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Swift recovery of *Sphagnum* nutrient concentrations after excess supply

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Abstract Although numerous studies have addressed the effects of increased N deposition on nutrient-poor environments such as raised bogs, few studies have dealt with to what extent, and on what time-scale, reductions in atmospheric N supply would lead to recovery of the ecosystems in question. Since a considerable part of the negative effects of elevated N deposition on raised bogs can be related to an imbalance in tissue nutrient concentrations of the dominant peat-former *Sphagnum*, changes in *Sphagnum* nutrient concentration after excess N supply may be used as an early indicator of ecosystem response. This study focuses on the N and P concentrations of *Sphagnum magellanicum* and *Sphagnum fallax* before, during and after a factorial fertilization experiment with N and P in two small peatlands subject to a background bulk deposition of 2 g N m^{-2} $year^{-1}$. Three years of adding N (4.0 g N m^{-2} $year^{-1}$) increased the N concentration, and adding P (0.3 g P m^{-2} $year^{-1}$) increased the P concentration in *Sphagnum* relative to the control treatment at both sites. Fifteen months after the nutrient additions had ceased, N concentrations were similar to the control whereas P concentrations, although strongly reduced, were still slightly elevated. The changes in the N and P concentrations were accompanied by changes in the distribution of nutrients over the capitulum and the stem and were congruent with changes in translocation. Adding N reduced the stem P concentration, whereas adding P reduced the stem N concentration in favor of the capitulum. *Sphagnum* nutrient concentrations quickly respond to reductions in excess nutrient supply, indicating that a management policy aimed at reducing atmospheric nutrient input to bogs can yield results within a few years.

Keywords Ecosystem recovery · Nitrogen deposition · Nutrient allocation · Phosphorus · Translocation

Introduction

Although numerous studies have addressed the effects of high N deposition on natural ecosystems (Matson et al. 2002), few studies deal with ecosystem recovery after a reduction in N stress and are mainly concerned with forest ecosystems (Strengbom et al. 2001; Melnychuk and Krebs 2005) or aquatic ecosystems (Brouwer et al. 1996). As a result it often remains unclear to what extent, and on what time-scale, a reduction in N deposition may result in ecosystem recovery.

Raised bogs are convenient ecosystems to study the effect of changes in atmospheric nutrient input because the vegetation, its bryophyte component in particular, depends on atmospheric deposition for its main nutrient supply. The bryophyte layer, which mainly consists of mosses from the genus *Sphagnum*, fulfils a key role in the functioning of the ecosystem; the mosses form the substrate in which the vascular plants root. As a result, all atmospheric N deposition that is not intercepted by the leaves of the vascular plants must first pass through the moss layer before becoming available for uptake by their roots (Malmer et al. 2003). As long as this nutrient filter works efficiently (Lamers et al. 2000), vascular plant cover is kept sparse and the ecosystem does not change much when N

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deposition increases. However, once vascular plants gain access to the atmospheric N and/or are less hampered in their growth by *Sphagnum* as a result of the N-induced decrease in *Sphagnum* competitiveness, they may expand and outcompete *Sphagnum* (Berendse et al. 2001; Bubier et al. 2007).

On the whole, expansion of vascular plants mainly depends on the absolute N deposition rate in combination with nutrient retention in the *Sphagnum* layer. The latter is mainly determined by the balance between moss growth and decomposition. In turn, *Sphagnum* growth depends, among other things, on the N concentration in the active growing part (capitulum); when concentrations become too high, growth is inhibited (Wiedermann et al. 2007) and the mosses may become vulnerable to parasites and epiphytes (Limpens et al. 2003a). As such, the speed at which *Sphagnum* nutrient concentrations decrease after the source of enrichment is removed can be interpreted as a sign of ecosystem recovery. It was shown earlier for *Sphagnum magellanicum* cores that the return to low tissue nutrient concentrations may occur quite fast (Limpens et al. 2003b); the nutrient concentrations in both pore water and *Sphagnum* decreased within 2 years after the source of enrichment was blocked by placing the cores under a roof. To what extent this recovery also occurs in situ at sites where the background N deposition is high, is unknown and is one of the aims of this study.

The mechanism responsible for the decrease in nutrient concentration is as yet unclear. In some vascular plants, a response to changes in the supply of a nutrient is a change in translocation or resorption efficiency; when the nutrient is limiting, translocation efficiency peaks and when there is an excess of the nutrient, translocation efficiency drops (van Heerwaarden et al. 2003; Rejmankova 2005). It seems that something similar may take place in *Sphagnum*; the moss is able to relocate nutrients from older tissues towards the capitulum (Rydin and Clymo 1989; Aldous 2002). Furthermore, the distribution of nutrients between stem and capitulum is affected by N deposition (Bragazza et al. 2004); the authors showed that the relative difference between N concentrations of capitulum and stem decreased with deposition, suggesting a negative relationship between N supply and N translocation.

