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Future climate conditions alter biomass of salt marsh plants in the Wadden Sea

Ketil Koop-Jakobsen[1,2] · Tobias Dolch[2]

Abstract

Understanding how the salt marsh vegetation will evolve under future climate conditions is essential for predicting the role of marsh ecosystem services in a warmer climate with higher CO_2-concentrations. In a mesocosm experiment in the northern Wadden Sea, the impact of increased temperature ($+3$ °C) and CO_2 (800 ppm) on salt marsh vegetation was investigated, assessing biomass production in the pioneer zone and low marsh. The pioneer zone, which was dominated by *Spartina anglica* and exposed to natural tidal inundations, demonstrated a differentiated response between belowground and aboveground biomass. Aboveground biomass increased in response to enhanced CO_2 availability, and belowground biomass increased in response to raised temperatures. Other plant species accounted for less than 18% of the aboveground biomass, and their biomass was suppressed under high CO_2 availability. Increased biomass by *Spartina anglica* may improve resilience toward sea level rise. Hence, the pioneer zone is expected to maintain its coastal protection and blue carbon storage capacity under future climate conditions. The low marsh, which was dominated by *Elymus athericus*, was exposed to higher than usual tidal inundations and resembled a scenario with increased sea level. The low marsh showed no response in biomass to increased CO_2 or temperature, which may be due to the increased flooding. The positive response of *Spartina anglica* (C_4 plant) and the lack of response in *Elymus athericus* (C_3 plant) counter the notion that C_3 plants are more productive under future climate conditions and demonstrate that C_4 plants can also thrive in future salt marshes.

Keywords Temperature · CO_2 · Pioneer zone · Climate change · *Sporobolus* · Sea level rise

Introduction

The salt marsh vegetation is susceptible to climate change, including increased CO_2 concentrations and temperatures, which may alter the vegetation composition and, thereby, also essential ecosystem services, such as nutrient remediation and blue carbon storage (Kirwan and Mudd 2012; FitzGerald and Hughes 2019; Duarte et al. 2021).

✉ Ketil Koop-Jakobsen
kkoopjakobsen@mbl.edu

1   The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA, USA

2   Wadden Sea Station Sylt, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research (AWI), List/Sylt, Germany

Understanding how salt marsh vegetation may change under future environmental conditions is the key to predicting the future role of salt marshes in the coastal landscape.

Increased temperatures and CO_2 availability may alter the salt marsh vegetation affecting the composition of C_3 and C_4 plants (Arp et al. 1993; Short et al. 2016). Increased CO_2 stimulates photosynthetic production more in C_3 plants than in C_4 plants, whereas C_4 plants exhibit higher productivity under elevated temperatures, which will negatively affect C_3 plants due to increased photorespiration (Bowes 1993; Sage and Kubien 2003). Hence, C_4 plants would be more competitive under lower CO_2 concentrations and higher temperatures, whereas C_3 would be more competitive under higher CO_2 concentrations and lower temperatures (Zhou et al. 2018). As climate change increases both temperature and CO_2, the effects on C_3 and C_4 plants are diverging, and the impact of future climate conditions on the salt marsh vegetation is unpredictable.

Salt marsh vegetation has been shown to increase biomass production in response to elevated CO_2 and temperature. (Gray

and Mogg 2001; McKee et al. 2012). Some salt marsh studies have shown that future climate conditions stimulate C_3 plants but do not affect C_4 plants (Arp et al. 1993; Lenssen et al. 1993). However, stimulation of C_4 plants in marshes is also commonly observed (Gray and Mogg 2001; Mateos-Naranjo et al. 2010a, b).

In a large-scale mesocosm experiment with a full-factorial design, we investigated the impact of increased CO_2 and temperature on biomass production in the European Wadden Sea salt marshes. Two marsh zones were studied, the frequently flooded pioneer zone dominated by *Spartina anglica* (C_4) at the water's edge and the low marsh dominated by *Elymus athericus* (C_3), which was located further inland and less frequently inundated. Large samples with intact rhizospheres (50 L) were grown for 100 days under environmental conditions resembling a future warmer climate with a 3-degree temperature increase and a CO_2 concentration of 800 ppm. These levels are consistent with model-projected levels for the year 2100, according to the IPCC (2014).

Material and methods

Experimental design

The study aimed to experimentally demonstrate the impact of increased temperature and CO_2 on biomass production in European salt marshes. The study targeted the pioneer zone dominated by *Spartina anglica* (C_4) and the low marsh dominated by *Elymus athericus* (C_3). The experiment was conducted in a large-scale mesocosm infrastructure at the *Alfred Wegener Institute-Wadden Sea Station* in Northern Germany (Fig. 1a). This facility was specifically developed to investigate the effects of future climate conditions on marine ecosystems (Pansch et al. 2016), allowing for control of CO_2 and temperature in the individual mesocosms.

Twelve independent mesocosms were set up in a 2×2-factorial design with true replication ($n = 3$) (Fig. 1c). The first factor was temperature, characterized by ambient water temperature and future climate conditions represented by warming to $+3\,°C$ above ambient temperature. The second factor was CO_2, characterized by the ambient CO_2 concentration and future climate conditions, represented by a doubling of CO_2 to 800 ppm. The effects of increased temperature and CO_2 were assessed as end-point measurements of above and belowground biomass and stem density after 100 days of incubation (May 11–August 19, 2022).

