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NITROGEN AND PHOSPHORUS MINERALIZATION IN FENS AND BOGS

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SUMMARY

(1) The release of inorganic nitrogen and phosphorus in ten mires in The Netherlands with different vegetation and hydrology was measured by incubating soil *in situ* in polyethylene bottles at depths of 10 and 25 cm. At the same time, cellulose decomposition was estimated by means of tensile strength loss of *in-situ* cotton strips.

(2) The size of the inorganic N pool was not related to depth, mire type or the presence of a *Sphagnum* cover. The labile inorganic P pool was significantly larger in *Sphagnum*-dominated bogs than in phanerogam-dominated fens.

(3) N and P mineralization were significantly faster in bogs with a *Sphagnum* cover than in phanerogam-dominated fens, and faster at 10 than at 25 cm.

(4) Cellulose decomposition rates were significantly higher in phanerogam-dominated fens than in *Sphagnum*-dominated bogs. The depth patterns of the decomposition rates also showed a difference between these mire types: in fens, the rates were relatively low at the surface but increased to a sustained higher value at 10 cm and below; in bogs, the rates were highest at the surface but decreased steeply to very low values.

(5) The inverse relation between N and P mineralization and decomposition is probably due to the chemical properties of *Sphagnum* litter predominant in bogs. The N- and P-rich protoplasm breaks down and releases nutrients quickly, whereas the bulk of cell walls is decomposed so slowly that not much N and P is immobilized in microbial tissues.

(6) Comparison of N mineralization measured in Dutch bogs with values from other regions found in the literature revealed no indications of an enhanced rate under the conditions of high atmospheric N deposition prevailing in The Netherlands.

INTRODUCTION

Mires are peat-forming wetland ecosystems in which primary productivity exceeds decomposition. Together with the organic matter that accumulates in the peat soil, substantial amounts of nitrogen and phosphorus are sequestered (Clymo 1978). Hence, recycling is not complete and plant growth may become more strongly limited by availability of nitrogen or phosphorus, or both, than it is in terrestrial systems that accumulate much less organic matter.

Mires differ markedly in vegetation and in water and soil chemistry (Sjörs 1950; Malmer 1962, 1963, 1986; Moore & Bellamy 1974); they are classified commonly into two main types, fen and bog. 'Minerotrophic' fens receive nutrients from surface water or groundwater as well as rainfall, have a neutral or basic soil and a vegetation dominated by graminoids (e.g. *Carex*, *Cladium*), whereas 'ombrotrophic' bogs are fed by precipitation only, have an acid soil and a vegetation dominated by peat mosses (e.g. *Sphagnum*).

Fens have a higher primary productivity than bogs (Brinson, Lugo & Brown 1981). It is commonly held that the availability of inorganic N and P to the vegetation is also higher in fens than in bogs (Moore & Bellamy 1974; Mitsch & Gosselink 1986). This view is based not only on the extra inputs of N and P from groundwater and surface water in fens, but also on the particularly adverse conditions for decomposition in bogs. Waughman (1980) compared the inorganic N and P pools of a whole range of South German mires and surprisingly found both inorganic pools to be significantly larger in bogs.

Mineralization processes are at least similar in importance to inputs in determining nutrient availability in systems with such a large soil organic N and P pool (Verhoeven, Koerselman & Beltman 1988); the study of these processes is essential for the understanding of the nutrient status of these systems. Reports of directly measured mineralization rates in fens and bogs are, however, very scarce in the literature. In previous studies of N and P mineralization in fens, the mineralization of both elements was shown to be faster in fens with a thick *Sphagnum* carpet than in those dominated by phanerogams and bryophytes other than *Sphagnum* (Verhoeven & Arts 1987; Verhoeven, Kooijman & Van Wirdum 1988). These studies involved only a small number of rather similar fen habitats, however, and did not include measures of decomposition.

This paper deals with a number of field experiments addressing the mineralization of N and P as well as the decomposition of cellulose in a greater variety of fens and bogs. In ten selected mire sites in The Netherlands, the release of inorganic N and P was measured using an *in-situ* incubation technique. At the same time, a standard measure of cellulose decomposition was obtained by determining tensile-strength loss of cotton strips. Relations of the rates of decomposition and N and P release with vegetation type, mire hydrology, total soil N and P, and soil pH were investigated. As atmospheric nitrogen deposition in The Netherlands is unusually high (40 kg ha^{-1} $year^{-1}$) due to the evaporation of ammonia in pastures and emissions by industries and traffic (Van Breemen *et al.* 1982), the N mineralization rates found were compared to estimates in the literature for bogs in other parts of the world.

METHODS

Site description

The ten mire sites are located in The Netherlands (*c.* 5°E, 53°N). Further information is summarized in Table 1. Sites 1 to 6 are small, quaking fens that have developed in ponds created by former peat excavations. These fens have a floating mat of vegetation on top of water or recently formed peat. They are all located in nature reserves and are mown annually in the summer, primarily to prevent further succession to carr woodland. The water levels in the fens are managed within narrow limits (Koerselman 1989).

