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OLD WORLD AND NEW

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Comparative study of nutrient-related processes in geographically separated wetlands: towards a science base for functional assessment procedures

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Abstract

We compared process rates related to nitrogen and phosphorus dynamics in similar types of wetlands that occurred in Maryland and The Netherlands. Process rates for decomposition, nitrogen mineralization, nitrous oxide emission, denitrification, and phosphorus release were measured and related to potentially important environmental factors (soil temperature, redox, pH, total plant and soil nitrogen and phosphorus, extractable soil nitrogen and phosphorus, soil organic matter, soil particle size distribution) in an attempt to identify easily measured variables that potentially could be used to assess wetland function(s). Rates of functions were different in wetlands dominated by mineral soils compared to wetlands dominated by peat substrates. Another important finding is that high nitrogen deposition in The Netherlands was reflected in higher pools of extractable nitrogen in the soil but not in higher process rates. The study demonstrates that it was possible to estimate rates of wetland processes using easily measured variables over a relatively short period of time. The results are especially encouraging because we have measured rates and variables in a range of wetland types in different parts of the world. We conclude that this is a valuable approach for improving our understanding of environmental controls on wetland functioning. The fact that the data from the two continents combined so well in correlative analyses and scatter diagrams underlines that nutrient-related processes can be unraveled and generalized across wetland types and geographic regions.

INTRODUCTION

Wetlands perform important functions (Adamus and Stockwell, 1983; Mitsch and Gosselink, 1986; Dugan, 1990; Gosselink et al., 1990; Risser, 1990; Finlayson and Moser, 1991; Whigham and Brinson, 1991; Mitsch, 1992) and attempts have been made to develop rapid functional assessment techniques for wetlands (e.g., Adamus et al., 1987; EPA, 1990; Bartoldus et al., 1992; Maltby et al., 1994; Brinson et al., 1994; Novitzki, 1994; Maltby and Verhoeven, in press). While these assessment approaches represent major advances in our ability to evaluate wetlands in a societal framework, their usefulness has been limited because of the lack of ecological information on most of the functions that they attempt to evaluate. For example, water quality improvement is an important wetland function that is primarily controlled by the nutrient dynamics of wetlands (Gopal, 1990). Wetlands have been shown to trap, store, transform and release nutrients, thus drastically modifying the chemistry of the through-flowing water and impacting water quality downstream (Nixon and Lee, 1986; Hemond and Benoit, 1988; Whigham et al., 1988; Maltby and Verhoeven, in press). Nitrogen and phosphorus are the most crucial nutrients in this respect because they can have strongly negative impacts on water quality and may limit plant growth in wetland ecosystems (Willis, 1963; Verhoeven et al., 1990; Verhoeven and Schmitz, 1991). This conclusion is, however, based on studies in only a small number of wetlands representing only a limited number of wetland types. Further, there is only a qualitative understanding of the way in which the processes that underlie the water quality function are influenced by environmental factors.

There is a clear need for more quantitative evaluations of wetland functions *in situ* in a wide variety of wetland types (Adamus and Preston, 1989; Maltby and Verhoeven, in press). The objectives of this study were: (1) to compare process rates related to nitrogen and phosphorus dynamics in similar types of wetlands that occurred in different parts of the world; (2) to relate process rates to a set of potentially important environmental factors; and (3) to identify easily measured variables that potentially could be used to assess wetland function(s). The experimental approach that we selected was to quantify rates of functional processes (decomposition, nitrogen mineralization, nitrous oxide emission, denitrification, and phosphorus release) at the same time that potentially important abiotic factors (soil temperature, redox, pH, total plant and soil nitrogen and phosphorus, extractable soil nitrogen and phosphorus, soil organic matter, soil particle size distribution, and water level relative to the soil surface) were being measured. All of the variables were evaluated during the 1991 growing season during a 6-week period in 8 wetlands in the USA and The Netherlands.

STUDY SITES

In both countries, 4 representative wetlands were selected to cover a range of environmental conditions and vegetation types (Table 1). Half of the sites were forested and the other half herbaceous. The sites selected in The Netherlands were all peatlands, a predominant wetland type in the country (Verhoeven, 1992). None of the Dutch sites received sediment from riverine inputs but water quality varied between them due to different sources of groundwater and surface water. The forested (NFF) and herb-dominated (NFH) Dutch fen sites were in contact with polder surface water which occasionally had high nitrate and ammonium concentrations (Beltman and Verhoeven, 1988). The Dutch forested bog site (NBF) had only limited contact with "lithotrophic" groundwater, and the surface waters had an "atmotrophic" water chemistry (Van Wirdum, 1991). The Dutch herb-dominated bog site (NBH) only received atmospheric inputs and was ombrotrophic (Vermeer and Joosten, 1992).

Two forested (AFF and AMF) and one herb-dominated site (AMH) in Maryland occurred along second order streams on the Inner Coastal Plain of Chesapeake Bay. The sites received most of their hydrologic inputs from small streams, were flooded during storm events, and the soils were dominated by mineral particles (Whigham et al., 1986). The Maryland bog site (ABH), referred to as Baltimore Corner by Tyndall et al. (1990), is one of a group (1,500–2,500) of small ombrotrophic depressional wetlands (Brinson, 1992) known as Carolina Bays that occur along the mid-Atlantic coast of North America (Sharitz and Gibbons, 1982). The Carolina Bays only occur on the Outer Coastal Plain on the Eastern Shore of Chesapeake Bay and they are found on a Pleistocene terrace at elevations between 12 and 24 m. They have been estimated to be between 16,000 and 21,000 years old (Stolt and Rabenhorst, 1987).