In the mesocosms, the samples were placed on a platform, which was lowered once a day for 2 h, submerging the marsh samples mimicking a natural tidal cycle. The applied inundation frequency was representative of the pioneer zone, whereas the low marsh experienced a higher inundation frequency than usual. Inundation frequency was monitored at

Fig. 1 Mesocosm infrastructure at the *Alfred Wegener Institute*—Wadden Sea Station *in* Northern Germany experimental set-up. **a** Mesocosms; **b** Biomass sample of *Spartina anglica* in open-sided folding boxes; **c** Experimental design: 2×2 factorial design with ambient and enhanced temperature, and CO_2

C	CO_2	
	Ambient	**800ppm**
Ambient	n=3	n=3
+3°C	n=3	n=3
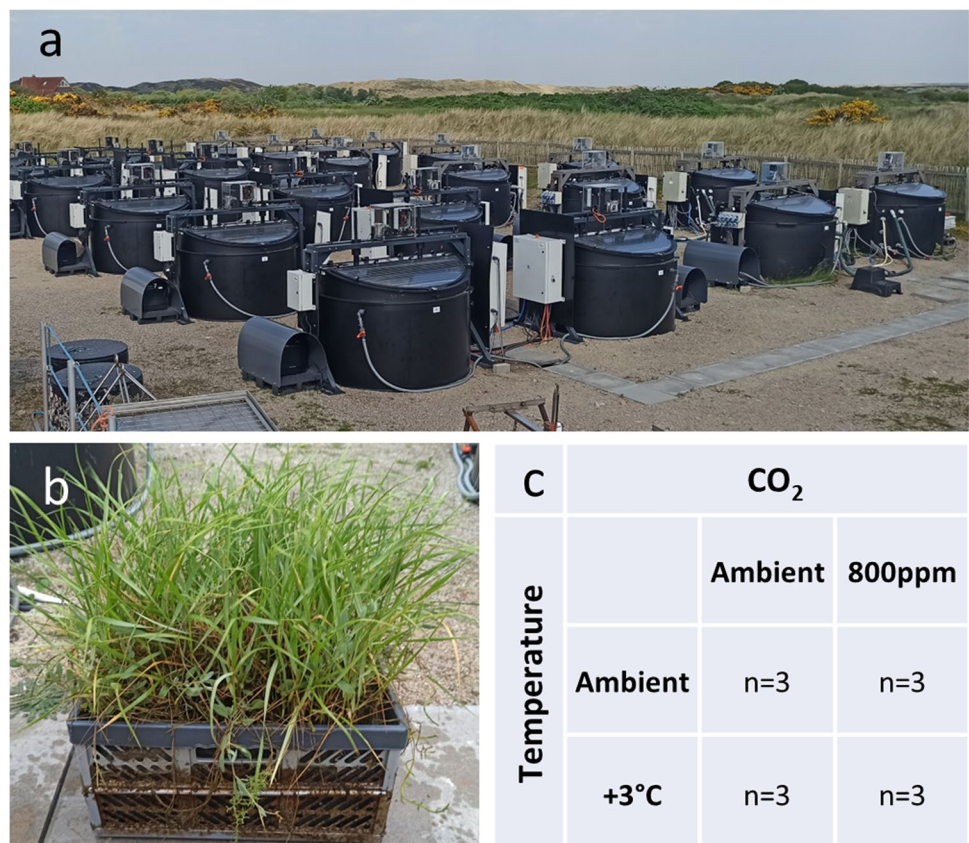
a closely located research site, about 200 m away from our sampling site, showing that the pioneer zone was inundated daily, ~ 300 days/year. The low marsh was flooded less frequently, approximately 50 days/year (Pers. Comm. Svenja Reents, AWI, Germany). Consequently, the experiment with the low marsh samples should be considered a future scenario with increased sea level rise. A differentiated tidal scheme for the low marsh and pioneer zone was not possible.

Sample collection and site description

Twelve samples were collected in the pioneer zone, which experienced daily flooding at high tide with seawater (salinity: ~ 33ppt). The samples were collected on the northern Wadden Sea coast at Hamburger Hallig (54°36″ 06N, 8°49′08E″), which has the largest natural marsh along the German Wadden Sea. Another twelve samples were collected 100 m further inland, in the low marsh, which was located at a higher elevation and experienced infrequent inundations, depending on the neap-spring tidal cycle and onshore winds affecting the tidal height. All samples were collected in mid-May 2021.

Large marsh samples (50 L soil) with intact rhizospheres were excavated and placed in open-sided folding boxes ($52 \times 37 \times 26$ cm) (Fig. 1b). The samples were cut to areal size (54×37 cm) in the field, cutting through the marsh surface with a long-bladed bread knife. Soil was removed in front of the sample, and the sample was cut out to a depth of ~ 25 cm. The whole piece was lifted from the marsh and placed in the open-sided folding boxes lined with permeable pond-lining fabric, allowing water movement in and out of the box, while the sediment was held back. In the mesocosm facility at the AWI Wadden Sea station, the samples were placed inside 12 mesocosms with one pioneer zone sample and one low marsh sample in each mesocosm.

The sampling areas were chosen due to their homogeneous vegetation distribution, assuring that the experiment's starting point was as uniform as possible. Each sample had 100% vegetation cover, avoiding patches without vegetation and areas with an alternative species composition. There were no noticeable differences in plant cover and composition among the samples from the pioneer zone and low marsh, respectively, based on the senescent plant material and early shoots at the time of collection.

Mesocosms

The mesocosm infrastructure is described in detail by Pansch et al. (2016). We here describe the aspects relevant to this study.

The mesocosms (Fig. 1a) consist of a basin tank with an inner diameter of 170 cm and a height of 85 cm and contain up to 1900 L of seawater. The top of the mesocosm consists of two sizeable transparent plexiglass lids allowing natural sunlight to enter. The mesocosms are set up as a slow flow-through system renewing the water approximately once a day with fresh seawater pumped in directly from the North Sea (28–30 ppt), which allows salinity to remain stable and nutrients to be replenished.

Temperature treatment: In the + 3 °C treatment, the water was warmed up 3 °C above ambient temperature and kept at this temperature by heaters and coolers. The ambient water temperature was identical to the temperature of the coastal water pumped into mesocosms ranging from 11 to 22 °C over the 100 days of incubation. The temperature of the mesocosms air compartments was not controlled. Since the mesocosms inevitably needed the lids closed to maintain the CO_2 treatment while still letting daylight in for photosynthesis, the air compartment above the water acted as a greenhouse on sunny days and heated up. This heating is an inevitable drawback of using closed mesocosms in a natural daylight setting. Although this effect was equal for all mesocosms, it could affect the growth of the plants investigated.

