

## PLANT-MEDIATED CONTROLS ON NUTRIENT CYCLING IN TEMPERATE FENS AND BOGS

R. AERTS,<sup>1,3</sup> J. T. A. VERHOEVEN,<sup>1</sup> AND D. F. WHIGHAM<sup>1,2</sup>

<sup>1</sup>Department of Plant Ecology and Evolutionary Biology, P.O. Box 800.84,  
NL-3508 TB Utrecht, The Netherlands

<sup>2</sup>Smithsonian Environmental Research Center, Edgewater, Maryland 20137 USA

**Abstract.** This paper reports on patterns in plant-mediated processes that determine the rate of nutrient cycling in temperate fens and bogs. We linked leaf-level nutrient dynamics with leaf-litter decomposition and explored how the observed patterns were reflected in nutrient cycling at the ecosystem level. Comparisons were made among growth forms (evergreen and deciduous shrubs and trees, graminoids and *Sphagnum* mosses) and between mire types (fens and bogs). A literature review showed that the predominant growth form was more important as a determinant of leaf-level nutrient-use efficiency (NUE) than mire type (fen vs. bog). Evergreens had the highest N and P use efficiency. The growth form differences in NUE were mainly determined by differences in N and P concentrations in mature leaves and not by differences in resorption efficiency from senescing leaves. *Sphagnum* leaves had lower N and P concentrations than the other growth forms, but because of a lack of data on nutrient resorption efficiency the NUE of these mosses could not be calculated. Nitrogen use efficiency did not differ among fen and bog species, whereas bog species had a higher P use efficiency than fen species. However, a complete evaluation of mire-type or growth-form effects on NUE is only possible when data become available about nutrient resorption from senescing *Sphagnum* leaves. As leaf-level NUE is negatively correlated with leaf-litter nutrient concentrations, there is a direct link between NUE and litter decomposition rate.

Rates of litter decomposition of *Sphagnum* mosses are lower than in the other growth forms, but there is still much speculation about possible reasons. The role of litter chemistry of *Sphagnum* mosses (including decay inhibitors and decay-resistant compounds) in decomposition especially warrants further study. The strongly deviating nutritional ecology of *Sphagnum* mosses clearly distinguishes fens and bogs from other ecosystems. Moreover, N and P concentrations in mature leaves from vascular plant species from fens and bogs are in almost all cases lower and leaf-level N use efficiency is higher than in species from other ecosystems, irrespective of the growth form considered.

Both literature data and data from a comparative study on soil nutrient cycling in temperate fens and bogs in the United States (Maryland), The Netherlands, and Poland showed that nutrient mineralization did not differ clearly between fens and bogs. The comparative study further showed that cellulose decomposition in bogs was lower than in fens and that nutrient mineralization was higher in forested than in herbaceous mires. The occurrence of dominant growth forms was clearly related to soil nutrient-cycling processes, and observed patterns were in agreement with patterns in the components of NUE as found in the literature study. We conclude that a protocol with standardized procedures for measuring various nutrient-cycling process rates that is used by scientists in various wetland types and geographical regions is a useful tool for unravelling large-scale patterns in soil nutrient-cycling processes in wetlands and for linking plant-mediated nutrient dynamics with ecosystem nutrient-cycling processes.

**Key words:** bogs, temperate; climate control of nutrient cycling; decomposition; evergreen; fens, temperate; leaf life-span; litter chemistry effects on decomposition; mineralization; nutrient cycling; nutrient resorption; nutrient-use efficiency; *Sphagnum*.

### INTRODUCTION

Mires (peat-forming ecosystems) are usually classified into fens and bogs. These wetland types are characterized by high water tables, accumulation of organic

matter (peat), and low nutrient availability. The nutrient supply to fens originates from nutrients contained in precipitation, surface water, and groundwater, whereas bogs are fed by the nutrients contained in precipitation only. In general, precipitation has a lower pH and a lower alkalinity than other water sources. As a result, the interstitial water in bogs has a low pH and low alkalinity in contrast to fens. Most fens and bogs are found in the temperate and (sub)arctic region of the Northern Hemisphere (Gore 1983). For purposes of this

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<sup>3</sup> Address for correspondence: Department of Systems Ecology, Vrije Universiteit, De Boelelaan 1087, NL-1081 HV Amsterdam, The Netherlands. E-mail: aerts@bio.vu.nl

study, the temperate region includes the Cf (warm temperate) and Df (cool temperate) climates as defined by Köppen (1931).

Fertilization experiments have shown that plant growth in temperate fens and bogs is nutrient limited (e.g., Vermeer 1986, Aerts et al. 1992, Verhoeven et al. 1996a). This raises the question of how plants from fens and bogs cope with low nutrient availability. Adaptations of perennials to different levels of nutrient availability are often evaluated by considering their nutrient-use efficiency (NUE). "NUE" is generally defined as the ratio between aboveground biomass production and nutrient loss in litterfall (Vitousek 1982). Thus, NUE covers a variety of processes, including tissue life-spans, tissue chemistry, and nutrient resorption from senescing tissues (Aerts and De Caluwe 1994, Aerts 1995). A widely used index of NUE is the inverse of litter nutrient concentrations (Vitousek 1982, Birk and Vitousek 1986). This index of NUE is strongly determined by the partitioning of nutrients between resorption and decomposition pathways (Aerts 1997a). High nutrient resorption contributes to high NUE, but leads to lower litter nutrient concentrations, and vice versa. This may have direct implications for litter decomposition rates and nutrient release, because decomposition and nutrient release from litter are often positively related to nutrient concentrations in litter and negatively related to carbon-to-nutrient ratios (Aber and Melillo 1982, Aerts 1997b). Thus, there may be a trade-off between leaf-level NUE and leaf-litter decomposition rate (Aerts 1997a).

The amount of nutrients available for plant uptake is determined by the balance between external inputs and outputs and by internal nutrient cycling. Nutrient-budget studies for fens and bogs in the temperate zone have shown that nutrient fluxes through internal cycling exceed external inputs by far (Urban and Eisenreich 1982, Hemond 1983, Morris 1991, Koerselman and Verhoeven 1992). This implies that plants exert a strong influence on nutrient availability through litter production, litter decomposition, and mineralization of nutrients contained in the litter. These processes show clear differences among various growth forms that occur in fens and bogs. In general, temperate bogs are dominated by *Sphagnum* mosses and to a lesser extent by slow-growing evergreen and deciduous shrubs and trees. Temperate fens are very often dominated by graminoids (mainly *Carex* and *Cladium* species) and by deciduous shrubs and trees and have, especially when water pH exceeds 5.5, a much lower *Sphagnum* cover (Malmer 1993, Bridgman et al. 1996).

