

Relative importance of macrophyte leaves for nitrogen uptake from flood water in tidal salt marshes

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ABSTRACT: Nitrogen limits plant growth in most salt marshes. As foliar N-uptake makes a significant contribution to the overall N-requirements of submerged plant species such as (e.g.) seagrasses, we tested if foliar N-uptake was also significant in *Spartina anglica* Hubbard, a species that dominates the lowest, regularly flooded areas of salt marshes in the SW Netherlands. Foliar N-uptake was compared for plants from 2 estuaries with contrasting N-loads in their water column. N-uptake was quantified by (1) flooding detached leaves in test tubes, (2) spraying leaves still attached to the plants, and (3) flooding whole plants, with solutions containing either $^{15}\text{NO}_3^-$ or $^{15}\text{NH}_4^+$. We found that detaching the leaves from the plant underestimated NH_4^+ uptake by between 30 and 50%. Higher salinity also reduced foliar N-uptake. Uptake rates were higher for NH_4^+ than for NO_3^- , as has been found for many submerged and terrestrial angiosperms and marine algae. Methodology also had a major effect on the uptake rate, with flooding of intact plants yielding higher uptake rates than spraying attached leaves. However, in general, foliar N-uptake rates were low at the NO_3^- and NH_4^+ concentrations that are actually present in the tidal waters during the growth season, and may at most contribute to around 10% of the growth requirement. This percentage is much less than for seagrasses, but in line with data for some terrestrial systems. We conclude that in contrast to seagrasses, foliar N-uptake does not form a significant contribution to the overall N-requirements of *S. anglica*. This low N-uptake capacity of the *S. anglica* leaves appears to be a consequence of adaptations to survive tidal flooding.

KEY WORDS: Foliar uptake · Nitrate · Ammonium · Tidal marsh · ^{15}N labelling

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INTRODUCTION

Some aquatic macrophytes such as seagrasses obtain a significant proportion of their nutrient requirements by uptake through their leaves, since N- and P-uptake from the soil may be limited by diffusion or uptake characteristics of their roots (Stapel et al. 1996, Lee & Dunton 1999). Foliar uptake can supply around 50% of the overall N-requirement of *Thalassia testudinum* (Lee & Dunton 1999) and *T. hemprichii* (Stapel et al. 1996), between 30 and 90% of the overall N-requirement of *Zostera marina* (Iizumi & Hattori 1982, Short

& McRoy 1984, Pedersen & Borum 1992, 1993) and, in extreme cases, the complete N-requirement of *Phyllospadix torreyi* (Terrados & Williams 1997). In the case of nitrogen, foliar uptake by seagrasses is generally higher for NH_4^+ than for NO_3^- (Touchette & Burkholder 2000). In terrestrial plants, foliar uptake is often severely restricted by the outer wall of the epidermal cells (Marschner 1995). Nevertheless, application of foliar nutrients can be useful in horticulture (e.g. Leacock & Syvertsen 1995, Reickenberg & Pritts 1996, Umar et al. 1999) and foliar N-uptake can constitute a significant component in the mineral nutrition cycle of some terrestrial ecosystems (Marschner 1995). For example, in the forestal ecosystems of Central Europe and Northern America, foliar uptake can comprise

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a large external N-source (3 to 10 kg N ha⁻¹ yr⁻¹: Brumme et al. 1992), even though it generally only meets a small fraction of the overall N-requirement of the trees (2 to 8%: Boyce et al. 1996; up to 5%: Wilson & Tiley 1998). Although leaching and the presence of epiphytic macroflora complicates interpretation of throughfall studies (Pearson & Stewardt 1993), it is also evident in terrestrial systems that foliar N-uptake is generally more efficient for NH₄⁺ than for NO₃⁻ (Wilson 1992, Peuke et al. 1998, Ignatova & Dambrine 2000). In this study, we address the question as to the extent in which foliar uptake of nitrogen contributes to the nutrient demand of halophytic species that grow in the lowest areas of tidal salt marshes.

Nitrogen limits plant growth in most marshes (Valiela & Teal 1974, Kiehl et al. 1997) so that foliar N-uptake would be beneficial to marsh plants. Plants that grow in the lowest parts of a salt marsh are flooded daily, which may enable them to take up any nutrients that are available in the tidal water. In contrast to seagrasses, which are generally flooded most of the time and may obtain a significant proportion of their nutrients by foliar uptake, halophytic salt marsh species are only flooded briefly. This difference in habitat may require different physiological characteristics in the 2 groups of species. The harsh conditions (windy and salty) of the relatively open-marsh environment may require halophytic salt-marsh species to have a relatively impermeable cuticle to prevent excessive water loss and excessive leaching of (in)organic solutes through the leaves. Such cuticle could hinder N-uptake by the leaves. As for the roots, the strongly reduced anoxic soil conditions that characterize the most frequently flooded parts of marshes (Armstrong et al. 1985, Ewing et al. 1997) may, to a certain degree, hinder nutrient uptake. Species from the low marsh need root systems that allow sufficient oxygen transport to facilitate aerobic metabolism and detoxification of the rhizosphere (Armstrong et al. 1991). This would be expected to result in relatively high carbon expenditure, which might make N-uptake by the leaves profitable from an efficiency perspective. To our knowledge, surprisingly little is known about the importance of foliar nutrient acquisition in salt-marsh ecosystems. Existing studies mainly focus on below-ground fertilization (e.g. Patrick & Delaune 1976, Broome et al. 1983), whereas studies that do examine fertilization at the soil surface (e.g. Mendelssohn 1979) or in the water column (e.g. Wright et al. 1996) do not quantify foliar uptake.

We quantified the uptake of ¹⁵NO₃⁻ and ¹⁵NH₄⁺ by the leaves of *Spartina anglica* Hubbard in an estuary with a high (i.e. Westerschelde) versus a low (i.e. Easterschelde) nitrogen concentration in the water column. In both estuaries, *S. anglica* dominates the

low-marsh areas that are flooded twice a day. Hence, we hypothesized that the uptake kinetics of *S. anglica* leaves would enable a significant contribution of foliar uptake to the overall N-demand for growth. Because of the lack of a standard method for studying foliar uptake in salt marshes, we measured uptake by (1) flooding detached leaves in test tubes, (2) spraying leaves still attached to the plant, and (3) flooding whole plants. Whereas Method 1 is easily applicable to large numbers of detached leaf samples, Methods 2 and 3 represent realistic simulations of leaves following and during a flood period, respectively. We also studied the effect of salt concentration, as the locations in the Westerschelde and Easterschelde differ in salinity. In the Westerschelde, we performed additional measurements on detached leaves of *Tiriglochin maritima* L. from the low/middle marsh and *Elymus pycnanthus* (Godron) Melderis from the high marsh. As the habitats from these species are less regularly flooded than that of *S. anglica*, we expected these species to have fewer adaptations facilitating foliar N-uptake.

