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The effects of changes in soil moisture on nitrogen cycling in acid wetland types of the New Jersey Pinelands (USA)

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ABSTRACT

Wetlands are subject to changes in soil moisture as a result of both short-term seasonal climate variations and long-term changes in regional water resource management, both of which can modify the dynamics of ground and surface water inputs. In the New Jersey Pinelands, forested wetlands that differ in both plant communities and soil structure occur along a topographic and hydrological gradient associated with an unconfined aquifer. Proposed groundwater withdrawals may affect water content of soils along this gradient. We hypothesized that prolonged changes in soil moisture would alter net nitrogen mineralization and nitrification rates in proportion to the amount of moisture change, and that these changes would be similar for the different soils along the drainage catena. Soils from two catenary sequences of wetlands, including pine-dominated (driest landscape position), hardwood-dominated, and Atlantic white-cedar-dominated (wettest landscape position) communities were used in long-term laboratory incubations (36 weeks). Production of NH_4^+–N, NO_3^-–N, and dissolved organic N were measured under two sets of conditions: constant moisture levels of 100%, 60% and 30% water-holding capacity (WHC), and fluctuating moisture levels (alternating 2 week periods at 100% and 30% WHC). In soils from most of the wetlands, we observed increases in net mineralization and nitrification when constant low-moisture conditions were established, but not under fluctuating conditions. Contrary to expectations, responses to the drying treatments varied between wetland types and between replicate wetlands of each type. Under constant-moisture conditions, nitrification increased more in cedar swamps than in either type of pine wetland. Under all conditions, soils from all the wetlands within one of the catenas produced more inorganic and organic soluble N than did the wetlands from the other catena, suggesting that area-wide effects are as important as wetland type in regulating production of soluble N. Within both catenas, pine-hardwood wetlands generated more soluble N under all moisture conditions than did either pine-dominated or cedar wetlands. Our results suggest that changes in soil moisture due to management of water resources will affect N cycling in wetland soils, but that the magnitude of the effects, and the potential for large releases of nitrate, will depend on the specific soil properties of affected wetlands.

1. Introduction

Nitrogen cycling in wetland soils is thought to be highly sensitive to variations in soil moisture, which is a controlling variable affecting the redox potential of the soil. As wetland soils become increasingly anoxic, oxygen-dependent processes, in particular nitrification, are reduced or eliminated. At the same time, processes that require anoxic conditions, notably denitrification, may increase (Pinay et al., 2002). Soil moisture in turn varies with soil properties such as texture and organic matter content, which affect the water-holding capacity of the soils (Bruland and Richardson, 2004; Wendroth et al., 2006; Sleutel et al., 2008), and the balance between inputs and outputs in the water budget of the soil profile. Changes to water budgets can be critical in wetlands, where small alterations to inputs of precipitation, surface and groundwater can have large effects on the moisture status of the soil. Variations in climate, both seasonal and inter-annual, and long-term changes in regional water resource management can both cause change in the moisture content of wetland soils. While nitrogen cycling in wetland soils has been extensively studied (Bridgham et al., 1998; Aerts et al., 1999; Butturini et al., 2003; Groffman et al., 2003; McHale et al., 2004; Sleutel et al., 2008), the comparative effects of

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constant versus fluctuating soil moisture conditions on nitrogen mineralization and the potentially-mineralizable nitrogen content of the soil have not been well studied. Studies in upland soils have shown that frequent fluctuations of moisture conditions can have long-term effects on microbial processes, including large increases in nitrifier populations (Fierer and Schimel, 2002), but whether wetland soils respond similarly is unknown. Moreover, most studies have concentrated on either mineral hydric soils or on histosols; there has been little work providing a comparison of the responses to long-term and short-term changes in moisture in these two types of wetland soils. We have carried out such a comparative study, contrasting the effects of constant vs. fluctuating moisture levels in both mineral and organic wetland soils.

Reduction in saturation of wetland soils has frequently been associated with increases in both net mineralization and nitrification, as reductions in moisture below saturation allow aerobic conditions to become established. For example, many observations of drained wetlands have found increases in both soluble inorganic N and N process rates (Regina et al., 1996, 1999; Freeman et al., 1997; Olde Venterink et al., 2002; Tiemeyer et al., 2007). Similar responses have been demonstrated in riparian wetlands subjected to drying during summer months (Bechtold and Naiman, 2006). However, Regina et al. (1996) found that the effects of drainage on nitrate production differed between minerotrophic fens and ombrotrophic bogs, suggesting that soil characteristics constrain the response of wetland soils to drying. In a now-classic series of studies, Bridgham and colleagues (Updegraff et al., 1995; Bridgham et al., 1998) showed that many types of histosol had higher rates of N mineralization and nitrification when incubated under aerobic conditions than under anaerobic conditions. However, they found that the relative amount of change in N process rates, and particularly the amount of nitrification as a fraction of total net mineralization, varied greatly among soil types, reflecting differences in substrate quality. In mineral wetland soils, N mineralization is maximal at intermediate levels of soil moisture (57–78% water-filled pore space) (Sleutel et al., 2008); the range of moistures producing maximal rates varied with soil texture and soil organic matter.

While these and other studies clearly suggest that the establishment of prolonged aerobic conditions in peatland soils frequently results in increased N mineralization and nitrification, the effects of alternating wet–dry conditions may not have the same effect. For example, Mentzer et al. (2006) found that the contrast between constant versus fluctuating moisture conditions had a large effect on N dynamics in mineral wetland soils, more so than other soil manipulations such as nutrient additions. Alternating conditions could result from a variety of environmental conditions. Even in climates with rainfall occurring throughout the year, periodic droughts of several weeks during the growing season can occur. Soil drying during these episodes will alternate with the re-establishment of wetter conditions after a rainfall. In wetlands subject to prolonged drying from lowered water tables due to drainage (Holden et al., 2004), periodic large rain events could re-wet dry soils. Fluctuating moisture conditions could result in either enhanced N mineralization and nitrification, if periodic droughts produce flushes of dead microbial biomass available for mineralization (Fierer and Schimel, 2002; Mikha et al., 2005), or alternatively could result in decreased net release of mineral N, as N that is mineralized and nitrified during dry periods is denitrified during wet periods. Indeed, observed increases in net nitrate production in drained wetland soils results from a combination of increased nitrification and decreased denitrification (Olde Venterink et al., 2002).

The New Jersey Pinelands is a large region in southern New Jersey which is characterized by highly porous, very sandy soils and an unconfined aquifer, resulting in extensive wetlands (Ehrenfeld, 1986; Forman, 1998). Wetlands dominated by pitch pine (*Pinus rigida*) occur on hydric mineral soils in the Atsion series, and wetlands dominated by hardwoods (mainly red maple, *Acer rubrum*, but with some pines intermixed) occur on similar soils but on lower positions on the hydrologic gradient. Atlantic white-cedar (*Chamaecyparis thyoides*) wetlands occur at the lowest positions, along stream channels, on Histosols (Manahawkin muck) (Tedrow, 1986). Pinelands soils, including both upland and mineral wetland soils, typically have very low to zero rates of net nitrification, and no or very low concentrations of nitrate in soil pore water (Ehrenfeld et al., 1997a,b) In a study of cedar swamp N dynamics, Zhu and Ehrenfeld (1999) found that net nitrification rates in soils from both hummocks and hollows were 1–40 μg N kg soil^{-1} day^{-1}, net mineralization rates were 3.6–4.9 mg N kg soil^{-1} day^{-1}, and extractable NO_3^-–N concentrations were at most 3 mg N kg^{-1}. However, because all Pinelands surface soils have very low pH (4 or less) (Soil Survey Staff; Tedrow, 1986; Lord et al., 1990), it might be expected that nitrification rates would be very low to below detection, as low pH is a well-known limiting condition for autotrophic nitrification (De Boer and Kowalchuk, 2001; Reddy and DeLaune, 2008), and therefore no change in nitrification with changes in soil moisture might be observed.