The aim of this paper is to summarize patterns in plant-mediated processes, which determine the rate of nutrient cycling in temperate fens and bogs. We are aware of the fact that nutrient cycling is determined by the interaction of both plant-mediated effects and abiotic effects. However, given the fact that in many wetlands the plant-mediated effects overrule the abiotic

effects (Urban and Eisenreich 1982, Hemond 1983, Morris 1991, Koerselman and Verhoeven 1992) we focus in this paper on the former. We collected literature data (Appendix) on NUE and other selected components, on litter decomposition (using the negative exponential decomposition model of Olson [1963]), and on nutrient mineralization. For the fen-bog classification we used the classification provided in the original papers. We organized the paper into four parts. First we review and summarize literature on NUE by comparing growth forms (evergreen species, deciduous species, graminoids, and *Sphagnum* mosses) and mire types (fens and bogs). We then investigate the link between NUE and litter decomposition rate by comparing published data on rates of leaf-litter decomposition using the same growth-form and mire-type classification as for NUE. Next, we determine if patterns of NUE and decomposition are expressed at the ecosystem level through patterns of nutrient cycling in fens and bogs. Unfortunately, there have been very few comparative studies on soil nutrient-cycling processes in fens and bogs. Therefore, most of this section deals with a synthesis of an ongoing comparative study of soil nutrient cycling in wetlands in the temperate zone using a standardized measuring protocol (Verhoeven et al. 1994, 1996b). Finally, we investigate if the patterns observed in our summary for fens and bogs deviate from those in terrestrial ecosystems.

#### NUTRIENT-USE EFFICIENCY AND ITS COMPONENTS

Since most data on nutrient-use efficiency (NUE) and its components refer to leaf studies, we present data for these plant parts only. NUE data are compared by growth form, irrespective of their origin, and by mire type (fen species and bog species, irrespective of their growth form). For most components of NUE, differences in plant growth form are more important than differences in mire type (fen vs. bog, Fig. 1). The leaf life-span of evergreens is considerably longer than for deciduous and graminoid species (Fig. 1A). Unfortunately, no data are available for leaf life-span of *Sphagnum* mosses, but field observations suggest that they are in the same range as those for evergreens. As bogs generally contain more evergreen species than do fens, the mean leaf life-span of bog species is higher than for fen species. A survey of the relation between leaf life-span and leaf physiology has shown that long leaf life-spans are negatively correlated with the maximum rate of photosynthesis (both per unit leaf area and per unit leaf mass), leaf N concentration (on a mass basis), and the specific leaf area (SLA = leaf area per unit leaf mass) (Reich et al. 1991, 1992). This suggests that there is a trade-off between plant traits that lead to long leaf life-spans and those that lead to high rates of productivity (Aerts 1990, Reich et al. 1992). This hypothesis is supported by the negative correlation between leaf life-span and the maximum relative growth rate (RGR = growth rate per unit plant mass) of seed-

