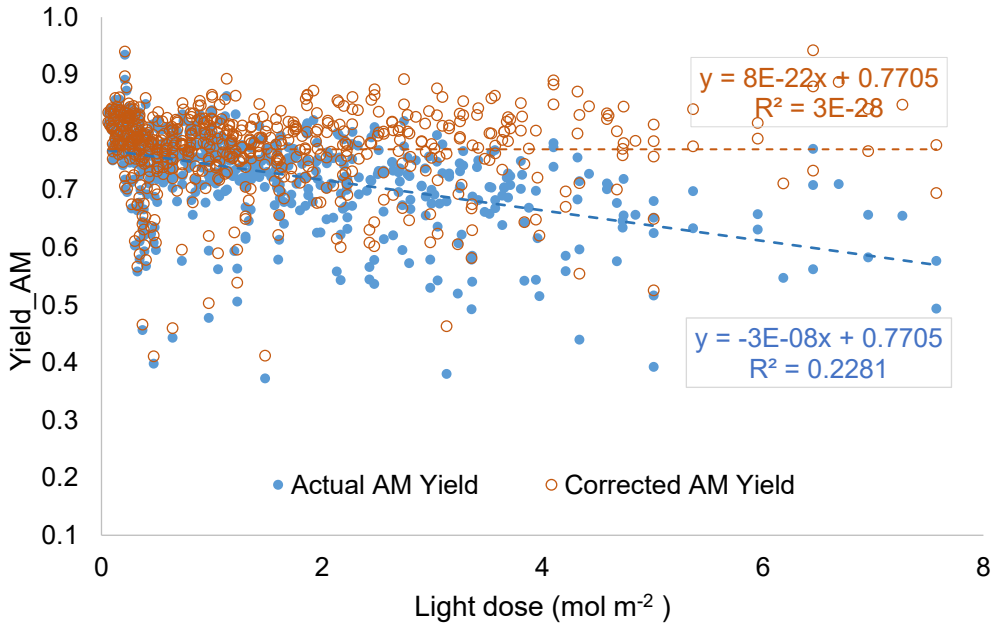

Figure 7. Chlorophyll fluoresence yield in the morning (AM Yield) of all species and treatments for 10 weeks. Circles are individual measurements; broken lines are linear regression line

2.3 Litter decomposition**

2.3.1 Experimental setup

Approximately 5 kg of senescent leaves of the most dominant species *P. australis* (*P. australis*$_{SM}$ from SM and *P. australis*$_{DM}$ from DM) and of the second dominant species from each site (*Carex* sp. in SM and *S. tabernaemontani* in DM) were collected in October 2019. Because we focused on the dominant species, *T. latifolia* was excluded from sampling. For *S. tabernaemontani,* instead of leaves, late-season stems were used as this plant is leafless and the stem is its photosynthetic organ. Samples were cleaned and cut into 10 cm length before weighing. A total of 240, 20 cm x 15 cm, litter bags made from fiberglass with a mesh size of 4 mm (Schwepa GmbH, Germany) were sewn using nylon thread, leaving one side open. Coarse mesh size (4mm) was used to allow colonization by larger macroinvertebrates responsible for much of the initial breakdown of plant material (Chimney and Pietro, 2006). A 20 g fresh litter sample of macrophyte was placed in each bag, then sealed with nylon thread and labeled accordingly. The average initial litter dry mass content was 10.20 g and 10.98 g for *P. australis*$_{SM}$ and *P. australis*$_{DM}$, respectively, while it was 11.07 g for *Carex* sp., and 3.77 g for *S. tabernaemontani.* The much lower dry mass of the latter is due to the high-water content of its stem compared to the leaves of the other species. Litter bags were transported in plastic bags to avoid losses before exposure at the two study sites.

At each site, 30 litter bags per species were equally distributed in five, 1 m x 1 m, plots (replicates per site) in monospecific stands of the same species. A reciprocal transplantation experiment was conducted for all macrophyte litter from both sites. This means that litter bags filled with litter from the freshwater peatland were deployed in the brackish environment and *vice versa*. Litter bags were buried at 10-15 cm depth (Moore et al., 2007) and covered immediately with the soil and litter material that had been removed to enable natural degradation conditions of buried litter.

A HOBO® U24 Conductivity Logger (U24-002-C, Onset, USA) was installed at each site during litter bag field exposure to monitor surface water temperature and EC. Approximately 1, 2, 4, 6 and 12 months (35, 62, 126, 186 and 371 days, respectively) from installation, 5 replicates per species per site (1 litter bag per plot) were retrieved to determine mass loss and change in elemental concentration. In the brackish site, no litter bag was left in the *Carex* plots during the last sampling due to animal (e.g. wild boar and deer) destruction of the site. Retrieved litter bags were immediately placed

**This section is from Batistel et al. 2021. Salinity exerted little effect of decompostion of emergent macrophytes in coastal peatlands. Aquatic Botany 175 (2021) 103446

individually in Ziploc® bags and brought to the laboratory for processing and analysis.

2.3.2 Remaining litter analysis

In the laboratory, retrieved litter bags were immediately stored at 5 °C and processed within 24 hours. Remaining litter per sample was gently cleaned by rinsing with tap water over a 1 mm-sieve to ensure that litter samples were not washed away. Samples were then oven-dried at 60 °C for 48 hours to determine dry weight. In the beginning, subsamples of the initial material of each species were also weighed, oven-dried at 60 °C, and reweighed to calculate moisture content. This value was applied to the starting mass (W_0) of litter used in subsequent calculations. Dry Mass Remaining (DMR, %) after each sampling period was calculated following Stagg et al. (2018) using the following equation:

$$DMR\ (\%) = (W_t/W_0) \times 100 \quad (10)$$

with W_0 the dry mass of the sample at time 0, and W_1 the dry mass at time *t* (days after installation). Using this value, the exponential decay coefficient (*-k* per day) was estimated using a single exponential decay model (Olson, 1963) as follows:

$$m_t = m_0 * e^{-kt} \quad (11)$$

with m_t (%) the mass remaining at time *t* (days after field burial), m_0 the initial mass (%), *t* the time in days, and *-k* the exponential decay coefficient per day. The mean DMR of the 5 replicates per species per site at each sampling time was used as m_t in calculating *-k* since the collected litter bags were different each time.

Oven-dried leaf litter was finely ground for analysis of carbon, nitrogen and sulfur (%) using a PYRO-Cube CNS analyzer (Elementar Analysensysteme GmbH, Hanau, Germany). Ash-free dry weight (AFDW) of subsamples was determined following the Loss on Ignition method by combustion for 4 hours at 550 °C in a muffle furnace. Ash remaining after combustion was digested with 25% HCl and filtered to determine concentrations of calcium, magnesium, potassium, sodium and phosphorus. Samples were analyzed using Inductively Coupled Plasma-Optical Emission Spectrometry (Perkin Elmer ICP-OES Optima 8300, Waltham, USA). Results are expressed as elemental concentration (mg g^{-1}) based on the dry mass of samples. The absence of data during the last sampling for *S. tabernaemontani* is due to the nearly complete decomposition of litter in the bags resulting in not having enough material for the macro-elemental (ICP-OES) analysis while for *Carex* sp., litter bags were lost due to disturbance by animals.

2.4 Statistical analyses

Individual plant height data from the acclimation study was fitted based on Richards growth model (Eq. 4) with R statistical software Version 4 (R Core Team, 2020) and the package BB (Varadhan and Gilbert, 2009). Resulting parameters (i.e. maximum height and maximum growth rate) were analysed according to the nested experimental design to determine the effects of salinity, species and their interaction using analysis of variance (ANOVA) for mixed linear models wherein salinity and species were fixed factors and the box was a random factor. Mean leaf area was analysed using mixed linear effects model with treatment, species by week as fixed factors and week and box as random factors. Additionally, chl a:b, chl a:car and root:shoot ratios were analysed using one-way ANOVA. For the ΔYield where requirements for ANOVA could not be met, Kruskal-Wallis test was used.

For the litter decomposition, data analyses were done using SPSS Version 27 (IBM SPSS Inc., Chicago, Illinois, USA). Nonlinear regression was used to estimate the decay coefficient of each species from a single exponential decay model. Simple one-way ANOVA was used to determine significant differences in the mean initial decay, 35 days after the field exposure of litter bags, between species and sites, and for the initial chemical contents of the litter to identify possible differences in starting values. The slope and intercept with linear regression were determined for each species per site using the remaining mass data from the third until the last retrieval period. Principal Component Analysis (PCA) was conducted using PRIMER Version 6 (PRIMER-E Ltd., 2009) to examine the complexity of the differences in the molar C:macroelemental ratios of all species across time.

All data were tested for standard distribution using Shapiro-Wilk-Test and homogeneity using Levene-Test. *Post hoc* pairwise multiple comparisons was performed after ANOVA using Tukey's Honestly Significant Difference (HSD) against an alpha-level of 0.05 to identify difference between treatments and/or species. For Kruskal-Wallis tests, Dunn's pairwise *post hoc* comparisons was used when results were significant at 0.05 alpha level.

3 Results

3.1 Species composition and diversity as affected by salinity

A total of 51 macrophyte species, belonging to 20 families, was recorded across sites and seasons (Tables 1 and 2). Of these, 26 were found in Schutower Moor, 21 in Diedriechshäger Moor, 14 in Hütelmoor1 and 12 in Hütelmoor2. Poaceae is the most represented family with 9 species contributing 18% of the macrophyte species composition (Table 2). This is followed by Cyperaceae (12%), Polygonaceae (10%), Onagraceae (10%). Lamiaceae (8%), Asteraceae (8%), Equitaceae (8%) and Typhaceae (8%) and a few other families with a single or 2 representative species are among the other families of macrophytes found in the assessed wetlands. *Phragmites australis* was the only species that was common to all sites while *Schoenoplectus tabernaemontani* and *Agrostis stolonifera* were found in all brackish sites. Of the 51 species, 17 were unique to the freshwater peatland, SM. Seasonal sampling shows no substantial difference in the phenology of macrophytes between sites. Two species of sedge could not be identified since they were only present in spring.

Table 1. List of grasses, sedges and other plants recorded in the four peatland sites

Family	Species	SM	DM	HM1	HM2
Poaceae	*Agrostis stolonifera*	0	1	1	1
Poaceae	*Alopecurus geniculatus*	0	0	1	0
Poaceae	*Deschampsia caespitosa*	1	0	0	0
Poaceae	*Festuca pratensis*	0	1	0	0
Poaceae	*Glyceria maxima*	1	0	0	0
Poaceae	*Phalaris arundinacea*	0	1	0	0
Poaceae	*Phragmites australis*	1	1	1	1
Poaceae	*Poa pratensis*	1	1	0	0
Poaceae	*Poa* sp.	0	1	0	0
Cyperaceae	*Bolboschoenus maritimus*	0	0	1	1
Cyperaceae	*Carex hirta*	0	0	1	0
Cyperaceae	*Carex acutiformis*	1	0	1	1
Cyperaceae	*Schoenoplectus tabernaemontani*	0	1	1	1
Cyperaceae	Sedge1	1	0	0	0
Cyperaceae	Sedge2	1	0	0	0
Polygonaceae	*Persicaria amphibia*	0	1	1	0
Polygonaceae	*Persicaria hydropiper*	1	0	0	0
Polygonaceae	*Rumex hydrolapathum*	0	0	1	0
Polygonaceae	*Rumex palustris*	0	1	1	0
Polygonaceae	*Persicaria* sp.	0	1	0	0
Onagraceae	*Epilobium hirsutum*	1	0	0	0
Onagraceae	*Epilobium palustre*	1	0	0	0
Onagraceae	*Epilobium* sp.	1	0	0	0
Onagraceae	*Epilobium* sp. $_1$	1	1	0	0
	Subtotal	12	11	10	5

Legend: 1 means present; 0 means absent

Table 2. Other species of macrophytes recorded in the four peatland sites

Family	Species	SM	DM	HM1	HM2
Lamiaceae	*Glechoma hederacea*	1	0	0	0
Lamiaceae	*Lycopus europaeus*	0	0	0	1
Lamiaceae	*Mentha aquatica*	0	1	1	0
Lamiaceae	*Scuttelaria galericulata*	1	0	0	0
Asteraceae	*Cirsium arvense*	0	1	0	1
Asteraceae	*Eupartorium cannabinum*	1	0	0	0
Asteraceae	*Tephroseris palustris*	0	0	1	0
Equisetaceae	*Equisetum fluviatile*	1	0	0	0
Equisetaceae	*Equisetum palustre*	1	0	0	0
Equisetaceae	*Equisetum* sp.	1	0	0	0
Typhaceae	*Sparganium erectum*	1	0	0	0
Typhaceae	*Sparganium sp.*	0	0	1	0
Typhaceae	*Typha latifolia*	1	0	0	0
Amaranthaceae	*Atriplex hastata*	0	1	0	0
Amaranthaceae	*Chenopodium album*	0	1	0	1
Juncaceae	*Juncus effusus*	0	0	0	1
Juncaceae	*Juncus inflexus*	1	0	0	0
Apaiceae	*Berula erecta*	1	0	0	0
Brachyteciaceae	*Brachythecium sp.*	1	1	0	0
Caprifoliaceae	*Valeriana dioica*	0	1	0	0
Convolvulaceae	*Calystegia sepium*	0	1	0	1
Fabaceae	*Vicia cracca*	0	0	0	1
Lythraceae	*Lythrum salicaria*	1	0	0	0
Ranunculaceae	*Ranunculus sceleratus*	1	1	1	0
Rubiaceae	*Galium palustre*	0	1	0	1
Solanaceae	*Solanum dulcamara*	1	1	0	0
	Subtotal	14	10	4	7
	Overall Total (Table 1 and 2)	26	21	14	12

Legend: 1 means present; 0 means absent

Of the four sites, the most diverse and most species-rich is the Schutower Moor with e^H = 9.81 and S = 26, respectively (Figure 8) followed by the oligohaline peatland, HM1 with an e^H = 8.37. In contrast, the more brackish peatlands DM and HM2 have almost three times lower effective species number of 3.44 and 3.70, respectively. Highest evenness index (J = 0.81) was recorded in HM1, followed by SM (J = 0.70) while the lowest was in DM (J = 0.40). Across season, the species richness per plot in SM ranges from 2-12 m^{-2}, 1-6 m^{-2} in DM, 2-7 m^{-2} in HM1 and 1-5 m^{-2} in HM2.

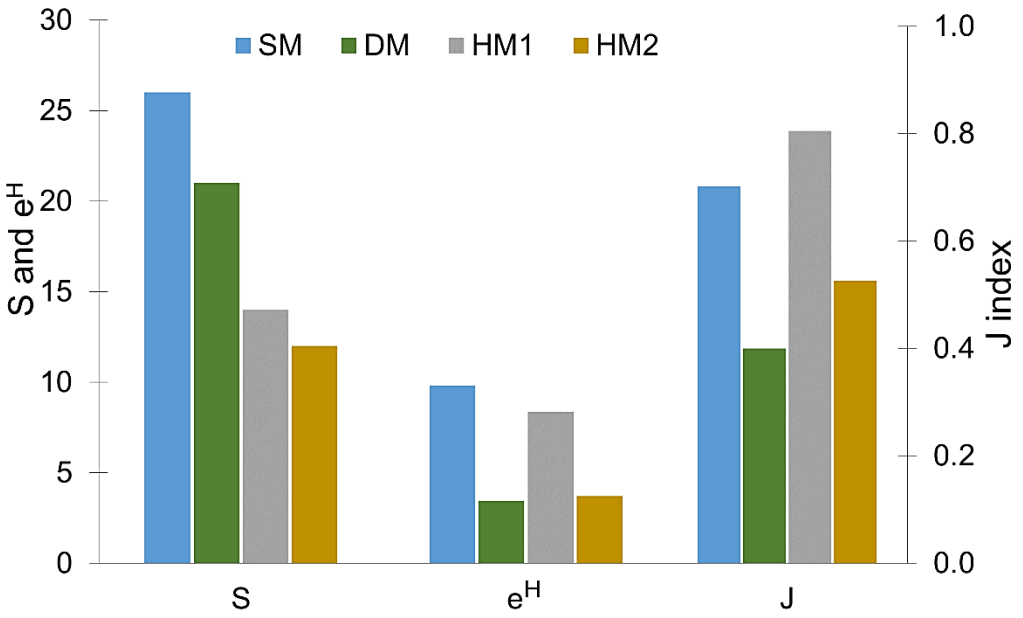

Figure 8. Species richness (S), Shannon diversity (H') expressed as the effective species number (e^H), and evenness (J) indices of macrophytes in Schutower Moor (SM), Diedrichshäger Moor (DM), Hütelmoor1 (HM1) and Hütelmoor2 (HM2)

3.2 Response of dominant emergent macrophytes to salinity and salinity pulses*

3.2.1 Plant height and growth rate

The maximum plant heights of the four emergent macrophytes relatively varied between treatments for each species (Figure 9). 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-) conditions ($P = 0.004$). The maximum height of *T. latifolia* exposed to A_{4b_4f} pulse was also significantly taller than C+ ($P = 0.006$). 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.

