Oecologia (1991) 85:375–380

Oecologia

The influence of salinity on the kinetics of NH_4^+ uptake in *Spartina alterniflora*

P.M. Bradley[1] **and J.T. Morris**[1,2]

[1] Marine Science Program and [2] Department of Biological Sciences, University of South Carolina, Columbia, SC 29208, USA

Received March 14, 1990 / Accepted in revised form August 15, 1990

Summary. The effects of short- and long-term exposure to a range in concentration of sea salts on the kinetics of NH_4^+ uptake by *Spartina alterniflora* were examined in a laboratory culture experiment. Long-term exposure to increasing salinity up to 50 g/L resulted in a progressive increase in the apparent K_m but did not significantly affect V_{max} (mean $V_{max} = 4.23 \pm 1.97$ μmole·g^{-1}·h^{-1}). The apparent K_m increased in a nonlinear fashion from a mean of 2.66 ± 1.10 μmole/L at a salinity of 5 g/L to a mean of 17.56 ± 4.10 μmole/L at a salinity of 50 g/L. These results suggest that the long-term effect of exposure to total salt concentrations within the range 5–50 g/L was a competitive inhibition of NH_4^+ uptake in *S. alterniflora*. No significant NH_4^+ uptake was observed in *S. alterniflora* exposed to 65 g/L sea salts. Short-term exposure to rapid changes in salinity significantly affected both V_{max} and K_m. Reduction of solution salinity from 35 to 5 g/L did not change V_{max} but reduced K_m by 71%. However, exposing plants grown at 5 g/L salinity to 35 resulted in an decrease in V_{max} of approximately 50%. Exposure of plants grown at 35 g/L to a total sea salt concentration of 50 g/L for 48h completely inhibited uptake of NH_4^+. For both experiments, increasing salinity led to an increase in the apparent K_m similar to that found in response to long-term exposure. Our data are consistent with a conceptual model of changes in the productivity of *S. alterniflora* in the salt marsh as a function of environmental modification of NH_4^+ uptake kinetics.

Key words: NH_4^+ uptake – Nitrogen limitation – Salinity – *Spartina alterniflora* – Sea salts

Along much of the eastern and Gulf Coasts of North America, *Spartina alterniflora* varies morphologically between a tall form greater than 1 m in height, found along the margins of tidal creeks, and a short form less than 50 cm in height, found at higher elevations within the marsh. Numerous studies indicate that this gradient in plant morphology and productivity is a consequence of nitrogen limitation. Several researchers have conclusively demonstrated that the addition of nitrogen fertilizer resulted in increased height and biomass accumulation in the high marsh, short form of *S. alterniflora*, while fertilization of the tall form had no significant effect on height or productivity (eg. Broome et al. 1975; Cavalieri and Huang 1981; Gallagher 1975; Patrick and DeLaune 1976; Valiela and Teal 1974).

Various observations suggest that nitrogen limitation in *S. alterniflora* is not a function of nitrogen availability per se, but a result of the environmentally induced inhibition of the kinetics of nitrogen uptake (Chalmers 1982; Morris 1980). After 4 years of fertilization, Valiela et al. (1978) found that the short form of *S. alterniflora* increased in height and productivity, but did not attain the same height as the tall form. Secondly, in several marshes which have a gradient in plant height, interstitial NH_4^+ (the primary source of available nitrogen in salt marsh sediments: Haines et al 1977; Mendelssohn 1979; Valiela and Teal 1974) concentrations are greatest in the high marsh (DeLaune et al. 1983; Mendelssohn 1979). Further, various well-studied marsh systems have been observed to export inorganic nitrogen during the growing season (Valiela et al. 1978; Whiting et al. 1987; Woodwell et al. 1979). Consequently, it has been hypothesized that hypoxia (Bradley and Morris 1990; Morris 1980, 1984; Morris and Dacey 1984), H_2S (Bradley and Dunn 1989; Bradley and Morris 1990; DeLaune et al. 1983; King et al. 1982; Mendelssohn and McKee 1988; Morris 1980) and salinity (Cavalieri and Huang 1981; Haines and Dunn 1976; Linthurst and Seneca 1980; Morris 1980; Smart and Barko 1980) influence NH_4^+ uptake in *S. alterniflora* in the marsh. For example, both sulfide concentration and oxygen availability have been shown to influence the kinetics of NH_4^+ uptake in *S. alterniflora*. In solution culture, the maximum rate of ammonium uptake in *S. alterniflora*, V_{max}, was 37–50% (Bradley and Morris 1990; Morris and Dacey 1984) lower under hyp-

