*Plant and Soil* **243:** 119–130, 2002.



# Impact of drying and re-wetting on N, P and K dynamics in a wetland soil

H. Olde Venterink[1,2,4,6], T.E. Davidsson[1,5], K. Kiehl[3] & L. Leonardson[1]
[1]*Department of Ecology-Limnology, Lund University, Ecology Building, S-22362 Lund, Sweden.* [2]*Department of Environmental Sciences, Utrecht University, PO Box 80115, 3508 TC Utrecht, The Netherlands.* [3]*Vegetation Ecology, Technische Universitaet Muenchen, Am Hochanger 6, D- 85350 Freising-Weihenstephan, Germany. Present addresses:* [4]*Laboratory of Plant Ecology, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands.* [5]*Ekologgruppen i Landskrona AB, Järnvägsgatan 19B, S-261 32 Landskrona, Sweden.* [6]*Corresponding author**

Received 25 October 2001. Accepted in revised form 4 April 2002

*Key words:* denitrification, mineralization, nitrogen, phosphorus, potassium, sulphate

**Abstract**

As increased nutrient availability due to drainage is considered a major cause of eutrophication in wetlands re-wetting of drained wetlands is recommended as a restoration measure. The effect of soil drying and rewetting on the contribution of various nutrient release or transformation processes to changed nutrient availability for plants is however weakly understood. We measured effects of soil drying and re-wetting on N mineralization, and denitrification, as well as on release of dissolved organic nitrogen (DON), phosphorus, and potassium in incubated soil cores from a wet meadow in southern Sweden. Additionally, the impact of re-wetting with sulphate-enriched water was studied. Soil drying stimulated N mineralization (3 times higher) and reduced denitrification (5 times lower) compared to continuously wet soil. In the wet cores, denitrification increased to 20 mg N $m^{-2}$ $d^{-1}$, which was much higher than denitrification measured in the field. In the field, increased inorganic-N availability for plants due to drainage seemed primarily to be caused by increased N mineralization, and less by decreased denitrification. Soil drying also stimulated the release of DON and K, but P release was not affected. Re-wetting of dried soil cores strongly stimulated denitrification (up to 160 mg N $m^{-2}$ $d^{-1}$), but N mineralization was not significantly decreased, neither were DON or K release. In contrast, the extractable P pool increased upon soil wetting. Re-wetting with sulphate-enriched water had no effect on any of the nutrient release or transformation rates. We conclude that caution is required in re-wetting of drained wetlands, because it may unintendently cause internal eutrophication through an increased P availability for plants.

*Abbreviations:* DON – dissolved organic nitrogen; WFPS – water filled pore space

## Introduction

Drainage of low-productive wetlands often leads to enhanced biomass production and changed vegetation composition. One explanation is that increased soil aeration promotes eutrophication by enhancing availability of growth limiting nutrients for plants (Bridgham and Richardson, 1993), which is in agreement with the increased nitrogen (N) availability after drainage as observed by Grootjans et al. (1985, 1986). All kinds of nitrogen flows – e.g. mineralization, denitrification, and organic-N release – may contribute to increased N availability. Also the relationships between drainage and availabilities of the other potentially growth limiting nutrients phosphorus (P) and potassium (K) (cf. Olde Venterink et al., 2001; Verhoeven et al., 1996b) is poorly understood.

With respect to N, it is known that mineralization increases after drainage and subsequent aeration of wet soils (Birch, 1960; Bridgham et al., 1998; Cabrera, 1993; Updegraff et al., 1995), whereas denitrification decreases as the consequence of decrease of anoxic regions (Groffman and Tiedje, 1988; Seitzinger, 1994). Both effects of drainage lead to increased N avail-

* E-mail: h.oldeventerink@biol.rug.nl

ability. Additionally – although little is known about plant uptake and transformation processes of dissolved organic nitrogen (DON) compounds – some DON-compounds may contribute to N availability for plants (Chapin, 1995; Kaye and Hart, 1997), and their availability may increase due to drainage (Paul and Tu, 1965).

Phosphorus availability for wetland plants is largely controlled by chemical equilibria in soil (Richardson and Marshall, 1986). Particularly in the pH range of 4–6, drainage of wet soils decreases plant phosphorus availability by Fe-P complexing (Patrick and Khalid, 1974; Richardson, 1985). Other studies, however, showed that microbial immobilization controls P availability for plants (Chapin et al., 1978; Walbridge, 1991). Whether this is related to soil wetness is unclear, but it seems plausible that along with mineralization, also immobilization will increase.

Potassium release in soils is primarily controlled by physical adsorption to clay particles (Mengel, 1982; Scheffer and Schachtschabel, 1989). Since K adsorption increases with drainage of the soil (Scheffer and Schachtschabel, 1989), K availability for plants likely decreases after drainage. However, data on the biogeochemistry of K in soils are rare. The availability of K for plants in relation to soil wetness is therefore still poorly understood.

Re-wetting of formerly drained areas has become common practice in wetland restoration (Pfadenhauer and Grootjans, 1999). If possible, the groundwater level is raised, but often surface water has to be applied. The aim of re-wetting is to reduce soil aeration and decrease N mineralization and hence to decrease N availability for wetland plants. Some studies have however shown that N-mineralization may increase – instead of decrease – after soil drying and re-wetting (Birch, 1960; Van Schreven, 1968). Moreover, also P and K availabilities may increase upon re-wetting; Chepkwony et al. (2001) indeed showed an increased P-availability for plants after soil drying and re-wetting. Besides, the chemical composition of surface water used for re-wetting generally differs from that of groundwater, which might affect nutrient release rates after re-wetting. For instance, sulphate-enrichment of the water may mobilize phosphate (Caraco et al., 1989; Lamers et al., 1998a, 1998b; Roelofs, 1991), and through sulphite production it may inhibit the coupled nitrification–denitrification (Joye and Hollibaugh, 1995) which may result in a higher N availability for plants.

*Table 1.* Soil characteristics at the start of incubation (mean ± 1 SE; $n$=8). All units are based on soil dry weight, except for moisture content which is based on soil fresh weight

| | |
|---|---|
| bulk density (g $cm^{-3}$) | 0.36 ± 0.02 |
| organic matter (%) | 27 ± 2 |
| moisture content (%) | 64 ± 1 |
| pH-KCL | 5.4 ± 0.1 |
| Kjeldahl N (g $kg^{-1}$) | 11 ± 1 |
| Kjeldahl P (g $kg^{-1}$) | 0.88 ± 0.07 |
| Kjeldahl K (g $kg^{-1}$) | 1.5 ± 0.1 |
| extractable Ca (g $kg^{-1}$) | 5.3 ± 0.3 |
| extractable Fe (g $kg^{-1}$) | 1.7 ± 0.2 |
| extractable Al (g $kg^{-1}$) | 0.32 ± 0.03 |

In this study, we evaluated the effects of drying and re-wetting of a wetland soil on N mineralization, and denitrification, as well as on changes in soil extractable pools of DON, P and K, in a laboratory experiment. We hypothesized that drying of incubated wetland soil will: (i) increase accumulation of inorganic-N, and (ii) that this increased N accumulation is caused by both an increased N mineralization rate and a decreased denitrification rate. Additionally, soil drying will (iii) increase soil extractable DON, (iv) decrease soil extractable P, and (v) decrease soil extractable K. We also hypothesized that re-wetting of dried wetland soil will act opposite to drying (reverse of hypotheses i–v), and that re-wetting with sulphate-enriched water will decrease denitrification and enhance extractable P in the soil compared to re-wetting with distilled water.