*This section is from Batistel et al. 2022. Response of four peatland emergent macrophytes to salinity and short salinity pulses. Wetlands 42:67. https://doi.org/10.1007/s13157-022-01592-0

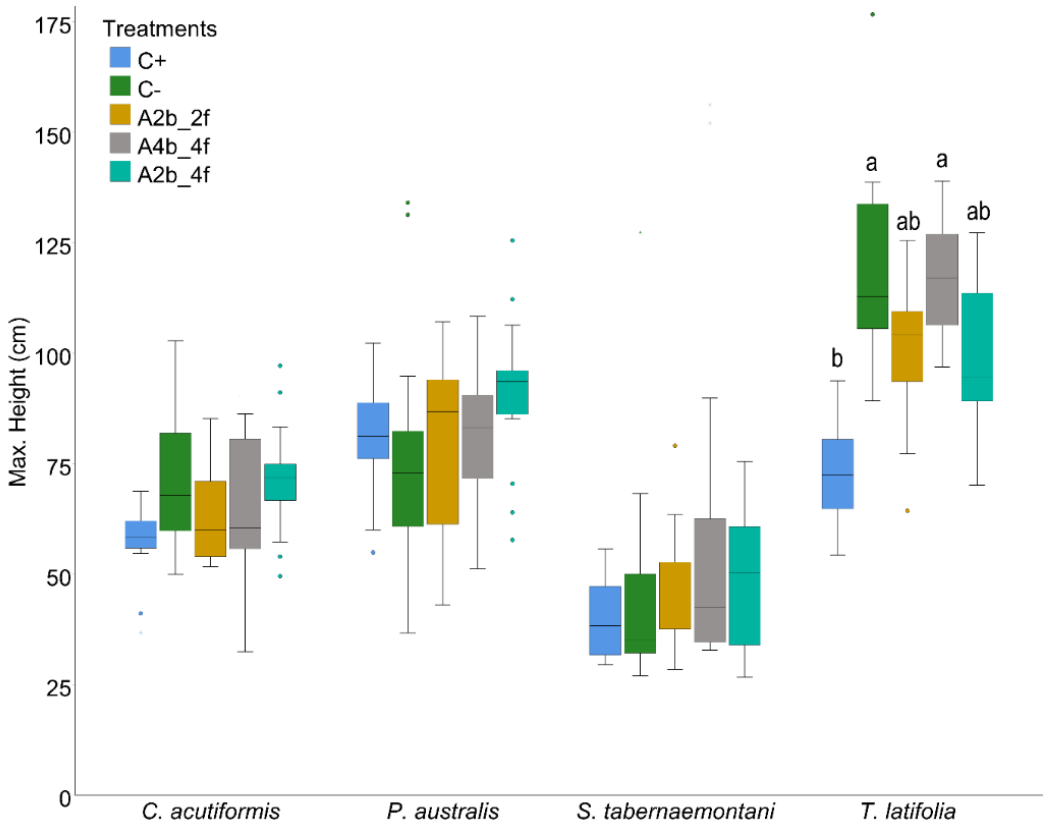

Figure 9. Maximum height (cm; n=15) of the four macrophytes under different treatments. Different letters above the boxes represent significant differences between treatments of the same species ($P \leq 0.05$) using Tukey's HSD multiple comparisons

The maximum growth rates of the four emergent macrophytes were neither significantly affected by salinity nor the different frequency of salinity pulses (Figure 10). For the daily growth grates (cm d^{-1}), values generally decreased three weeks after treatment application, except for *P. australis* specifically those under frequent salinity pulses (A_{2b_2f}, A_{4b_4f}, A_{2b_4f}) which showed the opposite pattern until week five (Figure11). Between treatments, C+ of both *C. acutiformis* and *T. latifolia* had the lowest growth rates from week six until nine and week four until ten, respectively. Treatment A2b_4f of *C. acutiformis* was relatively higher than the other treatments from week until seven but dropped thereafter. For *S. tabernaemontani*, growth rate slightly decreased until week six and then declined from week eight.

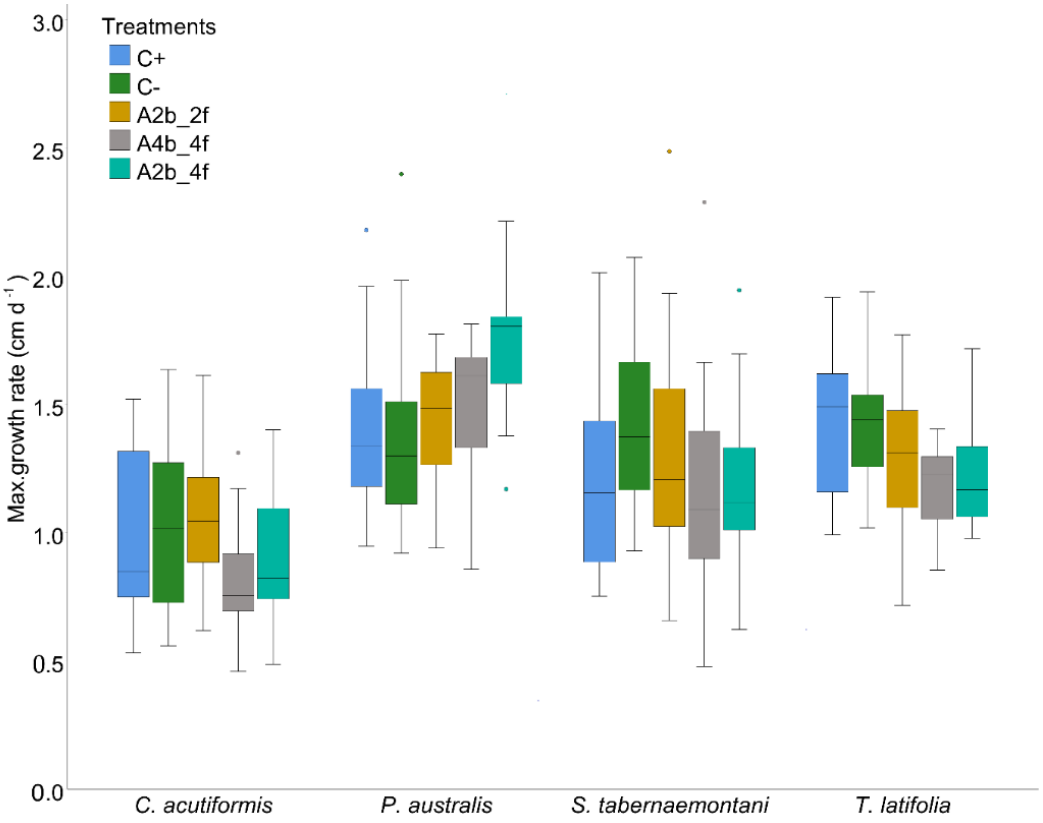

Figure 10. Maximum growth rate (cm d^{-1}; n=15) of the four macrophytes under different treatments. Different letters above thje boxes represent significant differences between treatments of the same species ($P \leq 0.05$) using Tukey's HSD multiple comparisons

3.2.2 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; Figure 12). In the first few weeks of brackish water flooding, 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 ($P < 0.05$) from the other treatments, except A_{4b_4f}, in week seven (Table 3). 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+.

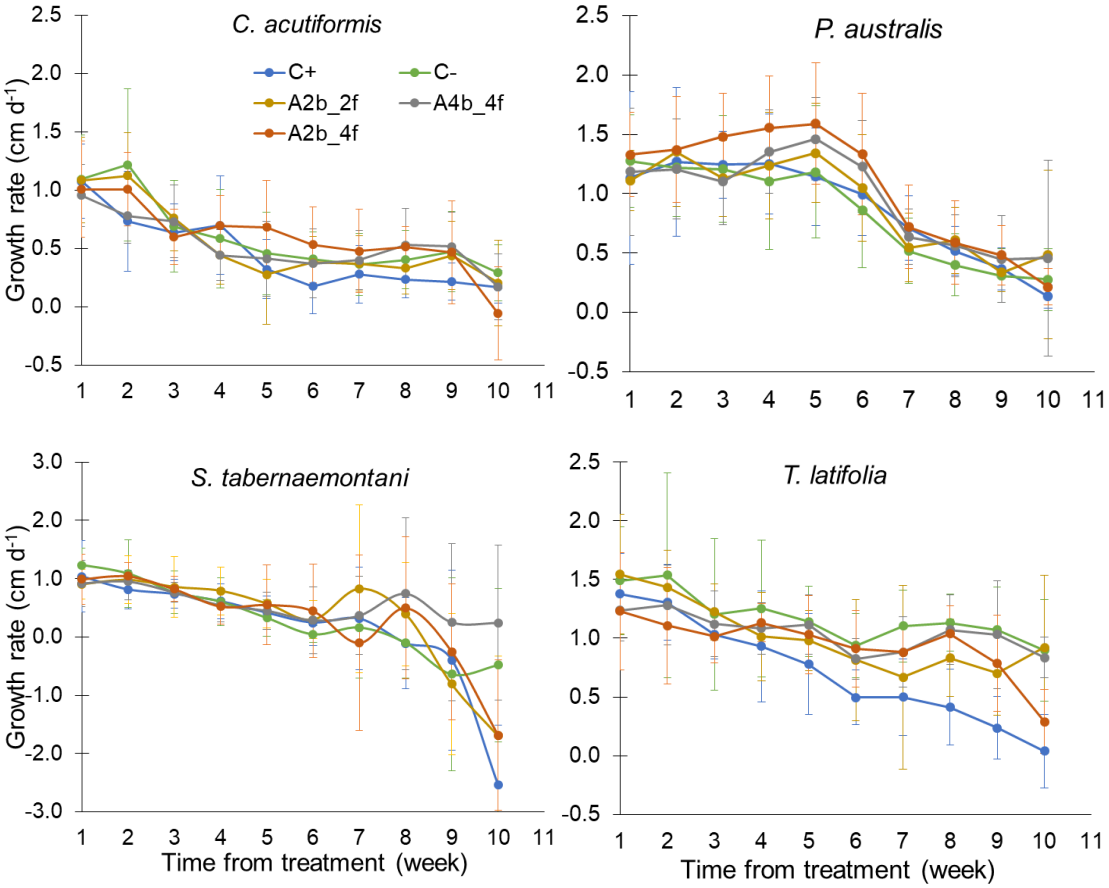

Figure 11. Mean growth rates (n=15) of the four emergent macrophytes under different treatments (C+: permanently brackish water; C- permanently freshwater; A_{2b_2f}: alternate 2 days brackish water, 2 days freshwater; A_{4b_4f}: alternate 4 days brackish water, 4 days freshwater; A_{2b_4f}: alternate 2 days brackish water, 4 days freshwater). Vertical bars represent standard deviation

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} ($P < 0.05$). In week six, the mean leaf area of C+ started to decline relative to the other treatments resulting in smaller leaves compared to C- ($P < 0.01$) from week six until termination. The mean leaf area under salinity pulse A_{2b_4f} was also smaller than C- ($P < 0.001$) 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 ($P < 0.01$). Salinity and salinity pulses did not cause significant effect on the mean leaf area ($P > 0.05$) of *P. australis* although A_{2b_4f} was generally larger than the other treatments.

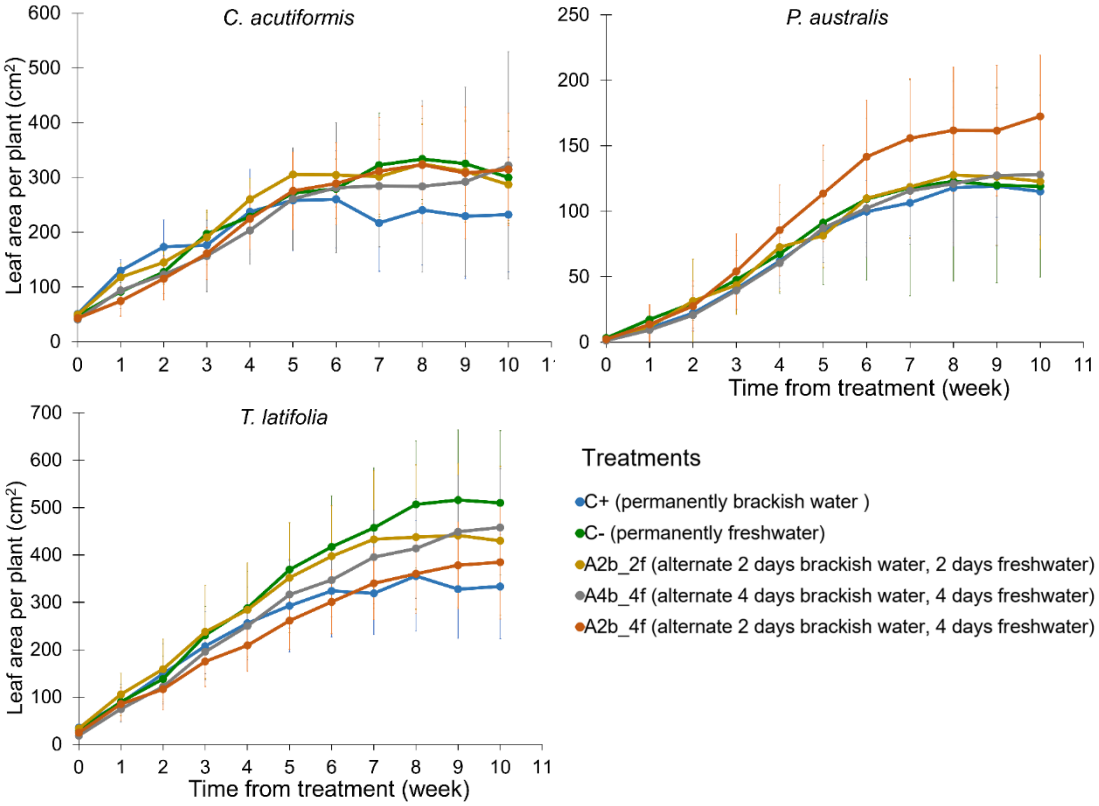

Figure 12. Mean leaf area per plant (n=15) per individual of under different treatments over time (weeks). Vertical lines represent standard deviation

Table 3. Results of 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 ($P \leq 0.05$); ⋮ represents weeks with $P > 0.05$

Species	Time (Week)	Treatments				
		C+	C-	A_{2b_2f}	A_{4b_4f}	A_{2b_4f}
Carex acutiformis	⋮					
	7	b	a	a	ab	a
	8	b	a	a	ab	a
	9	b	a	a	ab	ab
	10	b	ab	ab	a	a
Typha latifolia	⋮					
	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

3.2.3 Photosynthetic pigments

The chlorophyll a:b ratio across species and treatments on week ten ranged from 2.1 to 4.0 (Table 4). 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 ($P > 0.05$), except *P. australis* wherein Chl a:car of A_{4b_4f} was significantly lower than C- ($P = 0.039$).

Table 4. 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 ≤ 0.05) calculated with ANOVA post hoc multiple comparisons using Tukey's HSD

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

3.2.4 Photosynthetic yield

The difference in yield (ΔYield) between morning (AM) and noon (NN) under light dose classes varies between treatments for each species (Figure 13A–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.