Offprint requests to: P.M. Bradley

oxic conditions in comparison to oxygen saturated treatment. Further, under hypoxia the apparent K_m, a measure of the efficiency of NH_4^+ uptake, was 2X higher (ie. uptake was less efficient) than under oxygen saturation. Increasing sulfide concentration produced a greater change in the apparent K_m and V_{max} than hypoxia alone (Bradley and Morris 1990).

Interactions between salinity and NH_4^+ uptake in *S. alterniflora* have been postulated but not verified. Morris (1984) determined that the V_{max} of NH_4^+ uptake by *S. alterniflora* in solution culture did not differ significantly for plants exposed to salinities ranging from 3–32 g/L. However, the effect of this salinity range on the apparent K_m was not investigated, and changes in K_m, not V_{max}, are indicative of such salinity effects as competitive inhibition of ion uptake. Although, several investigators have proposed that the increased Na^+ concentration associated with high salinity may competitively inhibit NH_4^+ uptake in *S. alterniflora* (eg. Chalmers 1982; Haines and Dunn 1976; Linthurst and Seneca 1981; Smart and Barko 1980; Smart 1982), *S. alterniflora* demonstrates an apparent high affinity for NH_4^+ in the presence of 350 mmoles/L Na^+ (Smart and Barko 1980). Nevertheless, the salinities investigated by Morris (3–32 g/L: 1984) and Smart and Barko (15 g/L: 1980) are not extreme for *S. alterniflora* and may not significantly affect NH_4^+ uptake kinetics. In the following study, we examined the effect on uptake of various concentrations of total dissolved salts present in marsh interstitial water. To investigate long-term effects, we measured the apparent K_m and V_{max} of plants grown at and exposed to total sea salt concentrations of 5, 20, 35, 50 and 65 g/L. Because salinity in the salt marsh can fluctuate rapidly in response to tidal flooding, evaporation and rainfall, we made limited measurements of the short-term responses of K_m and V_{max} to rapid changes in salinity.

Material and methods

Prior to the laboratory experiment, we measured the salinity of the interstitial water in a series of salinity probes placed along a transect extending from the high marsh to the creek bank at the Belle W. Baruch Marine Institute at Georgetown, SC. Salinity probes were constructed of a 10 cm length of capillary tubing (6.5 mm OD × 1.0 mm ID) capped at the aboveground end with a sleeve stopper and at the belowground end with a 1.0 mL plastic pipette tip. A 2 mL aliquot of interstitial water was drawn by syringe into the probe through a screened (250 μm mesh) port cut in the side of the pipette tip. Four replicate probes were inserted in the marsh sediment to a depth of 10 cm (roots of *S. alterniflora* are typically concentrated in the top 20 cm of sediment) at 10 m intervals from the creek bank to a distance of 100 m inland. The salinity of the interstitial water was measured with a temperature compensated refractometer (Riechert Scientific Instruments).

The relative composition of major ions in the interstitial water along the transect and the compostion of the culture solutions used in the laboratory were determined using a Dionex 2000i ion chromatograph equipped with a conductivity detector. Three replicate samples were collected, as for salinity (19/06/89), at distances of 1.5, 41.5 and 81.5 m along the transect and stored at 4° C in evacuated glass containers until analysis. Prior to analysis, samples were filtered (0.2 μm syringe filters, Gelman Sciences) and diluted 1000X with deionized distilled water. Major anions (F^-, Cl^-, Br^- and SO_4^-) were eluted with a solution of 1.8 mmoles/L Na_2CO_3 and 1.7 mmoles/L $NaHCO_3$ at a rate of 2.0 mL/min on a Dionex HPIC–AS4A separatory column equipped with a HPIC–AG4A guard column. Background conductivity was reduced with a 25 mN H_2SO_4 (2.0 mL/min) regenerated micromembrane suppressor. Major cations (Na^+, K^+, Mg^{++} and Ca^{++}) were eluted with a solution of 30 mmoles/L HCl and 6 mmoles/L diamino-propionic acid (DAP.HCl) at a rate of 1.0 mL/min on a Dionex ION PAC CS3 separatory column equipped with an ION PAC CG3 guard column. Background conductivity was reduced by a micromembrane suppressor regenerated with 100 mmoles/L tetrabutylammonium hydroxide (TBAOH).

