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Seasonal flooding, nitrogen mineralization and nitrogen utilization in a prairie marsh

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Abstract. Flooding can be an important control of nitrogen (N) biogeochemistry in wetland ecosystems. In North American prairie marshes, spring flooding is a dominant feature of the physical environment that increases emergent plant production and could influence N cycling. I investigated how spring flooding affects N availability and plant N utilization in whitetop (*Scolochloa festucacea*) marshes in Manitoba, Canada by comparing experimentally spring-flooded marsh inside an impoundment with adjacent nonflooded marsh. The spring-flooded marsh had net N mineralization rates up to 4 times greater than nonflooded marsh. Total growing season net N mineralization was 124 kg N ha^{-1} in the spring-flooded marsh compared with 62 kg N ha^{-1} in the nonflooded marsh. Summer water level drawdown in the spring-flooded marsh decreased net N mineralization rates. Net nitrification rates increased in the nonflooded marsh following a lowering of the water table during mid summer. Growing season net nitrification was 33 kg N ha^{-1} in the nonflooded marsh but <1 kg N ha^{-1} in the spring-flooded marsh. Added NO_3^- induced nitrate reductase (NRA) activity in whitetop grown in pot culture. Field-collected plants showed higher NRA in the nonflooded marsh. Nitrate comprised 40% of total plant N uptake in the nonflooded marsh but $<1\%$ of total N uptake in the spring-flooded marsh. Higher plant N demand caused by higher whitetop production in the spring-flooded marsh approximately balanced greater net N mineralization. A close association between the presence of spring flooding and net N mineralization and net nitrification rates indicated that modifications to prairie marshes that change the pattern of spring inundation will lead to rapid and significant changes in marsh N cycling patterns.

Key words: ammonium, marsh, mineralization, nitrate, nitrification, nitrogen

Introduction

Seasonal water level fluctuations in shallow marshes of the northern North American great plains are a dominant feature of the physical environment that can regulate important ecosystem functions. Links between spring flooding and some functions, such as emergent plant production, are well established. Prairie marsh sedges and cool season grasses concentrate their growth in early spring during the period when flooding typically occurs. In years that marshes are flooded during May and June, growth begins before ice-out and flowering is complete by early July (Smith 1973a; Neckles et al. 1985). In the absence of spring flooding, growth is delayed and flowering does not occur. Plant biomass and productivity are higher in spring-flooded marshes compared with marshes that are not inundated (Smith 1973b; Clay & Nelson 1986; Neckles et al. 1985; Neill 1990).

Links between flooding and other functions, such as nitrogen (N) biogeochemistry are not as well known but potentially important. By controlling the duration of soil oxic and anoxic periods, flooding can be a major influence on wetland N biogeochemistry. Flooding affects organic matter decomposition and microbial N mineralization which regulate the net release of NH_4^+ to soil solution (Turner & Patrick 1968; Godshalk & Wetzel 1978). Understanding the controls on NH_4^+ production is important because NH_4^+ is an important plant nutrient. Recycled N is the most important source of plant-available N in many freshwater wetlands (Bowden 1987) and N typically limits emergent plant growth in prairie marshes (Neely & Davis 1988; Neill 1990). Nitrification of NH_4^+ during periods of soil drying can also influence N availability by controlling N losses (Groffman & Tiedje 1989; Zak & Grigal 1991) or by changing the relative availability of NH_4^+ and NO_3^- where plants have different capabilities to take up inorganic N forms (Mendelssohn 1979).

I investigated how flooding influences N biogeochemistry in a prairie marsh to determine if patterns of net N mineralization and N utilization caused by spring flooding were consistent with the early spring growth and higher plant production. To determine whether high net N mineralization coincided with the period of spring flooding, I compared soil extractable inorganic N concentrations, net mineralization rates and net nitrification rates in a marsh that was manipulated to be spring flooded and an adjacent nonflooded marsh. I also examined plant NH_4^+ and NO_3^- preference, NO_3^- utilization as indicated by nitrate reductase activity and total plant N uptake to determine if flooding results in a tight coupling between inorganic N forms, N mineralization and plant N utilization.

Methods

Study sites

Stands of whitetop (*Scolochloa festucacea* [Willd.] Link) in the Delta marsh, a 20,000 ha lacustrine prairie marsh at Delta, Manitoba, Canada (50°11′ N, 98°19′ W) served as study areas (Fig. 1). Whitetop covers large areas of the Delta marsh and other prairie wetlands on slightly to moderately saline soils (Stewart & Kantrud 1972). It forms essentially monospecific stands in areas that are flooded in spring but dry by mid summer of most years (Löve & Löve 1954).

Spring-flooded and nonflooded study sites were established inside and outside a 25 ha marsh impoundment (Fig. 1). Water level in the impoundment