The aims of this study were to assess the speed with which the nutrient concentration of living *Sphagnum* tissue would recover from deposition under field conditions and to explore whether this recovery would coincide with a change in the distribution of nutrients over the stem and the capitulum. We expected that: (1) the concentrations of N and P in the capitulum would decrease within 1 year after fertilization, (2) this decrease would be accompanied by a change in the distribution of N and P between the capitulum and the stem. To elucidate the above we sampled *Sphagnum* in experimental plots of a fertilization experiment with N and P at two sites before fertilization treatments started, at the end of 3 years of fertilization and 15 months after the fertilization treatments had ceased.

Materials and methods

Experimental set-up

Between 1998 and 2001 a fertilization experiment was conducted at two Dutch sites, Reigersplas and Rundeven, that were chosen because of their contrasting vegetation and nutrient limitation. The Reigersplas (52°50′N, 6°27′E) is a nutrient-poor fen with a *Sphagnum* layer limited by P and dominated by *Sphagnum magellanicum* (Brid.) and *Sphagnum papillosum* (Lindb.) with some *Sphagnum fallax* (Klinggr.), whereas the Rundeven (52°51′N, 6°23′E) is an eutrophic fen and is limited by N and P and dominated by *S. fallax*. For more extensive site descriptions see Limpens et al. (2004).

Plots measured 1 m × 1 m and were arranged in a randomized block design with five replicates per site. The fertilization treatments comprised a control treatment (C) receiving demineralised water only, an N treatment (N), a P treatment (P) and a treatment that received N as well as P (NP). Nutrients were dissolved in 2 l demineralised water and were applied with a watering can 6 times during the summer half year. N (4 g N m^{-2} $year^{-1}$) was applied as NH_4NO_3 at a concentration of 0.33 g N l^{-1} and P (0.3 g P m^{-2} $year^{-1}$) as $NaH_3PO_4.H_2O$ at a concentration of 0.025 g P l^{-1}.

The years from which we present data did not markedly differ from each other in regard to temperature or precipitation, although the summer of 1998 was somewhat wetter than those of the other 2 years. Mean annual precipitation measured at the two weather stations closest to our sites in Twente and Leeuwarden ranged from 981 mm in 1998, 914 mm in 2001, to 885 mm in 2002; the mean temperature from May until October varied between 14.9 and 15.9°C (Royal Netherlands Meteorological Institute, http://www.knmi.nl/klimatologie/maandgegevens/). The experimental sites were roughly situated between the indicated weather stations. Background bulk deposition at Reigersplas and Rundeven was 1.8 and 1.9 g N m^{-2} $year^{-1}$ and 0.01 and 0.02 g P m^{-2} $year^{-1}$ (Limpens et al. 2004).

Measurements

Sphagnum samples of *S. papillosum* and *S. magellanicum* in Reigersplas and *S. fallax* in Rundeven were taken from the plots before the first nutrients were added in July 1998, at the end of the experiment in September 2001 and

15 months later in January 2003. To be able to correct for the length of already senesced stem tissue we measured the distance from 1 cm below the capitulum to the transition point from colored to brown stem tissue with a ruler of a minimum of ten individuals per sample. Hereafter, the *Sphagnum* was cut into a capitulum section of 1 cm (0–1 cm) and a 2-cm stem section (1–3 cm), including the branches. All plant material was oven-dried at 70°C for 48 h after which dry weight was determined.

To correct for dilution of nutrients, *Sphagnum* growth was measured as height increment and biomass production between 1998 and 2001. Height increment was measured using a variation of the cranked wire method (Clymo 1970). Four plastic rods (diameter 1.5 mm) per plot were inserted to a depth of ca. 8 cm, and anchored by plastic broom bristles. The length of the rod extending above the moss surface was measured twice a year, in March–April and September–November. Since the *Sphagnum* surface around the rods was not markedly higher than the surrounding *Sphagnum*, we assumed the rods did not interfere with *Sphagnum* growth. Biomass production (A) over the experimental period was calculated as:

$$A = (B \times C) - (\Delta D)$$

with B = stem bulk density per cm depth at harvest time, C = cumulative height increment in cm, and ΔD = difference in capitulum bulk density between fertilization treatment and control at harvest time.

Dried and pulverized material was digested with H_2SO_4, salicylic acid, H_2O_2 and Se. Subsequently, the N and P concentrations were measured colorimetrically, using a continuous flow analyzer (Skalar San Plus system; Skalar, the Netherlands).