MATERIALS AND METHODS

Study area. The study was carried out in the salt marsh east of Waarde (approx. 90 ha) in the Westerschelde (WS) estuary (SW Netherlands; 51° 24' N, 4° 06' W) and the salt marsh of Rattekaai (approx. 135 ha) in the Easterschelde (ES) estuary (SW Netherlands; 51° 27' N, 4° 09' E). The WS estuary is part of an extensive salt, brackish, and freshwater tidal system. The high population density and intense agrarian and industrial activity around the Schelde river (Belgium) and WS estuary (Netherlands) result in high loads of nutrients in the water column. NO₃⁻ and NH₄⁺ concentrations are highest outside the growth season, when water temperatures are lowest (Fig. 1). The salinity in the Waarde marsh fluctuates around 18.5. Since the construction of the Volkerak dam in 1969, the ES estuary lacks freshwater input from any river, so that it in fact has become a tidal bay. Accordingly, the nutrient input is relatively low and the salinity is nearly constant around 31. The difference in salinity between the WS and ES marshes has caused distinct differences in the vegetation. However, the species that we used in the present study are readily found at both sites: *Spartina anglica* Hubbard is the dominant species in the lowest parts of the marsh (2.0 m NAP; de Leeuw et al. 1994), *Tiriglochin maritima* L. is a species found at the low/middle parts of the marsh (2.25 m NAP; de Leeuw et al. 1994) and *Elymus pycnanthus* (Godron) Melderis is dominant in the highest areas of the marsh (2.5 m NAP; de Leeuw et al. 1994). Elevation is given in meters above the Dutch Ordnance Level (m NAP), which is similar to mean sea level.

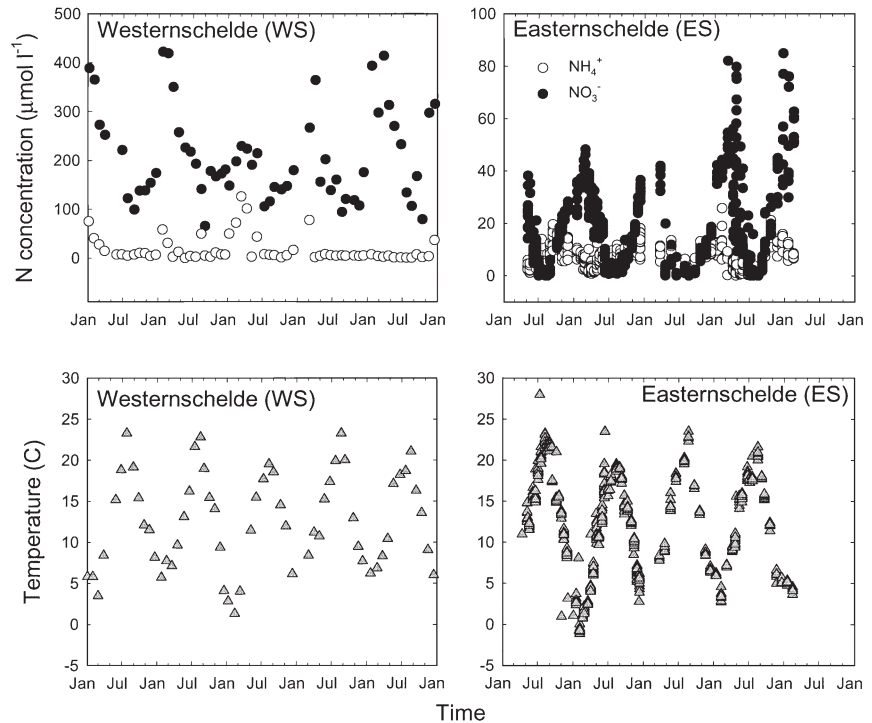


Fig. 1. Annual fluctuations in NO_3^- and NH_4^+ concentrations of the water column near the Westerschelde (WS) salt marsh east of Waarde and the Easternschelde (ES) salt marsh near Rattekaai. NO_3^- and NH_4^+ concentrations are highest outside the growth season, when water temperatures are lowest. In the WS the average NO_3^- and NH_4^+ concentrations ($\mu\text{mol l}^{-1}$) were 242 ± 17 ($n = 35$) and 21 ± 4.9 ($n = 35$) for the cold periods ($T < 15^\circ\text{C}$), and 156 ± 11 ($n = 23$) and 8.1 ± 2.6 ($n = 23$) for the warm periods ($T > 15^\circ\text{C}$), respectively. In the ES, the average NO_3^- and NH_4^+ concentrations ($\mu\text{mol l}^{-1}$) were 26.3 ± 0.6 ($n = 488$) and 8.1 ± 0.2 ($n = 484$) for the cold periods ($T < 15^\circ\text{C}$), and 5.3 ± 0.4 ($n = 330$) and 5.7 ± 0.2 ($n = 343$) for the warm periods ($T > 15^\circ\text{C}$)

Uptake experiments. To our knowledge, little is known about the importance of foliar nutrient acquisition in salt-marsh ecosystems. Accordingly, a standard method for studying foliar uptake in salt marshes is lacking. In our study, we used 3 methods to quantify the uptake of $^{15}\text{NO}_3^-$ and $^{15}\text{NH}_4^+$ by the leaves: (1) flooding detached leaves in test tubes, (2) spraying leaves still attached to the plants and (3) flooding whole plants (Table 1). Method 1 was used as an easily applicable method on large numbers of detached leaf samples. Method 2 simulates leaves following a flood period, when the leaves are still covered with water droplets, and is easily applied to a large number of leaves that are still attached to the plant. Method 3 is a realistic simulation of conditions during flooding, when intact leaves may take up nutrients from the flood water; applying this method in the field is however difficult. In all experiments, the ^{15}N -labeled and the artificial seawater solutions used for rinsing the plants had the following composition (g l^{-1}) to simulate local WS (13.2 NaCl, 1.75 Na_2SO_4 , 4.77 $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$, 0.30 KCl, 0.88 $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$) and ES (22.5 NaCl, 2.99 Na_2SO_4 , 8.11 $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$, 0.50 KCl, 1.50 $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$) waters, respectively. To maximize the sensitivity of measuring uptake at low N-concentrations, all solutions were fully labelled (i.e. the N in NO_3^- or NH_4^+ consisted of 98% ^{15}N).

In Method 1, test tubes were filled with a solution of either $^{15}\text{NO}_3^-$ or $^{15}\text{NH}_4^+$. The solution in each tube was well mixed by aeration. We placed 3 to 5 of the

youngest, freshly cut, full-grown leaves upside down in a test tube (height 160 mm; diameter 13 mm), taking care that the cut surface remained just above the solution. The leaves within a single tube were regarded as a single sample; replicates consisted of several independent tubes for each concentration. Incubations were in the field at ambient light and temperature. After 0.5 h, the leaves were briefly rinsed in 3 succeeding beakers with unlabelled NO_3^- or NH_4^+ solution, at a concentration (Table 1) similar to that used during the previous ^{15}N -uptake period. To determine the effect of salinity, some N-concentrations were duplicated at the salinity of the other location (i.e. 'contrasting' salinity: Table 1).

To test the effect of detaching leaves, we compared the ^{15}N -uptake of detached versus attached leaves for *Spartina anglica* plants cultivated in a climate room. In contrast to the field situation, the leaves of these control plants had not been previously exposed to regular flooding (Control 1: Table 1).

