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NITROGEN FIXATION, AS DETERMINED BY ACETYLENE REDUCTION, IN TWO SALT MARSHES OF MINAS BASIN[1]

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Rates of acetylene reduction to ethylene were measured and expressed as nitrogen fixation in two Minas Basin salt marshes subjected to tides of extremely high amplitude. Rates both at the soil surface and below ground were low throughout the season. The mean subsurface rate of reduction was equivalent to about 25 μg N $m^{-2}h^{-1}$, or 1 to 2% of the total requirements of the dominant angiosperm species (*Juncus gerardii, Spartina patens,* and *S. alterniflora).* At the soil surface the reduction rate was about 50 μg N $m^{-2}h^{-1}$, and was associated mainly with species of *Oscillatoria* and *Lyngbya* in the early and mid summer, as well as with *Anabaena* in late summer. Combined nitrogen (NO_3, NO_2, NH_4) was high in both soil and estuarine waters, but declined somewhat during the summer, and may possibly have inhibited N_2 fixation. Thus, these marshes may not be nitrogen limited.

Introduction

Salt marshes on the Atlantic coast of North America are among the most productive, non-agricultural ecosystems in the world (Odum 1971; Seneca 1974). As the annual production of these marshes decomposes, tidal action removes much of it in particulate form (Teal 1962), providing an important nutrient pool in surrounding waters (Teal 1962; Reed & Moisan 1971; Mann 1975). Marshes also contribute dissolved organic and sometimes inorganic nitrogen (Armstrong et al. 1975; Dawson & Armstrong 1975; Heinle & Flemer 1976), phosphate (Reimold 1972), and silica (Gardner 1975) to receding tidal waters.

Halophytic grasses and phorbes are the dominant angiosperms on salt marshes, and growth of these plants may be limited by lack of nitrogen (Valiela & Teal 1974; Broome et al. 1975). The apparent incongruity of net nitrogen export from a nitrogen limited system has led to the investigation of salt marshes for N_2 fixation (Carpenter et al. 1978; Patriquin & Keddy 1978; Patriquin & McClung 1978), with 2 major sites of N_2 fixation being identified: bacteria associated with the roots of angiosperms (belowground N_2 fixation), and cyanobacteria (blue-green algae), both heterocystous (Jones 1974; Van Raalte et al. 1974; Whitney et al. 1975) and non-heterocystous (Carpenter & Price 1977; Stewart 1975; 1977) species, growing on mud surfaces. Heterotrophic bacteria in sediments have been found to fix much less nitrogen than cyanobacteria (Jones 1974, Whitney et al. 1975). Patriquin and McClung (1978)

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estimated N_2 fixation associated with the roots of *Spartina alterniflora* to be 93 kg N ha^{-1} yr^{-1} in a marsh of the Atlantic coast of Nova Scotia, equivalent to 60% of the nitrogen accumulated by *S. alterniflora*. Carpenter et al. (1978) reported similar rates for a Massachusetts marsh. Patriquin and McClung (1978) estimated N_2 fixation at the mud surface of an Atlantic coastal marsh to be 22 kg N ha^{-1} yr^{-1}, attributing most of this activity to species of *Lyngbya*.

Extensive areas of salt marsh occur along the shores of Minas and Chignecto basins, at the head of the Bay of Fundy. These basins are characterized by large tidal amplitudes, rapid tidal currents, and large amounts of materials suspended in the water column (Bousfield & Leim 1960; Pelletier & McMullen 1972; Dalrymple et al.1975). We examined 2 sites on the Minas Basin marshland, for: N_2 fixation, nitrate reductase activity of the angiosperms, and combined nitrogen content of the soils and flooding waters.

Materials and Methods

Study Sites

Two transects were established at sites on Minas Basin, both in Kings Co., N.S., one near the community of Kingsport, the other near Grand Pré. The Kingsport marsh is well established and mature; the age of Grand Pré marsh is about 15 years, being the result of recent dyking. These transects were established in the spring of 1977. Data were collected biweekly from April through August. Acetylene reduction data are from 1977 and 1978; other data are from 1978 only.

Further details of the conformation and floristic composition of these transects is in the report of Smith (1978), and will be published separately.

Soil-Surface Algae

Circular, 8 cm diameter, samples of the mud surface were taken in the vicinity of each sampling station. These were examined microscopically, and the dominant species of cyanobacteria noted.