Sites 1, 2 and 4 are fens located in groundwater discharge areas. They receive substantial inputs of groundwater moderately rich in calcium and bicarbonate (Verhoeven, Koerselman & Beltman 1988; Beltman & Verhoeven 1988). The fens in groundwater recharge areas are supplied with surface water during the summer months to replace water losses through evapotranspiration. The quality of this water varies, and so does the degree to which specific sections of the fens are influenced by it. Sites 3 and 5 are the extremes of a gradient in a long, rectilinear fen; site 3 is near and site 5 very remote from the location where the lithotrophic (i.e. with a typical groundwater chemistry, see Van Wirdum 1981) surface water enters the fen. The mire water is lithotrophic near site 3 and atmotrophic (i.e. with a typical rain-water chemistry) near site 5 (Van Wirdum 1982; Verhoeven, Kooijman & Van Wirdum 1988). The surface water supplied to site 6 originates from the Rhine and is rich in nutrients and in NaCl. The section of this fen where the experiments were performed, however, has a predominantly atmotrophic water chemistry (Koerselman, Bakker & Blom 1990).

TABLE 1. Site characteristics and dominant plant species of ten mires in The Netherlands where mineralization was measured. F, fen; B, bog; S, *Sphagnum* carpet; N, no *Sphagnum* present; D, groundwater discharge; R, groundwater recharge. Percentage cover is indicated only for plant species with cover ⩾10%. Nomenclature of phanerogams and bryophytes follows Van der Meijden *et al.* (1983) and Margadant & During (1982), respectively. Mires have been ranked from fens without *Sphagnum* and with groundwater discharge toward bogs with *Sphagnum* and groundwater recharge.

Mire number*	1	2	3	4	5	6	7	8	9	10
Sphagnum/no *Sphagnum*	N	N	N	N	S	S	S	S	S	S
Fen/bog	F	F	F	F	F	F	B	B	B	B
Discharge/recharge	D	D	R	D	R	R	R	R	R	R
Phanerogams										
Total cover	70	75	60	55	30	25	25	30	20	35
Total number of spp.	24	16	13	10	13	8	5	5	5	7
Potentilla palustris	20									
Carex curta	10									
C. diandra		40	20							
C. acuta		10								
C. paniculata			15							
C. lasiocarpa				10						
C. hudsonii			30							
Drosera rotundifolia					10					
Phragmites australis			10	30	10	10	20			
Carex rostrata		10					5	15		
C. acutiformis						10				
Erica tetralix								10		
Eriophorum angustifolium									10	
E. vaginatum									10	
Andromeda polyfolia									10	
Oxycoccus palustris										35
Bryophytes										
Total cover	30	40	50	5	100	100	70	100	100	100
Total number of spp.	6	6	5	2	8	9	9	4	3	7
Bryum pseudotriquetrum	10									
Calliergon cordifolium	10	10								
Calliergonella cuspidata	12	10	20							
Plagiomnium affine		20								
Scorpidium scorpioides			20		10					
Mnium hornum			10		20					
Sphagnum flexuosum					20					
S. papillosum					20					
Polytrichum longisetum					20					
Sphagnum squarrosum						20				
S. palustre						20	20	10		
S. fallax						20	20	90	60	98
S. fimbriatum						20				
Polytrichum commune						20				
Pohlia nutans							10			
Drepanocladus fluitans							10			
Sphagnum cuspidatum									40	

* Key to mire locations:

1. Westbroek 'g'.
2. Westbroek 'l'.
3. Stobberibben 'III'.
4. Het Hol.
5. Stobberibben 'I'.
6. Molenpolder.
7. Korenburgerveen 'p'.
8. Korenburgerveen 'c'.
9. Meerstalblok.
10. Goudbergven.

Sites 7, 8 and 9 are located in large raised bog reserves that have lost some of their pristine character due to early buckwheat cultures and to water losses to their excavated surroundings. The sites are former bog pools, of which 7 and 8 are influenced by very slightly enriched bog water, and 9 is purely ombrotrophic. Site 10 is a floating island in an oligotrophic heath pool and also has an ombrotrophic character.

Table 1 indicates the presence of *Sphagnum* carpets at the sites studied. *Sphagnum* carpets have a strong effect on the water chemistry: they actively acidify the mire water, and may therefore directly influence decomposition and mineralization processes. Sites 1–4 are characterized by a dense, species-rich phanerogam vegetation with dominance of *Carex* species, and a relatively thin bryophyte cover with *Bryum*, *Calliergon* and *Calliergonella*. Sites 6–10 show a lower phanerogam cover and well-developed carpet of *Sphagnum* and *Polytrichum* species.

Field techniques

In-situ soil-incubation experiments for measuring N and P mineralization and cotton-strip experiments for measuring decomposition were carried out at five stations at each of the ten sites. The incubation period lasted for six weeks and started between 10 and 19 September 1987. Field procedures were as follows.

