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RESEARCH ARTICLE

Repetitive desiccation events weaken a salt marsh mutualism

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Abstract

1. Salt marshes suffered large-scale degradation in recent decades. Extreme events such as hot and dry spells contributed significantly to this, and are predicted to increase not only in intensity, but also in frequency under future climate scenarios. Such repetitive extreme events may generate cumulative effects on ecosystem resilience. It is therefore important to elucidate how marsh vegetation responds to repetitive stress, and whether changes in key species interactions can modulate vegetation resilience.
2. In this study, we investigated how moderate but repetitive desiccation events, caused by the combined effects of drought and high temperatures, affect cordgrass (*Spartina alterniflora*), the dominant habitat-forming grass in southeastern US salt marshes. In a 4-month field experiment, we simulated four consecutive desiccation events by periodically excluding tidal flooding and rainfall, while raising temperature. We crossed this desiccation treatment with the presence/absence of ribbed mussels (*Geukensia demissa*) – a mutualist of cordgrass known to enhance its desiccation resilience – and with grazing pressure by the marsh periwinkle (*Littoraria irrorata*) that is known to suppress cordgrass' desiccation resilience.
3. We found that each subsequent desiccation event deteriorated sediment porewater conditions, resulting in high salinity (53 ppt), low pH-levels (3.7) and increased porewater Al and Fe concentrations ($\approx 800 \mu\text{mol/L}$ and $\approx 1,500 \mu\text{mol/L}$) upon rewetting. No effects on porewater chemistry were found as a result of snail grazing, while ribbed mussels strongly mitigated desiccation effects almost to control levels and increased cordgrass biomass by approximately 128%. Importantly, although cordgrass generally appeared healthy above-ground at the end of the experiment, we found clear negative responses of the repetitive desiccation treatment on cordgrass below-ground biomass, on proline (osmolyte) levels in shoots and on the number of tillers (–40%), regardless of mussel and/or snail presence.

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4. Synthesis. Even though the mutualism with mussels strongly mitigated chemical effects in the sediment porewater throughout the experiment, mussels could not buffer the adverse ecophysiological effects observed in cordgrass tissue. Our results therefore suggest that although mussels may alleviate desiccation stress, the predicted increased frequency and intensity of hot dry spells may eventually affect saltmarsh resilience by stressing the mutualism beyond its buffering capacity.

KEYWORDS

drought, *Geukensia demissa*, *Littoraria irrorata*, mussel, mutualism, salt stress, *Spartina alterniflora*, water stress

1 | INTRODUCTION

Anthropogenic forcing is inducing both gradual and acute changes in climate patterns world-wide (IPCC et al., 2007; Myhre et al., 2013). In addition to the foreseen continued warming, predictions are that many ecosystems will continue to be increasingly exposed to extremes, such as heavy rainfall, heat spells or droughts that will likely increase in both severity and frequency (Hansen, Sato, & Ruedy, 2012; IPCC et al., 2007). Such climatic changes affect individual species and ecosystem structure and can result in species shifts, extinctions and ecosystem degradation (Grimm et al., 2013; Urban, 2015). While many studies have focused on how single extreme climate events affect ecosystem resilience (Jentsch & Beierkuhnlein, 2008), cumulative effects by repetitive exposure to extremes remain poorly studied (e.g. Smith, 2011), even though the limited work performed suggests that increased climatic variability can have severe impacts (e.g. Báez, Collins, Pockman, Johnson, & Small, 2013; Fay, Carlisle, Knapp, Blair, & Collins, 2003; Thomey, Collins, Friggens, Bron, & Pockman, 2014).

Ecosystem resilience to climatic extremes can be importantly mediated by both positive and negative biotic and abiotic interactions. In arid systems, for instance, overgrazing has been observed to interact with drought to intensify the rate of desertification (Li et al., 2000). In seagrass ecosystems, on the other hand, the mutualism between seagrass, bivalves and their endosymbiotic bacteria, prevents accumulation of the phytotoxin sulphide, but, at the same time, may make the system more vulnerable to drought-mediated desiccation and rapid ecosystem collapse (de Fouw et al., 2016; van der Heide et al., 2012). Understanding how such dominant interspecific interactions influence ecosystem sensitivity to climatic changes is therefore key to predicting temporal and spatial variability in ecosystem resilience.

Like most coastal ecosystems, salt marshes are degrading as a result of multiple anthropogenic impacts. In many regions, including the southeastern US, part of their increased deterioration has been associated with climatic changes such as desiccation events caused by the combined effects of drought and high temperatures (Alber, Swenson, Adamowicz, & Mendelssohn, 2008; Gedan &

Silliman, 2009; He, Silliman, Liu, & Cui, 2017; Li, Wen, & Yang, 2017; McKee, Mendelssohn, & Materne, 2004; Millennium Ecosystem Assessment, 2005; Silliman, van de Koppel, Bertness, Stanton, & Mendelssohn, 2005). In these marshes, several common species that can potentially alter ecosystem resilience interact with the dominant vegetation, *Spartina alterniflora* (hereafter cordgrass). Ribbed mussel (*Geukensia demissa*, hereafter mussels) live in aggregations around cordgrass stems in intermediate and high elevation marsh platforms. They have been found to generally enhance cordgrass production and persistence, and also increases cordgrass survival during desiccation events by enhancing water storage and reducing salinity stress (Angelini et al., 2016). In addition, mussels increase nutrient availability by excreting pseudofaeces and mitigate sulphide stress, thereby increasing cordgrass resilience to disturbance (Derksen-Hooijberg et al., 2018), and thus potentially its' resistance to desiccation events. The salt marsh periwinkle *Littoraria irrorata* (hereafter snails) on the other hand, grazes upon senesced leaves of cordgrass, but also inflicts wounds in healthy leaves to spread the infection of fungi. Snails feed on the fungus and both snails and fungi act synergistically in suppressing cordgrass growth (Silliman & Newell, 2003; Silliman & Zieman, 2001), and importantly, grazing impacts on cordgrass appear to be increased during desiccation-induced salt stress (Silliman et al., 2005).

During a desiccation event typically caused by lack of rainfall combined with high temperatures and limited tidal flooding, conditions may arise in which salt marsh soils dry out (Hughes, Wilson, & Morris, 2012; McKee et al., 2004). Throughout such an event, salt marsh plants may experience desiccation, increased salinity and osmotic stress (Hughes et al., 2012). Furthermore, when the normally waterlogged sediments are exposed to oxygen during desiccation events, compounds such as metal-sulphides are oxidised generating sulphuric acid, which results in a lowering of the pH upon rewetting (Palomo, Meile, & Joye, 2013; Smolders et al., 2006). Indeed, laboratory experiments demonstrated that salt marsh soil from dieback sites can reach low pH values after being dried (McKee et al., 2004). This drop in pH in turn, strongly enhances the solubility of metals such as aluminium (Al^{3+}) and iron (Fe^{2+}) that were previously bound to the sediment. These metals become available in the porewater

upon rewetting (Nordstrom, 1982), potentially resulting in toxicity for the plants (McKee et al., 2004). However, shortly after a climate event, when water tables increase again and several high tides flood the marsh interior, any accumulated salt, acid and metals may be quickly diluted, making it hard to pinpoint mechanistically which are the actual stressors that the vegetation experiences in a natural field setting.

To unravel the potentially cumulative effects of relatively short, but repetitive desiccation events (droughts + warming) and the underlying mechanisms in US salt marshes, we simulated drought combined with elevated temperatures, in a 4-month field experiment. We crossed the presence of mussels and snails – species known to interact with cordgrass during desiccation events – with the desiccation treatment to test the hypotheses that: (a) multiple chemical stressors accumulate after each successive desiccation event, (b) mussels facilitate cordgrass by mitigating chemical stressors and (c) snails reduce cordgrass' resilience to withstand these stressors over time.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in a salt marsh located within the National Estuarine Research Reserve on Sapelo Island, Georgia, USA (latitude 31.4081083, longitude -81.2897972) from April to August 2014. The experiment was carried out in a high elevation marsh platform with muddy, organic matter-rich sediments (organic matter content 6.7%–9.1%, silt fraction 12.8%–19.4%, clay fraction 18.9%–25.3%, sand fraction 60.6%–64.1%, bulk density 0.11–0.13 g/cm³). The vegetation is dominated by a healthy-appearing monoculture of short growth-form cordgrass, with scattered mussel aggregations of 5–70 mussels (Derksen-Hooijberg et al., 2018), and snails at moderate densities (~250 snails/m², personal observations by MD and CA) (Silliman et al., 2005). In the nearby area several, relatively small ($\pm 1,000$ m²) diebacks have occurred during a desiccation event between 2010 and 2012, indicating that the area is susceptible to die-back. In this period, the Palmer Drought Severity Index (PDSI) – a metric estimating relative dryness from temperature and rainfall on a scale from -10 and +10 – reached well below -4 in our study area, indicating severe drought (Angelini et al., 2016). During our experiment, PDSI was +3.1 in April 2013, followed by neutral to slightly negative values (0, -0.2, -0.7 and -1.3) in the following months (NOAA: <https://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers/>), indicating that our control treatments did not experience any significant desiccation stress.