## Methods

### *Soil and site characteristics*

Soil cores were collected at an abandoned wet meadow at the shore of lake Hammarsjön nearby Norra Åsum, SE Sweden. Characteristics of the sandy peat soil are presented in Table 1. Vegetation at the site showed intermediate productivity (dry weight of above-ground biomass in August 1999: 665±60 g $m^{-2}$). It was dominated by *Carex disticha* (80% coverage), and further characterized by *Filipendula ulmaria* and *Phalaris arundinacea*. Cores for the first and second lab experiment were taken on August 4 and 23 1999, respectively, all within a plot of 2.5-m × 2.5-m to minimize effects of soil heterogeneity. Soil cores (4.6

cm diameter, 10 cm depth) were carefully taken with sharpened PVC tubes, in between plant shoots; i.e. there were no plant shoots in the cores. To avoid soil compaction as much as possible, the tubes were cut by hand through the top 5-cm root layer, and further inserted in the soil by means of a hammer. Soil compaction could be checked in the field because the tubes were made of transparent PVC.

*Experimental design experiment 1*

The soil cores were incubated in a climate room within 1–3 h after collection. Air temperature was 17 °C throughout the experiments, corresponding to measured field temperature at August 4 (5-cm depth). The 17 °C can be considered maximum field temperature for this soil since it had been extremely warm for the region (30–34 °C maximal day temperature) for about a week. Due to high temperature and lack of rain, water filled pore space (WFPS) of the collected soil was 72%. Because we wanted to study the effect of drainage of a wet soil, this 'initial natural' drainage was unwanted in our experimental setting. We therefore simulated a rainfall by adding 20 mL of distilled water to all cores at incubation in the climate room, creating an average WFPS of 88% (Figure 2A). WFPS of all cores was calculated from measured moisture contents (loss of soil weight after 72 h at 70 °C), using the average amount of water (129±6 mL) in 44 water-saturated cores (cf. experiment 2) as 100% WFPS reference.

Immediately after rainfall simulation, initial denitrification rates and initial amounts of extractable nutrients were measured. Additionally, 48 cores were incubated at continuous wet conditions, and 96 cores were subjected to drying (cf. Figure 1). All cores were incubated in the PVC tubes in which they were taken. Tubes of the wet treatment were closed with lids on both ends, although small holes above the soil allowed gas exchange with the air. Tubes of the drying treatment were only closed on the bottom with nylon filter (1 mm mesh width). At regular intervals, all cores were weighed enabling *a posteriori* calculation of WFPS (Figure 2A). After 7 d of incubation, fans were positioned beneath the drying cores to simulate more severe drainage than the normal wetting-drying cycle. After 12 d of incubation, further drying of the drained cores was prevented by closing the tubes with lids; 24 cores were kept at this moisture content. Forty eight drained cores were re-wetted, with the average 65 mL water that was lost during drainage, of which 24 cores were re-wetted with distilled water and 24 cores with a 50 mg $L^{-1}$ $SO_4^{2-}$solution ($Na_2SO_4$). Because of possible long-term effects of acetylene on microbial processes (e.g. Hynes and Knowles, 1978; Seitzinger, 1994), every soil core was only used for either one denitrification measurement or one set of extractions (Figure 1). All measurements were carried out with 8 replicate cores.

The day before sampling of the experimental cores, 8 soil cores had been taken from the field site to determine amounts of soil extractable nutrients at field conditions. These cores were not initially wetted; analytical methods, however, were the same as for the laboratory experiment.

*Experimental design experiment 2*

By accident, average moisture contents of the denitrification cores immediately after re-wetting were significantly ($P$=0.032) higher in the cores re-wetted with distilled water than in the cores re-wetted with sulphate-enriched water. Because of this experimental error in the first experiment, a second re-wetting experiment was carried out. Therefore, 44 additional cores were collected from the same site as before. Initial WFPS was 100% this time since the site was flooded (water in the tubes was poured off). All 44 cores were subjected to the same drying treatment as described for the first experiment. After 12 days of drying, 32 cores were re-wetted with 65 mL to the initial 100% WFPS. Re-wetting was carried out with four types of water and 8 replicates: (i) distilled water, (ii) 50 mg $L^{-1}$ $SO_4^{2-}$solution ($Na_2SO_4$), (iii) 5 mg $L^{-1}$ $NO_3^-$-N solution ($NaNO_3$), and (iv) a combined 50 mg $L^{-1}SO_4^{2-}$ + 5 mg $L^{-1}NO_3^-$-N solution. No significant differences occurred in WPFS or moisture content. Additionally, 12 cores were re-wetted with different amounts of distilled water (duplicate re-wetting with 0, 10, 20, 30, 40 and 50 mL) to create a WFPS gradient after re-wetting. Denitrification was measured immediately after re-wetting.

*Denitrification*

Denitrification was determined by the acetylene-blockage method (Yoshinari and Knowles, 1976). At the start, and after 3, 6, 12, and 26 days of incubation, soil cores were carefully taken out of the tubes and rolled in aluminium foil with the top of the core left open. These cores were incubated in 1 L plastic jars with gas-tight lids and butyl septa facilitating headspace gas sampling. After closing each jar, 100 mL air