We hypothesized that 1) prolonged changes in moisture status of different types of wetland soils would affect nitrogen dynamics in similar ways, and in proportion to the amount of moisture change, and 2) that fluctuating moisture regimes would have different effects on N cycling than constant moisture regimes. In order to test these hypotheses, a laboratory incubation study was carried out to compare the three types of soil (two mineral hydric soils and one Histosols) under constant and fluctuating moisture regimes.

2. Methods and materials

2.1. Description

Two replicate sets of wetlands, in areas identified as 'M6' and 'M10' below, were established in the McDonald's Branch watershed in Brendan T. Byrne State Forest (39°53′05″N, 74°30′20″). The two study areas are in the middle and upper reaches, respectively, of the small watershed (6.1 km^2), below and above, respectively, a dirt road. The watershed is otherwise completely undisturbed. The region receives approximately 1100 mm precipitation annually, evenly distributed through the year. At each of two study areas, soils were taken from each of three wetlands arranged along the drainage catena, within pine wetland (PW), pine hardwood (PH) and cedar swamp (CS) communities. The PW and PH wetlands in each area are on hydric mineral soils, whereas the CS wetlands are on Histosols. These wetland communities have been previously described (Ehrenfeld and Gulick, 1981; Ehrenfeld, 1986, 1995; Ehrenfeld and Schneider, 1991; Zampella et al., 1992; Laidig and Zampella, 1999). Soils were taken along the boundaries of a 10 × 10 m plot established for separate studies of vegetation.

2.2. Soil sampling

Twenty-one cores of surface soil (0–5 cm) were sampled from each wetland at each sample area using a bulk density corer; soils were collected within aluminum cylinders, each 5-cm diameter and 5-cm deep. This volume of soil fit without further disturbance into the microlysimeters used in the incubations, as described below. In the PW and PH wetlands, mineral soils were collected after removing the organic layer while peat soils were taken in swamp hollows in the CS wetlands after detaching living moss (*Sphagnum*) material. Mineral soils were used because the thickness of the overlying organic horizon in the mineral soil wetlands was quite variable among the sample points, both within and between the two replicates of the PW and PH wetlands. Because N mineralization would be strongly affected by the amount of organic material in the soil, high variability in organic matter content would be likely to mask differences in the responses to the treatments. In both PW and PH wetlands, the organic horizon is a distinct mor layer, making its separation from the mineral soil straightforward, and allowing a similar mineral soil material to be tested.

Soil samples were kept in the cores and transported to the laboratory in an iced cooler. Nine intact cores per wetland were used for the constant-moisture laboratory incubation experiments, 6 cores use for the fluctuating-moisture incubations, 3 cores used for water-holding capacity (WHC, % gravimetric basis) and bulk density measurements, and 3 cores used or initial property determinations (moisture, pH deionized water at a 1:1 ratio) organic matter, total carbon, total nitrogen (Vario Max CN Elementar Americas, Inc.), and KCl-extractable nitrogen (NH_4^+ and $NO_2^- + NO_3^-$, extracted at a 1:4 ratio of soil to 2 mol KCl l^{-1}). Concentrations in extracts were analyzed using a flow injection analyzer (NH_4^+, Method 31-107-06-1-A; $NO_2^- + NO_3^-$, 31-107-04-1-C Lachat® QuickChem® FIA+ 8000, Milwaukee, WI, USA).

2.3. Laboratory incubation methodology

Two regimes of soil moisture were manipulated in the laboratory incubation experiments. The constant soil moisture regime had three levels (30%, 60%, and 100% WHC) while the dry-wet moisture regime alternated soil moisture between 30% and 100% WHC with a period of two weeks per soil moisture level (i.e. 2 weeks at 30% WHC and 2 weeks at 100% WHC). The two-week timing of moisture fluctuations was based on the hourly precipitation record of 2004–2005 obtained from the US Forest Service station at the Silas Little Experimental Forest, New Lisbon, NJ, located 8.6 km from the sampling location, in which the maximum rain-free period was 15 days. Moisture levels within the microcosms were established using distilled deionized water. A 36-week incubation protocol was applied to the incubation experiments using a microlysimeter as described by Nadelhoffer (1990) with soils incubated in a dark incubator at 30 °C. Intact cores were placed in the microlysimeters (115 ml Falcon filtration units, BD Labware, Lincoln Park, NJ, USA; model no. 7102), with as little disturbance as possible. Soil moisture was maintained at desired levels by adding nitrogen-free Hoagland's solution twice a week based on mass loss. Extractions were carried out by adding 100 ml of N-free Hoagland's solution to the top chamber of the microlysimeter for an hour, as recommended by Nadelhoffer (1990). This solution was used to ensure that other nutrients are replaced over the lengthy period of incubation, as their depletion can reduce mineralization rates (Weaver, 1994; Carter and Gregorich, 2008; Dijkstra et al., 2009), and also to efficiently extract exchangeable ammonium by using a solution with an appropriate electrolyte strength. The extractant solution was then removed by vacuum filtration and collected in 150 ml flasks, transferred to acid-washed vials, and stored in a freezer pending analysis.

In order to test the effects of constant moisture regimes, mineralized nitrogen was extracted first biweekly and then monthly, with 9 extractions over the 36-week period from each set of 3 replicate microlysimeters for each combination of wetland type and sample area. In order to test the effects of fluctuating moisture regimes, two sets of microlysimeters were set up in order to determine whether the time of extraction (after a dry period or after a wet period) would affect the cumulative amount of mineral nitrogen produced. Extraction after the dry period might remove NO_3^- that would be removed during the ensuing wet period, and thus give a different measure of total soluble N produced. Therefore one set of 3 replicate microlysimeters (per wetland type and per study area) was extracted after each two-week period (dry or wet); this treatment is referred to below as the 'D–W' treatment. A second set of three replicate microlysimeters per wetland type and study area was extracted after each dry-plus-wet cycle (4 weeks, at the end of the wet period); this treatment is referred to below as the 'D + W' treatment.

2.4. Measurement of nitrogen in filtrates

Concentrations of NH_4^+–N and $NO_2^- + NO_3^-$–N in the filtrates were measured directly using the Lachat® automatic flow injection analyzer. The concentration of total dissolved nitrogen (TDN) was determined by autoclave-digestion with potassium persulfate (Ameel et al., 1993) prior to analyzing NO_3^- concentrations as above. Dissolved organic nitrogen (DON) was calculated from the difference between TDN and mineral nitrogen ($NH_4^+ + NO_2^- + NO_3^-$) concentrations. Amounts of the different forms of nitrogen released were expressed by volume of soil (g N m^{-3} soil) in this study because of large differences in bulk density between mineral soils and peat soils.

2.5. Mineralization dynamic model

A two-pool exponential model (Molina et al., 1980; Richter et al., 1996) was employed to simulate the accumulated release of inorganic nitrogen under two soil moisture regimes in this study. Given that DON was extracted with inorganic nitrogen together at each extraction, the labile nitrogen pool was decreased by each extraction, over the course of incubation. The two-pool exponential model, therefore, was modified as Eq. (1):

$$\mathrm{TIN} = (N_L - \mathrm{DON})\left(1 - e^{-kt}\right) + (\mathrm{TN} - N_L)\left(1 - \mathrm{e}^{-ht}\right) \tag{1}$$

where TIN represents cumulative amount of inorganic nitrogen (NH_4^+–N + $NO_2^- + NO_3^-$–N, g N m^{-3}) released at time t; N_L is the size of labile nitrogen pool (g N m^{-3}) mineralized at a rate with a constant k(day^{-1}); DON is the cumulative amount of dissolved organic nitrogen (g N m^{-3}) extracted at time $t-1$; TN is the total soil nitrogen (g N m^{-3}); TN $-$ N_L represents the size of the slow-release nitrogen pool (SRNP) mineralized at a rate with a constant h (day^{-1}). Both labile and slow-release nitrogen pools are assumed as a constant in the model. The half-life ($t_{1/2}$) was calculated for both the labile nitrogen pool and the slow-release nitrogen pool using an exponential decay model as:

$$t_{1/2} = \frac{\ln 2}{k} \text{ or } \frac{\ln 2}{h} \tag{2}$$

respectively (Bridgham et al., 1998). The modified two-pool exponential model was fit to the incubation data using a PROC NLIN in SAS ver. 9.1, and initial values of parameters were manually adjusted to meet the default convergence criterion (10^{-5}).

