Interferences between Sphagnum and vascular plants: effects on plant community structure and peat formation

Malmer, Nils; Albinsson, C; Svensson, B M; Wallén, Bo

Published in:
Oikos

DOI:
10.1034/j.1600-0706.2003.12170.x

2003

Citation for published version (APA):
Malmer, N., Albinsson, C., Svensson, B. M., & Wallén, B. (2003). Interferences between Sphagnum and vascular plants: effects on plant community structure and peat formation. *Oikos*, *100*(3), 469-482. https://doi.org/10.1034/j.1600-0706.2003.12170.x

Total number of authors:
4

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

OIKOS 100: 469–482, 2003

Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation

Nils Malmer, Crister Albinsson, Brita M. Svensson and Bo Wallén

Malmer, N., Albinsson, C., Svensson, B. M. and Wallén, B. 2003. Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. – Oikos 100: 469–482.

The interference between vascular plants and peat mosses with respect to nitrogen and phosphorus was studied in a fertilization experiment and with respect to competition for light in a removal experiment in poor fens with either soligenous or topogenous hydrology using *Narthecium ossifragum* (L.) Huds. and three species of *Sphagnum* sect. *Sphagnum* as targets. Adding fertilizer either on the moss surface or below it confirmed the hypotheses of an asymmetric competition for nutrients, viz. that the *Sphagnum* mosses relied on the atmospheric supply while *Narthecium* depended on mineralization in the peat. The results of the removal experiments and the negatively correlated growth of *Narthecium* and *Sphagnum* mosses demonstrated a symmetric competition for light. The intensity of the competition for light increased as the availability of N and P increased. The nutrient resources in the total biomass decreased with decreasing standing crop of *Narthecium*. Only with a considerable amount of mineral nutrients in the biomass has *Narthecium* the capacity to grow ahead of *Sphagnum*, because the asymmetric competition for N and P gives *Sphagnum* the capacity to reduce the performance of vascular plants. The mosses are more efficient in their use of nutrients and produce a decay-resistant litter inducing low mineralization and increasing the peat accumulation rate, and that withdraws N and P from the rhizosphere. The *Sphagnum* mosses thus act as ecological engineers structuring the plant community and determining the carbon balance of the system. The development of ombrotrophic conditions through peat accumulation seems less probable on soligenous than on topogenous mires owing to the higher mineralization rate there supporting the growth of the vascular plants. Correspondingly, disturbances of the *Sphagnum* cover, such as through airborne pollutants, increase the productivity of the vascular plants and decrease the capacity for carbon accumulation.

N. Malmer, C. Albinsson, B. M. Svensson and B. Wallén, Dept of Ecology, Lund Univ., SE-223 62 Lund, Sweden (nils.malmer@planteco.lu.se). Present address for CA: Kalmar Univ., Box 905, SE-391 29 Kalmar, Sweden. Present address for BMS: Evolutionary Biology Centre, Dept of Plant Ecology, Uppsala Univ., Villavägen 14, SE-752 36 Uppsala, Sweden. Present address for BW: Faculty of Science, Lund Univ., Box 118, SE-221 00 Lund, Sweden.

In the globally most widespread peat forming systems, the mires of the arctic, boreal and temperate regions, mosses of the genus *Sphagnum* often form most of the biomass. They often have the greatest share as well of the primary production (Malmer 1993). The bryophytes also differ markedly in their life history strategy from the vascular plants (in *Sphagnum* mires various dwarf shrubs and sedges but few herbs). In *Sphagnum* mosses both photosynthesis and the accumulation of mineral nutrients take place over the entire plant surface whereas in vascular plants these two functions are divided between shoot and root. Most *Sphagnum* spp. are subjected to periods of drought whereas the water table very rarely sinks so much that the growth of the

Accepted 6 September 2002

ISSN 0030-1299

vascular plants is hampered by a shortage of water. At the same time the *Sphagnum* mosses are able to grow as long as the moss surface is not frozen and the capitula in the apex of the mosses are provided with the necessary moisture. For most vascular plants incremental growth is restricted to a few months in the earlier part of the vegetation period. This difference in growth phenology appears to facilitate the co-existence of both.

Peat formation can take place both in topographic depressions in the landscape with largely stagnant water (topogenous peat formation) and on gentle slopes with an outflow of sub-soil water (soligenous peat formation). In soligenous fens the subsurface water is more mobile and the peat layer is less deep and more humified and decomposed than in topogenous ones. In addition, the abundance of vascular plants is usually greater (Sjörs 1946, 1948, Havas 1961, McVean and Ratcliffe 1962, Fransson 1972, Banner et al. 1988, Albinsson 1996). Regardless of the type of mire involved the *Sphagnum* litter usually produces a larger proportion of the peat than of the primary production since many *Sphagnum* spp. form a litter more resistant to decay than the litter of most vascular plants (Coulson and Butterfield 1978, Johnson and Damman 1993).

Analyses of the mineral nutrients in the plant biomass suggest that N, P, and K limit primary productivity (Malmer 1962b, 1986, Koerselman and Meuleman 1996). In some experiments, an additional supply of N or P or both to the mire surface increased the growth of vascular plants at the expense of the mosses (Tamm 1955, Damman and Johnson 2000). In other experiments, only moss growth increased (Bayley et al. 1987, Aerts et al. 1992, 2000). An additional supply of N has also been shown to have detrimental effects on *Sphagnum* mosses (Gunnarsson and Rydin 2000). Vascular plants and *Sphagnum* mosses may rely on spatially different sources for mineral nutrients: vascular plants on the mineralization in decaying organic matter below the surface and mosses on atmospheric deposition on the surface (Malmer et al. 1994, Svensson 1995, Bridgham et al. 1996, Rydin 1997). In addition, peat formation always involves a sequestering of mineral nutrients, particularly of N and P, from the rhizosphere (Damman 1988), and may be as important as the low mineralization rate in the *Sphagnum* litter in reducing the availability of plant mineral nutrients in the surface layer of a mire (Scheffer et al. 2001).

In growing in close conjunction with *Sphagnum* mosses, vascular plants form a kind of matrix for the moss plants ("scaffolding") and enabling the moss carpet to rise above the water level (Malmer et al. 1994). However, the shading the vascular plants create also reduces the productivity of *Sphagnum* (Hayward and Clymo 1983, Murray et al. 1989), whereas the aboveground shoots of vascular plants are often observed being overgrown by *Sphagnum* (Backéus 1985, Redbo-Torstensson 1994, Svensson 1995). Interactions of this sort between vascular plants and *Sphagnum* mosses create a small-scale mosaic of patches with a high vascular plant cover and patches with a high moss cover. Such a pattern is very characteristic of the plant communities in most peat forming ecosystems.

All this taken together suggests that in peat-forming systems the proportion of *Sphagnum* mosses in the biomass can be assumed to strongly influence the decay and mineralization rates in the litter as well as the peat accumulation rate and accordingly the withdrawal of mineral nutrients from the rhizosphere. Thus, with an increasing share of *Sphagnum* mosses in the biomass the availability of mineral nutrients in the system may decrease and the peat accumulation rate increase. The present article reports experiments in which we have studied the competitive interactions determining the proportions of vascular plants and of *Sphagnum* mosses in the biomass found in mires of the poor fen type (Rydin et al. 1999) with a patchy vegetation. In particular we want to investigate whether the mutual interactions between vascular plants and *Sphagnum* mosses differ with the edaphic conditions and the mire type in a way that influences the availability of mineral nutrients, the structure of the plant community, the rate of peat formation and the development of a mire. In one fertilization experiment we examine the degree of asymmetry in the competition for nutrients between deep-rooted, scaffolding vascular plants and *Sphagnum* mosses assuming that they rely on different sources for mineral nutrients. In two biomass interference experiments, one at soligenous and the other at topogenous sites, we analyse the variation in the intensity of the interactions between vascular plants and *Sphagnum* mosses along a fertility gradient in the vegetation. Since we assume the competitiveness of the *Sphagnum* mosses to decrease in the aboveground biomass as the fertility is enhanced, we expect the influence of the *Sphagnum* mosses on the structure of the plant community to be greater at the topogenous than at the soligenous sites.

Methods

The species

Narthecium ossifragum (L.) Huds. (Liliaceae), a perennial, clonal plant with horizontal rhizomes 5–20 cm below the moss surface (Summerfield 1974), was the target species of the vascular plants (denoted henceforth by its generic name only). It has sterile aboveground shoots that develop from buds on the rhizome and have a short stem (< 1 cm) carrying a bunch of swordlike leaves, 5–45 cm in length. The fertile shoots have a longer stem with only small leaves. In mires in Scandinavia, *Narthecium* is most widespread in lawns (Rydin et al. 1999) in poor fen vegetation, and in the pH range of 4.0 to 6.0. Growing together with *Sphag-*

num in peat-forming systems, stands of *Narthecium* show a continuous variation from patches with dense stands of shoots in which the cover of mosses is low to patches containing only scattered shoots together with a vital and productive *Sphagnum* cover.

The three *Sphagnum* species included in the experiments, *Sphagnum affine* Ren. & Card., *S. magellanicum* Brid., and *S. papillosum* Lindb., all belong to the section *Sphagnum*. They are characteristic of lawns in peat-forming bog and poor fen vegetation. *S. magellanicum* is distinctly more acidophilous than the other two species (Malmer 1962a) whereas in Scandinavia *S. affine* only is found in fens (Flatberg 1984).