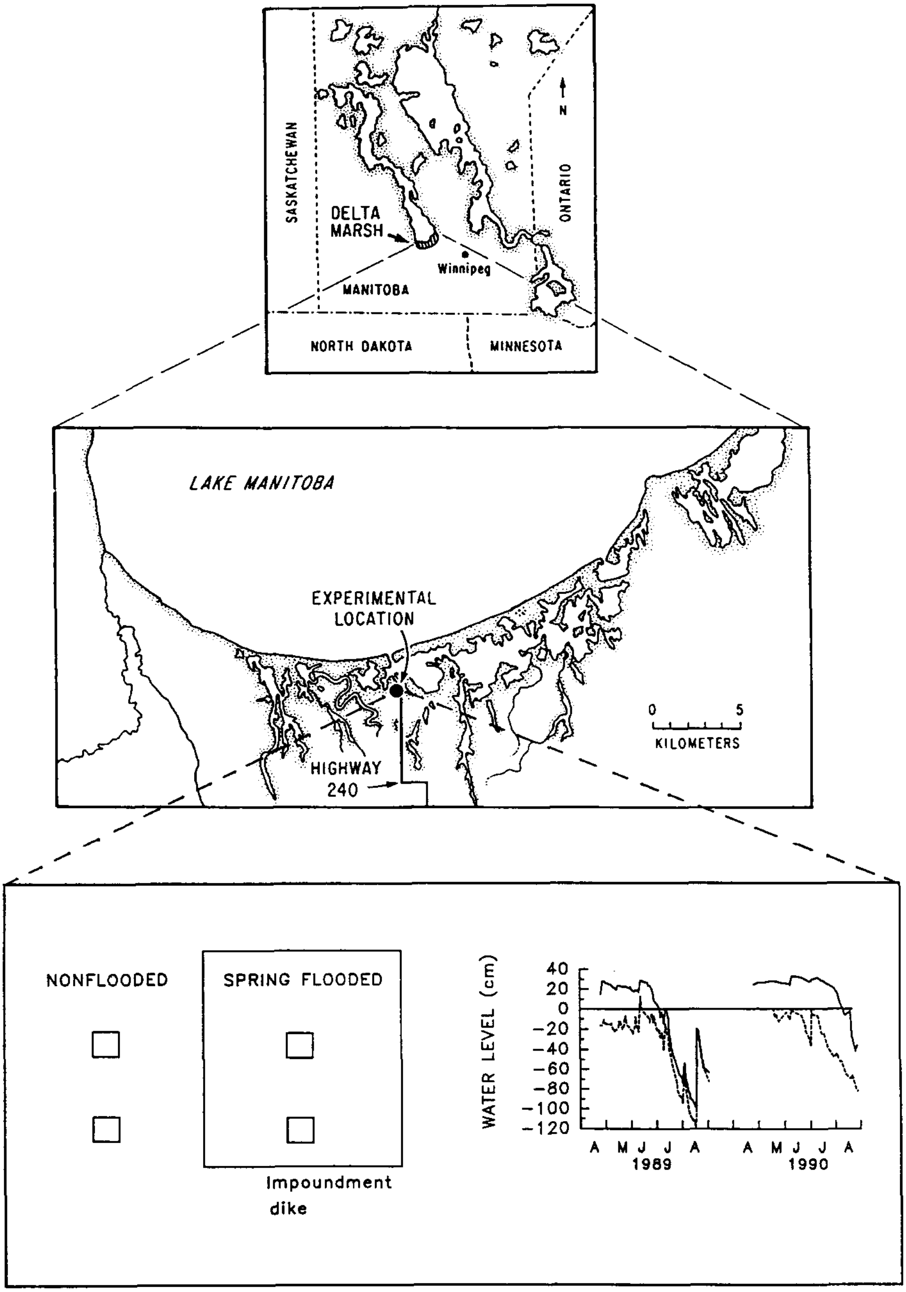

Fig. 1. Location, experimental design and water levels in the spring-flooded (——) and nonflooded (.....) whitetop marshes used in this study. The water level in the impoundment was maintained by pumping surface water from the Delta marsh. Samples were collected from two 30 m × 30 m plots in each marsh.

Table 1. Soil characteristics in the spring-flooded and the nonflooded marshes

	Spring flooded	Nonflooded
pH	7.1	7.2
Percent organic matter	23.6	24.6
Bulk density (g cm^{-3})	0.64	0.63
Mineral soil texture		
percent sand	47	57
percent silt	36	23
percent clay	17	21
Texture class	Loam	Sandy Loam
Classification	Humaquept	Humaquept

was raised to 20–30 cm in late April of 1989 and 1990 and drawn down below the soil surface on 10 July 1989 and 1 August 1990. This mimicked the spring-flooded water level regime during wet years when whitetop marshes are flooded through mid summer (Millar 1973; Neckles et al. 1985; Kantrud et al. 1989). Marsh directly outside the impoundment was not flooded. Higher water levels during the spring of 1990 inundated the area used as the nonflooded marsh in 1989 and required selection of a different area of nonflooded marsh on similar soil at slightly higher elevation in 1990. The flooded and nonflooded marsh soils had similar pH, organic matter content, bulk density and texture (Table 1). The water level regime in the nonflooded marshes was characteristic of dry years when whitetop marshes experience a high soil water table during spring but are not inundated.

Plant cover in the spring-flooded marsh was >99% whitetop. The nonflooded marshes contained whitetop and less than 20% cover of other species that are typical of prairie wet meadows, including sow thistle (*Sonchus arvensis* L.), Canada thistle (*Cirsium arvense* [L.] Scop.), orach (*Atriplex patula* L.) and asters (*Aster* spp.). Soils overlaid lacustrine deposits and had organic horizons 5 to 20 cm deep and buried horizons of sand and gravel that occurred to depths greater than 1 m.

All samples were collected from four 30 m × 30 m plots laid out in the spring-flooded and nonflooded marshes (Fig. 1). Requirements for dikes and pumping prevented replication of the flooding manipulation. Several factors, however, make it reasonable to interpret differences between these treatments as the consequence of the water level manipulation. First, the spring-flooded and nonflooded marshes were all part of a large, contiguous marsh before the construction of the water control dikes. Second, the marshes had a nearly identical flooding regime until 1987 when spring flooding was initiated in the impoundment. Third, soil characteristics of pH, organic matter content, bulk density and texture were similar among sites.