At each station, soil material was collected from depths of 10 cm and 25 cm. Living roots and coarse plant parts were removed and the material was divided between two 100-ml polyethylene bottles. The soil material was included in such a way that the bulk densities in the bottles were similar to that in the soil. The bottles were filled completely with mire water from the spot and closed with a lid to exclude air. One of the bottles was taken to the lab and the contents were analysed the next day. The other bottle was placed back into the soil at the sample depth and left there for six weeks. In all cases, the substrate consisted of a floating rhizome mat mixed with loose peat. Water levels were within 5 cm of the surface at all sites throughout the study.

At each station, close to the bottles, a cotton strip measuring 30 cm × 12 cm was inserted vertically in the soil to a depth of 25 cm in a sawn slit 15 cm wide. The position of the mire surface was marked on the strip. The strips were left in place for six weeks. A second strip was inserted and removed immediately to serve as a control.

Coverage of phanerogam and bryophyte species at the sampling stations was recorded by making vegetation relevés. The total area recorded at each site was 10 m^2.

Laboratory techniques

Substrate samples (fresh as well as incubated) were extracted the day after they were collected. A wet equivalent of 1 g dry soil was extracted with 100 ml of medium (1 h, 100 r.p.m.). Distilled water was used for extraction of nitrate and phosphate, and 0·2 mol KCl for extraction of ammonium. The extracts were filtered and stored in a refrigerator overnight. Analyses were made colorimetrically with a continuous-flow analyser (see also Verhoeven, Kooijman & Van Wirdum 1988). Soil pH was measured in the water extracts of the fresh samples.

The data from the soil extractions were treated as four variables, viz. nitrogen extractable from fresh soil (N_{ext}), phosphorus extractable from fresh soil (P_{ext}), mineralized nitrogen [= extractable nitrogen from incubated soil minus that from fresh soil (N_{min})] and mineralized phosphorus (P_{min}). For nitrogen, the amounts of nitrate and ammonium found in the water and the KCl extracts, respectively, were added as elementary nitrogen. As nitrate concentrations in the extracts were very low (below the detection limit in most cases), N_{ext} and N_{min} primarily represent extractable ammonium and ammonification, respectively.

The remaining part of the fresh samples was dried (70 °C, 48 h) and stored for later analysis of organic-matter content (loss on ignition) and total N and P. Total N and P were determined by acid digestion according to a salicylic-acid thiosulphate modification of the Kjeldahl method (Page, Miller & Keeney 1982). Ammonium and phosphate in the digests were determined colorimetrically.

Test and control cotton strips were washed gently in deionized water and air-dried before dispatch to the laboratory. Strips were cut into horizontal substrips 3 cm wide and reduced by fraying to 2 cm, to give test substrips corresponding to 0–2 cm, 3–5 cm, 6–8 cm, etc. Tensile strength was measured using a tensiometer (Monsanto Type W) with 7·5 cm-wide jaws set 3 cm apart. All measurements were carried out at 18–22 °C and with a relative humidity of 100% obtained by soaking strips in deionized water for 1 h. The general procedure is described in full and illustrated in Harrison, Latter & Walton (1988). Tensile-strength loss was calculated from the difference between test and control strips and duration of exposure.

RESULTS

Extractable nitrogen and phosphorus

The results for N_{ext} (Fig. 1a) show higher values at 10 cm than at 25 cm below the soil surface in the majority of sites. At three of the bog sites the situation is reversed, however. The two-way ANOVA (Table 2) shows significant effects of site as well as depth with a significant interaction factor. Further testing of the site effect by testing the significance of differences among three pairs of mire categories (bog vs. fen, groundwater discharge vs. groundwater recharge, *Sphagnum* carpet vs. no *Sphagnum*, see also Table 1) reveals no significant differences. Hence, the differences in extractable N are not unambiguously related to either depth, mire type, mire hydrology or the presence of a *Sphagnum* cover.

The results for P_{ext} (Fig. 1b) show proportionately larger differences among sites than those for N_{ext}. Here, the values at 10 cm below the surface are higher than those at 25 cm in nine out of ten cases. The two-way ANOVA (Table 2) indicates a highly significant site effect but no depth effect and a significant interaction term. The further testing of the site effect revealed that extractable phosphorus is significantly higher in bogs than in fens, also higher in groundwater recharge than in groundwater discharge mires, and higher in *Sphagnum*-covered mires than in those without *Sphagnum*.

Mineralized nitrogen and phosphorus

The values for nitrogen mineralization (N_{min}, Fig. 2a) exhibit more variation among sites and among depths than those for N_{ext}. The ANOVA (Table 2) shows highly significant site as well as depth effects with no interaction. Mineralization is faster at 10 cm than at 25 cm below the surface, and the contrast test shows that it is faster in bogs than in fens, faster in groundwater discharge than in recharge mires, and faster in *Sphagnum*-covered mires than in those without *Sphagnum*.