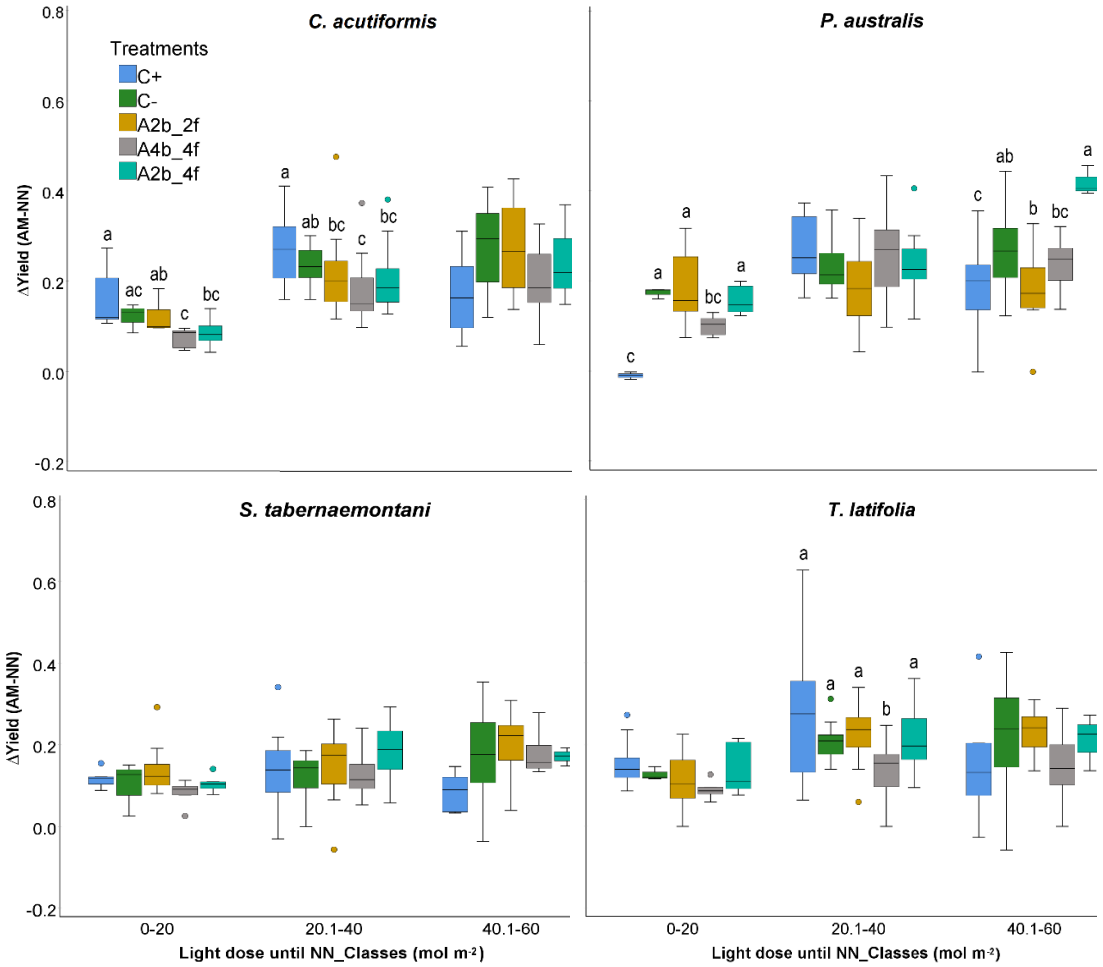

Figure 13. Differences in photosynthetic yield (Yield) between morning (AM) and noon (NN) measurements of the fours macrophytes under different treatments classified into light dose classes based on light dose received. Different letters above the boxes represent significant differences between treatments of the same species ($P \leq 0.05$; n ≥ 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.

3.2.5 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 (Figure 14). 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 ($P > 0.05$; n=3). However, a significantly lower root:shoot ratio ($P < 0.05$) of T. latifolia was observed under relatively frequent salinity pulses (A_{2b_2f} and A_{2b_4f}) compared to C+.

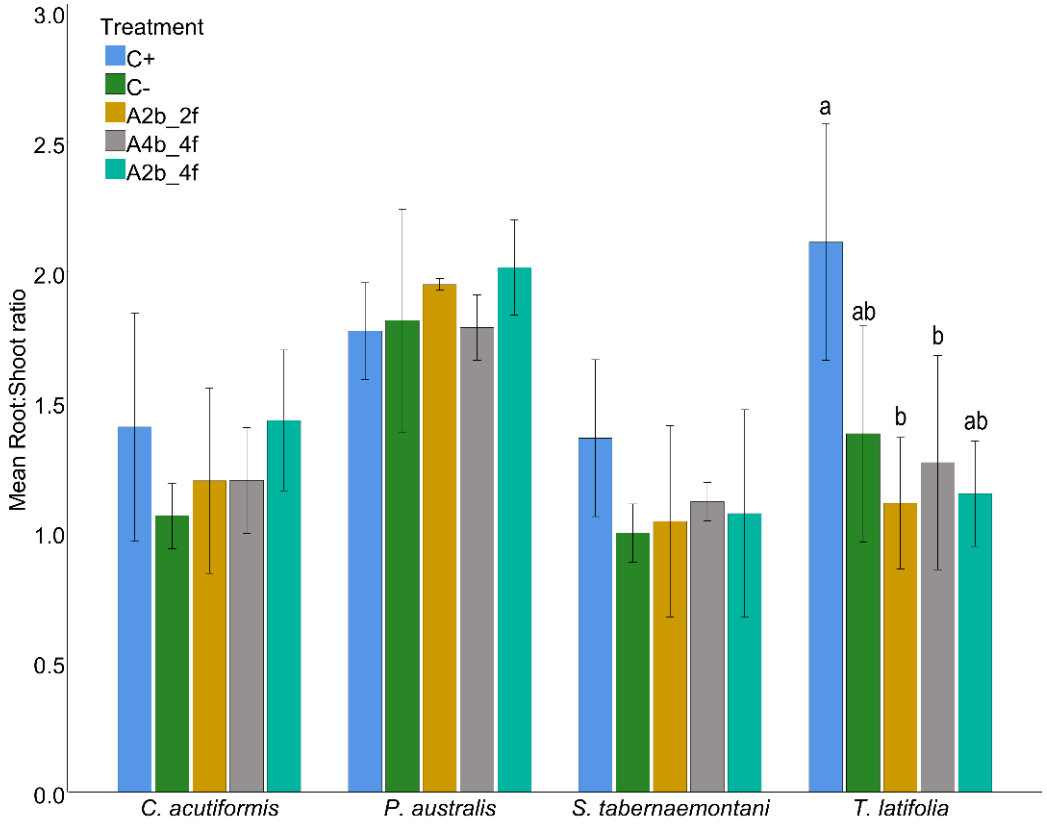

Figure 14. Mean root:shoot ratio of the macrophytes after 10 weeks of treatment application. Error bars represent standard deviation (n=3). Different letters above the boxes represent significant differences between treatments of the same species ($P \leq 0.05$; ANOVA post hoc multiple comparisons using Tukey's HSD); absence of letters above the boxes means no significant difference found between treatments.

3.3 Litter decomposition**

3.3.1 Mass loss

Changes in dry mass of *Phragmites australis*, *Carex* sp. and *Schoenoplectus tabernaemontani* litter versus incubation time are presented in Figure 15. Across site and species, 15% to 30% of the initial litter mass was lost in the first 35 days of decomposition. Mass loss of similar species exposed in the freshwater and brackish peatland were not statistically significant. However, species-specific differences were detected. *Schoenoplectus tabernaemontani* lost a significantly higher amount of its initial mass in both sites compared to the other species (Table 5). In SM, the litters from the other three species did not vary significantly, however, in DM (brackish), *P. australis*$_{DM}$ lost significantly more mass ($P < 0.05$) than *P. australis*$_{SM}$.

**This section is from Batistel et al. 2021. Salinity exerted little effect of decompostion of emergent macrophytes in coastal peatlands. Aquatic Botany 175 (2021) 103446

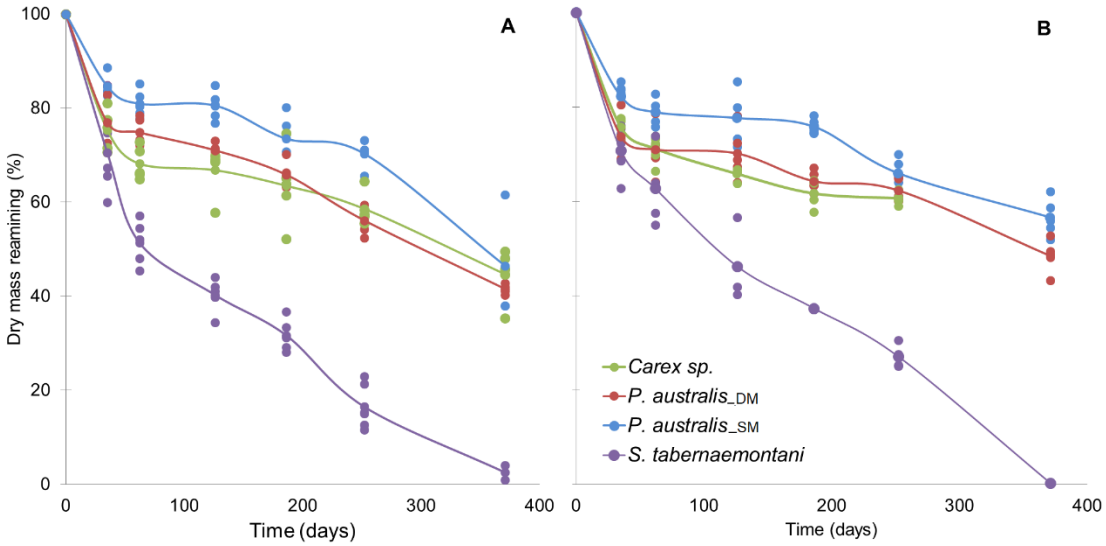

Figure 15. Dry mass remaining (%) of macrophyte litter after time (days) of exposure in A) Schutower Moor (freshwater); and B) Diedrichshäger Moor (brackish). Lines connect the mean (n≤5) while symbols are values of individual samples per species

Table 5. Initial decay (%, ± SD) at t=0-35 days, linear regression coefficient for the remaining time (t=62-371 days) and decay coefficient (-k d^{-1}) during the decomposition of macrophyte litter exposed in Schutower Moor (SM) and Diedrichshäger Moor (DM)

Site_Species	n	Time: 0-35 days	Time: 62-371 days		
SM (Freshwater)		Initial decay (%)	Slope	Intercept	r^2
P. australis$_{SM}$	5	15.38±2.36^{b}	-0.11	92.67	0.89
P. australis$_{DM}$	5	23.09±5.29^{b}	-0.11	84.03	0.98
Carex sp.	5	24.66±4.32^{b}	-0.08	75.73	0.93
S. tabernaemontani	5	29.50±9.58^{a}	-0.16	61.58	0.99
DM (Brackish)					
P. australis$_{SM}$	5	17.75±3.89^{c}	-0.08	86.37	0.93
P. australis$_{DM}$	5	26.24±4.50^{b}	-0.07	77.88	0.93
Carex sp.	5	24.30±2.19^{bc}	-0.06	73.62	0.92
S. tabernaemontani	5	29.20±5.25^{a}	-0.19	73.54	0.99

Different letter superscripts indicate significant differences in the initial decay between species per site ($P < 0.05$; ANOVA post-*hoc* multiple comparisons using Tukey's HSD). Similar species did not differ significantly between sites thus, results are not shown in the table.

Mass loss strongly decreased after 35 days with slopes of the remaining litter mass from 62 to 371 days ranging between -0.06 to -0.19. Of all the species, *S. tabernaemontani* had the highest daily loss of -0.16 and -0.19% as the remaining litter mass reached 62% and 74% in freshwater and brackish peatlands, respectively (Table 5). *P. australis*$_{SM}$, *P. australis*$_{DM}$ and *Carex* sp. had very flat slopes, indicating a slow decrease in the respective litter mass per day. For instance, in Schutower Moor, both *P. australis* decreased by 0.11% per day starting when the remaining mass was 84% (*P. australis*$_{SM}$) and 93% (*P. australis*$_{DM}$). In DM, their decay slopes were less than -0.1%.

The higher initial mass loss and slope in *S. tabernaemontani* are linked to a higher decay coefficient in both sites. These decay rates are up to four times higher compared to *P. australis*$_{SM}$ (Figure 16). This resulted in complete decomposition of *S. tabernaemontani* during field exposure time while about 40% to 60% litter mass remained for the other species a year after exposure.

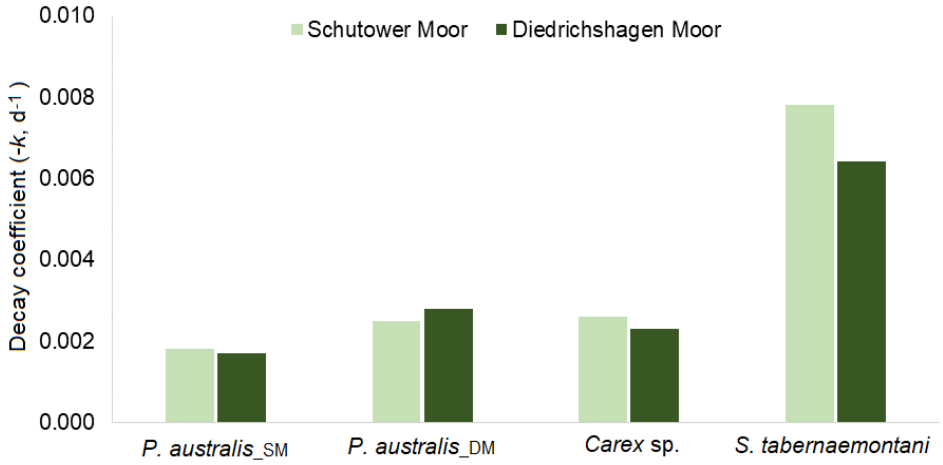

Figure 16. Decay coefficient (k, d^{-1}) of different macrophytes exposed in Schutower Moor (freshwater peatland) and Diedrichshäger moor (brackish peatland)

3.3.2 Litter chemical composition

3.3.2.1 Initial litter chemistry

The initial chemical composition of litter varied between species. The carbon content of *S. tabernaemontani* was significantly lower ($P < 0.01$) than that in *P. australis*$_{DM}$, *P. australis*$_{SM}$ and *Carex* sp. (Figure 17). The same pattern was observed in their initial nitrogen content with *S. tabernaemontani* containing 1.06% ± 0.06, which is about half of that found in *P. australis*$_{DM}$. In contrast, *S. tabernaemontani* had four

times higher sulfur content ($P < 0.01$) than macrophytes from the freshwater peatland. The phosphorus content of *P. australis*$_{SM}$ and *Carex* sp. was significantly lower ($P < 0.05$) than litter of the species from the brackish peatland, *P. australis*$_{DM}$ and *S. tabernaemontani*.

Molar ratios for C:N, C:K and N:P ratios differed significantly ($P < 0.05$) between species (Table 6). *S. tabernaemontani* litter obtained the highest molar C:N ratio but had the lowest C:P, C:K and N:P ratios. The initial C:P ratio in *S. tabernaemontani* was significantly lower than in *P. australis*$_{SM}$ or *Carex* sp. The low N and high P contents of the initial *S. tabernaemontani* litter resulted in a ~2-fold lower N:P ratio than that of *P. australis*. Further, *S. tabernaemontani* litter contained significantly more potassium and sodium ($P < 0.01$) resulting in significantly lower C:K and C:Na ratios ($P < 0.01$).

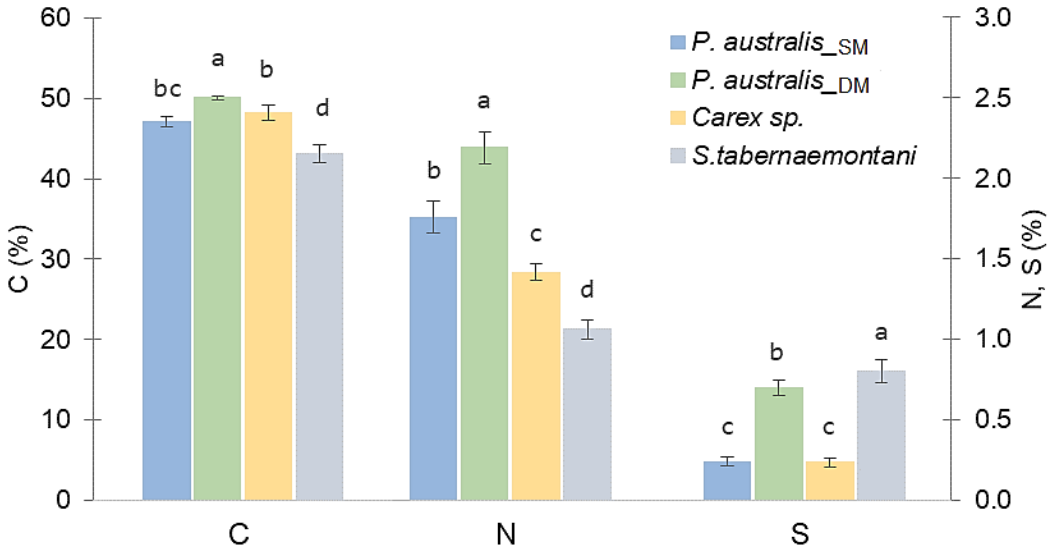

Figure 17. Mean initial C, N and S contents (%) of the macrophyte litter. Error bars denote standard deviation (n=5). Different letters on top of the bars indicate significant differences between species per element ($P < 0.05$; ANOVA post-hoc multiple comparisons using Tukey's HSD)

3.3.2.2 Decomposition stoichiometry

Changes in C:N, C:P and N:P ratios of the detritus from the start (day 0) to the end (day 371) of the decomposition study are shown in Figure 18. Generally, the C:N and C:P ratios (Figure 18A-D) of all litters initially increased in the first two months of decomposition and then stayed more or less constant, except for the C:N ratios of *S. tabernaemontani* which showed a slight decrease. The C:N ratios of *P. australis* and *Carex* sp. in both sites increased over time relative to their initial contents while *S.*

tabernaemontani demonstrated an opposite pattern (Figure 18A-B). Between species, *Carex* sp. had the highest C:N ratio from 35 to 371 days of field exposure. Higher values (8-22%) were recorded in DM than those exposed in its site of origin, SM.