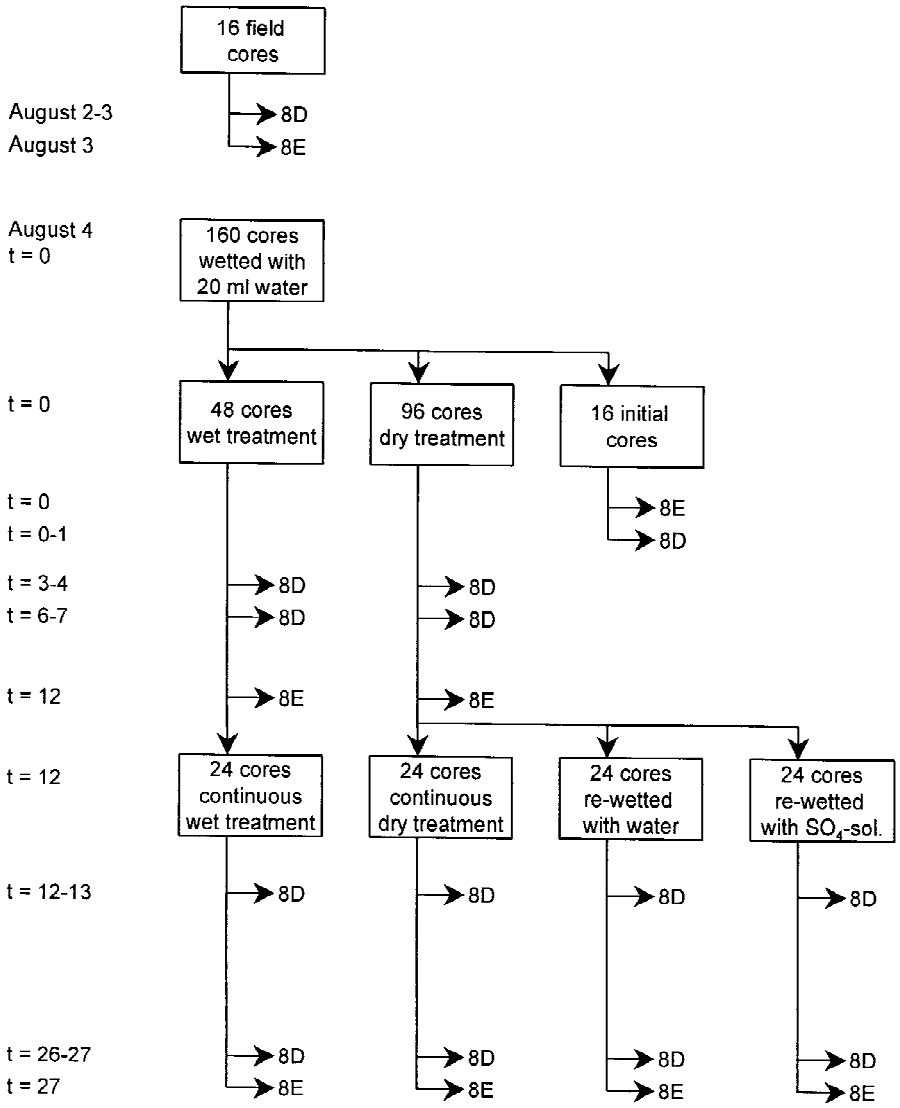


*Figure 1.* Experimental design of experiment 1. 8D = 8 soil cores used for denitrification measurements; 8E = 8 soil cores used for soil extractions; $t$ = number of days after August 4 1999.

from the headspace was replaced by 100 mL acetylene (purity >99%). After 1 and after 24 h of incubation, gas samples were taken from the headspace and immediately analysed for $N_2O$ concentration using a gas chromatograph (Varian 3300). $N_2O$ production was calculated by subtracting the 1 h concentration from the 24 h concentration, with corrections for time and soil core surface area. Denitrification in the field was determined in the same way by 8 cores incubated in jars in the soil, between 48 and 24 h before the main core sampling. Headspace samples were stored in blood tubes during transport.

*Extractable and total nutrients in soil*

Soil from 'field' cores, from initially wetted cores, and from cores incubated for 12 or 27 days, was extracted with 1 *M* KCl to determine extractable nitrogen (cf. Berendse et al., 1994), and with 0.1 *M* $NH_4OH$ + 0.1 *M* lactic acid + 0.4 *M* acetic acid (ALA) for extractable P and K (cf. Koerselman et al., 1993). Before extraction, soil was homogenized and large roots were removed. After extraction and centrifugation (10 min at 3000 rpm), ALA-extracts were acidified with 1 *M* $HNO_3$ for storage. Later, dissolved-P and K, as well as Ca, Fe and Al, concentrations were measured by

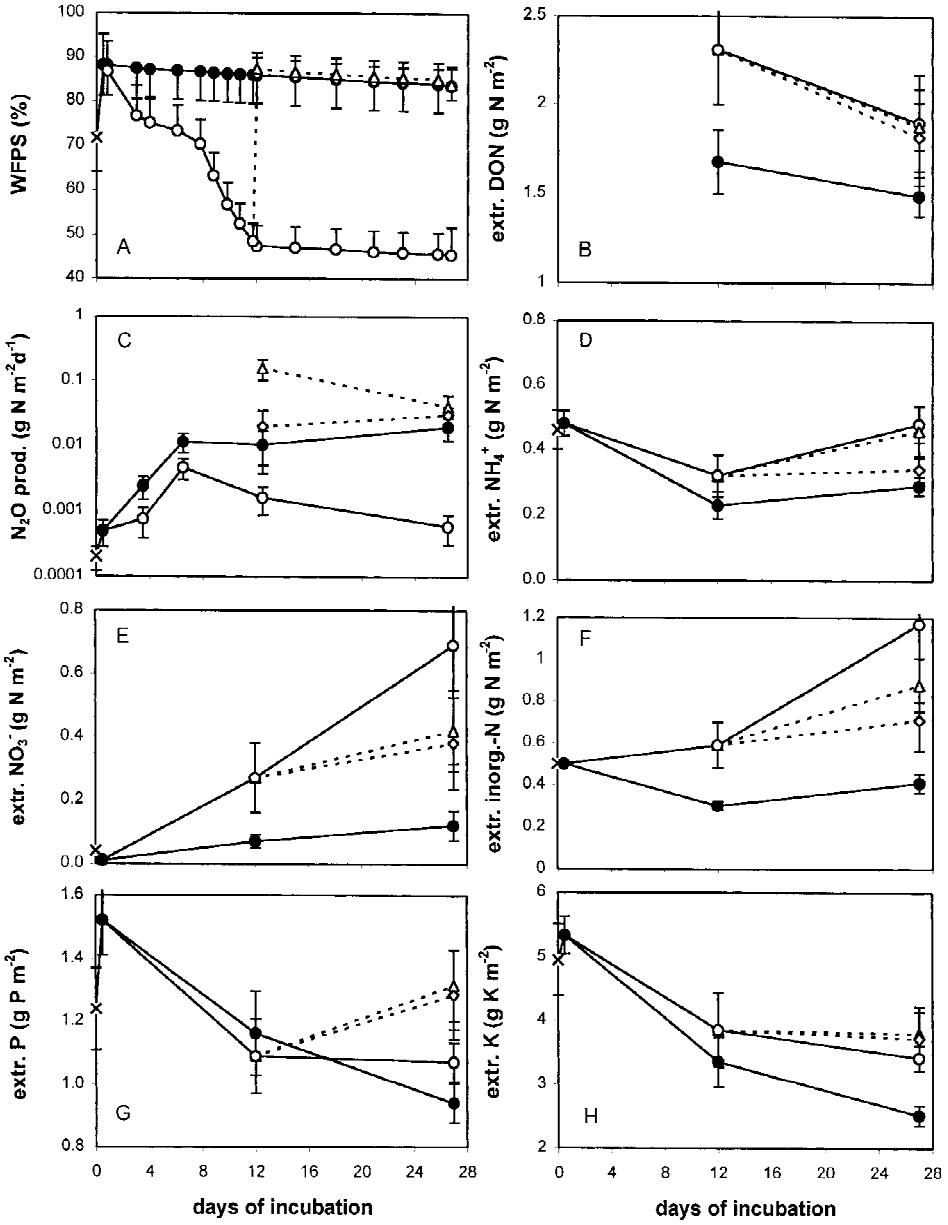


*Figure 2.* Effect of soil drying and re-wetting on water filled pore space (WFPS) (A), extractable amounts of dissolved organic nitrogen (DON) (B), ammonium (D), nitrate (E), ammonium+nitrate (F), phosphorus (G), and potassium (H), as well as denitrification (C) in intact soil cores. Denitrification was measured as $N_2O$-production after incubation with acetylene. Calculations are based on the upper 10 cm soil layer and mean bulk density. Symbols: x field cores, • constant wet cores, ◯ dried cores, Δ dried cores after 12 days re-wetted with destilled water, or ◊ re-wetted with sulphate-enriched water. Symbols represent means (±SE) of 8 replicate cores (2B–H); 2A shows mean (±SD) WFPS vs. time of 8 cores used for the final denitrification measurements ($t$=26-27), and 8 cores of the final soil extractions ($t$=27). Note the log-scale of 2C. For statistics see Table 2.

means of the inductively-coupled plasma technique. Centrifuged KCl extracts were stored overnight at 2 °C. The next day, $NH_4^+$ concentrations were analysed colorimetrically (Chaney and Marbach, 1962). Samples for nitrate and total nitrogen analysis were stored frozen. $NO_3^-$ concentrations were measured by flow injection analysis (Tecator 5042/5012). Total dissolved-N was measured with an ANTEK 9000 high temperature combustion total nitrogen analyser. DON

was estimated by subtracting $NH_4^+$-N and $NO_3^-$-N from total dissolved-N.