In Method 2, individual leaves that were still attached to plants in the field were sprayed with either a $^{15}\text{NO}_3^-$ or a $^{15}\text{NH}_4^+$ solution, until the whole leaf was covered (concentrations listed in Table 1). Although the amount of solution applied could represent a limiting N-supply, it represents the maximum amount that can be applied in this manner. To obtain independent replicates, we used different individual plants for different sprayings. After 2 h incubation at ambient light and temperature, the leaves were harvested and briefly rinsed as described for Method 1.

Table 1. *Spartina anglica* (Spa), *Tiriglochin maritima* (Tri) and *Elymus pycnanthus* (Ely). Overview of experiments on N-uptake by the leaves. Except for the experiment in the climate room, all measurements were in the field. Study areas WS and ES = Westernschelde salt marsh east of Waarde and Easternschelde salt marsh near Rattekaai, respectively; local salinity in WS and ES = 18.5 and 31, respectively, 'contrasting' salinity was the salinity of the other location; soil trenching = plant collars filled with ^{15}N -solution without agar. Replicates column indicates number of test tubes (Expt 1), number of individually sprayed leaves, each on a separate plant (Expt 2), and number of flooded plants (Expt 3) per N-concentration and N-form

Expt Species	Study area	Salinity	Experimental design (N-application + tissue type)	Light ($\text{mmol m}^{-2} \text{s}^{-1}$)	T ($^{\circ}\text{C}$)	N-form	N-conc. (mM)	N-exp. (h)	Repl.	Fig.
Expt 1										
Ely	WS	Local	Detached leaves in test tubes	863±132	17±0.6	NO_3^-	1,5,10,50, 100,500	0.5	4	3
	WS	Local	Detached leaves in test tubes	863±132	17±0.6	NH_4^+	1,5,10,50, 100,500	0.5	4	3
Tri	WS	Local	Detached leaves in test tubes	863±132	17±0.6	NO_3^-	1,5,10,50, 100,500	0.5	4	3
	WS	Local	Detached leaves in test tubes	863±132	17±0.6	NH_4^+	1,5,10,50, 500	0.5	4	3
Spa	WS + ES	Local	Detached leaves in test tubes	863±132	17±0.6	NO_3^-	1,5,10,50, 100,500	0.5	4	2
	WS + ES	'Contrasting'	Detached leaves in test tubes	863±132	17±0.6	NO_3^-	10,100	0.5	4	4
	WS + ES	Local	Detached leaves in test tubes	863±132	17±0.6	NH_4^+	1,5,10,50, 100,500	0.5	4	2
	WS + ES	'Contrasting'	Detached leaves in test tubes	863±132	17±0.6	NH_4^+	10,100	0.5	4	4
Control 1										
Spa	Climate room	0	Detached leaves in test tubes	350	20	NO_3^-	10,100	0.5	8	5
	Climate room	0	Detached leaves in test tubes	350	20	NO_3^-	10,100	0.5	8	5
	Climate room	0	Detached leaves in test tubes	350	20	NH_4^+	10,100	0.5	8	5
	Climate room	0	Detached leaves in test tubes	350	20	NH_4^+	10,100	0.5	8	5
Expt 2										
Spa	WS + ES	Local	Spraying attached leaves	815±54	19±0.2	NO_3^-	1,5,10,50	2	6	6
	WS + ES	Local	Spraying attached leaves	815±54	19±0.2	NH_4^+	1,5,10,50	2	6	6
Expt 3										
Spa	WS + ES	Local	Flooding intact plants	1007±89	19±0.5	NO_3^-	1,5,10,50	1.5	6	7
	WS + ES	Local	Flooding intact plants	1007±89	19±0.5	NH_4^+	1,5,10,50	1.5	6	7
Control 3										
Spa	WS + ES	Local	Soil trenching of intact plants	1007±89	19±0.5	NO_3^-	5	1.5	2	
	WS + ES	Local	Soil trenching of intact plants	1007±89	19±0.5	NO_3^-	50	1.5	3	
	WS + ES	Local	Soil trenching of intact plants	1007±89	19±0.5	NH_4^+	5	1.5	2	
	WS + ES	Local	Soil trenching of intact plants	1007±89	19±0.5	NH_4^+	50	1.5	3	

In Method 3, we put a small collar (height 160 mm; diameter 160 mm), around the base of individual plants in the field. Into these collars we poured agar solution (15 g l^{-1}) just above solidification temperature (36°C) until it reached approximately 4 cm in height. Immediately after pouring in the agar, we placed a tall transparent Plexiglas cylinder (height 450 mm; diameter 100 mm) inside each collar. After the agar had solidified, each Plexiglas cylinder was filled with an average of $2.9 \pm 0.02 \text{ l}$ ($n = 94$) of a $^{15}\text{NO}_3^-$ or a $^{15}\text{NH}_4^+$ solution (concentrations listed in Table 1). To determine if leakage occurred, we measured the level of the solution in each Plexiglas cylinder directly after filling and just before harvesting. If the leakage exceeded 10% of the total volume, the plant sample was discarded (maximum leakage was 314 ml, with an average of $115 \pm 8 \text{ ml}$; $n = 94$). The solution was well mixed

by aeration. After 1.5 h incubation at ambient light and temperature, the tall cores and small collars were removed, and the plants were cut just above the agar, whereafter they were briefly rinsed as described for Method 1, except that we used 10 l buckets instead of the small beakers. In the laboratory, the plants were separated into leaves, stems and (if present) flowering parts. To determine if leakage of ^{15}N -solution into the soil could have affected the ^{15}N -content of the leaves by uptake through the roots within the 1.5 h period, we filled a few small collars with 400 ml ^{15}N -solution, without agar (soil trenching; Control 3; Table 1).

In all experiments, samples were kept on ice during transport to the laboratory, where they were frozen and freeze-dried. After freeze-drying, the samples were analyzed for C, N and ^{15}N -content using an elemental analyzer (NA-1500, Carbo Erba) coupled via a

Finnigan con-flow II interface to an isotope-ratio mass spectrometer (Finnigan Delta S). N-uptake rates were calculated using the following equations:

$$N_{\text{tot}} = (\%N/100) \times DM \times 10^3 \quad (1)$$

$$^{15}N_{\text{upt}} = ([\%^{15}N_{\text{end}} - \%^{15}N_{\text{start}}]/100) \times N_{\text{tot}} \times 10^3 \quad (2)$$

$$V_{\text{upt}} = ^{15}N_{\text{upt}} \times 10^3 / (DM \times t_{\text{exp}}) \quad (3)$$

where N_{tot} = the total amount (mg) of N in the tissue studied; %N = the N-content as percentage of weight; DM = the dry mass (g) of the leaves; $^{15}N_{\text{upt}}$ = the amount of ^{15}N (μg) taken up from the flood water; $\%^{15}N_{\text{end}}$ = the ^{15}N -content as percentage of the weight in the plant tissue that was flooded with ^{15}N -solution; $\%^{15}N_{\text{start}}$ = the ^{15}N -content as percentage of the weight in the same type of plant tissue from a nearby control plant that was not flooded with ^{15}N -solution, V_{upt} = the N-uptake rate from the flood water per unit dry leaf mass ($\text{ng} [\text{g dry mass}]^{-1} \text{h}^{-1}$), t_{exp} = the experimental uptake period (h). Our calculation method can yield small negative values for the N-uptake rate if the difference between $\%^{15}N_{\text{end}}$ and $\%^{15}N_{\text{start}}$ is small compared to the natural variation in $\%^{15}N$. Such small negative (and also small positive) uptake rates are of course artifacts, and indicate that uptake rates are negligible. We also calculated the relative growth rate (RGR) that could be maximally supported by N-uptake from the flood water (RGR_{max} ; $\text{mg g}^{-1} \text{d}^{-1}$):