Table 6. Macroelement contents and C:macroelemental ratios (mean ± SD, n=5) of the initial litter samples of tested macrophytes

Macroelements/ Ratios	*P. australis*_SM	*P. australis*_DM	*Carex* sp.	*S. tabernaemontani*
P (mg g^{-1})	1.12±0.08^{b}	1.51±0.12^{a}	1.22±0.01^{b}	1.46±0.14^{a}
K (mg g^{-1})	4.03±0.59^{c}	5.30±0.32^{c}	11.84±0.70^{b}	26.12±2.55^{a}
Mg (mg g^{-1})	1.71±0.21^{b}	2.37±0.23^{a}	0.99±0.06^{c}	1.85±0.19^{b}
Na (mg g^{-1})	0.98±0.31^{b}	0.74±0.06^{b}	0.85±0.12^{b}	12.18±0.52^{a}
Ca (mg g^{-1})	8.45±0.56^{a}	9.27±0.47^{a}	4.13±0.39^{c}	6.82±1.10^{b}
C:N	31.28±1.78^{c}	26.69±1.13^{d}	39.71±0.85^{b}	47.55±2.69^{a}
C:P	1085.71±59.66^{a}	860.06±69.12^{b}	1021.59±72.66^{b}	770.35±83.63^{bc}
N:P	34.79±2.66^{a}	32.27±2.99^{a}	25.74±1.90^{b}	16.20±1.46^{c}
C:K	386.25±52.81^{a}	308.44±18.63^{b}	132.91±5.84^{c}	54.18±5.29^{d}
C:Mg	565.12±71.65^{b}	429.94±41.03^{c}	988.83±46.40^{a}	474.93±47.02^{bc}
C:S	533.25±65.44^{a}	191.42±12.10^{b}	550.97±51.63 ^{a}	144.55±10.96^{b}
C:Na	991.03±299.2^{a}	1303.63±108.4^{a}	1101.96±180.3^{a}	67.90±3.1^{b}
C:Ca	186.69±11.80^{b}	180.69±9.72^{b}	392.78±33.10^{a}	215.37±34.49^{b}

Different letter superscripts indicate significant differences in each macroelement/ C:macroelemental ratios between species ($P < 0.05$; ANOVA post-hoc multiple comparisons using Tukey's HSD)

The C:P ratio of all species increased relative to their initial values, except for *P. australis*_SM in SM wherein a decrease of 8.65% was recorded during the last sampling (Figure 18C-D). *Schoenoplectus tabernaemontani* litter had the lowest C:P ratio which is consistent throughout the course of decomposition. All species exposed in DM, except *S. tabernaemontani,* contained C:P ratios that were about 2-fold higher than those in SM. The N:P ratio (Figure 18E-F) in *S. tabernaemontani* was also lower compared to the other species. In both sites, *P. australis* litter had higher N:P ratio than the litter of the other species, however, with relatively lower values in SM than in DM.

The cation contents of most litter samples significantly dropped during the initial phase of decomposition (Figure 19). Magnesium concentration decreased by 43% to 88% across species and sites, except for *Carex* sp. and *S. tabernaemontani* in DM, which increased by 31% to 87%, respectively (Figure 19A-B). Calcium loss ranged from 48% to 63% for *P. australis* but not for *Carex* sp. and *S. tabernaemontani* (Figure 19C-D). Most of the K (73 to 98%) was lost during the initial phase (Figure 19E-F). After these initial losses, cation concentrations remained roughly constant. Of the tested species, *S. tabernaemontani* retained the highest amount of all cations in both sites. Between sites, *S. tabernaemontani* litter deployed in DM had more Mg and Ca throughout the decomposition period than those in SM.

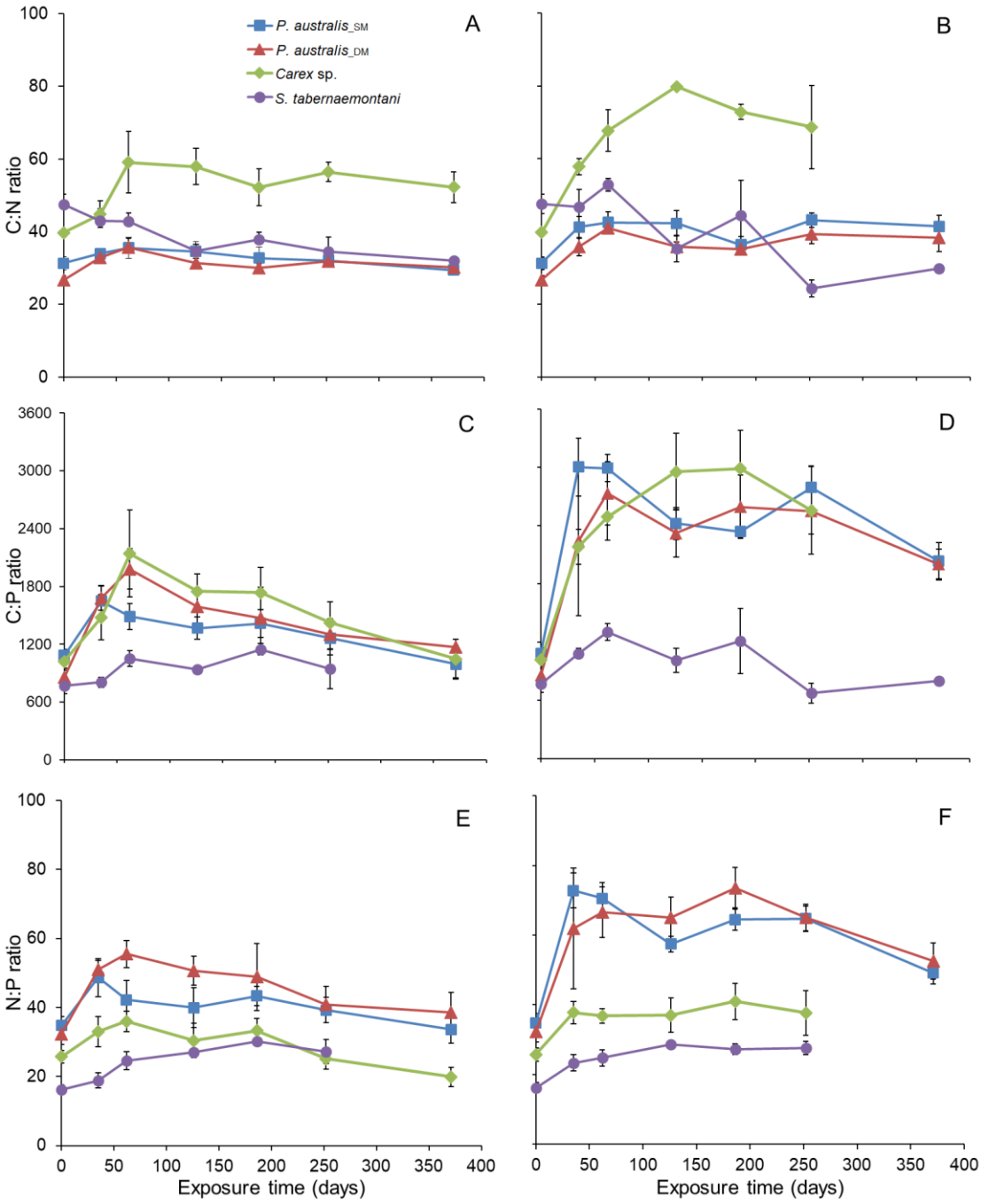

Figure 18. Molar C:N (A, B) , C:P (C, D) and N:P (E, F) ratios of macrophyte litter after time (days) of field exposure in Schutower Moor (freshwater, left column) and Diedrichshäger Moor (brackish, right column). Symbols represent the mean values, error bars show the standard deviation (± SD, n=5) per species

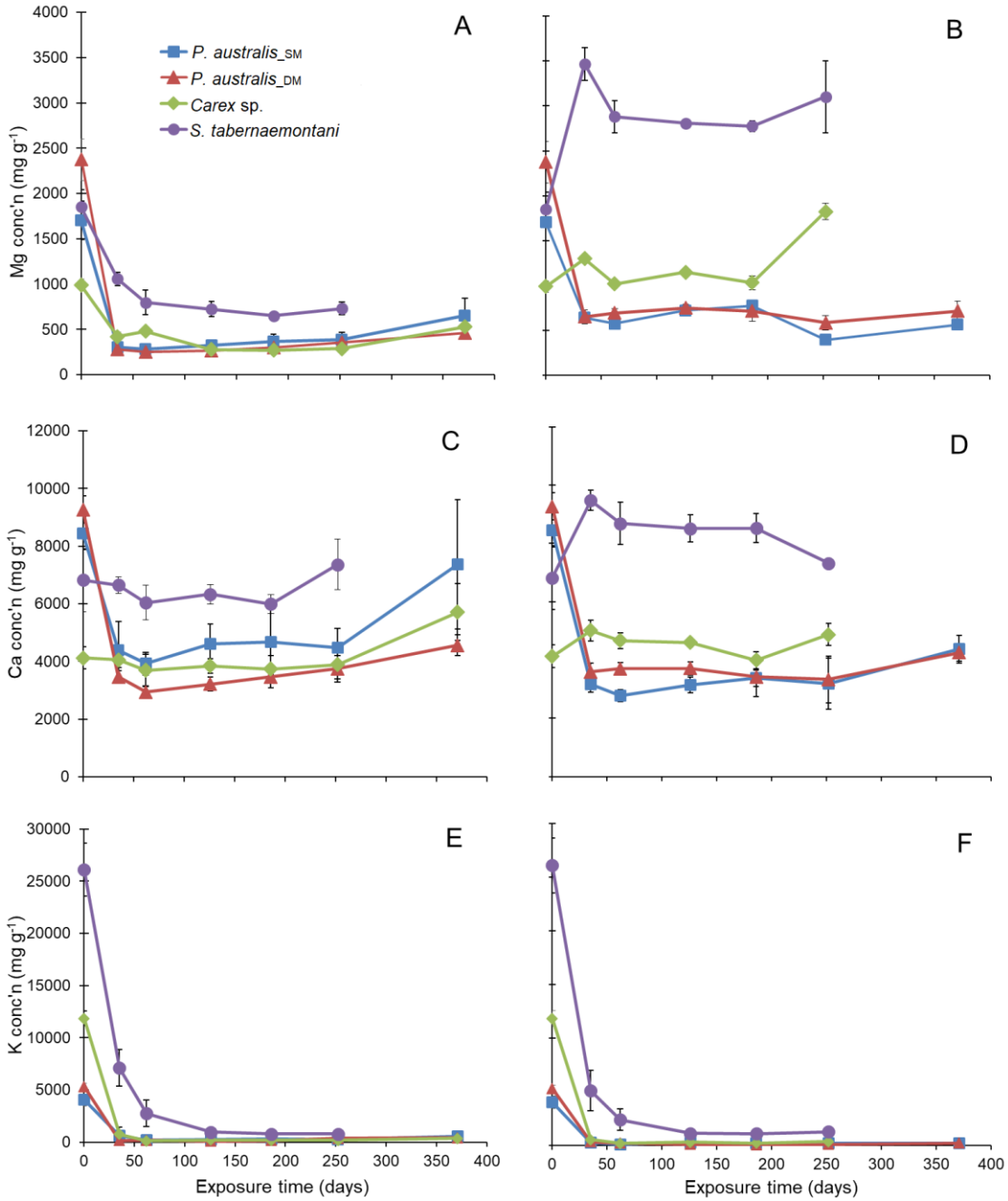

Figure 19. Concentrations of cations, Mg (A and B), Ca (C and D) and K (E and F) in macrophyte litter after time (days) of field exposure in Schutower Moor (freshwater, left column) and Diedrichshäger Moor (brackish, right column). Symbols represent the mean values and error bars show the standard deviations (± SD, n=5) per species

3.3.3 Principal component analysis

The first two principal components (axes) of the PCA that was constructed from the elemental stoichiometry of the decomposed litter across all sampling times cumulatively explained 71.0% of the variance in the dataset (Figure 20). The first principal component (PC1) explained 45.7% of the variation and was mainly defined by C:Mg (r = -0.50) and C:Ca (r = -0.49) ratios. The second principal component (PC2) explained 25.3% of the variation and was strongly determined by the C:P (r=0.62) and C:N (r=0.57) ratios.

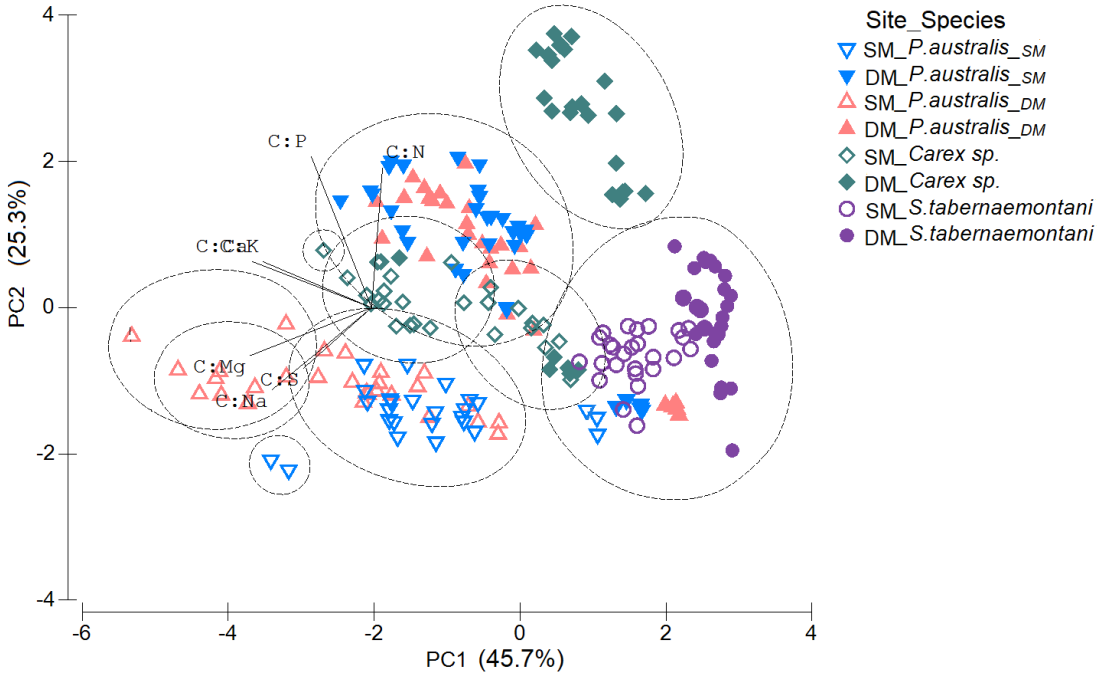

Figure 20. Principal component analysis (PCA) biplot of the molar C:macroelemental ratios of macrophyte litter in SM (freshwater) and DM (brackish) peatlands. Clusters are based on 2.5 Euclidean distance of normalized data (ratios)

4 Discussion

Emergent macrophytes in freshwater wetlands are mostly represented by only a few but large families of monocotyledons including Poaceae, Cyperaceae, Juncaceae and Typhaceae (Cronk and Fennessy, 2009, 2001; Khan et al., 2022). They added that other families with frequently encountered emergent species include Asteraceae, Lamiaceae and Polygonaceae. Oligohaline wetlands are inhabited by a mosaic of species including freshwater species that can grow under low salinity environments including *Typha* spp., *Juncus* spp., *Schoenoplectus* spp., *Scirpus* spp., *Phragmites australis* (Howard and Mendelssohn, 1999; Sharpe and Baldwin, 2009). Peatlands assessed in this study showed similar results with Poaceae and Cyperaceae being the most represented families (Table 1). Similar genera/species of macrophytes were also found although the other less abundant species were not exactly the same.