Soil not used for extraction was dried for 72 h at 70 °C to determine moisture content, after which the samples were ground and subjected to Kjeldahl digestion to analyse the total N, P and K contents (Allen, 1989). $NH_4^+$ concentration in the digests was measured photospectrometrically with a Skalar auto-analyser. Dissolved-P and K concentrations in the digests were measured as in the ALA extracts. Additionally, soil organic matter content was determined by loss of ignition at 550 °C during 4 h.

*Statistics*

Effects and interactions of drying and incubation time, or re-wetting and time, on nutrient variables and experimental control variables were examined by means of repeated measures ANOVA using polynomial contrasts (SPSS 7.5). Values of the initial soil cores were not included in examinations of the treatment effect (wet vs. dry), since initial cores were all wet. The effect of re-wetting on extractable nutrients was examined by one-way ANOVA, since there was only one measurement in time. Non-normal distributed variables or variables with unequal variances among means between treatments were log-transformed before statistical analysis.

## Results

*Effects of soil drying*

Extractable nitrate increased from almost zero in the initial soil cores to on average 120 mg N $m^{-2}$ in the wet cores and 690 mg N $m^{-2}$in the dried cores, after 27 d of incubation (Figure 2E). For all treatments, extractable ammonium first decreased and increased again afterwards (Figure 2D). The effects of drying and incubation time on extractable nitrate, ammonium, and on their sum (inorganic-N) were significant (Table 2). The difference in inorganic-N fractions between wet and dry cores did not increase significantly between 12 and 27 d of incubation (interaction terms Table 2), due to large variation at the final extraction.

Denitrification rates, measured by means of $N_2O$ production, increased from close to zero in the field and initial wetted soils, to on average 5 and 11 mg N $m^{-2}$ $d^{-1}$ after 6–7 d in the dried and wet cores, respectively (Figure 2C). After 26–27 d of incubation, denitrification was once more doubled in the wet cores, whereas it decreased to initial low rates in the dried cores (Figure 2C). The effects of time, drying and their interaction on denitrification were significant (Table 2).

On average a much larger fraction of the nitrate produced from nitrification was denitrified in the wet cores (60–82%) than in the dried cores (4–9%) (Figure 3). Taking these denitrification rates into account, N mineralization was 2–3.4 times higher in the dried cores than in the wet cores. Moreover, the difference in inorganic-N accumulation during 27 d of incubation (25– −3 = 28 mg N $m^{-2}$ $d^{-1}$) was to 68% caused by a higher mineralization rate in the dried cores (27–8=19 mg N $m^{-2}$ $d^{-1}$) and to 32% by a lower denitrification rate (11–2=9 mg N $m^{-2}$ $d^{-1}$) (Figure 3).

Soil extractable DON was on average 30% higher in the dried than in the wet cores (Figure 2B, Table 2). Extractable phosphorus and potassium decreased significantly in both the wet and dried soil cores during incubation. Extractable P did not differ between the wet and dried treatments, whereas extractable K decreased more in the wet cores than in the dried cores (Figure 2G–H, Table 2).

So, soil drying increased N mineralization, decreased denitrification, and increased DON and K release; P release was not affected.

*Effects of re-wetting*

Whether re-wetting was carried out with distilled water or sulphate-enriched water made no significant difference for extractable amounts of nutrients or denitrification (Figure 2, Table 2), although sulphate addition in the first experiment tended to decrease denitrification immediately after re-wetting. The second re-wetting experiment, however, showed that sulphate addition did not decrease denitrification, neither in the sulphate treatment compared to the distilled water treatment, nor in the sulphate+nitrate treatment compared to the nitrate treatment (Figure 4).

Because sulphate addition did not show an effect, we pooled the two re-wetting-treatments for comparison with the dry treatment. (Re)wetting of dried cores resulted in two significant effects. First, re-wetting strongly increased denitrification (Figure 2C, Table 2). Moreover, denitrification was positively related to WFPS, despite large variation (Figure 5). Second, wetting increased extractable amounts of P in the soil (Figure 2G), although this effect was only significant

*Table 2.* Effects of soil drying, re-wetting, re-wet water type (distilled water vs. sulphate-enriched water) and incubation time on nutrient variables of Figure 2 and on experimental control variables, examined by analysis of variance. Field measurements of Figure 2 are not included. *F*-values of repeated measures ANOVA (time, treatment and interaction) or one-way ANOVA are shown

| | $N_2O$ prod. | Extr. $NO_3^-$ | Extr. $NH_4^+$ | Extr. inorg-N | Extr. DON | Extr. P | Extr. K | WFPS N,P,K[b] | Total | $pH_{KCl}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| time[a] | 14.9** | 41.3*** | 15.4** | 4.8* | $1.4^{NS}$ | 38.6*** | 104*** | 1124*** | $2.0^{NS}$ | $2.0^{NS}$ |
| drying[a] | 16.5*** | 5.0* | 7.4* | 5.4* | 4.8* | $0.1^{NS}$ | 4.2* | 191*** | $1.2^{NS}$ | $0.1^{NS}$ |
| time*drying[a] | 11.1** | 3.3† | 3.7† | 4.0† | $0.1^{NS}$ | $0.9^{NS}$ | 6.8* | 819*** | $1.7^{NS}$ | $1.9^{NS}$ |
| time | $0.2^{NS}$ | | | | | | | 1615*** | | |
| re-wetting | 35.1*** | $0.2^{NS}$ | $1.6^{NS}$ | $0.6^{NS}$ | $0.1^{NS}$ | 3.1 | $0.6^{NS}$ | 154*** | $0.3^{NS}$ | 5.5* |
| time*re-wetting | $0.2^{NS}$ | | | | | | | 1605*** | | |
| time | $0.1^{NS}$ | | | | | | | 2697*** | | |
| water type | 3.5† | $0.5^{NS}$ | $2.2^{NS}$ | $0.3^{NS}$ | $0.3^{NS}$ | $0.1^{NS}$ | $0.1^{NS}$ | $0.5^{NS}$ | $1.0^{NS}$ | $0.5^{NS}$ |
| time*water type | 3.6† | | | | | | | $0.2^{NS}$ | | |

†$P<0.1$, * $P<0.05$, ** $P<0.01$, *** $P<0.001$, $^{NS}$ $P>0.1$.
[a] Initial cores were included in analysis for effects of time, and time*drying, but excluded for drying (wet vs. dry) since initial cores were all wet (see Figure1).
[b] The highest *F* value for total N, total P, or total K in the soil is shown.