The results for phosphorus mineralization (Fig. 2b) show relatively large differences among sites and also some depths. In a few cases, hardly any mineralization or even a net immobilization was found. As for nitrogen, the ANOVA (Table 2) indicates significant effects of site and depth with no significant interaction. Again, mineralization is faster at

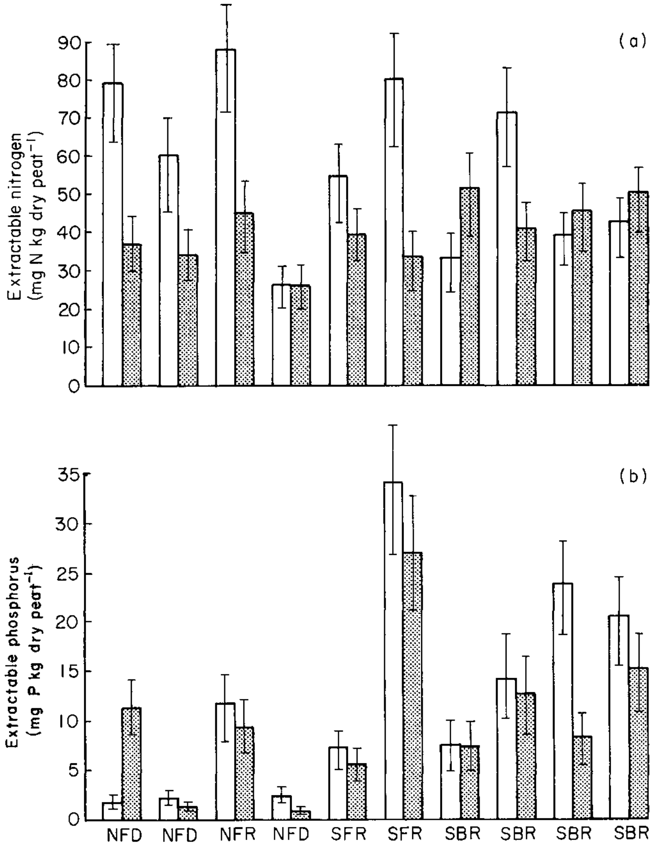

FIG. 1. Extractable nitrogen (a) and phosphorus (b) at 10 cm (□) and 25 cm (▨) in the soils of ten mires in The Netherlands. Vertical lines indicate standard errors. For a key to the mire sites, see Table 1.

TABLE 2. Two-way ANOVAS of the data for extractable N (N_{ext}), extractable P (P_{ext}), mineralized N (expressed as extractable N from incubated soil minus that from fresh soil, N_{min}) and mineralized P (P_{min}) and cotton tensile strength loss (TSL) with respect to the factors and depth. The hypothesis, that the differences among the pairs of mire categories indicated in Table 1 are zero, was tested with the CONTRAST statement in the GLM procedure (SAS 1985). d.f., degrees of freedom; all other figures are *P* values. If significant differences were found, the category where the variable is higher is indicated.

Factor	d.f.	N_{ext}	P_{ext}	N_{min}	P_{min}	TSL
Site	9	0·0057	<0·0001	<0·0001	0·0005	<0·0001
Depth	1	0·0001	0·8763	<0·0001	0·0245	0·7408
Site × depth	9	0·0110	0·0004	0·1416	0·4733	0·1715
Contrast						
Sphagnum/no *Sphagnum*	1	0·8059	<0·0001 S	<0·0001 S	0·0020 S	<0·0001 N
Bog/fen	1	0·8483	<0·0001 B	0·0184 B	0·0018 B	<0·0001 F
Recharge/discharge	1	0·0608	<0·0001 R	<0·0001 R	0·0032 R	<0·0001 D

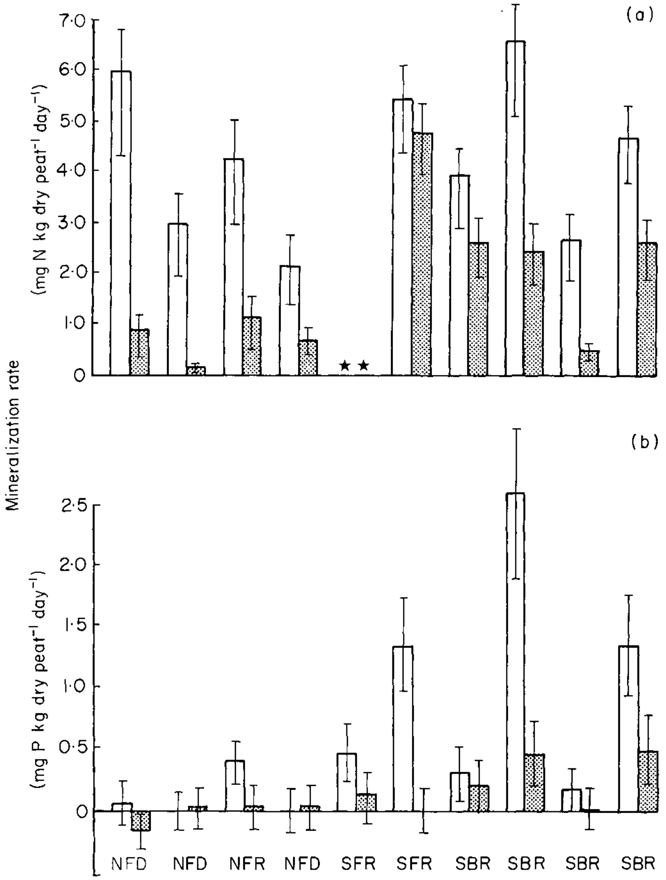

FIG. 2. Nitrogen (a) and phosphorus (b) mineralization rates at 10 cm (□) and 25 (▨) in the soils of ten mires in The Netherlands. Vertical lines indicate standard errors. ★, missing values. For a key to the mire sites, see Table 1.