CO_2 treatment: CO_2 in the mesocosms was regulated by continuously pumping in CO_2-regulated air, bubbling it through the water column at a flow of 800 L per hour. In the ambient CO_2 treatment, atmospheric air was pumped into the systems. However, since the atmospheric air was pumped in through a pressurized system, the concentration may have been slightly lower than at the atmospheric equilibrium. For the 800-ppm systems, atmospheric air enriched with CO_2 to a concentration of 800 ppm, regulated via a gas mixing system, was pumped in the mesocosm. CO_2 was sporadically monitored in the air phase. In the CO_2-enriched mesocosms, the concentrations were 50–150 ppm above the ambient concentrations, which showed values around 380 ppm. The high humidity in the air continuously destroyed the installed IR-based CO_2 sensors, which prevented continuous monitoring of CO_2 in the air.

Biomass assessment

The biomass was assessed at the end of the experiment after 100 days of exposure to the temperature and CO_2 treatments. *Spartina anglica* (C_3) and *Elymus athericus* (C_4) dominated the pioneer zone and low marsh, respectively, and were the primary targets for biomass investigations. Other plants growing in the marsh samples were also collected, identified, and measured.

Aboveground biomass: A 20- × 10-cm subsample was cut out from the middle of the marsh sample, so potential edge effects were avoided. The aboveground biomass was harvested by cutting off all shoots at the sediment surface, and the number of stems was counted. Subsequently, the aboveground biomass was dried at 70 °C for 48 h (to constant weight), and the sample weight was determined. Biomass

originating from plants other than *Spartina anglica* and *Elymus athericus* was identified, and their aboveground biomass was measured separately. *Salicornia europaea, Suaeda maritima, Elymus athericus*, and *Halimione portulacoides* were growing among *Spartina anglica* in the pioneer zone. Due to the infrequent distribution of these other plant species, their biomasses were merged for each marsh sample. In the low marsh, only *Atriplex prostrata* was found among *Elymus athericus*.

Stem density: The stem density was assessed before drying the biomass. The number of stems per sample area (20×10 cm) was counted.

Belowground biomass: The remaining belowground sample was cut to 10×10 cm. The depth of all pioneer marsh samples was adjusted to 20 cm to allow for an equal sample size. In the low marsh, the root system did not reach the bottom of the sample, so a height adjustment was rendered unnecessary. The root biomass was separated from the sediment by rigorously washing the sample in a 2-mm sieve in a bucket with seawater and flushing it with running seawater. Most of the root system could be extracted as one coherent piece of roots and rhizomes, while the sieve would catch smaller pieces of root material that had broken off. Separation of the belowground biomass by species was not possible, which was consequently evaluated as a whole, including the biomass contribution from other species. Based on the distribution of aboveground biomass, the vast majority of the belowground biomass is assumed to originate from *Spartina anglica* and *Elymus athericus*, respectively.

Statistical analysis

Statistical analyses were conducted using the Real Statistics Resource Pack software (Release 8.3.1, www.real-statistics.com). The effects of temperature and CO_2 increases on biomass production were analyzed statistically using a two-way ANOVA. The datasets were tested for normality and outliers and found suitable for ANOVA analyses.

Results

Biomass

Spartina anglica in the pioneer zone had a higher aboveground and belowground biomass than *Elymus athericus* in the low marshes. Aboveground biomass averaged 1025 ± 196 g DW m^{-2} in the pioneer zone (Fig. 2a) compared to 621 ± 141 g DW m^{-2} in the low marsh (Fig. 3a). Belowground biomass averaged 4139 ± 557 g DW m^{-2} in the pioneer zone (Fig. 2b) compared to 1553 ± 246 g DW m^{-2} in the low marsh (Fig. 3b) when averaged across treatments ($n = 12$).

Spartina anglica	SS	df	F	p-value
Temperature	114446	1	2.69	0.14
CO₂	216572	1	5.10	0.05
Temp x CO₂	57561	1	1.35	0.28
Other Plants	SS	df	F	p-value
Temperature	830	1	0.35	0.57
CO₂	16493	1	6.86	0.03
Temp x CO₂	3473	1	1.44	0.26

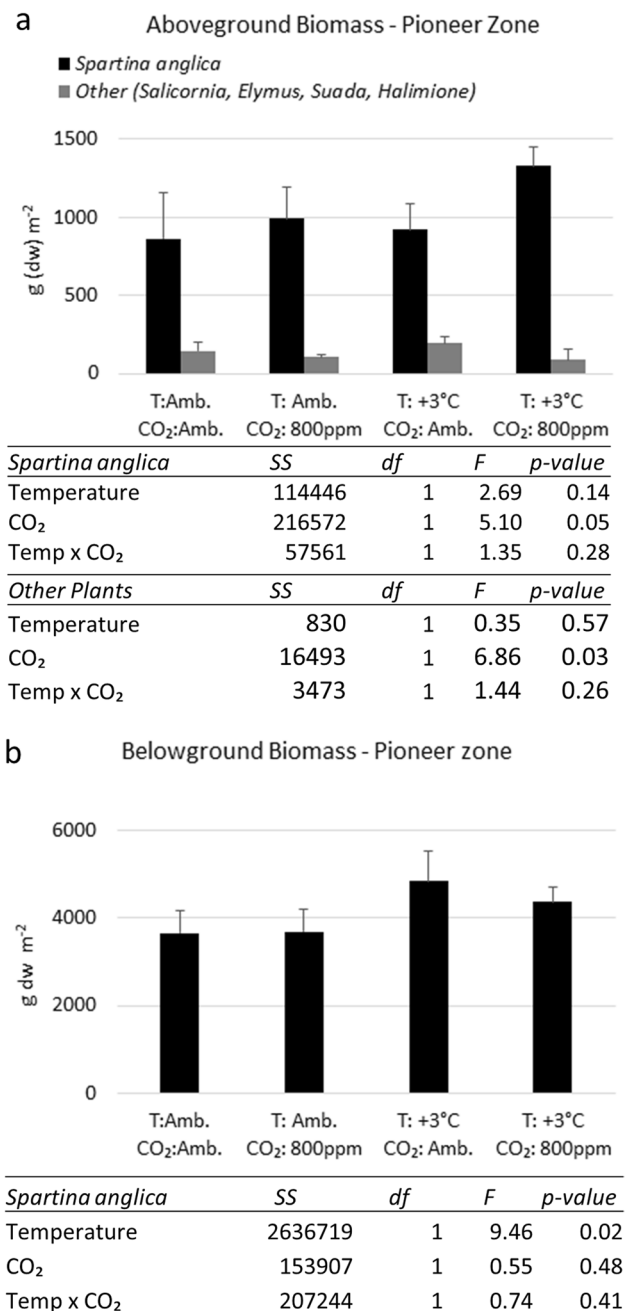| Spartina anglica	SS	df	F	p-value
Temperature	2636719	1	9.46	0.02
CO₂	153907	1	0.55	0.48
Temp x CO₂	207244	1	0.74	0.41