METHODS

At each site, 5 sampling locations were chosen and all of the measurements described below were taken at each station. Redox probes and porous cups were installed 2 weeks before the actual start

TABLE 1

Characteristics of the sites studied. All sites in Maryland were located between 38°30′–39°05′N and 76°32′–76°52′W; the sites in The Netherlands between 52°07′–52°41′N and 5°04′–6°51′E. Keys to the site designations are: A, Maryland, USA; N, The Netherlands; B, bog; F, fen; M, mineral soil; H, herbaceous; F, forested.

Site	Dominant tree/shrub	Dominant herbs	Dominant bryophytes
Maryland, USA			
ABH	*Cephalanthus occidentalis*	*Carex walteriana* *Panicum hemitomon*	*Sphagnum* spp.
AFF	*Alnus serrulata* *Acer rubrum* *Fraxinus americana*	*Cinna arundinacea* *Saururus cernuus* *Impatiens capensis*	
AMF	*Taxodium distichum* *Acer rubrum* *Ulmus americana*	*Saururus cernuus*	
AMH	None	*Carex* spp. *Saururus cernuus* *Hibiscus moscheutos* *Polygonum sagittatum* *Leersia orysoides*	
The Netherlands			
NBF	*Betula pubescens* *Rubus* spp.	*Phragmites australis* *Carex paniculata*	*Sphagnum* spp.
NBH	None	*Eriophorum vaginatum* *Oxycoccus palustris* *Andromeda polifolia*	*Sphagnum* spp.
NFF	*Alnus glutinosa* *Salix alba*	*Glyceria maxima* *Carex paniculata* *Sparganium erectum* *Lythrum salicaria* *Calamagrostis canescens*	*Calliergonella cuspidata*
NFH	None	*Carex diandra* *Equisetum fluviatile* *Caltha palutris* *Lycopus europaeus* *Peucedanum palustre* *Stellaria palustris* *Juncus subnodulosus*	*Calliergonella cuspidata*

of the 6-week field period. The field periods were 13 May–24 June in Maryland, and 30 May–10 July in The Netherlands.

Decomposition was evaluated using the cotton strip assay (Harrison et al., 1988). Duplicate cotton strips were placed vertically into the substrate at each site at the start of the study. One cotton strip from each sampling location served as a control and was immediately removed and returned to the laboratory where they were washed and dried. The second cotton strip in each pair was retrieved after six weeks, gently washed with water, and dried. Loss of cotton tensile strength was measured on the cleaned and dried samples (Maltby, 1988). *In situ* measurements of nitrogen mineralization and phosphorus release were made using the soil incubation procedure as described by Verhoeven et al. (1990). Soil samples were collected at each site and as much of the root material as possible was removed before the soil was placed in the incubation containers (stoppered aluminum tubes in Maryland and capped polyethylene bottles in The Netherlands). One container was returned to the laboratory for analysis and the other was placed in the soil and incubated for six weeks.

Fresh and incubated soil material was extracted immediately after collection with 0.2 M KCl (available ammonium and nitrate) and 0.1 M HCl in combination with 0.03 M NH_4F (Bray-II, available phosphate, Richardson and Marshall, 1986). The pH and the nitrogen and phosphorus concentrations in the interstitial water were measured at a depth of 5 cm at the start and at the end of the field period. Extracts and interstitial soil water samples were analyzed for ammonium, nitrate and phosphate with a Skalar continuous-flow analyzer.

Nitrous oxide emission and denitrification were measured at the start and at the end of the field period by *in situ* 24-hr incubations of soil. Glass jars (diameter 9.5 cm) were pushed upside down into a round slit sawed 7 cm into the soil. Two jars were installed at each sampling station; in one of these, 50 ml of acetylene was added to the headspace with a syringe via septa of silicon rubber. After 24 hr, 2 ml of gas was extracted from the headspace of both containers, stored in 25 ml helium-flushed bottles, and transferred to the lab. N_2O concentrations were determined with ECD (Electron Capture Detection) gas chromatography. N_2O emission and denitrification were calculated per m^2.

Soil temperatures were measured at the beginning and end of the study period using soil thermistors. Soil redox potential was measured using platinum-calomel probes that were placed into the soil at each site one week prior to the start of the study.

Extractable nitrogen and phosphorus, total nitrogen and phosphorus, and soil organic matter were only measured at the start of the field period. Plant nitrogen and phosphorus content were measured only at the end of the field period. Organic matter was determined as loss on ignition at a temperature of 550°C. Plant nitrogen and phosphorus content and total soil nitrogen and phosphorus were measured after acid digestion according to a salicylic-acid thiosulphate modification of the Kjeldahl method (Page et al., 1982).

Results were analyzed statistically with the SAS package (SAS, 1986). Stepwise multiple regression was used to correlate the rates measured with a range of soil parameters.

RESULTS

Comparison of the Sites

Soil temperatures (Table 2) were about 4°C lower in The Netherlands at the start of the experiment, but temperatures were similar in both countries (range: 17.3–20.7°C) at the end. Soil pH was distinctly lower in the Dutch (NBF, NBH) and Maryland (ABH) bog sites. Soil redox was spatially variable within and between sites. The two minerotrophic wetlands in Maryland (AMF, AMH) tended to have a higher soil redox than the other sites and in most instances there were large differences between the beginning and end of the experiment (Table 2).

Total soil nitrogen (Table 2) varied in the same way as soil organic matter, except for the comparatively low total nitrogen in the Dutch herbaceous bog (NBH). Total soil nitrogen and organic matter were highest in the two Dutch fens (NFF, NFH) and the forested bog (NBF). Total

TABLE 2

Data for soil variables at the beginning and/or end of the six week study period. Where differences between the two sampling dates were small (ammonium, nitrate, phosphate, organic matter, total nitrogen, total phosphorus, extractable nitrogen, extractable phosphorus) only end values are given in the Table. Values are means (N = 5)± 1 standard error. Codes for the study sites are given in Table 1 and they are described in the text. < 0.01 indicates that concentrations were below the level of detection.