Environmental conditions, plant production and nitrogen dynamics

Water level and water table depths were measured several times weekly in one plot of each marsh. To determine the effect of flooding on soil anoxia, oxidation-reduction potentials (Eh) at 5 cm depth were recorded in each plot in both marshes four times during the growing season. Eh was measured with polished platinum electrodes relative to a separate double-junction Calomel (Ag/AgCl) reference electrode following the method of Howes et al. (1981). Eh was calculated as +0.242 V relative to the measured value. Electrodes were allowed to equilibrate in place for 10 minutes before readings and were cleaned with emery cloth and deionized water between measurements. Eight measurements were made at each date in each plot. Sampling points in each plot were every 3 m beginning at a randomly selected point.

Aboveground production was estimated from six 0.25 m^2 quadrats clipped approximately monthly from each plot in the spring-flooded and nonflooded marshes from April to August 1990. Quadrat locations were chosen every 3 m in a line from a randomly selected point. Care was taken to avoid reclipping the same location. Standing crop is a good estimate of net aboveground production in whitetop marshes because growing season shoot turnover is low (Neill 1992).

Soil extractable inorganic N concentrations were determined from six 5- cm diameter, 15- cm deep soil cores from each plot in the flooded and nonflooded marshes collected monthly in 1989 and bimonthly in 1990. Collection locations at each date were points every 3 m in a line from a point selected at random. During 1990, buried bag incubations (Eno 1960; Nadelhoffer et al. 1983) were used to measure net N mineralization and net nitrification rates. Cores for incubation were set out at each date cores were collected for extractable N. They were paired <10 cm away from the initial cores, placed in sealed polyethylene bags and returned to their original core holes. The incubated cores were collected after 13–14 d when new cores for extractable N were collected and a new samples for incubation were set out.

Collected cores were stored at 4 °C and extracted within 48 h. In the laboratory, core wet weight was determined and a subsample was dried at 105 °C for wet/dry weight conversion and determination of dry bulk density. Each core was homogenized and roots were removed by hand. Soil was extracted by shaking 20 g of fresh soil in 100 ml of 2N KCl for 4 h.

Ammonium concentration in the KCl extracts was determined on the day of extraction colorimetrically by the salicylate-hypochlorite method (Bower & Holm-Hansen 1980). A subsample of the extract was immediately frozen for later analysis of NO_3^--N + NO_2^--N (hereafter referred to as NO_3^--N) by cadmium reduction on an Alpkem RFA autosampler. Net N mineralization rate was calculated as the concentration of NH_4^+-N and NO_3^--N in the incubated samples minus the concentration in the initial unincubated samples. Net nitrification rate was calculated as the difference in NO_3^--N between the beginning and end of the incubation. Net N mineralization and net nitrification rates for the growing season were converted to an areal basis using the mean of bulk density calculated for each site from cores collected for initial extractable N concentrations.

Plant nitrogen utilization

Whitetop N uptake for 1990 was calculated from monthly plant production and plant tissue N concentrations and from the buried bags. Because belowground production was not measured in 1990, production numbers were taken from monthly ingrowth into mesh bags measured in the spring-flooded and nonflooded marshes during 1989 (Neill 1994). Plant tissue N concentrations were determined from 3 samples of above- and belowground tissues chosen at random from the monthly above- and belowground biomass collections at each date, dried at 60 °C and ground to pass through a 1.3 mm mesh screen in a Wiley mill. Total N was analyzed on a Perkin Elmer 2400 elemental analyzer. From plant production and tissue N, total uptake by plants during the growing season was calculated as the sum of the product of monthly aboveground plus belowground biomass production and the monthly N concentration in tissues. Total growing season N uptake and percent uptake as NH_4^+ or NO_3^- was determined from the buried bag incubations following Nadelhoffer et al. (1984). N uptake for each 13–14 d period was calculated as the difference between NH_4^+ and NO_3^- produced in the incubated bags, where plant uptake was excluded, and outside the bags, where plant uptake occurred. This calculation assumes no inorganic N losses during the incubation, it provides a good estimate of plant N uptake if N losses are small (Nadelhoffer et al. 1984).

To determine relative whitetop growth with NH_4^+ or NO_3^- as N sources, a greenhouse experiment was conducted during 1990. Plants were collected from the spring-flooded marsh immediately after soil thaw in April by cutting blocks of sod to fit snugly into 7 L plastic pails. Eight pots selected at random were assigned to each of the following treatments: tap water, 25 g m^{-2} NH_4^+-N, 25 g m^{-2} NO_3^--N, and 25 g m^{-2} NH_4^+-N + 25 g m^{-2} NO_3^--N. The NH_4^+-N source was $(NH_4)_2SO_4$ and the NO_3^--N source was $NaNO_3$. One-eighth of the total treatment dose was provided weekly by line injections into each pot for 8 weeks. Pots were kept flooded with 3 cm of standing water and harvested after 10 weeks, when aboveground plus belowground biomass was collected, dried at 60 °C and weighed.

Nitrate reductase activity (NRA) was also measured as an indicator of the ability of whitetop to utilize NO_3^-. Assays were conducted both in the field and on plants grown in the greenhouse under the same N addition treatments (control, NH_4^+, NO_3^-, $NH_4^+ + NO_3^-$) described above. In the field, whitetop leaves or roots for NRA assays were collected 3 times (7 June, 17 July and 15 August) from the flooded and nonflooded marshes. The first two collections preceded the water level drawdown in the spring-flooded marsh and the last date followed the drawdown. To avoid diurnal changes in NRA, all samples were collected between 11 a.m. and 2 p.m. Leaves were collected in each plot from 5 points and roots from 3 points 3 m apart in a line beginning at a random location. Composite samples were formed from a minimum of 10 leaves or 50 root segments collected at each point. Only first or second expanded leaves and fresh healthy roots were collected. All tissues were placed immediately on ice and returned to the laboratory for processing within 1 h. In the greenhouse, 4 additional pots assigned to each of the 4 N source treatments provided plant tissues for NRA. One composite sample per pot was formed from 6 fresh leaves. Assays on greenhouse plants were performed on the same dates as those from the field.