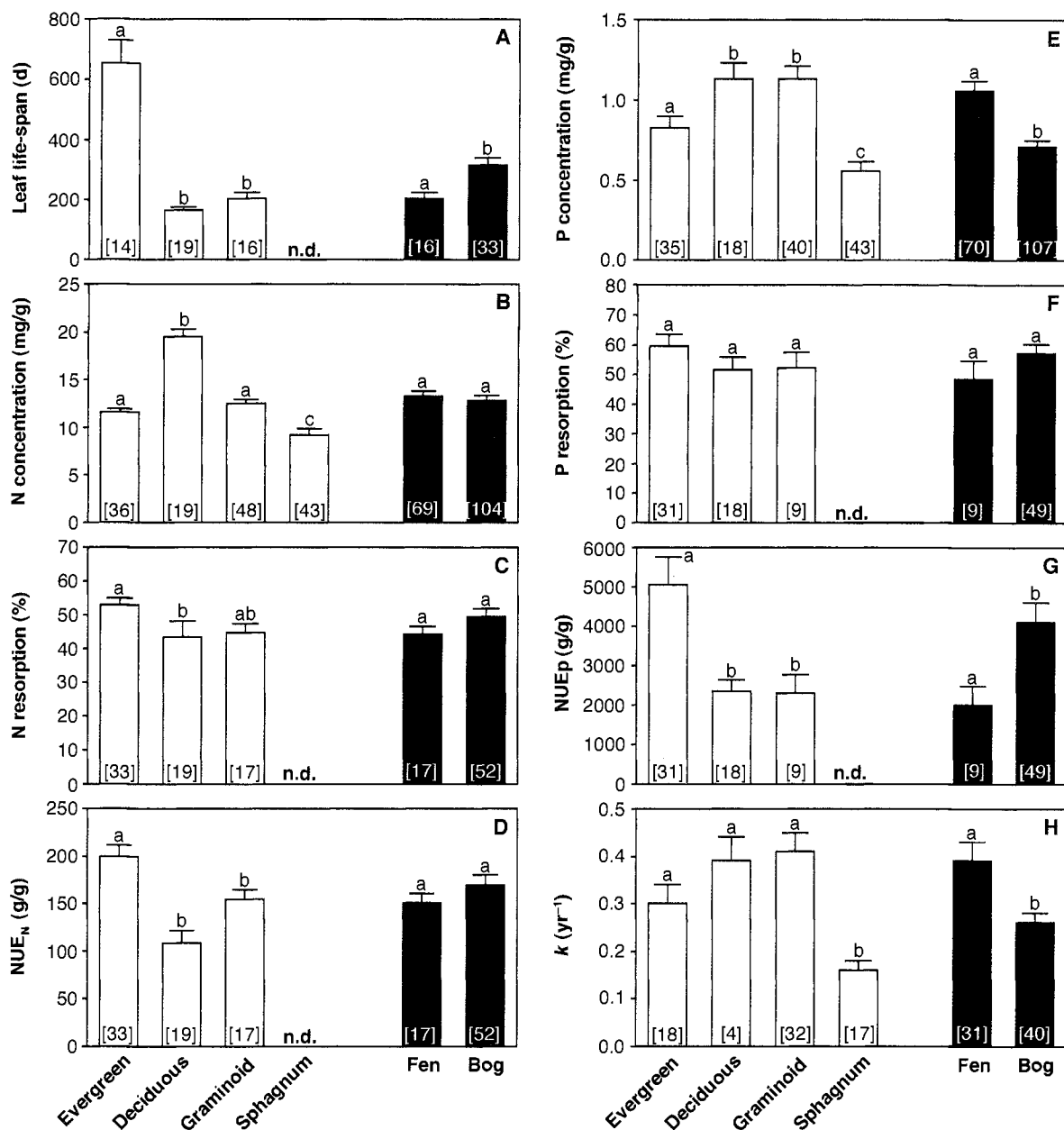


FIG. 1. Summary of literature data on leaf life-span, nitrogen-use efficiency ( $NUE_N$ ) and phosphorus-use efficiency ( $NUE_P$ ), N and P concentrations in mature leaves, N and P resorption from senescing leaves, and litter decomposition constants ( $k$  values) for species from fens and bogs in the temperate zone. Data are given as means and 1 SE; n.d. = no data available. The number of observations is given in brackets within the bars. Bars with the same lowercase letter above are not significantly different among growth forms (left) or among fen and bog species (right) ( $P < 0.05$ ). See Appendix for data sources.

lings (Reich et al. 1992). These data support the finding of Brinson et al. (1981) that bog species are less productive than fen species.

The N concentration in mature leaves of deciduous shrubs and trees is significantly higher than in other growth forms (Fig. 1B). *Sphagnum* mosses have the lowest leaf N concentrations, while evergreen shrubs and trees and graminoids have intermediate concentra-

tions. A similar pattern in N concentration was found in a broad-scale analysis of vascular species from a wide variety of habitats (Aerts 1996), suggesting that it is not specific for the wetland habitat types examined in this paper. We found no difference in leaf N concentration between fen species and bog species (Fig. 1B). As leaf carbon assimilation is linearly related to its N concentration (Field 1983, Hirose and Werger

1987, Evans 1989), our data indicate that deciduous shrubs and trees are more productive than the other growth forms. This is generally true, although evergreen species may compensate for lower productivity per unit leaf mass by having long leaf life-spans (Aerts 1995).

Nutrient-resorption efficiency ( $r$ ) is defined as

$$r = (\text{amount of nutrients resorbed from mature leaves} \div \text{maximum nutrient pool in mature leaves}) \times 100\% \quad (1)$$

in which the amounts are expressed in milligrams of nutrient per leaf. Nitrogen resorption from senescing leaves is generally between 40 and 50% and is highest in evergreens and lowest in deciduous species (Fig. 1C). The absolute differences are, however, small. As *Sphagnum* mosses have no anatomically specialized internal conducting system, it was believed for a long time that these mosses do not retranslocate nutrients during senescence. However, there are indications that nutrient resorption does occur in these mosses (Rydin and Clymo 1989). Unfortunately, no quantitative data are available for nutrient resorption from senescing *Sphagnum* leaves. The overall result of the observed differences between growth forms is that N resorption does not differ among fen species and bog species.

Nutrient use is calculated as the inverse of litter nutrient concentrations (nutrients in litter; Vitousek 1982), which is determined by the nutrient concentration in mature leaves (nutrients in mature leaves) and nutrient resorption efficiency ( $r$ ; see Eq. 1) according to the relation:

$$\text{NUE} = 1/(\text{nutrients in litter}) \\ = 1/[(\text{nutrients in mature leaves}) \times (1 - r)] \quad (2)$$

Due to lower N concentrations in mature leaves and higher N-resorption efficiency, leaf-level N-use efficiency ( $\text{NUE}_N$ ) of evergreen species is significantly higher than for any other growth form (Fig. 1D). However, N-use efficiency does not differ between fen and bog species (excluding the *Sphagnum* mosses for which there are no data). The results on NUE should be interpreted with caution, because patterns in leaf-level NUE are not necessarily similar to whole-plant patterns (Aerts 1990).

Mature-leaf P concentrations are lowest in *Sphagnum* mosses and highest in deciduous shrubs and trees and in graminoids (Fig. 1E). Evergreens have intermediate P concentrations. As bogs are mainly dominated by *Sphagnum* mosses and evergreens, we found that the P concentrations of bog species are significantly lower than for fen species. P-resorption efficiency from senescing leaves is higher than N-resorption efficiency (cf. Figs. 1C and 1F), but does not differ among growth forms. As was the case for N, there is no difference in P-resorption efficiency among fen species and bog species. Higher P- than N-resorption ef-

ficiency has been observed before (Walbridge 1991, Aerts 1996) suggesting that P may be more retranslocatable than N. As P-resorption efficiency is remarkably constant (Fig. 1F), patterns in P-use efficiency ( $\text{NUE}_P$ ) are entirely determined by variation in P concentrations in mature leaves (cf. Eq. 2). Thus,  $\text{NUE}_P$  is significantly higher in evergreens than in other growth forms and higher in bog species than in fen species (Fig. 1G). These conspicuous differences in  $\text{NUE}_P$  suggest that the high abundance of evergreens in bogs is related to low P availability in bogs compared with fens. However, a complete evaluation can only be made when data are available for the *Sphagnum* mosses as well.

Both N- and P-use efficiency are higher in evergreens than in the other growth forms (Figs. 1D and G). Thus, evergreens produce more leaf mass per unit of N or P taken up. It is generally assumed that a high NUE is beneficial in low-nutrient fens and bogs. However, the NUE index used in this and in other studies (the inverse of leaf-litter nutrient concentration) does not directly explain why a high NUE is beneficial in low-nutrient habitats. Two recently developed models (Aerts and van der Peijl 1993, Berendse 1994) show that a high NUE alone is not advantageous in nutrient-poor environments, but that selection is rather on features that minimize nutrient loss from the plant, such as low tissue nutrient concentrations, long tissue life-spans, and high nutrient resorption from senescing tissues. These models show that under conditions of nutrient-limited plant growth low nutrient-loss rates from the plant lead to a higher biomass and to competitive replacement of species with higher nutrient-loss rates. Unfortunately, for the present data set we know of no data on nutrient-loss rates, so we cannot test if these theories apply to temperate fen and bog species.