Variable	ABH	AFF	AMF	AMH	NBF	NBH	NFF	NFH
Ammonium (mg l^{-1})	0.72±0.23	1.50±0.60	1.41±0.70	0.12±0.05	4.05±0.92	0.17±0.09	0.96±0.18	0.07±0.02
Nitrate (mg l^{-1})	0.05±0.01	0.13±0.06	0.70±0.32	0.34±0.09	0.05±0.01	0.10±0.04	0.11±0.01	0.01±0.01
Phosphate (mg l^{-1})	0.09±0.09	<0.01	<0.01	<0.01	4.49±0.60	0.004±0.004	<0.01	<0.01
Organic matter (mg l^{-1})	0.53±0.08	0.40±0.03	0.15±0.01	0.13±0.01	0.74±0.02	0.85±0.03	0.67±0.06	0.72±0.01
Total soil N (mg l^{-1})	13.01±2.60	9.95±0.94	3.68±0.11	3.03±0.19	18.74±2.31	7.52±0.36	21.1±2.62	23.4±1.5
Total soil P (mg g^{-1})	0.82±0.17	2.48±0.03	1.70±0.18	1.68±0.15	0.54±0.10	0.15±0.03	0.95±0.10	0.98±0.11
Extractable N (mg kg^{-1})	2.82±0.54	14.27±1.75	19.28±2.77	3.49±0.51	37.81±12.75	25.00±4.01	60.60±4.78	67.85±14.63
Extractable P (mg kg^{-1})	28.6±24.0	566.2±232.5	184.7±32.4	272.4±15.1	37.2±4.1	13.9±6.1	25.4±3.8	22.9±4.0
pH: start	4.10±0.45	6.54±0.04	6.33±0.01	6.47±0.01	4.54±0.28	3.75±0.03	5.54±0.38	6.31±0.12
pH: end	4.62±0.22	5.40±0.20	5.87±0.15	5.52±0.22	4.49±0.09	3.56±0.03	5.75±0.28	6.41±0.10
Redox: start (mV)	−150±109	267±144	268±171	143±100	−130±46	10±84	−27±54	−70±39
Redox :end (mV)	8±39	−70±68	170±55	206±90	−9±85	57±64	151±24	−92±28
Temperature start (°C)	16.9±0.2	18.4±0.3	17.2±0.1	17.0±0.3	12.6±0.2	13.7±0.3	11.7±0.2	12.4±0.1
Temperature end (°C)	20.2±0.1	18.0±0.4	17.3±0.1	18.6±0.3	20.3±0.8	19.2±0.2	19.1±0.1	20.1±0.1

TABLE 3

Stepwise multiple regression results for process rates versus the environmental factors soil pH, redox, total soil nitrogen, total soil phosphorus, and soil organic matter. Also given are the partial R^2 (proportion of variance explained by single factor), model R^2 (proportion of variance explained by total model), F probability, and the standardized regression coefficient.

Dependent variable	Step	Variable	Partial R^2	Model R^2	Probability	Coeff.
Cotton tensile strength loss	1	Total soil P	0.6410	0.6410	0.0001	0.946
	2	Soil org.mat.	0.1130	0.7540	0.0002	–0.732
P release	No variable met the 0.2 significance level for entry into the model					
N mineralization	1	Total soil N	0.2456	0.2456	0.0013	1.131
	2	Soil org. mat.	0.1359	0.3815	0.0079	–0.840
	3	Soil redox	0.0605	0.4420	0.0595	–0.269
Nitrous oxide emission	1	Soil org. mat.	0.1048	0.1048	0.0444	–0.936
Denitrification	1	Soil redox	0.4311	0.4311	0.0001	0.781
	2	Total soil P	0.1009	0.5320	0.0117	1.051

phosphorus in the Maryland sites with stream sediment inputs (AFF, AMF and AMH) was distinctly higher than in the remaining sites, all peatland sites without such inputs. Total phosphorus was particularly low for the Dutch herbaceous bog (NBH).

Extractable soil nitrogen (Table 2) was distinctly higher in the Dutch sites. Extractable soil phosphorus was much higher in the Maryland sites which received sediment inputs (AFF, AMF, AMH). Extractable soil phosphorus in the Maryland bog site (ABH) was similar to values measured in the four Dutch sites.

Cotton tensile strength loss (Fig. 1a) was highest in the three Maryland sites with sediment input (AFF, AMF, AMH) and was lowest in the Dutch (NBF, NBH) and Maryland (ABH) bog sites. Cotton tensile strength loss was intermediate in the forested and herbaceous Dutch fen sites (NFF, NFH). Nitrogen and phosphorus mineralization rates (Fig. 1b) were lowest in the two herbaceous bog sites (ABH, NBH). Nitrogen mineralization was relatively high in the three other Dutch sites (NBF, NFF, NFH), whereas phosphorus mineralization was high in two (AFF, AMH) of the Maryland riverine sites.

Nitrous oxide emission rates were lower at the start than at the end of the experiment (Fig. 2a). Rates of nitrous oxide emission were lowest in the bog (ABH, NBF, NBH) and herbaceous fen (NFH) sites, and highest in the two Maryland forested sites (AFF, AMF) with sediment input. Denitrification patterns were similar to the pattern of nitrous oxide emission (Fig. 2b). Denitrification rates were higher at the end than at the start of the experiment, lower rates were measured in the bogs, and the highest rates occurred in the two Maryland forested sites (AFF, AMF) with sediment input.