10 cm than at 25 cm below the surface, and is more rapid in bogs, groundwater recharge mires and *Sphagnum*-covered sites.

Tensile-strength loss (TSL) of cotton strips

There were remarkable differences in cellulose decomposition between mires with and those without a *Sphagnum* cover (Fig. 3). Decomposition is distinctly faster in the mires without *Sphagnum* (sites 1–4): the rate of tensile strength loss (TSL) of cotton strips amounts to more than 1% day^{-1} at almost all sampling points, whereas it is generally lower than 0·5% daily in mires that have a *Sphagnum* carpet (sites 5–10). A further difference is the depth pattern of C_{tsl}. In mires 1–4, decomposition is relatively slow at the soil surface, and increases in the first 5 cm. In mires 1 and 2, TSL stays at a level higher than 1·5% day^{-1} until about 15 cm and decreases to the rate observed for the surface level further down. In mires 3 and 4 it remains rather constant at about 1·1. An almost opposite pattern occurs in mires 5–10: C_{tsl} is highest at the soil surface and decreases sharply in the first 5 cm to very low levels, particularly in the bog sites (7–10).

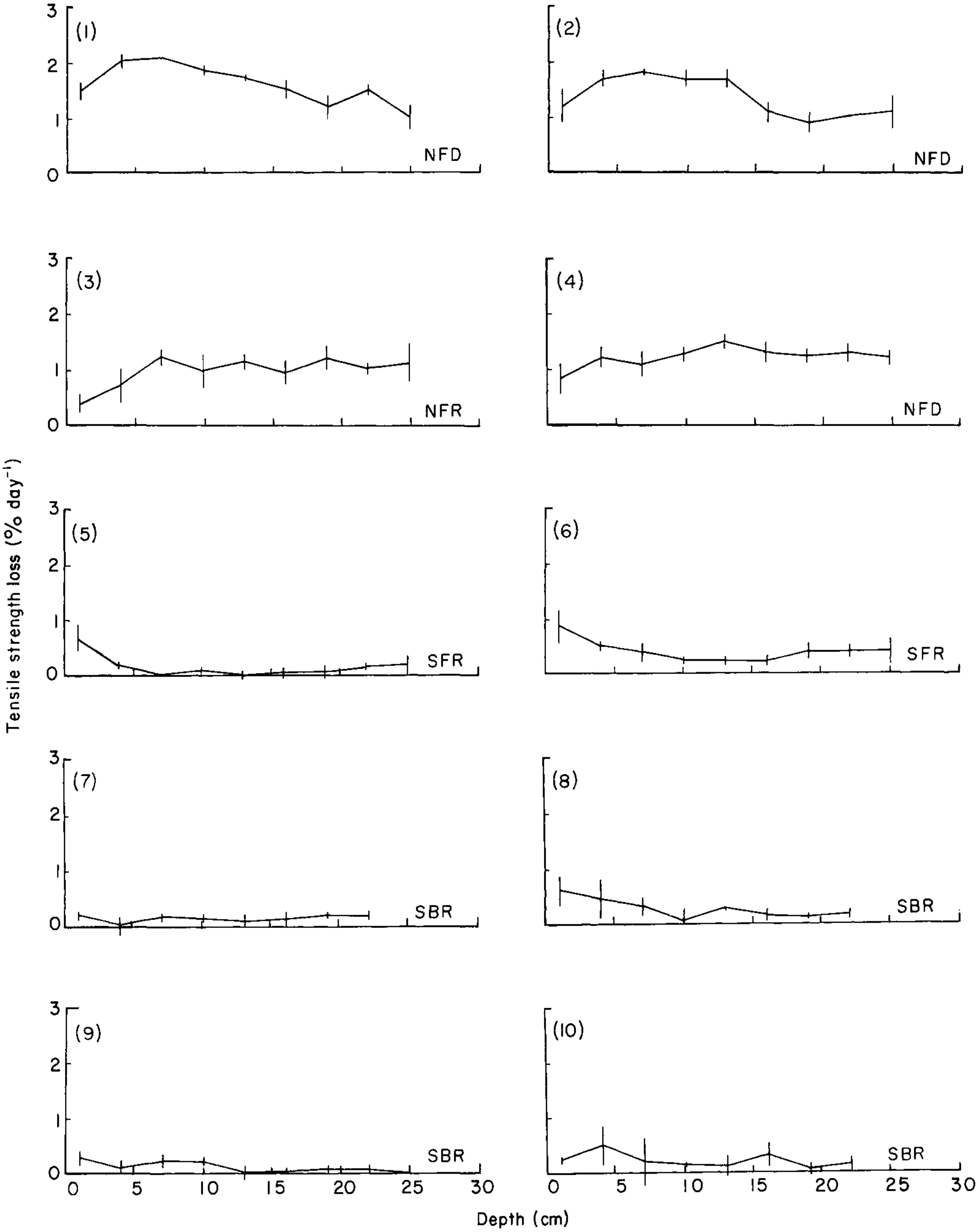

FIG. 3. Tensile strength loss (%TSL day^{-1}) plotted against depth for ten mire sites in The Netherlands. Vertical lines indicate ±1 S.E. For a key to the mire sites, see Table 1.