2.2 | Experimental setup

We conducted a full-factorial experiment in which three factors were crossed: desiccation – control, mussels – no mussels and snails – no snails, resulting in eight treatments ($N = 6$ replicates per treatment, totalling 48 plots). Plot size (0.02 m²) was chosen such that

(a) the isolated cordgrass plots are large enough to grow on their own (Silliman et al., 2015), and (b) it encompassed the spatial scale of the relevant interactions – that is, millimetre to centimetre-scale rhizosphere interactions (Derksen-Hooijberg et al., 2018), leaf to shoot-scale snail grazing (Davidson et al., 2015) and decimetre-scale mussel mounds (Angelini et al., 2015). Plots were spaced at least 1 m apart, and positioned such that cordgrass stem density was standardised at 11–16 shoots with a canopy height of 25–30 cm at the start of the experiment.

For mussel treatments, we positioned the plots in the centre of naturally present mussel mounds ranging between 28 and 47 cm in diameter. We utilised naturally present mounds, as opposed to transplanting mussels into marsh plots to form mussel treatments, because previous experiments have shown that mussel effects on soil chemistry and plant growth took >1 year to develop and maintaining this current experiment that entailed manipulating drought stress was infeasible over that time-scale. Because soil temperature, inundation level/surface elevation, exposure to grazers and predators and other physical and biotic factors did not vary measurably across the experimental plots, we argue that effects of factors confounded with mussels are likely to be limited, though they cannot be ruled out.

We designed our experimental setup such that the desiccation treatment would generate the suite of adverse conditions reported from earlier work – that is, enhanced salinity levels ultimately reaching from 45 to beyond 55 ppt (Angelini et al., 2016; Silliman et al., 2005), and soil acidification down to pH 3–4 with associated dissolution of heavy metals (Feijtel, DeLaune, & Patrick, 1988; McKee et al., 2004). To simulate such events in a repetitive manner, we installed climate and control chambers in the field. Below-ground PVC tubes (41 cm length by 16 cm diameter) were glued to a PVC connector socket (9 cm overlapping, total length of socket 18 cm), creating a 50 cm long below-ground structure with an open bottom (Figure 1a,b) to prevent water from flowing horizontally into plots below-ground. For the desiccation treatments, we then inserted a transparent PVC tube (84 cm length and 16 cm diameter) (EnviroKingUV Harvel Plastics Inc., Easton, PA) into the top 9 cm of the below-ground connector socket, creating an above-ground chamber that extended 73 cm above the marsh surface. We sealed the transparent tube to the connector socket by squeezing a layer of plumbers' putty (Hercules-Sta Put, Passiac, NJ) between the outer ring of the socket and the transparent tube. To prevent rain from entering while still allowing air exchange, we installed sloping transparent acrylic roofs 4–6 cm above each climate chamber (size 254 × 203 × 0.20 mm; OPTIX, Columbus, OH). In control treatments, the same below-ground structure was installed, but instead of transparent PVC, a white Vexar mesh tube (84 cm length and 16 cm diameter) was installed on top of the connector socket (Figure 1b), so that tidal water could freely move through the mesh. Prior to the start of the experiment, snails were removed from all plots, and, in snail treatments, five adult snails (standardised shell length of 11–15 mm) were added, corresponding to ambient snail densities.

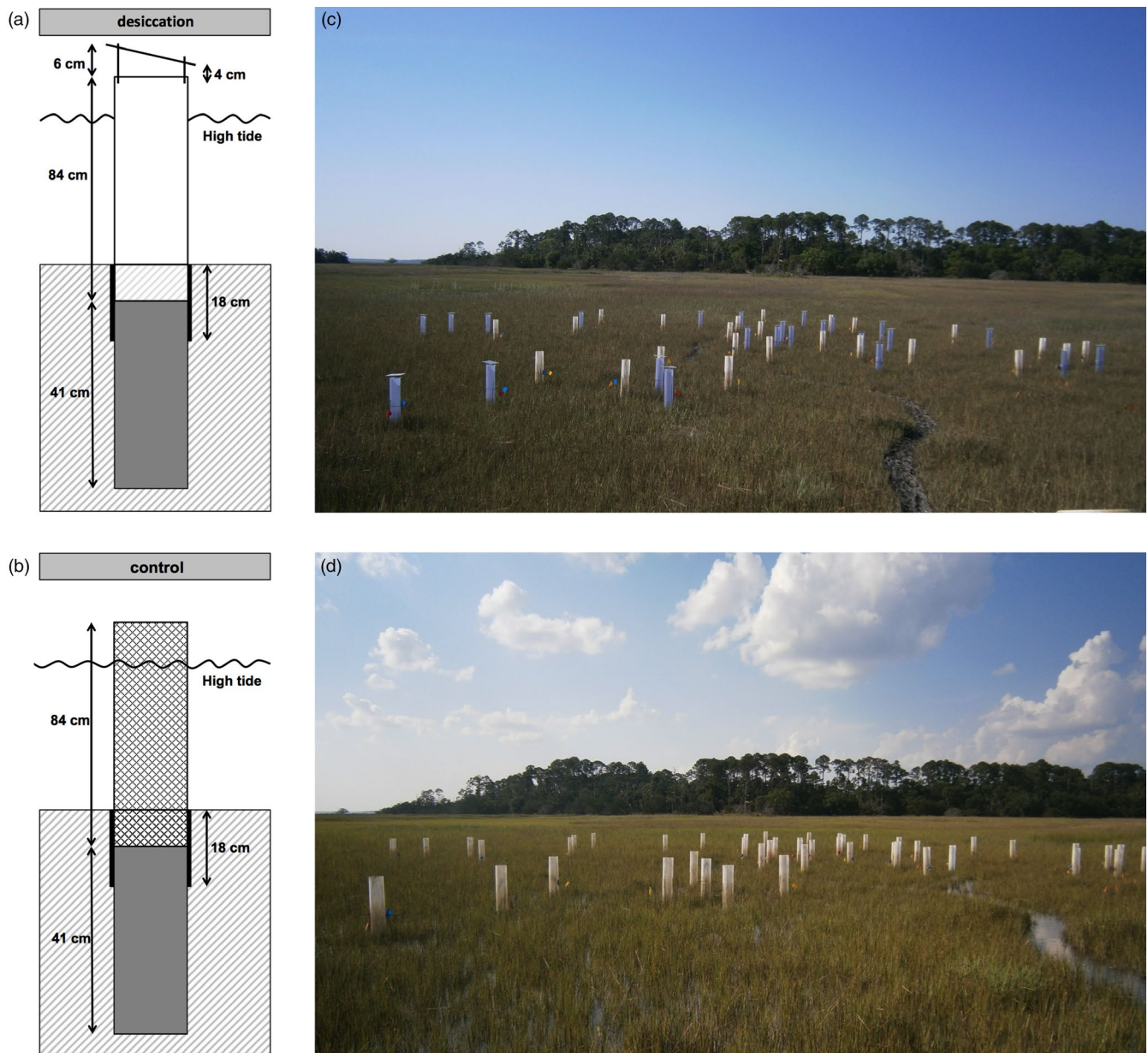


FIGURE 1 Schematic setup of desiccation and control treatments consisting of a below-ground PVC tube and an (a) above-ground transparent PVC tube and sloping roof, or (b) a Vexar permeable mesh tube. (c) Experiment during simulated desiccation event: tidal water and rain were excluded from half of the plots. (d) Experiment in between desiccation events: all plots were exposed to tidal inlet and rain [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Simulated repetitive desiccation events