After chemical analyses the relative difference in nutrient concentrations between the capitulum and the stem (referred to as capitulum nutrient enrichment, C) was calculated as (Bragazza et al. 2004):

$$C = (A - B)/(A),$$

with A = capitulum nutrient concentration, and B = stem nutrient concentration. As we combined capitulum and stem data derived from the same plot, and we did not have matching data for all of the plots in 1998, we could not calculate the capitulum nutrient enrichment for the control plots in 1998.

Data analyses

Data were tested for normality, equality of variance and slopes, in the case of analysis of covariance (ANCOVA), and when necessary, were ln-transformed prior to analysis. In general we had five replicates for each factor and treatment combination, but for some specific combinations (indicated in figure legends or text) we had less than five, due to sample loss or unmatched capitulum, stem and growth data. For Reigersplas, four out of 15 plots (2 × C, 1 × P and 1 × N&P treatment) had two *Sphagnum* species per plot. Data for the different species were used as extra replicates (species nested within site) or aggregated (no species in design) depending on the statistical design used.

The capitulum nutrient concentrations as well as the distribution of nutrients over capitulum and stem were tested for each separate year with an ANOVA with N, P, site and species as fixed factors, with species nested within site. We choose to enter N ($df = 1$) and P ($df = 1$), and not treatment ($df = 3$) to gain df: the effects of N and P were additive and did not interact. We treated each year separately to exclude the variation due to differences in sampling season, and the concomitant differences in nutrient demand by *Sphagnum*. Differences in nutrient concentration between capitulum and stem were tested by a paired sample t-test, as their concentrations were highly correlated.

The effects of the individual *Sphagnum* growth parameters (cumulative height increment, production etc.) on nutrient concentration and distribution were tested with an ANCOVA with N, P and site as fixed factors and the growth parameter as a co-variable; for these analyses we lumped species within the Reigersplas site to obtain one value per plot, as growth had been measured for the dominant species only.

Results

Nutrient concentrations

In 1998 *Sphagnum* cover was above 90% and the capitulum nutrient concentrations tended to reflect the nutrient availability (Limpens et al. 2004) at the sites (Fig. 1; Table 1); generally *Sphagnum* from Reigersplas had the higher capitulum N concentrations (N_{cap}) whereas *Sphagnum* from Rundeven had the higher P concentrations (P_{cap}). As a result the *Sphagnum* N:P ratio ($N:P_{cap}$) differed markedly between the sites, with a N:P ratio of around 40 at Reigersplas and 14 at Rundeven for the control plots. Although nutrient additions had not yet started, there was already a significant P effect on P_{cap}, particularly for Rundeven by chance. The smaller sample size ($n = 3$ for P plots and $n = 1$ for C plots) may have contributed to this anomaly.

In 2001 *Sphagnum* cover was still above 80% and N_{cap} had increased with adding N, irrespective of site or species (Fig. 1a, b; Table 1). In turn, P_{cap} remained unaffected by adding N but was elevated by adding P irrespective of site and species (Fig. 1c, d; Table 1). As a result $N:P_{cap}$ increased with the addition of N, but decreased with the addition of P, irrespective of site. This P effect was more