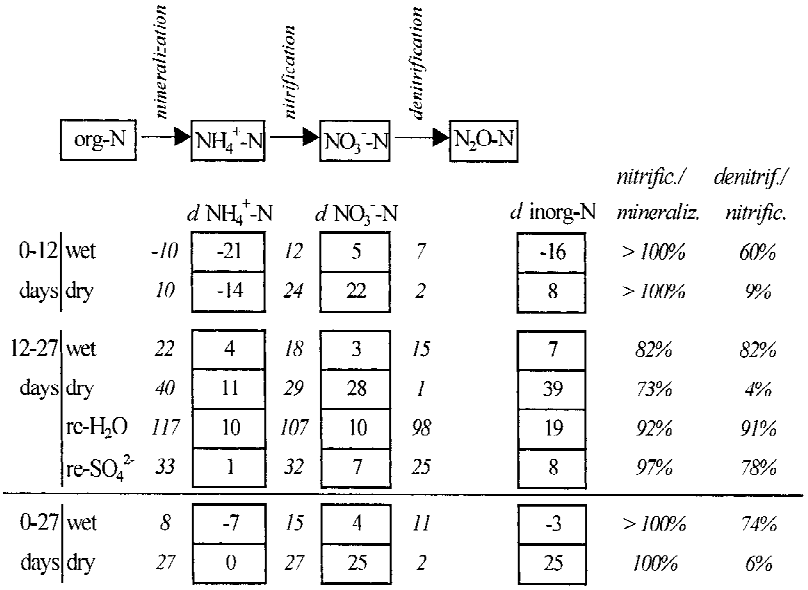


*Figure 3.* Effect of soil drying and re-wetting on average rates (mg N $M^{-2}$ $d^{-1}$) of mineralization, nitrification, denitrification, and accumulation of ammonium (*d* $NH_4^+$-N), nitrate (*d* $NO_3^-$-N) and inorganic-N (*d* inorg-N) in incubated soil cores. Accumulation rates of nitrate, ammonium, and inorganic-N were calculated from differences in time in Figure 2D–F, denitrification rates from Figure 2C, assuming linear change between measurements. Nitrification = nitrate accumulation + denitrification; mineralization = ammonium accumulation + nitrification. Immobilization of produced ammonium or nitrate is not included. Because calculations were based on several variables, true variances were unknown and differences between treatments could not be tested.

($F$=5.77, $p$=0.022) when the two wetting events (initial wetting and re-wetting) were combined in a two-way ANOVA with wetting and date of wetting as factors. Both wetting events had similar effects on extractable P since the date of wetting as well as the interaction term were not significant.

So, re-wetting increased denitrification and P release, but did not affect N mineralization, DON or K

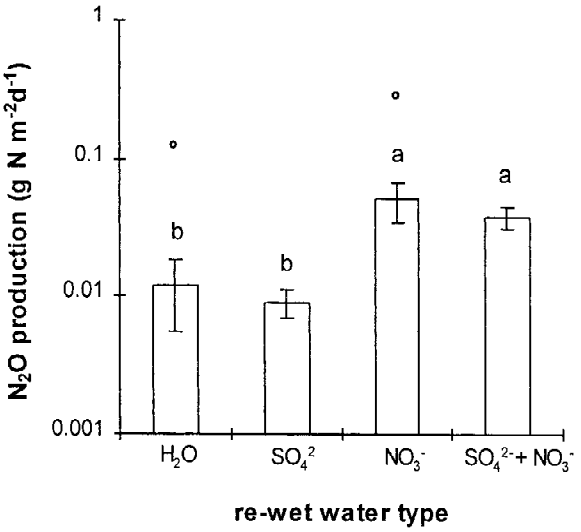


*Figure 4.* Effect of re-wetting with distilled water ($H_2O$), sulphate solution ($SO_4^{2-}$), nitrate solution ($NO_3^-$), or sulphate + nitrate solution ($SO_4^{2-}$+$NO_3^-$) on denitrification in intact soil cores. Before re-wetting, cores were dried for 12 d. Denitrification was measured as $N_2O$-production after incubation with acetylene. Calculations are based on the upper 10 cm soil layer and mean bulk density. Bars indicate means ±SE ($n$=7–8). Two outliers (◯, values > mean + 2SD) were excluded from calculation of means, but were included in calculation of significant differences between treatments as indicated by different letters ($p$<0.05, Mann-Whitney $U$-test).

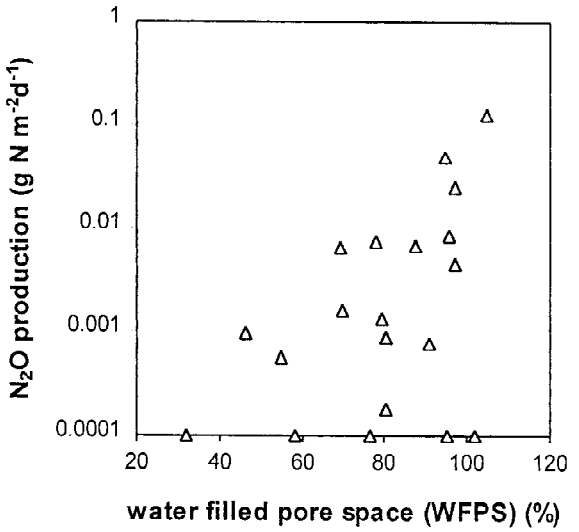


*Figure 5.* Denitrification after re-wetting vs. water filled pore space (WFPS) in intact soil cores. Cores were dried for 12 days and re-wetted with different amounts of distilled water. Denitrification was measured as $N_2O$-production after incubation with acetylene. Calculations are based on the upper 10 cm soil layer and mean bulk density. (Spearman's $r$=0.40; $p$<0.05). $N_2O$ production was enhanced with 0.0001 to allow plots on a log-scale.

release. Sulphate had no effect on nutrient transformation or release rates.

## Discussion

### *Nitrogen dynamics during soil drying and wetting*

Drainage or aeration of wetland soils has been shown to increase N mineralization and subsequent N availability for plants (Grootjans et al., 1985, 1986). Also in our experiment, soil drying lead to higher N mineralization and an increased inorganic-N content compared to wet soil. Our N-mineralization rates fell in the range of rates measured at field conditions in wetland soils (cf. Olde Venterink et al. 2002). Moreover, the on average 3 times higher N mineralization rate in our dried cores was consistent with differences between aerobic and anaerobic mineralization rates observed in a range of wetland soils (Bridgham et al., 1998; Updegraff et al., 1995). Remarkably, ammonium contents decreased in both wet and dried cores during the first 12 days of incubation (Figure 2D), resulting in negative net mineralization rates in the wet cores (Figure 3). Negative net N mineralization rates, which have also been reported for other wet soils (Aerts et al., 1999; Giblin et al., 1991), may be explained by high ammonium concentrations in the initial soil cores (possibly due to ammonium leakage from damaged roots by core sampling) and a higher affinity for ammonium of heterotrophic bacteria compared to nitrifying bacteria (Verhagen et al., 1995; Zak et al., 1990).