During the experiment, we simulated four consecutive desiccation events. Below-ground PVC structures were left untouched for the full duration of the experiment. We started each simulated desiccation event at neap tide each month (when water tables are naturally lowest) by installing the transparent PVC chambers in desiccation treatments (Figure 1c) on top of the below-ground structures, so that plants, mussels and snails were exposed to dry and warmer conditions for a period of 10 days in May. After this period, the climate chambers were replaced by Vexar control chambers, thereby allowing rain and tidal water to re-flood the plots once more. The control chambers

were also lifted and reinstalled to correct for handling biases. This process was repeated and prolonged each month, resulting in desiccation events of 10 days in May, 12 days in June, 15 days in July and 20 days in August. Vexar and transparent PVC tubes were cleaned between each implementation to prevent shading effects from dirt or fouling. Hygrochron iButtons (Embedded Data Systems, Lawrenceburg, KY), programmed to record temperature and relative humidity every 5 min, were deployed on the marsh surface in the centre of each plot and in adjacent open field locations for 6 hr on 1 day in July.

The experimental setup was effective in simulating repetitive desiccation events. In addition to effectively preventing tidal water flooding and excluding rain, desiccation treatments raised the temperature

6°C and reduced relative humidity by 11%, on average, compared to controls ($F_{2,26} = 389.36$; $p < 0.001$ and $F_{2,26} = 50.28$; $p < 0.001$; Appendix S1). In the GCE LTER Marsh Landing weather station database, there are numerous records of >10 consecutive days (and up to 20 days) without precipitation and temperatures exceeding 6°C above the mean (i.e. >34°C with mean: 28°C) during summer months since 2003 (). Humidity in control treatments was similar to open field conditions ($p = 0.13$), while temperatures were 2°C lower in control treatments than in open field conditions ($p < 0.001$), most likely due to slight shading by the Vexar mesh. Nevertheless, even though differences between control plots and open field conditions are minor, we cannot exclude the possibility that plant growth deviated somewhat in the slightly cooler and shaded control chambers relative to ambient field conditions. We did not collect additional vegetation data from unmanipulated open field areas, as snail densities fluctuate over time in open marsh areas, and potential plots placed here would very likely experience levels of snail grazing incomparable to those imposed within the experimental treatments.

2.4 | Response variables of the desiccation events

We installed 5 cm rhizon soil moisture samplers (Rhizosphere Research Products, The Netherlands) into the top 5 cm of sediment in each plot. After each first tide that rewetted the plots following each simulated desiccation event, we connected the rhizons to 60 ml syringes to collect sediment porewater. Porewater pH and salinity were measured with a handheld multimeter (340i; WTW, Germany) connected to a pH electrode (sentix 41; WTW, Germany), and a conductivity sensor (TetraCon 325; WTW, Germany) respectively. A third porewater subsample was stored at -20°C for further analyses. In the laboratory, porewater ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were analysed on Auto Analyzer III systems (Bran and Luebbe, Norderstedt, Germany). Another portion of the porewater was diluted three times with Milli-Q water (ELGA LabWater PURELAB flex, Lane End, UK) and acidified with nitric acid (HNO_3) prior to ion- and metal-concentration measurements (sodium, aluminium, iron and calcium) on an inductively coupled plasma emission spectrophotometer (ICP-OES, model Iris Intrepid II; Thermo Fisher Scientific, Waltham, MA).

After the final simulated desiccation event in August, mussels from each plot were collected, washed, categorised as alive or dead and as recruits (<30 mm) or adults based on their shell lengths. Above-ground biomass of cordgrass was harvested from the entire plot and rinsed with fresh water and separated in live and dead tissue. In each cordgrass sample, we recorded the number of live shoots and live tillers (new emerging shoots smaller than 5 cm). Of a subset of the plots in each treatment ($N = 3$ or 4), live root and rhizome biomass were quantified in the top 15 cm of the sediment as described by (Derksen-Hooijberg et al., 2018). Fresh tillers ($N = 5$ per plot) from each plot were pooled and stored at -20°C for measurement of the free amino acid proline, which acts as a plant osmolyte (Delauney & Verma, 1993). Briefly, samples were freeze-dried with liquid nitrogen, ground in a ball-mill and 50 mg of dried tissue was extracted in

extraction fluid. 500 ml extraction fluid consisted of 164 ml demineralized water, 336 ml ethanol, 20 ml 25% thiodiglycol and 350 mg citric acid monohydrate and 500 nmol norvaline was added as an internal standard. Samples were shaken and centrifuged and the precipitate diluted in chloroform. After the samples were shaken overnight, the supernatant was freeze-dried, diluted in ml 0.01 M HCL and filtered (Dynagard, 0.2 μm). Finally, free aminoacids were analysed after derivatization with FMOC-Cl and separation with a reversed phase column on High Pressure Liquid Chromatography system (HPLC Model Varian 920-LC, Palo Alto, CA).

2.5 | Data analyses

To assess main and interactive effects of desiccation treatment, mussels and snails on cordgrass metrics, three-way factorial ANOVAs were conducted with R statistical software version 3.1.2 (R Core Team, 2014). Effects of desiccation treatment and snails on mussel metrics were analysed with two-way factorial ANOVA's. Assumptions of heterogeneity of variances and normality of the residuals were checked and if found unsatisfactory, data were Box-Cox transformed. Repetitive data (salinity, pH and metal concentrations in sediment porewater) were analysed in a repeated measures design using 'ez' package in R. Sphericity was checked with Mauchly's Test and if violated, Greenhouse-Geisser corrections were applied. Four experimental plots were excluded from the final data analyses: three units were excluded because the number of cordgrass stems declined by over 50% within the first few weeks, unrelated to treatment and presumably caused by damage during construction, and one climate plot was excluded due to tidal water leaking into the plot. Final number of replicates per treatment were: (Desiccation [D], Control [C], Mussels [M], no Mussels [nM], Snails [S] and no Snails [nS]): D M S = 6, D M nS = 5, D nM S = 5, D nM nS = 6, C M S = 5, C M nS = 5, C nM S = 6, C nM nS = 6, totalling 44 experimental plots.

3 | RESULTS

3.1 | Sediment porewater and cordgrass chemistry

The desiccation treatment greatly increased potential chemical stress in sediment porewater for cordgrass. Over the course of the four simulated desiccation events, porewater salinity almost doubled compared to control treatments ($F_{1,36} = 348.1$; $p < 0.001$; Figure 2a). Mussel presence reduced salinity ($F_{1,36} = 344.6$; $p < 0.001$), interacting with desiccation ($F_{1,36} = 171.4$; $p < 0.001$). Mussel presence completely buffered salinity effects of the desiccation treatment resulting in similar average salinities (28 ppt) in the 'climate + mussel', the 'control + mussel' and the 'control + no mussel' treatments, whereas in 'climate + no mussel treatment' salinities reached 53 ppt on average. Snail presence did not affect salinity.