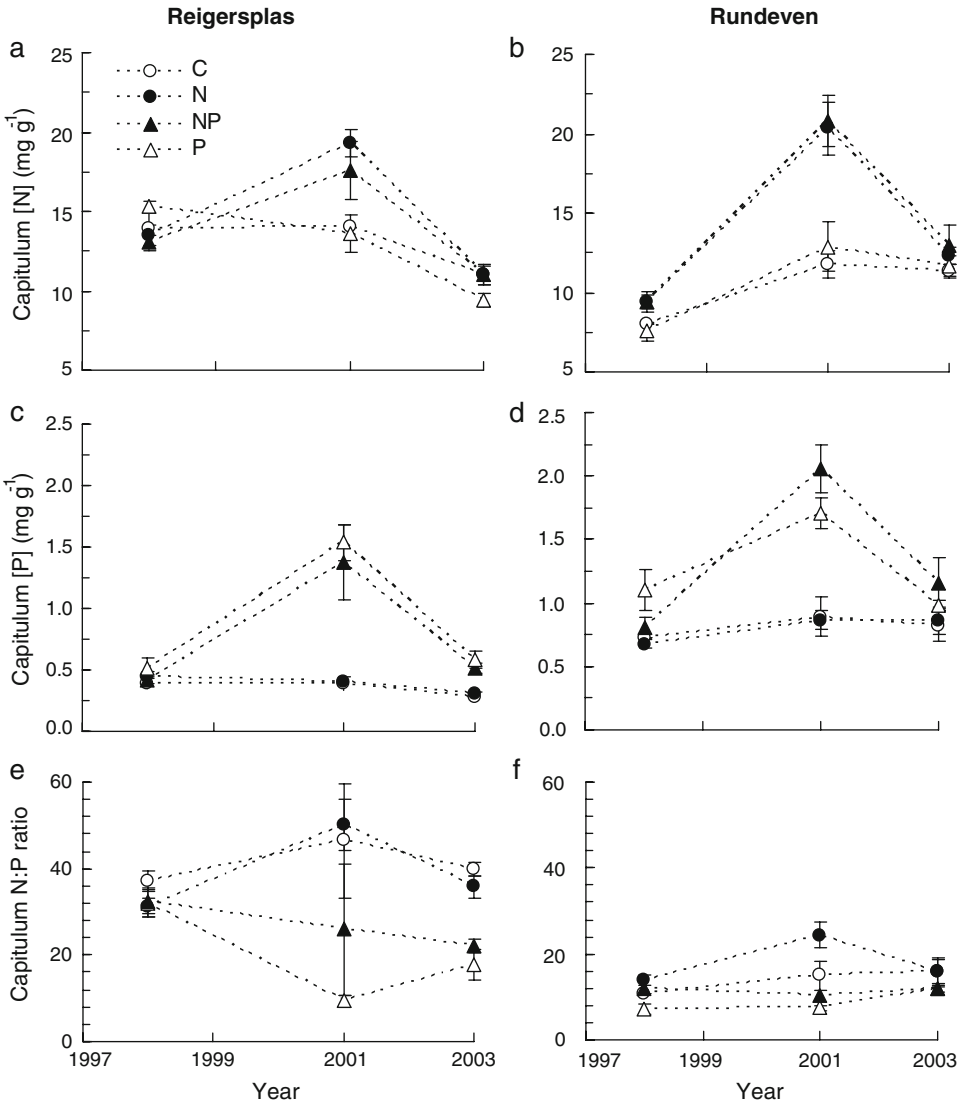

Fig. 1a–f Capitulum N and P concentrations and N:P ratio per treatment per site per year (means ± 1 SE). N = 4 g N m^{-2} $year^{-1}$, P = 0.3 g P m^{-2} $year^{-1}$, NP = 4 g N m^{-2} $year^{-1}$ and 0.3 g P m^{-2} $year^{-1}$. Means for Reigersplas include both *Sphagnum papillosum* and *Sphagnum magellanicum* data. See Table 1 for statistics. *C* Control

pronounced in Reigersplas, resulting in a significant interaction between P fertilization and site (Fig. 1e, f; Table 1).

In 2003 *Sphagnum* cover roughly resembled that in 2001 and the N fertilization effect on N_{cap} had sharply decreased at both sites, but was still significant (Fig. 1a, b; Table 1). The effect of adding P on P_{cap} had disappeared for Rundeven but was still significant for Reigersplas (Fig. 1c, d; Table 1). As a result the sites differed in their capitulum N:P ratio response. In Reigersplas N:P_{cap} was around 20 in the P and N&P plots whereas N:P_{cap} had reached 40 in the C and N plots. In Rundeven N:P_{cap} was around 16 and no longer differed between the treatments (Fig. 1e, f).

Nutrient distribution

Stem and capitulum nutrient concentrations did not differ in the direction of their response to addition of N and P (Fig. 2; Table 2), but for some treatments the strength of their response did differ, however, leading to changes in the capitulum nutrient enrichment (Fig. 3; Table 3).

In 2001 N_{cap} did not differ from stem N concentration (N_{ste}) for all treatments except for the P treatment, where N_{cap} exceeded N_{ste} for both sites (Fig. 2). Yet, adding N seemed to have affected N_{cap} less than N_{ste}, as when analyzed over all treatments, adding N did depress capitulum N enrichment (N_{enr}) irrespective of site (Fig. 3; Table 3). In contrast to adding N, adding P increased N_{cap} more than N_{ste}, concomitantly increasing N_{enr} irrespective of site (Fig. 3; Table 3). P_{cap} exceeded P_{ste} in Reigersplas for the N treatment only and for all treatments in Rundeven (Fig. 2). The capitulum P enrichment (P_{enr}) was not affected by adding N, but was affected by adding P. P increased P_{cap} slightly less than P_{ste}, leading to lower P_{enr}, particularly for Reigersplas (Fig. 3; Table 3).