Study sites

All experiments were performed in lawn vegetation in mires with a *Sphagnum*-dominated poor fen type of vegetation (Rydin et al. 1999) located in the boreonemoral zone of southern Sweden in the province of Småland. Together, the sites included most of the variation in this type of vegetation found in the region. The experiments (plot size throughout 0.20 × 0.20 m) were carried out in part in a large topogenous fen area on the Åkhult mire (57°10′N, 14°30′E; altitude 230 m, Malmer 1962a) in the central part of the province, and in part in six soligenous mires in the eastern part of the province (centred on 56°55′N, 15°30′E; altitude 150–250 m, Albinsson 1996). The mean annual precipitation in the region is 650–700 mm (Eriksson 1983), the mean temperature of the warmest month (July) being 17°C. The vegetation period (daily mean temperature > 4°C) is 205–215 days (Malmer 1962a). The mosses are able to grow from early spring to late autumn, the greatest growth in length often taking place in the autumn (Malmer and Wallén, pers. obs.). In contrast, *Narthecium* reaches its peak aboveground standing crop in mid-July (Malmer 1962b).

The three sites in the topogenous fen (slope < 1‰) followed a direct vegetational and edaphic gradient from Site A (water-pH 4.2) close to an ombrotrophic part of the mire lacking *Narthecium*, over Site B (pH 4.4), to Site C (pH 4.6) in the marginal part of the mire. On Site A *Sphagnum magellanicum* was the dominant moss plant in the lawns and *Narthecium* and scattered *Eriophorum angustifolium* Honck. the only plants indicating minerotrophic conditions (Gunnarsson et al. 2002). Site B was characterized by vegetation with more of exclusive fen plants (e. g. *Menyanthes trifoliata* L., *Carex lasiocarpa* Ehrh.) and with *Sphagnum papillosum* as dominant in the lawns. At Site C the vegetation was of the mire margin type (Malmer 1962a, 1986, Rydin et al. 1999) with a few, lowgrown pines and species such as *Carex canescens* L., *C. echinata* Murr. and *C. nigra* (L.) Reich. together with *Sphagnum papillosum* and *S. apiculatum* H. Lindb. as dominants in the moss layer.

The six sites in the soligenous fens (slope 2.5–25‰) were dominated either by *Sphagnum papillosum* and *S. magellanicum* (three sites, pH around 4.4) or by *S. affine* (three sites, pH around 4.8). The vegetation at these two types of sites was of the *Calluna* community type and the *Molinia* community type, respectively, as described in Albinsson 1996. The former community type is characterized by a richer occurrence of dwarf shrubs (*Calluna vulgaris* (L.) Hull, *Erica tetralix* L.) and *Eriophorum* spp. and much less of *Molinia caerulea* (L.) Moench than in the latter. The two site types are referred to as the *Sphagnum papillosum* and *S. affine* sites, respectively.

The biomass interference experiments

The topogenous fen

The experiments started in September 1993. In each of the three sites there were 25 plots arranged in five blocks placed in lawns with *Narthecium* as the dominat among the vascular plants. In each block, two of the plots (Table 1) were placed in stands with a low moss cover (5–50%), and randomly assigned to either control (nothing done) or clipping of all the aboveground biomass of *Narthecium* and other vascular plants. The other three plots in each block were placed in stands with high moss cover (70–100%). Each of these plots was randomly assigned to one of the following three treatments, viz. untreated (control), all faded, greyish aboveground biomass from a dense stand (size 0.2 × 0.2 m) of *Narthecium* nearby laid onto the moss surface, and clipping of the *Sphagnum* biomass. (The *Sphagnum* biomass comprises those parts of the mosses that were not faded or decaying. Cf. also next paragraph!) During 1994 one plot at site C with the mosses clipped became destroyed by flooding and was thus excluded.

Clipping was carried out four times during the vegetation periods in 1994 and 1995 and the adding of litter repeated in September 1994. Early in September 1994 and in the third week in August 1995, in each plot we

Table 1. Survey of treatments in the biomass interference experiments.

Treatment	Topogenous sites	Soligenous sites
Plots with high moss cover:		
Untreated (control)	+	+
Narthecium clipped	−	+
Sphagnum clipped	+	+
Litter added	+	−
N and P in biomass	+	−
Plots with low moss cover:		
Untreated (control)	+	+
Narthecium clipped	+	+
Sphagnum clipped	−	+
N and P in biomass	+	−

estimated the percentage moss cover visually, counted the sterile *Narthecium* shoots, and measured their length. In 1995 all the aboveground plant biomass was harvested, taken to the laboratory, and sorted into five fractions: *Narthecium*, other herbs, woody plants, gramineous plants, and *Sphagnum* mosses. At the same time the number of fertile *Narthecium* shoots was counted and the length of the moss plants measured as the distance from the top to the uppermost branches with fading and decaying leaves, a limit which could be determined with sufficient accuracy. All samples were then dried at 40°C and weighed. To establish the fertility gradient and the biomass content of mineral nutrients the samples of *Narthecium* (fertile shoots excluded), gramineous plants and *Sphagnum* were also analysed for N and P. Four plots had to be excluded because the samples were too small.

The soligenous fens

At each one of the six sites, 30 plots were arranged in six blocks and were so placed as to minimise the presence of vascular plants other than *Narthecium*. Within each block one of the following three treatments (Table 1) were randomly assigned to one of the plots, viz. control (nothing done), *Sphagnum* biomass clipped together with all shoots of vascular plants except *Narthecium*, and all aboveground biomass of vascular plants clipped.

The treatments were begun in May 1993 and repeated four times during the vegetation periods in 1993 and 1994. In early September 1993 and 1994 the number of *Narthecium* shoots in each plot was counted, the length of the sterile *Narthecium* shoots measured, and their percentage cover visually estimated in 5 × 5 cm quadrates, from which a mean cover per plot was calculated. A rough estimate of the aboveground biomass of *Narthecium* was calculated using the linear regression:

$$y = a + k \times l_s \times d_s, \qquad (1)$$

where y is the *Narthecium* biomass (g m^{-2}) and l_s and d_s the shoot length (cm) and the shoot density (shoots per m^2) of *Narthecium*, respectively. The constants a and k were calculated using data obtained in the untreated plots on sites A and B at the topogenous fen ($a = 13.6$, $k = 0.00631$, $R^2 = 0.87$, $p < 0.001$, $n = 20$).

Moss cover was estimated in the same way as the cover of *Narthecium* at the start of the experiments and in September 1993 and 1994. The height increment of the *Sphagnum* plants during the summer periods was measured with one cranked wire (Clymo 1970) in each plot with the moss cover being kept intact. Using the data from the start of the experiments the blocks were divided into two groups, one with a mean moss cover > 67% and one with < 67% (mean cover 84% and 34%, respectively; total range 2.5%–94%). Both groups included at least two blocks from each site.

The fertilization experiment

The effects of supplying N and P were studied at site A at the topogenous mire in patches with a high moss cover of *Sphagnum magellanicum* and only sparse shoots of *Narthecium* and other vascular plants. The nutrients were added in an aqueous solution of NH_4NO_3 (2.8 mM) and NaH_2PO_4 (0.52 mM). Twenty plots (size 20 × 20 cm) were arranged in five blocks and randomly assigned to one of the following four treatments: 200 ml of nutrient solution sprayed on the moss surface, 200 ml of distilled water sprayed on the moss surface, 200 ml of nutrient solution added through a funnel 6–8 cm below the moss surface on five, uniformly spaced points, and 200 ml of distilled water added in the same way. Owing to disturbance by animals one of the plots fertilized below the surface had to be discarded.

The treatments were begun at the beginning of May 1994 and were repeated every fifth week until September of that year, and again in 1995 from the end of April through July. Calculated on an annual basis, the added N and P (2.0 and 0.40 g m^{-2} yr^{-1}) represent, respectively, 4–5 and 50–100 times the ambient supply rate (Malmer 1988) whereas the water added corresponds to only 4% of the mean annual precipitation. At the end of August in 1995 the plots were harvested and treated in the same way as in the biomass interference experiments on the topogenous sites except that only the *Narthecium* shoots and the *Sphagnum* mosses were analysed for N and P.

Chemical analyses

Prior to the analyses, the entire sample was ground in a Wiley mill. Two portions were taken out and analysed separately in a Tecator flow injection analyser following wet digestion in H_2SO_4. Nitrogen was analysed as NH_4^+ (gas-diffusion) and P as PO_4^{3-} using vanado molybdate as reagent. All analyses were duplicated, the differences in nearly all cases being < 5% of the mean.

Statistical analyses

To test for differences between treatments and sites, two-way analyses of variance (ANOVA, Zar 1984, the SYSTAT package) were employed throughout. Whenever necessary, the data were log transformed to obtain normality. Average values are presented together with SE. The data from the soligenous and the topogenous mires and from the plots with high and with low moss cover were analysed separately. No statistically significant differences between the control and the treated plots were found in the non-destructive measurements at the start of the experiments (data not shown). Unless stated otherwise, the data referred to concern the measurements made at the end of the experiments.