We hypothesized that a higher accumulation of inorganic-N in dried soil compared to wet soil would not only be due to an increased mineralization rate but also by a decreased denitrification rate. Calculations of average N transformation rates over 27 d, indeed, showed that the difference in inorganic-N accumulation between our wet and dried cores was to 68% caused by a higher mineralization rate in the dried cores, and to 32% by a lower denitrification rate (Figure 3). We emphasize, however, that these percentages count for incubated soil; the contribution of a decreased denitrification rate seems less important under field conditions where denitrification rates were much lower than in the incubated wet soil. Denitrification rates in the incubated wet cores were much higher than rates in the field site were the cores were taken (Figure 2C), as well as in four nearby located sites of which two sites were very wet (data not shown). Field

denitrification rates in other wetlands, were mostly consistent with our sites: lower than 1 mg N $m^{-2}$ $d^{-1}$ (e.g. Aerts et al., 1999; Bowden, 1987; Groffman et al., 1991; Koerselman et al., 1989; Merrill and Zak, 1992; Urban et al., 1988); although sometimes higher denitrification rates were measured, particularly during winter (Ambus and Christensen, 1993; Berendse et al., 1994), or due to external nitrate supply or repeated drying-wetting conditions (Davidsson and Leonardson, 1998; Leonardson et al., 1994). Combined field measurements of mineralization and denitrification in temperate wetlands also showed that denitrification rates were generally much lower than mineralization rates (Aerts et al., 1999; Verhoeven et al., 1996a, 2001; Zak and Grigal, 1991). We conclude that increased inorganic-N availability in most drained wetlands will primarily be caused by increased mineralization and less by decreased denitrification.

Differences in denitrification rates between incubated dried and wet soil cores, as well as between incubated soil and field conditions, can be explained by the concept of Davidson and Swank (1986) in which denitrification is primarily controlled by soil nitrate concentration and WFPS; particularly in our carbon-rich wetland soil. In the field – and at the start of our experiment– denitrification was likely limited by a low nitrate concentration as a consequence of ammonium and nitrate uptake by plants (cf. Smith and Tiedje, 1979; Verhagen et al., 1995; Zak et al., 1990). In the wet cores, denitrification could strongly increase due to coupled mineralization – nitrification and constantly high WFPS (Figure 2A–E), whereas WFPS was too low for denitrification in the drained cores (cf. Figure 4; Riley and Vitousek, 1995), despite a high nitrate concentration.

We hypothesized that higher N availability for plants due to drainage would not only be a result of mineralization and denitrification, but would also be caused by a higher organic-N availability (cf. Chapin, 1995; Kaye and Hart, 1997; Raab et al., 1999). Indeed, differences in DON between wet and dried cores were comparable to the maximum difference in inorganic-N (Figure 2, Table 2). We only measured differences in total DON amounts, but Paul and Tu (1965) showed that soil drying might increase plant acquirable amino acids. Although still little is known about plant uptake of DON (but see Chapin, 1995; Kaye and Hart, 1997; Van Beusichem and Neeteson, 1982), dynamics of organic-N compounds in relation to soil wetness clearly merits further study.

Re-wetting strongly stimulated denitrification (Figure 2C) as could be expected from the accumulated nitrate in the dried cores and the sudden rise in WFPS (cf. Davidson and Swank, 1986; Davidson et al., 1993; Groffman and Tiedje, 1988; Mulvaney and Kurtz, 1984). The higher denitrification was however not reflected in significantly lower extractable amounts of inorganic-N in the re-wetted soil cores compared to the dried cores; i.e. re-wetting did not significantly decrease net N mineralization. We note however, that particularly average nitrate concentrations tended to be lower in the re-wetted cores (Figure 2E); a longer incubation time or more replicates might have shown a significant decrease in net N mineralization, similar to the results of Berendse et al. (1994). The other component of N availability, DON, was also not reduced after re-wetting. This indicates that a hysteresis effect concerning N availability versus soil drying and re-wetting might not only be created by N mineralization, but also by availability of organic-N.

In the first experiment an indication arose that re-wetting with sulphate-enriched water might tone down denitrification (Figure 2), but results of the second experiment showed that sulphate did not inhibit denitrification, whether additional nitrate was supplied or not (Figure 4). Sulphide – which is highly toxic for nitrifying bacteria (Joye and Hollibaugh, 1995) – was obviously not built up to toxic levels in our soil, as also nitrate production and coupled nitrification-denitrification were not reduced by sulphate addition at the end of the first experiment; i.e. after 12 d of incubation with sulphate. So, if sulphate did not inhibit denitrification, the difference in denitrification between cores re-wetted with water or with sulphate-enriched water in the first experiment (Figure 2C) was likely caused by an unintended difference in soil wetness after re-wetting (see 'Methods'). Moreover, the importance of soil wetness for denitrification was also demonstrated in the second experiment (Figure 5). The large variation in denitrification after re-wetting is most likely a result of variation in soil nitrate concentrations after soil drying (cf. Figure 2E), due to large small-scale variation in decomposable organic matter and consequently in coupled mineralization-nitrification. Large small-scale variation in denitrification, because of variation in soil nitrate, was also found in other flooded meadows (Davidsson et al., 1998; Leonardson et al., 1994).

*Phosphorus dynamics during soil drying and wetting*

While drying had no significant effect on extractable P in the soil, wetting significantly increased P concentrations. The lack of effect of drainage on extractable P is in contrast with our hypothesis that soil extractable P would decrease due to redox sensitive Fe-P complexing (cf. Patrick and Khalid, 1974; Richardson, 1985). The $pH_{KCl}$ of 5.4, corresponding to $pH_{water}$ of 5.6–6.4 (Bolt and Bruggenwert, 1978; Olde Venterink, unpublished data), however, suggets that P was not chemically complexed with Fe, but with Ca (Lindsay and Moreno, 1960). Ca-$PO_4$ complexing is supported by Pearson correlation coefficients between lactic acid extractable amounts of P and Ca ($R$=0.74; $P$<0.001) and between P and Fe ($R$=0.05; $P$=0.69). This indicates that soil redox status, as affected by soil wetness, was less important for P availability in our soil. Another explanation for the increased extractable P pools after re-wetting could be through increased mineralization of organic matter, as was suggested by Chepkwony et al. (2001) in a comparable soil drying - re-wetting experiment. In our study, however, an increased mineralization rate was not supported by increased extrable inorganic N-pools.

A strong decrease in extractable P in both wet and drained cores was observed during incubation (Figure 2G, Table 2). If this decrease was not caused by Fe-P complexing, microbial immobilization seems the most likely explanation (cf. Chapin et al., 1978; Wood et al., 1984; Walbridge, 1991). From this point of view, initial wetting apparently dissolved a part of the Ca-$PO_4$, which was readily immobilized by micro-organisms in both the wet and dried cores (Figure 2G). Re-wetting the dried cores again dissolved some Ca-$PO_4$, but probably due to a diminished microbial P-demand during this second P burst, less of the released P was immobilized. A strong P release after drying and re-wetting was also observed by Olila et al. (1997) in a wetland soil of similar acidity (5.7–6.3).

Re-wetting with sulphate-enriched water had no significant effect on extractable P compared to re-wetting with distilled water in our soil (Table 2). The major mechanism for sulphate-induced P release as reported in other studies is sulphate reduction associated with P release from iron phosphates (Caraco et al., 1989; Koerselman et al., 1993; Lamers et al., 1998a). This mechanism seems indeed less relevant in our soil when P release appeared to be controlled by Ca-$PO_4$ complexing and microbial immobilization, and not by Fe-P complexing.