Angiosperm Nitrogen Requirements

Aboveground angiosperm production (maximum seasonal standing crop) was measured by cutting, drying, and weighing the biomass contained in 0.25 m^2 quadrats. The percentage of nitrogen in above- and belowground tissue was determined by Kjeldahl analyses.

Acetylene Reduction Assay

Reduction of acetylene to ethylene, a widely used procedure for expressing nitrogenase activity (Carpenter et al. 1978; Patriquin & McClung 1978; Hardy et al. 1968), was measured by the in situ method as was done previously (Patriquin & Denike 1978). Acetylene (10 kPa) was generated inside each cylinder by the addition of water to calcium carbide. Areas of mud surfaces (200 cm^2) were incubated with acetylene (10 kPa) in 500 ml specimen jars, allowing separation of surface and belowground acetylene reduction. Five ml samples of gas were removed from the cylinders and jars at 2 and 26 h. Nitrogen fixation was calculated using a ratio of 3 acetylene molecules reduced for each molecule of nitrogen (N_2) assumed to be fixed (Hardy et al. 1968). As no ethylene production was detected in aerobic or anaerobic controls, the measured rates of acetylene reduction were applied directly to the calculations.

Combined Nitrogen Determinations

Water samples were collected in 500-ml acid-washed, polyvinylchloride bottles. Samples were taken from: estuarine water at the end of the Grand Pré transect, water seeping into holes (15 cm deep) dug in the marsh (soil water), and water draining out of the marsh soil. The latter was collected from small streams draining the marshes; only Zones 1, 2 and 3 of the Kingsport marsh yielded soil water. Samples were frozen on dry ice immediately, and held at -40° until analysis. Nitrate, nitrite, and ammonium were determined by the methods given in Strickland and Parsons (1972).

Assay of Nitrate Reductase Activity

Sods of *Juncus gerardii, Spartina patens,* and *S. alterniflora* were transported to the laboratory and held overnight in a growth chamber (25°, 16:8 h L:D, darkness commencing at 2000 h). The following day the soil was washed from the sods, and 200 mg of shoot and root tissue were taken from each. Tissue samples were chopped into 1 mm segments and incubated in darkness at 25° for 1 h in 25 ml flasks each containing: 1.6 ml 25% *n*-propanol, 3.0 ml 0.2 M KNO_3, 1.0 ml NaOH (1 Mg) solution, 2.0 ml 0.5 M potassium phosphate buffer (pH 7.5), 2.4 ml water, and 0.15 g NaCl (modified from Jaworski 1971). Immediately before dark incubation, flasks containing samples were evacuated (4 withdrawals with a 50-ml syringe) and backfilled with dinitrogen.

Samples of shoot tissue were always taken from the youngest, fully expanded blade. Root tissue was taken from near the root tips. One-ml samples of the medium were removed from each flask at 0 and 60 min, and analysed for nitrite (Strickland & Parsons 1972). Dry weight of the plant material was determined after the assay.