Nitrate reductase assays were conducted using a method similar to that of Al Gharbi & Hipkin (1984). Tissues were chopped into <1 mm^2 pieces and each sample was divided into three 300 mg analytical replicates. Fresh samples were placed in a 0.1 M KH_2PO_4 buffer solution with 40 mM KNO_3 and 1.5% (v,v) n-propanol, infiltrated and incubated at 30 °C for 2 h at -60 mbar. The reaction was terminated by placing vials in a boiling water bath for 5 min. Nitrite produced was measured colorimetrically after addition of Griess Ilovsay reagent.

Statistical comparisons

Analysis of variance (GLM procedure of SAS) was used to test for differences in oxidation-reduction potential, extractable inorganic NH_4^+-N and NO_3^--N, net N mineralization rate, net nitrification rate and NRA between the spring-flooded and nonflooded marshes. When multiple measurements were made over the growing season (e.g., oxidation-reduction, extractable NH_4^+-N and NO_3^--N, net mineralization and net nitrification rate), they were treated as repeated measures from the same plot. When measurements were from a single date, they were analyzed in a two-way ANOVA with marsh and plot nested within marsh as main effects. Separate analyses were performed before and after the dates of water level drawdown. Treatment means in the greenhouse experiments were compared using one-way analysis of variance and Bonferroni t-tests.

Results

The spring-flooded marsh had higher aboveground plant biomass (Fig. 2, Table 2). Flooding led to lower soil oxidation reduction potentials before and after the drawdown in both years (Fig. 2, Table 2). Potentials in the spring-flooded marsh became progressively more reducing until late summer during both years, when they increased in response to the water level drawdown. Potentials in the nonflooded marsh were >200 mV, except during a period in June 1989 that followed heavy rains.

Extractable NH_4^+ concentrations showed no consistent seasonal pattern and no consistent differences between flooding regimes (Fig. 2). Spring NH_4^+ concentrations in both marshes were higher in 1989 than in 1990. Ammonium concentrations before and after the drawdown were higher in the nonflooded marsh in 1989 but higher in the spring-flooded marsh in 1990 (Fig. 2, Table 2). Even though significant, these differences were small compared with the magnitude of seasonal variation. Extractable NO_3^- concentrations in both marshes were higher in 1989 (Fig. 2). The nonflooded marsh had higher NO_3^- concentrations before the drawdown in both years (Table 2), but these differences disappeared after the drawdown (Table 2).

Spring flooding led to higher net N mineralization rates over the portion of the growing season when standing water was present (Fig. 3). After the drawdown, net N mineralization rates rose in the nonflooded marsh and fell in the spring-flooded marsh, eliminating the difference between marshes (Table 2). The spring-flooded marsh had higher total net N mineralization (Table 3). Mean growing season net N mineralization was 124 kg N ha^{-1} in the spring-flooded marsh and 62 kg N ha^{-1} in the nonflooded marsh (Table 3).

Net nitrification was detectable in May but remained low through June in both marshes (Fig. 3). Rates increased sharply in the nonflooded marsh in July and remained high through August (Fig. 3). Positive net nitrification was detectable in the spring-flooded marsh only in August and was highly variable as soils dried after the drawdown (Fig. 3). Total growing season net nitrification was greater in the nonflooded marsh. Net nitrification was 40 kg N ha^{-1} in the nonflooded marsh and <1 kg N ha^{-1} in the spring-flooded marsh (Table 3). Fifty-three percent of net N mineralized was nitrified in the nonflooded marsh compared with <1% in the spring-flooded marsh (Table 3).

Table 2. Results of analyses of variance to test for the effect of marsh (spring flooded or nonflooded) on plant aboveground biomass, soil oxidation-reduction potential, soil extractable NH_4^+-N, soil extractable NO_3^--N, net N mineralization rate and net nitrification rate. For oxidation-reduction potential, extractable NH_4^+-N and NO_3^--N, net mineralization and net nitrification rate, *F*-values and probabilities are for the main effect of marsh in a repeated measures ANOVA with multiple sampling times treated as repeated measures from the same plot. Because aboveground biomass was sampled only once, *F*-values and probabilities are for the main effect of marsh in a two-way ANOVA with marsh and plots within marsh as main effects. Sample sizes are the number of measurements made in each plot at each date. NS = not significant ($p > 0.05$), – = data not collected.