For the uptake study, rhizomes of *S. alterniflora* were collected in May 1989 from the sandy substrate of a high marsh site located at North Inlet, SC. Rhizomes were potted in sand and placed in plastic tubs which contained sufficient dilute seawater (5 g/L) to completely cover the surface of the sand. Plants were grown under nutrient limiting conditions for 2 weeks to promote root growth. Subsequently, the solution salinity was gradually increased over a period of 1 month to give final growth salinities of 5, 20, 35, 50, and 65 g/L. Throughout this paper the salinity of culture treatments and field samples is given as g/L of total dissolved salts. The % compostion by weight of major ions is summarized in Table 1. Plants were exposed to their final growth salinity for approximately 1 month before uptake experiments were initiated.

NH_4^+ uptake rates were measured in solution culture as a function of salinity (concentration of dissolved sea salts). Healthy plants (3–7 g total dry weight) were transferred to the laboratory, washed free of sand and placed in the appropriate saline solution for a 3–4 day recovery period. For the uptake experiment, individuals were transferred to 600 mL glass chambers identical to that described in Bradley and Morris (1990). Chamber solutions consisted of seawater collected at the Belle W. Baruch Marine Lab and diluted as needed. In order to maintain the same relative composition of major ions, 50 and 65 g/L salinities were achieved by adding artificial sea salts (Dayno Mfg Inc.) to seawater. During the uptake experiment the solution pH was maintained at 6.5 ± 0.5 (± SD) and temperature at 25 ± 1° C. For all treatments, the culture solution was deoxygenated by continuously bubbling with He gas. Solution oxygen concentration was monitored periodically with a YSI model 5700 oxygen electrode and remained less than 0.05 mg/L (1.6 μmole/L 0_2) throughout the experiment. Ammonium was added to solution as $(NH_4)_2SO_4$ to give an initial NH_4^+ concentration of approximately 100 μmole/L. Uptake was measured as the decrease in NH_4^+ concentration over a period of 10–30 h. Solution samples of 2.5 mL were withdrawn periodically at 0.25–3.0 h intervals and analyzed for NH_4^+ using a colorimetric technique modified from Solarzano (1969). The plants were harvested after each experiment and dry root biomass was determined after drying 7 days at 110° C.

Table 1. Percent composition by weight (± SD) of major ions contained in the culture solutions (autoclaved seawater and artificial sea salts) and measured at the field transect (means of sites 1.5, 41.5 and 81.5 m). Differences between culture solutions and interstitial water are not significant according to the Tukey-Kramer Test ($p \leq 0.05$)

ION	CULTURE SOLUTION n = 6	INTERSTITIAL WATER n = 9
Cl^-	52.39 ± 5.09	52.20 ± 6.20
Na^+	29.46 ± 1.85	31.23 ± 0.31
$SO_4^=$	9.13 ± 1.06	9.23 ± 0.34
Mg^{++}	3.30 ± 1.35	5.06 ± 0.37
Ca^{++}	0.73 ± 0.30	0.77 ± 0.37
F^-	0.79 ± 0.62	0.40 ± 0.03
Br^-	0.68 ± 0.53	0.60 ± 0.40
K^+	0.59 ± 0.30	0.34 ± 0.20