From Eq. 2 it is clear that variation in NUE can be determined by variation in nutrient concentration in mature leaves and/or by variation in nutrient-resorption efficiency. Our data show that growth-form differences in N- and P-use efficiencies are mainly determined by differences in N and P concentrations in mature leaves and not by differences in N- or P-resorption efficiency. This appears to be a general phenomenon, because this was also found in an extensive analysis of species from other habitat types (Aerts 1996). As we have already seen, high NUE, and thus low litter nutrient concentrations, may have consequences for litter decomposition and nutrient release. Thus, our analysis predicts that leaf litter from evergreen species growing in temperate fens and bogs will decompose slower and release less nutrients than the litter from other growth forms. In a large literature review on the nutritional ecology of wild plant species, it was found indeed that leaves from evergreens decompose slower than leaves from deciduous species (Aerts and Chapin 1999). Due to the dominance of evergreens in nutrient-poor mires, this implies that there might be a positive feedback between

low soil fertility and dominance of evergreens (cf. Hobbie 1992, Aerts 1995).

#### LITTER DECOMPOSITION

Peatlands from the northern hemisphere (including sub-arctic and arctic peatlands) store an estimated 455 Pg ( $\text{Pg} = 10^{15} \text{ g}$ ) of carbon (which is about one third of the total global soil C pool) and currently serve as a net sink for atmospheric carbon. The annual C accumulation rate is estimated at 0.076 Pg C/yr (Houghton et al. 1990, Gorham 1991). In peat-forming ecosystems, such as fens and bogs, low litter decomposition mainly determines the rate of peat accumulation rather than high primary productivity (Clymo 1984). Moreover, the amount of carbon returned to the atmosphere by decomposition of dead organic matter is an important component of the global carbon budget (Shaver et al. 1992, Coûteaux et al. 1995). We explore the relationships between decomposition rates and the growth form and habitat characteristics of the litter.

The decomposition data from our review originate from measurements of leaf decomposition using litter bags. In many studies, published decomposition constants ( $k$  values) were based on the single exponential decay model proposed by Olson (1963):

$$W_t = W_0 e^{-kt} \quad (3)$$

in which  $W_t$  and  $W_0$  are litter masses at time  $t$  and time 0;  $k$  is the decomposition constant (in 1/years) and  $t$  is time (in years). When  $k$  values were not provided, we calculated them from tabulated data or from graphs in which mass remaining was depicted against time. The decomposition constants presented here are based on the first year of decomposition. The decomposition rate of *Sphagnum* litter is significantly lower than that of the other growth forms, which do not show any statistical difference from each other (Fig. 1H). These data support our hypothesis that the decomposition rate of leaf litter of *Sphagnum* species is lower than that of other growth forms. However, we did not find evidence for our hypothesis that this is also the case for evergreen species. Due to the dominance of *Sphagnum* mosses in bogs, the decomposition rate of bog species is lower than in fen species (Fig. 1H). Slower decay in bogs compared with fens has also been found in comparative studies using cellulose strips (Farrish and Grigal 1988, Verhoeven et al. 1990). This points to the fact that the abiotic conditions in bogs are also a cause for low litter-decomposition rates. The low decomposition rate of *Sphagnum* litter and the high abundance of *Sphagnum* mosses in many peatlands clearly illustrate why *Sphagnum* mosses are such important peat formers in fens and bogs (cf. Clymo 1984).

The low decomposition rates of *Sphagnum* are determined by the chemistry of these mosses and by abiotic conditions in *Sphagnum*-dominated sites. From an analysis of literature data, Johnson and Damman (1993) concluded that intrinsic litter chemistry overrules site

factors in regulating *Sphagnum* decay rates. They concluded that low nutrient concentrations in *Sphagnum* litter may contribute to low decay rates, but there is little experimental evidence to support this hypothesis. In contrast, already a century ago the phenolic compounds ("sphagnol") of *Sphagnum* mosses were considered as decay inhibitors because of their antibiotic properties (Czapek 1899). Rudolph and Engman (1967) and Rudolph (1972) determined the chemical structure of sphagnol, which in reality appeared to be a complex of various phenolic compounds. Work by Painter (1991) suggested that sphagnan, a polyuronic acid, may act as a tanning agent and that it may suppress microbial activity by interfering with microbial exo-enzymes and by sequestering essential nutrients, which leads to nutrient shortages for the microbes. Recently, Verhoeven and Toth (1995) found that the addition of a small amount of homogenized *Sphagnum fallax* capitula to litter of *Carex diandra* and of *S. fallax* reduced the decomposition rate of both litter types significantly, whereas addition of homogenized leaves of *C. diandra* had no effect. This confirms the hypothesis that living *Sphagnum* cells do indeed leach a substance that reduces decomposition. The slow decay of *Sphagnum* can also be caused by high concentrations of decay-resistant compounds (Johnson and Damman 1993). Although *Sphagnum* does not contain true lignin, its cell walls contain various phenolic compounds, waxes, and polymerized lipids, which are all very decay resistant. These results show that decay inhibitors and decay-resistant compounds are probably the main cause for low *Sphagnum* decay rates, but it is clear that at present many questions still need to be answered.

#### SOIL NUTRIENT CYCLING

Nutrient budgets of fens and bogs in the temperate zone have shown that mineralization contributes a greater percentage to total plant uptake than do external inputs. There have been, however, surprisingly few studies in which nutrient-mineralization rates were compared between fens and bogs. A notable exception is the study by Verhoeven et al. (1990) in which N and P mineralization were studied in a number of fens and bogs in the Netherlands. They found that N and P mineralization were significantly higher in bogs with a *Sphagnum* cover than in fens dominated by other growth forms. This result is contrary to the generally observed higher productivity and plant nutrient uptake in fens compared with bogs (Waughman 1980, Verhoeven 1986). Therefore, primary production in bogs is probably limited by factors other than N and P availability, such as low pH and other water-chemistry features (e.g., soluble toxic compounds). This is clearly a topic that needs further investigation.