2.6. Statistical analyses

Differences between the soils of the three types of wetlands in response to the moisture treatments were tested by analyses of variance (ANOVA). The two replicate sample areas (M6 and M10) were compared as a random factor in the model nested within combinations of wetland type (cedar swamp, pine hardwood, pine wetland) and moisture treatments (5 levels, including 100%, 60%, and 30% WHC constant treatments, D + W and D–W fluctuating treatments). Initial soil properties, total amounts of different forms of cumulative released nitrogen, and parameter estimates of the model were tested with this three-way ANOVA model. Because the 'sample area' factor was significant in all analyses, the data were re-analyzed separately by area with 2-factor factorial analyses of variance (ANOVAs) followed by Tukey's HSD test to better identify patterns among wetland types and among moisture treatments. A MANOVA-Repeated Measures test was employed to test effects of moisture regime and incubation period and of area and wetland type on net rates of mineralization and nitrification in the wetland soils over time. These analyses allowed us to test differences among wetland types, among moisture treatments, and the interactions between wetland types and moisture regimes. All tests were executed using SAS for Windows version 9.1 (SAS Institute, 2001).

3. Results

3.1. Soil properties

The wetland soils had very low pH values, 3.20–3.58 (Table 1). The organic soils from both CS had significantly higher organic matter, lower bulk density, higher WHC, lower C:N ratios and higher concentrations of extractable NH_4^+–N than did the mineral wetland soils from the PW and PH plots. Soils from the M6 sample area had higher WHC, total C, total N, and extractable NH_4^+–N than did soils from the M10 sample area (Table 1). Median water table depths were significantly different among the three wetlands in each sample area (Table 1).

3.2. Cumulative nitrogen release

Soils from all wetland types in the M6 sample area released more NH_4^+–N, total inorganic N (TIN) and DON than soils in the M10 sample area (Table 2). In contrast, the M10 sample area soils released more NO_3^-–N than did wetlands at the M6, particularly from the CS muck soils (Fig. 1, Table 2). In all sample areas, inorganic N production was highly dominated by NH_4^+–N; nitrate accounted for <2% of all mineral N produced, except in the 60% and 30% moisture treatments of the M10CS soils, in which nitrate accounted for about 35% of total inorganic N (TIN). There was a trend of higher net production of NH_4^+–N in the constant-moisture treatments in the M10 sample area (Table 3), but not in the M6 (Table 3). In both sample areas, net nitrate production in the CS soils showed the largest response to drying (the largest absolute amounts of NO_3^-–N), but only in the constant-moisture treatments. Dissolved organic N accounted for 46–73% of total soluble N production, and was least responsive to the moisture treatments, only showing effects (reductions) in the fluctuating-moisture treatments in the M10 series. Fluctuating-moisture treatments produced lower amounts of dissolved N than the two constant-moisture drained treatments (60% and 30% WHC) in most of the M10 soils and for all forms of N (Fig. 1), but only showed this pattern for the CS soils in the M6 sample area. The M10 series of wetlands also had more complex responses to the moisture treatments, as demonstrated by the significant interactions between moisture and wetland type in the 2-way ANOVAs (Table 3), which were not apparent in the M6 soils. However, both sample areas were similar in that the mineral hydric soils of the PH wetland type tended to produce as much or more extractable nitrogen, both inorganic and organic, than did the organic CS soils or the similar mineral soils of the PW wetland type. Indeed, the difference between pine hardwoods and the other wetland types was the most consistent source of differences in N release (Table 3). Dissolved organic N (DON) was higher from PH wetlands than from the other types in both study areas, and showed a trend in M10 of less release in the fluctuating-moisture treatments (Table 3).

The results also show that there is not a linear response of nitrogen cycling to reductions in soil moisture content, in that the 30% and 60% treatments were not significantly different from each other in any treatment (Table 3), although one or both are frequently different from the 100% treatment. Thus, "dry" can be a wide range of moisture levels that are less than saturation (100% WHC).

The fluctuating-moisture treatments under both patterns of extraction resulted either less N release (M10 wetlands) or N release no greater than the constant-moisture drying treatments (M6 wetlands). Surprisingly, there were few significant differences between the two extraction patterns; thus the removal of NH_4^+–N and DON after each two-week dry period vs. retention of this N during the wet periods did not affect the net production of N. However, analyses of the N extracted after each two-week period in the D–W treatment showed that although the amounts of extracted NH_4^+–N did not differ between extraction periods, the amounts of NO_3^-–N and DON were significantly higher during the dry periods than during the wet periods ($F = 7.52$, $p < 0.05$ for NO_3^-–N, $F = 4.52, p < 0.05$ for DON; data not shown).

3.3. Net rates of N mineralization and nitrification

In the constant-moisture treatments, patterns of change of mineralization rate over time were very different between the sample areas (Fig. 2; between-subjects factor, Table 4), and the patterns of change over time differed among the moisture levels (within-subject factors; Table 4). In the M10 sample area, rates increased gradually over time, whereas in the M6 sample area, they rapidly increased to a maximum, and then declined slowly (Fig. 2). There were also significant differences in the responses of mineralization rates to wetland types and moisture levels (significant between-subjects interactions among all the factors; Table 4). Mineralization rates were consistent with the patterns of cumulative N release: the M6 sample area had higher rates than the M10 sample area during the first 130 days of the incubation ("sample area" factor in three-way analyses of variance for the first 6 dates significant at $p < 0.001$). In both sample areas, mineralization rates tended to be greatest in PH wetlands under all moisture regimes and lowest in PW wetlands (Fig. 2; for both sample areas, 'wetland type' significant in two-way ANOVAs at $p < 0.05$ for 8 dates (M10) and 5 dates (M6); for all dates in both sample areas except the first, the PH rates were highest and the PW rates were lowest). In the M6 sample area, there were larger effects of the moisture treatments the PH and PW mineral soil wetlands than in the histosols of the CS wetland, whereas in the M10 sample area, there was an opposite pattern (Fig. 2). Patterns of response of net nitrification rates in the constant-moisture treatments were similar to those of net mineralization, with significant interactions among, wetland type, and time factors (Table 4). In the M10 sample area, only the CS soils showed a significant increase in nitrification with the drying treatments, whereas in the M6 sample area, all three wetland types showed increases in nitrification with drying (Fig. 3).

When extractable N was measured after combined dry–wet cycles (D + W), net mineralization rates were significantly higher in the M6 than the M10 sample area on every date ($p < 0.01$ for all dates, two-way ANOVAs, and $F = 45.54$, $p < 0.001$ in repeated measures ANOVA for 'sample area' factor; Fig. 4). PH wetlands had higher rates of net mineralization on most dates ($p < 0.05$, two-way ANOVAs for each date, wetland type factor). In contrast, net rates of soil nitrification did not differ between wetland types or between sample areas (two-way ANOVAs for each date non-significant), and in all wetland soils, the rates were very low, <1.0 mg N m^{-3} day^{-1}

Table 1
Initial soil properties (mean ± standard error, $n = 2$), 2-way analyses of variance for each soil property (F value), and significance of differences among sites and soils using Tukey's HSD test. Ns = not significant; * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Water tables are cm below the ground surface; ANOVA results are for monthly median values.