The two-way ANOVA for the data on C_{tsl} (Table 2) shows a highly significant site effect and a non-significant depth effect. The interaction term site × depth reflects the various depth effects in mires 1–4 vs. those in mires 5–10 described above. A further testing of the site effect reveals that decomposition is significantly faster in fens than in bogs, and the

TABLE 3. Soil pH, organic matter and total N and P contents at the sites investigated. Values are means of five samples ± 1 S.E. For keys to sites and codes see Table 1.

Site	Code	Depth	pH	Organic matter	Total N	Total P
1	NFD	10	6·1±0·1	89·1±0·4	19·3±0·9	1·08±0·05
		25	6·0±0·1	88·9±0·4	15·6±0·6	0·86±0·05
2	NFD	10	6·2±0·1	87·0±0·9	21·2±1·2	0·82±0·04
		25	6·6±0·1	60·5±9·6	14·7±0·9	0·68±0·08
3	NFR	10	5·8±0·2	93·7±0·5	13·3±1·0	0·56±0·05
		25	6·3±0·1	89·0±1·1	16·4±1·1	0·56±0·05
4	NFD	10	5·9±0·1	94·4±0·4	12·2±0·6	0·37±0·02
		25	5·9±0·1	92·5±0·6	15·1±1·2	0·45±0·03
5	SFR	10	4·3±0·1	96·3±0·4	9·1±0·8	0·35±0·03
		25	5·0±0·1	92·6±1·2	15·2±1·3	0·47±0·05
6	SFR	10	4·1±0·1	96·8±0·6	13·7±1·4	0·62±0·04
		25	5·2±0·2	96·2±0·6	19·9±1·0	0·75±0·05
7	SBR	10	3·8±0·1	96·3±0·6	14·6±0·7	0·54±0·03
		25	3·8±0·1	95·6±0·4	13·9±0·5	0·45±0·02
8	SBR	10	3·8±0·1	95·5±0·4	18·1±0·6	0·62±0·04
		25	3·7±0·1	95·8±0·4	14·6±0·6	0·51±0·04
9	SBR	10	3·6±0·1	97·7±0·4	9·7±0·4	0·31±0·02
		25	3·7±0·1	96·6±0·3	8·9±0·3	0·18±0·02
10	SBR	10	4·2±0·1	97·9±0·4	7·1±0·3	0·36±0·03
		25	4·3±0·1	97·3±0·3	6·9±0·8	0·28±0·03

same applies to groundwater discharge vs. recharge mires and to mires without vs. those with a *Sphagnum* cover.

Soil covariables: pH, organic matter, total N and total P

Soil pH (Table 3) is distinctly higher in the fen (mires 1–6) than in the bog sites (7–10). Further, fens with a *Sphagnum* cover (mires 5–6) are more acidic at 10 cm than at 25 cm; these fens have subsurface inflows of well-buffered water, while the surface layer is being acidified by the *Sphagnum*.

All soils investigated are highly organic peat soils with organic matter contents above 90%, except for somewhat lower values in some of the fens (sites 1 and 2).

Total N and total P are relatively high in fen sites 1 and 2 and particularly low in bog sites 9 and 10. Neither of these factors shows a significant depth effect.

Stepwise multiple regression of the dependent variables to the covariables

The multiple regression of each of the dependent variables against five covariables (Table 4) shows that extractable nitrogen is positively related to total P and to total N; however, together these covariables explain only 8% of the variance. As neither of them is correlated with depth, the covariables only explain part of the significant site effect found in the ANOVA.

Extractable phosphorus shows a significant relation with *Sphagnum* cover. The regression coefficient and the proportion of variance explained are both high. This result corresponds well with that of the ANOVA where the highly significant site effect was partly explained by *Sphagnum* presence.

Nitrogen mineralization is positively related to soil organic matter and total P, and negatively related to pH; together the covariables explain 33% of the variance. The regression coefficients show that the effect is by far the strongest for soil organic matter.

TABLE 4. Stepwise multiple regression of five dependent variables against the covariables *Sphagnum* cover, soil pH, soil organic matter, total N and total P. Only the significant relations that eventually stayed in the model are given. R.C. = standardized regression coefficient; explained = proportion of variance explained by covariable.