Fig. 2 Biomass in the pioneer zone (gram dry weight per area): **a** aboveground biomass and **b** belowground biomass, after 100-day exposure to four treatments of temperature (*T*) and CO_2 (*C*): (1) ambient *T*/ambient *C*; (2) ambient *T*/800 ppm *C*; (3) +3 °C *T*/ambient *C*; (4) +3 °C *T*/800 ppm *C*. Tables: Results of 2-way ANOVA examining the effects of temperature and CO_2-concentration on biomass

Effects of increased temperature and CO₂

In the pioneer zone, aboveground biomass (Fig. 2a) varied significantly in response to CO_2 ($F = 5.10$, $p = 0.05$), increasing biomass in response to increasing CO_2, whereas there was no temperature or combined temperature and CO_2
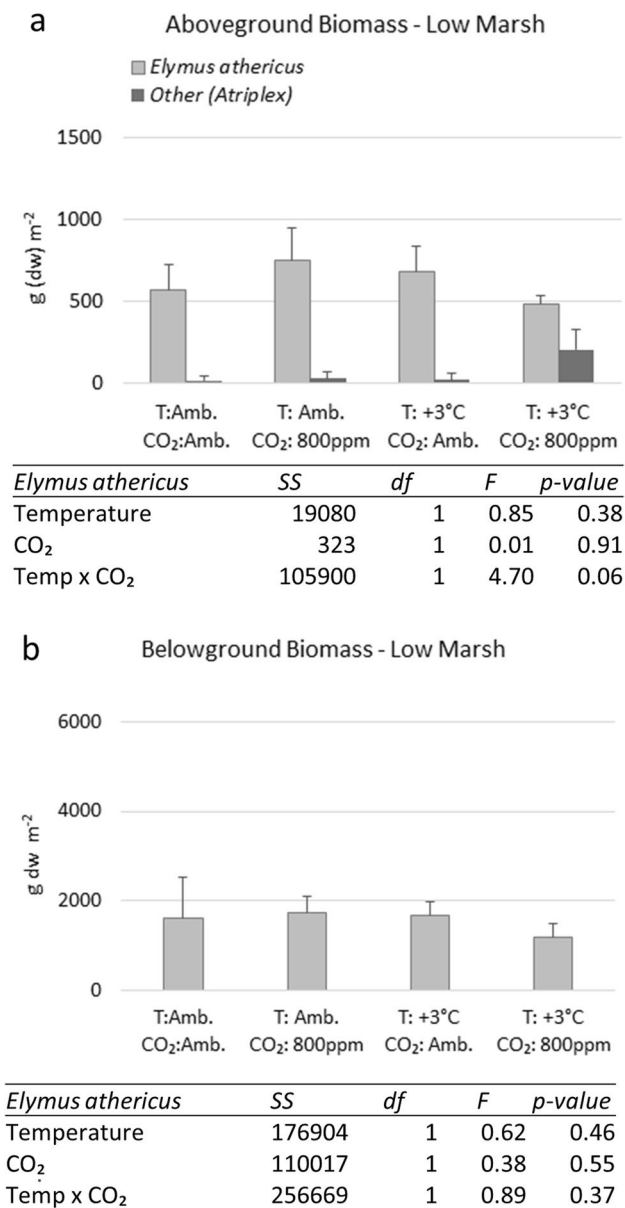
a   Aboveground Biomass - Low Marsh

☐ *Elymus athericus*
■ *Other (Atriplex)*

Elymus athericus	SS	df	F	p-value
Temperature	19080	1	0.85	0.38
CO_2	323	1	0.01	0.91
Temp x CO_2	105900	1	4.70	0.06

b   Belowground Biomass - Low Marsh

Elymus athericus	SS	df	F	p-value
Temperature	176904	1	0.62	0.46
CO_2	110017	1	0.38	0.55
Temp x CO_2	256669	1	0.89	0.37

Fig. 3 Biomass in the low marsh (gram dry weight per area): **a** aboveground biomass and **b** belowground biomass, after 100-day exposure to four treatments of temperature (*T*) and CO_2 (*C*): (1) ambient *T*/ambient *C*; (2) ambient *T*/800 ppm *C*; (3) + 3 °C T/ambient *C*; (4) + 3 °C T/800 ppm C. Tables: Results of 2-way ANOVA examining the effects of temperature and CO_2-concentration on aboveground and belowground biomass

effect. Although the samples exposed to both increased temperature and CO_2 on average had 32% higher biomass than the samples of any other treatment, this difference was not statistically significant ($F = 1.35$, $p = 0.28$).

The belowground biomass (Fig. 2b) in the pioneer zone varied significantly in response to temperature ($F = 9.5$, $p = 0.02$), increasing biomass in response to rising temperatures. In contrast, there was no CO_2 or combined

temperature and CO_2 effect. In the low marsh, there was no effect of increased temperature or CO_2 ($p > 0.05$) on either aboveground (Fig. 3a) or belowground biomass (Fig. 3b).

It is, however, noteworthy that the aboveground biomass, which was exposed to the combination of high temperature and CO_2, had lower biomass than in any other treatment. The statistical analysis showed that the combined effect of temperature and CO_2 was statistically significant at $p = 0.06$.