Results

The biomass interference experiments

The topogenous sites

Both the number and length of the shoots and the aboveground biomass of *Narthecium* decreased as the moss biomass increased (Fig. 1). Site C stood out from the other sites through the sterile *Narthecium* shoots being of greater length and lower density and having the greatest density of fertile shoots (data not shown). In the plots with low moss cover the aboveground *Narthecium* biomass was significantly higher at site C than at sites A + B (320 ± 50 and 190 ± 20 g m^{-2}, respectively; $p = 0.03$) whereas in the plots with high moss cover it did not differ (130 ± 50 and 72 ± 9 g m^{-2}; $p = 0.16$). At site C the moss plants were significantly longer than at sites A + B both in plots with high (8.0 ± 0.5 and 4.2 ± 0.3 cm, respectively) and in those with low (4.4 ± 1.0 and 2.5 ± 0.6 cm) moss cover ($F_{2,24} = 21.6$, $p < 0.001$ and $F_{2,24} = 4.68$, $p = 0.019$, respectively). The moss biomass at site C was at most about 4 times that of the aboveground vascular plant biomass as compared with about 14 times at the other two sites (Fig. 1). However, at all three sites the cover of mosses ranged from < 10% to > 90%. Thus, if moss biomass in Fig. 1 is replaced by moss cover as independent variable, the slopes of the regressions for site C would be more or less parallel with those calculated for sites A and B.

Clipping *Sphagnum* increased the shoot density of *Narthecium* (Fig. 2). At site C also the *Narthecium* biomass increased by 59% although not significant ($p = 0.12$; t-test). Adding litter onto the mosses did not affect the growth of *Narthecium* (Fig. 2d–f).

Clipping vascular plants resulted in greater cover and biomass of *Sphagnum* whereas the length of the moss plants was hardly affected (Fig. 3a–c). Adding litter to plots with high moss cover decreased length, cover and biomass of the *Sphagnum* plants (Fig. 3d–f). In plots with dense stands of *Narthecium*, the ratio of vascular plant litter relative to vascular plant biomass (except dwarf shrubs) in August 1995 was less at site C (0.34 ± 0.09; n = 10) than at the sites B (1.08 ± 0.18) and A (0.84 ± 0.17). This suggests that the smaller effect of litter addition at site C than at the other sites be due to a higher initial litter decay rate there.

The soligenous sites

Just as at the topogenous sites growth of the *Narthecium* shoots at the soligenous sites were negatively correlated with the moss cover (Fig. 4). The shoots were taller but grew more sparsely at the *Sphagnum affine* than at the *S. papillosum* sites. With low moss cover the aboveground standing crop of *Narthecium* was significantly higher at the sites of the *Sphagnum affine* type than of the *S. papillosum* type (210 g m^{-2} and 120 g m^{-2}, respectively; cf. eq. 1), whereas it was similar (approx. 55 g m^{-2}) with high moss cover. With a high moss cover the moss biomass may be at most 10–15 times that of the aboveground vascular plant

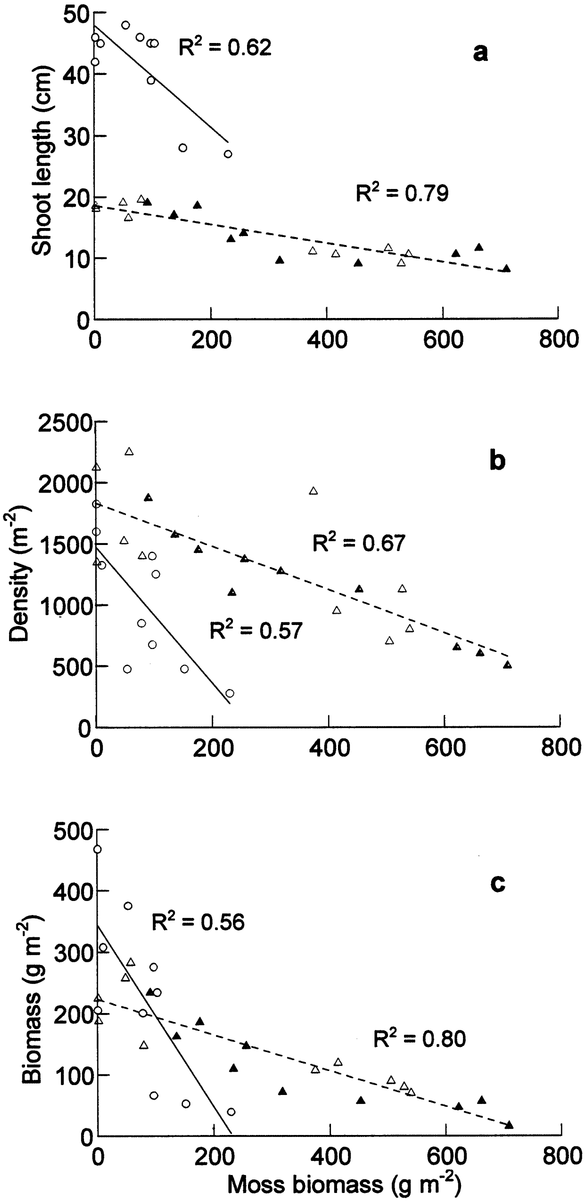

Fig. 1. Shoot length (a), shoot density (b), and aboveground biomass (c) of *Narthecium* in relation to moss biomass at the topogenous sites. Data from the untreated plots in 1995. Circles and full drawn regression line represent site C; triangles and hatched line represent site A (open symbols) and B (filled symbols). R^2 ($p \leq 0.01$) for the two regressions indicated.

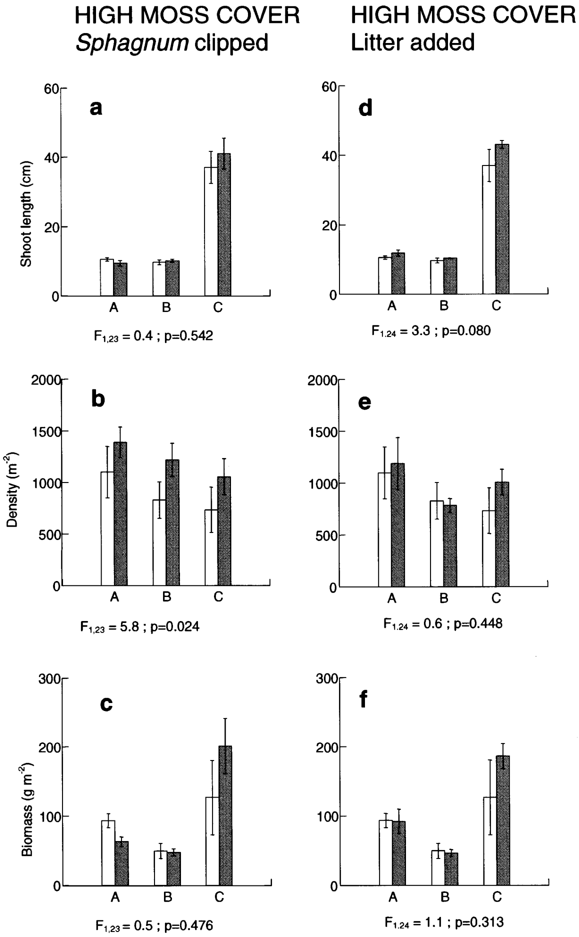

Fig. 2. Response of *Narthecium* shoots in plots with high moss cover to clipping of the *Sphagnum* biomass (a–c) and to addition of extra litter (d–f) in length (a and d), density (b and e), and standing crop (c and f) at the topogenous sites (A, B, and C). Values are mean ± SE. Open and filled bars for unclipped and clipped plots, respectively. F- and p-values refer to the effect of treatment in the analysis of variance. No significant interactions treatment × site.

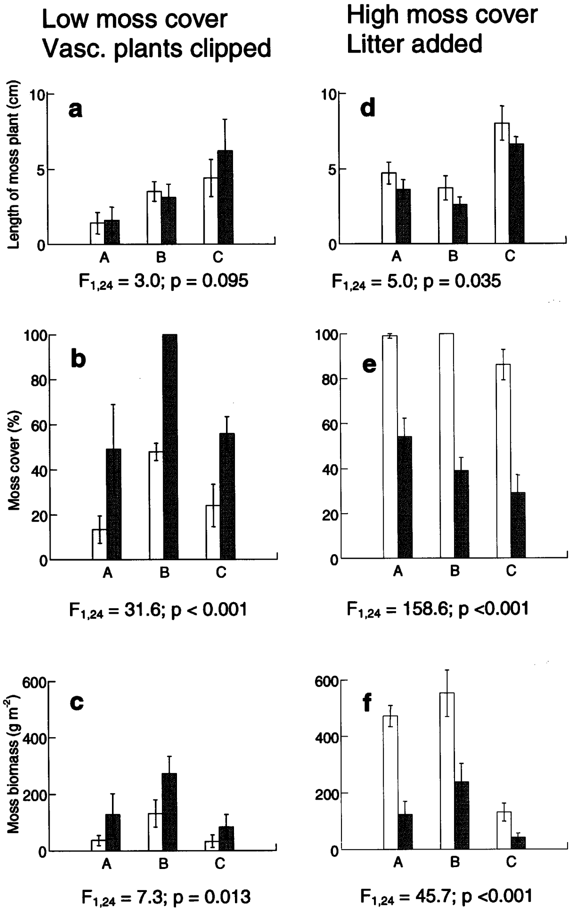

Fig. 3. Response of *Sphagnum* in plots with low moss cover to clipping of the aboveground vascular plant biomass (a–c) and in plots with high moss cover to addition of litter (d–f) in length of the moss plants (a and d), percentage cover (b and e), and biomass (c and f) at the topogenous sites (A, B, and C). Values are mean ± SE. Open and filled bars for control and treated plots, respectively. F- and p-values refer to the effect of treatment in the analysis of variance. A significant interaction treatment × site only for moss biomass in the plots with litter added ($F_{2,24} = 4.8$; $p = 0.017$).

biomass since a moss biomass of 500–800 g m^{-2} can be inferred at both types of sites (Albinsson 1996, part II, Fig. 9). During the study period, the moss cover in the control plots increased on average by 24 percentage units, more in plots with low than with high moss cover. This increase in moss cover could represent a recovery of the moss layer from disturbances caused by an extreme summer drought in 1992, which affected other experimental sites in the region as well (Aerts et al. 2000).