Variable	Covariables	R.C.	*F*	*P*	Explained
N_{ext}	total P	0·39	3·09	0·082	0·031
	total N	0·055	4·91	0·029	0·047
P_{ext}	*Sphagnum* cover	0·55	49·97	<0·0001	0·338
N_{min}	organic matter	0·49	20·58	<0·0001	0·190
	total P	0·025	8·71	0·0041	0·074
	pH	−0·086	8·68	0·0041	0·068
P_{min}	pH	−0·061	10·81	0·0014	0·099
TSL	*Sphagnum* cover	−0·74	134·02	<0·0001	0·598
	pH	0·030	7·17	0·0088	0·030

As neither of the three covariables is correlated to depth, the results here are a further explanation of the highly significant site effect detected with the ANOVA.

Phosphorus mineralization, having shown significant site and depth effects in the ANOVA, only correlates with soil pH, and the regression coefficient as well as the proportion of variance explained are low. Factors other than those measured apparently play a role here.

Cotton tensile-strength loss is strongly negatively related to *Sphagnum* cover. Together with soil pH this factor explains 62% of the total variance. This is in agreement with the result of the ANOVA, where the contrasts were highly significant.

DISCUSSION

The incubation experiments were carried out in September and October, when soil temperatures were in the range 10–20 °C. Previous experiments with repeated incubations showed that mineralization rates were rather constant from May to October, and distinctly lower in April and November (Verhoeven & Arts 1987; Verhoeven, Kooijman & Van Wirdum 1988). The soil moisture conditions among the ten mire sites studied were similar. All stations were in floating mats; as these mats move up and down together with fluctuations in the water table, the soil conditions remain constantly wet. For these reasons, the mineralization and cellulose decomposition rates measured in September and October can be considered as representative for those prevailing throughout most of the growing season.

N and P mineralization are faster at a depth of 10 cm than at a depth of 25 cm. This is due probably to an effect of temperature and/or redox conditions on microbial metabolic activity. A change in substrate quality with depth could also have an effect, but none of the soil covariables related to substrate quality (organic matter, total N, total P) showed a correlation with depth.

The tensile-strength loss of cotton strips provides a relative measure of cellulose decomposition (Harrison, Latter & Walton 1988) and shows differences among sites almost exactly opposite to those for N and P mineralization. They are in agreement with the results of many decomposition studies in mires that all indicate that the breakdown of carbon compounds is severely inhibited in bogs (Clymo 1965; Maltby & Crabtree 1976; Swift, Heal & Anderson 1979; Damman 1988; Farrish & Grigal 1988; Maltby 1988).

TABLE 5. C/N quotient of peat and N/P quotients of peat, extractable pool and mineralized amounts (C contents were estimated as 0·41 organic matter). Values are means of five samples ± 1 S.E. For keys to sites and codes see Table 1.

Site	Code	Depth	C/N	N_{peat}/P_{peat}	N_{ext}/P_{ext}	N_{min}/P_{min}*
1	NFD	10	18·5±0·8	18·2±1·5	33·4±9·4	113
		25	22·8±0·8	18·4±1·3	3·6±0·6	†
2	NFD	10	16·7±1·1	25·7±1·1	21·5±8·4	†
		25	16·3±1·4	21·9±0·7	23·7±9·6	8
3	NFR	10	29·1±2·8	24·3±2·3	11·1±3·7	10
		25	22·1±1·6	30·0±2·4	5·9±2·2	30
4	NFD	10	31·2±1·4	33·6±1·8	14·8±4·5	†
		25	25·8±2·9	33·0±1·9	26·4±3·4	15
5	SFR	10	44·2±3·9	25·9±0·9	12·1±3·9	‡
		25	25·5±3·0	32·6±0·9	8·6±1·9	‡
6	SFR	10	31·0±3·4	21·9±2·4	2·4±0·5	4
		25	19·5±1·0	27·0±1·3	1·2±0·4	†
7	SBR	10	26·5±1·1	27·7±2·5	4·6±0·8	12
		25	27·7±1·2	30·8±0·9	6·6±2·7	12
8	SBR	10	21·1±1·3	29·8±1·6	5·1±0·6	3
		25	26·4±1·0	29·0±1·1	3·2±0·7	5
9	SBR	10	40·5±1·6	31·8±0·9	3·3±1·1	14
		25	43·6±1·1	50·4±3·4	6·2±1·5	38
10	SBR	10	55·0±2·0	20·4±1·5	3·1±0·8	3
		25	59·4±4·5	25·9±2·0	3·3±0·6	5

* No S.E. is given because of frequent values near or below 0 for P_{min} in the data set; † mean value $P_{min} < 0$; ‡ missing values for N_{min}.

The inverse relation of N and P mineralization to decomposition in the mires studied is contrary to expectation. Inorganic N release in soils is associated with microbial decomposition of organic matter and is a net result of the N mineralization of the substrate and the N uptake by the microbes (i.e. immobilization). Whether there is net N mineralization or immobilization generally depends on substrate quality: net N immobilization occurs at C/N quotients above 15–20, and net mineralization at lower values for this quotient (Parnas 1975; Swift, Heal & Anderson 1979). In the present study high N mineralization was associated with very low (cellulose) decomposition in all mires with a *Sphagnum* carpet. C/N quotients in some of these mires were well above 40 (Table 5). In bogs, net N mineralization has been detected at C/N quotients between 60 and 100 (Malmer & Holm 1984; Damman 1988).