Similar to salinity, desiccation treatment, mussel presence and their interaction strongly influenced porewater pH ($F_{1,36} = 136.6$; $p < 0.001$, $F_{1,36} = 11.4$; $p < 0.001$ and $F_{1,36} = 14.2$; $p < 0.001$ respectively; Figure 2b). In control treatments, mussel presence did not

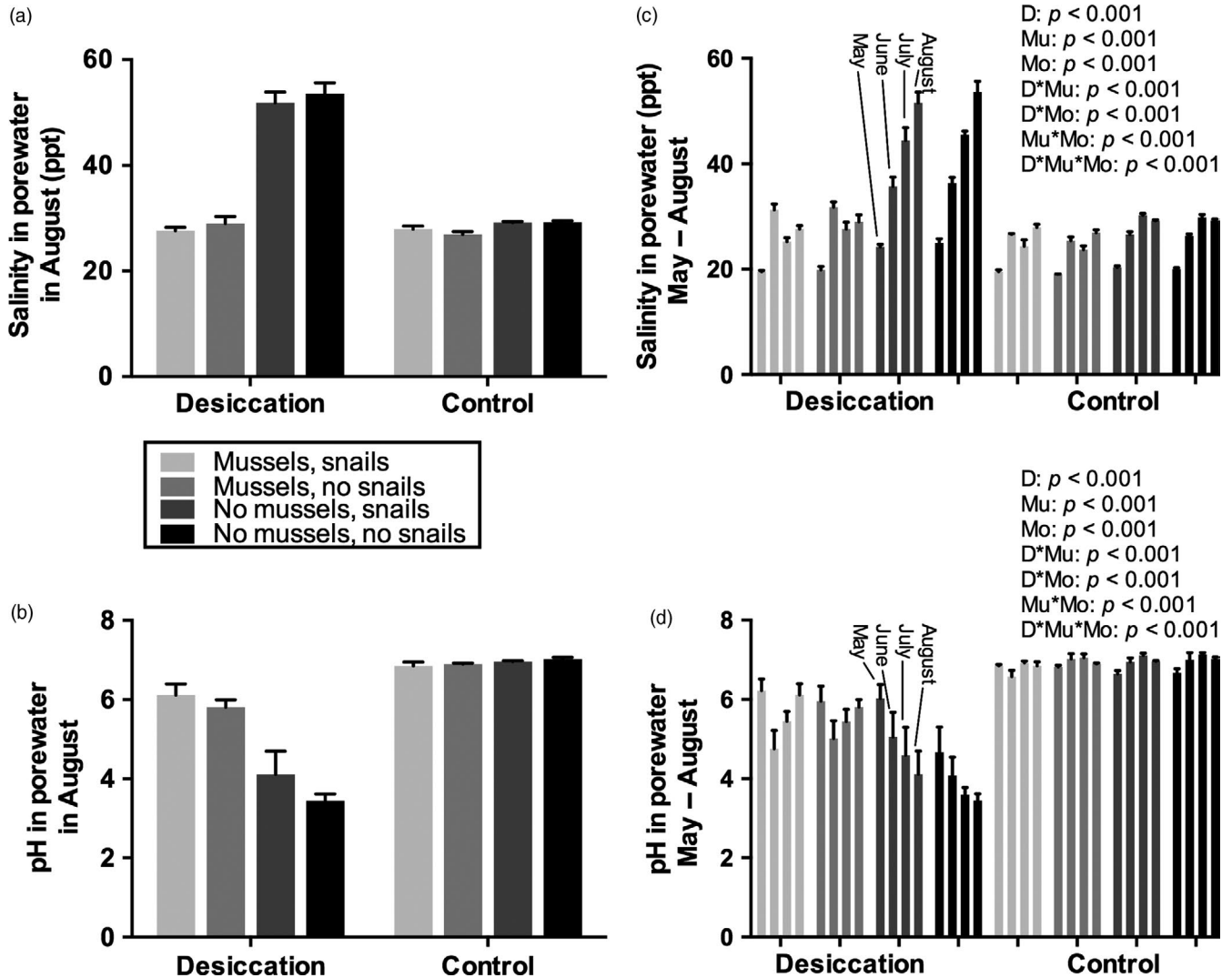


FIGURE 2 (a, b) Salinity and pH in the porewater of the top 5 cm of the sediment, at the end of the final desiccation event in August after 1 tide had rewetted the plots. (c, d) Salinity and pH upon rewetting after each subsequent desiccation event in May, June, July and August 2014. D, Mu and Mo represent main effects of desiccation, mussels and month and their interactions respectively. Error bars represent SE

affect pH (average pH of 7). In desiccation treatments, pH decreased strongly (pH 3.7), while mussels largely mitigated this effect (pH 6). Importantly, we observed a gradual increase in salinity and pH stress over time, which was also demonstrated by a significant three-way interaction between month, desiccation and mussels (salinity: $F_{3,108} = 47.0$; $p < 0.001$ and pH: $F_{3,108} = 6.6$; $p < 0.001$, Figure 2c,d).

As pH in the porewater declined, porewater iron (Fe) and aluminium (Al) concentrations increased. After four desiccation events, porewater Fe concentrations had strongly increased in desiccation treatments, but this effect was mitigated by mussel presence ($F_{1,36} = 285.8$; $p < 0.001$, $F_{1,36} = 19.1$; $p < 0.001$ and interaction effect: $F_{1,36} = 25.2$; $p < 0.001$; Figure 3a). In control treatments, Fe concentrations remained below 20 μM regardless of mussel presence, whereas in desiccation treatments without mussels Fe concentrations increased to 1,600 μM . Mussels strongly mitigated this desiccation effect, more than halving Fe concentrations to 650 μM . Likewise, porewater Al concentrations in August 2014 were affected by desiccation, mussels

and their interaction ($F_{1,36} = 8.8$; $p = 0.005$, $F_{1,36} = 7.3$; $p = 0.010$ and $F_{1,36} = 7.3$; $p = 0.010$; Figure 3b). We detected no Al in control treatments with and without mussels, whereas Al was high in the desiccation treatment without mussels (770 μM). This effect, however, was largely mitigated by mussel presence (35 μM). Concentrations of both Fe and Al built up in the porewater over time in desiccation treatments without mussels (Figure 3c,d), which was confirmed by a significant three-way interaction between month, desiccation and mussels (Fe: $F_{3,108} = 7.2$; $p < 0.001$ and Al: $F_{3,108} = 4.6$; $p = 0.0327$).

Interestingly, we found no increase in Fe and Al in cordgrass shoots in desiccation treatments (data not shown). Further investigation of porewater calcium concentrations in August 2014 (hereafter Ca) revealed that porewater Ca concentrations were very high, ranging between 5,000 and 15,000 μM (Appendix S2) and were at all times higher than Al concentrations with Ca:Al ratios ranging between 5 and 1,000. Finally, the concentrations of the amino acid proline measured in cordgrass leaves were increased in desiccation treatments