Clipping *Sphagnum* resulted in shorter *Narthecium* shoots whereas shoot density and cover increased (Fig. 5). Proportionally, the increase in density and cover was greatest in the plots with a high moss cover at the *Sphagnum affine* sites. At these sites also an increase in the standing crop of *Narthecium* by 70% might be inferred from eq. (1) compared to only about 20% at the *S. papillosum* sites.

Growth in length of the moss plants was positively correlated with the length of the *Narthecium* shoots (Fig. 6). However, clipping the vascular plants had no significant effect on the *Sphagnum* cover, either on the plots with low moss cover ($F_{1,30} = 0.012$, $p = 0.913$) or on those with high cover ($F_{1,34} = 0.006$, $p = 0.937$). Nor did the increment in height of *Sphagnum* plants differ between treated and untreated plots ($F_{1,68} = 0.410$, $p = 0.524$), or between the untreated plots with high and low moss cover ($F_{1,32} = 0.5$, $p = 0.482$).

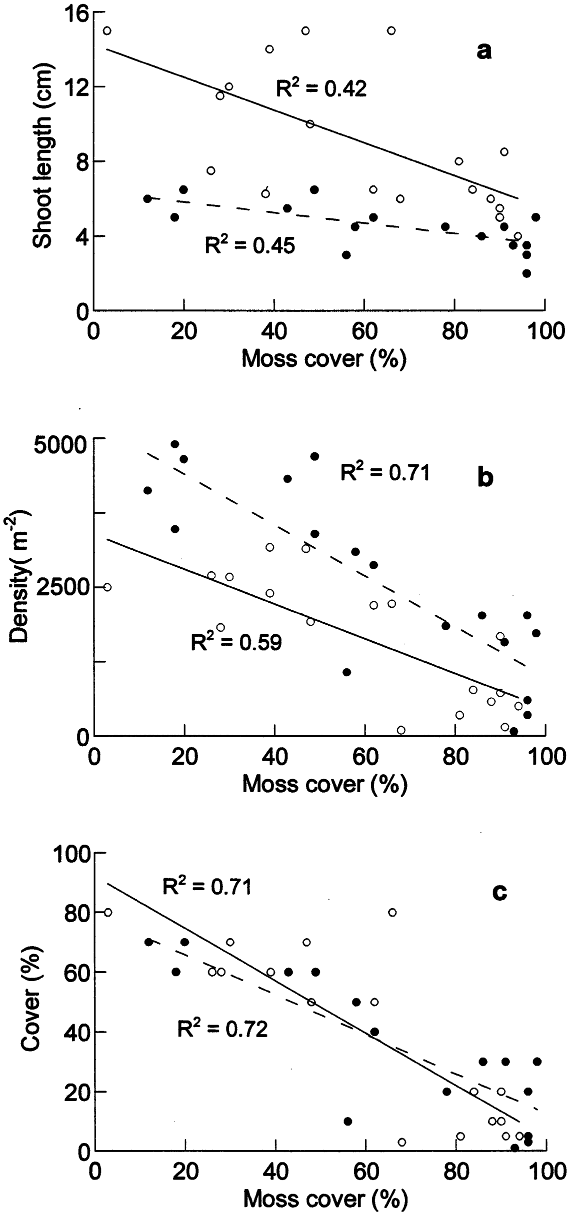

Fig. 4. Shoot length (a), shoot density (b), and percentage cover (c) of *Narthecium* in relation to *Sphagnum* cover at the soligenous mires. Data from the untreated plots in September 1993. Open symbols and full drawn regression line represent sites with *Sphagnum affine*, filled symbols and hatched line sites with *S. papillosum*. R^2 ($p < 0.005$) for the regressions indicated.

The fertilization experiment

No significant differences were found between watering the plots above the moss surface and below, in the growth of either *Narthecium* or *Sphagnum magellanicum*, or in the concentrations or the total N and P in the plant biomass (data not shown, but cf. Fig. 7–10).

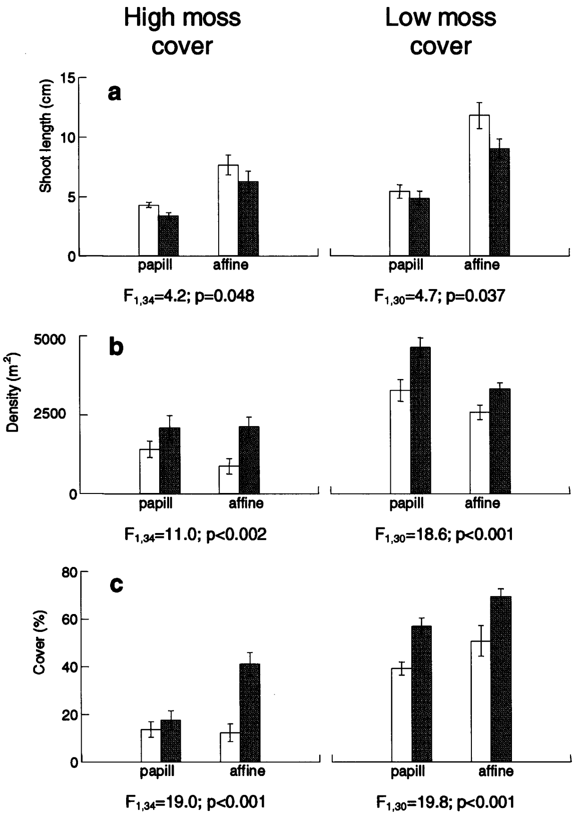

Fig. 5. Response of *Narthecium* shoots in plots with high and low moss cover (left and right panel, respectively) to clipping of the *Sphagnum* biomass in length (a), density (b), and percentage cover (c) at the soligenous mires. Values are mean ± SE and given separately for the *Sphagnum affine* (affine) and *S. papillosum* (papill) sites. Open and filled bars for unclipped and clipped plots, respectively. F- and p-values refer to the effect of treatment in the analysis of variance. A significant effect of treatment × site only for cover in the plots with high moss cover $F_{1,34} = 11.2$; $p = 0.002$).

For *Narthecium*, the addition of N and P on the moss surface resulted in longer shoots (Fig. 7a) but lower shoot density (Fig. 7b; $F_{1,13} = 5.31$, $p = 0.038$) as an effect of the increased growth of the mosses (Fig. 8). In the plots fertilized below the moss surface the shoot density increased from 1994 to 1995 with 45% (from 1160 ± 100 to 1690 ± 170 per m^{-2}; $p = 0.030$) but not in the controls (1610 ± 90 and 1590 ± 90, respectively). Otherwise the effects were too weak to be significant (Fig. 7a–c). Maybe, the experiments were of to short duration to give strong effects on the performance of *Narthecium*.

For the *Sphagnum* mosses addition of N and P on the surface resulted in the plants becoming twice as long as in the control plots, whereas the increases in biomass did not reach significance (Fig. 8). Adding N and P below the moss surface had no effects on the growth of the mosses.

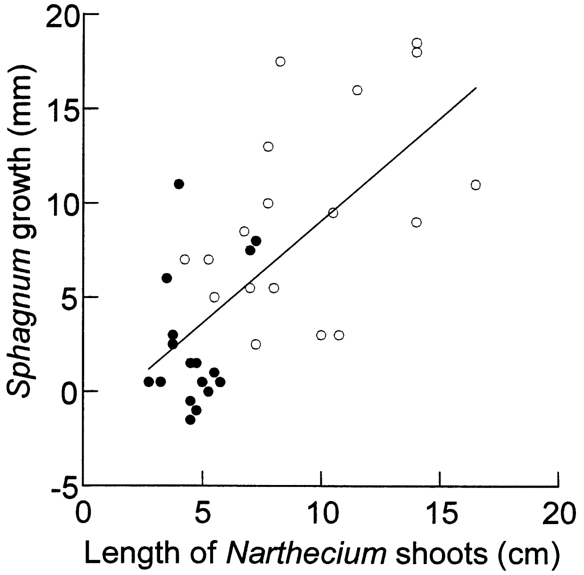

Fig. 6. Increase in length (mm) of *Sphagnum affine* (open symbols) and *S. papillosum* (filled symbols) during the summer period in relation to the length (cm) of the *Narthecium* shoots in the untreated plots at the soligenous mires. The lengths of the mosses are means of the readings at the end of the two summer periods. $R^2 = 0.44$ ($p < 0.001$) for the indicated regression.