We summarize a set of studies on nutrient dynamics in temperate fens and bogs in the Netherlands, Eastern Poland, and Maryland (USA) (Verhoeven et al. 1994, 1996b). The fens and bogs studied in each area have

similar plant communities. The areas primarily differ in regional hydrology and in atmospheric N inputs. Fens in the Netherlands are located in polders with strictly controlled water levels, whereas those in Maryland and Poland are subject to natural seasonal fluctuations in water table. Fens and bogs in the Netherlands receive an atmospheric deposition of  $45 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ , in comparison with  $5\text{--}15 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  in Poland and Maryland (Erisman 1991, Jordan and Weller 1996, W. Bleuten, *personal communication*). Besides the fen-bog classification, sites in each area were also classified according to dominant growth forms of vegetation. Forested fens in all three areas are dominated by deciduous trees, with abundant representatives of the genus *Alnus*. All bog sites have a high cover of *Sphagnum*, which is the dominant growth form. The herbaceous fen sites have a vegetation dominated by graminoids, except for a transitional fen in Poland, which was dominated by evergreen shrubs.

A detailed description of sampling and chemical analyses is given in Verhoeven et al. (1994, 1996b). In short, decomposition was evaluated using the cotton-strip assay (Harrison et al. 1988), N mineralization and P release from soil P pools were measured using a soil incubation procedure, and denitrification rates were measured by in situ 24-h incubations of soil using the acetylene inhibition technique.

Cotton tensile-strength loss, an index of decomposition, was generally higher in fens than in the bogs (Fig. 2A, Table 1). Tensile-strength loss was particularly low in an ombrotrophic Dutch bog and particularly high in a riparian fen forest in Maryland. In Poland, decay rates were variable among the herbaceous fen sites. Nitrogen mineralization was high in the riparian forest in Maryland, and in both fen sites and the bog forest in the Netherlands (Fig. 2B, Table 1). Herbaceous bogs in The Netherlands and Maryland showed very low N mineralization. Mineralization was low in the Polish sites, particular for two herbaceous fens, one of which exhibited net N immobilization. Phosphorus release showed strong differences among sites (Fig. 2C, Table 1). A very high P-release rate was found for the riparian forest in Maryland, whereas the herbaceous bog in the same region showed P immobilization. In the Netherlands, P release was higher in the forested than in the herbaceous sites. The values were generally higher for the Dutch than for the Polish sites, except for the high value in the Polish transitional fen. Denitrification was highest in the fen forests in all three areas (Fig. 2D, Table 1) with generally higher rates in Maryland. Even the Maryland bog site showed a higher denitrification rate than most European sites. The values for the Dutch sites were higher than those of the Polish sites, except for the fen forests.

Further interpretation of these differences has been achieved by factor analysis of the data shown in Fig. 2 and of physicochemical and biological characteristics of the sites (Verhoeven et al. 1994, 1996b). Higher

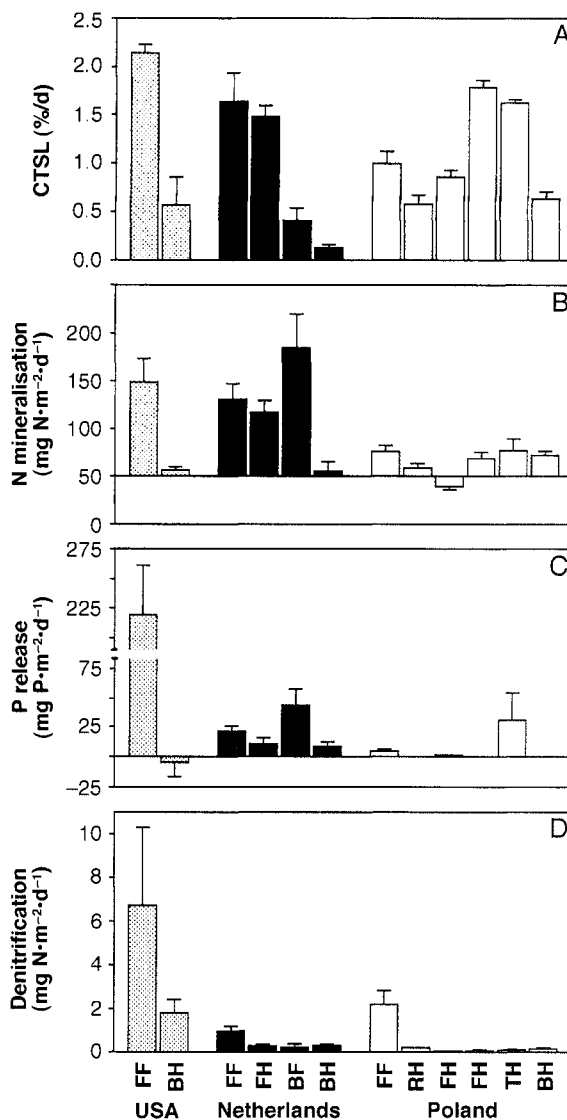


FIG. 2. Comparison of soil nutrient dynamics parameters in forested or herbaceous mires from the temperate zone in the United States (Maryland), the Netherlands, and Poland. Data are means and 1 SE and are based on five replicates. CTSL = cotton-strip tensile-strength loss. The first letter of site codes refers to mire type: F = fen (sensu strictu), T = transitional fen, R = rheophilous fen, B = bog; second letter refers to vegetation type: F = forested, H = herbaceous. Data sources: Verhoeven et al. (1994, 1996b).

N-mineralization rates in the Dutch sites were positively related to high atmospheric N deposition in the Netherlands. Higher N-mineralization rates are not related to higher denitrification rates possibly because of the stable, controlled water levels in the Netherlands. The three sites with the highest denitrification rates in the study areas were forests dominated by alders (*Alnus* spp.), which have symbiotic nitrogen fixation, and with strong water-level drops during the study periods. High P-release rates in the Dutch mires compared to the

TABLE 1. Cotton-strip tensile-strength loss (CTSL) and soil nutrient dynamics parameters in temperate mires in Poland, the Netherlands, and Maryland (USA), separated by the dominant growth form and by type.