Results

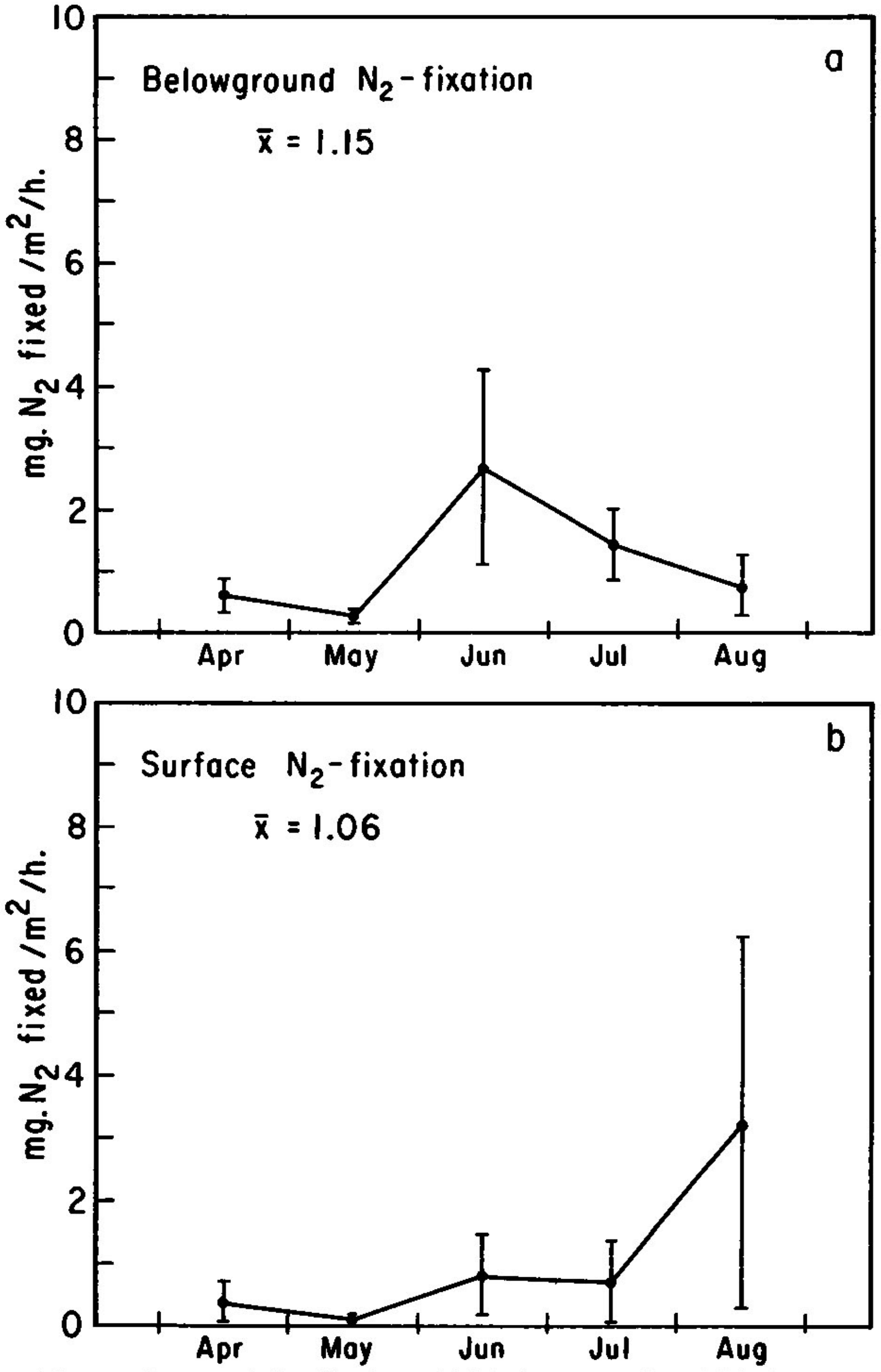
Belowground Nitrogen Fixation

On both Kingsport and Grand Pré marshes, there was a peak in N_2 fixation in spring (Figs 1 and 2). The average rates of belowground N_2 fixation were similar in both marshes, and were low compared with values reported for other Atlantic coast marshes (Table I). *Spartina alterniflora* and *J. gerardii* fixed similar amounts of nitrogen, whereas *S. patens* fixed only about one-half this amount (Table II).

Mud Surface Nitrogen Fixation

Rates of N_2 fixation by organisms on the mud surfaces of both marshes were low until late August when an abrupt increase was observed (Figs 1 and 2). From April to July, when the rates were low, species of the non-heterocystous genera, *Oscillatoria* and *Lyngbya* were the dominant cyanobacteria of the mud surfaces. In August, coincident with the sudden increase in N_2 fixation, there was an increase in biomass of *Anabaena* (Table II), with circular mats up to 20 cm in diameter appearing on the surface of the mud. These mats were more common in the lower zones of the marshes where the biomass of cyanobacteria had previously been low. One such mat reduced acetylene at the rate of 400 $\mu M\ m^{-2}\ h^{-1}$. Within 2 weeks of the last sampling, autumn storms had fragmented and to a large extent buried these mats.

The fine surface sediments of the lower zones of *S. alterniflora* are subjected to twice daily tidal resuspension, and resulting substrate instability may be responsible for low numbers of cyanobacteria and thus low rates of N_2 fixation observed in these areas. In general, surface N_2 fixation was associated with photosynthetic organisms in the sediments, and Table II lists dominant species of cyanobacteria noted on the marshes during each of the summer months.



Figs 1 and 2. Seasonal distribution of (a) belowground and (b) aboveground N_2 fixation at Grand Pré (Fig 1) and Kingsport (Fig 2). Each point is the average of 8 or 16 measurements. The vertical bars represent $\pm 25\bar{x}$. The measurements for these averages were taken during 2 summer seasons.