We examined the change in the kinetics of NH_4^+ uptake by *S. alterniflora* in response to both short- and long-term exposure to a given salinity regime. To evaluate long-term responses, we followed NH_4^+ uptake by plants exposed to the salinity at which they were grown. Subsequently, uptake by plants grown at 5 g/L salinity then exposed to 35 g/L, was followed after a 10–12 h equilibration period. Similarly, plants grown at 35 g/L were allowed to equilibrate in 5 g/L for 10–12 h and then NH_4^+ uptake in 5 g/L salinity was followed. Subsequently, uptake was reevaluated at 35 g/L salinity. Finally, these plants (grown at 35 g/L) were allowed to equilibrate for 10–12 h at a salinity of 50 g/L. NH_4^+ uptake at 50 g/L was measured immediately following the 10–12 h equilibration period and again after 48 h of exposure.

Morris (1980) concluded that the Michaelis-Menten equation for enzyme kinetics adequately describes the kinetics of ammonium uptake by *S alterniflora*:

$$d[NH_4^+]/dt = \frac{-V_{max}\cdot(\text{root dry weight})\cdot[NH_4^+]}{K_m + [NH_4^+]}$$

where $d[NH_4^+]/dt$ is the rate of NH_4^+ uptake. According to this model, uptake is a function of root dry weight, NH_4^+ concentration, and two empirical parameters: V_{max} (the maximum rate of uptake expressed per g dry weight) and the apparent K_m, the half saturation constant (the substrate concentration at which the rate of uptake is 0.5 V_{max}).

The Michaelis-Menten parameters, V_{max} and K_m, for each salinity treatment were determined in a manner similar to that described previously (Bradley and Morris 1990, Classen and Barber 1974, Wilkinson 1961). Provisional estimates of the apparent K_m (μmole/L) and V_{max} (μmole·g^{-1}·h^{-1}) were determined using the method of Wilkinson (1961). Fine adjustment of the provisional estimates was made using a dynamic nonlinear parameter estimation procedure which numerically integrated the Michaelis-Menten equation and calculated the K_m and V_{max} that gave the least-squares fit to the time series of NH_4^+ concentration (Bard 1967). V_{max} and K_m were determined for 3–10 individuals per treatment and mean values of V_{max} and K_m were compared using the SAS general linear model procedure multivariate analysis of variance (MANOVA) and the Tukey-Kramer (HSD) Studentized Range Test ($p \leq 0.05$:SAS Institute 1985). The Tukey-Kramer test controls the mean experiment-wise error rate at p and is considered a conservative (ie. small Type I error rate) estimate of significant differences for unequal sample sizes (Montgomery 1984; Neter et al. 1985).

Results

The V_{max} of plants grown at treatment salinities less than or equal to 50 g/L did not differ significantly (Fig. 1). This result is consistent with the lack of variation in the V_{max} of *S. alterniflora* plants exposed to 3–32 g/L salinity reported earlier (Morris 1984). The mean V_{max} for 5–50 g/L salinity treatment plants of 4.2 ± 2.0 (± SD) μmole·g^{-1}·h^{-1} is similar to previous estimates under hypoxic conditions (4.83–10.4 μmole·g^{-1}·h^{-1}: Bradley and Morris 1990; Morris 1980, 1984; Morris and Dacey 1984). The V_{max} for NH_4^+ uptake by *S. alterniflora* grown at and exposed to 65 g/L did not differ significantly from 0 nor did the biomass of these plants change significantly during the month of exposure to 65 g/L salinity in the greenhouse.

A 6-fold increase in the apparent K_m of NH_4^+ uptake as a function of increasing salinity was observed in plants that were grown at these salinities (Fig. 2). K_m increased from a mean of 2.7 ± 1.1 μmole/L at a salinity of 5 g/L to 9.3 ± 3.9 μmole/L at 35 g/L to a mean of 17.6 ± 4.1 μmole/L at a salinity of 50 g/L. The K_m at 20 g/L salinity was an intermediate 4.8 ± 2.3 μmole/L but did not differ significantly from that of the 5 or 35 g/L plants (according to the Tukey-Kramer Test at $p \leq 0.05$). K_m was not determined for the 65 g/L treatment plants.