In 2003, the N-fertilization effect on N_{enr} had disappeared at both sites (Fig. 3; Table 3). The effect of adding

Table 1 ANOVA testing the effects of adding N and P, site and *Sphagnum* species on capitulum nutrient concentrations per year. *Sig.* Significance

Source	*df*	1998[a]		2001		2003	
		F	Sig.	*F*	Sig.	*F*	Sig.
Capitulum [N]							
N	1	0.9	NS	51.6	***	5.9	*
P	1	<0.1	NS	<0.1	NS	0.1	NS
Site	1	85.3	***	<0.1	NS	8.7	**
Species(Site)	1	2.1	NS	1.6	NS	2.5	NS
N × P	1	0.1	NS	0.4	NS	1.3	NS
N × Site	1	8.4	**	3.3	NS	0.1	NS
P × Site	1	0.5	NS	1.0	NS	2.3	NS
N × P × Site	1	1.0	NS	0.1	NS	0.4	NS
R^2		0.76		0.54		0.26	
Capitulum [P]							
N	1	3.0	NS	0.2	NS	0.3	NS
P	1	6.7	**	89.8	***	28.2	***
Site	1	43.6	***	15.6	***	100.9	***
Species(Site)	1	0.2	NS	<0.1	NS	0.1	NS
N × P	1	2.9	NS	0.1	NS	0.3	NS
N × Site	1	1.6	NS	1.1	NS	0.3	NS
P × Site	1	3.1	NS	0.1	NS	4.3	*
N × P × Site	1	0.1	NS	1.7	NS	0.8	NS
R^2		0.65		0.73		0.77	
Capitulum N:P							
N	1	3.4	*	7.5	**	<0.1	NS
P	1	4.7	*	48.5	***	42.6	***
Site	1	170.0	***	15.2	***	77.6	***
Species(Site)	1	0.1	NS	0.1	NS	0.1	NS
N × P	1	2.2	NS	0.1	NS	1.5	NS
N × Site	1	7.8	**	<0.1	NS	<0.1	NS
P × Site	1	2.0	NS	3.8	*	17.4	***
N × P × Site	1	0.1	NS	1.2	NS	1.6	NS
R^2		0.87		0.65		0.78	

* $0.05 > P > 0.01$, ** $0.01 > P > 0.001$, *** $P < 0.001$, *NS* $P > 0.05$

[a] Significant effects for the N concentration data in 1998 should be interpreted with caution since the variances were not homogeneously distributed over the treatments (Levene's test: $F = 5.5$, $P < 0.001$)

P on N_{enr} had also disappeared at Rundeven but lingered at the Reigersplas, resulting in a strong interaction between P treatment and site (Fig. 3; Table 3). The P fertilization effect on P_{enr} found earlier had disappeared.

Sphagnum growth

Cumulative height increment over the experimental period (1998–2001), height increment in 2001 and *Sphagnum* production (Table 4) responded roughly similarly to the nutrient treatments. In general there was a negative effect of N and a positive effect of P fertilization at both sites, although the response to P at Reigersplas was more pronounced than for Rundeven. The length of colored stem was an exception to the above. The colored stem section for *S. fallax* from Rundeven (3.0 cm) was longer than for *S. magellanicum* and *S. papillosum* from Reigersplas (1.6 cm) and was not affected by the fertilization treatments (Table 4).

Similar to cumulative height increment (Table 3), neither *Sphagnum* growth in 2001 nor total *Sphagnum* production affected N_{cap}, N_{ste}, P_{cap} or P_{ste} in 2001. As a result, N_{enr} and P_{enr} in 2001 also remained unaffected by *Sphagnum* growth (data not shown).

Discussion

Recovery

Our results show that *Sphagnum* nutrient concentrations can recover within 15 months from substantial enrichment with N and P, even under suboptimal conditions such as the high background N deposition in the Netherlands (Fig. 1). Recovery of nutrient concentrations took place roughly within 1 year, although the effect of adding P on P_{cap} lingered. Possibly, the further decrease in P_{cap} was slowed when a favorable N:P ratio had been reached (Fig. 1). The longer recovery time after P fertilization relative to N fertilization has been reported for other ecosystems as well, such as fen meadows (van der Hoek et al. 2004).

When compared to other ecosystems and species, the swift recovery in tissue N concentration is remarkable and mostly resembles the recovery time of 1–2 years reported for the concentrations of exchangeable N in forest soils (Bredemeier et al. 1998; Boxman et al. 1998) that were measured under similar high N deposition rates. As can be expected from bryophytes that can take up nutrients across their entire surface (Brown and Wells 1990), the nutrient concentrations in the *Sphagnum* closely followed the shifts in nutrient availability and did not show a time lag such as in tissue nutrient concentrations in trees (Bredemeier et al. 1998; Boxman et al. 1998). In addition the fast recovery of the nutrient concentrations shows that translocation of previously supplied nutrients cannot offset the effects of major changes in supply on the *Sphagnum* nutrient concentrations, at least not at the high end of the N deposition spectrum where *Sphagnum* is metabolically saturated with N. Adding N to *Sphagnum* unsaturated with N (tissue concentration <7–8 mg N g^{-1}; Lamers et al. 2000) is likely to lead to increases in production as the N added is used to increase photosynthetic efficiency (Tomassen et al. 2003; Vitt et al. 2003). Only when nutrient concentrations are elevated beyond the metabolic saturation point, it is likely that concentrations will decrease rapidly after the source of enrichment is reduced.