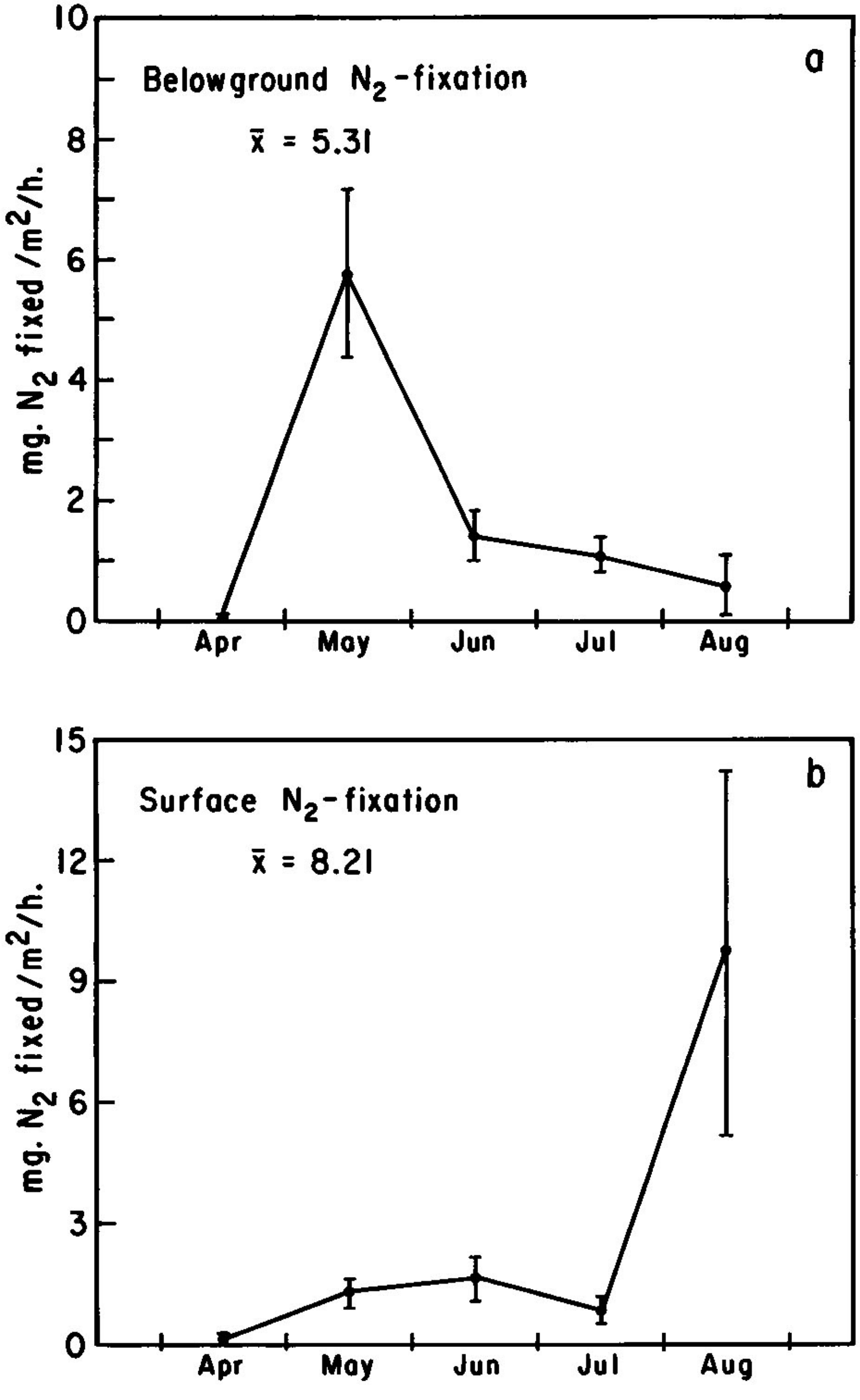

10
8
6
4
2
0
mg. N₂ fixed /m²/h.
Belowground N₂-fixation
x̄ = 5.31
a
Apr
May
Jun
Jul
Aug
15
12
9
6
3
0
mg. N₂ fixed /m²/h.
Surface N₂-fixation
x̄ = 8.21
b
Apr
May
Jun
Jul
Aug

Fig. 2

Table I. Above- and belowground rates of N_2 fixation on Grand Pré, Kingsport, and several other marshes of the Atlantic coast.