In general, the low marsh experienced inundation frequency higher than usual, and these sea-level-rise conditions may have inhibited biomass development in all samples.

Other plant species

In the pioneer zone, plants other than *Spartina* consisted of a mixture of typical salt marsh species in the Wadden Sea, predominantly *Salicornia europaea* (present in all 12 samples), but also including *Elymus athericus* (present in 7 samples), *Suaeda maritima* (present in 4 samples), and *Halimione portulacoides* (present in 2 samples). Due to the patchy distribution of individual species, the biomass of plants other than *Spartina* was merged. This biomass was less than 18% of the total aboveground vegetation in all treatments (Fig. 2a). The biomass of other plants was negatively affected by increasing CO_2 ($p = 0.02$) but was not affected by temperature.

In the low marsh, plants other than *Elymus* consisted of only a single species: *Atriplex prostrata* (present in 7 samples). Due to its sporadic occurrence, statistical analysis was not possible, but we found its substantial presence in the combined high temperature and CO_2 treatment noteworthy. *Atriplex prostrata* accounted for 30% of the total aboveground biomass in the treatment with both high temperature and high CO_2 but less than 10% in any other treatment, where it was primarily absent (Fig. 3a).

Stem density

In the pioneer zone, *Spartina anglica* showed a significantly higher stem density in response to increased CO_2 concentration ($p = 0.03$) (Fig. 4a). Hence, the increased biomass production was driven by the production of more shoots, rather than an increase in the biomass of the individual shoot.

In contrast, in the low marsh, there was no effect of either temperature of CO_2 on the stem density in *Elymus athericus* (Fig. 4b).

Discussion

In our experiments, the increase in CO_2 and temperature represents the predicted levels reached by 2100. By this year, the Bern carbon cycle-climate model, one of the models used by the IPCC, predicts atmospheric CO_2 concentrations
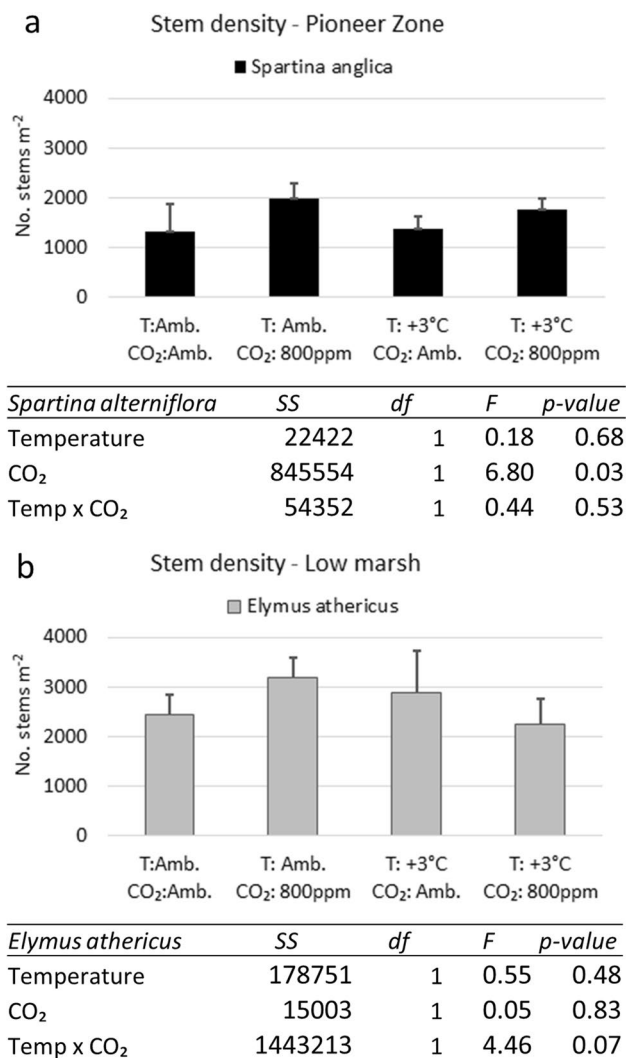
a   Stem density - Pioneer Zone

■ Spartina anglica

Spartina alterniflora	SS	df	F	p-value
Temperature	22422	1	0.18	0.68
CO_2	845554	1	6.80	0.03
Temp x CO_2	54352	1	0.44	0.53

b   Stem density - Low marsh

☐ Elymus athericus

Elymus athericus	SS	df	F	p-value
Temperature	178751	1	0.55	0.48
CO_2	15003	1	0.05	0.83
Temp x CO_2	1443213	1	4.46	0.07

Fig. 4 Stem density in **a** *Spartina anglica* in the pioneer zone and **b** *Elymus athericus* in the low marsh, after 100-day exposure to four treatments of temperature (*T*) and CO_2 (*C*): (1) ambient *T*/ambient *C*; (2) ambient *T*/800 ppm *C*; (3) +3 °C T/ambient *C*; (4) +3 °C T/800 ppm *C*. Tables: Results of 2-way ANOVA examining the effects of temperature and CO_2-concentration on stem density

to reach 836 ppm. This doubling of the atmospheric CO_2 concentration will likely result in a temperature increase from 2 to 4.5 °C, with 3 °C being the most likely value (Meehl et al. 2007). Therefore, we consider our experiment to represent a realistic scenario of the future impact of climate change on salt marsh vegetation.

Spartina anglica was chosen to represent the vegetated pioneer zone due to its essential ecosystem services and increased spread along the Wadden Sea coastline (Loebl et al. 2006). *Elymus athericus* was chosen to represent the low marsh, as it is increasingly becoming more dominant in northern European salt marshes, spreading from the high marsh into the low marsh (Valéry et al. 2017). It was the dominant species in the low marsh samples used in this

study, but it can also be found in mixed vegetation (Hartmann and Stock 2019).