Multivariate Correlations Between Process Rates and Environmental Factors

The stepwise multiple regression for cotton tensile strength loss (Table 3) showed that more than 75% of the variance was explained by total soil phosphorus (positive correlation) and soil organic matter (negative correlation). Phosphorus release or uptake was correlated with none of the factors

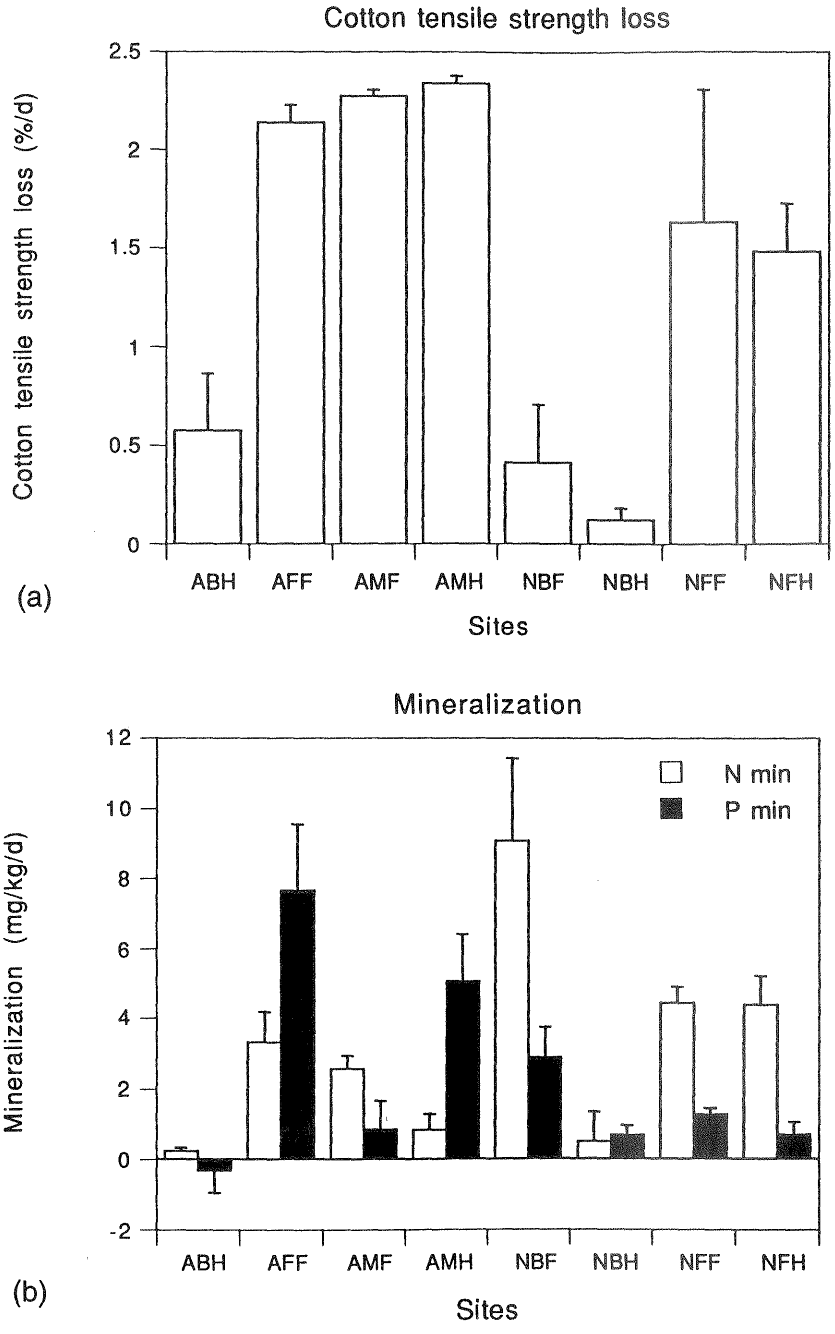


Fig. 1. Comparison of characteristics of wetlands in Maryland, USA (A) and The Netherlands (N): (a) cotton tensile strength loss; (b) nitrogen mineralization and phosphorus release. Abbreviations as in Table 1.

tested. Total soil nitrogen, soil organic matter, and soil redox accounted for 44% of the variance in nitrogen mineralization. Nitrous oxide emission was negatively correlated with soil organic matter which, however, only explained 10% of the variance. Denitrification rates were positively correlated with soil redox and total soil phosphorus, which together accounted for 53% of the variance.