Site	Grand Pré*	Kingsport*	Other
$\mu g\ N\ m^{-2}\ h^{-1}$ (surface) n = 56)	66.8 ± 47.3	47.3 ± 36.5	625 (Carpenter et al. 1978) 800 (Patriquin and McClung 1978)
$\mu g\ N\ m^{-2}\ h^{-1}$ (below ground) (n = 56)	28.6 ± 24.8	23.8 ± 17.8	3,300 (Carpenter et al. 1978) 3,000 (Patriquin and McClung 1978)
Mud Flats			
$\mu g\ N\ m^{-2}\ h^{-1}$ (n = 14)	9.8 ± 9.6	15.2 ± 10.5	

* average of 2 summer seasons

Table II. Dominant species of cyanobacteria of the Kingsport and Grand Pré transects during the periods indicated.

Month	Kingsport	Grand Pré
April	*Oscillatoria brevis*	*Oscillatoria brevis*
May	*Oscillatoria brevis*	*Oscillatoria brevis*
June	*Oscillatoria brevis* *Oscillatoria margaritifera* *Lyngbya confervoides* *Microcoleus* sp	*Oscillatoria brevis* *Lyngbya confervoides*
July	*Oscillatoria brevis* *Oscillatoria corallinae* *Lyngbya confervoides* *Microcoleus* sp	*Oscillatoria brevis* *Oscillatoria margaritifera* *Lyngbya confervoides*
August	*Anabaena spherica* *Anabaena subcylindrica* *Oscillatoria brevis* *Oscillatoria corallinae* *Oscillatoria princeps*	*Anabaena subcylindrica* *Oscillatoria brevis* *Oscillatoria princeps* *Lyngbya confervoides*

The rates of N_2 fixation by organisms living on the surface of the mud beyond the angiosperms cover were comparable for the 2 study sites, and much lower than rates amongst the angiosperms (Table I). The instability of the sediments may restrict the types of species, in addition to numbers, capable of inhabiting the sediments. No cyanobacteria were noted in the mud sediments, and quite possibly N_2 fixation here was associated with heterotrophic bacteria.

Nitrogen Accretion in Angiosperms

Concentrations of nitrogen in shoot and root tissue declined throughout the sampling period (Table III), except in root tissue of *J. gerardii* which showed an abrupt increase near the end of the growing season. For all angiosperm species, belowground N_2 fixation could have supplied only 1 to 2% of the total nitrogen accumulated (Table IV).

Nitrate Reductase Activity

In the aboveground tissues of all 3 species assayed, and in belowground tissues of *J. gerardii* and *S. patens,* nitrate reductases activity (per g dry wt) declined during summer. The root tissue of *S. alterniflora,* both tall and short forms, also declined throughout most of the summer, but increased markedly in late July (Fig 3) just prior to the onset of flowering. A similar pattern of nitrate reductase activity was observed in a marsh of the Atlantic coast of Nova Scotia by Livingstone (1978), although the absolute rates observed were about 100 fold greater than ours.

Combined Nitrogen in Soil and Estuarine Waters

Concentrations of nitrate, nitrite, and ammonium, in both soil and seepage waters, declined as the growing season progressed (Table V). Nitrate in the estuarine waters also declined during this time.

We found that the concentration of nitrate in the estuary water showed a strong positive correlation with the amount of sediment suspended in the water column. This relations best fitted the line $y = 7.15 + 0.69$, where y is the concentration of nitrate in μg -at l^{-1} and x is g dry weight of sediment l^{-1} ($r = 0.95$). For this reason nitrate concentrations in Table V are given in μg at g dry sediment $^{-1}$. Both sediment and nitrate levels varied inversely with tide height. Sediment and nitrate concentrations were as low as 1.5g dry weight l^{-1} and 7.2μg-at l^{-1}, respectively, at high tide and as high as 28g dry weight l^{-1} and 24μg-at l^{-1}, respectively, at low tide.