It is suggested that the atmospheric enrichment of CO_2 will favor the growth of C_3 plant species (such as *Elymus athericus*) in wetlands. As a result, the competitive balance between C_3 and C_4 plant species may change markedly (Rozema et al. 1991). This effect may impose changes to coastal vegetation and, thereby, the morphology and function of the salt marshes, in both terms of ecosystem services and loss of biodiversity (Duarte et al. 2014). Our results suggest that C_4 plants, here represented by *Spartina anglica*, will also be stimulated by future climate conditions with increased CO_2 availability and temperatures. When grown under experimental conditions mimicking the natural pioneer marsh with water-saturated soils and frequent tidal inundations, the aboveground *Spartina* biomass increased in response to increased CO_2 (Fig. 2a), driven by an increase in the number of stems produced (Fig. 4a). In contrast, the belowground biomass increased in response to increased temperatures (Fig. 2b).

This differentiated response in aboveground and belowground biomass to increases in CO_2 availability and temperature is noteworthy, as it suggests that the total biomass would increase in a future climate, based on different drivers. This complex interaction makes it more difficult to predict the response of biomass production. It is also possible that the lack of temperature control of the air compartment and the occasional heating events on sunny days have caused the absence of a temperature response in the aboveground biomass. However, given that the biomass was four times higher belowground than aboveground (Fig. 2), our results demonstrated that increased temperature would significantly increase the total biomass production in the pioneer zone.

This demonstration of increases in biomass in the pioneer zone supports previous observations of a positive response by various *Spartina* species to future climate conditions, including *Spartina densiflora* (Mateos-Naranjo et al. 2010a) and *Spartina maritima* (Mateos-Naranjo et al. 2010b) and *Spartina anglica* (Gray and Mogg 2001).

In contrast, our results showed no response in biomass production of the C_3 plant *Elymus athericus* in the low marsh to future climate conditions (Fig. 3). Instead, markedly lower biomass was demonstrated in the treatment with high temperature and high CO_2 concentrations, which suggests an adverse effect of future climate conditions. However, this was not statistically significant ($p = 0.06$). This result diverges from previous studies, where *Elymus* responded positively to future climate conditions, particularly increased CO_2 (Lenssen et al. 1993; van de Staaij et al. 1993; Rozema et al. 1997).

Although recent studies have demonstrated that some *Elymus athericus* genotypes possess traits enabling it to inhabit flooded sediments (Koop-Jakobsen et al. 2021; Mueller et al.

2021; Reents et al. 2021), the sudden increase in inundation frequency that Elymus plants experienced in the mesocosms may have markedly influenced the results inhibiting biomass production. Consequently, the low marsh experiment should be considered a scenario where rising sea level plays a role in Elymus's performance.

Also, in the low marsh, the lack of temperature control of the air compartment and the occasional heating events on sunny days may have caused the absence of temperature response in the aboveground biomass. As the primary production of C_3 plants is negatively affected at higher temperatures due to increased photorespiration (Bowes 1993), it may have affected *Elymus athericus* (C_3) in the low marsh samples more than *Spartina anglica* (C_4) in the pioneer zone.

However, the increased inundation and temperature effects do not explain the observed tendency towards lower aboveground biomass when both temperature and CO_2 are increased ($p = 0.06$). There could be several reasons for this divergence. In our experiment, competition with *Atriplex prostrata*, is a plausible explanation. *Atriplex prostrata* have been more frequently observed in the Wadden Sea vegetation in recent years (Hartmann and Stock 2019). Our results support the notion that this may be a response to climate change as *Atriplex prostrata* had the highest biomass in the treatment with elevated CO_2 and raised temperature, accounting for 33% of the aboveground biomass (Fig. 3a). In the other treatments, it was absent or occurred only in small amounts. Due to this absence in many samples, statistical analysis was not possible, and it cannot be ruled out that the observed distribution of *Atriplex prostrata* was due to a predisposition in the distribution of seeds.

Also, in the pioneer zone samples, there was a sporadic presence of other plant species: *Salicornia europaea*, *Halimione* portulacoides, *Suaeda maritima*, and *Elymus athericus*, which combined accounted for less than 18% of the total aboveground biomass in all samples. The combined biomass of these plant species was inversely affected by increased CO_2 ($p = 0.03$) (Fig. 2a). This effect is likely caused by increased competition for space by *Spartina*, which increased its stem production in response to increased CO_2 (Fig. 4a).

Marshes' future role in coastal protection and carbon burial

Coastal protection is an important ecosystem service provided by salt marshes, which is directly dependent on the morphology and strength of the vegetation (Shepard et al. 2011). The biomechanic traits affecting plants' interaction with hydrodynamic forcing were investigated in an additional study of the mesocosm vegetation from this experiment. The measurements showed an increase in diameter and flexural rigidity in response to increased temperature

and CO_2 in *Spartina anglica* (Paul et al. 2022). Combined with our results showing increased biomass and stem density under elevated temperature and CO_2 conditions, a stronger and more resilient pioneer zone maintaining its coastal protection properties is expected under future climate conditions. Increased belowground biomass will stabilize the sediment, and increased aboveground biomass will improve wave attenuation, prevent erosion, and increase sedimentation. This change will enhance the marshes' coastal protection properties. Although no direct effects were shown on *Elymus athericus* (Paul et al. 2022), the low marsh may also benefit from a more robust pioneer zone, improving protection from wave and wind action.

The effects of sea level rise will also have a significant influence on the development of European salt marshes. Recent studies have shown that both *Spartina anglica* and *Elymus athericus* in the Wadden sea marshes demonstrate resilience against sea level rise (Granse et al. 2021; Reents et al. 2021). In this study, the low marsh experiment resembled a "sea level rise" — scenario with increased inundation frequency. Although the biomass tended to be lower with increased temperature and CO_2 combined, the difference was not statistically significant, and the low marsh biomass was generally unaffected by increased temperature and CO_2. Hence, there is no weakening of the low marsh coastal protective capability, but whether the status quo is sufficient to withstand future increases in hydrodynamic forcing needs further attention. In contrast, the biomass increased in *Spartina anglica* in response to temperature and CO_2. Although the experiment for the pioneer zone was not a sea level rise scenario, it suggests that future climate conditions may improve resilience toward sea level rise.