Parameters	Growth forms				Mire type	
	Evergreen (n = 5)	Deciduous (n = 15)	Graminoid (n = 20)	<i>Sphagnum</i> (n = 20)	Fens (n = 40)	Bogs (n = 20)
CTSL (%/d)	1.62 <sup>a</sup> ± 0.04	1.59 <sup>a</sup> ± 0.16	1.18 <sup>a</sup> ± 0.12	0.44 <sup>b</sup> ± 0.06	1.38 <sup>a</sup> ± 0.09	0.44 <sup>b</sup> ± 0.06
N mineralization (mg N·m <sup>-2</sup> ·d <sup>-1</sup> )	27.7 <sup>ab</sup> ± 10.9	67.5 <sup>a</sup> ± 12.7	20.7 <sup>b</sup> ± 7.4	42.0 <sup>ab</sup> ± 15.0	37.8 <sup>a</sup> ± 6.9	42.0 <sup>a</sup> ± 15.0
P release (mg P·m <sup>-2</sup> ·d <sup>-1</sup> )	30.7 <sup>ac</sup> ± 22.6	82.3 <sup>a</sup> ± 29.1	3.1 <sup>bc</sup> ± 1.6	11.4 <sup>bc</sup> ± 5.8	36.3 <sup>a</sup> ± 12.6	11.4 <sup>a</sup> ± 5.8
Denitrification (mg N·m <sup>-2</sup> ·d <sup>-1</sup> )	0.11 <sup>b</sup> ± 0.03	3.29 <sup>a</sup> ± 1.31	0.15 <sup>b</sup> ± 0.03	0.60 <sup>b</sup> ± 0.21	1.32 <sup>a</sup> ± 0.54	0.60 <sup>a</sup> ± 0.21

Notes: Data are means ± 1 SE; n is number of sampling stations. In each row, means with the same lowercase superscript letter(s) are not significantly different ( $P < 0.05$ ) among growth forms or among fens and bogs.

Polish mires were due to the higher calcium and iron concentrations in groundwater feeding into the Polish fens. As a result, phosphate will be bound by calcium and iron ions and thus P release will decrease. Differences in cotton tensile-strength loss were mainly correlated with soil base status, i.e., acidic sites showed lower values than basic sites.

We also tested whether the occurrence of dominant growth forms of vegetation (evergreen and deciduous shrubs and trees, graminoids and *Sphagnum* mosses) were related to decomposition and nutrient dynamics (Table 1) and if there was a possible interaction of growth form with the region where the samples were taken. Cotton tensile-strength loss showed significantly lower values in the *Sphagnum*-dominated sites (bogs) than in those dominated by the other three growth forms, which showed quite similar rates. The region effect was significant and there was a significant interaction of region with growth form (Table 2), indicating a region-dependent effect on the species composition within a particular growth form and thereby on CTSL. Nitrogen mineralization was highest in sites dominated by deciduous plants, intermediate in *Sphagnum*-dominated sites, and low in the remaining sites. Only the difference between the highest and lowest values was statistically significant ( $P < 0.05$ ). Although there was a significant region effect, with highest values in The Netherlands, there was no significant interaction term. P release showed a wider range, with

the highest values again for sites with deciduous plants and lowest values for the graminoid-dominated sites. P release differed strongly between the various regions, with highest values in Maryland and much lower values in The Netherlands and Poland (Fig. 2). Phosphorus release had a significant interaction of growth form and site. Denitrification rates were higher, on average, by one order of magnitude in the deciduous (tree-)dominated sites than in all other sites ( $P < 0.05$ ). The highest values were measured in the Maryland sites.

This comparative field study shows that the occurrence of dominant growth forms in temperate fens and bogs is clearly related to ecosystem nutrient dynamics. Fen forests with a dominance of deciduous trees generally show the highest rates for all four processes studied, particularly for P release from soil P pools and denitrification. These results support our analysis of NUE (nutrient-use efficiency) and some of its underlying components, which showed that deciduous species are highly productive, have high leaf-litter nutrient concentrations, and high nutrient-loss rates from the plant through litter production. *Sphagnum*-dominated mires show the lowest decomposition rates, as has been reported in many earlier studies (Verhoeven et al. 1990, Johnson and Damman 1993). In our field study, we have not measured the decomposition of *Sphagnum* but rather of cotton as a standard substrate. The slower breakdown in *Sphagnum*-dominated sites points to negative effects of dead *Sphagnum* on microbial processes, as was also discussed above (see *Litter decomposition*). Graminoid-dominated sites showed low N-mineralization and P-release rates, and did not differ from the evergreen-dominated sites for any of the rates measured. This means that the hypothesized slower breakdown and mineralization of evergreen-derived organic matter is not confirmed by our studies of soil-based processes.

#### HOW UNIQUE ARE FENS AND BOGS?

Fens and bogs are characterized by high water tables, accumulation of organic matter (peat), and low nutrient availability. This combination of features clearly distinguishes these wetland types from other terrestrial ecosystems. Does this lead to other patterns in plant-mediated processes in nutrient cycling? To answer this

TABLE 2. Results of  $3 \times 2$  ANOVAs for cotton-strip tensile-strength loss (CTSL) and soil nutrient dynamics parameters as dependent on the dominant growth form and region (see Table 1).

Parameters	Growth form (df = 3)	Region (df = 2)	Growth form × Region (df = 6)
CTSL	30.20****	6.78**	5.19**
N mineralization	3.00*	8.43****	2.07
P release	19.35****	26.67****	28.05****
Denitrification	6.17**	6.98**	1.61

Note: The  $F$  values are presented for main effects (growth form and region) and their interaction, with levels of significance indicated (model df = 8, error df = 51).

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; \*\*\*\*  $P < 0.0001$ .

TABLE 3. Comparison of plant-mediated nutrient-cycling parameters between species from fens and bogs and species from terrestrial ecosystems in general.