Discussion

Studies of salt marshes bordering bodies of water with much smaller tidal amplitudes than the Bay of Fundy suggest that the amounts of combined nitrogen imported into these marshes each season are insufficient to account for the observed productivity. This topic has been reviewed by Hanson (1977). High levels of N_2 fixation are characteristic of these marshes (Carpenter et al. 1978; Patriquin & McClung 1978; Patriquin & Keddy 1978), and may supply the balance of the nitrogen required. Even so, these marshes are considered to be nitrogen limited (Valiela & Teal 1974; Broome et al. 1975).

The rates of belowground N_2 fixation in Minas Basin marshes are much lower than those reported for other marshes. Assuming complete transfer of fixed nitrogen from rhizosphere bacteria to the host angiosperm, nitrogen from this source, based on our in situ measurements, should supply only 1 to 2% of the requirements of the higher plants. Even if the rate is 5-fold higher as suggested by Patriquin & Denike

Table III Percent nitrogen in above- and belowground angiosperm tissue at various times during the summer. Each value is the average of 2 replicates differing at most from each other by 3%.

Zone	Tissue	Percent Nitrogen				Species
		June 14	July 12	July 27	August 9	
KP1*	Shoot	2.15	1.38	1.01		*Juncus*
	Root	0.95	0.38	1.14		*gerardii*
KP2*	Shoot	1.03	0.95		0.60	*Spartina*
	Root	0.93	0.83		0.74	*patens*
KP4*	Shoot	2.11	1.02		0.97	*Spartina*
	Root	1.66	1.21		1.09	*alterniflora* (tall form)
GP2**	Shoot	1.92	1.34		0.95	*Spartina*
	Root	0.79	0.74		0.55	*alterniflora* (short form)

* Kingsport
** Grand Pré

Table IV. Comparison of annual accumulation of nitrogen in angiosperms with total annual nitrogen fixation.

Species	% N at max biomass		g m^{-2} yr^{-1}	N fixed x 100	
	Shoot	Root	N accumulated	N accumulated	
Juncus gerardii	1.38	0.83	13.39	0.210	1.57
Spartina patens	0.60	0.74	9.19	0.137	1.49
Spartina alterniflora	0.99	0.76	13.62	0.243	1.78

