Climatic modifiers of the response to nitrogen deposition in peat-forming *Sphagnum* mosses: a meta-analysis

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Summary

- Peatlands in the northern hemisphere have accumulated more atmospheric carbon (C) during the Holocene than any other terrestrial ecosystem, making peatlands long-term C sinks of global importance. Projected increases in nitrogen (N) deposition and temperature make future accumulation rates uncertain.
- Here, we assessed the impact of N deposition on peatland C sequestration potential by investigating the effects of experimental N addition on *Sphagnum* moss. We employed meta-regressions to the results of 107 field experiments, accounting for sampling dependence in the data.
- We found that high N loading (comprising N application rate, experiment duration, background N deposition) depressed *Sphagnum* production relative to untreated controls. The interactive effects of presence of competitive vascular plants and high tissue N concentrations indicated intensified biotic interactions and altered nutrient stochiometry as mechanisms underlying the detrimental N effects. Importantly, a higher summer temperature (mean for July) and increased

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annual precipitation intensified the negative effects of N. The temperature effect was comparable to an experimental application of almost 4 g N m^{-2} yr^{-1} for each 1°C increase.

• Our results indicate that current rates of N deposition in a warmer environment will strongly inhibit C sequestration by *Sphagnum*-dominated vegetation.

Introduction

At the scale of millennia, peatlands in the northern hemisphere have significantly affected the earth's atmosphere (Frolking & Roulet, 2007) by steadily sequestering CO_2 in the form of partly decomposed organic material (peat), mostly formed by peat forming *Sphagnum* mosses (Rydin & Jeglum, 2006). Although fairly resilient to small disturbances in climate (Belyea & Baird, 2006), *Sphagnum*-dominated peatlands are now experiencing a hitherto unprecedented combination of stresses such as increases in nitrogen (N) deposition (Galloway *et al.*, 2008), temperature, and drought frequency (Dise, 2009). To what extent these stresses will affect future carbon (C) sequestration requires urgent attention (Dise, 2009).

Sphagnum-dominated peatlands are extremely nutrient poor ecosystems and commonly rely on atmospheric inputs as their sole sources of external nutrients, resulting in a plant community sensitive to increases in N deposition (Bobbink *et al.*, 2003). The vegetation consists mainly of slow-growing ericaceous dwarf shrubs and cyperaceous graminoids rooting in a soil matrix of living and dead peat mosses. The competitive balance between *Sphagnum* and vascular plants is maintained by their asymmetrical competition for nutrients. *Sphagnum* uses N derived from atmospheric deposition, and efficiently relocates nutrients from older tissue (Rydin & Clymo, 1989), whereas vascular plants depend more on N released during decomposition of organic material (Malmer *et al.*, 2003). *Sphagnum* restricts the N supply to vascular plants by intercepting deposited N (Lamers *et al.*, 2000), and by slowing down decomposition through its recalcitrant litter and acidity (Van Breemen, 1995). Once competition from *Sphagnum* is reduced, or the nutrient limitation is lifted, vascular plants may gain a competitive advantage and, being taller, outcompete the mosses for light (Hautier *et al.*, 2009). Shifts from a moss- to a vascular plant-dominated state can depress C sequestration rates (Bubier *et al.*, 2007) and even mobilize the N and C stored in the underlying peat by stimulating decomposition (Freeman *et al.*, 2004). Since estimates of the peatland C-store range between 34 and 46% of the 796 PgC currently held in the atmosphere as CO_2 (IPCC, 2007), ensuing release to the atmosphere and local environment may be substantial (Limpens *et al.*, 2008).

It is generally hypothesized that increasing N deposition rates lead to progressive N saturation of the moss layer,

shifting the competitive balance in favour of vascular plants and depressing *Sphagnum* production and cover (Limpens *et al.*, 2006). In turn, this reduces C sequestration rates (Gunnarsson *et al.*, 2008), despite the increased productivity of vascular plants (Bubier *et al.*, 2007). N-depressed moss production has been related to direct effects of enhanced tissue N concentration, such as nutrient imbalance (Bragazza *et al.*, 2004) and increased sensitivity to pests and pathogens (Wiedermann *et al.*, 2007), or indirect effects such as light competition from leaves and litter of taller vascular plants (Berendse *et al.*, 2001) or other mosses (Mitchell *et al.*, 2002). Moreover, the response of *Sphagnum* to N can be modified by climatic factors, such as temperature (Gunnarsson *et al.*, 2004), summer drought (Gerdol *et al.*, 2007), and phosphorus (P) limitation (Aerts *et al.*, 2001). Although there are many hypotheses about which factors may affect *Sphagnum* production and its response to N enrichment, we do not yet know the importance of these factors in relation to each other, nor if their effects can be extrapolated beyond the scope of single studies. The growing number of N-addition experiments in peatlands enables us for the first time to test these hypotheses comprehensively and to quantify the effects of environmental factors on N application over a wider geographic range using meta-regressions.