Site	Wetland	pH (H_2O)	Organic matter (g kg soil^{-1})	Bulk density (g cm^{-3})	Water-holding capacity (% w/w)	Total carbon (kg C m^{-3})	Total nitrogen (kg N m^{-3})	C/N ratio	NH_4^+–N (g m^{-3})	NO_2^- + NO_3^-–N (g m^{-3})	Median water table (max, min)
M10	Pine wetland (PW)	3.38 ± 0.10	65.6 ± 19.9	0.91 ± 0.13	58.90 ± 3.95	39.23 ± 7.07	1.05 ± 0.22	37.89 ± 1.27	8.07 ± 2.32	0.00	22.6 (83.4, 37.4)
	Pine hardwood (PH)	3.20 ± 0.09	81.3 ± 19.8	0.62 ± 0.10	66.74 ± 12.63	22.21 ± 5.39	0.57 ± 0.14	38.98 ± 1.43	8.04 ± 2.45	0.00	24.8 (59.1, 13.8)
	Cedar swamp (CS)	3.58 ± 0.04	406.1 ± 68.1	0.15 ± 0.02	299.53 ± 41.10	20.00 ± 5.60	0.81 ± 0.23	24.74 ± 1.19	22.60 ± 2.19	0.09 ± 0.09	−2.9(29.8, −13.3)
M6	Pine wetland (PW)	3.42 ± 0.09	102.4 ± 22.8	1.03 ± 0.20	67.41 ± 4.64	40.15 ± 5.06	1.17 ± 0.17	34.38 ± 0.81	11.16 ± 0.59	0.00	25.5 (69.9, 11.3)
	Pine hardwood (PH)	3.48 ± 0.10	186.6 ± 42.3	1.01 ± 0.18	128.55 ± 39.57	65.97 ± 0.41	1.96 ± 0.32	34.19 ± 4.03	32.82 ± 8.34	0.00	19.3 (10.18, 47.6)
	Cedar swamp (CS)	3.45 ± 0.02	874.9 ± 5.6	0.21 ± 0.004	740.19 ± 83.81	55.74 ± 6.25	2.35 ± 0.21	23.68 ± 0.60	58.22 ± 8.58	0.20 ± 0.20	5.6 (33.9, −3.5)
Wetland type	*F* value	ns	146.59***	22.04***	74.08***	ns	ns	26.54***	18.34***	ns	109.64***
	Tukey's HSD		CS > PH, PW	PW, PH >> CS	CS >> PH, PW			PH, PW >> CS	CS >> PH, PW		PW > PH > CS
Site	*F* value	ns	48.08***	ns	24.92***	24.53***	31.17***	ns	25.25***	ns	ns
	Tukey's HSD		M6 > M10		M6 >> M10	M6 >> M10	M6 >> M10		M6 >> M10		
Site × wetland type	*F* value	ns	20.84***	ns	15.90***	5.90*	6.05*	ns	5.16*	ns	ns

(Fig. 4). The rates of both mineralization and nitrification changed significantly over time (Table 5, "Time" factor); nitrification rates varied over time differently in the different wetland types, whereas patterns of change over time varied between the two sample areas for net mineralization (interaction factors; Table 5).

When the extractions were carried out after each 2-week incubation period (D–W), the net mineralization rates did not differ between the dry and wet periods (Table 5, between-subject "moisture regime" factor). Nitrification rates, however, responded to the fluctuating conditions, the dry periods produced higher nitrification rates than during the wet periods in all types of wetland soils (Table 5, Fig. 5). While nitrification rates varied significantly over time (Table 5, within-subjects factor), there were no apparent long-term trends of increase or decrease. In the cedar swamps, measurable nitrification occurred during dry incubation periods, but disappeared during the wet periods in both sample areas. In the other wetland types, dry periods had consistently higher net nitrification during dry periods than the rates measured during wet periods. Large differences between sample areas were again observed; nitrification in the M6CS and M6PH soils were higher than in the M10CS and M10PH soils respectively, but rates were comparable (except for one anomalous measurement at day 150) in soils from the two PW wetlands (Fig. 5).

3.4. Dynamics of N mineralization

The modified two-pool exponential model (Eq. (1)) fit the net mineralization data for both the constant-moisture and the D + W treatment for most but not all of the M6 wetland incubations, and only for the fluctuating-moisture treatment (D + W) in the M10 wetland incubations, with R^2 values ranging from 0.845 to 0.984 (except a replicate of PW soil under D + W moisture regime, $R^2 = 0.197$; Table 6). Because the analyses did not produce significant model results for all incubations, and because the distribution of calculated values was highly skewed, the calculated values were analyzed for differences among wetland types and moisture regimes using non-parametric Kruskal–Wallis tests.

The D + W regime was the only moisture treatment for which calculations were successful for wetlands within both sample areas. In the M6 sample area, the labile N pool (N_L) estimated by the model was 146.9–648.1 g N m^{-3}, equivalent to 7.92–33.1% of TN, and in the M10 wetlands was 63.2–191.9 g N m^{-3}, equivalent to 11.1–23.7% of TN (Table 6). These differences were marginally different ($\chi^2 = 3.57$, $p = 0.06$), but the pattern of difference (M6 > M10) was consistent with the observed trend of larger amounts of all forms of N released in the M6 compared to the M10 sample area (Table 2, Fig. 1).

The different moisture regimes did not result in statistical differences in N_L, but some differences among wetland types were found. Total mineralizable N differed among the wetlands ($\chi^2 = 7.02$, $p = 0.030$; sequence of types PH > CS > PW), again consistent with the observed pattern of higher amounts of production of all forms of N from the PH wetlands (Table 1). The rate constants ('k') did not differ among sample areas, wetland types, or moisture treatments (all Kruskal–Wallis tests non-significant). The wetlands did differ in the percent of TIN within the total N pool ($\chi^2 = 11.84$, $p = 0.003$, PH > PW > CS). The half-life of N_L ranged from 19.2 to 128.1 weeks (Table 6), but neither wetland type nor moisture regime significantly affected this value. The half-life of the slow-release nitrogen pool is essentially infinite, since the estimates of h, the mineralization rate constant for this pool, were very small ($<10^{-6}$). This suggests that the slow-release pool did not play an important role in the N mineralization

Table 2
Nested analyses of variance results for the cumulative production of nitrogen components testing all moisture treatments and wetland types, with 'site' nested within. *F* values are given, with significance indicated by asterisks. The patterns of main effect differences, following Tukey's HSD test. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, 'ns' = not significant.

Nitrogen fraction	Site (S)	Wetland type	Moisture regime	Interaction (V × M)
NH_4	8.84***	31.45***	ns	ns
NO_3	10.29***	18.67***	9.47***	7.38***
Total inorganic N	8.41***	30.28***	2.76*	ns
Dissolved organic N	4.41***	22.20***	10.67***	ns
Total dissolved N	5.54***	30.03***	7.17***	2.27*

processes in these wetland soils, even after draining for the full 36-week incubation period.

4. Discussion

Soils along the drainage catena of wetland types proved to be heterogeneous in their response to variations in moisture regimes. Some, but not all wetland soils from different types of wetland plant communities responded to decreases in soil moisture with the increases in net mineralization rates; all showed increased nitrification under dry conditions. However, these responses were not uniformly observed across all wetland types and patterns of moisture change, and across the two apparent replicate sample areas. One sample area (M6) maintained higher rates of mineralization in all wetland types, produced more mineral N, and had larger pools of mineralizable N under both constant and fluctuating moisture regimes than did wetlands in the other sample area (M10); these differences were associated with differences in N_L, but not in the rate constants of N mineralization. Moreover, within both sets of wetlands, the pine-hardwoods wetland soils tended to produce significantly more extractable N than did either the pine wetland mineral soils or the cedar swamp organic soils, a result that was also in line with the calculated labile N. Although nitrification and extractable nitrate showed consistent increases as soil moisture decreased in most wetlands, the absolute amounts and changes in rate were very small. Our results are in line with studies of drainage in peatlands and other wetlands that report increases in nitrification and mineralization, but with significant variation in amounts and in responsiveness to moisture changes among wetland types (Regina et al., 1996, 1999; Freeman et al., 1997; Olde Venterink et al., 2002).