With addition below the surface fertilization significantly increased the concentration and total amount of P accumulated in the aboveground *Narthecium* shoots (Fig. 9b; $F_{1,12} = 23.3$; $p < 0.001$ and Fig. 9d; $F_{1,12} = 7.4$; $p = 0.018$, respectively) whereas neither concentration nor content of N was affected (Fig. 9a and c). However, in *Narthecium* the aboveground shoots make up only 12.5% of the total biomass (Malmer, unpubl.). Since the concentrations of N and P in the belowground biomass are roughly half of that in the leaves (6.3 and 0.19 mg g^{-1}, respectively; cf. Table 2), the share of N and P in the aboveground shoots is only about 25% of the total biomass content. The increase in the content of P in the *Narthecium* shoots (Fig. 9d) corresponded to about 35% of what had been added and the rest of the added P may well have been accumulated in the belowground parts.

In *Sphagnum* only a supply onto the surface affected the concentrations (Fig. 10). The increase in P was then highly significant whereas the decrease in N (because of increased growth) only approached significance ($F_{1,13} = 3.6$; $p = 0.080$). The total amount of P accumulated in the moss biomass was four times that in the control plots (Fig. 10d) and corresponded to 92% of the P added with the fertilizer.

In contrast to P hardly any of the added N was recovered in the aboveground biomass despite of the fact that the annually added N corresponded to as much as nearly one third of the total content in both *Narthecium* and *Sphagnum magellanicum*. The high concentration of N in *S. magellanicum* (Fig. 10a) in the untreated plots may perhaps indicate a kind of N saturation in the moss layer and that no more of N could be taken up there (Malmer 1993, Lamers et al. 2000). Most of the added N may thus either have been assimilated by the microorganisms (Damman 1988, Malmer and Wallén 1996, 1999) or leached (Aerts et al. 1992, 2000).

Biomass content of mineral nutrients

At the topogenous sites, both the concentrations (Table 2) and the total content of N and P in the aboveground vascular plant biomass (Fig. 11) were higher at site C than at the other two sites. In *Sphagnum* the concentrations of N and P differed according to the same pattern (Table 2). For N they are high as compared with what has been reported for regions with pristine conditions whereas the concentrations of P more closely agree with those found for such areas previously (Malmer 1988, Malmer et al. 1992). For the total aboveground

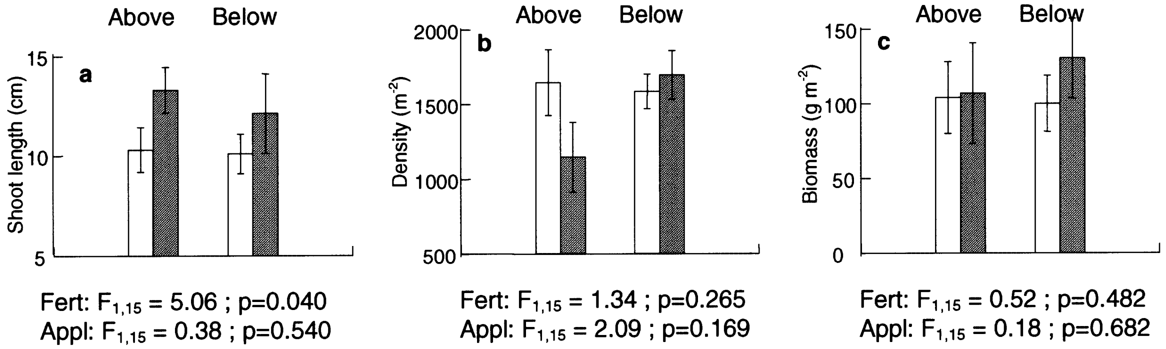

Fig. 7. Response of *Narthecium* shoots to the application of fertilizer above and below the moss surface in length (a), density (b), and standing crop (c). Values are mean ± SE. Open and filled bars for untreated and treated plots, respectively. F- and p-values refer to effect of the treatment in the analysis of variance. The interaction fertilizer × application near significance only for density ($F_{1,15} = 3.24$; $p = 0.092$).

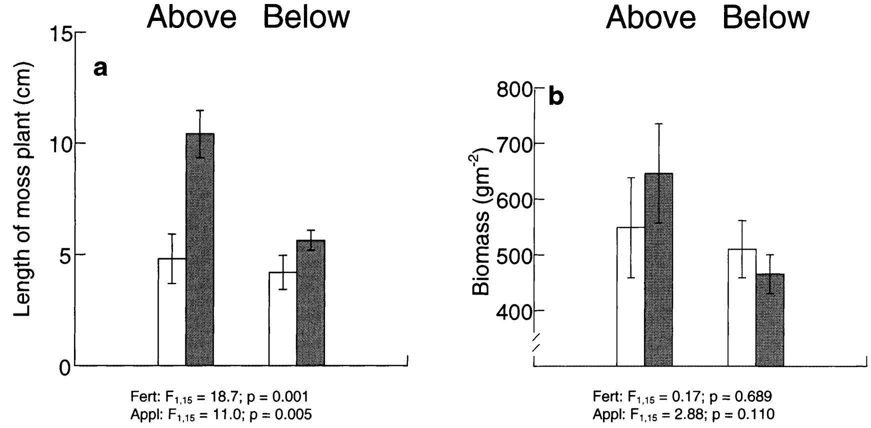

Fig. 8. Response of *Sphagnum* to the application of fertilizer above and below the moss surface in (a) length of moss plants and (b) biomass. Values are mean ± SE. Open and filled bars for untreated and treated plots, respectively. F- and p-values refer to the effect of treatment in the analysis of variance. The interaction fertilizer × application significant only for the length of the moss plants ($F_{1,15} = 6.6$; p = 0.021).

biomass (mosses + vascular plants; Fig. 11) the difference in the total content between sites approaches significance only for phosphorous ($F_{2,20} = 3.47$; p = 0.051). Since the N/P-quotients (Table 2) are well above the range 14–16 (Koerselman and Meuleman 1996) P may also be the growth-limiting element for both *Narthecium* and the *Sphagnum* spp.

At the same site, neither shoot concentrations nor total amounts of N and P in the aboveground plant biomass (mosses + vascular plants) differed much between stands with high and with low moss cover (Table 2, Fig. 11). With a moss biomass > 300 g m^{-2}, the content of N and of P in the moss layer usually exceeded that in the aboveground parts of the vascular plants (except dwarf shrubs). In *Narthecium*, however, the belowground biomass may contain as much as 75% of the total N and P content of the plant (Malmer, unpubl.). Therefore, in the dense *Narthecium* stands the content of N and P per unit area in the biomass as a whole may be inferred to be considerably greater than in the stands with a high moss cover. In addition, in stands with high moss cover the total N and P content of the vascular plants may either be about equal to that of the *Sphagnum* mosses, as at sites A and B, or be greater than this as at site C.

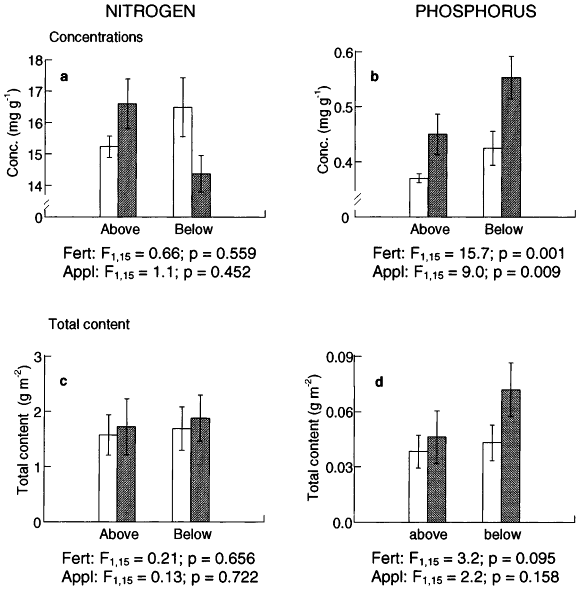

Fig. 9. Response of the *Narthecium* shoots in concentrations (a and b, mg g^{-1}) and total content in the aboveground biomass (c and d, g m^{-2}) of N (left panel) and P (right panel) with the fertilizer added either above or below the moss surface. Values are mean ± SE. Open and filled bars for untreated and treated plots, respectively. F- and p-values refer to the effect of the treatment in the analysis of variance. The interaction fertilizer × application significant only for the concentration of N in *Narthecium* ($F_{1,15} = 7{,}7$; p = 0.014).

Discussion

Supply of mineral nutrients

The performance of *Narthecium* in mire vegetation has been seen as related both to the water level (Daniels 1975) and to the supply of mineral nutrients (Malmer 1962b, Summerfield and Rieley 1975, Spink and Parsons 1995). Through resulting in an increased aeration of the peat, a low water level provides beneficial conditions for mineralization processes. This is particularly favourable for a species such as *Narthecium* lacking aerenchymatic tissue in the belowground parts (Daniels 1975, Miles 1976). Both the fertilization experiment and the N/P-quotients (Table 2) suggest that P is a growth-limiting element for both *Narthecium* and *Sphagnum* in this region (Malmer 1988, Aerts et al. 1992, Koerselman and Meuleman 1996). Moreover, since hardly any of the added N was taken up by the plants that element may even be supplied in excess by the recent atmospheric deposition, particularly on sites with low productivity (Spink and Parsons 1995, Lamers et al. 2000, Gunnarsson and Rydin 2000).