Parameters	Fens/bogs	Terrestrial ecosystems	P†
Leaf N concentration (mg/g)			
Evergreen shrubs and trees	11.6 ± 2.6 (36)	13.7 ± 5.2 (95)	**
Deciduous shrubs and trees	19.5 ± 3.6 (19)	22.2 ± 7.4 (95)	*
Graminoids	12.5 ± 2.7 (48)	16.0 ± 4.0 (22)	***
<i>Sphagnum</i> species	9.2 ± 4.5 (48)	n.p.	
Leaf P concentration (mg/g)			
Evergreen shrubs and trees	0.83 ± 0.43 (35)	1.02 ± 0.56 (74)	*
Deciduous shrubs and trees	1.13 ± 0.42 (18)	1.60 ± 0.92 (78)	*
Graminoids	1.13 ± 0.50 (40)	0.95 ± 0.51 (13)	
<i>Sphagnum</i> species	0.56 ± 0.38 (43)	n.p.	
Leaf NUE <sub>N</sub> (g/g N)			
Evergreen shrubs and trees	200 ± 67 (33)	169 ± 70 (92)	*
Deciduous shrubs and trees	109 ± 54 (19)	119 ± 59 (101)	
Graminoids	155 ± 38 (17)	125 ± 56 (53)	*
Leaf NUE <sub>P</sub> (g/g P)			
Evergreen shrubs and trees	5064 ± 3904 (31)	4290 ± 6410 (71)	
Deciduous shrubs and trees	2331 ± 1294 (18)	1963 ± 1398 (79)	
Graminoids	2292 ± 1292 (9)	3947 ± 3838 (25)	
Leaf-litter decomposition constants (k; yr <sup>-1</sup> )			
Evergreen shrubs and trees	0.30 ± 0.15 (18)	0.31 ± 0.09 (33)	
Deciduous shrubs and trees	0.39 ± 0.08 (4)	0.45 ± 0.20 (32)	
Graminoids	0.40 ± 0.23 (32)	0.29 ± 0.11 (22)	*
<i>Sphagnum</i> species	0.16 ± 0.07 (17)	n.p.	

Notes: Data are means ± 1 SD; number of observations is given in parentheses. All data for terrestrial ecosystems are from Aerts (1996) except leaf-litter decomposition constants, which are from Aerts et al. (1997b); n.p. = not present.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

† Differences between fens/bogs and terrestrial ecosystems were tested with one-way ANOVAs.

question, we first compare some of the data from this paper with data from Aerts (1996, 1997b) on the nutritional ecology of terrestrial plants. This comparison shows that N and P concentrations in mature leaves from species from fens and bogs are in almost all cases lower than in species from other ecosystems, irrespective of the growth form considered (Table 3). This suggests that the nutrient-poor character of fens and bogs is not only reflected in the high abundance of evergreens (cf. Monk 1966, Aerts 1995), but within that growth form it is also reflected in lower N and P concentrations in mature leaves. Moreover, leaf-level nitrogen-use efficiency is also higher than in other ecosystems, except for deciduous shrubs and trees. However, with regards to phosphorus-use efficiency there is no difference between species from fens and bogs and species from other ecosystems. Leaf-litter decomposition constants do not differ clearly between the vascular plant growth forms (Table 3), except for graminoids.

The most conspicuous difference between fens and bogs compared to other ecosystems is the strongly deviating nutritional ecology of the *Sphagnum* mosses. These mosses are, in terms of both biomass and productivity, a very important component of fens, but especially of bogs (Malmer 1993, Bridgham et al. 1996). *Sphagnum* mosses have much lower N and P concentrations in mature leaves than the other growth forms

and have much lower leaf-litter decomposition constants (Table 3). The low decomposition constants are caused by high concentrations of decay-resistant compounds and the water-logged and very acidic conditions in bogs. As a result, peat accumulation occurs. This feature clearly distinguishes fens and bogs from other ecosystems.

#### CONCLUSIONS AND FUTURE RESEARCH

Our literature review of nitrogen-use efficiency (NUE) and litter decomposition and the comparative study of ecosystem nutrient cycling in temperate fens and bogs has shown that nutrient-use efficiency and its components differ clearly between the predominant growth forms, with evergreens having the highest NUE. Growth-form differences in NUE are mainly determined by differences in nutrient concentrations in mature leaves and not by differences in nutrient-resorption efficiency. *Sphagnum* mosses have much lower N and P concentrations than other growth forms, but unfortunately no quantitative data are available for nutrient-resorption efficiency in these species. Thus, for a complete evaluation of growth-form differences in nutrient-use efficiency in temperate fens and bogs we need data on resorption efficiency and NUE for *Sphagnum* mosses. The conspicuous difference in phosphorous NUE (NUE<sub>P</sub>) between fen and bog species raises the question of whether or not this is a special adaptation to low-P



conditions in bogs compared with fens. However, a complete evaluation of mire-type or growth-form differences in NUE can only be made when data are available for the *Sphagnum* mosses as well.

Litter decomposition rates of *Sphagnum* species are lower compared with vascular species. This is partly due to the abiotic conditions in bogs, as is shown by the low cotton-strip tensile-strength loss in those ecosystems (Fig. 2). As *Sphagnum* mosses are—both in terms of biomass and productivity—important components of fens and bogs, this clearly illustrates why *Sphagnum* mosses are such important peat formers. However, there is still much uncertainty about the reasons for the low decomposition rate of *Sphagnum* litter. Therefore, more research effort should be focused on the role of litter chemistry of *Sphagnum* mosses (including decay inhibitors and decay-resistant compounds in litter decay) (cf. Johnson and Damman 1993). The strongly deviating nutritional ecology of *Sphagnum* mosses clearly distinguishes fens and bogs from other ecosystems. Moreover, N and P concentrations in mature leaves from vascular plant species from fens and bogs are in almost all cases lower and leaf-level nitrogen-use efficiency is higher than in species from other ecosystems, irrespective of the growth form considered.

Available data limit our conclusions about possible differences in soil nutrient cycling between temperate fens and bogs. Literature data and the field data presented here indicate that nutrient mineralization does not differ clearly between these mire types. This suggests that the low primary productivity in bogs is probably caused by factors other than low N and P availability, such as low pH and the presence of soluble toxic compounds. This is clearly a topic that needs further investigation.

In our opinion, a protocol with standardized procedures for measuring various nutrient-cycling process rates, which is used by scientists in various wetland types and geographical regions, is a useful tool for unravelling large-scale patterns in soil nutrient-cycling processes in wetlands and for linking plant-mediated nutrient dynamics with ecosystem nutrient-cycling processes. Using the method described by Verhoeven et al. (1994, 1996b) for temperate mires it was determined that cellulose decomposition in bogs is lower than in fens and that nutrient mineralization is higher in forested than in herbaceous mires. The occurrence of dominant growth forms was clearly related to soil nutrient-cycling processes and the observed patterns were in agreement with the patterns in the components of NUE as found in the literature study. However, the data sets currently available are still relatively few. Thus, comparative studies on soil nutrient dynamics in a range of wetland types and climatic regions would be useful.