		1989				1990			
		Before drawdown		After drawdown		Before drawdown		After drawdown	
	n	*F*	p<	*F*	*p*<	*F*	*p*<	*F*	*p*<
Aboveground biomass	6	–	–	162.08	0.0001	–	–	31.40	0.0001
Oxidation-reduction potential	8	87.16	0.0001	16.05	0.0002	402.56	0.0001	284.12	0.0001
Extractable NH_4^+-N	6	26.35	0.0001	6.25	0.0164	6.86	0.0001	6.09	0.0163
Extractable NO_3^--N	6	6.99	0.0105	0.04	NS	62.52	0.0001	0.19	NS
Net N mineralization rate	6	–	–	–	–	144.32	0.0001	2.92	NS
Net nitrification rate	6	–	–	–	–	22.70	0.0001	4.21	0.0467

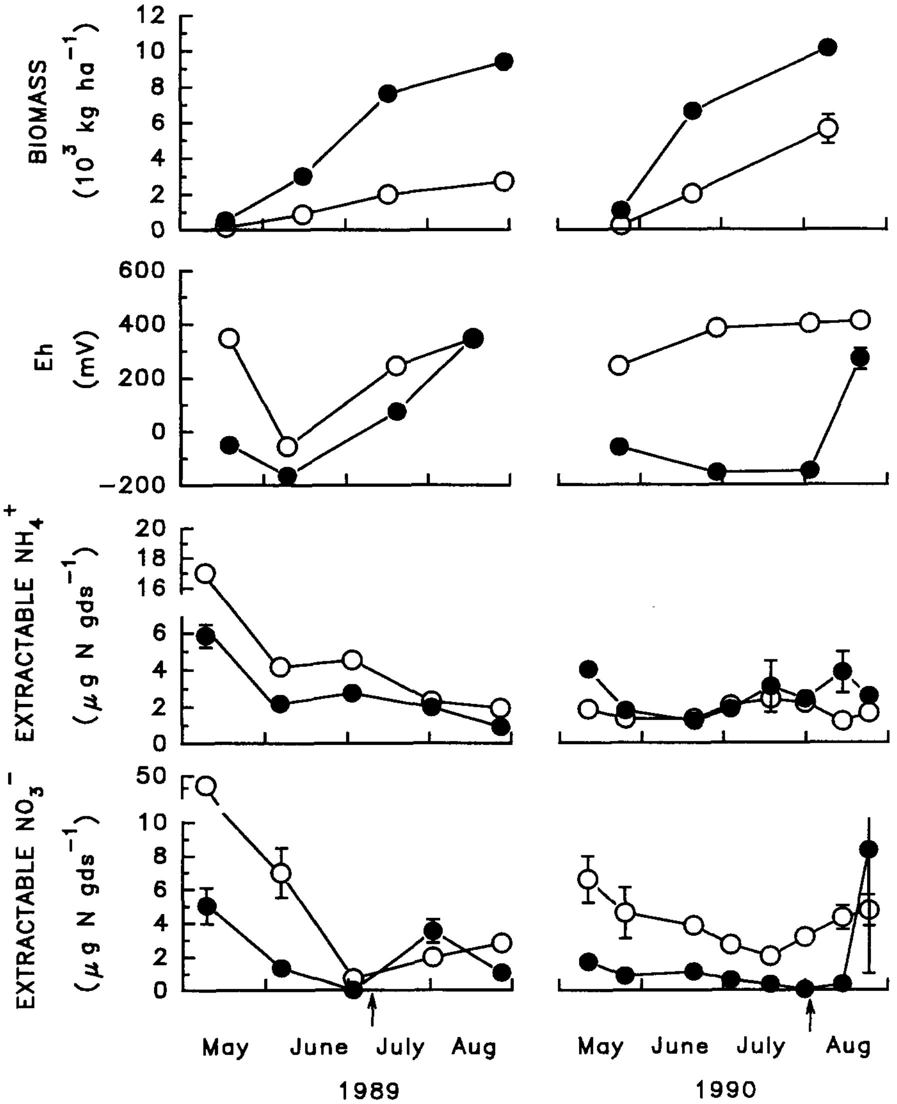

Fig. 2. Whitetop aboveground biomass, soil oxidation-reduction potential (Eh), extractable NH$_4^+$ and extractable NO$_3^-$ over two years in the spring-flooded (●) and nonflooded (○) marshes. NH$_4^+$ and NO$_3^-$ concentrations are μg N per gram dry soil. Values are means ±se. Error bars are not shown when they are smaller than the symbol. The arrows indicate the drawdown dates in the spring-flooded marsh.

Whitetop growth in pot culture was greater when nitrogen was supplied as NH$_4^+$ compared with NO$_3^-$ (Fig. 4). Treatment with NH$_4^+$ or NH$_4^+$ + NO$_3^-$ approximately doubled whitetop aboveground biomass compared with the