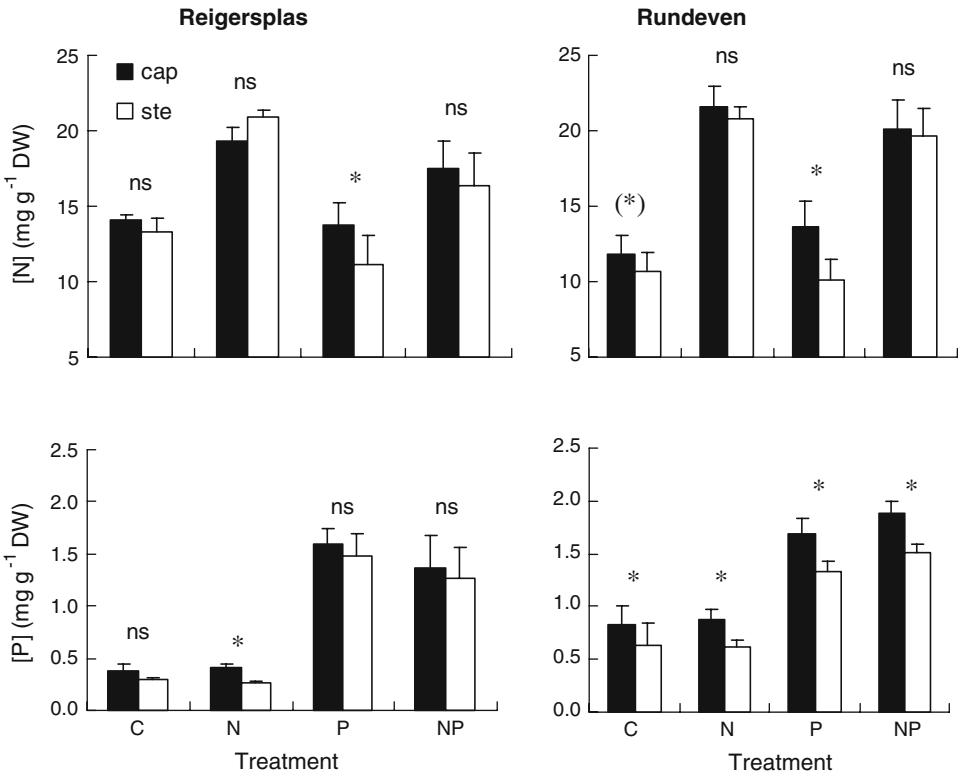

Fig. 2 N and P concentrations in capitulum (*filled bars*) and stem (*open bars*) per site in 2001 (means +1 SE). N = 4 g N m^{-2} $year^{-1}$, P = 0.3 g P m^{-2} $year^{-1}$, NP = 4 g N m^{-2} $year^{-1}$ and 0.3 g P m^{-2} $year^{-1}$. Means for Reigersplas include both *S. papillosum* and *S. magellanicum* data. See Table 2 for statistics. *$P < 0.10$ [significant difference between capitulum and stem concentrations (paired *t*-test)]. *DW* Dry weight, *ns* $P > 0.05$

Table 2 Analysis of covariance testing the effects of cumulative *Sphagnum* height increment, N and P additions, site and *Sphagnum* species on capitulum and stem nutrient concentrations in 2001

Source	*df*	Capitulum		Stem	
		F	Sig.	*F*	Sig.
N concentration 2001					
Height increment 1998–2001	1	0.3	NS	0.6	NS
N	1	32.4	***	45.7	***
P	1	0.0	NS	1.1	NS
Site	1	<0.1	NS	0.3	NS
N × P	1	0.2	NS	0.3	NS
N × Site	1	3.8	*	2.9	NS
P × Site	1	0.3	NS	0.5	NS
N × P × Site	1	0.0	NS	0.1	NS
R^2		0.50		0.63	
P concentration 2001					
Height increment 1998–2001	1	0.4	NS	0.1	NS
N	1	0.2	NS	0.1	NS
P	1	53.8	***	35.7	***
Site	1	12.5	**	7.2	***
N × P	1	<0.1	NS	0.1	NS
N × Site	1	1.0	NS	0.8	NS
P × Site	1	<0.1	NS	2.7	NS
N × P × Site	1	2.0	NS	0.3	NS
R^2		0.73		0.70	

* $0.05 > P > 0.01$, ** $0.01 > P > 0.001$, *** $P < 0.001$, *NS* $P > 0.05$

It should be stressed that the recovery from nutrient stress within a few years can only be expected when the *Sphagnum* layer is still mostly present; once the vegetation type has changed, particularly when *Sphagnum* cover has declined, a much longer period of recovery has to be taken into account (Maksimova and Yudina 1999; Strengbom et al. 2001), because of increased competition as a consequence of the expansion of vascular plants (Heijmans et al. 2002; Tomassen et al. 2003). When the *Sphagnum* layer is still intact, then the vegetation will likely recover faster, although a certain lag time can be expected when mineralization of the N-enriched *Sphagnum* litter may lead to a transient increase in N availability for the vascular plants (Limpens and Berendse 2003).