We assessed the role of N deposition on peatland C sequestration potential and its relation to N saturation, using the effects of experimental N addition on the production and N concentration of *Sphagnum*. After checking for bias caused by artifacts of adding N, we analysed experimental outcomes of 29 fertilization studies spanning 18 countries in North America and Eurasia to test our prediction that N application depresses *Sphagnum* production and enhances *Sphagnum* N concentration and to quantify the importance of interactions with N loading (N application rate and background N deposition rate), climatic factors (precipitation, temperature), and local factors (position above the water table, P addition, presence of vascular plants, *Sphagnum* species). We expected that, at constant N loading, an elevation in temperature, increased precipitation rate, a position close to the water table, P addition and removal of vascular plants would dilute *Sphagnum* N content by stimulating biomass production (Breeuwer *et al.*, 2009), thus postponing negative effects associated with high tissue N concentration (Limpens *et al.*, 2006).

Description

Data acquisition

Nitrogen fertilization studies conducted on *Sphagnum*-dominated vegetation were located by searching the Web of Science and Google Scholar using key words *Sphagnum*, nitrogen, peatlands, mires, fertilisation and fertilization, as well as using our contacts within the small peatland researcher community. Hereafter, all first authors were approached for access to raw data, enabling accurate calculation of treatment effects. When raw data turned out irretrievable (three studies, Supporting Information, Table S1), we extracted the data from published manuscripts. The dataset was further expanded with unpublished production, growth or N concentration data related to published experiments of the co-authors. We selected all studies where: *Sphagnum* was exposed to diurnal and seasonal changes in solar irradiance and temperature; and where the control was subject to the same temperature regime as the fertilization treatments. As a result we excluded all glasshouse studies, but included fertilization studies carried out in the field or in mesocosms and studies using pots kept under a roof. These selection criteria left us with 29 separate studies from 14 countries (Table S1), yielding 107 experiments focusing on *Sphagnum* production or height increment and 87 on *Sphagnum* N concentration.

From these studies we compiled a dataset on three response variables and 12 explanatory variables. Response variables were *Sphagnum* production, height growth and *Sphagnum* N concentration, whereas explanatory variables were N application rate, background N deposition, annual precipitation, mean July temperature, position above the water table, P addition, presence of vascular plants, *Sphagnum* species, experiment duration, N dose concentration, and form and frequency in which fertilizer was applied. We calculated or extracted mean and standard deviation of the response variables for all N treatments per study, treating different species subject to the same treatment, or the same species subject to different treatments, as separate experiments (Gurevitch & Hedges, 1999). For three studies we used the response ratio (*rr*) of *Sphagnum* height increment instead of production, as production data were unavailable. Before doing so we compared the *rr*-values of both variables for a subset of field fertilization studies where both length increment and production had been reported. The *rr*-values were well correlated and closely followed the 1 : 1 line (production $rr = -0.01 + 0.98 \times$ length rr, $R^2 = 0.79$, $n = 86$). Excluding the height-increment studies from our meta-analysis did not affect the model coefficients but did slightly widen the 95% credible intervals.

To allow comparison of N-application effects over different studies, the *Sphagnum* response to N application was standardized, expressing the effect relative to the control. For each experiment, the effect size was calculated as the natural logarithm ($\log_e$) of the *rr* of *Sphagnum* production (PROD) or N concentration (N). The *rr* is defined as the mean of the experimental group (*E*) divided by the mean of the control group (*C*). The $\log_e rr$ was used to linearize the metric and achieve a more normal distribution (Hedges *et al.*, 1999). A negative $N\log_e rr$ indicates that applying N reduced the N concentration, whereas a positive $N\log_e rr$ indicates that applying N increased the N concentration relative to the control. Assuming treatment and control are independent, the variance (var) of $\log_e rr$ is var ($\log_e E - \log_e C$) and is calculated as $SD_E^2/n_E E^2 + SD_C^2/n_C C^2$ (Hedges *et al.*, 1999), where SD is the standard deviation and *n* is the sample size. To compare the relative importance of the explanatory variables, we standardized their regression coefficients from our models by subtracting the mean and dividing by two times SD (Gelman, 2008). Regression coefficients are then directly comparable with each other, including untransformed binary variables (Gelman, 2008). The standardized coefficients are given in tables and nonstandardized coefficients are presented in Table S2 and in all figures.