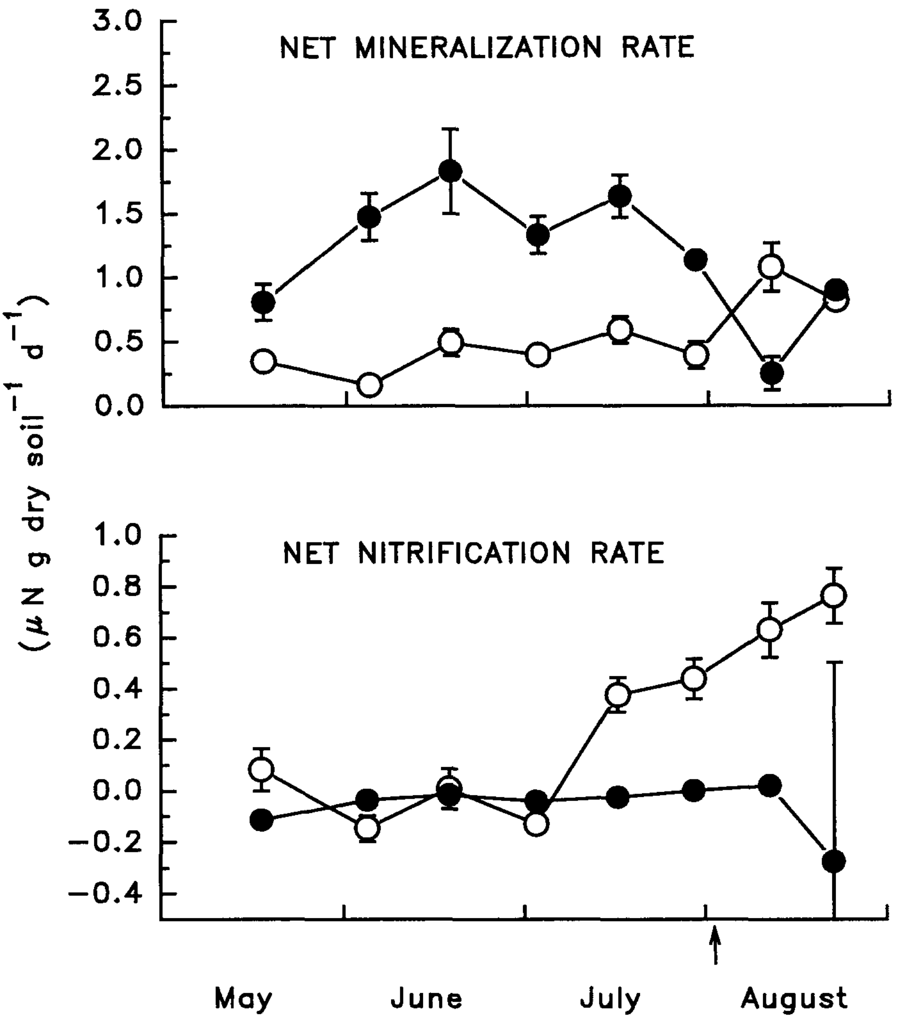

Fig. 3. Net N mineralization and net nitrification rates in the spring-flooded (●) and nonflooded (○) marshes during 1990. Rates are μg N per gram dry soil per day and were calculated from the mean of 12 cores in each marsh at each date. Values are mean ±se. Error bars are not shown when they are smaller than the symbol. The arrow indicates the drawdown date in the spring-flooded marsh.

control, while aboveground biomass with NO_3^- alone did not differ from the control (Fig. 4). Effects of N source on belowground biomass showed a similar pattern, but the absolute growth differences were smaller than for aboveground biomass.

In pot culture, fertilization of whitetop with NO_3^--N increased leaf and root NRA compared with all other treatments (Fig. 5), indicating that exposure

Table 3. Estimates of total annual net N mineralization and net nitrification and their relationship to annual plant N requirements.

		Spring-flooded	Nonflooded
Net primary production			
aboveground	kg dry mass ha^{-1}	10140	5990
belowground	kg dry mass ha^{-1}	4120	1920
Plant N uptake (tissue concentrations)	kg N ha^{-1}	167	81
Plant N uptake (buried bags)	kg N ha^{-1}	124	61
Net mineralization	kg N ha^{-1}	124	62
Net nitrification	kg N ha^{-1}	<1	33
Percent of mineralized N nitrified		<1	53
Percent of N uptake as NO_3^-		0	40

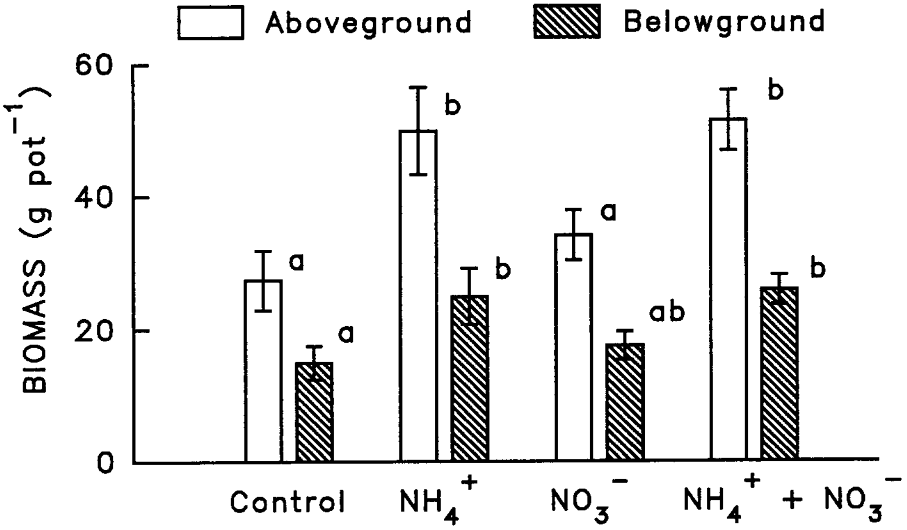

Fig. 4. The effect of N source on the above- and belowground biomass of whitetop in pot culture experiments. Plants were provided either $(NH_4)_2SO_4$, $NaNO_3$, or equal amounts of $(NH_4)_2SO_4$and $NaNO_3$. Control plants received no nitrogen addition. Error bars represent ±1 se. Values for above- or belowground biomass with the same letters indicate no significant differences among treatments (Bonferroni *t*-test, $p < 0.05$, $n = 8$).

to NO_3^- induced NRA. Fertilization with NH_4^+ alone did not increase NRA relative to the control. Plants treated with NH_4^+ + NO_3^- had NRA similar to those treated with NH_4^+ alone (Fig. 5), suggesting that when added NH_4^+ satisfied plant N demand, they used little NO_3^-. Plants in pot culture showed