Furthermore, increased biomass will provide a larger pool of organic matter, which can be permanently buried in the marsh, maintaining marshes' role as a critical blue carbon ecosystem mitigating the increase in atmospheric CO_2 concentrations. These effects combined will confirm salt marshes' importance in future coastal ecosystems.

Methodological considerations

The study was conducted in large mesocosm*s* at the *Alfred Wegener Institute-Wadden Sea Station* in Northern Germany. Access to this infrastructure gave the experiment several advantages, allowing for true replication of treatments and the use of large natural marsh samples while maintaining tidal exposure with natural seawater. Experimental studies of marsh plants are challenging. Many salt marsh plants produce a massive and complex underground root system (Granse et al. 2022), which is difficult to investigate in a regular greenhouse experiment using potted samples. Furthermore, in salt marshes, tidal inundations control plant composition and zonation (Silvestri et al. 2005). Consequently, experimental studies of marsh plants shall ideally

resemble a natural tidal scheme, and these conditions require facilities with access to large quantities of seawater.

The large mesocosms allowed for simulations of daily tidal inundation, which resembled the tidal scheme of the pioneer zone better than the low marsh, where the soil can experience air entry between inundations (Keshta et al. 2020). We chose this tidal scheme to take advantage of the mesocosm facility's tidal simulation opportunities, which are difficult to reproduce in a laboratory setting. Differentiated tidal simulation of the pioneer zone and low marsh samples was not possible, as the height of the mesocosm was too low to have one sample placed higher than the other.

Our experiments emphasized maintaining natural conditions while manipulating temperature and CO_2 availability. Consequently, we used large samples with a soil volume of 50 L collected in the field and avoided culturing, replanting, and potting. This sample size allowed a large part of the rhizosphere to remain intact, and we could avoid edge effects by subsampling from the middle of the samples.

Conclusion and perspectives

In general, biomass production of the vegetation in the pioneer zone was stimulated by enhanced CO_2 and temperature. The biomass of species other than *Spartina* was low and became even lower with increased CO_2, likely due to increased competition from *Spartina* that increased its shoot density. Hence, future climate conditions may cause the already low diversity of the pioneer zone to become even more inferior and support the development of *Spartina* monocultures.

The low marsh was unaffected by changes in temperature and CO_2. However, in the treatment combining high CO_2 and temperature, the aboveground and belowground biomass of *Elymus athericus* was lower than in the other treatments, although not significant. In contrast, a different species, *Atriplex prostrata*, was present in larger numbers here but was almost absent in the other treatments. This alteration indicates a change in vegetation composition under future climate conditions, which is supported by field observations showing an increase in *Atriplex prostrata* distribution in the Wadden sea in recent years (Hartmann and Stock 2019). However, our data could not confirm these changes statistically. In addition, the low marsh was more frequently inundated than under natural conditions. These results should therefore be considered a scenario with increased flooding and wetter soils that may have inhibited plant growth. Further studies of the low marsh are needed to determine the impact of future climate conditions on species composition. These results emphasize the need for long-term and large-scale studies that allow successional changes to be evaluated.

In conclusion, the salt marsh pioneer zone is expected to maintain its vegetation-derived ecosystem services under future climate conditions. Increased CO_2 and temperature will improve plant traits that enhance the resilience towards sea level rise and harsher weather patterns. The low marsh may be more susceptible since the vegetation here was unaffected by CO_2 and temperature. However, the low marsh may also benefit from a more robust pioneer zone with improved coastal protection traits.

Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval No animal testing was performed during this study.

Sampling and field studies All necessary permits for field sampling were obtained by the authors from Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein (LKN) - Nationalparkverwaltung Schleswig-Holsteinisches Wattenmeer.

Data availability Data is available through PANGAEA — data publisher. https://doi.pangaea.de/10.1594/PANGAEA.955057.

Author contribution KKJ and TD conceived and designed this research. KKJ conducted the fieldwork and experiment, and wrote the manuscript. All authors read and approved the manuscript.

References

Arp WJ, Drake BG, Pockman WT, Curtis PS, Whigham DF (1993) Interactions between C_3 and C_4 salt marsh plant species during four years of exposure to elevated atmospheric CO_2. In: Rozema J, Lambers H, Van de Geijn SC, Cambridge ML (eds) CO2 and biosphere. Springer, Dordrecht, pp 133–143

Bowes G (1993) Facing the inevitable: plants and increasing atmospheric CO_2. Annu Rev Plant Physiol Plant Mol Biol 44:309–332. https://doi.org/10.1146/annurev.pp.44.060193.001521

Duarte B, Santos D, Silva H, Marques JC, Caçador I (2014) Photochemical and biophysical feedbacks of C_3 and C_4 Mediterranean halophytes to atmospheric CO_2 enrichment confirmed by their stable isotope signatures. Plant Physiol Biochem 80:10–22. https://doi.org/10.1016/j.plaphy.2014.03.016

Duarte B, Carreiras J, Caçador I (2021) Climate change impacts on salt marsh blue carbon, nitrogen and phosphorous stocks and ecosystem services. Appl Sci 11:1969. https://doi.org/10.3390/app11041969

FitzGerald DM, Hughes Z (2019) Marsh processes and their response to climate change and sea-level rise. Annu Rev Earth Planet Sci 47:481–517. https://doi.org/10.1146/annurev-earth-082517-010255

Granse D, Suchrow S, Jensen K (2021) Long-term invasion dynamics of *Spartina* increase vegetation diversity and geomorphological resistance of salt marshes against sea level rise. Biol Invasions 23:1–13. https://doi.org/10.1007/s10530-020-02408-0

Granse D, Titschack J, Ainouche M, Jensen K, Koop-Jakobsen K (2022) Subsurface aeration of tidal wetland soils: root-system structure and aerenchyma connectivity in *Spartina* (Poaceae). Sci Total Environ 802:149771. https://doi.org/10.1016/j.scitotenv.2021.149771