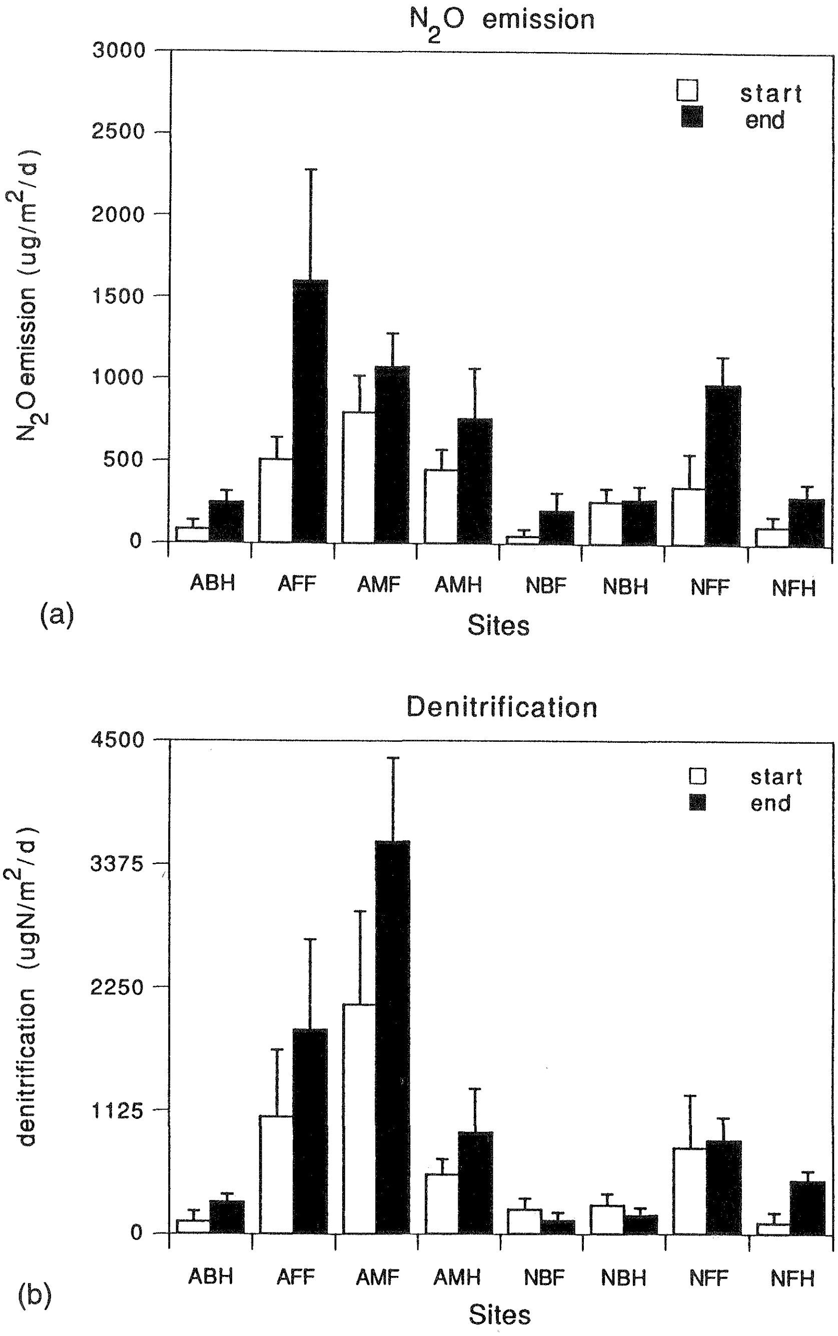


Fig. 2. Comparison of (a) nitrous oxide emission and (b) denitrification for wetlands in Maryland, USA (A) and The Netherlands (N). Abbreviations in Table 1.

Seventy-four percent of the variance in plant phosphorus content (Table 4) was explained by 5 factors, of which extractable phosphorus and ammonium in soil water were the most important. Extractable nitrogen, ammonium and nitrate in soil water and cotton tensile strength loss together accounted for 60% of the variance in plant nitrogen content.

TABLE 4

Stepwise multiple regression results for plant phosphorus and nitrogen concentration versus soil pH, redox, total soil nitrogen, total soil phosphorus, extractable soil nitrogen, extractable soil phosphorus, nitrogen mineralization, phosphorus release, cotton tensile strength loss, organic matter, NH_4 in soil water, NO_3 in soil water and PO_4 in soil water. **: because of removal of a variable during stepwise procedure only total model R^2 given. For further explanation, see Table 2.

Dependent variable	Step	Variable	Partial R^2	Model R^2	Probability	Coeff.
Plant P	1	P-extractable	0.5014	0.5014	0.0001	0.516
concentration	2	NH_4 soil water	0.1377	0.6391	0.0007	0.321
	3	Cotton loss	0.0357	0.6749	0.0579	0.637
	4	Total soil P	0.0365	0.7114	0.0457	–0.323
	5	PO_4 soil water	0.0263	0.7377	0.0777	0.267
Plant N	1	N-extractable	**	**	0.0036	0.112
concentration	2	NH_4 soil water			0.0281	0.328
	3	Cotton loss			0.0294	0.065
	4	NO_3 soil water		0.6037	0.0378	0.414

DISCUSSION

Any useful functional assessment methodology must be able to evaluate wetland functions using easily obtained data and it must be robust enough to use in almost any situation. None of the functional assessment protocols that have been developed thus far (Adamus et al., 1987; Hunsaker and Carpenter, 1990; Bartoldus et al., 1992; Maltby et al., 1994; Brinson et al., 1994; Novitzki, 1994; Maltby and Verhoeven, in press) have met these requirements because the scientific data base for wetland functions is small. One objective of this study was to determine if it would be possible to begin to develop an assessment methodology based on the use of standard analytical procedures for measuring wetland functions. The approach that we chose was to measure ecological functions and potentially important control variables in widely separated wetlands that represented a range of ecological conditions.

The sites that were selected were geographically widely separated and had both similarities and dissimilarities (Tables 1 and 2). Floristically, the dominant herbaceous genera in the bog sites in both countries were *Carex, Eriophorum* and *Sphagnum.* The forested sites had few woody species in common (see Whigham et al., 1986; Wiegers, 1992) even though the genus *Alnus* occurred at all sites.

No vegetation management is practiced in the Maryland sites while hydrologic and vegetation management have been practiced for centuries in The Netherlands (Borger, 1992). Currently, however, only the NFH site is actively managed with annual mowing to insure that trees do not become established and to maintain a high species diversity. Mowing also removes large amounts of nutrients that can influence rates of nutrient cycling (Koerselman et al., 1990).

The major site differences were the composition of the substrate and the amount of atmospheric nitrogen loading. All Maryland sites except ABH had substrates dominated by mineral sediments that are typical of watersheds on the Inner Coastal Plain of Chesapeake Bay (Correll et al., 1992). The Maryland bog site (ABH) had a substrate with a high organic matter content. All of the Dutch sites had highly organic sediments that formed during the development of peatlands over a relatively flat landscape (Verhoeven, 1992). Three of the Dutch sites developed over the last 70 years in ponds that had been formed by earlier peat excavations. The NBH site is part of a bog complex that formed during the Pleistocene (Barkman, 1992). None of the Dutch sites received direct stream sediment inputs but they differ greatly in water quality because of differences in the degree that the sites are isolated from groundwater and/or different sources of surface water. Ammonium as well as phosphate in the interstitial soil water are particularly high in the Dutch bog forest (Table 2). Here, a low pH and primarily "atmotrophic" water chemistry, in combination with the existence of Sphagnum hummocks lead to a high leaching. As indicated, all of the Dutch sites are hydrologically managed which leads to comparatively stable water tables.