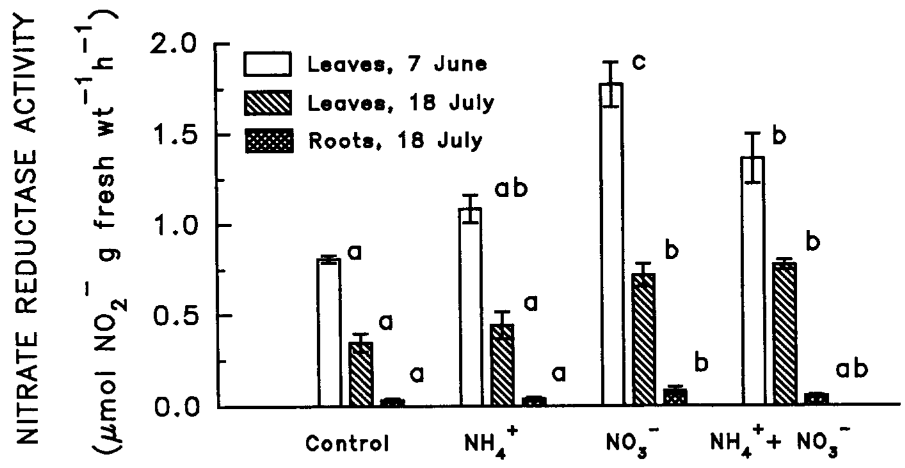

Fig. 5. Nitrate reductase activity of whitetop leaves and roots (±se) from plants in pot culture fertilized with either $(NH_4)_2SO_4$, $NaNO_3$ or equal amounts of $(NH_4)_2SO_4$ and $NaNO_3$. Different letters indicate significant differences among N treatments (Bonferroni *t*-test, $p < 0.05$, $n = 4$).

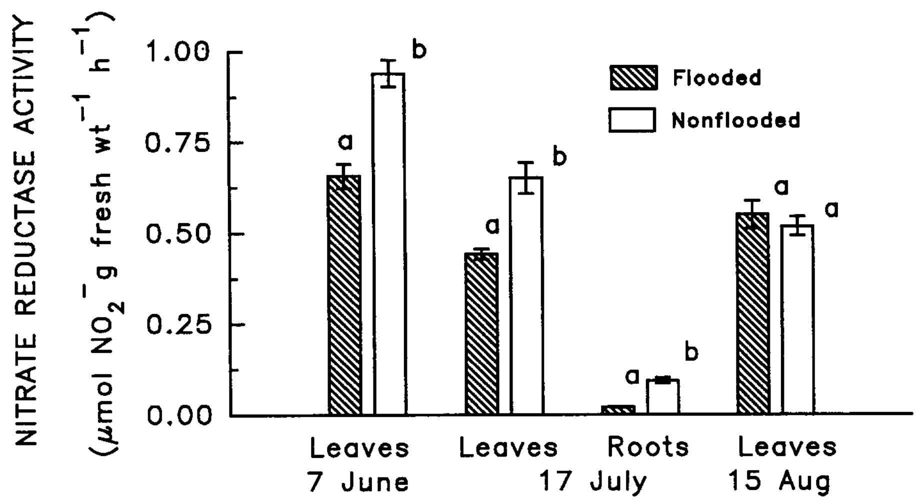

Fig. 6. Comparison of nitrate reductase activity in whitetop leaves and roots in spring-flooded and nonflooded marshes. Leaf NRA was determined at two dates before the water level drawdown in the spring-flooded marsh and one date after the drawdown. Root NRA was determined once before the drawdown. Values followed by a different letter indicate significant differences between marshes (Bonferroni *t*-test, $p < 0.05$).

higher NRA during June compared with later in the growing season. NRA was lower in roots than in leaves.

In the field, NRA in whitetop leaves was higher in the nonflooded marsh than in the spring-flooded marsh during June and July (Fig. 6). This indicated a greater utilization of NO_3^- in the nonflooded marsh. Differences in NRA between flooding regimes disappeared after water level drawdown in the spring-flooded marsh (Fig. 6). A slight increase in NRA in the spring-flooded marsh after the drawdown contrasted with a general pattern of seasonal decline in NRA in the nonflooded marsh. This suggested that even when the marsh was flooded, whitetop utilized NO_3^- as a N source despite low extractable NO_3^- concentrations and low net nitrification rates. Roots showed lower NRA than leaves, and differences between sites during July were greater for leaves than for roots (Fig. 6).

Total growing season N uptake calculated from plant tissue N concentrations was 167 kg N ha^{-1} in the spring-flooded marsh and 81 kg N ha^{-1} in the nonflooded marsh (Table 3). Growing season N uptake calculated from the buried bags was 124 kg N ha^{-1} in the spring-flooded marsh and 61 kg N ha^{-1} in the nonflooded marsh (Table 3). Nitrate-N accounted for 40% of total growing season plant N uptake in the nonflooded marsh, while all nitrogen uptake in the flooded marsh was as NH_4^+ (Table 3).

Discussion

The spring period of rapid plant growth in shallow prairie marshes coincided with a period of high net N mineralization brought about by flooding. Because higher plant production in the flooded marsh increased plant N demand, net mineralized N equaled approximately the same proportion of plant N uptake (74 to 77%) in both marshes. This indicated the potential for tight coupling between net N mineralization and plant growth. This study probably underestimated total net N mineralized because cores were restricted to the top 15 cm and because soil incubations were not performed in September when soil microbes remained active. N inputs in groundwater could also account for the remaining discrepancies in the soil N budget. Groundwater inputs were not measured but can be important in some wetlands (Grootjans et al. 1985).