Gray AJ, Mogg RJ (2001) Climate impacts on pioneer saltmarsh plants. Clim Res 18:105–112. http://www.jstor.org/stable/24861564

Hartmann K, Stock M (2019) Long-term change in habitat and vegetation in an ungrazed, estuarine salt marsh: man-made foreland compared to young marsh development. Estuar Coast Shelf Sci 227:106348. https://doi.org/10.1016/j.ecss.2019.106348

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, pp 151

Keshta A, Koop-Jakobsen K, Titschack J, Mueller P, Jensen K, Baldwin A, Nolte S (2020) Ungrazed salt marsh has well connected soil pores and less dense sediment compared with grazed salt marsh: a CT scanning study. Estuar Coast Shelf Sci 245:106987. https://doi.org/10.1016/j.ecss.2020.106987

Kirwan ML, Mudd SM (2012) Response of salt-marsh carbon accumulation to climate change. Nature 489:550–553. https://doi.org/10.1038/nature11440

Koop-Jakobsen K, Meier RJ, Mueller P (2021) Plant-mediated rhizosphere oxygenation in the native invasive salt marsh grass *Elymus athericus*. Front Plant Sci 12:669751. https://doi.org/10.3389/fpls.2021.669751

Lenssen GM, Lamers J, Stroetenga M, Rozema J (1993) Interactive effects of atmospheric CO_2 enrichment, salinity and flooding on growth of C_3 (*Elymus athericus*) and C_4 (*Spartina anglica*) salt marsh species. Vegetatio 104–105:379–388. https://doi.org/10.1007/BF00048167

Loebl M, van Beusekom JEE, Reise K (2006) Is spread of the neophyte *Spartina anglica* recently enhanced by increasing temperatures? Aquat Ecol 40:315–324. https://doi.org/10.1007/s10452-006-9029-3

Mateos-Naranjo E, Redondo-Gómez S, Álvarez R, Cambrollé J, Gandullo J, Figueroa ME (2010) Synergic effect of salinity and CO_2 enrichment on growth and photosynthetic responses of the invasive cordgrass *Spartina densiflora*. J Exp Bot 61:1643–1654. https://doi.org/10.1093/jxb/erq029

Mateos-Naranjo E, Redondo-Gómez S, Andrades-Moreno L, Davy AJ (2010) Growth and photosynthetic responses of the cordgrass *Spartina maritima* to CO_2 enrichment and salinity. Chemosphere 81:725–731. https://doi.org/10.1016/j.chemosphere.2010.07.047

McKee K, Rogers K, Saintilan N (2012) Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In: Middleton BA (ed) Global change and the function and distribution of wetlands. Springer, Netherlands, Dordrecht, pp 63–96

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ, Zhao Z-C (2007) Global climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) IPCC, 2007: Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Mueller P, Do HT, Smit C, Reisdorff C, Jensen K, Nolte S (2021) With a little help from my friends: physiological integration facilitates invasion of wetland grass *Elymus athericus* into flooded soils. Oikos 130:431–439. https://doi.org/10.1111/oik.07863

Pansch A, Winde V, Asmus R, Asmus H (2016) Tidal benthic mesocosms simulating future climate change scenarios in the field of marine ecology. Limnol Oceanogr Methods 14:257–267. https://doi.org/10.1002/lom3.10086

Paul M, Bischoff C, Koop-Jakobsen K (2022) Biomechanical traits of salt marsh vegetation are insensitive to future climate scenarios. Sci Rep 12:21272. https://doi.org/10.1038/s41598-022-25525-3

Reents S, Mueller P, Tang H, Jensen K, Nolte S (2021) Plant genotype determines biomass response to flooding frequency in tidal wetlands. Biogeosciences 18:403–411. https://doi.org/10.5194/bg-18-403-2021

Rozema J, Lenssen GM, Arp WJ, Van De Staaij JWM (1991) Global change, the impact of the greenhouse effect (atmospheric CO_2 enrichment) and the increased UV-B radiation on terrestrial plants. In: Rozema J, Verkleij JAC (eds) Ecological responses to environmental stresses. Springer, Netherlands, Dordrecht, pp 220–233

Rozema J, Lenssen GM, van de Staaij JWM, Tosserams M, Visser AJ, Broekman RA (1997) Effects of UV-B radiation on terrestrial plants and ecosystems: interaction with CO_2 enrichment. Plant Ecol 128:183–191. https://doi.org/10.1023/A:1009762924174

Sage RF, Kubien DS (2003) Quo vadis C_4? An ecophysiological perspective on global change and the future of C_4 plants. Photosynth Res 77:209–225. https://doi.org/10.1023/A:1025882003661

Shepard CC, Crain CM, Beck MW (2011) The protective role of coastal marshes: a systematic review and meta-analysis. PLOS ONE 6:e27374. https://doi.org/10.1371/journal.pone.0027374

Short FT, Kosten S, Morgan PA, Malone S, Moore GE (2016) Impacts of climate change on submerged and emergent wetland plants. Aquat Bot 135:3–17. https://doi.org/10.1016/j.aquabot.2016.06.006

Silvestri S, Defina A, Marani M (2005) Tidal regime, salinity and salt marsh plant zonation. Estuar Coast Shelf Sci 62:119–130. https://doi.org/10.1016/j.ecss.2004.08.010

Valéry L, Radureau A, Lefeuvre J-C (2017) Spread of the native grass *Elymus athericus* in salt marshes of Mont-Saint-Michel bay as an unusual case of coastal eutrophication. J Coast Conserv 21:421–433. https://doi.org/10.1007/s11852-016-0450-z

van de Staaij JWM, Lenssen GM, Stroetenga M, Rozema J (1993) The combined effects of elevated CO_2 levels and UV-B radiation on growth characteristics of *Elymus athericus* (= *E. pycnanathus*). Vegetatio 104:433–439. https://doi.org/10.1007/BF00048172

Zhou H, Helliker BR, Huber M, Dicks A, Akçay E (2018) C_4 photosynthesis and climate through the lens of optimality. Proc Natl Acad Sci 115:12057–12062. https://doi.org/10.1073/pnas.1718988115