Statistical model building

To test our hypotheses, we used a meta-regression approach, a method increasingly used for meta-analyses in ecology (Gurevitch & Mengersen, 2010). Meta-regression models are similar to multiple regression models, in that they allow inclusion of continuous explanatory variables and the exploration of response curves. Before constructing the main models referred to in our results we first pre-specified the variables of interest related to our hypotheses and predictions. This theory-driven approach avoids problems associated with stepwise procedures, such as biased estimates (Harrell, 2001), and other pitfalls in meta-regression modelling, such as data dredging, confounding variables and too many explanatory variables (Thompson & Higgins, 2002; Lajeunesse, 2010). After this we identified potential covariates associated with experimental design that could bias our results and investigated colinearity among explanatory variables to ensure that modelled variables could be estimated independently. Here we also looked at the distribution to ensure relatively even distribution of data within the range. We tested if the covariates had an effect on the response variables. If this were the case they were included in the main model. Finally, we assembled the two main regression models referred to in our results and Tables 1, S2. If submodels, model checking or theory strongly suggested interaction or quadratic terms, we included them in the model, while keeping the number of parameters as low as possible for reasons mentioned earlier. Data on all explanatory variables are given in Table S1, together with

Table 1 Results of the Bayes linear models with PRODlog$_e$rr and Nlog$_e$rr with standardized coefficients

	Standardized coefficient	Upper	Lower	P	τ^2	% explained
PRODlog$_e$rr (n_{exp} = 107)						
Intercept	0.19	0.35	0.03	0.02	0.06	53
Nitrogen (N) application rate	−0.15	−0.01	−0.28	0.03		
Background N deposition	−0.32	−0.13	−0.52	< 0.01		
Mean July temperature	−0.06	0.17	−0.28	0.61		
Microhabitat (hummock)	−0.16	0.03	−0.34	0.09		
Microhabitat (hummock) × Mean July temperature	−0.53	−0.15	−0.91	< 0.01		
Mean annual precipitation	−0.30	−0.07	−0.54	0.01		
Phosphorus application	0.30	0.51	0.08	0.01		
Presence vascular plants	−0.42	−0.21	−0.63	< 0.01		
Nlog$_e$rr (n_{exp} = 87)						
Intercept	0.62	0.72	0.51	< 0.01	0.01	61
N-application rate (linear term)	0.37	0.48	0.26	< 0.01		
N-application rate (quadratic term)	−0.28	−0.18	−0.38	< 0.01		
Background N deposition	−0.19	−0.10	−0.28	< 0.01		
Experiment duration	0.17	0.26	0.09	< 0.01		
Mean July temperature	0.07	0.17	−0.02	0.13		
Microhabitat (hummock)	−0.21	−0.11	−0.31	< 0.01		
Phosphorus application	−0.06	0.03	−0.15	0.15		
Mean annual precipitation	0.11	0.23	−0.01	0.07		
N dose concentration	−0.08	0.01	−0.17	0.07		
PRODlog$_e$rr − simplified model (n_{exp} = 55)						
Intercept	−0.07	0.06	−0.19	0.30	0.07	59
Sphagnum N concentration	−0.30	−0.03	−0.57	0.03		
Mean July temperature	−0.54	−0.26	−0.82	< 0.01		
Mean annual precipitation	−0.37	−0.06	−0.68	0.02		

n_{exp}, number of experiments. See Supporting Information Table S2 for nonstandardized coefficients and the range and SD for the continuous explanatory variables. Negative coefficients indicate that an increase in the predictor makes *Sphagnum* more sensitive to nitrogen (N) addition. Categorical levels are compared with the intercept which is set to without phosphorus (P) addition (and without vascular plants in the PRODlog$_e$rr model) in the lawn microhabitat. Upper and lower, 95% credible intervals; *P*, two-sided *P*-value derived from the posterior probability corresponding to the hypothesis that the regression coefficient is zero; τ^2, residual heterogeneity. % explained is a measure of model performance and represents the variation among experiment outcomes explained by the explanatory variables (see the Description section).

details on the data sources used. We now briefly describe the variables that were included in our two main models (one main model for each response variable).

N-application rate Amounts of N (g N m^{-2} yr^{-1}) applied by the experimenters. For multiple-year experiments we only used data from the last year.