Phragmites australis highly dominates in the assessed coastal peatlands, covering up to 100% in most plots, and a few other emergent species occurring at the margins. Its abundance is attributed to the extensive rhizomes and stolons that allow the plant to spread into dense monotypic stands (Welsh, 2003). Being present in all sites confirms that it has wider salinity tolerance than the other species. This support previous studies reporting that it thrives in a variety of habitats throughout its range including tidal and non-tidal wetlands, marshes and other wetlands (Hickmann, 1993; Welsh, 2003), and even occupies salty tidal marshes with soil salinity greater than 20 (Burdick et al., 2001; Chambers, 1997). Common reed is also adapted to frequent, prolonged flooding, although plant mortality has been reported after 3 or more years with more than 1 m of water (Shay and Shay, 1986). Thus, *P. australis* is considered as the most widely distributed angiosperm with geographical range extending from 70° N to the tropics (Cronk and Fennessy, 2009).

The presence of *Schoenoplectus tabernaemontani* and *Agrostris stolonifera* in all brackish sites confirms that these species can tolerate a slightly saline environment. *Bolboschoenus maritimus* was found, although sparsely, in Hütelmoor plots. Koch et al. (2017) observed in 2011 that *S. tabernaemontani* and *B. maritimus* co-occurred in many plots in this area with higher abundances of the latter. However, years after the 2010 rewetting, *S. tabernaemontani* increased in both frequency and abundance whereas *B. maritimus* declined. Koch et al. (2017) further reported that before rewetting, “Hütelmoor and Heiligensee” was dominated by helophytic species such as

P. australis, B. maritimus, S. tabernaemontani and *C. acutiformis*. This infers shifting of vegetation communities resulting from increased water level and salinity following permanent inundation.

The generally low effective species number of macrophytes (e^H = 3.44 – 9.81, Figure 8) in these peatlands can be explained by the low species richness and the low evenness of species distribution, having only a single species, *P. australis*, dominating in most plots. This is common in wetland habitats since they are susceptible to plant invasions due to high disturbance and often high nutrients that facilitate the rapid expansion of invading species leading to the formation of monocultures while displacing the native vegetation and allowing only a few co-occurring plants to persist (Rejmánková, 2011). The recorded species richness in Schutower Moor (26) and Diedrichshäger Moor (21) is comparable to Cranes Moor in Southern England with a mean species richness of 20.38 ± 1.16 (Lovegrove et al., 2020). In Hütelmoor, the lower species richness is due to lesser number of plots (5). In terms of species dominance, peatlands in Rostock are vastly occupied by common reeds (*P. australis*) while the Cranes Moor is dominated by *Sphagnum* spp. In Finland, sedges (i.e. *Carex* spp.) and mosses dominate the eutrophic fens while *Sphagnum* spp. mainly dominates the open fens (Seppä, 2002). The difference in vegetation type could be mainly attributed to the difference in pH, nutrient status and moisture, the most important ecological gradients that affect peatland vegetation (Seppä, 2002).

Salinity is one of the main factors controlling the distribution and abundance of macrophytes in coastal wetlands (Grillas et al., 1993; Watt et al., 2007). Many studies have shown that salinity reduces diversity and abundance of macrophyte species (Grillas et al., 1993; Smith et al., 2009). This study found similar trend having lower species richness in brackish peatlands, resulting in lower beta diversity, compared to the Schutower Moor. The low species richness results from the colonization of *P. australis* in most sites, which in turn resulted in low species evenness. Lowest evenness was recorded in the more brackish sites (DM, J = 0.40; HM2, J = 53) since 90% of the plots were totally covered with *P. australis* with a single or two undergrowth species, which are very low in both abundance and frequency. Subsequently, DM had the lowest effective species number. In contrast, freshwater peatland, SM, had the highest effective species number (e^H = 9.81) due mainly to both higher species richness and higher evenness index compared to the brackish sites.

This assessment shows that species composition and distribution change with salinity as shown by the lower species richness and diversity in brackish peatlands than in the freshwater site. This suggests that different species are adapted to certain

salinity levels. Across sites, *P. australis* is the most dominant except in HM2, where the common reed was replaced by *S. tabernaemontani* apparently due to higher water level, which is favored by the latter. Of all the species, *P. australis* and *Carex* spp. occur in the coastal wetlands with salinity up to 7. Other species such as *S. tabernaemontani* are limited to slightly saline environments. These results, however, may not be valid for other coastal wetlands with higher salinity. Also, due to the relatively small area covered here, results may differ from others and therefore not conclusive. Nevertheless, because of these findings, the question of how these dominant emergent macrophytes would potentially react to future sea-level rise and the predicted frequent and extreme storms and flooding events arise. Hence, the emergent macrophytes, *P. australis*, *S. tabernaemontani, Carex* sp. and *T. latifolia* were subjected to salinity acclimation experiment to prove the second hypothesis that salinity and frequent brackish water flooding affect their growth and productivity to different degrees.

Results of the acclimation study 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 (C+) than those in freshwater (C-, Figure 9) suggests high sensitivity 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 salinity ≥ 25 (Glenn et al., 1995; Macek and Rejmánková, 2007; Shay and Shay, 1986). *Typha latifolia* under brackish water had consistently lower relative growth rate than in freshwater from week one until week ten (Figure 11). 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 (Figure 10) 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 (Supplementary Table 1). 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 (Cramer, 2003; Munns and Tester, 2008; Wang and Nii, 2000). 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 *Carex 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+ (Figure 11). More pronounced effect of salinity stress on the species is manifested in the leaf area (Fig. 12A). The smaller leaf area under treatment C+ from week seven resulted from the lower expansion rate starting week five (Supplementary Table 1). 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 finding supports 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- (Figure 12, Table 3), the concentration of their photosynthetic pigments as well as the ratios did not differ (Table 4). 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 ΔYield, were also similar even under high light doses (Figure 13). 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 (James et al., 2002; Kurban et al., 1999; Rajesh et al., 1998). 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* (≤32%) and *T. latifolia* (≤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. 14). 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 (Acosta-Motos et al., 2017; Hsiao and Xu, 2000).

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 9.6 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 soil 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). This was also observed in this experiment as some individuals under treatments C+, A_{2b_2f} and A_{2b_4f} started to wither after eight weeks of treatment application, thus the sharp decrease in growth rates (Fig. 11).

The significantly lower ΔYield of *P. australis* under constant brackish water (C+) than in freshwater (C-) at light dose classes <20 mol m^{-2} and 40.1–60 mol m^{-2} (Fig. 13) shows that this species peculiarly acclimated to increased salinity. Salt stress is shown to inhibit photosystem II (PS II) activity in some higher plants (Mishra and Tanna, 2017; Parida et al., 2003) whereas others observed no effect on PS II (Morales et al., 1992). However, a decreased ΔYield 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 et al., 1993; Schubert and Hagemann, 1990), resulting in a shift of P/I-characteristics as suggested here. The reason for this was seen in increased energy demand for osmoregulation, which was fulfilled by cyclic electron transfer driven by photosystem I (PS I) and indicated by both increased energy transfer towards PS 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.

Results of this study further suggest that the four emergent macrophytes respond differently to frequent brackish water flooding. *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-, Fig 9). 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 (Cramer, 2003; Munns and Tester, 2008). Additionally, reducing the leaf canopy area could be a mechanism to minimize water loss by transpiration (Acosta-Motos et al., 2017; Munns and Termaat, 1986). 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 constantly 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 height, maximum growth rate, and root:shoot ratios between C- and the other treatments (Figures 9, 10, 14, respectively). 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 (Chambers et al., 2003; Mauchamp and Mesleard, 2001). 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 a decrease 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 ΔYield 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} (Figure 13) implies that when there is no limitation in irradiance, photosynthetic efficiency of *P. australis* decreases. This most probably resulted 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 (Acosta-Motos et al., 2017; Maxwell, 2000; Murchie and Lawson, 2013). However, this higher ΔYield 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 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} (Table 4) is due to low Chl a (267.2 µg g^{-1} FM) and Chl b (89.3 µg 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*, a significantly lower Chl a:car was also observed under similar treatment (A_{4b_4f}). However, we only had pigment data available for week 10 and, hence, this

idea cannot be proven here. We recommend further investigation of this aspect to gain a better understanding of this phenomenon. Yet, in both species, this has not impaired biomass production.

Overall, this salinity acclimation study demonstrates that *P. australis* has the highest tolerance to salinity and frequent brackish water flooding among the four emergent macrophytes tested. Although *S. tabernaemontani* can tolerate brackish environment, it can only stand under a salinity of 9.6 for up to 8 weeks. Beyond that, the plant growth starts to deteriorate due probably to salinity stress. This suggests that with more brackish water influx into coastal wetlands, increased salinity may induce expansion of area covered by *P. australis*. However, if this coastal flooding is combined with increased precipitation, surface runoff will increase which would eventually drain into coastal wetlands. This may not significantly increase the salinity of the coastal peatland but an increment in the water level may be expected. This will result in the expansion of *S. tabernaemontani* as it favors relatively deeper, oligohaline water than the other species. Still, both scenarios may induce the flourishing of either species while the salt-sensitive species, *T. latifolia* and *C. acutiformis* may be outcompeted. New species may also colonize the area in the future. In contrast, change in biomass allocation pattern may occur resulting from salinity stress. Specifically, the aboveground biomass of *T. latifolia* and *C. acutiformis* will, most likely, decrease. As a result, other equally relevant ecological processes including nutrient cycling and peat formation may be affected. Therefore, litter decomposition study was carried out to prove the third hypothesis that changes in salinity alters decomposition patterns of these dominant emergent macrophytes even at low salinity levels.

Results of the decomposition study showed that the decomposition of the emergent macrophyte litters varies with species mainly due to their differences in chemical composition. The significantly higher initial mass loss in *S. tabernaemontani* compared to the other species (Figure 15; Table 5) indicates that this species contains more labile organic compounds leached from the decomposing litter (Brinson et al., 1981; Webster and Benfield, 1986). Thereafter, the decomposition rate continued to be relatively fast for *S. tabernaemontani* suggesting sustained litter decay throughout the study period that led to complete decomposition a year after litter field exposure. For *P. australis* and *Carex* sp., decomposition rates slowed down, implying that the remaining mass was mainly composed of recalcitrant compounds that were more resistant to decay (Webster & Benfield, 1986), providing a low-quality food source for the decomposers (Chapin III et al., 2011).

The measured mass loss and decay coefficients of the tested species, presented in Figure 16, are within the range found by other studies (*P. australis* 0.0003-0.009, Van der Valk et al., 1991; Menéndez et al., 2001; *Carex* spp. 0.0009-0.0028 d^{-1}, Longhi et al., 2008. Even though no comparable values were found for *S. tabernaemontani*, the rates can be compared with *Scirpus* spp. (syn. *Schoenoplectus*) (0.002-0.008 d^{-1}, Chimney and Pietro, 2006). Based on our measurements, *S. tabernaemontani* has a medium decay rate while the *P. australis* and *Carex* sp. are slow. From this, we can conclude that only these species but not *S. tabernaemontani* contribute to peat formation.

C:N, C:P and N:P ratios are considered good predictors of litter decomposition (Aerts, 1997; Heal et al., 1997). Previous studies (Nguyen et al., 2006) reported that higher nitrogen concentrations in plant tissues lead to faster decay rates. Therefore, litter with a low C:N ratio generally decomposes rapidly (Ágoston-Szabó and Dinka, 2008). However, other studies (Longhi et al., 2008) claimed that initial nutrient content alone does not explain differences in decomposition rates. This is supported by our results for *S. tabernaemontani* that had the lowest initial nitrogen content (Figure 17) and highest C:N ratios (Table 6) and decomposed the fastest suggesting that low initial nitrogen does not necessarily limit initial decomposition. Instead, low initial nitrogen might stimulate microbial decomposers to sequester N from the surrounding environment to meet their growth requirements (Tezuka, 1990). Previous findings showed that litter with low initial nutrient concentrations can accumulate more nitrogen (Van der Valk et al., 1991). The initial C:N ratio of *S. tabernaemontani* (~48:1) was higher than the reported optimal value for microbial degradation (20:1 to 30:1), which may have led to easier N immobilization (Heal et al., 1997). This is supported by the declining C:N ratio for *S. tabernaemontani* both in freshwater (32:1) and even lower ratio in brackish water (30:1) towards termination (Figure 18A-B).

Carex sp., however, showed an opposite pattern due to ~50% net loss of the initial N content. Without a concrete explanation for this, it is speculated that this may have been caused by phenolic compounds known to occur in this species (Rahman et al., 2013; Schellekens et al., 2012). Many phenolic compounds have antibacterial effects that could prevent or inhibit microbial activity (Swift et al., 1979), thus possibly also N immobilization. Moreover, the relatively similar decomposition rates of *Carex* sp. and *P. australis,* despite the lower C:N of the latter, indicates that N might have been integrated into aromatic compounds or other recalcitrant compounds (Chapin et al., 2011), and would, therefore, not be available for microbial decomposers. This is supported by their nearly constant C:N values after the initial increase.

The higher initial P content in *S. tabernaemontani,* that resulted in faster decomposition, is consistent with other studies (Berg and McClaugherty, 2008; Rejmánková and Houdková, 2006). Its low and nearly constant C:P ratio throughout decomposition suggests sustained P availability supporting microbial growth that fuels decomposition (Chapin III et al., 2011). At the beginning, C:P ratios of all litter substantially increased due to P release during the leaching phase (Nguyen et al., 2006) and later decreased due to some degree of P immobilization. The different P immobilization rates between species and sites could be attributed to the difference in microbial communities that colonize and proliferate on the decomposing litter (Dinka et al., 2004).

Nitrogen and phosphorus uptake, by microbial decomposers associated with the litters, decreases the N:P ratio that results in faster decomposition (Dinka et al., 2004) as confirmed here by *S. tabernaemontani* having the lowest N:P ratio (16:1) among the species. Previous studies (Güsewell and Gessner, 2009) revealed that bacteria are abundant at low N:P ratios (N-limited) while fungi colonize and proliferate at high N:P ratios. This may explain the higher net N immobilization rates in *S. tabernaemontani* (DM 103%, SM 68% after 371 days) as some bacterial decomposers are capable of N fixation (Marino and Howarth, 2009). In the beginning, the litter samples of other species showed P-limitation (N:P >25:1; Koerselman and Meuleman, 1996) and decomposition was, thus, most likely dominated by fungi since they require lower nutrient levels than bacteria (Van Der Wal et al., 2006). This nutrient limitation appeared to be the main reason for the slow decomposition of *P. australis* and *Carex*. However, this thesis lacks the microbial community data to support these so, these findings may not be conclusive. Inclusion of such data in future similar studies is recommended to provide a better understanding of this topic.

Calcium concentration and decomposition rates showed an inverse relationship. Higher initial Ca concentration in *P. australis* (Table 6) seemed to support larger fungal colonization producing calcium-rich hyphae encrustations that hamper litter decay (Virzo De Santo et al., 2009). Calcium oxalate provides a hydrophobic covering that prevents hyphae from becoming hydrated, therefore reducing microbial attack (Whitney and Arnott, 1987). The formation of calcium oxalate by certain fungi may also explain the increasing Ca concentrations in some litter during decomposition (Blair, 1988). Lower initial Ca losses in other litter and the sustained concentration, thereafter, confirmed that its release is correlated with decomposition rates since this is more dependent on biotic activity (Blair, 1988).

Magnesium and potassium concentrations in most litter bags decreased steeply during the initial phase (Figure 19), which is linked to leaching (Eid et al., 2014). The rapid initial potassium loss observed here is in line with comparable studies (Han et al., 2011), suggesting high K mobility is due to its loose ionic bonding with organic tissues (Chimney and Pietro, 2006). The remaining K is attached to refractory components explaining the slow release (Blair, 1988). The increase in the relative amount of Mg in some litter samples in DM may be attributed to microbial uptake from the surrounding water, as well as colonization and proliferation of microbes on the decomposing litter (Dinka et al., 2004).