The results support the conclusion that prolonged drainage is likely to produce environmentally significant amounts of nitrate in these wetland soils. The increase in nitrate production may be due

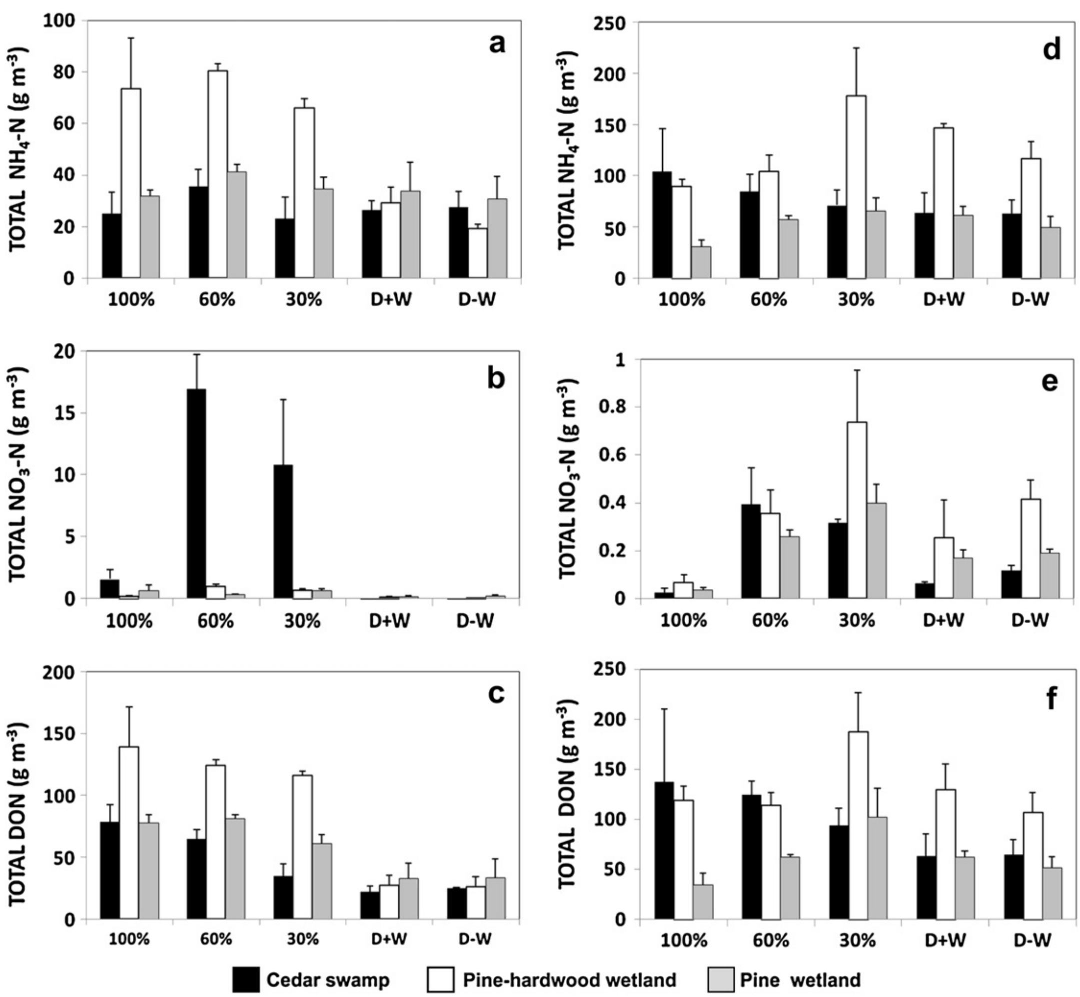

Fig. 1. Net nitrogen production accumulated during long-term incubations of soils from three wetland types in two sample areas. Cumulative amounts of (a) and (d) NH_4–N in the M10 sites and M6 sites respectively; (b) and (e) NO_3–N in the M10 and M6 sites respectively; and (c) and (f), dissolved organic N in the M10 and M6 sites respectively. All data are in g N m^{-3} ± s.e, $n = 3$. Note the differences in *y*-axis scales between forms of N and between sample areas.

Table 3

Two-way analyses of variance comparing cumulative production of N fractions among Wetland types and moisture regimes (F values for each factor and significance levels are give). Means comparisons (Tukey's HSD tests) show treatments and groups of treatments that are significantly different from each other at $p = 0.05$, listed in order of decreasing mean values. The "Moisture regime" factor includes 5 levels (constant moisture at 100%, 60%, 30% WHC, D + W and D–W fluctuating regimes).

Site (S)	Nitrogen fraction	Wetland type	Moisture regime	Interactions
M10	NH_4	14.97*** PH > PW = CS	5.67** 60 = 100 = 30 > 100 = 30 = D + W = D-W	3.72**
	NO_3	20.44*** CS >> PH = PW	8.92*** 60 = 30 > 30 = 100 > 100 = D-W = D + W	7.49***
	Total inorganic N	11.02*** PH > CS > PW	8.51*** 30 = 60 = 100 > 30 = 100 = D + *W* > 100 = D + W = D-W	3.36**
	Dissolved organic N	16.66*** PH > PW = CS	24.74*** 100 = 60 > 60 = 30 > D–W = D + W	3.03*
	Total dissolved N	15.49*** PH > PW = CS	18.09*** 60 = 100 = 30 > D + W = D–W	2.98*
	% DON	ns	13.95*** 100 = 60 > 60 = 30 = D–W > D–W = D + W	ns
M6	NH_4	21.38*** PH > CS = PW	ns	ns
	NO_3	5.49** PH > PW = CS	9.39*** 30 = 60 > 60 = D + W = D-W> D + W = D-W = 100	ns
	Total inorganic N	21.33*** CS > PH = PW	ns	ns
	Dissolved organic N	12.27*** PH > CS = PW	ns[a] 30 = 60 = 100 = D + *W* > 60 = 100 = D + W = D-W	ns
	Total dissolved N	18.71*** PH > CS = PW	ns	ns
	%DON	6.58**	5.57**	ns

[a] $p = 0.06$; significant Tukey's test.

to either increased gross nitrification rates or to decreased denitrification rates, or both (Olde Venterink et al., 2002); our results do not allow us to separate these different causes. Although there was some evidence of increased nitrification during the dry periods of the fluctuating treatment, the absolute amounts were very small, and the lack of significant difference in NO_3^-–N production between the D + W and D–W treatments suggests little denitrification occurred. As noted above, even though nitrification increased during the two-week dry periods, the absolute amounts of nitrification were extremely small. The effects of anthropogenic drainage must, therefore be evaluated in terms of whether they will produce consistent, long-term changes in soil moisture, despite the periodic input of precipitation, rather than short-term increases in dry conditions even during drought spells.

Only 2.6–9.6% of soil total nitrogen was mineralized during the 36-week incubation. Because the labile nitrogen estimated from the two-pool exponential models ranged from 7.3 to 33.1% of soil total nitrogen (Table 6), the 36-week period was evidently too short to allow the entire pool to mineralize. This suggests that the consecutive extraction procedure used in our study might underestimate N