The other major difference between the Dutch and Maryland sites is the amount of nitrogen received as atmospheric inputs. The total atmospheric nitrogen deposition in The Netherlands may be as high as 45 kg-N ha^{-1} yr^{-1} (Koerselman and Verhoeven, 1992) which is much higher than in the Chesapeake Bay region (Jordan et al., in press). Another difference is in the forms of nitrogen. In The Netherlands, a large percentage of nitrogen is in the form of ammonium, primarily the result of inputs from livestock. In Maryland, there is little ammonium in the atmospheric inputs but a higher level of nitrate than in The Netherlands (Jordan et al., in press).

While the rates of the ecological processes varied within and between sites, stepwise multiple regression analysis demonstrated that the rates were strongly related to differences in substrate characteristics (Table 3), especially the presence or absence of stream sediment inputs and/or the amount of soil organic matter. The three Maryland sites that received sediment inputs had distinctly higher total soil phosphorus and lower values of soil organic matter (Table 2), the two factors that showed the most significant correlations with the process rates measured (Table 3).

Cotton tensile strength loss was positively related to total soil phosphorus and negatively related to soil organic matter content (Table 3). Nitrogen mineralization, nitrous oxide emission, and denitrification were also positively related to total soil phosphorus or negatively related to soil organic matter content (Table 3).

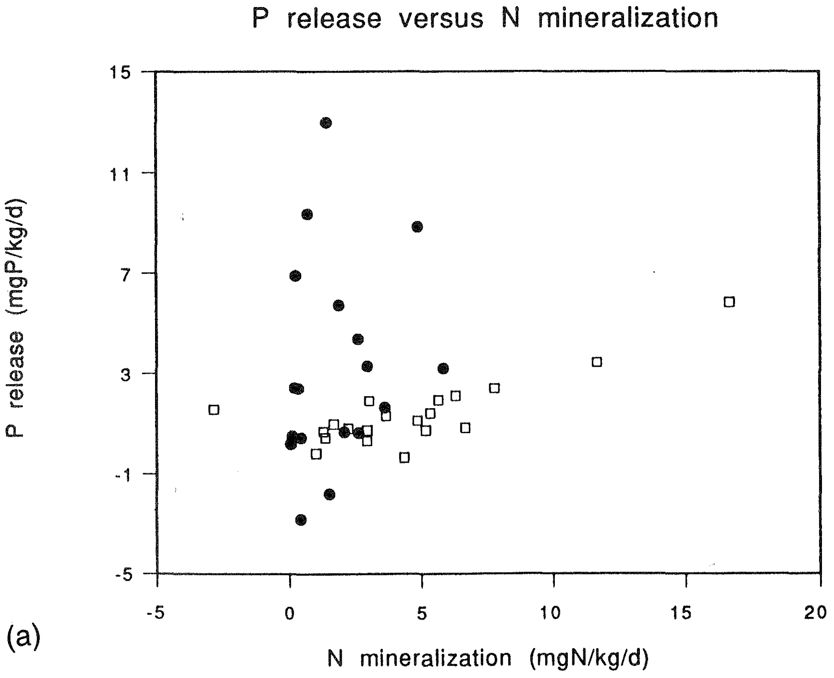


Fig. 3. (a) Phosphorus release plotted versus nitrogen mineralization. See opposite for (b) and (c).:

