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Water column ammonium concentration and salinity influence nitrogen uptake and growth of *Spartina alterniflora*

Rachel M. MacTavish *, Risa A. Cohen

Department of Biology, Georgia Southern University, PO Box 8042-1, Statesboro, GA 30460, USA

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ABSTRACT

Salt marsh macrophytes, such as *Spartina alterniflora*, play a critical role in uptake and transformation of inorganic nitrogen before it reaches coastal waters, but it may be possible to exceed *S. alterniflora* nitrogen uptake capacity, particularly when salinity is elevated. While it is well known how inorganic nitrogen availability or salinity influences *S. alterniflora* nitrogen uptake individually, investigating the combined effects of both factors is essential because changes in inorganic nitrogen supply often occur simultaneously with altered freshwater flow. Nitrogen uptake and growth responses of *Spartina alterniflora* to inorganic nitrogen (0, 10, or 100 μM ammonium, NH_4^+) and salinity (20, 30, or 40) treatments were measured in greenhouse microcosms with tidal simulation. Water column NH_4^+ uptake decreased as salinity increased with the addition of 10 μM NH_4^+ after 48 h. In contrast, with 100 μM NH_4^+ addition uptake rates were twice as high in the lowest (20) and highest (40) salinity compared to the mid-level (30) salinity treatment. After 6 months, above and belowground *S. alterniflora* plant tissue NH_4^+ uptake ($\delta^{15}N$) decreased by 50% with increasing salinity across all NH_4^+ addition treatments. Furthermore, at the highest salinity, above and belowground biomass, stem density and culm height were greater in the 10 μM NH_4^+ addition compared to the 0 and 100 μM NH_4^+ addition, indicating potential for low-level NH_4^+ additions to mitigate salinity-induced stress. Overall the effects of salinity on *S. alterniflora* nitrogen uptake and biomass generally outweighed those of water column N concentration, suggesting the interaction of salinity and nutrient loading should be considered when developing predictive models for the fate of coastal ecosystems under changing environmental conditions.

1. Introduction

Increasing human pressure on estuaries worldwide underscores the importance of investigating the effects of nitrogen loads and salinity on salt marsh function (Scavia et al., 2002; Flemer and Champ, 2006). Nutrient loading to coastal waters is still on the rise (Verity, 2002; Weston et al., 2009). In addition, dams, hydroelectric plants, and freshwater diversions that are likely a function of agriculture influence salinity regimes by altering freshwater supply to the coast (Rodriguez et al., 2001; Acharyya et al., 2012). Further, anthropogenic activities coupled with rising sea levels are predicted to increase nutrient delivery, change coastal salinity regimes and marsh structural morphology, subsequently altering valuable nutrient retention services provided by tidally influenced marshes along the coast (Craft et al., 2009; Deegan et al., 2012).

Salt marsh nutrient retention prevents excess nitrogen (N) and phosphorous (P) from reaching adjacent waters where they could otherwise accelerate coastal eutrophication resulting in an increase in algal blooms and subsequent low dissolved oxygen conditions (Nixon, 1995; Verity, 2002; Sousa et al., 2008; Verity, 2010). Nitrogen retention in temperate salt marshes occurs via microbial transformations and immobilization by plants such as the marsh macrophyte *Spartina alterniflora* (Weston et al., 2009), but plants appear to have a major role (Anderson et al., 1997). For example, *S. alterniflora* may remove >40% of available nitrogen, compared to 1–25% by denitrifiers in non-vegetated salt marsh sediments (Buresh et al., 1981; White and Howes, 1994; Drake et al., 2009). Thus the ability of a salt marsh to retain nitrogen is heavily dependent on the presence of salt marsh vegetation.

While salt marsh vegetation is typically limited by N availability in temperate salt marshes (Valiela and Teal, 1974; Pennings et al., 2005), it is possible for inorganic N loads to exceed uptake capacity on multiple time scales. Exposing *S. alterniflora* to inorganic N enrichment resulted in sequestration of a smaller fraction of the total nitrogen load than untreated plants over two days (Drake et al., 2009) and on the scale of months (Morris, 1980). Furthermore, increased ammonium (NH_4^+) export from a *S. alterniflora* dominated marsh to the overlying water column increased linearly with fertilizer additions over a 40-year study (Brin et al., 2010). This potential for export of excess nutrients from *S.*

* Corresponding author.
E-mail addresses: rmactavish@uga.edu (R.M. MacTavish), rcohen@georgiasouthern.edu (R.A. Cohen).

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alterniflora marshes to nearby coastal waters can have severe economic and ecological consequences (Scavia and Bricker, 2006; Bromberg Gedan et al., 2009).

Salinity also plays an important role in controlling *S. alterniflora* N uptake capacity (Odum, 1988; Crain, 2007), both directly and indirectly. Increased salinity reduced *S. alterniflora* ammonium uptake rates by 62% via direct competition between sodium and NH_4^+ ions at the roots in hydroponic solutions (Bradley and Morris, 1991a). Indirect inhibition of *S. alterniflora* NH_4^+ uptake can also occur due to increased dissolved sulfide concentrations and decreased water potential, growth and sexual reproduction associated with tissue damage under more saline conditions (Nestler, 1977; DeLaune et al., 1983; Touchette et al., 2009; Xiao et al., 2011). Thus, examining *S. alterniflora* N uptake in response to alterations in both nutrient concentration and salinity simultaneously is needed to determine marsh nitrogen retention capacity.