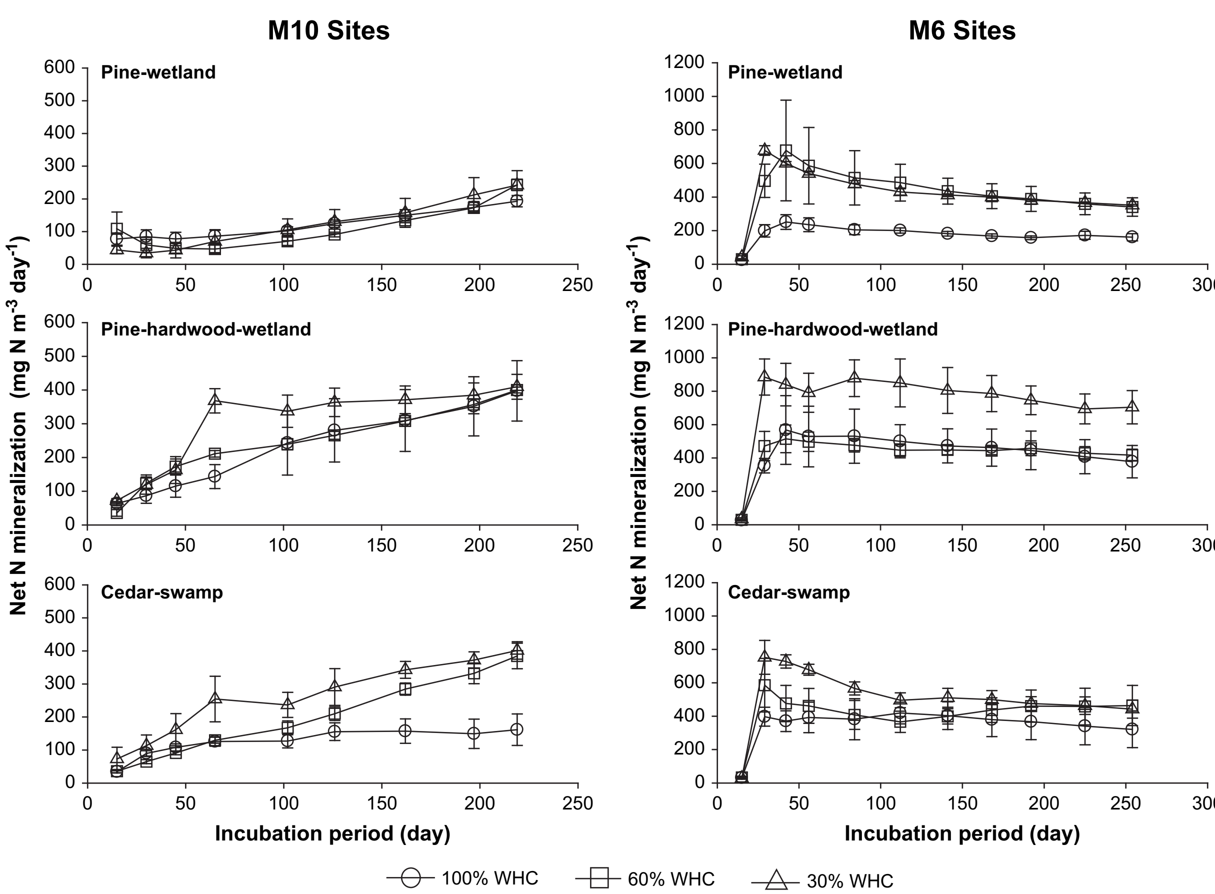

Fig. 2. Net N mineralization rates (mg N m^{-3} d^{-1} ± se, $n = 3$) calculated for each 2-week incubation period for the constant-moisture treatments. Note the difference in y-axis scale for M10 and M6.

Table 4
Repeated measures analyses of mineralization and nitrification rates in the constant-moisture incubations (T = 'time' as the repeated within-subject factor, S = 'site', W = 'wetland type' and M = 'moisture level' as between-subject factors). Factors and factor interactions not listed were not significant. P values for univariate tests of within-subject factors are values adjusted with the Huynh-Feldt epsilon. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Source	Soil net mineralization		Soil net nitrification	
	F value of Wilks' λ	*F* value of repeated measures	*F* value of Wilks' λ	*F* value of repeated measures
Between subjects				
Moisture		8.54***		4.65*
Sample area		35.00***		22.42***
Wetland type		14.81***		18.05***
Wetland type × moisture				3.91**
Sample area × moisture				3.69*
Sample area × wetland type				18.16***
Sample area × wetland type × moisture				3.88**
Within subjects (*Time*)				
Time	94.60***	28.94***	8.79***	3.87**
Time × sample area	37.7***	40.70***	31.51***	3.83**
Time × moisture	4.50***	3.38***	8.08***	
Time × wetland type	4.65***		11.76***	3.38**
Time × sample area × moisture	3.25***	2.94***	10.94***	
Time × sample area × wetland type			10.53***	3.37**
Time × wetland type × moisture			5.46***	2.00*
Time × wetland type × moisture × sample area			5.13***	1.97*

mineralization because each extraction of mineralized inorganic nitrogen also extracted dissolved organic nitrogen from incubated soils. The dissolved organic nitrogen is a ready-mineralizable portion of soil labile nitrogen pool (Haynes, 2005). The accumulated amount of dissolved organic nitrogen we extracted in this study accounted for 19.8–64.0% of estimated soil labile nitrogen pool size (Table 6). Both total released inorganic nitrogen (TIN) and dissolved organic nitrogen (DON) were linearly related to the estimated labile nitrogen pool in the incubated wetland soils (TIN: $R^2 = 0.67$, $p < 0.001$; DON: $R^2 = 0.69$, $p < 0.001$; $n = 40$). Although other studies have shown that the labile N pool is affected by land management practices (Haynes, 2005; Gregorich et al., 2006), the labile N pool was not affected by moisture regimes in this study. This result suggests that N_L may be more sensitive to the quality and quantity of plant inputs, as well as long-term (multi-year) soil conditions, than short-term moisture manipulations (duration of weeks).

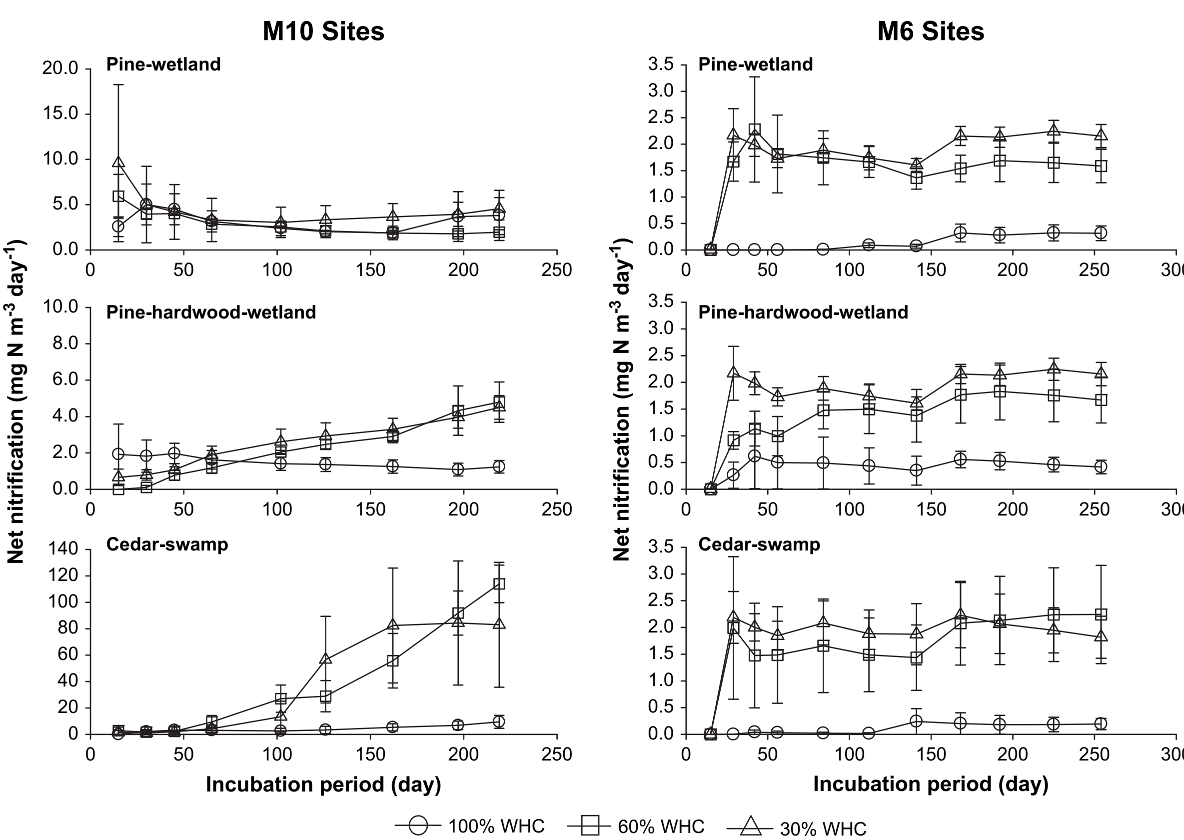

Fig. 3. Net nitrification rates (mg N m^{-3} d^{-1} ± se, $n = 3$) calculated for each 2-week incubation period for the constant-moisture treatments. Note the difference in *y*-axis scales for the different graphs.