The complete uptake of P in the moss layer if supplied to the surface demonstrates the efficiency in *Sphagnum* as a filter for atmospheric supply of a nutri-

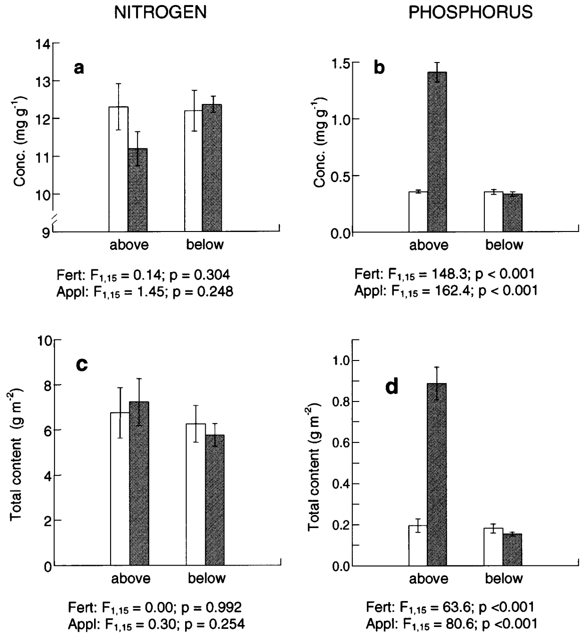

Fig. 10. Reponse of *Sphagnum* in concentrations (a and b, mg g^{-1}) and biomass content (c and d, g m^{-2}) of N (left panel) and P (right panel) with the fertilizer added either above or below the moss surface. Values are mean ± SE. Open and filled bars for untreated and treated plots, respectively. F- and p-values refer to the effect of treatment in the analysis of variance. The interaction fertilizer × application significant both for the concentration and total content of P ($F_{1,15}$ = 160.2; $p < 0.001$ and $F_{1,15}$ = 74.4; $p < 0.001$, respectively).

Table 2. Concentrations of N and P and the N/P-quotient in the aboveground shoots of *Narthecium* and in the *Sphagnum* biomass on the control plots used in the clipping experiments at the topogenous mire. Mean values and (within parentheses) SE presented (n = 5).

Species/site	N mg g^{-1}	P mg g^{-1}	N/P
Narthecium, low moss cover			
Site A	17.8	0.43	41.4
	(0.9)	(0.02)	(0.8)
Site B	17.2	0.45	38.5
	(0.3)	(0.01)	(0.9)
Site C	23.4	0.71	32.8
	(0.3)	(0.04)	(1.6)
Narthecium, high moss cover			
Site A	15.6	0.34	46.5
	(0.3)	(0.01)	(0.9)
Site B	16.6	0.41	40.1
	(0.4)	(0.01)	(1.5)
Site C	22.4	0.71	31.7
	(0.5)	(0.03)	(1.5)
Sphagnum spp., high moss cover			
Site A	11.9	0.38	31.1
	(0.4)	(0.01)	(0.8)
Site B	11.0	0.35	31.5
	(0.5)	(0.01)	(1.3)
Site C	13.7	0.66	20.7
	(1.0)	(0.05)	(0.1)

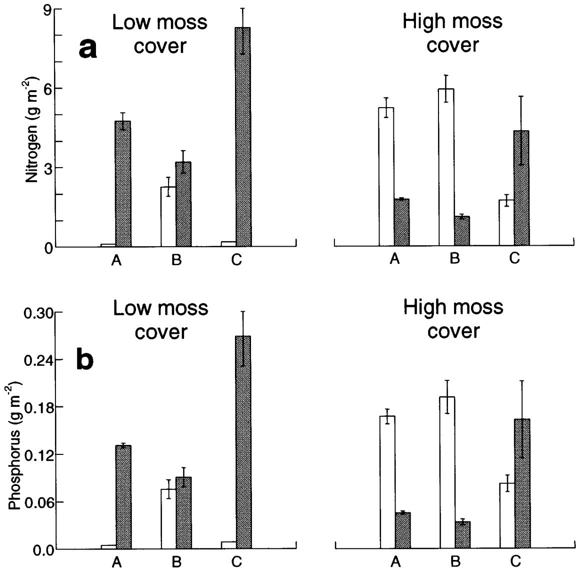

Fig. 11. Total amounts of (a) nitrogen and (b) phosphorus in the aboveground vascular plant biomass (except dwarf shrubs) and the *Sphagnum* biomass (filled and open bars, respectively) in the untreated plots of the biomass interference experiment at the topogenous sites (A, B, and C). Values are mean ± SE. In the left panel plots with low moss cover and a dense stand of *Narthecium*, in the right panel plots with high moss cover and sparse *Narthecium*.

ent provided it is not supplied in excess to the growth of *Sphagnum* (Lee et al. 1986, Aerts et al. 1992, van Breemen 1995). In *Sphagnum fuscum* (Schimp.) Klinggr. (Woodin and Lee 1987, Lee and Woodin 1988) and *Rhacomitrium lanuginosum* (Hedw.) Brid. (Jónsdóttir et al. 1995), such a filter effect has also been shown for N in regions with low atmospheric supply of that element. In the present experiments, however, this filter effect did not function for N because of the high atmospheric deposition (Aerts et al. 1992). The high concentrations of N and the high N/P-quotients in the *Sphagnum* mosses may even indicate the atmospheric supply rate to have negative effects on the growth and performance of the species studied (Gunnarsson and Rydin 2000).

As a consequence of this filter effect, the deep-rooted vascular plants like *Narthecium* growing together with a dense cover of *Sphagnum* have no direct access to the mineral nutrients supplied in low concentrations by atmospheric deposition. For N and P, therefore, these plants have to rely on mineralization of the peat (Malmer 1962b, 1986, Chapin et al. 1978) and on the very low concentrations in the mire water (Malmer 1962a, Malmer and Nihlgård 1980, Clymo 1984, Gignac 1990, Westling 1990). Only vascular plants such as *Drosera rotundifolia* L. and *Vaccinium oxycoccos* L., with their roots close to the moss surface, compete directly with the mosses for mineral nutrients (Moizuk and Livingston 1966, Svensson 1995). Thus, the low mineralization rate and the decrease in resources through the withdrawal of N and P from the rhizosphere during peat formation affect only the deep-rooted vascular plants. Since the peat accumulation rate is greater at topogenous than at soligenous sites the removal of mineral nutrients from the rhizosphere may also be greater there.

The mineral nutrients included in the plant cover are not uniformly distributed over the mire surface. Patches with a dense stand of *Narthecium* form "islands" in which the biomass (shoots and roots) contains greater mineral nutrient resources than the surrounding patches with a high cover of *Sphagnum* and only few shoots of vascular plants. In *Sphagnum* the response to the fertilization was an immediate increase in growth whereas in *Narthecium* the responses obtained were weaker (Fig. 7 and 8; Spink and Parsons 1995 and Albinsson 1996), probably at least partly because of the short duration of the experiments. This points to the high efficiency of *Sphagnum* in the use of dissolved nutrients (Clymo 1970, Malmer 1993), considerably increasing its competitive power relative to deep-rooted vascular plants when the availability of N and P is low. This asymmetric competition for and more efficient use of mineral nutrients is presumably a major reason for the competitive strength of *Sphagnum* mosses in relation to *Narthecium* demonstrated in the experiments here. The success of the *Sphagnum* mosses depends partly on their access to the airborne supply immediately replacing what is lost in the litter, partly on their formation of litter resistant to decay and restricting the release of mineral nutrients to vascular plants. The deposition of peat, with its content of N and P, also continuously remove these elements from the acrotelm, thus creating and maintaining a low level of availability of mineral nutrients in the rhizosphere. This removal should in principle be equal to the supply rates in order to maintain the vegetation and its productivity in a steady state.

Structure of the plant community

The negative correlation between the abundance of *Narthecium* shoots and *Sphagnum* mosses (Fig. 1, 4 and 6) may result from direct interactions through shading in the symmetric competition for light (Clymo and Hayward 1982, Hayward and Clymo 1983, Rydin 1997, Ohlson et al. 2001). In the aboveground standing crop of *Narthecium*, however, both on the topogenous and soligenous mires a difference between sites differing in fertility was noted only for plots with low moss cover, i.e. in stands in which *Sphagnum* mosses had only weak impact on the growth. This suggests that vascular plants such as *Narthecium* have a capacity to grow ahead of *Sphagnum* mosses only with a considerable amount of mineral nutrients accumulated in their biomass. Heijmans et al. (2002) also suggest that a vascular plant cover of at least 60% is needed for a reduction of *Sphagnum* growth because of shading.

An increase in shoot density was the most obvious effect that the clipping of *Sphagnum* had on *Narthecium* (Fig. 2 and 5). *Sphagnum* mosses have also been shown to have capacity to reduce the growth of other vascular plants such as *Betula nana* (Hobbie et al. 1999) and *Eriophorum angustifolium* (Heijmans et al. 2002). Experiments in Icelandic heathlands involving the removal of dense cover of *Rhacomitrium lanuginosum* have likewise shown that this species hampers the growth of *Carex bigelowii* Torr. ex. Schwein., particularly through reduction of the aboveground shoot density (I. Jónsdóttir, pers. com.). The increase in performance of *Narthecium* when *Sphagnum* was clipped was more evident at the soligenous than at the topogenous sites. In contrast, *Sphagnum* responded only to the removal of the standing crop and the litter of vascular plants at the topogenous sites. The soligenous mires have a more constant and abundant flow of water than the topogenous ones, which increases the decay and mineralization rates there. A possible explanation for the difference between the mire types may thus be that the growth of *Narthecium* was nutrient-limited to a greater extent at the topogenous sites than at the soligenous ones. At the latter sites it was instead more strongly limited by competition for light from the *Sphagnum* mosses, contrary to our expectations on the basis of the vegetation. The greater increase in *Narthecium* biomass at the *Sphagnum affine* than at the *S. papillosum* sites, which the clipping of *Sphagnum* resulted in, points in that direction too.