*Potassium dynamics during soil drying and wetting*

Although potassium is a potentially growth-limiting nutrient in some wetlands (Olde Venterink et al., 2001; Verhoeven et al., 1996b), its biogeochemistry in wetlands is only rarely reported. Two major effects on $NH_4$-exchangeable K were observed in this experiment: (1) A significant decrease in time, and (2) a stronger decrease in the wet than in the dried cores (Figure 2F, Table 2).

Among other explanations for the decrease of exchangeable K during incubation, it seems most likely that potassium, just like ammonium, leached out of roots damaged by core sampling. Potassium rapidly leaches out of dead plant material (Verhoeven, 1986). During incubation this leached K was adsorbed or in another way immobilized in the soil.

The stronger decrease of exchangeable K in the wet compared to the dried cores was not expected according to our hypothesis that K availability would decrease due to an increased K adsorption to soil particles upon drying. However, adsorption of K is affected by soil acidity (Mengel, 1982). A higher exchangeable K-pool in dried cores may be caused by $H^+$ production in the mineralization process; mineralization was higher in the dried cores than in the wet cores (cf. Figure 3) although this was not reflected in a lower $pH_{KCl}$ (Table 2). An increased K release after drainage and increased mineralization was reported for other wet meadows (Grootjans et al., 1985; Johnston et al., 1995). Other authors observed, however, a decreased K release after soil drying (Koerselman et al., 1993; Lamers et al., 1998b), or an unaffected K release (Grootjans et al., 1986). The strong increase in exchangeable K after soil wetting as observed by Koerselman et al. (1993) was also different from the lack of K response on re-wetting in our study. Additional studies are required to distinguish general patterns between K release, soil wetness and other site characteristics.

## Conclusions

Our experimental data support field studies which showed that drainage of wetlands increases N availability for plants. In dried incubated soil, increased N availability was caused by both increased mineralization and decreased denitrification. In most wetlands, however, decreased denitrification will be less important. Soil drying also stimulated the release of DON

and K, but P release was not affected. We conclude that, in N-limited wetlands, and to a lesser extent in K-limited wetlands, drainage will often cause eutrophication whereas drainage will probably not cause eutrophication in many P-limited wetlands.

Although re-wetting of drained wetlands may increase denitrification, it could not be concluded from our study that N mineralization or N availability will be reduced after re-wetting. Caution must, however, be taken in re-wetting of drained wetlands for the benefit of nature restoration, particularly when plant growth is P-limited. Both in acid soils as well as in base-rich soils, re-wetting may severely increase P availability for plants and stimulate biomass production. Hence, in such wetlands re-wetting will not solve the problem of eutrophication, but will create eutrophication instead.

## Acknowledgements

We are very grateful for the support in the labs in Lund and Utrecht. We thank P. de Ruiter and M. Wassen for comments on the manuscript, B. Zielman for statistical advice, and H. Cronert for the introduction to the field site. Financial support was provided by the EU TMR research network "Wetland Ecology and Technology" (WET, contract ERBFMRX-CT960051).

## References

Aerts R, Verhoeven J T A and Whigham D F 1999 Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology 80, 2170–2181.

Allen S E 1989 Chemical Analysis of Ecological Material. Blackwell, Oxford, UK. 386 p.

Ambus P and Christensen S 1993 Denitrification variability and control in a riparian fen irrigated with agricultural drainage water. Soil Biol. Biochem. 25, 915–923.

Berendse F, Oomes M J M, Altena H J and De Visser W 1994 A comparative study of nitrogen flows in two similar meadows affected by different groundwater levels. J. Appl. Ecol. 31, 40–48.

Bolt G H and Bruggenwert M G H 1978 Soil Chemistry, Basic Elements. Elsevier, Amsterdam, The Netherlands. 281 p.

Bowden W B 1987 The biogeochemistry of nitrogen in freshwater wetlands. Biogeochemistry 4, 313–348.

Bridgham S D and Richardson C J 1993 Hydrology and nutrient gradients in North Carolina peatlands. Wetlands 13, 207–218.

Bridgham S D, Updegraff K and Pastor J 1998 Carbon, nitrogen, and phosphorus mineralization in northern wetlands. Ecology 79, 1545–1561.

Cabrera M L 1993 Modelling the flush of nitrogen mineralization caused by drying and rewetting soils. Soil Sci. Soc. Am. J. 57, 63–66.

Caraco N F, Cole J J and Likens G E 1989 Evidence for sulphate-controlled phosphorus release from sediments of aquatic systems. Nature 341, 316–318.

Chapin III F S 1995 New cog in the nitrogen cycle. Nature 377, 199–200.

Chapin III F S, Barsdate R J and Barel D 1978 Phosphorus cycling in Alaskan coastal tundra: a hypothesis for the regulation of nutrient cycling. Oikos 31, 189–199.

Chaney A and Marbach E P 1962 Modified reagents for determination of urea and ammonia. Clin. Chem. 8, 130–132.

Chepkwony C K, Haynes R J, Swift R S and Harrison R 2001 Mineralization of soil organic P induced by drying and rewetting as a source of plant-available P in limed and unlimed samples of an acid soil. Plant Soil 234, 83–90.

Davidson E A, Matson P A, Vitousek P M, Riley R, Dunkin K, Garcia-Méndez G and Maass J M 1993 Processes reguating soil emissions of NO and $N_2O$ in a seasonally dry tropical rain forest. Ecology 74, 130–139.

Davidson E A and Swank W T 1986 Environmental parameters regulating gaseous nitrogen losses from two forested ecosystems via nitrification and denitrification. Appl. Environ. Microb. 52, 1287–1292.

Davidson E A, Swank W T and Perry T O 1986 Distinguishing between nitrification and denitrification as sources of gaseous nitrogen production in soil. Appl. Environ. Microb. 52, 1280–1286.

Davidsson T E and Leonardson LG 1998 Seasonal dynamics of denitrification activity in two water meadows. Hydrobiologia 364, 189–198.

Davidsson T E, Leonardson L G and Balkhag P 1998 Small-scale variation in denitrification, nitrate, dissolved organic carbon and nitrous oxide in a flooded wetland soil. Verh. int. Ver. Limnol. 26, 1328–1333.

Giblin A E, Nadelhoffer K J, Shaver G R and Laundre J A 1991 Biogeochemical diversity along a riverside toposequence in arctic Alaska. Ecol. Monogr. 61, 415–435.

Groffman P M, Axelrod E A, Lemunyon J L and Sullivan W M 1991 Denitrification in grass and forest vegetated filter strips. J. Environ. Qual. 20, 671–674.

Groffman P M and Tiedje J M 1988 Denitrification hysteresis during wetting and drying cycles in soil. Soil Sci. Soc. Am. J. 52, 1626–1629.

Grootjans A P, Schipper P C and Van der Windt H J 1985 Influence of drainage on N-mineralization and vegetation response in wet meadows: I *Calthion palustris* stands. Acta Oecol. 6, 403–417.

Grootjans A P, Schipper P C and Van der Windt H J 1986 Influence of drainage on N-mineralization and vegetation response in wet meadows: II *Cirsio-Molinietum* stands. Acta Oecol. 7, 3–14.