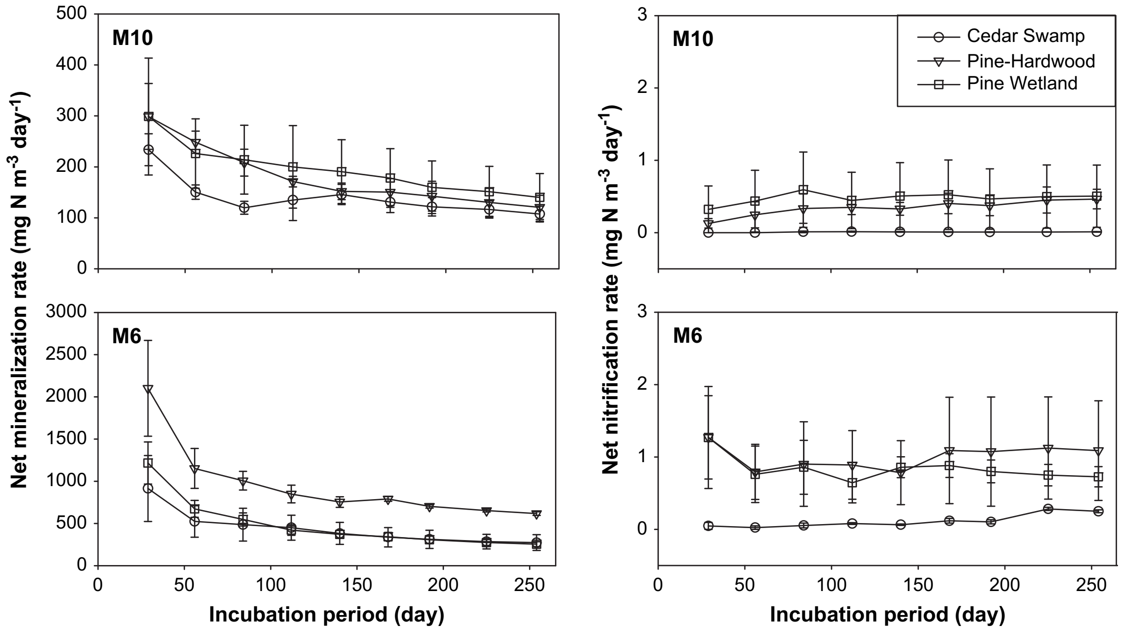

Fig. 4. Patterns of net mineralization and nitrification (mg N m^{-3} d^{-1} $\pm$ se, $n = 3$) in the fluctuating-moisture incubations extracted after each D + W cycle. Note the difference in *y*-axis scale for net mineralization in the two study areas.

The very low absolute rates of nitrification observed in all the wetland soils is likely to be a result of the very low soil pH values observed (Table 1). Low pH is a well-known limiting condition for nitrification (Bridgham et al., 1998; Ste-Marie and Paré, 1999; Paul, 2007). Studies in European forests subjected to high rates of nitrogen deposition (largely as NH_4^+–N) have found that hardwood forests with soil pH values over 4.5 can almost fully nitrify ammonia (Falkengren-Grerup et al., 1998). In our study, net total nitrate production accounted for less than 0.6% of TIN. The net nitrification rates and percentages of NH_4^+–N nitrified of our wetland soils were much lower than wetland soils from northern Minnesota (Bridgham et al., 1998), southeastern Alaska (Fellman and D'Amore, 2007), and northwestern Quebec, Canada (Ste-Marie and Paré, 1999) whereas net mineralization rate and NH_4^+–N production were in a comparable range as these studies. In all of these studies, soil pH values were higher than those we observed in the Pinelands soils, supporting our inference that the very low pH values highly constrained nitrification in our samples. In previous studies of nitrogen cycling in Pinelands cedar swamps (Zhu and Ehrenfeld, 1999), increases in pH were clearly associated with increased amounts of nitrification and nitrate in soil water. Other studies have also associated nitrification in wetland soils with higher pH conditions (Bridgham et al., 2001). Thus, very low pH may buffer wetlands subjected to drying conditions against large increases in nitrification.

Most of the statistical analyses reported above showed that there were consistent differences among the wetland types, in both sets of sample areas. The pine hardwood wetlands had the highest

Table 5

Repeated measures analyses of mineralization and nitrification rates in the fluctuating-moisture incubations ('time' as the repeated within-subject factor, and 'Wetland type' and 'moisture level' as between-subject factors). Factors and factor interactions not listed were not significant. P values for univariate tests of within-subject factors are values adjusted with the Huynh-Feldt epsilon. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Moisture regime	Source	Soil net mineralization		Soil net nitrification	
		F value of Wilks' λ	*F* value of repeated measures	*F* value of Wilks' λ	*F* value of repeated measures
D + W	*Between subjects*				
	Wetland type		9.27*		
	Sample area		45.53***		
	Within subjects (*Time*)				
	Time	16.77***	19.57***	5.04*	2.53*
	Time × wetland type			3.12*	
	Time × sample area	5.22*	11.17***	7.83*	
D–W	*Between subjects*				
	Moisture regime (dry or wet)				5.22*
	Wetland type		5.09*		4.29*
	Site		46.44***		10.70**
	Within subjects (*Time*)				
	Time	56.88***	22.46***	12.90***	3.19**
	Time × moisture regime	55.91***	46.98***	12.46***	9.03***
	Time × Wetland type	4.31***	1.27	0.85	0.69
	Time × site	20.98***	8.30***	8.45***	1.62

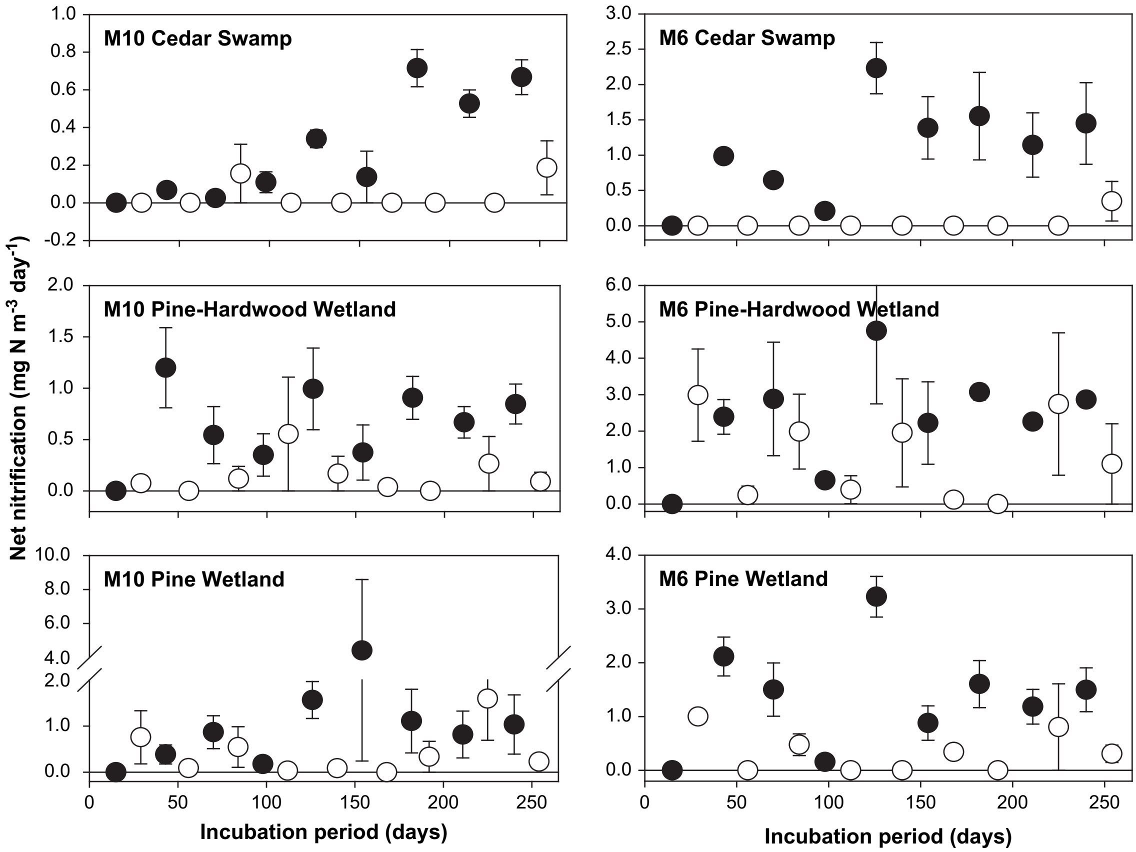

Fig. 5. Net nitrification (mg N m^{-3} d^{-1} $\pm$ se, $n = 3$) patterns in fluctuating-moisture incubations extracted after each two-week period (D–W). The solid line denotes the 0 rate. Note the different *y*-axis scales for each graph. Closed circles: nitrification rates during 30% WHC periods. Open circles: nitrification rates during 100% WHC periods.