$$\text{RGR}_{\text{max}} = V_{\text{upt}} \times t_{\text{flood}} / (N_{\text{con}} \times 10^3) \quad (4)$$

where N_{con} = the N-content (mg N g^{-1}) in the tissue studied, and t_{flood} = the daily flood period (h d^{-1}). Finally, we calculated the maximum percentage of the overall N-demand needed for a linear increase of plant biomass with time, which could be taken up by the shoot from the flood water ($U_{\%}$; %):

$$U_{\%} = 100 \times \sum (V_{\text{upt}} \times 10^{-6} \times DM_t \times t_{\text{flood}}) / \sum (\text{GR} \times N_{\text{con}}) \quad (5)$$

where \sum indicates monthly integration intervals, DM_t is the dry plant biomass at time t (g m^{-2}), and GR is the linear rate ($\text{g m}^{-2} \text{d}^{-1}$) by which plant biomass increased.

Statistical analysis. Analysis of variance (ANOVA) was used to test for effects of salinity, detaching leaves, location, N-concentration, N-form and possible interactions, using STATISTICA software (StatSoft). It was noted that the variance was not homogeneous. Due to the negative values this could not be solved by log-transformation. As our experiment generally included 3 factors, the possibilities for using non-parametric tests were limited. Because of the simple experimental design and the straightforward results with clearly visible differences, we chose to restrict our statistical analysis to ANOVA even though the variance was not homogeneous. When the ANOVA revealed significant

differences, we did a post-hoc analysis using Tukey's honestly significant difference test (5% significance level). All independent variables, interactions, and F and p values are summarized in Table 2. Regression analyses were performed with STATISTICA software (StatSoft) and p values, R^2 values, and the number of observations are given in the legends of the relevant figures. For all experiments, the exact number of replicates is listed in Table 1.

RESULTS

The rate of N-uptake by the youngest, freshly cut, full-grown leaves (Method 1) increased linearly with increasing N-concentration in the incubation medium for *Spartina anglica* from both the WS and ES (Fig. 2), as well as for *Elymus pycnanthus* and *Triglochin maritima* (Fig. 3) from the WS (regression equations in the relevant figure legends). In *S. anglica* and *E. pycnanthus*, foliar N-uptake was greatest when ^{15}N was supplied as $^{15}\text{NH}_4^+$ (Figs. 2 & 3). Only in *T. maritima* was ^{15}N -uptake independent of the N-form (Fig. 3). Small negative (and small positive) values for the N-uptake rate are artifacts of our calculation method (Eqs. 1 to 3) that occur when the difference between $\%^{15}N_{\text{end}}$ and $\%^{15}N_{\text{start}}$ (Eq. 2) is small compared to the natural variation in $\%^{15}N$ (0.37265 ± 0.00066 [$n = 10$] in the WS vs 0.36973 ± 0.00012 [$n = 10$] in the ES). Such small negative and positive values indicate that the N-uptake rate is negligible. Regeneration can be excluded, as we used fully labelled ^{15}N -solutions, whereas the internal pools of field-grown plants consist to more than 99% of ^{14}N . Exposing *S. anglica* leaves collected from the WS and the ES to both their local salinity and the salinity of each other revealed that a higher salinity reduced foliar N-uptake (Fig. 4, Table 2). This effect however was not evident when directly comparing the uptake rates of leaves collected in the WS (Salinity = 18.5) and ES (Salinity = 31), respectively (Fig. 2).

In all species, uptake rates were low (Figs. 2 & 3) at the N-concentrations that are actually present in the column water during the growth season: i.e. $156 \pm 11 \mu\text{mol NO}_3^- \text{ l}^{-1}$ and $8.1 \pm 2.6 \mu\text{mol NH}_4^+ \text{ l}^{-1}$ in the WS vs $5.3 \pm 0.4 \mu\text{mol NO}_3^- \text{ l}^{-1}$ and $5.7 \pm 0.2 \mu\text{mol NH}_4^+ \text{ l}^{-1}$ in the ES (Fig. 1). This suggests that N-uptake by leaves is only of minor importance with respect to the N-requirements for plant growth, both for the frequently flooded *Spartina anglica* plants and the occasionally flooded *Triglochin maritima* and *Elymus pycnanthus* plants. However, a control experiment with climate-room-grown *S. anglica* plants indicated that foliar N-uptake may be underestimated by 30 to 50% in leaves detached from the shoot (Fig. 5, Table 2). To exclude artifacts due to leaf-excision, we repeated our experiments on intact plants by spraying the leaves (Method 2) or flooding whole plants (Method 3).

Table 2. *Spartina anglica*. Results of analysis of variance (ANOVA) of data in Figs. 4–7. We tested the effect of leaf detachment (Control 1: Table 1) only for NH_4^+ , as the uptake of NO_3^- was 0 (Fig. 5). CR: climate room. Independent variables are underlined; *, a, b, c significant differences