The lengths of the *Sphagnum* plants and the *Narthecium* shoots were positively correlated with each other at both the soligenous and topogenous sites whereas clipping of *Sphagnum* resulted in shorter *Narthecium* shoots. In the fertilization experiment, the fewer but longer *Narthecium* shoots that resulted from the increase in *Sphagnum* growth indicate the intensity of the interspecific competition increasing with an increase in the availability of mineral nutrients, just as the intraspecific competition within the *Sphagnum* population did. Similarly, the intensity of competition may be greater at the soligenous than at the topogenous sites. At the soligenous sites the intensity of the competition for light increases with productivity (Fig. 6) and should thus be greater at the *Sphagnum affine* than at the *S. papillosum* sites. At the topogenous sites, we might also expect the intensity of the competition to be greater at site C, than at the other two sites.

Recently Jonasson and Shaver (1999) proposed that in wetlands "characteristics of the plants (nutrient resorption, tissue type and longevity) mirror the functioning of the system rather than play a major role in regulating overall element cycling". In principle, the reverse proportions of *Narthecium* and *Sphagnum* in the photosynthesising biomass (Fig. 1 and 4) can be established in two ways, either by the growth of *Narthecium* shading *Sphagnum* and increasing the litter fall or by the growth of *Sphagnum* hampering the development of aboveground *Narthecium* shoots. However, in the long term a high proportion of *Sphagnum* litter in the system contributes strongly to decrease the availability of N and P but the decrease will affect only the vascular plants. Therefore, the result of this asymmetric competition for mineral nutrients between *Sphagnum* and vascular plants often involves a competitive exclusion of several vascular plant species. In this way the *Sphagnum* mosses act as ecological engineers (Jones et al. 1994, Svensson 1995, Ohlson et al. 2001) for the peat forming system. When there are only few or no vascular plants present, however, the moss plants are exposed to full daylight and longer periods of reduced moisture, conditions that reduce their growth (Murray et al. 1989). On the other hand, scaffolding by vascular plants is needed to develop lawns and hummocks with *Sphagnum* mosses (Malmer et al. 1994). Thus a moderate growth of the vascular plants promotes the growth of the *Sphagnum* mosses.

Peat accumulation rate

Expanding *Sphagnum* mosses structuring the plant community and depleting the rhizosphere of mineral nutrients, tend to increase the peat accumulation rate. This may be the biological part of the process leading to the development of ombrotrophic bogs with hydrological regimes that are independent of the surroundings (Svensson 1988, Malmer et al. 1997). On the other hand, if vascular plants, in obtaining a sufficient supply of mineral nutrients through mineralization, are able to maintain a level of productivity sufficient to limit the growth of *Sphagnum*, they may be able to prevent the increase in the peat accumulation rate that such a development requires. The dense stands of vascular plants on soligenous fens (cf. the densities of *Narthecium* shoots in Fig. 1 and 4) may contribute in that way to the maintenance of a low peat accumulation rate and thus prevent development of an ombrotrophic bog. In this manner, the interactions between the vascular plants and *Sphagnum* mosses exert a strong influence on the carbon accumulation rate in peatlands.

During the growth of the *Sphagnum* plants N and P are relocated from the senescing, lower part of the plant to the capitulum (Malmer 1988, Rydin and Clymo 1989, Aldous 2000). Therefore, under pristine conditions the N and P lost from the moss layer together with the litter may be expected to balance the input by atmospheric deposition. However, the productivity of the *Sphagnum* mosses is determined also by the moisture and temperature conditions (Malmer and Wallén 1993). Moreover, because of the internal shading that occurs between the moss plants (Clymo and Hayward 1982), the biomass of the moss layer has an upper limit. The capacity of a moss layer of *Sphagnum* to accumulate N and P is therefore restricted (Lamers et al. 2000, Berendse et al. 2001) and differs between climatic regions. If the supply exceeds the accumulation capacity, N and P are leached and become available for the vascular plants (Aerts et al. 1992, 2000). Such a leaching can be assumed to result sooner or later in an increased growth of the vascular plants, which in turn reduces the growth of the *Sphagnum* mosses. Still more important may perhaps be that N, if supplied in excess, would reduce the productivity of *Sphagnum* (Gunnarsson and Rydin 2000) and its competitiveness in relation to the vascular plants. Over a period of time, it would be possible then for *Narthecium* (and certainly also other vascular plants) to accumulate nutrients and increase the aboveground biomass over large areas to a size as great as that found in the dense stands of the species. Such processes brought about by an increased deposition of anthropogenic N, for example, could be one reason for the decrease in the abundance of *Sphagnum* mosses and the expansion of vascular plants noted in many ombrotrophic bogs in recent decades (Aaby 1994, Malmer 1998, Risager 1998, Gunnarsson et al. 2002). The increase in supply of N results then in a less decay resistant litter and greater decay losses in the acrotelm. In that way, the N-pollution also tends to reduce the peat accumulation rate and the capacity for carbon accumulation in mires (Malmer and Wallén 1999, 2003, Berendse et al. 2001).

Acknowledgements – C. Albinsson carried out the experiments on the soligenous mires with the assistance of D. and M. Albinsson, N. Malmer and B. Wallén those on the topogenous mire. M. Varga assisted with the experiments on the topogenous mire and made all the chemical analyses. The work was supported by grants from the Swedish Natural Science Research Council to N. Malmer.

References

Aaby, B. 1994. Monitoring Danish raised bogs. – In: Grünig, A. (ed.), Mires and man. Mire conservation in a densely populated country – the Swiss experience. Kosmos, pp. 284–300.

Aerts, R., Wallén, B. and Malmer, N. 1992. Growth-limiting nutrients in *Sphagnum*-dominanted bogs subject to low and high atmospheric nitrogen supply. – J. Ecol. 80: 131–140.

Aerts, R., Wallén, B., Malmer, N. and de Caluwe, H. 2000. Nutritional constraints on *Sphagnum*-growth and potential decay in northern peatlands. – J. Ecol. 89: 292–299.

Albinsson, C. 1996. Vegetation structure and interactions on mires. – PhD-thesis, Lund Univ.

Aldous, A. R. 2000. Nitrogen translocation in *Sphagnum* mosses: response to atmospheric nitrogen deposition. – In: Crowe, A. and Rochefort, L. (eds), Québec 2000: Millenium Wetland Event, Program with Abstracts.

Backéus, I. 1985. Aboveground production and growth dynamics of vascular bog plants in central Sweden. – Acta Phytogeogr. Suec. 74: 98.

Banner, A., Hebda, R. J., Oswald, E. T. et al. 1988. Wetlands of Pacific Canada. – In: Wetlands of Canada, Wetlands

Working Group, Canada Committee on Ecological Land Classification. Polyscience Publication Inc., pp. 307–346.

Bayley, S. E., Vitt, D. H., Newbury, R. W. et al. 1987. Experimental acidification of a *Sphagnum*-dominated peatland: first year results. – Can. J. Fish. Aquat. Sc. 44 (Suppl. 1): 194–205.

Berendse, F., van Breemen, N., Rydin, H. et al. 2001. Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. – Global Change Biol. 7: 591–598.

van Breemen, N. 1995. How *Sphagnum* bogs down other plants. – Trends Ecol. Evol. 10: 270–275.

Bridgham, S. D., Pastor, J., Janssens, J. A. et al. 1996. Multiple limiting gradients in peatlands: a call for a new paradigm. – Wetlands 16: 45–65.

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

Clymo, R. S. 1970. The growth of *Sphagnum*: methods of measurements. – J. Ecol. 58: 13–49.

Clymo, R. S. 1984. *Sphagnum*-dominated peat bogs: a naturally acid ecosystem. – Philos. Trans. R. Soc. Lond. B 305: 487–499.

Clymo, R. S. and Hayward, P. M. 1982. The ecology of *Sphagnum*. – In: Smith, A. J. E. (ed.), Bryophyte ecology. Chapman and Hall, pp. 229–289.

Coulson, J. C. and Butterfield, J. 1978. An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. – J. Ecol. 66: 631–650.

Damman, A. W. H. 1988. Regulation of nitrogen removal and retention in *Sphagnum* bogs and other peatlands. – Oikos 51: 291–305.

Damman, A. W. H. and Johnson, L. C. 2000. Individualistic plant species' response to N and P fertilization of an ombrotrophic fertilized bog. – In: Crowe, A. and Rochefort, L. (eds), Québec 2000: Millennium wetland event, Program with Abstracts, p. 150.

Daniels, R. E. 1975. Observations on the performance of *Narthecium ossifragum* (L.) Huds. and *Phragmites communis* Trin. – J. Ecol. 63: 965–977.

Eriksson, B. 1983. Data concerning the precipitation climate of Sweden. Mean values for the period 1951–80. – Swed. Meteorol. Hydrol. Inst. – Report 1983: 28.

Fransson, S. 1972. Myrvegetation i sydvästra Värmland. – Acta Phytogeogr. Suec. 57 (in Swedish with summary in English.)

Flatberg, K. I. 1984. A taxomonic revision of the *Sphagnum imbricatum* complex. – Det Kongelige Norske Videnskabers Selskab Skrifter 3: 1–80.