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## APPENDIX

Tabulation and description of studies used in our review of plant-mediated processes that affect nutrient cycling in temperate fens and bogs, by plant growth form, together with the availability of relevant data. A “+” indicates that data on that parameter were taken from the referenced paper.

Study	Description	Life-span	N resorp- tion [N]	P resorp- tion [P]	k†
Evergreen shrubs and trees					
Watt and Heinselman (1965)	<i>Picea mariana</i> in an American fen and bog	...	+	...	...
Small (1972)	Evergreen shrubs and trees in a Canadian bog	+	+	+	...
Reader and Stewart (1972)	Evergreen species in a Canadian fen and bog	...	...	...	+
Reader (1978)	Evergreen shrubs in a Canadian bog	+	+	+	...
Coulson and Butterfield (1978)	<i>Calluna vulgaris</i> in a British blanket bog	...	...	...	+
Brinson et al. (1981)	Evergreen species from a wide variety of locations	...	...	...	+

## APPENDIX. Continued.

Study	Description	Life-span	[N]	N resorp-tion	[P]	P resorp-tion	k <sup>†</sup>
Tyrrell and Boerner (1987)	<i>Picea mariana</i> in an American bog	+	+	+	...	...	...
Wallbridge (1991)	Evergreen shrubs in American pocosin and bay forest	...	+	+	+	+	...
Bartsch (1994)	<i>Chamaedaphne calyculata</i> in an American bog	...	+	...	+	...	...
Francez (1995)	<i>Calluna vulgaris</i> in a French bog	...	...	...	...	...	+
Deciduous shrubs and trees							
Small (1972)	Deciduous shrubs and trees in a Canadian bog	+	+	+	+	+	...
Reader and Stewart (1972)	Deciduous species in a Canadian fen and bog	...	...	...	...	...	+
Tilton (1977)	<i>Larix laricina</i> in an American fen and in a bog	...	+	+	+	+	...
Brinson et al. (1981)	Deciduous species from a wide variety of locations	...	...	...	...	...	+
Tyrrell and Boerner (1987)	<i>Larix laricina</i> in an American bog	+	+	+	...	...	...
Graminoids							
Latter and Cragg (1967)	<i>Juncus squarrosus</i> in a British bog	...	...	...	...	...	+
Reader and Stewart (1972)	Graminoids in a Canadian fen and bog	...	...	...	...	...	+
Bernard (1976)	<i>Carex rostrata</i> in an American fen	+	...	...	...	...	...
Bernard and Solsky (1977)	<i>Carex lacustris</i> in an American fen	+	+	+	+	+	...
Bernard and Hankinson (1979)	<i>Carex rostrata</i> in an American fen	+	+	...	+	...	...
Auclair (1977)	Graminoids in a Canadian fen	...	+	...	+	...	...
Auclair (1982)	<i>Carex</i> species in a Canadian fen	...	+	+	+	+	...
Coulson and Butterfield (1978)	<i>Eriophorum vaginatum</i> a British blanket bog	...	...	...	...	...	+
Brinson et al. (1981)	Graminoids from a wide variety of locations	...	...	...	...	...	+
Ganzert and Pfadenhauer (1986)	<i>Schoenus ferrugineus</i> in a German fen	+	+	+	+	+	...
Pfadenhauer and Twenhöven (1986)	Graminoids in a German fen	...	+	+	+	+	...
Bedford et al. (1988)	<i>Carex lasiocarpa</i> in an American fen	+	...	...	...	...	...
Verhoeven et al. (1983)	Graminoids in Dutch fens	...	+	...	+	...	...
Verhoeven et al. (1988)	<i>Carex</i> species in Dutch fens	+	...	...	...	...	...
Verhoeven and Arts (1992)	<i>Carex</i> species in Dutch fens	...	...	...	...	...	+
Ohlson and Malmer (1990)	<i>Rhynchospora alba</i> in a Swedish bog	...	+	+	+	+	...
Konings et al. (1992)	<i>Carex</i> species in Dutch fens	...	+	+	+	+	...
Aerts and De Caluwe (1994, 1995)	<i>Carex</i> species from Dutch fens	+	+	+	...	...	...
Aerts and De Caluwe (1997)	<i>Carex</i> species from Dutch fens	...	...	...	...	...	+
Wassen et al. (1995)	Graminoids in Polish fens and a bog	...	+	...	+	...	...
Francez (1995)	<i>Carex rostrata</i> and <i>Eriophorum vaginatum</i> in a French fen and bog	...	...	...	...	...	+
<i>Sphagnum</i> species							
Malmer (1962)	<i>Sphagnum</i> species in a Swedish fen and a bog	...	...	...	+	...	...
Malmer (1988)	<i>Sphagnum</i> species in Swedish bogs	...	+	...	+	...	...
Malmer et al. (1992)	<i>Sphagnum</i> species in Swedish fens and bogs	...	+	...	+	...	...
Clymo (1965)	<i>Sphagnum</i> species in British bogs	...	...	...	...	...	+
Reader and Stewart (1972)	<i>Sphagnum fuscum</i> in a Canadian bog	...	...	...	...	...	+
Pakarinen (1978)	<i>Sphagnum</i> species in Finnish bogs	...	+	...	+	...	...
Coulson and Butterfield (1978)	<i>Sphagnum recurvum</i> in a British blanket bog	...	...	...	...	...	+
Ferguson et al. (1984)	<i>Sphagnum</i> species in British bogs	...	+	...	+	...	...
Lieffers (1988)	<i>Sphagnum warnstorffii</i> in a Canadian fen	...	...	...	...	...	+
Brock and Bregman (1989)	<i>Sphagnum recurvum</i> in a Dutch alder carr	...	+	...	+	...	+
Rocheftort et al. (1990)	<i>Sphagnum</i> species in a Canadian fen	...	...	...	...	...	+
Johnson and Damman (1991)	<i>Sphagnum</i> species in a Swedish bog	...	...	...	...	...	...
Gerdol (1991, 1995)	<i>Sphagnum</i> species in Italian bogs	...	+	...	+	...	...
Misceallenous							
Waughman (1980)	A wide array of unidentified species in German fens and bogs	...	+	...	+	...	...

† Litter-decomposition constant.