Background N deposition The wet N-deposition rate (g N m^{-2} yr^{-1}) at the experimental site. For those experiments where vegetation was moved under a roof, we used wet deposition rate at the collection site. If not provided by the experimenters, wet N-deposition rate was extracted from the EMEP website (http://webdab.emep.int/Unified_Model_Results/AN/) for the year the *Sphagnum* N-concentration data were collected. We selected wet deposition rather than total deposition because of its smaller estimation error (Boring *et al.*, 1988).

Mean annual precipitation (mm yr^{-1}) at the experimental site was weakly correlated with background N deposition ($r = 0.26$ for production data and $r = 0.12$ for N-concentration data, both $P > 0.1$), allowing inclusion of both variables in the main models. Their coefficients in the models did not change substantially if they were fitted individually or together, supporting our choice.

Temperature Mean July temperature at the study site in °C. This was strongly correlated with mean summer temperature (June–August, $r = 0.98$), and yielded similar model outcomes (not shown). We chose July temperature to facilitate data retrieval from weather stations.

Depth of the water table expressed as hummock vs lawn microhabitats. As information on water tables was inconsistent, we used microhabitat as a proxy. Microhabitat was assigned according to dominant moss species (Andrus,

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1986). If vegetation was co-dominated by two *Sphagnum* species, we selected the lowest microhabitat as the maximum position of *Sphagnum* species above the water table is physiologically constrained (Rydin & Jeglum, 2006).

P-addition P (PO_4^{3-}) added vs no P added.

Experimental duration The number of growing seasons over which N was applied.

Presence of vascular plants Presence vs removed by the experimenter by clipping above-ground parts. Plant abundance was measured in only a few studies and could therefore not be used. Presence of vascular plants was confounded with experimental duration, as removal of vascular plants by clipping was mainly restricted to short-term studies. To choose which of the two variables to select for our main models, we first tested their individual effects on data subsets. Presence of vascular plants was tested using data recorded after one growing season only, including first-year data from long-term studies. The effect of duration was tested on another subset using only studies where vascular plants had not been removed. The presence of vascular plants seemed to affect the *Sphagnum* production response (PROD$\log_e rr$) to N application (regression coefficient (upper, lower credible interval)) = -0.19 (0.074, -0.45), $P = 0.15$, $n = 52$), whereas the effect of duration was negligible (0.04 (0.28, -0.20), $P = 0.74$, $n = 74$). The pattern was reversed for change in N concentration (N$\log_e rr$). Here vascular plants did not affect N$\log_e rr$ substantially (-0.055 (0.052, -0.16), $P = 0.30$, $n = 57$) but duration did (0.16 (0.28, 0.045), $P = 0.006$, $n = 60$). Based on this, we included presence of vascular plants for our main model testing PROD$\log_e rr$ and experimental duration in the model testing N$\log_e rr$.

***Sphagnum* species** The dominant *Sphagnum* species in the experimental plots. Because sample size differed widely among species, we did not include species as a variable in the main model. Instead, we ran individual models for those species with a substantial amount of data that covered a broad range of our explanatory variables. We performed this analysis for *Sphagnum magellanicum* and *Sphagnum fuscum*.

Covariates associated with experimental design that could bias our results included the N concentration (g l^{-1}) of the fertilizer solution applied to the vegetation (**N dose concentration**), the form (NH_4^+, NO_3^-, NH_4NO_3) in which N was applied (**N form**) and the frequency (low, medium, high; see Table S1) in which N fertilization was applied (**N frequency**). They were included in the main models when they significantly affected the response variables, as was the case for N dose concentration only. The lack of effects of N form and N frequency are probably a result of the relatively

few studies that applied an N form other than NH_4NO_3 or fertilized < six times a year (see Table S1).

Sampling dependence and hierarchical Bayes linear model (HBLM)

In a meta-analysis, the linear mixed model can be written as: $y = X\beta + \delta + \varepsilon$, where y is the vector of effect size estimates ($\log_e rr$); X is the design matrix with the explanatory variables; β is a vector of parameters (including an intercept term and the effects of the explanatory variables); δ is a identity matrix with τ^2 along the diagonal. τ^2 is the residual heterogeneity, that is the variability among experimental outcomes that is not accounted for by the explanatory variables included in the model. ε is the sampling variance-covariance matrix. This matrix is assumed to be known and has the experiment-specific variances on the diagonal.

To address our research question, we needed to calculate effect sizes for different N-application rates. As single studies often involved multiple N-application rates, and only one control treatment, the same samples were used as control for > one experimental group when calculating rr for these studies. This created a sampling dependence in our responses which needed to be accounted for (Gurevitch & Hedges, 1999). We did so by including covariances between related experiments (off-diagonal blocks) in ε (Hedges *et al.*, 2010). Our choice of effect size ($\log_e rr$) enabled us to obtain approximated covariances between experiments using the delta method. The variance (var) of $\log_e rr$ is: $\log_e E - \log_e C$, E referring to the experimental group and C the control group. The covariance (cov) between two values for $\log_e rr$ is cov($\log_e E1 - \log_e C$, $\log_e E2 - \log_e C$), which equals var($\log_e C$), calculated as $SD_C^2 / n_C C^2$ (Hedges *et al.*, 1999).