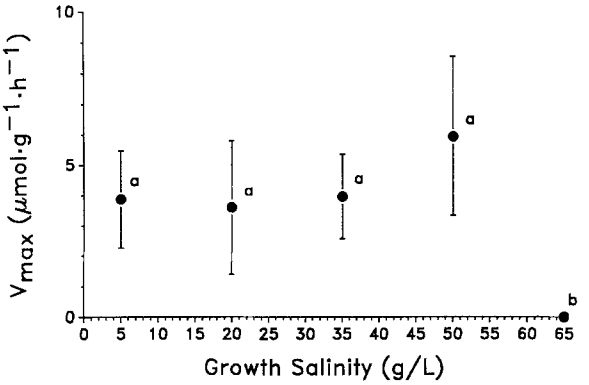

Fig. 1. The effect of salinity (g/L) on the V_{max} (μmole·g^{-1}·h^{-1}) of NH_4^+ uptake by *S. alterniflora* plants that were grown at those salinities for 1 month. Error bars are ± 1SD. Superscripts denote significantly different subsets according to the Tukey-Kramer Test ($p \leq 0.05$)

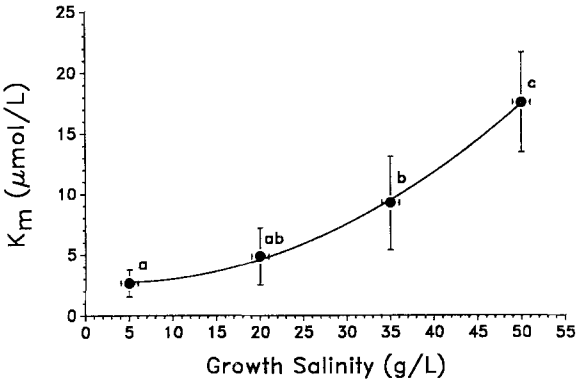

Fig. 2. The effect of salinity (g/L) on the K_m (μmole/L) of NH_4^+ uptake by *S. alterniflora* plants that were grown at those salinities for 1 month. Error bars are ± 1SD. Superscripts denote significantly different subsets according to the Tukey-Kramer Test ($p \leq 0.05$)

Short-term variation in solution salinity significantly affected both V_{max} and K_m of NH_4^+ uptake by *S. alterniflora*. Exposing plants grown at 35 g/L to 5 g/L salinity did not significantly affect V_{max} (Fig. 3). However, the V_{max} of plants grown at 5 g/L decreased by 62% from 3.9 ± 1.6 μmole·g^{-1}·h^{-1} at 5 g/L salinity to 1.5 ± 0.2 μmole·g^{-1}·h^{-1} when exposed to 35 g/L (Fig. 3). No significant difference in V_{max} was detected following the exposure of 35 g/L plants to 50 g/L for 12 h, but after 36 h of exposure no significant uptake was observed. Subjecting plants grown at 5 g/L salinity to 35 g/L led to a significant increase in K_m from 2.7 ± 1.1 μmole/L at 5 g/L to 5.9 ± 2.0 at 35 g/L (Fig. 4). Similarly, the K_m of 35 g/L plants increased from 2.8 ± 1.8 μmole/L at 5 g/L, to 9.3 ± 3.9 μmole/L at 35 g/L, to 12.9 ± 2.4 μmole/L at 50 g/L salinity.

Along the North Inlet marsh transect, the root zone salinity of *S. alterniflora* typically ranged from 34 g/L at the creek bank to 63 g/L in the high marsh (Fig. 5) during

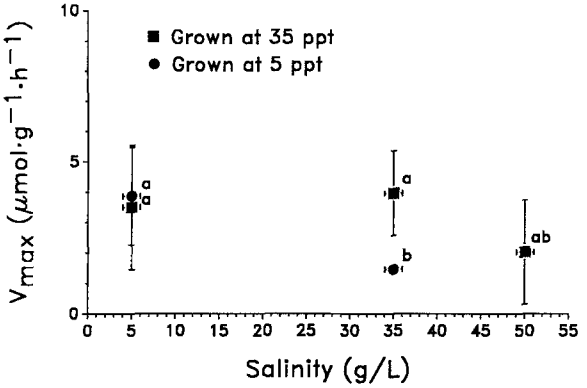

Fig. 3. The effect of a rapid change in salinity (g/L) on the V_{max} (μmole·g^{-}·h^{-1}) of plants grown at 5 or 35 g/L. Uptake was measured after 12 h of acclimation at the new salinity. Error bars are ± 1SD. Superscripts denote significantly different subsets according to the Tukey-Kramer Test ($p \leq 0.05$)