The results indicate a severe inhibition of microbial decomposition by the presence of a *Sphagnum* carpet. This inhibition may not only be due to acidification but also to the chemical composition of *Sphagnum* litter that contains refractory cell-wall material (Clymo 1965), or to toxic products produced by living *Sphagnum* plants. Brock & Bregman (1989), who studied the decomposition of *Sphagnum recurvum*, found that the litter of this species lost only 18% of its dry weight in the first year, whereas it lost 45% of its N. Furthermore, they found remarkably small changes in the cell-wall structures and low microbial activity associated with them.

The high N mineralization in mire soils with predominantly *Sphagnum*-derived organic matter may be caused by the virtual absence of immobilization due to low microbial activity. Easily degradable N-rich compounds are decomposed by a sparse microbial community and the bulk of the carbon compounds are hardly decomposed at all, so that inorganic N is not incorporated in microbial biomass but released into the environment.

For phosphorus the picture is more complicated. Apart from mineralization associated with microbial decomposition, there are transfers between the inorganic 'labile' phosphate pool (as measured in the extractions) and the inorganic 'bound' phosphate pool consisting of chemically adsorbed and precipitated P (Nichols 1983). The extractant used, distilled water, is mild; it releases the labile phosphate pool, and leaves the inorganic bound P intact (Richardson 1985; Verhoeven & Arts 1987). The P release found during the incubation is the net result of both the microbial and the physico-chemical release of phosphates.

Further insight can be obtained by comparing the N/P quotients in the peat, the extractable pools and the amounts mineralized (Table 5). The values in the peat are between 20 and 50 and are not different among mire categories. The N/P quotients in the extractable pools are generally lower in the mires with *Sphagnum*, which is due to the relatively high amounts of P in these pools. High values for the N/P quotient of the amounts mineralized, and cases of P immobilization, occur primarily in sites 1, 2 and 4 (fens without *Sphagnum* under a regime of groundwater discharge). Most of the other values in this column are of the same order of magnitude as those for the peat, indicating similar relative release rates for N and P.

The generally lower pH in sites with a thick *Sphagnum* carpet is one of the factors explaining the higher pools of labile phosphates at these sites. In the stepwise multiple regression, *Sphagnum* cover proved the main factor explaining differences in P_{ext}, and soil pH did so for P_{min}. These two covariables proved to be mutually correlated. The low inorganic P pools and low P mineralization in the fens with groundwater discharge are probably caused by the adsorption of phosphates to calcium, iron and aluminium compounds that are supplied by the inflowing groundwater (e.g. Boyer & Wheeler 1989). The water extraction is too mild to desorb these phosphates but they may be partly available to plants and microbes (Richardson & Marshall 1986). The extraction procedure may therefore have underestimated P availability in these fens.

The main conclusion of these experiments, that the nitrogen and phosphorus mineralization is higher in ombrotrophic than in minerotrophic mires, seems at variance with the generally higher productivity and plant nutrient uptake in the latter type of mires (Moore & Bellamy 1974; Waughman 1980; Howard-Williams 1985; Verhoeven 1986). Plant growth in bogs is probably limited by factors other than N and P availability. Low pH and other water chemistry features may play a role.

The question can be raised if N mineralization in bogs in The Netherlands is exceptionally rapid as a result of their gradual enrichment with this element from rainfall or dry deposition. Average atmospheric N deposition levels are as high as 40 kg N ha^{-1} $year^{-1}$ due to the evaporation of ammonia from pastures and emissions by traffic and industries (Van Breemen *et al.* 1982; Koerselman, Beltman & Verhoeven 1988). *Sphagnum* plants are known to capture N efficiently from atmospheric deposition (Lee & Woodin 1988). A comparison of the present results with the scarce data on N mineralization rates measured by various methods in mires in other parts of the world (Table 6) gives no indication of more rapid N mineralization in the Dutch mires. Effects of high N deposition on mineralization may be long-term and only detectable in the future. The inputs are small relative to the total N stock in the soil and are second in importance to the quantities mineralized (Verhoeven, Kooijman & Van Wirdum 1988; Koerselman *et al.* 1990). More data, especially from a comparative study, using standardized methods in bogs subject to different levels of N deposition, are now needed if a valid comparison is to be made.

TABLE 6. Mineralization rates in fens and bogs. Values are given as μg N cm^{-2} day^{-1}. F, fen; B, bog, BB, blanket bog.

Reference		Mineralization rate	Method
This study*	F	1·25 ± 0·68	field incubations
This study	B	1·53 ± 0·53	field incubations
Urban & Eisenreich (1988)	B	3·1 ± 1·1	lab incubations 22 °C
Hemond (1983)	B	1·43†	comparison of N content along profile
Martin & Holding (1978)	BB	2·77	lab incubations/ microbiological study

*An active depth of 40 cm was assumed; the value measured at 10 cm was generalized for the range 0–15 cm, that measured at 25 cm for 16–40 cm.

†Calculated from an annual estimate; an active season of 150 days was assumed.

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