Expt Independent variables	df _{effect,error}	F	p	N-uptake rates (ng g ⁻¹ h ⁻¹)			
				<u>NO_3^-</u>	<u>NH_4^+</u>		
Salinity, WS (Fig. 4)							
1: N-form	1, 24	13.2	0.001*	<u>-25^a</u>	<u>711^b</u>		
2: N-conc.	1, 24	5.3	0.031*	<u>10 μM</u>	<u>100 μM</u>		
3: salinity	1, 24	5.3	0.031*	<u>18.5 ppt</u>	<u>31 ppt</u>		
1 × 2	1, 24	2.8	0.108				
1 × 3	1, 24	5.3	0.031*	<u>NO_3^--18.5 ppt</u>	<u>NO_3^--31 ppt</u>	<u>NH_4^+-18.5 ppt</u>	<u>NH_4^+-31 ppt</u>
2 × 3	1, 24	6.8	0.015*	<u>10 μM-18.5 ppt</u>	<u>10 μM-31 ppt</u>	<u>100 μM-18.5 ppt</u>	<u>100 μM-31 ppt</u>
1 × 2 × 3	1, 24	3.9	0.060	-24 ^a	-25 ^a	1174 ^b	247 ^a
				79 ^a	143 ^a	1071 ^b	79 ^a
Salinity, ES (Fig. 4)							
1: N-form	1, 24	67.7	0*	<u>77^a</u>	<u>413^b</u>		
2: N-conc.	1, 24	109.6	0*	<u>10 μM</u>	<u>100 μM</u>		
3: salinity	1, 24	30.9	0*	<u>18.5 ppt</u>	<u>31 ppt</u>		
1 × 2	1, 24	38.8	0*				
1 × 3	1, 24	0.9	0.350				
2 × 3	1, 24	1.8	0.190				
1 × 2 × 3	1, 24	0.7	0.421				
				<u>10 μM NO_3^-</u>	<u>100 μM NO_3^-</u>	<u>10 μM NH_4^+</u>	<u>100 μM NH_4^+</u>
				-9.1 ^a	164 ^b	72 ^{ab}	753 ^c
Leaf detachment, CR (N-form = NH_4^+) (Fig. 5)							
1: N-conc.	1, 28	13.5	9.9E-04*	<u>10 μM NH_4^+</u>	<u>100 μM NH_4^+</u>		
2: tissue	1, 28	6.5	0.017*	<u>Attached</u>	<u>Detached</u>		
1 × 2	1, 28	0.1	0.719	1092 ^a	2163 ^b		
				1998 ^b	1257 ^a		
Spraying, WS + ES (Fig. 6)							
1: location	1, 79	12.4	0.001	<u>WS</u>	<u>ES</u>		
2: N-form	1, 79	0.0	0.953*	20 ^a	82 ^b		
3: N-conc.	3, 79	1.4	0.263				
1 × 2	1, 79	0.1	0.769				
1 × 3	3, 79	0.0	0.995				
2 × 3	3, 79	0.7	0.543				
Flooding, WS + ES leaves (Fig. 7)							
1: location	1, 76	26.6	0*	<u>WS</u>	<u>ES</u>		
2: N-form	1, 76	46.9	0*	872 ^a	3953 ^b		
3: N-conc.	3, 76	10.0	0*	<u>NO_3^-</u>	<u>NH_4^+</u>		
1 × 2	1, 76	18.2	0*	368 ^a	4458 ^b		
1 × 3	3, 76	4.5	0.006*	<u>1 μM</u>	<u>5 μM</u>	<u>10 μM</u>	<u>50 μM</u>
2 × 3	3, 76	8.2	0*	389 ^a	1227 ^a	3659 ^b	4375 ^b
1 × 2 × 3	3, 76	3.5	0.019*				
Flooding, WS + ES Stem (Fig. 7)							
1: location	1, 77	5.8	0.018*	<u>WS</u>	<u>ES</u>		
2: N-form	1, 77	45.9	0*	909 ^a	1652 ^b		
3: N-conc.	3, 77	9.6	0*	<u>NO_3^-</u>	<u>NH_4^+</u>		
1 × 2	1, 77	2.7	0.102	235 ^a	2325 ^b		
1 × 3	3, 77	1.0	0.382	<u>1 μM</u>	<u>5 μM</u>	<u>10 μM</u>	<u>50 μM</u>
2 × 3	3, 77	8.1	0*	155 ^a	829 ^{ab}	1893 ^{bc}	2245 ^c
1 × 2 × 3	3, 77	0.6	0.603				

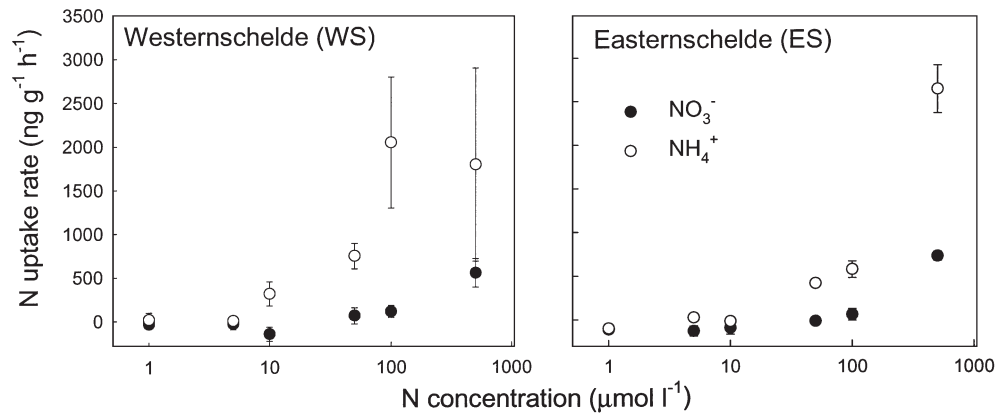


Fig. 2. *Spartina anglica*. Effects of N-concentration (C ; $\mu\text{mol l}^{-1}$) on NO_3^- and NH_4^+ uptake rates (V_{upt} ; $\text{ng [g dry mass]}^{-1} \text{h}^{-1}$) of detached leaves from plants growing in the WS vs plants growing in the ES. We ^{15}N -labeled the leaves by placing them upside down in a test tube. The linear regression equations for NO_3^- and NH_4^+ uptake rates by plants from the WS were $V_{\text{upt}} = 1.0793 C$; $R^2 = 0.5908$, $p = 7.18 \times 10^{-6}$ ($n = 24$) and $V_{\text{upt}} = 4.325 C$; $R^2 = 0.0979$, $p = 0.1278$ ($n = 24$), respectively. The linear regression equations for NO_3^- and NH_4^+ uptake rates by plants from the ES were $V_{\text{upt}} = 5.3195 C$; $R^2 = 0.9457$, $p = 4.44 \times 10^{-16}$ ($n = 24$) and $V_{\text{upt}} = 1.4005 C$; $R^2 = 0.8209$, $p = 4.65 \times 10^{-10}$ ($n = 24$), respectively. Linear regression lines are not shown because of the log-transformed x-axes

Spraying the leaves with $^{15}\text{NO}_3^-$ and $^{15}\text{NH}_4^+$ again resulted in low N-uptake rates (Fig. 6). This is probably due to the aggregation of the sprayed solution in droplets, which results in a minimal contact surface between the leaf and ^{15}N -labeled solution. Such problem does not exist when intact plants are flooded with a well-stirred solution that thus yields a more accurate estimate of the ^{15}N -uptake rates. Accordingly, we found much higher uptake rates for such flooded plants (Fig. 7). The absence of ^{15}N in shoots from the plants that received the soil trenching treatment with ^{15}N -solution (data not shown) excludes the possibility

that such higher uptake rates could in part be due to uptake by the roots.

To quantify the potential importance of N-uptake by the shoots for plant growth we calculated Eq. (4) the maximum relative growth rate that could be achieved under the assumptions that (1) flood water was the only N-source and (2) the total shoots would on average be fully submerged for 2.4 h d^{-1} . The 2.4 h d^{-1} period was based on the fact that the lowest *Spartina anglica* plants that grow around 2.0 m above the Dutch Ordnance Level (m NAP) are flooded by approx. 25 cm water 10% of the time (Fig. 8). Our calculation showed