Nutrient distribution

As hypothesized, the fertilization-induced changes in N_{cap} and P_{cap} coincided with changes in N_{enr} and P_{enr}, with the added nutrient generally accumulating more in the stem and the alternative nutrient accumulating in the capitulum (Fig. 2, 3). Because of the indirect nature of the evidence, we cannot distinguish between the mechanism(s) responsible for the observed changes. However, we think that translocation from older tissue (stem) to growing tissue (capitulum) most likely explains the capitulum enrichment. Although absolute differences in nutrient concentration between capitulum and stem (Fig. 2) were small, they were

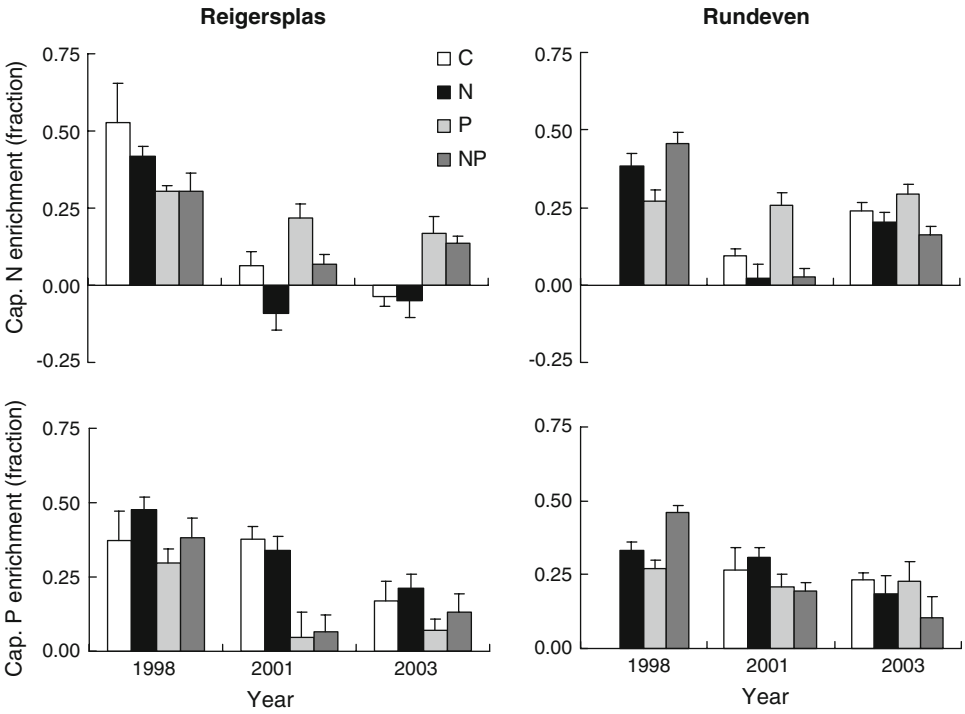

Fig. 3 Capitulum (*Cap*) nutrient enrichment per treatment per site per year (means +1 SE or −1 SE). Positive values—capitulum N concentration (N_{cap}) > stem N concentration (N_{ste}); negative values—$N_{cap} < N_{ste}$. The absence of data for the control treatment in Rundeven in 1998 is due to missing values. Means for Reigersplas include both *S. papillosum* and *S. magellanicum* data. See Table 3 for statistics

Table 3 ANOVA testing the effects of adding N and P, site and *Sphagnum* species on the distribution of N and P over stem and capitulum per year. See Materials and methods for definition of capitulum N enrichment

Source	*df*	1998[a]		2001		2003	
		F	Sig.	*F*	Sig.	*F*	Sig.
Capitulum N enrichment							
N	1	0.3	NS	23.2	***	3.7	NS
P	1	2.1	NS	15.7	***	14.2	***
Site	1	<0.1	NS	0.4	NS	36.1	***
Species(Site)	1	<0.1	NS	4.3	*	0.0	NS
N × P	1	0.9	NS	2.1	NS	1.1	NS
N × Site	1	1.6	NS	0.0	NS	1.3	NS
P × Site	1	1.9	NS	1.4	NS	12.2	***
N × P × Site	1	–	–	1.3	NS	0.4	NS
R^2		0.15		0.50		0.61	
Capitulum P enrichment							
N	1	5.3	*	0.1	NS	0.1	NS
P	1	<0.1	NS	26.3	***	2.4	NS
Site	1	0.8	NS	0.7	NS	0.4	NS
Species(Site)	1	<0.1	NS	3.8	NS	1.3	NS
N × P	1	0.0	NS	0.0	NS	0.2	NS
N × Site	1	0.5	NS	<0.1	NS	2.6	NS
P × Site	1	3.0	NS	8.9	**	0.3	NS
N × P × Site	1	–	–	0.3	NS	0.2	NS
R^2		0.048		0.37		0.027	