The PCA (Figure 20) shows that C:macroelemental ratios, namely: C:Mg, C:Ca, C:P and C:N, differ strongly among the incubated macrophyte litter samples. The clustering indicates that species-specific chemical composition dominates over salinity effects. Apparent differences in decomposition kinetics between *S. tabernaemontani* and the other species indicate that the litter quality, specifically C:Ca, C:Mg, C:P and C:N, is of great importance both for microbial colonization (initial phase) as well as for sustaining decomposition after colonization. For colonization, initial C:N, C:P and N:P ratios have been identified as determinants for the rate of the decomposition process (Aerts, 1997; Ágoston-Szabó and Dinka, 2008; Rejmánková and Houdková, 2006). To what extent the conditions during the initial phase affect composition of the microbiome and, consequently, determine kinetics of the further decomposition process needs in-depth investigation.

With respect to salinity, it has been reported to both increase (Morrissey et al., 2014) and decrease (Rejmánková and Houdková, 2006) decomposition rates in wetland ecosystems. Connolly et al. (2014) also found that salinity did not significantly affect the decay rate, specifically of *P. australis.* This is consistent with our results for *P. australis, Carex* sp. and *S. tabernaemontani,* which were exposed in freshwater and brackish peatlands with an annual EC difference of 1.2 to 8.0 mS cm^{-1} (mean = 4.77 mS cm^{-1}).

Litter chemistry might explain the observed decreasing decay rates of *P. australis* and *Carex* sp. over time (specifically day 62 to 371) while the decay rates of *S. tabernaemontani* showed less reduction in decay rate in both peatlands. This can be supported by the stoichiometry of the remaining mass from the two sites displaying distinct patterns (e.g. higher C:P and N:P in DM than SM; Figure 18). We assume that these might have been caused by the different microbial communities present in the peatlands. Microbial community composition can be influenced by salinity (Wu et al., 2006) and different elemental requirements for their metabolic activities (Ágoston-

Szabó and Dinka, 2008). Again, this study does not have the microbial community data to support these claims hence this remains a speculation. Examination of this matter is advantageous for better understanding. Yet, despite these possible variations in microbial community composition, litter decomposition rates were not significantly affected, which support the findings of Bani et al. (2019) that site-specific microbial decomposers do not lead to greater mass loss. Therefore, this thesis suggests that sea level rise coupled with increased precipitation resulting from climate warming may not have a significant impact on the litter decomposition of these macrophytes in the future.

5 Conclusions and Future Research

Species composition of the coastal peatlands on the southern Baltic Sea coasts are widely dominated by *Phragmites australis* with patches of *Carex* spp., and *Typha latifolia* co-occurring in freshwater peatland margins while mostly *Schoenoplectus tabernaemontani* co-occur at the margins of brackish peatland. The wider salinity range and the clonal and sexual reproductive mechanisms of *P. australis* (McCormick et al., 2010) enable the species to colonize both freshwater and brackish coastal wetlands. Increasing salinity in the future may not seem to affect its distribution since it can tolerate a relatively wide salinity range however, when water level increases due to frequent and intense precipitation, species composition and distribution will perhaps shift. Given the unique, non-tidal condition of the Baltic Sea, the increased precipitation may result in much longer periods of freshwater conditions in the coastal wetlands. Increasing water levels may trigger the expansion of *S. tabernaemontani* since it is often found in standing water up to 1.5 m deep along water body margins (Nicol et al., 2015) while *P. australis* cannot survive after long exposure to water deeper than one meter for at least three years (Shay and Shay, 1986). When salinity level also increases, *S. tabernaemontani* may expand in previously freshwater-dominated peatlands as this species establishes best in oligohaline conditions. However, peatland salinity range covered in this study is only up to 10 so these results may not be assumed accurate in areas that are more brackish. Therefore, similar study needs to be conducted covering wetlands with higher salinity levels.

This study proves that all of the tested emergent macrophytes can survive under brackish water conditions with a salinity of 10 of short but frequent brackish-water flooding. *Typha latifolia*, however, will most likely exhibit more negative responses to both salinity and frequent brackish water flooding than the other species. The other species, including the salt-sensitive *Carex acutiformis*, seemed to be more resilient to 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 outcompeted eventually by the less salt-sensitive species, especially the *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. If so, carbon cycling in coastal peatlands may be altered since *S. tabernaemontani* is a non-peat-forming species. It is noteworthy, however, that the salinity tested in this study is only classified as ß-

mesohaline so results may vary for coastal wetlands having higher salinity levels hence, further study is necessary.

Litter decomposition study shows that the decomposition rates of *P. australis*, *Carex* sp. and *S. tabernaemontani* are not significantly affected by low salinity. Site-specific differences in decomposition of similar litter exposed in freshwater and brackish peatland with annual electrical conductivity difference of 1.2 to 8.0 mS cm^{-1} could not be detected in this study. This implies that site-specific microbial decomposers do not lead to different decomposition rates. Nonetheless, chemical composition of the litters played more important role resulting in species-specific differences in percent initial mass loss specifically between *S. tabernaemontani* and the other species. The decay coefficient of the former is also up to four times higher than *P. australis*$_{SM}$. After a year of field exposure, *S. tabernaemontani* was totally decomposed while the other species still had up to 60% of the litter mass. This confirms that of the tested species, both *P. australis* and *Carex* sp. are peat-forming while *S. tabernaemontani* is not. With this, if in the future *P. australis* expands its coverage area due to salinity increase, peat in these coastal wetlands may continuously accumulate. However, if *S. tabernaemontani* thrives due to increased water level while keeping the salinity level at around 5, which is favored by the species, dead plants may not add up to the existing carbon stock due to its high decomposition rate. In contrast, the less salt-tolerant species, *Carex* sp. and *T. latifolia,* may negatively be affected by increased salinity. Aboveground biomass of both species may decrease as duration and frequency of exposure to salinity increases as shown in the salinity acclimation study. Subsequently, the contribution of *Carex* in the peat formation may also decrease. For *T. latifolia*, litter decomposition study still needs to be done since it was not included in this thesis.

This study also reveals that low initial nutrient concentration does not necessarily result in slow decomposition rate. In fact, *S. tabernaemontani* had significantly lower initial N or higher C:N ratio than the other litters but decomposed the fastest. Ratios of C:Mg, C:Ca, C:N and C:P appear to strongly influence microbial colonization at the beginning of litter decay and in sustaining decomposition after colonization. To what extent the conditions during the initial phase affect composition of the microbiome and, consequently, determine kinetics of the further decomposition process needs in-depth investigation. Additionally, determination of microbial community composition in both freshwater and brackish peatlands would be recommended to prove the assumption that difference in microbial community does not affect the rate of litter decay. Still, based on the findings, sea level rise coupled with

increased precipitation resulting from climate warming may not have a significant impact on the litter decomposition of these macrophytes in the future.

References

Acosta-Motos, J.R., Ortuño, M.F., Bernal-Vicente, A., Diaz-Vivancos, P., Sanchez-Blanco, M.J., Hernandez, J.A., 2017. Plant responses to salt stress: Adaptive mechanisms. Agronomy 7, 1–38.

Aerts, R., 1997. Climate, Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems : A Triangular Relationship. Oikos 79, 439–449.

Ágoston-Szabó, E., Dinka, M., 2008. Decomposition of Typha angustifolia and Phragmites australis in the littoral zone of a shallow lake. Biologia (Bratisl). 63, 1104–1110.

Allakhverdiev, S.I., Sakamoto, A., Nishiyama, Y., Inaba, M., Murata, N., 2000. Ionic and osmotic effects of NaCl-induced inactivation of photosystems I and II in Synechococcus sp. Plant Physiol. 123, 1047–1056.

Ashraf, M., Harris, P.J.C., 2013. Photosynthesis under stressful environments: An overview. Photosynthetica 51, 163–190.

BACC II Author Team, 2015. Assessment of Climate Change for the Baltic Sea Basin, Assessment of Climate Change for the Baltic Sea Basin.

Bani, A., Borruso, L., Matthews Nicholass, K.J., Bardelli, T., Polo, A., Pioli, S., Gómez-Brandón, M., Insam, H., Dumbrell, A.J., Brusetti, L., 2019. Site-specific microbial decomposer communities do not imply faster decomposition: Results from a litter transplantation experiment. Microorganisms 7, 1–15.

Baur, O., Kuhn, M., Featherstone, W.E., 2013. Continental mass change from GRACE over 2002-2011 and its impact on sea level. J. Geod. 87, 117–125.

Bełdowska, M., Jędruch, A., Łęczyński, L., Saniewska, D., Kwasigroch, U., 2016. Coastal erosion as a source of mercury into the marine environment along the Polish Baltic shore. Environ. Sci. Pollut. Res. 23, 16372–16382.

Berg B., McClaugherty C., Johansson M-B., 1997. Chemical changes in decomposing plant litter can be systemized with respect to the litter's initial. Reports from the Departments in Forest Ecology and Forest Soil, Swedish University of Agricultural Science. Report 74:85

Blair, J.M., 1988. Nutrient release from decomposing foliar litter of three tree species with spicial reference to calcium, magnesium and potassium dynamics. Plant Soil 110, 49–55.

Brinson, M.M., Lugo, A.E., Brown, S., 1981. Primary Productivity, Decomposition and Consumer Activity in Freshwater Wetlands. Annu. Rev. Ecol. Syst. 12, 123–161.

Brock, M.A., Nielsen, D.L., Crosslé, K., 2005. Changes in biotic communities developing from freshwater wetland sediments under experimental salinity and water regimes. Freshw. Biol. 50, 1376–1390.

Burdick, D.M., Buchsbaum, R., Holt, E., 2001. Variation in soil salinity associated with expansion of Phragmites australis in salt marshes. Environ. Exp. Bot. 46, 247–261.

Burdick, D.M., Konisky, R.A., 2003. Determinants of expansion for *Phragmites australis*, common reed, in natural and impacted coastal marshes. Estuaries 26, 407–416.

Chambers, P.A., Lacoul, P., Murphy, K.J., Thomaz, S.M., 2008. Global diversity of aquatic macrophytes in freshwater. Hydrobiologia 595, 9–26.

Chambers, R.M., 1997. Porewater chemistry associated with *Phragmites* and *Spartina* in a Connecticut tidal marsh. Wetlands 17, 360–367.

Chambers, R.M., Osgood, D.T., Bart, D.J., Montalto, F., 2003. *Phragmites australis* invasion and expansion in tidal wetlands: Interactions among salinity, sulfide, and hydrology. Estuaries 26, 398–406.

Chapin III, F.S., Matson, P.A., Mooney, H.A., 2011. Principles of terrestrial ecosystem ecology, New York, USA. Springer.

Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D.M., Jackson, S.T., Korhola, A., Mauquoy, D., Mitchell, F.J.G., Prentice, I.C., Van Der Linden, M., De Vleeschouwer, F., Yu, Z.C., Alm, J., Bauer, I.E., Corish, Y.M.C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Sillasoo, U., Swindles, G.T., Tuittila, E.S., Ukonmaanaho, L., Väliranta, M., Van Bellen, S., Van Geel, B., Vitt, D.H., Zhao, Y., 2013. Climate-related changes in peatland carbon accumulation during the last millennium. Biogeosciences 10, 929–944.

Chaves, M.M., Flexas, J., Pinheiro, C., 2009. Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. Ann. Bot. 103, 551–560.

Chimney, M.J., Pietro, K.C., 2006. Decomposition of macrophyte litter in a subtropical constructed wetland in south Florida (USA). Ecol. Eng. 27, 301–321.

Connolly, C.T., Sobczak, W. V., Findlay, S.E.G., 2014. Salinity effects on phragmites decomposition dynamics among the hudson river's freshwater tidal wetlands. Wetlands 34, 575–582.

Cowardin, L.M., Carter, V., Golet, F.C., Laroe, E.T., 1979. Classification of Wetlands and Deepwater Habitats of the United States. US Fish and Wildlife Service FWS/OBS 79/31.

Cramer, G.R., 2003. Differential effects of salinity on leaf elongation kinetics of three grass species. Plant Soil 253, 233–244.

Cronk, J.K., Fennessy, M.S., 2009. Wetland Plants, in: Wetland. Elsevier Inc., pp. 590–598.

Cronk, J.K., Fennessy, S.M., 2001. Wetland Plants: Biology and Ecology. Lewis Publishers, Florida.

Davis, A.F., 1993. Rare Wetland Plants and Their Habitats in Pennsylvania. Proc. Acad. Nat. Sci. Philadelphia 144, 254–262.

Delphine, S., Alvino, A., Zacchini, M., Loreto, F., 1999. Consequences of salt stress on conductance to CO_2 diffusion, Rubisco characteristics and anatomy of spinach leaves. Aust. J. Plant Physiol. 25, 395–402.

Dinka, M., Ágoston-Szabá, E., Tóth, I., 2004. Changes in nutrient and fibre content of decomposing *Phragmites australis* litter. Int. Rev. Hydrobiol. 89, 519–535.

Eid, E.M., Shaltout, K.H., Al-Sodany, Y.M., 2014. Decomposition dynamics of *Phragmites australis* litter in Lake Burullus, Egypt. Plant Species Biol. 29, 47–56.

Ellenberg, H., 1974. Zeigerwerte der Gefäßpflanzen Mitteleuropas. Scripta Geobotanica.

European Union, 2000. Peatlands for LIFE. Luxemburg. https://doi.org/10.2826/619188

Flowers, T.J., Colmer, T.D., 2008. Salinity tolerance in halophytes. New Phytol. 179, 945–963.

Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim. Biophys. Acta - Gen. Subj. 990, 87–92.

Gerdol, R., Brancaleoni, L., Lastrucci, L., Nobili, G., Pellizzari, M., Ravaglioli, M., Viciani, D., 2018. Wetland Plant Diversity in a Coastal Nature Reserve in Italy: Relationships with Salinization and Eutrophication and Implications for Nature Conservation. Estuaries and Coasts 41, 2079–2091.

Glenn, E., Thompson, T.L., Frye, R., Riley, J., 1995. Effects of salinity on growth and evapotranspiration. Water 52, 75–91.

Goodman, A.M., Ganf, G.G., Dandy, G.C., Maier, H.R., Gibbs, M.S., 2010. The response of freshwater plants to salinity pulses. Aquat. Bot. 93, 59–67.

Gopal, B., Ghosh, D., 2008. Natural Wetlands. Encycl. Ecol. Five-Volume Set 2493–2504.

Grillas, P., Wijck, C., Bonis, A., 1993. The effect of salinity on the dominance-diversity relations of experimental coastal macrophyte communities. J. Veg. Sci. 4, 453–460.

Groh, A., Richter, A., Dietrich, R., 2017. Recent baltic sea level changes induced by past and present ice masses. Coast. Res. Libr. 19, 55–68.

Güsewell, S., Gessner, M.O., 2009. N:P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. Funct. Ecol. 23, 211–219.

Hadad, H.R., Mufarrege, M.M., Di Luca, G.A.D., Maine, M.A., 2017. Salinity and pH effects on floating and emergent macrophytes in a constructed wetland. Water Sci. Technol. 270–275.

Han, M.Y., Zhang, L.X., Fan, C.H., Liu, L.H., Zhang, L.S., Li, B.Z., Alva, A.K., 2011. Release of nitrogen, phosphorus, and potassium during the decomposition of apple (Malus domestica) leaf litter under different fertilization regimes in Loess Plateau, China. Soil Sci. Plant Nutr. 57, 549–557.

Harff, J., Lemke, W., Lampe, R., Lüth, F., Lübke, H., Meyer, M., Tauber, F., Schmölcke, U., 2007. The Baltic Sea coast - A model of interrelations among geosphere, climate, and anthroposphere. Spec. Pap. Geol. Soc. Am. 426, 133–142.

Heal O.W., Anderson, J.M., Swift M.J., 1997. Plant litter quality and decomposition: an historical overview. In: Driven by Nature. Plant Litter Quality and Decomposition. Cadish G. and Giller K.E. (Eds.), CAB International, Walling- ford, pp. 3 –30.

Herbert, E.R., Boon, P., Burgin, A.J., Neubauer, S.C., Franklin, R.B., Ardon, M., Hopfensperger, K.N., Lamers, L.P.M., Gell, P., Langley, J.A., 2015. A global perspective on wetland salinization: Ecological consequences of a growing threat to freshwater wetlands. Ecosphere 6, 1–43.