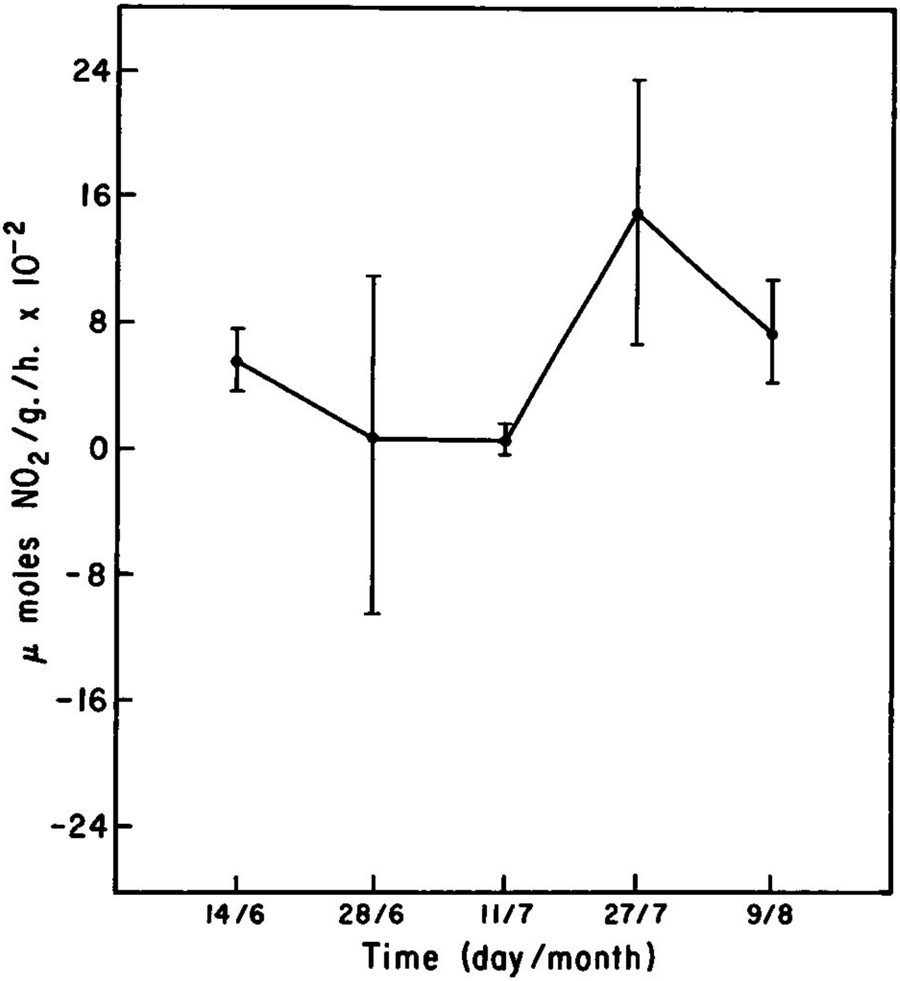


Fig 3. The seasonal distribution of nitrate reductase activity in the root tissue of *S. alterniflora* from zone 4 of the Kingsport marsh. The points are the averages of 3 values and are given $\pm 2S\bar{x}$.

(1978), nitrogen fixed belowground in Minas Basin marshes could have supplied only about 7.5% of the angiosperm requirement.

Nitrogen fixation is suppressed by some forms of combined nitrogen (Shanmugam & Morand 1974; Burns & Hardy 1975), and suppression in situ by ammonium may occur in some marshes (Patriquin & Keddy 1978). The large tidal amplitudes of Minas Basin results in rapidly flowing currents, large loads of suspended matter, and complete mixing of the water column. This is probably the cause of the high concentrations of combined nitrogen in soil and estuarine waters which may possibly supply the nitrogen requirements of the marsh angiosperms and inhibit N_2 fixation. It is further possible that the high levels of ammonium and nitrate observed in the reducing marsh soils supply much of the angiosperms nitrogen and bring about the low rates of nitrate reductase activity observed in these plants (Fig. 2).

The lower levels of combined nitrogen in the soil and estuarine waters during late

Table V. Concentration of combined nitrogen in soil water, drainage water, and estuarine water of the Kingsport marsh during the summer season.

		Soil water (μg-at ℓ^{-1})		
Zone	Date	Nitrate	Nitrite	Ammonium
1	6 June	21.0 + 2.8	10.7 + 1.2	1.1 + 0.2
1	7 July	18.9 + 0.6	7.6 + 0.6	0.8 + 0.1
2	28 June	14.9 + 1.1	7.3 + 0.2	0.3 + 0.4
2	27 July	12.1 + 0.7	6.7 + 0.3	0.1 + 0.0
3	12 July	9.8 + 0.8	3.5 + 0.7	0.1 + 0.0
3	27 July	5.2 + 0.1	1.3 + 0.2	Trace

		Drainage water (μg-at ℓ^{-1})		
Site	Date	Nitrate	Nitrite	Ammonium
Kingsport	28 June	14.5 + 5.7	3.6 + 0.1	0.03 + 0.01
Kingsport	27 July	9.2 + 0.1	3.2 + 0.2	0.02 + 0.01
Grand Pré	14 June	29.6 + 0.3	11.1 + 0.1	1.2 + 0.1
Grand Pré	27 July	14.7 + 0.1	5.5 + 0.9	1.1 + 0.1

	Estuarine water
Date	(μg-at NO_3 g sediment dry wt^{-1})
June 14	93.0 91.2
July 11	85.1 81.1
July 27	73.4 71.3
August 9	55.5 53.3

Values are the average of 3 measurements and are given ± 25$\bar{x}$.

summer may have conferred a slight advantage to the more efficient N_2-fixing heterocystous cyanobacteria, resulting in the proliferaton of *Anabaena* in August However, similar changes in species composition have not been noted on other marshes.

As with belowground N_2 fixation, the amounts of nitrogen fixed at the marsh surface during the growing season was low (Table I). Here again it is likely that high levels of combined nitrogen in the marsh soils and estuarine waters inhibited N_2 fixation.

The nitrate-sediment correlation was surprising as nitrate concentrations were determined after the water samples had been filtered. Possibly nitrate ions are associated with positively charge ions bound to the clay particles suspended in the water, and they are removed during the filtration process.

We suggest that, unlike salt marshes on the Atlantic coast of the province, Minas Basin marshes are not nitrogen limited. The rapidly flowing tidal currents of the Basin result in high levels of combined nitrogen in the water column. This in turn results in high levels of soil nitrogen in the marshes which supplies most of the requirements of the marsh species. However, data presented by Smith (1978) suggest that other factors may limit productivity on these marshes.

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