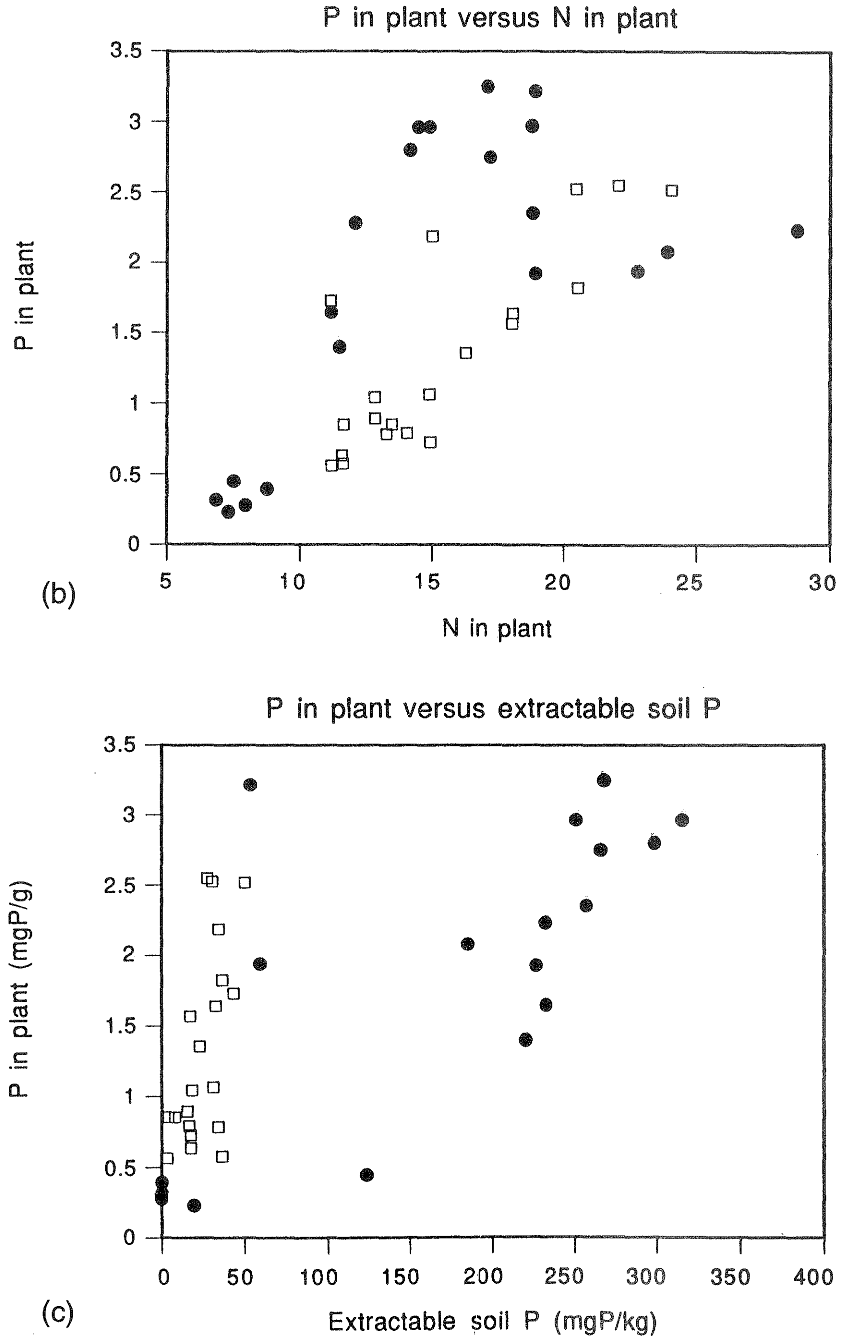


Fig. 3 *continued.* (b) Plant phosphorus concentrations plotted versus plant nitrogen concentrations; (c) plant phosphorus concentrations plotted versus extractable soil phosphorus. ● Maryland; □ The Netherlands.

The two herb-dominated bog sites on both sides of the Atlantic had the lowest rates of nitrogen mineralization and phosphate release. The rates of phosphorus release were also related to the amounts of nitrogen mineralized, especially in the sites with a high amount of organic matter in the substrate (Fig. 3a). This indicates a similar mechanism for nitrogen and phosphorus release in the peat sites, i.e., bacterial mineralization, whereas phosphorus release in the mineral sites is obviously controlled by other factors, i.e., inorganic precipitation and dissolution.

The much higher atmospheric nitrogen deposition in The Netherlands may be responsible for the generally higher values for extractable nitrogen in the Dutch peat soils. There are no indications, however, of a higher nitrogen mineralization, nitrous oxide emission, or denitrification in these soils. The remarkably similar behavior of the two herbaceous bog sites in Maryland (ABH) and The Netherlands (NBH) is especially noteworthy because it suggests that soil nutrient dynamics are controlled more by internal substrate related processes than they are influenced by atmospheric nitrogen inputs.

The positive correlation of denitrification with soil redox and the fact that nitrate levels in the soil were low indicated that nitrification (i.e., nitrate production) was in fact the process controlling the rate of denitrification. The latter process showed the highest values in the sites with average redox about +200 mV (see also Table 2), the value recognized in other studies as a threshold between nitrification and denitrification. With the large spatial variation in redox found, circumstances suitable for nitrification (> 200 mV) and denitrification (< 200 mV) will occur in close proximity at these sites.

Phosphorus concentrations in plant tissues correlated strongly with phosphorus availability. When plant phosphorus concentrations were plotted against plant nitrogen concentrations (Fig. 3b), the majority of data points show a linear relationship. Phosphorus concentrations were relatively higher for plant tissues at sites with mineral soils (AMF and AMH) and at the bog forest with high soil interstitial phosphorus (NBF).

The most significant correlation for plant phosphorus, i.e., extractable phosphorus 6 weeks prior to plant sampling (Fig. 3c), showed two linear relationships and the peat soils showed a much steeper correlation than the two sites with mineral soils. The phosphate extractant used, Bray II, thus gave a reliable indication of phosphorus available to plants, but with different coefficients for mineral and organic soils.

With respect to our primary objectives for this study, i.e., finding indicators for wetland functioning, we have investigated the value of three easily measured ratios as predictors of process

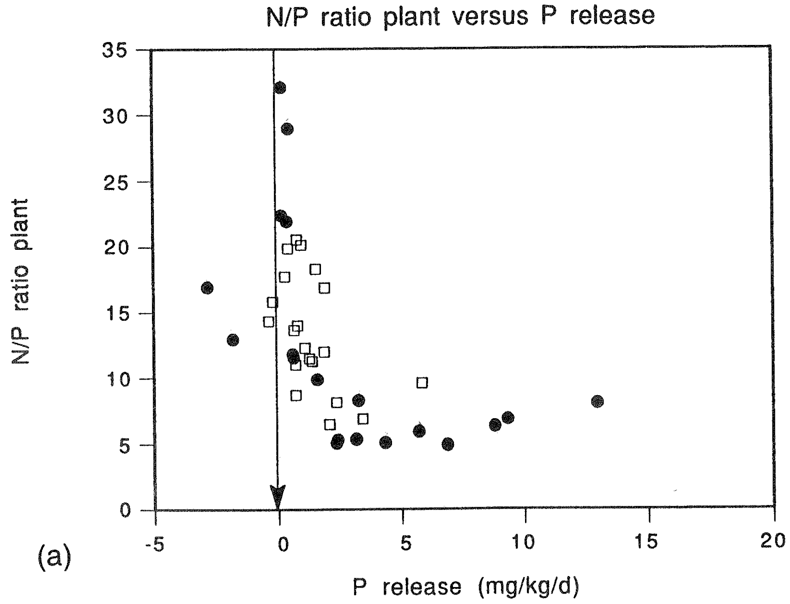
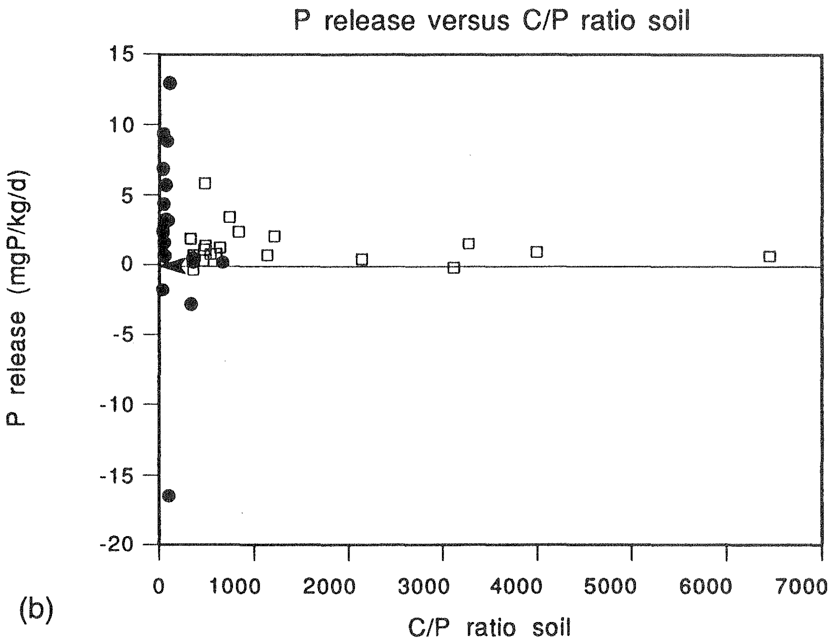