Hernández, J.A., Olmos, E., Corpas, F.J., Sevilla, F., del Río, L.A., 1995. Salt-induced oxidative stress in chloroplasts of pea plants. Plant Sci. 105, 151–167.

Hickmann, J.C., 1993. The Jepson manual : higher plants of California. University of California Press, Berkeley.

Hill, M.O., Preston, C.D., Roy, D.B., 2004. Plantatt Atributes of British and Irish Plants: Status, Size, Life history, Geography and Habitats. Cent. Ecol. Hydrol. 80.

Hopkinson, C.S., Cai, W.J., Hu, X., 2012. Carbon sequestration in wetland dominated coastal systems-a global sink of rapidly diminishing magnitude. Curr. Opin. Environ. Sustain. 4, 186–194.

Howard, R.J., Mendelssohn, I.A., 1999a. Salinity as a constraint on growth of oligohaline marsh macrophytes. II. Salt pulses and recovery potential. Am. J. Bot. 86, 795–806.

Howard, R.J., Mendelssohn, I.A., 1999b. Salinity as a constraint on growth of oligohaline marsh macrophytes. Species variation in stress tolerance. Am. J. Bot. 86, 785–794.

Howard, R.J., Rafferty, P.S., Johnson, D.J., 2020. Plant Community Establishment in a Coastal Marsh Restored Using Sediment Additions. Wetlands 40, 877–892.

Hsiao, T.C., Xu, L.K., 2000. Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport Theodore. J. Exp. Bot. 51, 1595–1616.

Hutchinson, I., 1988. Salinity tolerance of plants of estuarine wetlands and associated uplands. Washingt. State Shorelands Coast. Zo. Manag. Progr. Wetl. Sect.

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, M.A., Howard, C.M., Erisman, J.W., Billen, G., Bleeker, A., Grennfelt, P., van Grinsven, H., Grizzetti, B. (Eds.), . Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1–32.

IPCC, 2019: Summary for Policymakers, 2019. IPCC The Ocean and Cryosphere in a Changing Climate Summary for Policmakers, IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.

James, R.A., Rivelli, A.R., Munns, R., Von Caemmerer, S., 2002. Factors affecting CO2 assimilation, leaf injury and growth in salt-stressed durum wheat. Funct. Plant Biol. 29, 1393–1403.

Joosten, H., 2015. Peatlands, climate change mitigation and biodiversity conservation Peatlands, climate change mitigation and biodiversity conservation. Copenhagen, Denmark.

Jurasinski, G., Janssen, M., Voss, M., Böttcher, M.E., Brede, M., Burchard, H., Forster, S., Gosch, L., Gräwe, U., Gründling-Pfaff, S., Haider, F., Ibenthal, M., Karow, N., Karsten, U., Kreuzburg, M., Lange, X., Leinweber, P., Massmann, G., Ptak, T., Rezanezhad, F., Rehder, G., Romoth, K., Schade, H., Schubert, H., Schulz-Vogt, H., Sokolova, I.M., Strehse, R., Unger, V., Westphal, J., Lennartz, B., 2018. Understanding the coastal ecocline: Assessing sea-land interactions at non-tidal, low-lying coasts through interdisciplinary research. Front. Mar. Sci. 5, 1–22.

Kadlec, R.H., Wallace, S., 2008. Treatment Wetlands, 2nd editio. ed, Treatment Wetlands. CRC Press Taylor & Francis Group.

Kao, W.Y., Tsai, H.C., Tsai, T.T., 2001. Effect of NaCl and nitrogen availability on growth and photosynthesis of seedlings of a mangrove species, kandelia candel (L.) Druce. J. Plant Physiol. 158, 841–846.

Karl, T.R., Knight, R.W., Plummer, N., 1995. Trends in high-frequency climate variability in the twentieth century. Nature 377, 217–220.

Keddy, P.A., 2010. Wetland ecology:Principles and conservation, Second. ed, Wetland Ecology: Principles and Conservation. Cambridge University Press, New York.

Khan, K., Shah, G.M., Saqib, Z., Rahman, I.U., Haq, S.M., Khan, M.A., Ali, N., Sakhi, S., Aziz-ud-din, Nawaz, G., Rahim, F., Rasheed, R.A., Al Farraj, D.A., Elshikh, M.S., 2022. Species Diversity and Distribution of Macrophytes in Different Wetland Ecosystems. Appl. Sci. 12.

Koch, M., Koebsch, F., Hahn, J., Jurasinski, G., 2017. From meadow to shallow lake: Monitoring secondary succession in a coastal fen after rewetting by flooding based on aerial imagery and plot data. Mires Peat 19, 1–17.

Koebsch, F., Glatzel, S., Hofmann, J., Forbrich, I., Jurasinski, G., 2013. CO2 exchange of a temperate fen during the conversion from moderately rewetting to flooding. J. Geophys. Res. Biogeosciences 118, 940–950.

Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J. Appl. Ecol. 33, 1441–1450.

Kreuzburg, M., Ibenthal, M., Janssen, M., Rehder, G., Voss, M., Naumann, M., Feldens, P., 2018. Sub-marine Continuation of Peat Deposits From a Coastal Peatland in the Southern Baltic Sea and its Holocene Development. Front. Earth Sci. 6.

Kurban, H., Saneoka, H., Nehira, K., Adilla, R., Premachandra, G.S., Fujita, K., 1999. Effect of salinity on growth, photosynthesis and mineral composition in leguminous plant Alhagi pseudoalhagi (Bieb.). Soil Sci. Plant Nutr. 45, 851–862.

Latham, P.J., Pearlstine, L.G., Kitchens, W.M., 1991. Spatial distributions of the softstem bulrush, *Scirpus validus*, across a salinity gradient. Estuaries 14, 192–198.

Lentz, K.A., Dunson, W.A., 1999. Dintinguishing characteristics of temporary pond habitat of endangered northeastern bulrush, *Scirpus ancistrochaetus* 19, 162–167.

Leppäranta, M., K. Myrberg. 2009. Physical oceanography of the Baltic Sea, Springer-Praxis books in geophysical sciences, Springer/Praxis Pub., Berlin, Chichester, UK.

Longhi, D., Bartoli, M., Viaroli, P., 2008. Decomposition of four macrophytes in wetland sediments: Organic matter and nutrient decay and associated benthic processes. Aquat. Bot. 89, 303–310.

Lovegrove, A.T., Newton, Adrian C., Evans, P.M., Diaz, A., Newton, Arthur C., Davy, L., Newbould, P.J., 2020. Changes in vegetation structure and composition of a lowland mire over a sixty-five-year interval. Ecol. Evol. 10, 13913–13925.

MacArthur, R.H., 1965. Patterns of Species Diversity. Biol. Rev. 40, 510–533.

Macek, P., Rejmánková, E., 2007. Response of emergent macrophytes to experimental nutrient and salinity additions. Funct. Ecol. 21, 478–488.

Maoka, T., 2020. Carotenoids as natural functional pigments. J. Nat. Med. 74, 1–16.

Marino, R.W., Howarth, R., 2009. Nitrogen Fixation: Introduction to Biological Nitrogen Fixation in Aquatic Systems. Inorg. Chem. 65–72.

Mauchamp, A., Mesleard, F., 2001. Salt tolerance in *Phragmites australis* populations from coastal Mediterranean marshes. Aquat. Bot. 70, 39–52.

Maxwell, K. and J.G.N., 2000. Chlorophyll fluorescence—a practical guide. J. Exp. Bot. 51, 659–668.

McCormick, M.K., Kettenring, K.M., Baron, H.M., Whigham, D.F., 2010. Extent and reproductive mechanisms of *Phragmites australis* spread in brackish wetlands in Chesapeake bay, Maryland (USA). Wetlands 30, 67–74.

McKee, K.L., Mendelssohn, I.A., 1989. Response of a freshwater marsh plant community to increased salinity and increased water level. Aquat. Bot. 34, 301–316.

McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Front. Ecol. Environ. 9, 552–560.

Menéndez, M., Martinez, M., Hernández, O., Comín, F.A., 2001. Comparison of leaf decomposition in two Mediterranean rivers: A large eutrophic river and an oligotrophic stream (S Catalonia, NE Spain). Int. Rev. Hydrobiol. 86, 475–486.

Mishra, A., Tanna, B., 2017. Halophytes: Potential resources for salt stress tolerance genes and promoters. Front. Plant Sci. 8, 1–10.

Mitra, S., Wassmann, R., Vlek, P.L., 2005. An appraisal of global wetland area and its organic carbon stock. Curr. Sci. 88, 25–35.

Mitsch, W.J., Gosselink, J.G., 2016. Wetlands (5th edition), Reference Reviews.

Moore, P.D., 2006. Wetlands - Biomes of the Earth. Chelsea House Publishers, New York.

Moore, T.R., Bubier, J.L., Bledzki, L., 2007. Litter decomposition in temperate peatland ecosystems: The effect of substrate and site. Ecosystems 10, 949–963.

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. Physiol. Plant. 86, 419–426.

Morrissey, E.M., Gillespie, J.L., Morina, J.C., Franklin, R.B., 2014. Salinity affects microbial activity and soil organic matter content in tidal wetlands. Glob. Chang. Biol. 20, 1351–1362.

Munns, R., 2002. Comparative physiology of salt and water stress. Plant, Cell Environ. 25, 239–250.

Munns, R., Termaat, A., 1986. Whole-plant responses to salinity. Aust. J. Plant Physiol. 13, 143–160.

Munns, R., Tester, M., 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 59, 651–681.

Murchie, E.H., Lawson, T., 2013. Chlorophyll fluorescence analysis: A guide to good practice and understanding some new applications. J. Exp. Bot. 64, 3983–3998.

Neubauer, S.C., Craft, C.B., 2009. Global Change and Tidal Freshwater Wetlands: Scenarios and Impacts, Tidal Freshwater Wetlands.

Newell, N., 2013. Review: Effects of Soil Salinity on Plant Growth. Plant Physiol. 1–4.

Nguyen, K.L., Asaeda, T., Manatunge, J., 2006. Decomposition of aboveground and belowground organs of wild rice (*Zizania latifolia*): Mass loss and nutrient changes. Aquat. Ecol. 40, 13–21.

Nicholls, R.J., Hoozemans, F.M.J., Marchand, M., 1999. Increasing flood risk and wetland losses due to global sea-level rise: Regional and global analyses. Glob. Environ. Chang. 9, 69–87.

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.

Nielsen, D.L., Brock, M.A., Rees, G.N., Baldwin, D.S., 2003. Effects of increasing salinity on freshwater ecosystems in Australia. Aust. J. Bot. 51, 655–665.

Novotny K., G. Liebsch, E. Dietrich, A. Lehmann. 2005. Combination of sea level observations and an oceanographic model for geodetic applications in the Baltic Sea. *In*: A Window on the Future of Geodesy. IAG Symp 128:195-200

Olson, J.S., 1963. Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. Ecology 44, 322–331.

Oppenheimer, M., Glavovic, B., 2019. Chapter 4: Sea Level Rise and Implications for Low Lying Islands, Coasts and Communities. IPCC SR Ocean and Cryosphere, IPCC Special Report on the Ocean and Cryosphere in a Changing Climate [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, M. Nicolai, A. Okem, J. Petzold, B. Rama, N. Weyer (eds.)]. In press.

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 Divers. 38, 183–189.

Pantin, F., Simonneau, T., Rolland, G., Dauzat, M., Muller, B., 2011. Control of leaf expansion: A developmental switch from metabolics to hydraulics. Plant Physiol. 156, 803–815.

Parida, A.K., Das, A.B., 2005. Salt tolerance and salinity effects on plants: A review. Ecotoxicol. Environ. Saf. 60, 324–349.

Parida, A.K., Das, A.B., Mittra, B., 2003. Effects of NaCl stress on the structure, pigment complex composition, and photosynthetic activity of mangrove *Bruguiera parviflora* chloroplasts. Photosynthetica 41, 191–200.

Parish, F., Sirin, A., Charman, D., Joosten, H., Minayeva, T., Silvius, M., Stringer, L., 2008. Assessment on Peatlands, Biodiversity and Climate Change: Main Report. Global Environment Centre, Kuala Lumpur and Wetlands International, Wageningen., Assessment on peatlands, biodiversity and climate change: main report.

Passaro, M., Müller, F.L., Oelsmann, J., Rautiainen, L., Dettmering, D., Hart-Davis, M.G., Abulaitijiang, A., Andersen, O.B., Høyer, J.L., Madsen, K.S., Ringgaard, I.M., Särkkä, J., Scarrott, R., Schwatke, C., Seitz, F., Tuomi, L., Restano, M., Benveniste, J., 2021. Absolute Baltic Sea Level Trends in the Satellite Altimetry Era: A Revisit. Front. Mar. Sci. 8, 1–16.

Porra, R.J., Thompson, W.A., Kriedemann, P.E., 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. Biochim. Biophys. Acta 384–394.

Qu, W., Li, J., Han, G., Wu, H., Song, W., Zhang, X., 2018. Effect of salinity on the decomposition of soil organic carbon in a tidal wetland. J. Soils Sediments 19, 609–617.

R Core Team, 2020. R: A language and environment for statistical computing, in: R Foundation for Statistical Computing. Vienna, Austria.

Rahman, M.M., Tsukamoto, J., Tokumoto, Y., Shuvo, M.A.R., 2013. The Role of Quantitative Traits of Leaf Litter on Decomposition and Nutrient Cycling of the Forest Ecosystems. J. For. Environ. Sci. 29, 38–48.

Rajesh, A., Arumugam, R., Venkatesalu, V., 1998. Growth and photosynthetic characteristics of Ceriops roxburghiana under NaCl stress. Photosynthetica 35, 285–287.

Ramsar Convention Secretariat, 2010. National Wetland Policies: Developing and Implementing National Wetland Policies., 4th ed, Ramsar handbooks for the wise use of wetlands. Ramsar Convention Secretariat, Gland, Switzerland.

Rasmuson, K.E., Anderson, J.E., 2002. Salinity affects development, growth, and photosynthesis in cheatgrass. J. Range Manag. 55, 80–87.

Reddy, K. R., Delaune, R. D. 2008. Biogeochemistry of Wetlands: Science and Applications. CRC Press, Boca Raton.

Rejmánková, E., 2011. The role of macrophytes in wetland ecosystems. J. Ecol. F. Biol. 34, 333–345.

Rejmánková, E., Houdková, K., 2006. Wetland plant decomposition under different nutrient conditions: What is more important, litter quality or site quality? Biogeochemistry 80, 245–262.

Rich, F.J., 2015. Peat: Its Origins, Characteristics, and Geological Transformations, Coal and Peat Fires: A Global Perspective. Elsevier.

Richards, F.J., 1959. A flexible growth function for empirical use. J. Exp. Bot. 10, 290–301.

Richter, A., Groh, A., Dietrich, R., 2012. Geodetic observation of sea-level change and crustal deformation in the Baltic Sea region. Phys. Chem. Earth 53–54, 43–53.

Romero-Aranda, R., Soria, T., Cuartero, J., 2001. Tomato plant-water uptake and plant-water relationships under saline growth conditions. Plant Sci. 160, 265–272.

Sardinha, M., Müller, T., Schmeisky, H., Joergensen, R.G., 2003. Microbial performance in soils along a salinity gradient under acidic conditions. Appl. Soil Ecol. 23, 237–244.

Schellekens, J., Buurman, P., Kuyper, T.W., 2012. Source and transformations of lignin in Carex-dominated peat. Soil Biol. Biochem. 53, 32–42.

Schönfeld-Bockholt, R., Roth, D., Dittmann, L. 2005. Friends of the natural history in Mecklenburg. Ch. Teilflächenbezogene ökologische und futterwirtschaftliche Beurteilung des Grünlandes im Naturschutzgebiet Heiligensee und Hütelmoor

Schoor, A., Schubert, H., Hagemann, M., 1995. Immediate effects of a salt shock on energy distribution to the photosystem of Synechocystis sp. PCC 6803, in: International Photosynthesis Congress; 10th, Photosynthesis: From Light to Biosphere. Kluwer Academic;, Dordrecht, Netherlands, Montpellier; France, pp. 697–700.

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. J. Plant Physiol. 142, 291–295.

Schubert, H., Hagemann, M., 1990. Salt effects on 77K fluorescence and photosynthesis in the cyanobacterium *Synechocystis* sp. PCC 6803. FEMS Microbiol. Lett. 71, 169–172.

Schumann, M., Joosten, H., 2008. A Global Peatland Restoration Manual 64pp.

Seppä, H., 2002. Mires of Finland: Regional and local controls of vegetation, landforms, and long-term dynamics. Fennia 180, 1–2, 43–60.