Few studies to date have specifically addressed the combined effects of water column salinity and nutrient concentrations on *S. alterniflora* N uptake and growth, but yielded different results (Haines and Dunn, 1976; Linthurst and Seneca, 1981). Using microcosms containing hydroponic solutions with elevated NH_4^+ and salinity, Haines and Dunn (1976) observed that the highest NH_4^+ concentration enhanced total *S. alterniflora* dry weight, but only at low and intermediate salinities. In contrast, Linthurst and Seneca (1981) found that *S. alterniflora* transplanted to NH_4^+ enriched sediment increased growth and foliar tissue N at all salinities tested. Both studies were conducted under permanently flooded conditions, but tidal influence under field conditions can result in pulsing of salinity by periodic flushing of accumulated salts, coupled with replenishment of nutrients (Smart and Barko, 1980).

The conflicting effects of NH_4^+ and salinity on *S. alterniflora* growth in the aforementioned studies were most likely due to differences in how treatment solutions were administered to the plants (hydroponics vs. sediments). Although *S. alterniflora* is capable of nitrogen uptake from both sediment and the water column (Mozdzer et al., 2011), nutrient delivery to marshes via the water is more common (Johnson et al., 2016). The presence of sediments also affects N removal via bacterial denitrification and anaerobic oxidation of NH_4^+, processes shown to be sensitive to changes in salinity and N availability (Rysgaard et al., 1999; Weston et al., 2010; Teixeira et al., 2016). Therefore, to better constrain how water column NH_4^+ and salinity influence *S. alterniflora* N uptake and growth, the aim of this study was to examine plant responses to both variables concurrently in the presence of marsh sediments under tidal conditions.

To test the hypothesis that concurrent alterations of both water column inorganic N concentration and salinity affect *S. alterniflora* N uptake and growth, a greenhouse experiment using microcosms with tidal simulation was conducted. Higher N uptake rates and more growth with increasing N concentration were predicted, while increasing salinity was anticipated to reduce *S. alterniflora* N uptake and growth. Finally, increasing N availability was expected to alleviate some of the negative effects of high salinity on *S. alterniflora*. Results from this study enhance

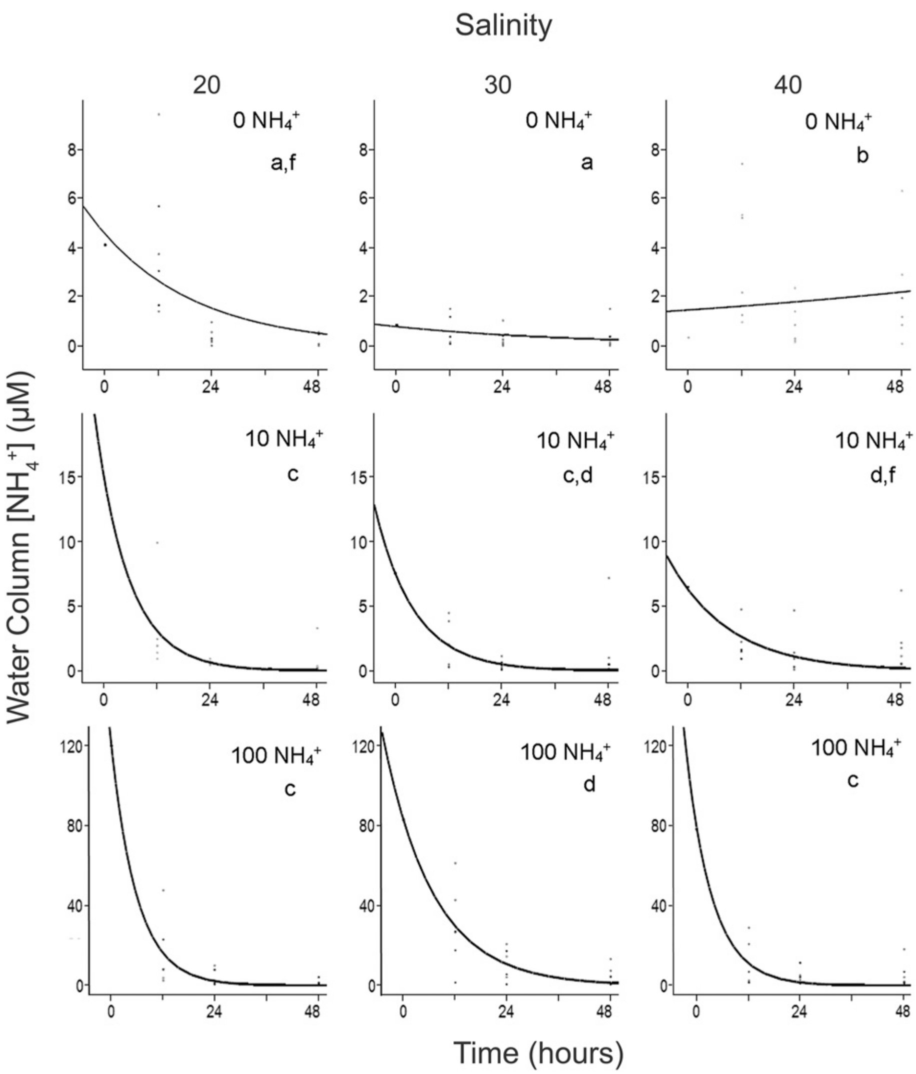

Fig. 1. Short-term water column NH_4^+ uptake by *Spartina alterniflora* over 48 h of exposure to 0, 10 or 100 μM NH_4^+ addition and salinity of 20, 30 or 40 in August 2013 (n = 6).