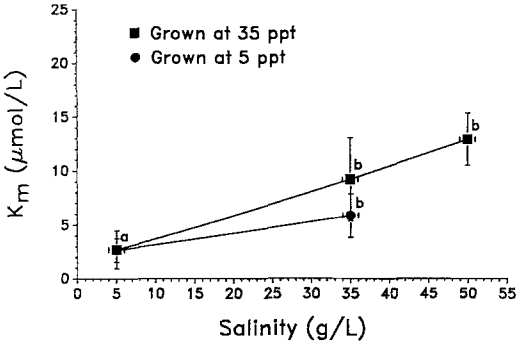

Fig. 4. The effect of a rapid change in salinity (g/L) on the K_m (μmole/L) of plants grown at 5 or 35 g/L. Uptake was measured after 12 h of acclimation at the new salinity. Error bars are ± SD. Superscripts denote significantly different subsets according to the Tukey-Kramer Test ($p \leq 0.05$)

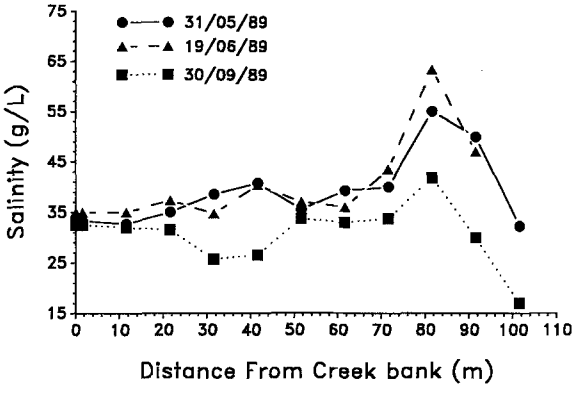

Fig. 5. Salinity profiles for dates 31/05/89, 19/06/89 and 30/09/89. These are typical of variation in salinity (g/L) with distance (m) from the creek bank found at the Oyster Landing Site during the summer months

the summer months. Hence our treatment salinities covered the range of salinity normally found at this site during the summer. After a period of intense rain, salinity ranged from 16 g/L at the edge of the high marsh to 34 g/L at the creek bank with the maximum 42 g/L at a distance of 80 m. The major ion composition of the transect interstitial water and the culture solutions are given in Table 1. The composition of major ions was the same for autoclaved seawater collected from the Baruch Lab and solutions of artificial sea salts. Consequently, the salinity treatments examined in the study differed in the absolute concentration of total and individual ions, but the relative composition remained constant. Further, we found no apparent difference in the relative composition of major ions in the interstitial water of the 3 transect sites examined.

Discussion

Salinity has been implicated as a factor influencing the productivity of *S. alterniflora* in the marsh. A negative correlation between sediment salinity and productivity of *S. alterniflora* was found at Sapelo Island, GA (Nestler 1977), and reduced survival of *Spartina* has been observed at salinities within a range of 40–50 g/L (Haines and Dunn 1976, Phleger 1971, Shiflet 1963, Woodhouse et al. 1974). The optimum growth salinity of *S. alterniflora* has been variously estimated between 0–20 g/L (Adams 1963; Haines and Dunn 1976; Linthurst and Seneca 1980). Salinities in excess of 35 g/L are common in Eastern and Gulf coast marshes (Cavalieri and Huang 1981; Nestler 1977; Webb 1983). Moreover, Webb (1983) reported that salinities greater than 60 g/L occurred at the higher elevations within the range of *S. alterniflora* along the coast of Texas.