Shannon, C.E., 1948. A Mathematical Theory of Communication. Bell Syst. Tech. J. 27, 379–423.

Sharpe, P.J., Baldwin, A.H., 2009. Patterns of wetland plant species richness across estuarine gradients of Chesapeake Bay. Wetlands 29, 225–2325.

Shay, J.M., Shay, C.T., 1986. Prairie marshes in western Canada, with specific reference to the ecology of five emergent macrophytes. Can. J. Bot. 64, 443–454.

Sinicrope, T.L., Hine, P.G., Warren, R.S., Niering, W.A., 1990. Restoration of an impounded salt marsh in New England. Estuaries 13, 25–30.

Smith, M.J., Ough, K.M., Scroggie, M.P., Schreiber, E.S.G., Kohout, M., 2009. Assessing changes in macrophyte assemblages with salinity in non-riverine wetlands: A Bayesian approach. Aquat. Bot. 90, 137–142.

SMHI: Swedish Meteoroligcal and Hydrological Institute. www.smhi.se accessed on 26 July 2022

Snoeijs-Leijonmalm, P., Schubert, H., Radziejewska, T., 2017. Biological Oceanography of the Baltic Sea, Springer. Springer.

Spalding, E.A., Hester, M.W., 2007. Interactive effects of hydrology and salinity on oligohaline plant species productivity: Implications of relative sea-level rise. Estuaries and Coasts 30, 214–225.

Stagg, C.L., Baustian, M.M., Perry, C.L., Carruthers, T.J.B., Hall, C.T., 2018. Direct and indirect controls on organic matter decomposition in four coastal wetland communities along a landscape salinity gradient. J. Ecol. 106, 655–670.

Stepien, P., Johnson, G.N., 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 Physiol. 149, 1154–1165.

Stofberg, S.F., Klimkowska, A., Paulissen, M.P.C.P., Witte, J.P.M., van der Zee, S.E.A.T.M., 2015. Effects of salinity on growth of plant species from terrestrializing fens. Aquat. Bot. 121, 83–90.

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. Environ. Exp. Bot. 70, 192–203.

Sudhir, P., Murthy, S.D.S., 2004. Effects of salt stress on basic processes of photosynthesis. Photosynthetica 42, 481–486.

Swift, M.J., Heal, O.W. and Anderson, M.J., 1979. Decomposition in terrestrial ecosystems, Oxford. Blackwell Scientific Publications

Tanneberger, F., Tegetmeyer, C., Busse, S., Barthelmes, A., Shumka, S., Mariné, A.M., Jenderedjian, K., Steiner, G.M., Essl, F., Etzold, J., Mendes, C., Kozulin, A., Frankard, P., Milanović, Ganeva, A., Apostolova, I., Alegro, A., Delipetrou, P., Navrátilová, J., Risager, M., Leivits, A., Fosaa, A.M., Tuominen, S., Muller, F., Bakuradze, T., Sommer, M., Christanis, K., Szurdoki, E., Oskarsson, H., Brink, S.H., Connolly, J., Bragazza, L., Martinelli, G., Aleksāns, O., Priede, A., Sungaila, D., Melovski, L., Belous, T., Saveljić, D., De Vries, F., Moen, A., Dembek, W., Mateus, J., Hanganu, J., Sirin, A., Markina, A., Napreenko, M., Lazarević, P., Stanová, V.Š., Skoberne, P., Pérez, P.H., Pontevedra-Pombal, X., Lonnstad, J., Küchler, M., Wüst-Galley, C., Kirca, S., Mykytiuk, O., Lindsay, R., Joosten, H., 2017. The peatland map of Europe. Mires Peat 19, 1–17.

Tanneberger, F., Wichtmann, W., 2011. Carbon credits from peatland rewetting Climate - biodiversity - land use. Schweizerbart Science Publishers, Stuttgart, Germany.

Tezuka, Y., 1990. Bacterial regeneration of ammonium and phosphate as affected by the carbon:nitrogen:phosphorus ratio of organic substrates. Microb. Ecol. 19, 227–238.

Tiner, R.W., 2018. Hydrology of coastal wetlands. Wetl. B. I Struct. Funct. Manag. Methods 217–231.

Van der Valk, A.G., Rhymer, J.M., Murkin, H.R., 1991. Flooding and the decomposition of litter of four emergent plant species in a prairie wetland. Wetlands 11, 1–16.

Van Der Wal, A., Van Veen, J.A., Smant, W., Boschker, H.T.S., Bloem, J., Kardol, P., Van Der Putten, W.H., De Boer, W., 2006. Fungal biomass development in a chronosequence of land abandonment. Soil Biol. Biochem. 38, 51–60.

Varadhan, R., Gilbert, P.D., 2009. BB: An R package for solving a large system of nonlinear equations and for optimizing a high-dimensional nonlinear objective function. J. Stat. Softw. 32, 1–26.

Vasander, H., Tuittila, E.-S., Lode, E., Lundin, L., Ilomets, M., Sallantaus, T., Heikkilä, R., Pitkänen, M.-L., Laine, J., 2003. Status and restoration of peatlands in northern Europe. Wetl. Ecol Manag. 11, 51–63.

Vasquez, E.A., Glenn, E.P., Brown, J.J., Guntenspergen, G.R., Nelson, S.G., 2005. Salt tolerance underlies the cryptic invasion of North American salt marshes by an introduced haplotype of the common reed *Phragmites australis* (Poaceae). Mar. Ecol. Prog. Ser. 298, 1–8.

Virzo De Santo, A., De Marco, A., Fierro, A., Berg, B., Rutigliano, F.A., 2009. Factors regulating litter mass loss and lignin degradation in late decomposition stages. Plant Soil 318, 217–228.

Vymazal, J., Greenway, M., Tonderski, K., Brix, H., Mander, Ü., 2006. Wetlands and Natural Resource Management, in: Verhoeven, J.T.A., Beltman, B., Bobbink, R., Whigham, D.F. (Eds.), Ecological Studies. Springer-Verlag, Berlin Heidelberg, pp. 475–477.

Walsby, A.E., 1997. Modelling the daily integral of photosynthesis by phytoplankton: Its dependence on the mean depth of the population. Hydrobiologia 349, 65–74.

Wang, Y., Nii, N., 2000. Changes in chlorophyll, ribulose bisphosphate carboxylase-oxygenase, glycine betaine content, photosynthesis and transpiration in Amaranthus tricolor leaves during salt stress. J. Hortic. Sci. Biotechnol. 75, 623–627.

Watt, S.C.L., García-Berthou, E., Vilar, L., 2007. The influence of water level and salinity on plant assemblages of a seasonally flooded Mediterranean wetland. Plant Ecol. 189, 71–85.

Webster, J.R., Benfield, E.F., 1986. Vascular plant breakdown in freshwater ecosystems. Annu. Rev. Ecol. Syst. Vol. 17 567–594.

Welsh, S.L., 2003. A Utah flora. Print Services, Brigham Young University, Provo, Utah, U.S.A.

Whitney, K.D., Arnott, H.J., 1987. Calcium oxalate crystal morphology and development in Agaricus bisporus. Mycology 79, 180–187.

Wolanski, E., Perillo, G.M.E., Cahoon, D.R., 2009. Coastal wetlands: A synthesis, in: Hopkinson, C.S., Wolanski, E., Cahoon, D.R., Perillo, G.M.E., Brinson, M.M. (Eds.), Coastal Wetlands: An Integrated Ecosystem Approach. Elsevier B.V., pp. 1–75.

Wright, J.P., Jones, C.G., Flecker, A.S., 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132, 96–101.

Wu, Q.L., Zwart, G., Schauer, M., Kamst-Van Agterveld, M.P., Hahn, M.W., 2006. Bacterioplankton community composition along a salinity gradient of sixteen high-mountain lakes located on the Tibetan Plateau, China. Appl. Environ. Microbiol. 72, 5478–5485.

Xi, H., Feng, Q., Zhang, L., Si, J., Chang, Z., Yu, T., Guo, R., 2016. Effects of water and salinity on plant species composition and community succession in Ejina Desert Oasis, northwest China. Environ. Earth Sci. 75, 1–16.

Yu, Z., Beilman, D.W., Frolking, S., MacDonald, G.M., Roulet, N.T., Camill, P., Charman, D.J., 2011. Peatlands and their role in the global carbon cycle. Eos (Washington. DC). 92, 97–108.

Zerbe, S., Steffenhagen, P., Parakenings, K., Timmermann, T., Frick, A., Gelbrecht, J., Zak, D., 2013. Ecosystem service restoration after 10 years of rewetting peatlands in NE Germany. Environ. Manage. 51, 1194–1209.

Zhu, J., 2007. Plant Salt Stress, in: Encyclopedia of Life Sciences (ELS). John Wiley & Sons, Ltd, Chichester.

Supplementary Data

Supplementary Table 1. Mean leaf elongation rates (± SD, cm d^{-1}; n=15) of the four emergent macrophytes under different treatments namely, C_+: permanently brackish water, C_-: permanently freshwater, A_{2b_2f}: alternate 2 days brackish water then 2 days freshwater, A_{4b_4f}: alternate 4 days brackish water then 4 days freshwater, and A_{4b_4f}: alternate 2 days brackish water then 4 days freshwater; (-) in week 1 means no data yet

Species_Time (Week)	Treatments				
Carex acutiformis	C_+	C_-	A_{2b_2f}	A_{4b_4f}	A_{2b_4f}
1	-	-	-	-	-
2	0.08 ± 0.58	0.38 ± 0.68	0.44 ± 0.34	0.25 ± 0.46	0.35 ± 0.38
3	0.54 ± 0.31	0.39 ± 0.25	0.40 ± 0.25	0.35 ± 0.22	0.29 ± 0.27
4	0.46 ± 0.24	0.34 ± 0.30	0.55 ± 0.18	0.49 ± 0.30	0.72 ± 0.27
5	0.39 ± 0.47	0.60 ± 0.36	0.58 ± 0.30	0.50 ± 0.34	0.57 ± 0.33
6	0.39 ± 0.36	0.47 ± 0.40	0.37 ± 0.29	0.61 ± 0.55	0.70 ± 0.28
7	0.43 ± 0.42	0.31 ± 0.43	0.43 ± 0.39	0.43 ± 0.54	0.45 ± 0.30
8	0.11 ± 0.84	0.39 ± 0.31	0.36 ± 0.35	0.34 ± 0.49	0.53 ± 0.54
9	0.18 ± 0.45	0.59 ± 0.66	0.41 ± 0.21	0.15 ± 0.91	0.36 ± 0.51
10	0.35 ± 0.38	0.24 ± 0.51	0.38 ± 0.39	0.49 ± 1.00	0.38 ± 0.78
Phragmites australis					
1	-	-	-	-	-
2	0.39 ± 0.52	0.42 ± 0.22	0.68 ± 0.71	0.43 ± 0.24	0.64 ± 0.35
3	0.29 ± 0.16	0.17 ± 0.18	0.29 ± 0.13	0.38 ± 0.20	0.39 ± 0.24
4	0.31 ± 0.15	0.45 ± 0.32	0.36 ± 0.20	0.33 ± 0.14	0.50 ± 0.15
5	0.25 ± 0.16	0.29 ± 0.32	0.09 ± 0.61	0.26 ± 0.21	0.25 ± 0.20
6	0.18 ± 0.20	0.12 ± 0.29	0.22 ± 0.16	0.18 ± 0.18	0.38 ± 0.21
7	0.07 ± 0.20	0.18 ± 0.44	0.20 ± 0.21	0.21 ± 0.21	0.08 ± 0.25
8	0.11 ± 0.14	0.07 ± 0.30	0.07 ± 0.13	0.06 ± 0.22	0.03 ± 0.10
9	0.01 ± 0.21	0.06 ± 0.28	0.07 ± 0.15	0.01 ± 0.25	0.04 ± 0.18
10	0.07 ± 0.23	0.05 ± 0.28	0.05 ± 0.18	0.02 ± 0.14	-0.08 ± 0.12
Typha latifolia					
1	-	-	-	-	-
2	1.36 ± 0.82	1.21 ± 0.82	0.88 ± 0.30	1.28 ± 0.73	0.77 ± 0.43
3	0.51 ± 0.28	0.77 ± 0.40	0.72 ± 0.27	0.59 ± 0.29	0.53 ± 0.20
4	0.75 ± 0.29	0.76 ± 0.54	0.87 ± 0.24	0.81 ± 0.37	0.93 ± 0.22
5	0.81 ± 0.30	1.02 ± 0.33	0.70 ± 0.25	0.92 ± 0.42	0.88 ± 0.35
6	0.55 ± 0.39	0.81 ± 0.37	0.98 ± 0.53	0.82 ± 0.38	0.81 ± 0.25
7	0.29 ± 0.69	1.25 ± 0.45	0.61 ± 0.69	0.85 ± 0.37	0.81 ± 0.40
8	0.65 ± 0.67	0.69 ± 0.37	0.86 ± 0.60	0.91 ± 0.37	0.78 ± 0.34
9	0.55 ± 0.46	1.04 ± 0.39	0.59 ± 0.40	0.92 ± 0.56	1.01 ± 0.37
10	0.27 ± 0.24	0.87 ± 0.63	0.71 ± 0.55	0.78 ± 0.50	0.62 ± 0.33

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– Cheryl

Declaration of Authorship

I hereby declare that I have written the thesis submitted today independently and have not used any other sources or aids other than those indicated, and I have clearly marked the citations. The copies of this thesis are completely identical in words and pictures.

Furthermore, I declare that the figures are prepared by myself or are clearly labeled otherwise.

Lastly, I declare that as the first author of the two papers I used in this thesis, I primarily carried out the research from conceptualization, data gathering and analysis, visualization and write-up of the manuscripts.

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Publications

- **Batistel, C. C.**, C. Porsche, G. Jurasinski and H. Schubert. Response of four peatland emergent macrophytes to salinity and short salinity pulses. Wetlands. In press.

- **Batistel, C.C.**, G. Jurasinski and H. Schubert. 2021. Salinity exerted little effect on decomposition of macrophytes in coastal peatlands. Aquatic Botany. 175 (2021) 103446

- Malanguis, JM T., **C. C. Batistel** and MJ M. Bande. 2017. Microbial respiration as indicator of soil quality of different land uses in Cienda, Gabas, Baybay City, Leyte. Annals of Tropical Research 39 (2): 55-66.

- Dargantes, B. B., **Batistel, C. C.** and MA B. Manahan. 2012. Springs of Hope: Alternatives to Commercialization of Water Resources and Services in Asia. In Alternatives to Privatization in the Global South. Eds. McDonald, D. and G. Ruiters. Routledge Studies in Development and Society. UK. pp 222-255.

- **Batistel, C. C.,** and V.B. Asio. 2008. Effects of leaf decomposition of selected exotic and native tree species on forest soil quality. Annals of Tropical Research 30(1):29-39. Visayas State University, Baybay City, Leyte, Philippines.

Work Experiences

02/2019 – 08/2022	Research Associate; Baltic TRANSCOAST Project; University of Rostock, Faculty of Mathematics and Natural Sciences, Aquatic Ecology
06/2013 – 12/2019	Instructor; Visayas State University, Department of Biological Sciences, Baybay City, Leyte, Philippines
06/2011 – 05/2013	Instructor; College of Arts and Sciences, Camarines Norte State College, Daet, Camarines Norte, Philippines
05/2009 – 05/2011	Research Assistant; Visayas State University, Institute for Strategic Research and Development Studies, Baybay City, Leyte, Philippines
02/2008 – 12/2008	Scientific Assistant; University of Hohenheim, Institute of Agroecology and Plant Production in the Tropics and Subtropics, Stuttgart, Germany
09/2007 – 01/2009	Scientific Assistant; University of Hohenheim, Institute of Agroecology and Plant Production in the Tropics and Subtropics, Stuttgart, Germany
02/2007 – 10/2007	Science Research Assistant; University of Hohenheim, Institute of Phytomedicine, Stuttgart, Germany
06/2006 – 10/2006	Part-time Instructor; Visayas State University, Department of Biological Sciences, Baybay City, Leyte, Philippines
05/2004 – 06/2006	Science Research Assistant; Visayas State University, Department of Agronomy and Soil Science, Baybay City, Philippines

Scholarships/Grants

07/2020	German Academic Exchange Service (DAAD); International DAAD-Alumni Summer School Hanoi, Vietnam
10/2006 – 12/2007	Father and Son Eiselen Foundation, Ulm Scholarship