The mechanism that links spring flooding with higher net N mineralization could not be determined directly from this study. Higher net N mineralization may follow from higher gross N mineralization in spring-flooded marsh. More likely, gross N mineralization rates are lower with flooding, but lower microbial N immobilization under flooded conditions increases the net amount of N mineralized. Greater N immobilization in the absence of flooding is consistent with results of studies of whitetop litter decay. Buried whitetop litter exhibits greater mass loss but retains a greater portion of its original N in the absence of flooding (Neckles & Neill 1994). Bowden (1986) demonstrated a similar phenomenon where N was immobilized by freshwater marsh litter under nonflooded oxidizing conditions and mineralized under flooded anoxic conditions. In the Delta marsh, Kadlec (1986) found that soil water NH_4^+ concentrations increased following flooding of the marsh with above-normal water levels.

The range of growing season net N mineralization of 62 to 124 kg N ha^{-1} was similar to rates observed in other wetlands on mineral soils at similar latitudes. Bowden et al. (1991) calculated an annual net N mineralization rate of 180 kg N ha^{-1} for a Massachusetts tidal freshwater marsh. Berendse et al. (1987) measured annual net mineralization rates of 100 to 115 kg N ha^{-1} for wet heathlands in the Netherlands. Zak & Grigal (1991) reported lower annual net N mineralization rates of 15 kg N ha^{-1} for swamp forest and rates up to 35 kg N ha^{-1} for associated upland systems.

The net nitrification of 33 kg N ha^{-1} measured in the nonflooded marsh is very high for wetland ecosystems. This differs from many wetlands where nitrification rates are zero (Martin & Holding 1978; Rosswall & Granhall 1980) or remain low throughout the year (Bowden 1987), but it supports evidence from wetlands that experience periodic drying, where nitrification can make up an important component of the ecosystem inorganic N economy. Giblin et al. (1991) found evidence for nitrification in tundra ecosystems. Zak & Grigal (1991) observed increased nitrification rates in a Minnesota swamp forest as soils dried during late summer. Soil NO_3^- pools in sedge and grass wetlands associated with beaver ponds increase in response to water level drawdown (Pinay & Naiman 1991), as do nitrification rates in wet meadows upon soil drainage (Grootjans et al. 1985). Bowden et al. (1991) reported an annual nitrification rate of 11 kg N ha^{-1} from a tidal freshwater marsh.

Despite preference for NH_4^+, elevated NRA in the nonflooded marsh and after water level drawdown in the spring-flooded marsh indicated whitetop utilized NO_3^- when it was available. Other emergent marsh plants also prefer to take up NH_4^+ (Tyler 1967; Mendelssohn 1979). This preference is thought to reflect the dominance of NH_4^+-N in the flooded soil of the environments the plants evolved (Haynes & Goh 1978). Nitrate reductase assays showed that even in a species adapted to flooded soils, NO_3^- utilization can be induced quickly upon changes in soil moisture status and can comprise an important nitrogen source at times when NO_3^- is available. Other measurements of NRA in marsh plants suggest that the ability to utilize NO_3^- may be common despite the predominance of NH_4^+ as the form of available mineral N in flooded soil habitats (Stewart et al. 1973; Rozema & Bloom 1967; Mendelssohn 1979). Nitrification may be important even in wetlands where drying is infrequent.

High net nitrification rates in the nonflooded marsh and whitetop preference for NH_4^+ over NO_3^- suggest that nitrification could lower plant N availability. However, the timing of the onset of nitrification in summer indicated that it had little direct influence on whitetop productivity. Spring plant growth and flowering were complete and differences between flooding regimes were well established by July, when increases in net nitrification rates occurred in the nonflooded marsh.

Although the co-occurrence of flooding and elevated N mineralization suggest a link between N supply and whitetop spring growth response to flooding, these results do not demonstrate a direct cause and effect relationship because flooding is also associated with other environmental changes that can influence whitetop growth. For example, spring flooding lowers soil salinities (as measured by electrical conductivity) from 13–15 dS m^{-1} in nonflooded marsh to 7–11 dS m^{-1} in flooded marsh (Neill 1993). Spring flooding also maintains lower salinities for a longer portion of the growing season compared with nonflooded marsh (Neill 1993). Soil conductivities as low as 4 dS m^{-1} reduce whitetop growth in greenhouse experiments, and decreasing soil salinity by 5 to 7 dS m^{-1} can double whitetop aboveground biomass in nonflooded marsh (Neill 1993). These increases compare with 28 to 33% increases in aboveground biomass that follow N fertilization of flooded and nonflooded whitetop marshes (Neill 1990). Reduced salinity and higher net N mineralization associated with spring flooding likely both play a role in increasing emergent plant growth. Field experiments that alter soil salinity without changing the flooding regime could determine which factor is the dominant influence on plant production.

Rapid spring plant growth has been proposed as a mechanism that prevents ecosystem N loss (Muller & Bormann 1976). Microbial immobilization can also be an important early spring N sink in forests (Zak et al. 1990), but flooding influences this dynamic by decreasing N immobilization (Groffman et al. 1993). In marshes, flooding would likely favor N uptake by emergent plants at the expense of microbial immobilization. I did not measure N losses or immobilization that would allow me to evaluate the role of spring flooding in N retention, but rapid spring growth, high plant N uptake, close agreement between net N mineralized and plant N demand and reduced net nitrification with flooding all suggest that N could be tightly cycled with spring flooding despite conditions that would otherwise favor N loss by denitrification (Patrick & Tusneem 1972).

The close coupling between the presence of spring flooding, net N mineralization and net nitrification rates in these prairie marshes indicates that modifications that change the pattern of spring inundation will lead to rapid and significant changes in marsh N cycling patterns. The widespread occurrence of spring flooding in mid- and high-latitude wetland ecosystems suggest that similar responses of soil N dynamics controlled by seasonal flooding could occur across a variety of ecosystem types.

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