Hynes R K and Knowles R 1978 Inhibition by acetylene of ammonia oxidation in *Nitrosomonas europaea*. FEMS Microb. Lett. 4, 319–321.

Johnston C A, Pinay G, Arens C and Naiman R J 1995 Influence of soil properties on the biogeochemistry of a beaver meadow hydrosequence. Soil Sci. Soc. Am. J. 59, 1789–1799.

Joye S B and Hollibaugh J T 1995 Influence of sulfide inhibition of nitrification on nitrogen regeneration in sediments. Science 270, 623–625.

Kaye J P and Hart S C 1997 Competition for nitrogen between plants and soil organisms. Trend. Ecol. Evol. 12, 139–143.

Koerselman W, De Caluwe H and Kieskamp W M 1989 Denitrification and dinitrogen fixation in two quaking fens in the Vechtplassen area, The Netherlands. Biogeochemistry 8, 153–165.

Koerselman W, Van Kerkhoven M B and Verhoeven J T A 1993 Release of inorganic N, P and K in peat soils; effect of temperature, water chemistry and water level. Biogeochemistry 20, 63–81.

Lamers L P M, Tomassen H B M and Roelofs J G M 1998a Sulphate induced eutrophication and phytotoxicity in freshwater wetlands. Environ. Sci. Technol. 32, 199–205.

Lamers L P M, Van Roozendaal S M E and Roelofs J G M 1998b Acidification of freshwater wetlands: combined effects of non-airborne sulfur pollution and dessication. Water Air Soil Poll. 105, 95–106.

Leonardson L, Bengtsson L, Davidsson T, Persson T and Emanuelsson U 1994 Nutrient retention in artificially flooded meadows. Ambio 23, 332–341.

Lindsay W L and Moreno E C 1960 Phosphate phase equilibria in soils. Soil Sci. Soc. Am. Proc. 24, 177–182.

Mengel K 1982 Dynamics and availability of major nutrients in soils. Adv. Soil Sci. 2, 65–131.

Merrill A G and Zak D R 1992 Factors controlling denitrification rates in upland and swamp forests. Can. J. Forest. Res. 22, 1597–1604.

Mulvaney R L and Kurtz L T 1984 Evolution of dinitrogen and nitrous oxide from nitrogen-15 fertilized soil cores subjected to wetting and drying cycles. Soil Sci. Soc. Am. J. 48, 596–602.

Olde Venterink H, Pieterse N M, Belgers J D M, Wassen M J and De Ruiter P C 2002 N, P and K budgets along nutrient availability and productivity gradients in wetlands. Ecol. Appl. 12, in press.

Olde Venterink H, Van der Vliet R E and Wassen M J 2001 Nutrient limitation along a productivity gradient in wet meadows. Plant Soil 234, 171–179.

Olila O G, Reddy K R and Stites DL 1997 Influence of draining on soil phosphorus forms and distribution in a constructed wetland. Ecol. Eng. 9, 157–169.

Patrick W H and Khalid R A 1974 Phosphate release and sorption by soils and sediments: effect of aerobic and anaerobic conditions. Science 186, 53–55.

Paul E A and Tu C M 1965 Alteration of microbial activities, mineral nitrogen and free amino acid constituents of soils by physical treatment. Plant Soil 22, 207–219.

Pfadenhauer J and Grootjans A 1999 Wetland restoration in Central Europe: aims and methods. Appl. Veg. Sci. 2, 95–106.

Raab T K, Lipson D A and Monson R K 1999 Soil amino acid utilization among species of the Cyperaceae: plant and soil processes. Ecology 80, 2408–2419.

Richardson C J 1985 Mechanisms controlling phosphorus retention capacity in freshwater wetlands. Science 228, 1424–1427.

Richardson C J and Marshall P E 1986 Processes controlling movement, storage, and export of phosphorus in a fen peatland. Ecol. Monogr. 56, 279–302.

Riley R H and Vitousek P M 1995 Nutrient dynamics and nitrogen trace gas flux during ecosystem development in montane rain forest. Ecology 76, 292–304.

Roelofs J G M 1991 Inlet of alkaline river water into peaty lowlands: effects on water quality and *Stratiotes aloides* L. stands. Aquat. Bot. 39, 267–293.

Scheffer F and Schachtschabel P 1989 Lehrbuch der Bodenkunde. Enke Verlag, Stuttgart, Germany. 491 p.

Seitzinger S P 1994 Linkages between organic matter mineralization and denitrification in eight riparian wetlands. Biogeochemistry 25, 19–39.

Smith M S and Tiedje J M 1979 The effect of roots on soil denitrification. Soil Sci. Soc. Am. J. 43, 951–955.

Updegraff K, Bridgham S D, Pastor J and Johnston C A 1995 Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecol. Appl. 5, 151–163.

Urban N R, Eisenreich S J and Bayley S E 1988 The relative importance of denitrification and nitrate assimilation in midcontinental bogs. Limnol. Oceanogr. 33, 1611–1617.

Van Beusichem M L and Neeteson J J 1982 Urea nutrition of young maize and sugar-beet plants with emphasis on ionic balance and vascular transport of nitrogenous compounds. Neth. J. Agric. Sci. 30, 317–330.

Van Schreven D A 1968 Mineralization of the carbon and nitrogen of plant material added to soil and of the soil humus during incubation following periodic drying and rewetting of the soil. Plant Soil 28, 226–245.

Verhagen F J M, Laanbroek H J and Woldendorp J W 1995 Competition for ammonium between plant roots and nitrifying and heterotrophic bacteria and the effects of protozoan grazing. Plant Soil 170, 241–250.

Verhoeven J T A 1986 Nutrient dynamics in minerotrophic peat mires. Aquat. Bot. 25, 117–137.

Verhoeven J T A, Keuter A, Van Logtestijn R, Van Kerkhoven M B and Wassen M J 1996a Control of local nutrient dynamics in mires by regional and climatic factors: a comparison of Dutch and Polish sites. J. Ecol. 84, 647–656.

Verhoeven J T A, Koerselman W and Meuleman A F M 1996b Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. Trend. Ecol. Evol. 11, 494–497.

Verhoeven J T A, Whigham D F, Van Logtestijn R and O'Neill J 2001 A comparative study of nitrogen and phosphorus cycling in tidal and non-tidal riverine wetlands. Wetlands 21, 210–222.

Walbridge M R 1991 Phosphorus availability in acid organic soils of the lower North Carolina coastal plain. Ecology 72, 2083–2100.

Wood T, Bormann F H and Voigt G K 1984 Phosphorus cycling in a northern hardwood forest: biological and chemical control. Science 223, 391–393.

Yoshinari T and Knowles R 1976 Acetylene inhibition of nitrous oxide reduction by denitrifying bacteria. Biochem. Bioph. Res. Co. 69, 705–710.

Zak D R and Grigal D F 1991 Nitrogen mineralization, nitrification and denitrification in upland and wetland ecosystems. Oecologia 88, 189–196.

Zak D R, Groffman P M, Pregitzer K S, Christensen S and Tiedje J M 1990 The vernal dam: plant-microbe competition for nitrogen in northern hardwood forests. Ecology 71, 651–656.

*Section editor: C. van Kessel*