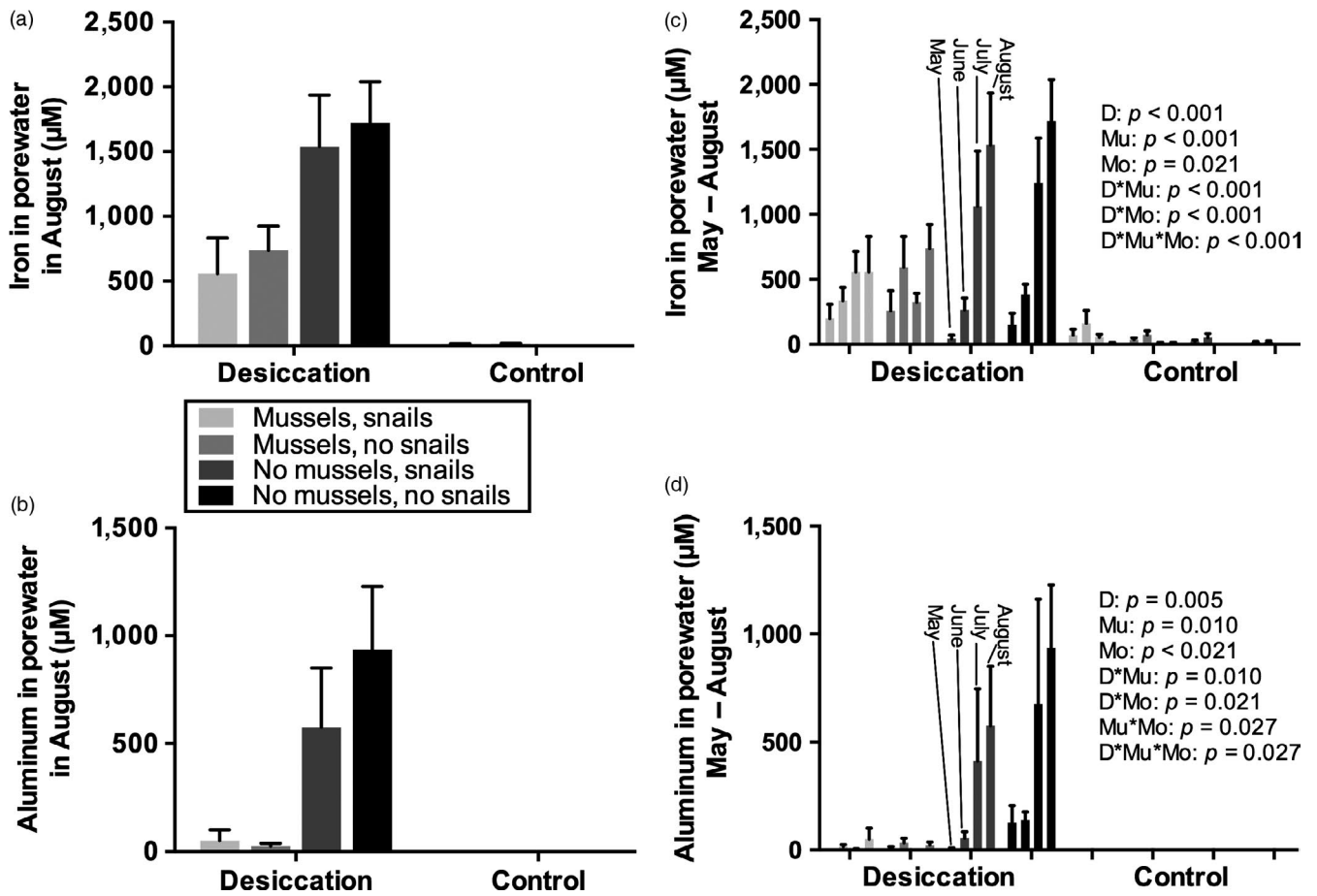


FIGURE 3 (a, b) Iron and aluminium concentrations in the porewater of the top 5 cm of the sediment, at the end of the final desiccation event in August after 1 tide had rewetted the plots. (c, d) Iron and aluminium concentrations upon rewetting after each subsequent desiccation event in May, June, July and August 2014. D, Mu and Mo represent main effects of desiccation, mussels and month and their interactions respectively. Error bars represent SE

($F_{1,36} = 70.9$; $p < 0.001$; Figure 4), indicating that the vegetation was experiencing salt and/or desiccation stress. Mussel presence interacted with desiccation ($F_{1,36} = 9.2$; $p = 0.005$), such that mussel presence only resulted in lower proline concentrations in control plots.

Desiccation and mussels both enhanced nitrogen availability in the porewater (Figure S3). Porewater ammonium concentrations almost doubled in the desiccation treatment ($F_{1,36} = 4.5$; $p = 0.042$). Mussels significantly enhanced nitrate levels ($F_{1,36} = 19.1$; $p < 0.001$), and interacted with desiccation ($F_{1,36} = 18.0$; $p < 0.001$) to increase nitrate by almost five times compared to controls. Finally, mussels also stimulated phosphorus availability in the porewater ($F_{1,36} = 14.4$; $p < 0.001$), while desiccation caused these levels to drop to almost zero across all other treatments ($F_{1,36} = 60.1$; $p < 0.001$).

3.2 | Cordgrass and mussels

At the time of harvest, live above-ground biomass of cordgrass was doubled by mussel presence ($F_{1,36} = 97.375$; $p < 0.001$; Figure 5a), while no effects of desiccation treatment or snails were found ($F_{1,36} = 2.688$; $p = 0.11$ and $F_{1,36} = 0.042$; $p = 0.839$). Desiccation treatment, however, reduced the number of live cordgrass stems by

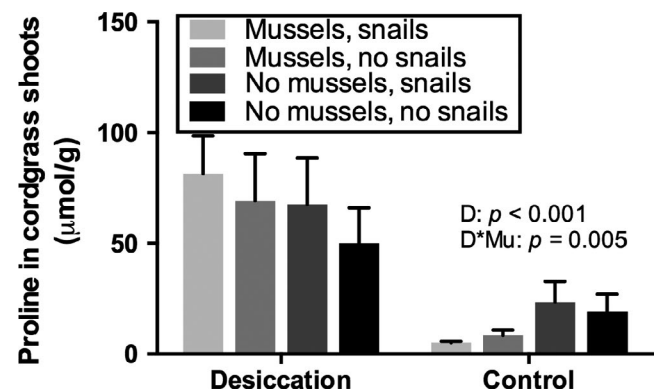


FIGURE 4 Proline concentrations in cordgrass shoots (tillers) at the end of the final desiccation event in August. D and Mu represent main effects of desiccation, mussels and their interactions respectively. Error bars represent SE

13% compared to control plots ($F_{1,36} = 11.3$; $p = 0.002$; Figure 5c). Snails also reduced live stem density by 11% ($F_{1,36} = 5.9$; $p = 0.023$), whereas mussel presence enhanced the number of stems by 24% ($F_{1,36} = 68.5$; $p < 0.001$). Furthermore, we found an interaction

between mussels and snails ($F_{1,36} = 5.2$; $p = 0.029$), wherein the negative effects of snails were more pronounced in plots with mussels compared to plots without mussels. Desiccation effects were even more distinct in the number of cordgrass tillers, which were reduced by 40% ($F_{1,36} = 16.1$; $p < 0.001$; Figure 5d). Mussel presence enhanced tiller density ($F_{1,36} = 6.9$; $p = 0.012$), but only in control treatments (interaction effect, $F_{1,36} = 6.0$; $p = 0.019$). Mussel treatments increased below-ground biomass (roots and rhizomes summed) by 94% ($F_{1,36} = 68.5$; $p < 0.001$), while it was reduced by 16% in desiccation treatments ($F_{1,36} = 7.4$; $p = 0.012$; Figure 2b) and reduced by 17% in snail treatments ($F_{1,36} = 5.9$; $p = 0.023$). Finally, the number of adult mussels found in the plots did not differ between treatments, while recruitment was decreased by over 50% in the desiccation treatment, presumably due to a shortened settlement period caused by periodic tidal exclusion and/or desiccation stress (see Appendix S4).

4 | DISCUSSION

Recent work revealed that ribbed mussels are able to mitigate desiccation stress by enhancing water storage and reducing salinity

(Angelini et al., 2016). In contrast, grazing activity by marsh periwinkle snails dramatically aggregates stress during severe desiccation events (Silliman & Newell, 2003; Silliman & Zieman, 2001). Here, we experimentally demonstrate that, although mussels were able to strongly mitigate chemical stressors within the sediment, they are not able to sufficiently buffer the effects of relatively short, but repetitive desiccation events. Even though cordgrass appeared healthy above-ground after the four events, our field experiment revealed that the desiccation treatment resulted in osmotic stress demonstrated by increased proline levels in leaves, and had important negative effects on cordgrass by reducing below-ground biomass and decreasing the numbers of live shoots and tillers.

4.1 | Desiccation effects

Compared to unmanipulated open conditions, Vexar-enclosed controls may have experienced somewhat reduced evaporation due to slightly lower temperatures. Despite this experimental limitation, however, salinity remained around 30 ppt in the control plots, which is common for this area (Angelini et al., 2016). Our simulated desiccation events probably underestimated shifts in physical stress