* $0.05 > P > 0.01$, ** $0.01 > P > 0.001$, *** $P < 0.001$, *NS* $P > 0.05$

[a] Due to missing values, we did not have enough *df* to run the three-way interaction for 1998

consistent (Fig. 3), and as such may be indicative of sink and source functions of the two plant parts.

The nutrient concentration in the capitulum (0–1 cm) is a result of nutrient uptake from the environment, translocation from older tissue, dilution by growth and losses by for example leaching (Rydin and Clymo 1989). For the stem (1–3 cm) similar processes apply with additional nutrient loss through chlorophyll breakdown as a result of increased self-shading by the growing upper moss parts. Our results show that dilution by growth did not explain the observed patterns, since not one of the growth parameters tested, including cumulative height increment (Table 2), affected nutrient concentration or distribution in 2001. Additionally, the observed treatment effects on N_{enr} and P_{enr} could not be completely explained by changes in nutrient uptake from the environment and nutrient losses. In general, the following arguments could be used against the first two explanations. If nutrient supply from the atmosphere increases, N retention in the capitulum decreases (Bragazza et al. 2004). As a consequence the nutrients penetrate deeper into the *Sphagnum* layer, making uptake by stem tissue possible. Although this process could explain some of the observed changes in the distribution of the applied nutrient itself, i.e. the decrease in P_{enr} with P supply, it does not explain the increase in N_{enr} as a result of P supply (Fig. 3). The latter could be related to a P-induced increase in N assimilation mediated through increased photosynthetic activity (Gordon et al. 2001) of the metabolically more

Table 4 *Sphagnum* growth parameters (means ± 1 SE, $n = 5$). *F*-values and significant main effects are given for the addition of N and P and site (ANOVA)

	C	N	P	NP
Reigersplas				
Height increment 2001 (cm)	−0.1 ± 0.2	−0.4 ± 0.2	2.0 ± 0.8	1.3 ± 0.5
Height increment 1998–2001 (cm)	9.5 ± 1.1	5.0 ± 0.3	15.1 ± 1.9	12.6 ± 1.2
Production 1998–2001 (g m^{-2})	821 ± 139	482 ± 38	1,166 ± 122	831 ± 122
Colored stem (cm)	1.4 ± 0.1	1.5 ± 0.0	1.7 ± 0.1	1.7 ± 0.4
Rundeven				
Height increment 2001 (cm)	2.4 ± 1.2	0.2 ± 0.5	1.8 ± 1.0	1.9 ± 1.4
Height increment 1998–2001 (cm)	7.2 ± 1.2	5.7 ± 0.2	7.0 ± 1.4	7.1 ± 1.6
Production 1998–2001(g m^{-2})	318 ± 44	134 ± 33	497 ± 136	216 ± 42
Colored stem (cm)	3.3 ± 0.8	2.7 ± 0.9	3.0 ± 0.7	3.2 ± 0.7
Significant main effects		N (*df* 1)	P (*df* 1)	Site (*df* 1)
Height increment 2001 (cm)		NS	4.5*	NS
Height increment 1998–2001 (cm)		5.6*	17***	18***
Production 1998–2001		16***	7.2*	51***
Colored stem (cm)		NS	NS	14**

* $0.05 > P > 0.01$,
** $0.01 > P > 0.001$,
*** $P < 0.001$, *NS* $P > 0.05$

active capitulum section. Alternatively, the effects could also be explained by increased N translocation. Finally, one could argue that differences in nutrient loss from the sampled part of the stem could have been responsible for the fertilization effects on N_{enr} and P_{enr}. Indeed the length of stem sampled in 2001 (2 cm) regularly exceeded the length of colored stem (Table 4), especially for the Reigersplas. However, since the length of colored stem was not affected by adding N or P (Table 4) and the distributions of nutrients over the capitulum and the stem were similar for both sites (Fig. 3), this explanation seems unlikely.

On the whole, the observed changes in nutrient distribution over capitulum and stem in response to the treatments seem most consistent with nutrient translocation as their main driver. However, a fertilization experiment using tracers such as ^{15}N and ^{32}P is needed to further elucidate the mechanisms responsible for the observed distribution effects.

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