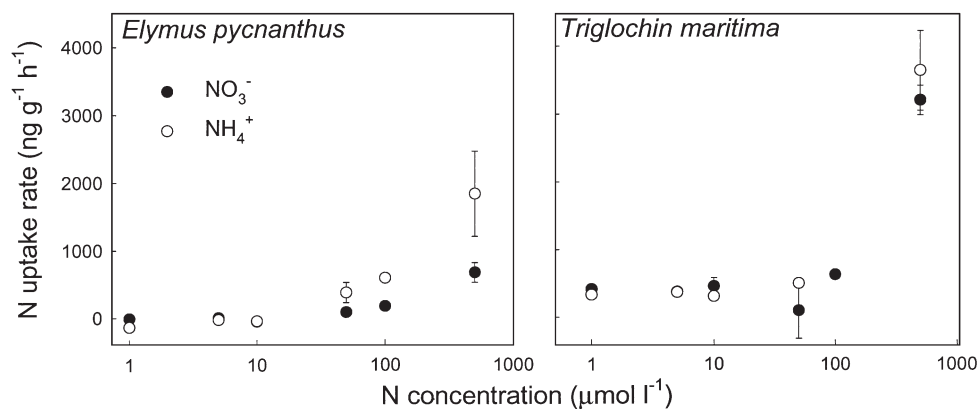


Fig. 3. *Elymus pycnanthus* and *Triglochin maritima*. Effects of N-form and N-concentration (C ; $\mu\text{mol l}^{-1}$) on uptake rates (V_{upt} ; $\text{ng [g dry mass]}^{-1} \text{h}^{-1}$) of detached leaves of plants sampled in the WS. The linear regression equations for NO_3^- and NH_4^+ uptake rates by *E. pycnanthus* were $V_{\text{upt}} = 1.3436 C$; $R^2 = 0.8066$, $p = 1.13 \times 10^{-9}$ ($n = 24$) and $V_{\text{upt}} = 3.7681 C$; $R^2 = 0.6574$, $p = 8.89 \times 10^{-7}$ ($n = 24$), respectively. The linear regression equations for NO_3^- and NH_4^+ uptake rates by *T. maritima*, were $V_{\text{upt}} = 6.3708 C$; $R^2 = 0.8401$, $p = 8.12 \times 10^{-10}$ ($n = 22$) and $V_{\text{upt}} = 7.3075 C$; $R^2 = 0.8598$, $p = 1.51 \times 10^{-9}$ ($n = 20$), respectively. Linear regression lines are not shown because of the log-transformed x-axes

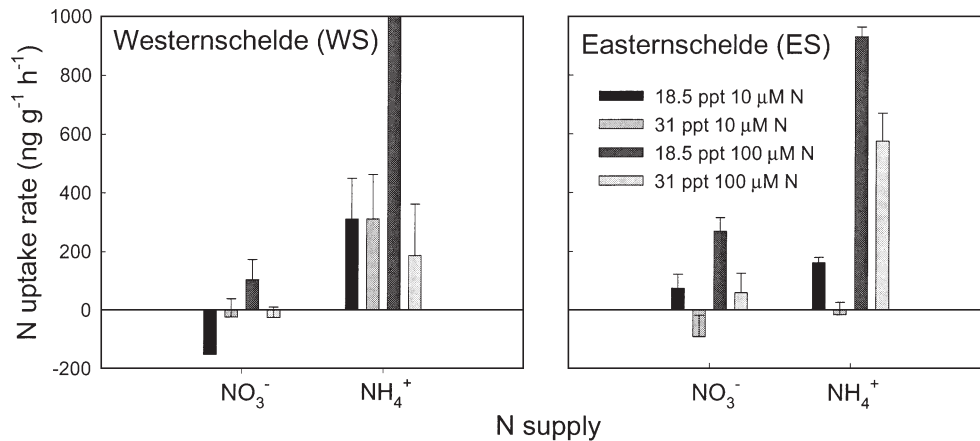


Fig. 4. *Spartina anglica*. Effects of salinity and N-concentration ($\mu\text{mol l}^{-1}$) on uptake rates ($\text{ng [g dry mass]}^{-1} \text{h}^{-1}$) of NO_3^- and NH_4^+ by detached leaves sampled from plants growing in the WS vs plants growing in the ES

that N-uptake by the shoots could only support a very low relative growth rate, even when we used the highest ^{15}N -uptake rates obtained for intact plants (Table 3). Since exponential growth mainly occurs at the early seedling growth stage we also calculated Eq. (5) the potential contribution of N-uptake by the shoots as a percentage of the N-requirements needed for the approximately linear increase in biomass that occurs from May to September. We maintained our assumption that the total shoots would on average be fully submerged for 2.4 h d^{-1} . In addition, we assumed a leaves/stem-ratio of 0.91 over the whole growth period (average for 225 *S. anglica* plots harvested in September 1999). Our calculations indicated that vegetation with a relatively high biomass per m^2 , as would be present later in the growth season, could receive a substantial NH_4^+ -supply from the shoots (30% max.: Table 4), provided that (1) NH_4^+ concentrations and

(2) flood frequency were sufficiently high. The reason is that during linear growth, new biomass is constantly being produced by a continuously increasing standing biomass (i.e. the RGR decreases over time). However, during the periods when the standing biomass is highest, the NH_4^+ concentrations in the flood water are generally very low (average of ca. $5 \mu\text{M}$: Fig. 1), thus enabling only a much smaller contribution of N-uptake by the shoots (10% max.: Table 4). In addition, complete flooding for 2.4 h d^{-1} becomes less realistic when plants grow taller (Fig. 8), as is the case towards the end of the growth season. Shorter periods of complete flooding proportionally decrease the relative contribution of N-uptake by the shoots to the N-requirements for growth. Hence, we conclude that N-uptake by leaves makes only a minor contribution (up to around 10%) to the N-requirements for plant growth in the frequently flooded *S. anglica* plants in the low marsh.

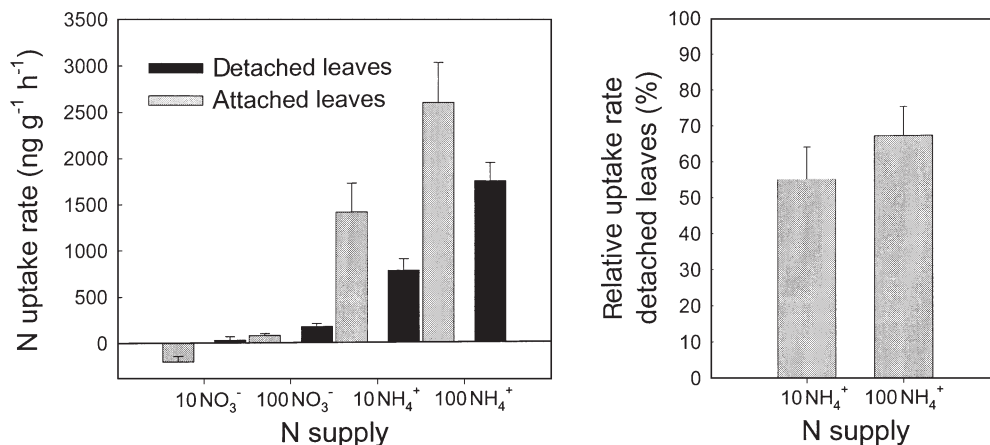


Fig. 5. *Spartina anglica*. Effects of leaf detachment on uptake rates ($\text{ng [g dry mass]}^{-1} \text{h}^{-1}$) of NO_3^- and NH_4^+ by leaves from plants cultivated in a climate room. NO_3^- and NH_4^+ were supplied at concentrations of 10 and $100 \mu\text{mol l}^{-1}$. For the NH_4^+ treatments the uptake rate of the detached leaves is expressed as a percentage of that of the attached leaves