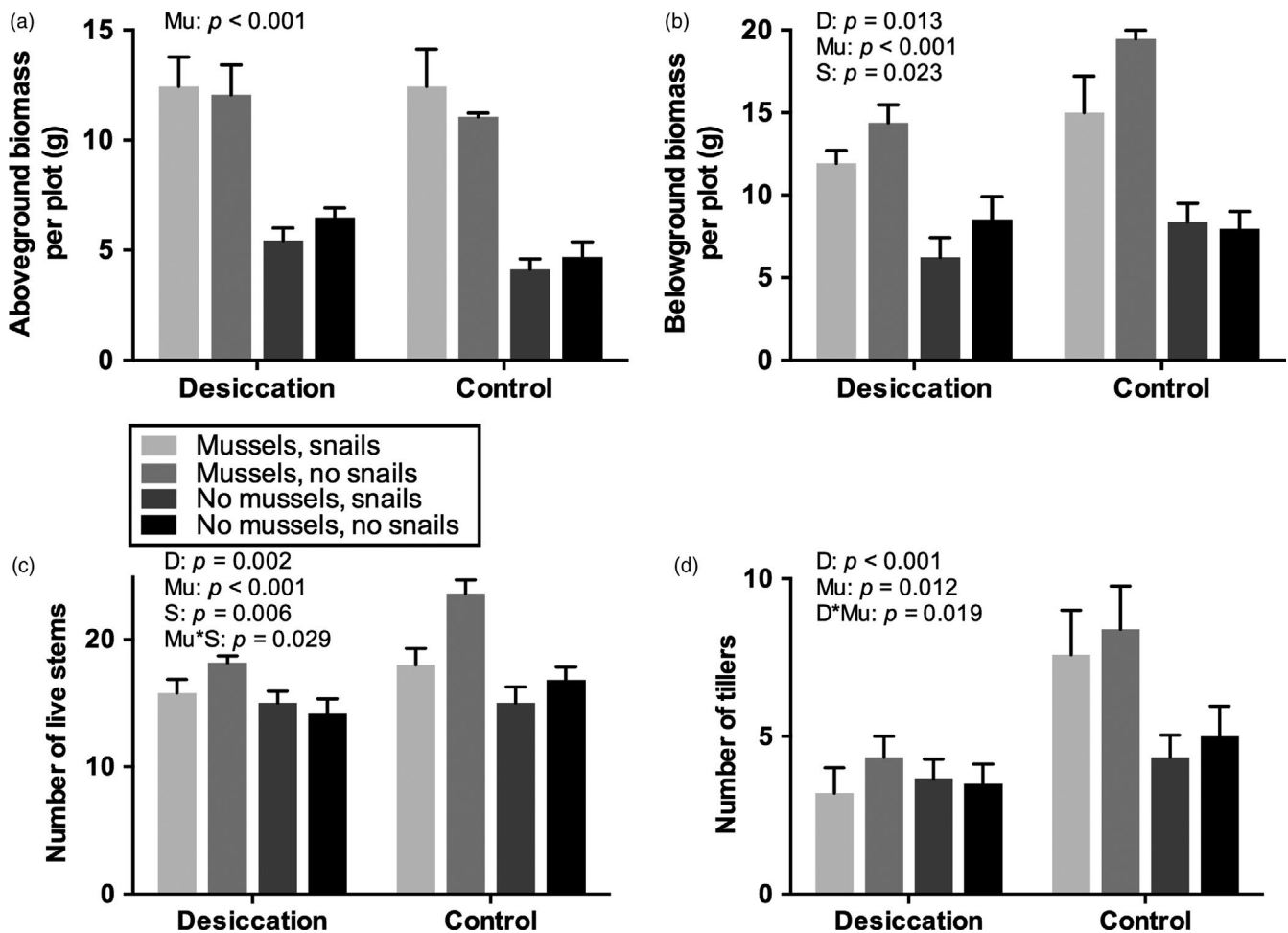


FIGURE 5 Cordgrass above-ground biomass (a), below-ground biomass (roots and rhizomes) (b), number of live stems (c) and number of tillers (d) in plots exposed to desiccation or control conditions, with and without mussels and with and without snails. D, μ and S represent main effects of desiccation, mussels, snails and their interactions respectively. Error bars represent SE

associated with real dry spells occurring in the field that coincide with neap tides in a natural setting. In particular, the climate tubes obstructed wind action, thereby decreasing air exchange and slowing down soil drying and direct desiccation of the vegetation. Nonetheless, porewater analyses showed that chemical stressors increased at each subsequent desiccation event of increasing length, resulting in sublethal salinities for cordgrass, low pH values and high porewater Fe and Al concentrations, confirming findings from earlier work (Angelini et al., 2016; McKee et al., 2004; Silliman et al., 2005). In addition, however, our findings also demonstrate that dissolved nitrogen and phosphorus levels are also significantly affected. Specifically, we found that desiccation greatly stimulated ammonium availability, and in the presence of mussels, also nitrate, indicating that the drying out of the marsh soil increased decomposition rates likely due to increasing oxygen availability. In contrast, dissolved phosphorus was reduced, most likely because phosphate precipitated with iron (iii) in the dried, oxidised soils (Smolders et al., 2006).

4.2 | Mussels and desiccation

Ribbed mussels strongly mitigated the effects of desiccation on the marsh soil; salinities in mussel plots remained similar to control levels even after four climate events. Mussels are known to reduce salinity during desiccation events by enhancing soil water content, via the additional layer on top of the sediment consisting of excreted pseudofaeces (Angelini et al., 2016). This enhanced water storage – resulting in less sediment drying, and hence less oxidation of iron-sulphide compounds and consequent H^+ release upon rewetting – may also partially explain the observed mitigation in the decline of pH (acidification) and of metal solubility. Furthermore, when these physical effects of mussel presence do not fully negate pH changes as observed, mussel shells may provide a chemical line of defence as the dissolution of calcium carbonate by the acids formed can buffer pH changes. Finally, mussels increased cordgrass biomass, thereby indirectly providing a buffer against snail herbivory damage, and demonstrating the strong resilience-enhancing potential of this mutualism. However, as mussels did not negate desiccation effects on shoot formation, as shown by the strong cordgrass tillers reduction in the desiccation treatments, our results suggest that cordgrass production and standing biomass maybe negatively impacted over longer time periods.

4.3 | Snails and desiccation

By grazing on cordgrass, snails reduced the number of live cordgrass stems, and interestingly, also decreased below-ground cordgrass biomass, whereas above-ground biomass remained unaffected. This may well be explained by cordgrass compensating for grazing pressure by allocating more resources to above-ground structures at the expense of below-ground biomass, a strategy that has been observed in the vegetation of many ecosystems (Gao et al., 2008; Ruess, Hendrick, & Bryant, 1998; Thornton & Millard, 1996; Väre, Ohtonen, & Mikkola, 1996). We, however, found no interactions

between snail grazing and desiccation, contradicting results reported by Silliman et al. (2005), who found increased negative effects of snails when cordgrass was exposed to high soil salinities. The discrepancy in results may be explained by the difference in snail densities. While moderate densities of snails were used in our study (250 snails/m²), the aforementioned study investigated a more extreme scenario, testing dieback situations where large densities of snails congregate (400–2,600 snails/m²). Nevertheless, snails did affect cordgrass even in these modest densities, acting as a subtle additive stressor to the repetitive desiccation treatments.

4.4 | Metals and proline in cordgrass shoots

As metal toxicity has been proposed as a factor contributing to desiccation stress-related sudden dieback events (McKee et al., 2004; Palomo et al., 2013) we examined if this metric would play a role in a moderate but repetitive desiccation scenario. Indeed, at the end of our experiment, we found high porewater Fe and Al concentrations in desiccation treatments without mussels. However, we observed no increases in their concentrations in cordgrass tissue, and no signs of Al or Fe toxicity were observed by visually inspecting cordgrass leaves. As the main symptom of Al toxicity in plants is the inhibition of root growth (Kochian, 1995; Rout, Samantaray, & Das, 2001), and root biomass decreased in desiccation treatments, we scanned cordgrass roots to inspect for signs of aluminium toxicity – that is, lateral roots becoming thickened and brown and lack fine branching (Rout et al., 2001). Although roots in the top layer of soil were rust coloured in desiccation treatments indicating the formation of oxidised iron-plaques vs. off-white coloured in controls (Derksen-Hooijberg et al., 2018; Mendelsohn & Morris, 2002), we found no pronounced shifts in root morphology. Hence, metal toxicity was presumably not a strong contributing factor to the observed negative effects on cordgrass in our experiment. A possible explanation may be found in the short exposure time of cordgrass to this stressor. Metals would become available for uptake for cordgrass after each simulated climate event ended and water re-flooded the plots. However, accumulated acid and metals are likely to have been diluted after a few tides inundated the plots, leaving a narrow window for acute toxicity to occur. Furthermore, a second explanation may be found in the observed high Ca concentrations in sediment porewater, as high concentrations of bivalent base cations such as Ca^{2+} and Mg^{2+} can negate Al^{3+} uptake and toxicity effects in plants (De Graaf, Bobbink, Verbeek, & Roleofs, 1997; Kochian, 1995).