Gignac, L. D. 1990. Mineral content of mire surface water and hummock-forming *Sphagnum* species in peatlands in western Canada. – Lindbergia 15: 151–160.

Gunnarsson, U. and Rydin, H. 2000. Nitrogen fertilization reduces *Sphagnum* production in bog communities. – New Phytol. 147: 527–537.

Gunnarsson, U., Malmer, N. and Rydin, H. 2002. Dynamics or constancy in *Sphagnum* dominated mire ecosystems: – a 40-year study. – Ecography 25: 685–704.

Havas, P. 1961. Vegetation und Ökologie der ostfinnischen Hangmoore. – Ann. Bot. Soc. Zool. Bot. Fenn. 'Vanamo' 31: 2.

Hayward, P. M. and Clymo, R. S. 1983. The growth of *Sphagnum*: experiments on, and simulations of some effects of light flux and water table depth. – J. Ecol. 71: 845–863.

Heijmans, M. M. P. D., Klees, H. and Berendse, F. 2002. Competition between *Sphagnum magellanicum* and *Eriophorum angustifolium* as affected by raised CO_2 and increased N deposition. – Oikos 97: 415–425.

Hobbie, S. E., Shevtsova, A. and Chapin, F. S. III. 1999. Plant responses to species removal and experimental warming in Alaskan tussock tundra. – Oikos 84: 417–434.

Johnson, L. C. and Damman, A. W. H. 1993. Decay and its regulation in *Sphagnum* peatlands. – Adv. Bryol. 5: 249–296.

Jonasson, S. and Shaver, G. R. 1999. Within-stand nutrient cycling in Arctic and Boreal wetlands. – Ecology 80: 2139–2150.

Jones, C. G., Lawton, J. H. and Shachak, M. 1994. Organisms as ecosystem engineers. – Oikos 69: 373–386.

Jónsdóttir, I. S., Callaghan, T. C. and Lee, J. A. 1995. Fate of added nitrogen in a moss-sedge Arctic community and effects of increased nitrogen deposition. – Sci. Total Environ. 160/161: 677–685.

Koerselman, W. and Meuleman, A. F. M. 1996. The vgetation N:P ratio: a new tool to detect the nature of nutrient limitation. – J. Appl. Ecol. 33: 1441–1450.

Lamers, L. P. M., Bobbink, R. and Roelofs, J. G. M. 2000. Natural nitrogen filter fails in polluted raised bogs. – Global Change Biol. 6: 583–586.

Lee, J. A. and Woodin, S. J. 1988. Vegetation structure and the interception of acidic deposition by ombrotrophic mires. – In: Verhoeven, J. T. A., Heil, G. W. and Werger, M. J. A. (eds), Vegetation structure in relation to carbon and nutrient economy. SPB Academic Publisher, pp. 137–147.

Lee, J. A., Press, M. C., Woodin, S.J. and Fergusson, N. P. 1986. Resposes to acidic deposition in ombrotrophic mires. – In: Hutchinson, T. C. and Meema, K. (eds), Effects of acidic deposition and air pollutants on forests, wetlands and agricultural ecosystems. Springer, pp. 549–560.

Malmer, N. 1962a. Studies on mire vegetation in the archaean area of southwestern Götaland (South Sweden). I. Vegetation and habitat conditions on the Åkhult mire. – Op. Bot. 7: 1.

Malmer, N. 1962b. Studies on mire vegetation in the archaean area of Southwestern Götaland (South Sweden). II. Distribution and seasonal variation in elementary constituents on some mire sites. – Op. Bot. 7: 2.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. – Can. J. Bot. 64: 375–383.

Malmer, N. 1988. Patterns in the growth and the accumulation of inorganic constituents in the *Sphagnum*-cover on ombrotrophic bogs in Scandinavia. – Oikos 53: 105–120.

Malmer, N. 1993. Mineral nutrients in vegetation and surface layers of *Sphagnum*-dominated peat-forming systems. – Adv. Bryol. 5: 223–248.

Malmer, N. 1998. Våt- och torvmarkers känslighet för klimatförändringar. – Kungliga Skogs- och Lantbruksakademiens Tidskrift 137: 87–107. (in Swedish.)

Malmer, N. and Nihlgård, B. 1980. Supply and transport of mineral nutrients in a subarctic mire. – In: M. Sonesson (ed.), Ecology of a subarctic mire, Ecol. Bull. 30: 63–95.

Malmer, N. and Wallén, B. 1993. Accumulation and release of organic matter in ombrotrophic bog hummocks – processes and regional variation. – Ecography 16: 193–211.

Malmer, N. and Wallén, B. 1996. Peat formation and mass balance in sub-arctic ombrotrophic peatlands around Abisko, northern Scandinavia. – In: P. S. Karlsson and T. V. Callaghan (eds), Plant ecology in the subarctic Swedish Lapland. – Ecol. Bull. 45: 79–92.

Malmer, N. and Wallén, B. 1999. The dynamics of peat accumulation on bogs: mass balance of hummocks and hollows and its variation throughout a millenium. – Ecography 22: 736–750.

Malmer, N. and Wallén, B. 2003. Input rates, decay losses and accumulation rates of carbon in bogs during the last millennium: internal processes and environmental changes. – The Holocene (in press).

Malmer, N., Vitt, D. H. and Horton, D. G. 1992. Elemental concentrations in mosses and surface waters of western Canadian mires relative to precipitation chemistry and hydrology. – Ecography 15: 114–128.

Malmer, N., Svensson, B. M. and Wallén, B. 1994. Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. – Folia Geobot. Phytotax. 29: 483–496.

Malmer, N., Svensson, G. and Wallén, B. 1997. Mass balance and nitrogen accumulation in hummocks on a south Swedish bog during late Holocene. – Ecography 20: 535–549.

McVean, D. N. and Ratcliffe, D. A. 1962. Plant communities of the Scottish Highlands. – Monographs of the Nature Conservancy 1. Her Majesty's Stationery Office, London.

Miles, J. 1976. The growth of *Narthecium ossifragum* in some southern English mires. – J. Ecol. 64: 849–858.

Moizuk, G. A. and Livingston, R. B. 1966. Ecology of read maple (*Acer rubrum* L.) in a Massachusetts upland bog. – Ecology 66: 942–950.

Murray, K. J., Tenhunen, J. D. and Kummerow, J. 1989. Limitations on *Sphagnum* growth and net primary production in the foothills of the Philip Smith mountains, Alaska. – Oecologia 80: 256–262.

Ohlson, M., Ökland, R. H., Nordbakken, J. F. and Dahlberg, B. 2001. *Sphagnum* and *Pinus* – interacting engineers in bog ecosystems. – Oikos 94: 425–432.

Redbo-Torstensson, P. 1994. The demographic consequences of nitrogen fertilization of a population of sundew, *Drosera rotundifolia*. – Acta Bot. Neerlandica 43: 175–188.

Risager, M. 1998. Impacts of nitrogen on *Sphagnum* dominated bogs with emphasis on crtical load assessment. – PhD-thesis, Univ. of Copenhagen.

Rydin, H. 1997. Competition among Bryophytes. – Adv. Bryol. 6: 135–168.

Rydin, H. and Clymo, R. S. 1989. Transport of carbon and phosphorus compounds about *Sphagnum*. – Proc. R. Soc. Lond., B 237: 63–84.

Rydin, H., Sjörs, H. and Löfroth, M. 1999. Mires. – Acta Phytogeogr. Suec. 84: 91–112.

Scheffer, R. A., van Logtestijn, R. S. P. and Verhoeven, J. T. A. 2001. Decomposition of *Carex* and *Sphagnum* litter in two mesotrophic fens differeing in dominant plant species. – Oikos 92: 44–54.

Sjörs, H. 1946. Myrvegetationen i övre Långanområdet i Jämtland. – Arkiv för Botanik 33A: 1–96. (in Swedish.)

Sjörs, H. 1948. Myrvegetation i Bergslagen. – Acta Phytogeogr. Suec. 21: 1–299. (in Swedish with summary in English.)

Spink, A. J. and Parsons, A. N. 1995. An experimental investigation on the effects of nitrogen deposition to *Narthecium ossifragum*. – Environ. Poll. 90: 191–198.

Summerfield, R. J. 1974. Biological Fora of the British Isles: *Narthecium ossifragum* (L.) Huds. – J. Ecol. 62: 325–339.

Summerfield, R. J. and Rieley, J. O. 1975. Relationships between mineral supply and growth of *Narthecium ossifragum* (L.) Huds. on mire ecosystems. – J. Ecol. 63: 643–656.

Svensson, B. M. 1995. Competition between *Sphagnum fuscum* and *Drosera rotundifolia*: a case of ecosystem engineering? – Oikos 74: 205–212.

Svensson, G. 1988. Bog development and environmental conditions as shown by the stratigraphy of Store Mosse mire in southern Sweden. – Boreas 17: 89–111.

Tamm, C. O. 1955. Some observations on the nutrient turnover in a bog community dominated by *Eriophorum vaginatum* L. – Oikos 5: 189–194.

Westling, O. 1990. Strong and organic acid in the run-off from peat and woodland. – In: Mason, B. J. (ed.), The surface waters acidification program. Univ. Press, pp. 137–148.

Woodin, S. J. and Lee, J. A. 1987. The fate of some components of acidic deposition on ombrotrophic mires. – Environ. Poll. 45: 61–72.

Zar, J. H. 1984. Biostatistical analysis. – Prentice Hall.