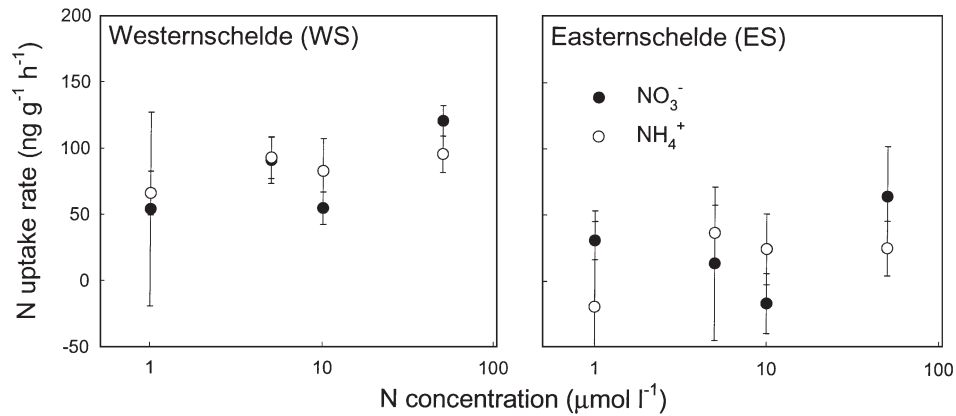


Fig. 6. *Spartina anglica*. Effects of N-concentration ($\mu\text{mol l}^{-1}$) on uptake rates ($\text{ng [g dry mass]}^{-1} \text{h}^{-1}$) of NO_3^- and NH_4^+ by attached leaves from plants growing in the WS vs plants growing in the ES. ^{15}N -labeling was provided to the plants by spraying the attached leaves

DISCUSSION

The present results clearly show that (1) selection of a proper application method (i.e. flooding intact plants) is essential for quantifying the N-uptake rate by leaves of salt-marsh species, and that (2) N-uptake by the shoots makes only a small contribution to the

N-requirements for growth in the salt-marsh species we studied. Under favorable conditions, N-uptake by the shoots could only cover the N-demand required to support a relative growth rate (RGR) of around $2.5 \text{ mg g}^{-1} \text{ d}^{-1}$ (Table 3) whereas most slow-growing species can easily reach an RGR of around $100 \text{ mg g}^{-1} \text{ d}^{-1}$ (Poorter & Remkes 1990, Poorter et al. 1991). In vege-

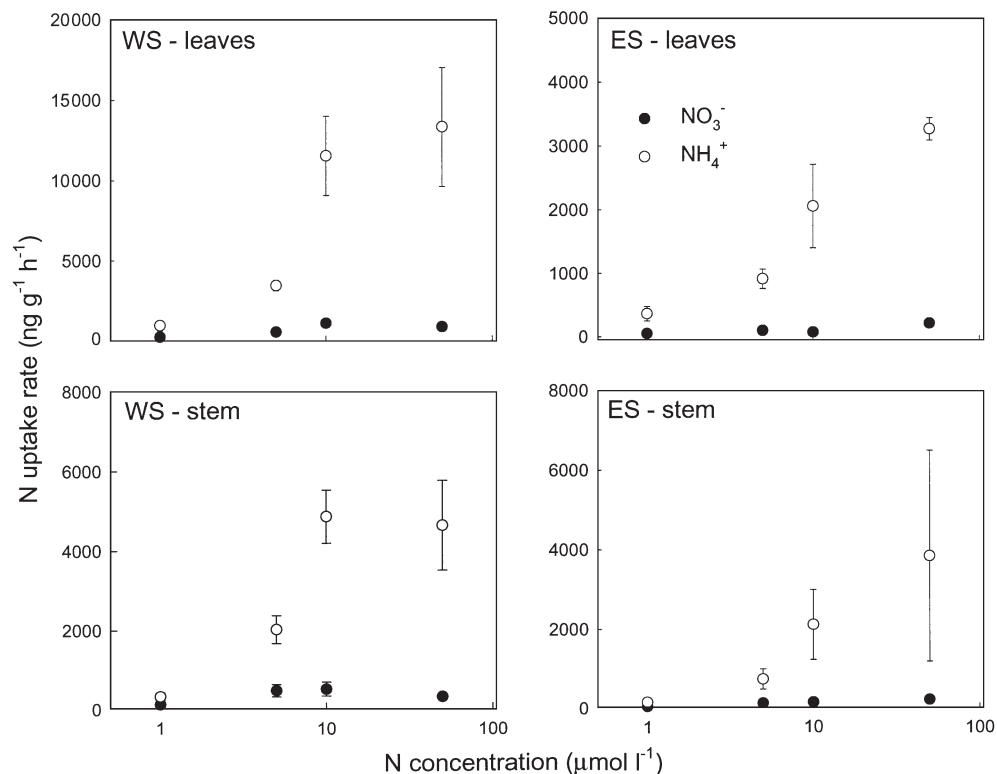


Fig. 7. *Spartina anglica*. Effects of N-concentration on uptake rates ($\text{ng [g dry mass]}^{-1} \text{h}^{-1}$) of NO_3^- and NH_4^+ by intact shoots (leaves plus stems), from plants growing in the WS vs plants growing in the ES. ^{15}N -labeling was provided to the plants by flooding

Table 3. *Spartina anglica*. Calculation of the maximum relative growth rate (RGR_{max} : $mg\ g^{-1}\ d^{-1}$; Eq. 4) that could be achieved under the assumptions that (a) flood water is the only N-source and (b) total shoot would on average be fully submerged for $2.4\ h\ d^{-1}$ (cf. Fig. 8). RGR_{max} was calculated for a range of NO_3^- and NH_4^+ concentrations similar to those observed in the field (Fig. 1), and for which we measured the uptake rates (Fig. 7)

Parameter	WS		ES	
	Leaves	Stem	Leaves	Stem
N-content	12.5	7.1	17.5	9.1
RGR_{max} at $1\ \mu M\ NO_3^-$	0.04	0.04	0.01	0.01
RGR_{max} at $5\ \mu M\ NO_3^-$	0.10	0.16	0.01	0.03
RGR_{max} at $10\ \mu M\ NO_3^-$	0.20	0.17	0.01	0.03
RGR_{max} at $50\ \mu M\ NO_3^-$	0.15	0.11	0.03	0.05
RGR_{max} at $1\ \mu M\ NH_4^+$	0.18	0.11	0.05	0.04
RGR_{max} at $5\ \mu M\ NH_4^+$	0.66	0.68	0.12	0.19
RGR_{max} at $10\ \mu M\ NH_4^+$	2.21	1.64	0.28	0.55
RGR_{max} at $50\ \mu M\ NH_4^+$	2.55	1.56	0.45	1.01