Contrary to the results on plant metal concentration, we observed an increased stress response to desiccation by cordgrass in a fourfold increase in proline concentrations in cordgrass tiller leaves. Importantly, mussels did not ameliorate the build-up of proline even though they strongly mitigated porewater salinity increases in desiccation treatments. Cordgrass can accumulate sodium ion (Na^+) in its leaves and excrete excess salts through salt glands (Bradley & Morris, 1991) and can therefore grow well in environments exposed to moderate salinities (<35 ppt), although lower salinities result in increased biomass production (Brown, Pezeshki, & DeLaune, 2006;

Vasquez, Glenn, Guntenspergen, Brown, & Nelson, 2006). Proline accumulation can be a sign of salt, drought, higher temperatures and other physical stresses (Verbruggen & Hermans, 2008), and mussels did not negate proline build-up. As proline levels were also raised in (drought × mussel) where salinity was at control levels, it is likely that in our experiment the increased temperature, rather than salt stress, provoked the increased accumulation of proline in cordgrass leaves, demonstrating that the plants were indeed stressed.

4.5 | Ecosystem resilience

The results from our experiment suggest that desiccation events of a moderate but repetitive nature may pose a risk to the long-term persistence of cordgrass in these systems. For instance, the observed reduction in root biomass indicates a downward spiral: as cordgrass is a perennial plant, its potential to cope with future climate event may be compromised, as it will have less root and rhizome biomass available for water uptake. Likewise, the severe reductions in cordgrass' remaining tillers indicate that cordgrass' ability to generate new shoots was already compromised after these four short, but consecutive desiccation events, potentially leading to more pronounced declines in biomass in subsequent months or years. Such a desiccation-induced gradual decline in cordgrass biomass was furthermore recently found by a 28-year analysis with remote sensing techniques (O'Donnell & Schalles, 2016).

Cordgrass' facultative mutualist ribbed mussel is known to enhance the persistence of southeastern US salt marshes, and also aid in the natural and designed (transplanted) recovery of degraded marshes (Angelini et al., 2015, 2016; Bertness, Brisson, & Crotty, 2015; Derksen-Hooijberg et al., 2018). However, our experiment demonstrates the first signs of a limitation to the buffering capacity of ribbed mussels, shown by the inability of mussels to negate the build-up of proline and reduction in cordgrass tillers. It seems that the mutualism is able to buffer short bursts of stress, but reaches its limits as climate perturbations progress with climatic changes. Similar cumulative processes can be observed in other ecosystems dominated by mutualism-dependent foundation species. Examples are for instance the mass bleaching events in coral-zooxanthellae mutualisms (Hoegh-Guldberg et al., 2007), and the accelerated seagrass collapse in seagrass-lucinidae clam mutualism systems (de Fouw et al., 2016). Overall, these findings illustrate that it is of vital importance to understand the resistance of such mutualisms to climate events. We suggest that proxies for physiological stress as found in our experiment may serve as valuable early warning indicators for loss of resilience and imminent ecosystem degradation.

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AUTHORS' CONTRIBUTIONS

M.D.-H., T.v.d.H., J.R.H.H. and C.A. designed the experiment; M.D.-H., C.A., T.v.d.H., J.R.H.H., L.P.M.L., A.S., A.B., S.F.H. and L.L.G. conducted the field experiment; M.D.-H., J.R.H.H. and T.v.d.H. analysed the data; M.D.-H. wrote the first draft of the manuscript, all authors contributed to revisions and gave approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6h0k74n> (Derksen-Hooijberg et al., 2019).

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REFERENCES

- Alber, M., Swenson, E. M., Adamowicz, S. C., & Mendelssohn, I. A. (2008). Salt Marsh Dieback: An overview of recent events in the US. *Estuarine, Coastal and Shelf Science*, 80, 1–11. <https://doi.org/10.1016/j.ecss.2008.08.009>
- Angelini, C., Griffin, J. N., van de Koppel, J., Lamers, L. P. M., Smolders, A. J. P., Derksen-Hooijberg, M., ... Silliman, B. R. (2016). A key-stone mutualism underpins resilience of a coastal ecosystem to drought. *Nature Communications*, 7, 12473. <https://doi.org/10.1038/ncomms12473>
- Angelini, C., van der Heide, T., Griffin, J. N., Morton, J. P., Derksen-Hooijberg, M., Lamers, L. P. M., ... Silliman, B. R. (2015). Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. *Proceedings of the Royal Society B*, 282, 20150421. <https://doi.org/10.1098/rspb.2015.0421>
- Báez, S., Collins, S. L., Pockman, W. T., Johnson, J. E., & Small, E. E. (2013). Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. *Oecologia*, 172, 1117–1127. <https://doi.org/10.1007/s00442-012-2552-0>
- Bertness, M. D., Brisson, C. P., & Crotty, S. M. (2015). Indirect human impacts turn off reciprocal feedbacks and decrease ecosystem resilience. *Oecologia*, 178, 231–237. <https://doi.org/10.1007/s00442-014-3166-5>
- Bradley, P. M., & Morris, J. T. (1991). Relative importance of ion exclusion, secretion and accumulation in *Spartina alterniflora* Loisel. *Journal of Experimental Botany*, 42, 1525–1532. <https://doi.org/10.1093/jxb/42.12.1525>
- Brown, C., Pezeshki, S., & DeLaune, R. (2006). The effects of salinity and soil drying on nutrient uptake and growth of *Spartina alterniflora* in a simulated tidal system. *Environmental and Experimental Botany*, 58, 140–148. <https://doi.org/10.1016/j.envexpbot.2005.07.006>
- Davidson, A., Griffin, J. N., Angelini, C., Coleman, F., Atkins, R. L., & Silliman, B. R. (2015). Non-consumptive predator effects intensify grazer-plant interactions by driving vertical habitat shifts. *Marine Ecology Progress Series*, 537, 49–58. <https://doi.org/10.3354/meps11419>
- de Fouw, J., Govers, L. L., van de Koppel, J., van Belzen, J., Dorigo, W., Cheikh, M. A. S., ... Piersma, T. (2016). Drought, mutualism breakdown, and landscape-scale degradation of seagrass beds. *Current Biology*, 26, 1051–1056. <https://doi.org/10.1016/j.cub.2016.02.023>