rates of N mineralization, the largest amounts of cumulative production of both inorganic extractable and dissolved organic N (Table 3), across moisture treatments (Table 5), and had the largest amounts of readily mineralizable N (Table 6). The only departure from this pattern was the production of nitrate and rates of nitrification, which were consistently higher in the cedar swamps than the other wetland types. This latter result may reflect the lower C:N ratio of the cedar swamp soils (Table 1), and also the significantly larger amounts of NH_4^+–N that are present (initial, pre-treatment measurements; Table 1). None of the soil properties reported in Table 1 adequately explain the greater availability of N in the PH stands. The relatively high N availability in PH wetlands may be a result of the plant community, in that the litter of the dominant hardwood trees should be more rapidly decomposed than that of the coniferous litter in the PW (pine needle) or CS (white cedar needle) stands. It may also reflect an optimal soil structure: the PH stands have higher total nitrogen than the PW stands, but better drainage than the CS stands due to the presence of sandy mineral material not present in CS mucks. This combination of conditions may promote optimal conditions for microbial activity, resulting in

Table 6
Estimated parameters for the two-pool exponential nitrogen mineralization model fitted to data from the 36-week laboratory incubations of wetland soils. N_L = potentially mineralizable (labile) N; TIN = total inorganic N; DON = dissolved organic N; TN = total N. Values are means ± standard errors ($n = 3$) of calculations made for each replicate microcosm of each treatment.

Site	Wetland type	Moisture regime	Percent of TIN in TN (%)	Labile nitrogen pool (N_L) (g N m^{-3})	K ($\times10^{-3}$ d^{-1})	h ($\times10^{-6}$ d^{-1})	Half-life of N_L (week)	Percent of N_L in TN (%)	Percent of DON in N_L (%)	R^2
M10	CS	D + W	3.4 ± 0.5	191.9 ± 112.2	1.6 ± 0.6	0.01 ± 0	128.1 ± 83.2	23.7 ± 13.9	19.8 ± 6.9	0.878–0.952
M10	PH	D + W	4.5 ± 1.0	63.2 ± 27.4	5.1 ± 2.3	0.01 ± 0	24.3 ± 11.0	11.1 ± 4.8	36.1 ± 1.9	0.938–0.965
M10	PW	D + W	3.4 ± 1.1	116.7 ± 41.6	2.7 ± 0.7	0.01 ± 0	42.4 ± 11.4	11.1 ± 4.0	30.6 ± 2.7	0.934–0.980
M6	CS	D + W	3.0 ± 1.0	185.0 ± 59.0	3.3 ± 0.4	0.01 ± 0	31.4 ± 4.4	7.9 ± 2.5	37.0 ± 2.3	0.853–0.959
M6	PH	D + W	8.1 ± 0.4	648.1 ± 94.6	1.8 ± 0.7	0.01 ± 0	65.1 ± 24.2	33.1 ± 4.8	25.4 ± 10.1	0.905–0.969
M6	PW	D + W	5.5 ± 0.6	146.9 ± 15.3	5.4 ± 0.9	0.01 ± 0	19.2 ± 2.9	12.5 ± 1.3	45.1 ± 1.3	0.197–0.881
M6	CS	100% WHC	4.7 ± 1.8	606.0 ± 301.5	1.2 ± 0.2	0.01 ± 0	83.3 ± 13.1	25.8 ± 12.9	23.2 ± 1.5	0.919–0.979
M6	PH	100% WHC	4.6 ± 0.5	347.4 ± 70.6	2.2 ± 0.2	0.01 ± 0	46.0 ± 4.0	17.7 ± 3.6	33.9 ± 0.6	0.951–0.970
M6	PW	100% WHC	2.6 ± 1.0	117.4 ± 33.6	2.0 ± 0.4	0.01 ± 0	52.4 ± 11.7	10.0 ± 2.9	32.5 ± 7.0	0.970–0.971
M6	CS	60% WHC	3.2 ± 0.4	521.9 ± 112.5	1.0 ± 0.4	0.01 ± 0	125.7 ± 52.9	22.7 ± 4.8	24.0 ± 8.2	0.935–0.951
M6	PH	60% WHC	5.9 ± 1.0	436.7 ± 86.0	1.8 ± 0.3	23.7 ± 23.7	59.5 ± 12.1	22.3 ± 4.4	31.5 ± 4.8	0.951–0.984
M6	PW	60% WHC	5.1 ± 0.4	171.5 ± 11.2	3.4 ± 0.6	0.01 ± 0	31.6 ± 7.0	14.6 ± 1.0	37.9 ± 4.0	0.940–0.975
M6	CS	30% WHC	3.1 ± 0.7	172.1 ± 42.1	4.2 ± 0.5	44.2 ± 43.6	24.4 ± 3.5	7.3 ± 1.8	64.0 ± 14.2	0.845–0.948
M6	PH	30% WHC	9.6 ± 2.4	607.1 ± 129.4	2.5 ± 0.4	0.01 ± 0	42.3 ± 6.5	31.0 ± 6.6	32.9 ± 0.6	0.969–0.976
M6	PW	30% WHC	5.9 ± 1.2	267.6 ± 110.7	2.8 ± 0.7	20.5 ± 20.0	42.6 ± 13.7	22.8 ± 9.4	46.0 ± 7.6	0.952–0.972

higher rate of N production. The pine wetland stands, in contrast, had the lowest values of available N (measured as extractable concentrations and as process rates), although the quantitative amounts were most frequently not significantly different from those of the cedar swamps. Regionally, the PW communities are characterized by abundant to dominant populations of broadleaf evergreen trees (*P. rigida*) and shrubs (*Kalmia angustifolia*, *Ilex glabra*, *Gaultheria procumbens*), whereas in the PH wetlands, the only evergreen species present is *P. rigida*, at low densities, interspersed with deciduous trees. The presence of evergreen species has been related to low nutrient cycling rates and low nutrient availability (Aerts et al., 1999; Aerts and Chapin, 2000); the high abundance of evergreen broadleaved understory species in the PW communities may thus create a more recalcitrant organic matter than the predominantly deciduous vegetation of the PH swamps. The cedar swamps are characterized by a monospecific canopy of needle-leaved evergreen (*C. thyoides*, Atlantic white cedar), and few evergreen shrubs. We speculate that the low nutrient content of litter from the dominant evergreen shrubs in the PW community may contribute to the low N mineralization rates and therefore amounts of extractable N observed in both PW wetlands in this study. Ste-Marie and Paré (1999) also found that despite similar soil types in hardwood and conifer forest types in northern Quebec, the conifer stands, and particularly the low-pH jack pine stands, had much lower rates of N cycling and amounts of extractable N than did the hardwood stands of aspen and birch.

In summary, the response of N mineralization and nitrification rates in wetlands soils to reductions in soil moisture depends on both the length of time of the reduction and the intrinsic quality of the soil organic matter, as reflected in the mineralizable N. Differences among wetland types, which integrate differences in soil composition and the nature of plant inputs, appear to drive consistent differences in nitrogen cycling. Thus, long-term changes in soil moisture conditions may affect N cycling rates not only through changes in the amount of N mineralized from the labile pool, but possibly also by changing the composition of the plant community.

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