Several mechanisms have been proposed by which salinity can influence the productivity of *S. alterniflora* in the marsh. Salinity induced water stress can reduce stomatal conductance and net photosynthesis (Giurgevich and Dunn 1979; Longstreth and Strain 1977). Exposure to a high salt environment can result in an internal accumulation of ions leading to ion toxicity or increased energy allocation to enhance salt gland function and ion compartmentation (Haines and Dunn 1976). Finally, salinity can inhibit production in *S. alterniflora* by contributing to nitrogen limitation (Cavalieri and Huang 1979, 1981; Morris 1980, 1984). The tendency of *S. alterniflora* to accumulate the nitrogen containing osmotica, proline and glycine-betaine, in response to salinity results in the reallocation of internal nitrogen away from growth and toward osmoregulation (Cavalieri and Huang 1979, 1981).

This study demonstrates that increasing salinity inhibits the uptake of new NH_4^+. Over the 5–50 g/L range, salinity affects the apparent K_m (Fig. 3) but not V_{max} (Fig. 2). Based on the carrier mediated model of nutrient uptake in plants (for nutrient concentrations ≤ 1 mmole/L: Epstein and Hagen 1952, Nye and Tinker 1977), V_{max} can be viewed as a function of the saturated uptake rate of the carrier and the concentration per surface area of root of active carrier sites, while K_m is a measure of the ability of each carrier system to bind with and take up substrate as a function of relative substrate concentration. Epstein and Hagen (1952) proposed that the presence of competing ions can reduce the efficiency of the active uptake mechanism by effectively diluting the concentration of substrate. Since increasing the substrate concentration will overcome this competitive effect, the maximum rate of uptake, V_{max} remains unchanged in the case of competitive inhibition. The fact that salinity in the range 5–50 g/L increased K_m but did not effect V_{max} strongly suggests that long-term exposure to a given

salinity competitively inhibits NH_4^+ uptake in *S. alterniflora*. This conclusion is supported by the fact that the effect on K_m of changing solution salinity was reversible (Fig. 4).

Several researchers have suggested that the Na^+ concentration associated with high salinity may exceed the capacity of *S. alterniflora* to selectively absorb NH_4^+ (eg. Chalmers 1982; Haines and Dunn 1976; Linthurst and Seneca 1981; Smart and Barko 1980; Smart 1982). This hypothesis presumes that a single carrier mechanism is responsible for Na^+ and NH_4^+ in *S. alterniflora* (Chalmers 1982) as has been suggested for wheat (Tromp 1962). A $Na^+:K^+$ ratio greater than 125:1 was shown to inhibit K^+ uptake in *Avicennia marina* (Rains and Epstein 1967). Over the 5–65 g/L range in total salinity investigated in the present study, the $Na^+:NH_4^+$ molar ratio varied from 641:1 to 8329:1 (assuming $[NH_4^+]=100$ μmol/L = 1.8 mg/L). Although these observations are highly suggestive, a detailed investigation of the effects of specific ions such as Na^+ and K^+ on NH_4^+ uptake is required to conclusively resolve the mechanism of overall salinity effects.

High salinity and/or rapid changes in salinity appear to be toxic to *S. alterniflora*. Plants exposed to a salinity of 65 g/L did not take up NH_4^+ at a measurable rate even when exposed to NH_4^+ concentrations in excess of 150 μmole/L over the period of this experiment (Fig. 1). This result is consistent with the low productivity within the high salinity zone of the marsh. In the high marsh region where salinity can rise to 60 g/L, the bulk of active NH_4^+ uptake may be restricted to times when salinity is relatively low. Growth which occurs during the summer months of high salinity may result from the translocation of internal nitrogen to the growing tissues at the expense of older tissues as suggested by Hopkinson and Schubauer (1984). Hopkinson and Schubauer (1984) estimate that approximately 54% of the total above ground nitrogen requirements are met by recycling nitrogen internally. It should be noted that although typically reduced, these sediments may become oxidized during periods of high evapotranspiration (associated with elevated salinity) and this oxidation may 1) significantly improve NH_4^+ uptake as well as 2) permit nitrification and subsequent NO_3^- uptake. Consequently, these results may be a poor predictor of the growth potential of *S. alterniflora* in sediments where significant oxidation occurs. Additional study is required to evaluate the interaction of salinity and oxygen concentration on NH_4^+ uptake and the extent to which the sediments at this site are oxidized by water loss to evapotranspiration.