- De Graaf, M. C., Bobbink, R., Verbeek, P. J., & Roleofs, J. G. (1997). Aluminium toxicity and tolerance in three heathland species. *Water, air, and soil pollution*, 98, 229–239. <https://doi.org/10.1007/BF02047036>
- Delauney, A. J., & Verma, D. P. S. (1993). Proline biosynthesis and osmoregulation in plants. *The Plant Journal*, 4, 215–223. <https://doi.org/10.1046/j.1365-313X.1993.04020215.x>
- Derksen-Hooijberg, M., Angelini, C., Hoogveld, J. R. H., Lamers, L. P. M., Borst, A., Smolders, A., ... van der Heide, T. (2019). Data from: Repetitive desiccation events weaken a salt marsh mutualism. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.6h0k74n>
- Derksen-Hooijberg, M., Angelini, C., Lamers, L. P. M., Borst, A., Smolders, A., Hoogveld, J. R. H., ... van der Heide, T. (2018). Mutualistic interactions amplify salt marsh restoration success. *Journal of Applied Ecology*, 55, 405–414. <https://doi.org/10.1111/1365-2664.12960>
- Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., & Collins, S. L. (2003). Productivity responses to altered rainfall patterns in a C4-dominated grassland. *Oecologia*, 137(2), 245–251. <https://doi.org/10.1007/s00442-003-1331-3>
- Fejtel, T. C., DeLaune, R. D., & Patrick, W. H. (1988). Biogeochemical control on metal distribution and accumulation in Louisiana sediments. *Journal of Environmental Quality*, 17, 88–94. <https://doi.org/10.2134/jeq1988.00472425001700010013x>
- Gao, Y. Z., Giese, M., Lin, S., Sattelmacher, B., Zhao, Y., & Brueck, H. (2008). Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. *Plant and Soil*, 307, 41–50. <https://doi.org/10.1007/s11104-008-9579-3>
- GCE LTER Data Portal. Georgia coastal ecosystem long term ecological research data portal. Retrieved from <https://gce-lter.marsci.uga.edu/portal/>
- Gedan, K., & Silliman, B. (2009). Patterns of salt marsh loss within coastal regions of North America: Presettlement to present. In B. R. Silliman, E. D. Grosholz, & M. D. Bertness (Eds.), *Human impacts on salt marshes: A global perspective* (pp. 253–266). Berkeley, CA: University of California Press.
- Grimm, N. B., Chapin, F. S., Bierwagen, B., Gonzalez, P., Groffman, P. M., Luo, Y., ... Raymond, P. A. (2013). The impacts of climate change on ecosystem structure and function. *Frontiers in Ecology and the Environment*, 11, 474–482. <https://doi.org/10.1890/120282>
- Hansen, J., Sato, M., & Ruedy, R. (2012). Perception of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 109, E2415–E2423. <https://doi.org/10.1073/pnas.1205276109>
- He, Q., Silliman, B. R., Liu, Z., & Cui, B. (2017). Natural enemies govern ecosystem resilience in the face of extreme droughts. *Ecology Letters*, 20(2), 194–201. <https://doi.org/10.1111/ele.12721>
- Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... Hatzioioli, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, 318, 1737–1742. <https://doi.org/10.1126/science.1152509>
- Hughes, A. L. H., Wilson, A. M., & Morris, J. T. (2012). Hydrologic variability in a salt marsh: Assessing the links between drought and acute marsh dieback. *Estuarine, Coastal and Shelf Science*, 111, 95–106. <https://doi.org/10.1016/j.ecss.2012.06.016>
- IPCC, Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., ... Miller, H. (Eds.) (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. Chapter 11. Regional climate projections*, 996 pp. Cambridge: Cambridge University Press.
- Jentsch, A., & Beierkuhnlein, C. (2008). Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. *Comptes Rendus Geoscience*, 340, 621–628. <https://doi.org/10.1016/j.crte.2008.07.002>
- Kochian, L. V. (1995). Cellular mechanisms of aluminum toxicity and resistance in plants. *Annual review of plant biology*, 46, 237–260. <https://doi.org/10.1146/annurev.pp.46.060195.001321>
- Li, S. G., Harazonob, Y., Oikawa, T., Zhaoc, H. L., He, Z. Y., & Chang, X. L. (2000). Grassland desertification by grazing and the resulting micrometeorological changes in Inner Mongolia. *Agricultural and Forest Meteorology*, 102, 125–137. [https://doi.org/10.1016/S0168-1923\(00\)00101-5](https://doi.org/10.1016/S0168-1923(00)00101-5)
- Li, X., Wen, B., & Yang, F. (2017). Effects of alternate flooding-drought conditions on degenerated *Phragmites australis* salt marsh in Northeast China. *Restoration Ecology*, 25(5), 810–819. <https://doi.org/10.1111/rec.12500>
- McKee, K. L., Mendelssohn, I. A., & Materne, M. D. (2004). Acute salt marsh dieback in the Mississippi River deltaic plain: A drought-induced phenomenon? *Global Ecology and Biogeography*, 13, 65–73. <https://doi.org/10.1111/j.1466-882X.2004.00075.x>
- Mendelssohn, I. A., & Morris, J. T. (2002). Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. In M. P. Weinstein, & D. A. Kreeger (Eds.), *Concepts and controversies in tidal marsh ecology* (pp. 59–80). Dordrecht, the Netherlands: Springer.
- Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: Wetlands and water*. Washington, DC: World Resources Institute.
- Myhre, G., Shindell, D., Bréon, F.-M., Collins, W., Fuglestvedt, J., Huang, J., ... Zhang, H. (2013). Anthropogenic and natural radiative forcing. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 658–740). Cambridge, UK and New York, NY: Cambridge University Press.
- Nordstrom, D. K. (1982). Aqueous pyrite oxidation and the consequent formation of secondary iron minerals. In J. A. Kittrick, D. S. Fanning, & L. R. Hossner (Eds.), *Acid sulfate weathering* (pp. 37–56). Madison, WI: Soil Science Society of America.
- O'Donnell, J., & Schalles, J. (2016). Examination of abiotic drivers and their influence on *Spartina alterniflora* biomass over a twenty-eight year period using Landsat 5 TM satellite imagery of the Central Georgia Coast. *Remote Sensing*, 8, 477. <https://doi.org/10.3390/rs8060477>
- Palomo, L., Meile, C., & Joye, S. B. (2013). Drought impacts on biogeochemistry and microbial processes in salt marsh sediments: A flow-through reactor approach. *Biogeochemistry*, 112, 389–407. <https://doi.org/10.1007/s10533-012-9734-z>
- R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>
- Rout, G., Samantaray, S., & Das, P. (2001). Aluminium toxicity in plants: A review. *Agronomie*, 21, 3–21. <https://doi.org/10.1051/agro:2001105>
- Ruess, R. W., Hendrick, R. L., & Bryant, J. P. (1998). Regulation of fine root dynamics by mammalian browsers in early successional Alaskan taiga forests. *Ecology*, 79, 2706–2720. [https://doi.org/10.1890/0012-9658\(1998\)079\[2706:rofrdb\]2.0.co;2](https://doi.org/10.1890/0012-9658(1998)079[2706:rofrdb]2.0.co;2)
- Silliman, B. R., & Newell, S. Y. (2003). Fungal farming in a snail. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 15643–15648. <https://doi.org/10.1073/pnas.2535227100>
- Silliman, B. R., van de Koppel, J., Bertness, M. D., Stanton, L. E., & Mendelssohn, I. A. (2005). Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science*, 310, 1803–1806. <https://doi.org/10.1126/science.1118229>
- Silliman, B. R., & Zieman, J. C. (2001). Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology*, 82, 2830–2845. [https://doi.org/10.1890/0012-9658\(2001\)082\[2830:tdcosa\]2.0.co;2](https://doi.org/10.1890/0012-9658(2001)082[2830:tdcosa]2.0.co;2)

- Silliman, B. R., Schrack, E., He, Q., Cope, R., Santoni, A., van der Heide, T., ... van de Koppel, J. (2015). Facilitation shifts paradigms and can amplify coastal restoration efforts. *Proceedings of the National Academy of Sciences*, 112(46), 14295–14300. <https://doi.org/10.1073/pnas.1515297112>.
- Smith, M. D. (2011). The ecological role of climate extremes: Current understanding and future prospects. *Journal of Ecology*, 99, 651–655. <https://doi.org/10.1111/j.1365-2745.2011.01833.x>
- Smolders, A. J. P., Moonen, M., Zwaga, K., Lucassen, E. C. H. E. T., Lamers, L. P. M., & Roelofs, J. G. M. (2006). Changes in pore water chemistry of desiccating freshwater sediments with different sulphur contents. *Geoderma*, 132, 372–383. <https://doi.org/10.1016/j.geoderma.2005.06.002>
- Thomey, M. L., Collins, S. L., Friggens, M. T., Bron, R. F., & Pockman, W. T. (2014). Effects of monsoon precipitation variability on the physiological response of two dominant C₄ grasses across a semi-arid ecotone. *Oecologia*, 176(3), 751–762. <https://doi.org/10.1007/s00442-014-3052-1>
- Thornton, B., & Millard, P. (1996). Effects of severity of defoliation on root functioning in grasses. *Journal of Range Management*, 49, 443–447. <https://doi.org/10.2307/4002927>
- Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348, 571–573. <https://doi.org/10.1126/science.aaa4984>
- van der Heide, T., Govers, L. L., de Fouw, J., Olff, H., van der Geest, M., van Katwijk, M. M., ... Smolders, A. J. (2012). A three-stage symbiosis forms the foundation of seagrass ecosystems. *Science*, 336, 1432–1434. <https://doi.org/10.1126/science.1219973>
- Väre, H., Ohtonen, R., & Mikkola, K. (1996). The effect and extent of heavy grazing by reindeer in oligotrophic pine heaths in northeastern Fennoscandia. *Ecography*, 19, 245–253. <https://doi.org/10.1111/j.1600-0587.1996.tb01251.x>
- Vasquez, E. A., Glenn, E. P., Guntenspergen, G. R., Brown, J. J., & Nelson, S. G. (2006). Salt tolerance and osmotic adjustment of *Spartina alterniflora* (Poaceae) and the invasive M haplotype of *Phragmites australis* (Poaceae) along a salinity gradient. *American Journal of Botany*, 93, 1784–1790. <https://doi.org/10.3732/ajb.93.12.1784>
- Verbruggen, N., & Hermans, C. (2008). Proline accumulation in plants: A review. *Amino Acids*, 35, 753–759. <https://doi.org/10.1007/s00726-008-0061-6>

SUPPORTING INFORMATION

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