Fig. 4. (a) N/P ratio of plant material plotted versus phosphorus release. See opposite for (b) and (c).



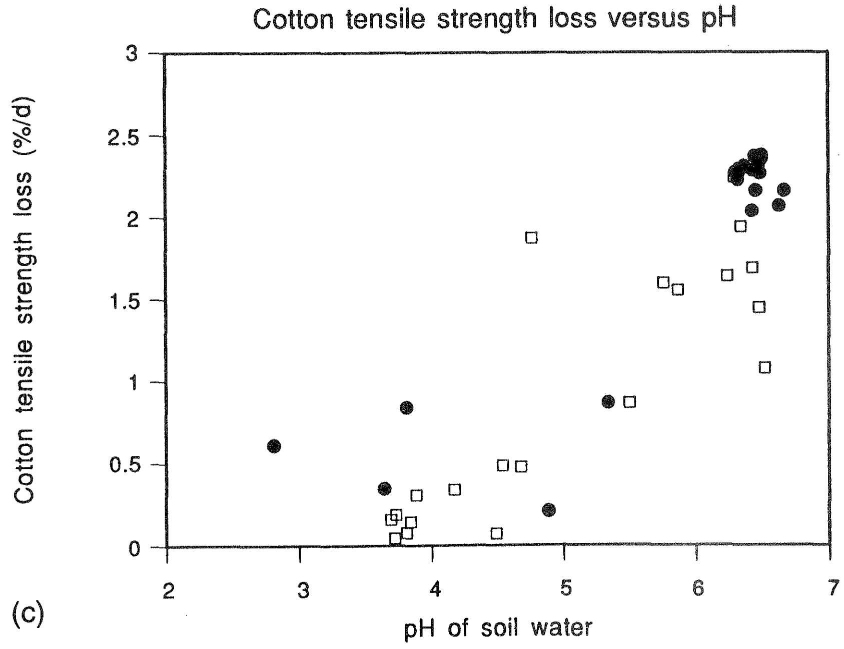


Fig. 4 continued. (b) phosphorus release plotted versus C/P ratio in soil; (c) cotton tensile strength loss plotted versus pH of interstitial water.

rates. Plant N/P ratio plotted versus phosphorus release (Fig. 4a) gave a distinct "threshold relationship" as ratios above 10 were found at very low phosphorus release or even immobilization (–2.5 to +2.1 mg-P kg-soil^{-1} day^{-1}), while ratios below 10 occurred at release rates above 2.5 (up to 13) mg-P kg-soil^{-1} day^{-1}. The N/P ratio plotted versus nitrogen mineralization gave a similar relationship but with much more scatter. C/P and C/N ratios (Figs. 4b) also gave threshold relationships with phosphorus and nitrogen mineralization, respectively. For nitrogen, this threshold corresponded to the widely reported C/N value of 15 below which mineralization occurs. For phosphorus, the low C/P values in the mineral wetlands were not at all related to mineralization rates. The threshold for the remaining peat soils is about 750, which is substantially higher than previously reported (Swift et al., 1979).

For cotton tensile strength loss we tested the relation with pH as an easily measured parameter (Fig. 4c). There is a good linear relationship although it should be realized that the actual pH values measured are not forming a continuous range but are clustered around the two extremes.

This study has demonstrated that it was possible to estimate wetland functions using easily measured variables over a relatively short period of time. The results are especially encouraging because we have measured rates and variables in a range of wetland types in different parts of the world. We conclude that this is a valuable approach for improving our understanding of environmental controls on wetland functioning. The fact that the data from the two continents combined so well in correlative analyses and scatter diagrams suggests that nutrient-related processes can be unraveled and generalized across wetland types and geographic regions.

An important outcome of this study has been the demonstration that rates of functions are quite different in wetlands dominated by mineral soils compared to wetlands dominated by peat substrates. Another important finding is that high nitrogen deposition in The Netherlands was reflected in higher pools of extractable nitrogen in the soil but not in higher process rates.

There are also several limitations that need to be noted. First, our approach neglected seasonal and/or annual rates for the functions that we measured. We chose a relatively short period of time to make our measurements with the knowledge that it will not be possible to make long-term measurements of wetland functions in most cases where an assessment protocol is being used. Second, we sampled areas where the water was not more than 3–5 cm below the wetland surface. We are aware that the depth to the groundwater will often be deeper and that there is a strong seasonal component to the location of the groundwater. Finally, we have not attempted to examine details of the mechanisms behind the various relationships that we have evaluated. This approach rather gives a "fingerprint" of functioning which may be valuable in quantifying wetland functions as part of an assessment protocol. Clearly, we need to evaluate this methodology using more types of wetlands under different environmental conditions and in many more geographic areas. These initial findings show, however, that fairly easily measured variables can be used to assess important wetland functions

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