Our short-term experiments indicate that a rapid increase in salinity, such as may occur during tidal inundation of infrequently flooded high marsh areas, affects both the maximum rate and the apparent K_m of NH_4^+ uptake in *S. alterniflora* (Figs. 3 and 4). Moreover, exposure of 35 g/L plants to a salinity of 50 g/L for a period of 48 h completely inhibited NH_4^+ uptake and induced chlorosis and death in all plants. The fact that the short-term exposure of 5 g/L plants to 35 g/L resulted in no obvious chlorosis and continued uptake of NH_4^+ even after 36 h of exposure is consistent with the observation of Linthurst and Seneca (1981) that an increase in salinity from 30 to 45 g/L is more deleterious to the growth of *S. alterniflora* than an increase from 15 to 30 g/L.

Our field measurements demonstrate that salinity fluctuates in the marsh in response to tidal inundation and rainfall. During the summer, evaporation resulted in a steady increase in salinity at the higher elevations of the marsh. A period of heavy rainfall (30/09/89) resulted in a rapid decrease in the salinity of these sites (Fig. 5). Based on present results, these rapid changes in sediment salinity are expected to strongly influence NH_4^+ uptake and growth in *S. alterniflora* in the field.

The major ion composition of interstitial water along the field transect at the Baruch lab on 19/06/89 did not vary significantly with distance inland (data not shown). This observation suggests that selective ion exclusion by the roots of *S. alterniflora* was not significant at this time. However, it should be noted that these measurements, made once early in the growing season, do not give any information about the temporal variation in ion composition which would be expected to result from growth of *S. alterniflora* (Smart and Barko 1980). During growth experiments, the interstitial water $Na^+:K^+$ ratio was positively related to above ground biomass of *S. alterniflora* during growth experiments (Smart 1982).

The results of this study are consistent with a conceptual model of changes in the kinetics of NH_4^+ uptake by *S. alterniflora* as a function of environmental gradients in the salt marsh (Bradley and Morris 1990, Morris 1984). In the relatively low stress environment of the creek bank, the V_{max} is expected to be comparatively high while K_m should be low. A higher V_{max} is consistent with the higher rate of growth typical of creek bank *Spartina*, while a low K_m is consistent with the demonstrated failure of creek bank populations to respond to nitrogen fertilization. In contrast, a relatively low V_{max} and a high K_m are expected to occur in the high stress environment of the upper marsh. A low V_{max} in the high marsh plants is consistent with the slow growth of these individuals. A large K_m associated with stunted high marsh plants would explain the increased growth resulting from nitrogen fertilization in the high marsh. Although it has been demonstrated that V_{max} does not change with salinity, for those salt marshes where salinity increases with elevation, the increase in K_m observed in this study in response to increasing salinity is consistent with the decrease in efficiency of NH_4^+ uptake hypothesized to occur in the high marsh.

In conclusion, this study is consistent with previous research suggesting that nitrogen limitation is a proximate mechanism by which environmental factors affect the growth of *S. alterniflora* in the salt marsh. In addition to other direct physiological responses to osmotic and salt stress, our data indicate that an effect of relatively constant long-term exposure to a salinity within the range 5–50 g/L is a competitive inhibition of NH_4^+ uptake in *S. alterniflora*. Furthermore, relatively rapid increases in salinity and long-term exposure to high salinity (salinity > 50 g/L) appear to be toxic to *S. alterniflora* resulting in a reduction in V_{max} and an increase in K_m for NH_4^+ uptake.

Acknowledgements. The authors wish to acknowledge the assistance of C. Coleman, B. Haskins and Y–H Hwang in the completion of

this project. We gratefully acknowledge an anonymous reviewer whose comments resulted in significant improvements in the manuscript. This paper is contribution 824 of the Belle W. Baruch Institute for Marine Science. This research was supported by a fellowship from the Slocum-Lunz Foundation to P. Bradley.

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