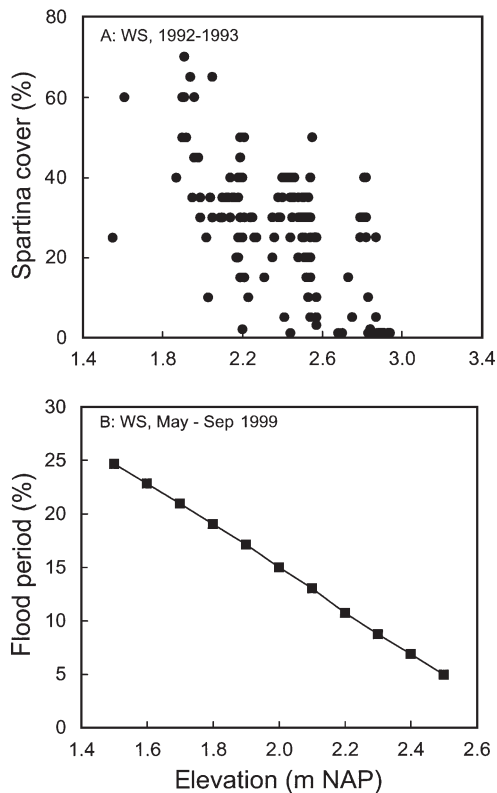


Fig. 8. *Spartina anglica*. Cover of (8A) and fraction of time that flooding occurs (B) as a function of elevation. Elevation is given in m above the Dutch Ordnance Level (m NAP). The data on cover were obtained at the Westernschelde marsh near Waarde during 1992 and 1993. The relative flood period was derived from measurements taken at Hansweert, situated about 10 km east of the Waarde marsh, over the period 1 May 1999 to 30 September 1999

tation with a relatively high biomass per m^2 as seen later in the growth season, N-uptake by the shoots could theoretically make a substantial contribution to the N-requirements for a linear increase in biomass (30% max.: Table 4). However, such a substantial contribution would require, at the end of the growth season, unrealistically high NH_4^+ concentrations in the flood water ($\geq 10\ \mu M\ NH_4^+$ for the period between June and September) and unrealistically long flood periods ($\geq 2.4\ h\ d^{-1}$ fully submerged). Lower NH_4^+ concentrations ($\sim 5\ \mu M$; Fig. 1) and shorter flood periods would, together, reduce the contribution of N-uptake by the shoots proportionally, so that a maximum contribution of around 10% seems a more realistic estimate (Table 4). Our findings thus emphasize the importance of other N-sources for plant growth. The present results suggest that in addition to N-recycling within

Table 4. *Spartina anglica*. Calculation of the maximum percentage of overall N-requirements for aboveground growth that could be met by NO_3^- and NH_4^+ taken up by the shoot from flood water ($U_{\%}$; %; Eq. 5). $U_{\%}$ was calculated over consecutive months, for the range of NO_3^- and NH_4^+ concentrations for which we measured uptake rates (Fig. 7). Our calculation was based on the assumptions that during the growth season (1) plant biomass increases linearly over time at a rate of $6.9\ g\ m^{-2}\ d^{-1}$, starting at $50\ g\ m^{-2}$ on 1 May (cf. Fig. 2 in Groenendijk 1984), (2) total shoot would on average be fully submerged for $2.4\ h\ d^{-1}$ (cf. Fig. 8), and (3) leaves/stem-ratio is 0.91 (average of 225 plots harvested in September 1999). ***Bold-italics:*** values $\geq 10\%$

	WS		ES	
	NO_3^-	NH_4^+	NO_3^-	NH_4^+
1 $\mu M\ N$				
May	0.1	0.3	0.0	0.1
June	0.2	0.8	0.0	0.2
July	0.3	1.2	0.1	0.4
August	0.5	1.6	0.1	0.5
September	0.6	2.1	0.1	0.6
5 $\mu M\ N$				
May	0.3	1.6	0.0	0.4
June	0.7	3.6	0.1	0.9
July	1.1	5.6	0.2	1.3
August	1.5	7.7	0.2	1.8
September	1.9	9.7	0.3	2.3
10 $\mu M\ N$				
May	0.4	4.5	0.0	1.0
June	1.0	10	0.1	2.3
July	1.6	16	0.2	3.6
August	2.1	22	0.2	4.9
September	2.7	28	0.3	6.1
50 $\mu M\ N$				
May	0.3	4.7	0.1	1.7
June	0.7	11	0.2	4.0
July	1.1	17	0.4	6.2
August	1.5	23	0.5	8.5
September	1.9	30	0.6	11

the plant, the root systems are the main source for acquiring external N, regardless of the strongly reduced anoxic soils that characterize the low marsh where these halophytes grow (Armstrong et al. 1985, Ewing et al. 1997). In other studies we have focussed on the root growth strategies (i.e. root architecture, root plasticity in relation to elevational height of a species habitat) that enable halophytic species to cope with such unfavorable soil conditions in the low marsh (Bouma et al. 2001a,b).

The relatively low uptake capacity of *Spartina anglica* leaves contrasts with the situation for rooted, submerged, aquatic plant species such as seagrasses, in which foliar uptake can contribute up to 90% of the overall N-requirement (see 'Introduction'). However, a 10% contribution of foliar N-uptake to the overall N-requirements for plant growth is not too different from the percentages in (e.g.) forest ecosystems (2 to 8%: Boyce et al. 1996; up to 5%: Wilson & Tiley 1998). Similarly, as found for aquatic (Touchette & Burkholder 2000) and terrestrial (Wilson 1992, Peuke et al. 1998, Ignatova & Dambrine 2000) angiosperms and marine algae (Lotze & Schramm 2000), we found that foliar uptake is generally higher for NH_4^+ than for NO_3^- . A linear increase in the uptake rate (Figs. 2 & 3) with increasing N-concentration has also been reported for other plant species, and possible implications of such a linear increase for the uptake mechanism have been discussed in detail by Wilson (1992).

The main question that arises is why halophytic plant species that grow in the low parts of N-limited tidal salt marshes (Valiela & Teal 1974, Kiehl et al. 1997) do not have a higher N-uptake capacity of their leaves. There may be a trade-off between having a high uptake capacity in the leaves and living in a tidal area. If a high uptake capacity of the leaves reduces survival during low tide, it will be selected against, as plants are only flooded during a short period of the day. One adaptation of *Spartina anglica* in our experiments is the strong hydrophobic characteristics of the upper layer of its leaves. During flooding, the upper leaves are shielded from the water by a thin layer of air (data not shown). This air layer not only prevents water intrusion through the stomata into the leaves, but also reduces the plant's capacity for foliar N-uptake and may thus represent a trade-off against living in a frequently flooded area. No such air layer is however present around the lower leaves, which lack stomata. The low N-uptake despite the absence of a hydrophobic layer at the lower leaf level indicates that the lower leaves must have a relatively impermeable cuticle with few carriers for N-transport. Such an impermeable cuticle will help to prevent the leaves from excessive water loss during low tide and excessive leaching from (in)organic solutes during high tide.

Summarizing, even though nitrogen limits plant growth in most salt marshes, we found that foliar N-uptake from the tidal water does not make an important contribution to *Spartina anglica*'s N-requirement at the NO_3^- and NH_4^+ concentrations present in the tidal water during its growth season. This is in contrast to the foliar uptake seen in many submerged aquatic species. Its low capacity for N-uptake is probably (at least partly) due to the hydrophobic characteristics of the upper layer of its leaves and the impermeable cuticle of the lower leaves, representing a trade-off against living in a habitat that is regularly flooded.

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