To account for the sampling dependence in our dataset, we used a HBLM. The HBLM is a method that allows controlling for sampling dependence (Kulmatiski *et al.*, 2008; Stevens & Taylor, 2009), something that is particularly important in our dataset which had many multiple-treatment studies (see Table S1). We also ran a mixed-model meta-analysis using method of moments for estimation while accounting for sampling dependence. This method yielded similar estimates but narrower 95% intervals. In this paper we only present the more conservative HBLM results. The analyses were performed in R (R Development Core Team, 2010), using the package metahdep (Stevens & Nicholas, 2009). For a HBLM, metahdep uses a noninformative normal prior on $\beta | (\tau)$, and a log-logistic prior on τ. See Stevens & Taylor (2009) for computational details. The uncertainty in the regression coefficients is given by 95% credible intervals, which in Bayesian statistics means that the posterior probability that β lies within the interval is 0.95. Credible intervals were calculated as two times the posterior standard deviation of

the coefficients. Two-sided *P*-values for the coefficients were also calculated for a more familiar interpretation of significant effects. To give an estimate of the overall performance of our models, we calculated the % reduction in τ^2 (the residual heterogeneity) as a result of including the explanatory variables: (τ^2, model with intercept only − τ^2, model with explanatory variables)/(τ^2, model with intercept only). To test how well our simplified model (see the Results section) would predict the sign (positive, negative) of the N effect on production, we used a leave-one-out procedure (Harrell, 2001). Each observation was tested, or predicted, by using a model trained by the other observations; that is, in our case 55 model runs with 54 observations. Predicted and observed values were compared to assess the quality of the model.

Model checking

We checked for sample size bias in our dataset by examining plots of effect size vs variance and number of replicates (Fig. S1a–d). Residual analyses were used for model checking. For the two main meta-analysis models we assessed the fit of the model by predictive model checking (Gelman & Hill, 2007). This entailed using the model parameters, and the known sampling error covariance matrix, to simulate 1000 hypothetical replications of the data. If the model is reasonably accurate, the hypothetical data should resemble the original data. We investigated whether the minimum and maximum values or standard deviation of the replicated data differed significantly from the original data. A *P*-value was calculated as the proportion of cases in which the simulated values of PRODlog$_e rr$ or Nlog$_e rr$ exceeded the original value. Furthermore, we re-ran the model on the replicated data sets and checked the 95% coverage of the model coefficients. Ideally, in 95% of the replicated data sets, the 95% interval of the coefficient should cover the coefficient obtained by the original model (Gelman & Hill, 2007).

To test how well the effect of N addition mimicked that of N deposition, we compared the relationship between *Sphagnum* N concentration and the sum of background N and applied N (N influx) for our data with the relationship reported independently by Bragazza *et al.* (2005) for unfertilized peatlands. The authors presented a nonlinear relationship between N concentration and N deposition in *Sphagnum* (N concentration = μ + log$_e$N deposition). We applied a similar relationship to our own data, by fitting a generalized least-squares regression (GLS) using mean N concentration in control and N-treated plots as the response variable. One-year experiments were excluded, as they might not have reached equilibrium with the N influx. A GLS model was applied to account for the within-study correlation with a compound symmetry correlation structure, using the R package *nlme* (Pinheiro *et al.,* 2009).

Results

N addition mimics N deposition

Despite the N influx in our study being higher, up to 6 g m^{-2} yr^{-1} compared with maximum of 2 g N m^{-2} yr^{-1} background deposition in Bragazza *et al.* (2005), both datasets show high similarity. The absolute N concentration as well as the relationship between *Sphagnum* N concentration and N influx was very similar between both studies (Fig. 1). Moreover, our coefficient estimates were within two times the standard error of those reported by Bragazza *et al.* (2005). These results support the assumption that the *Sphagnum* response to experimental N addition can be used to predict its response to natural atmospheric N deposition, even at more extreme N influx.

Sphagnum production

Taken over all studies, adding N depressed *Sphagnum* production (Fig. 2a, Table 1), but the direction and strength of the response to N application depended more on the other explanatory variables than on the N application rate. Applying low rates of N in areas with low N background deposition stimulated or did not affect production relative
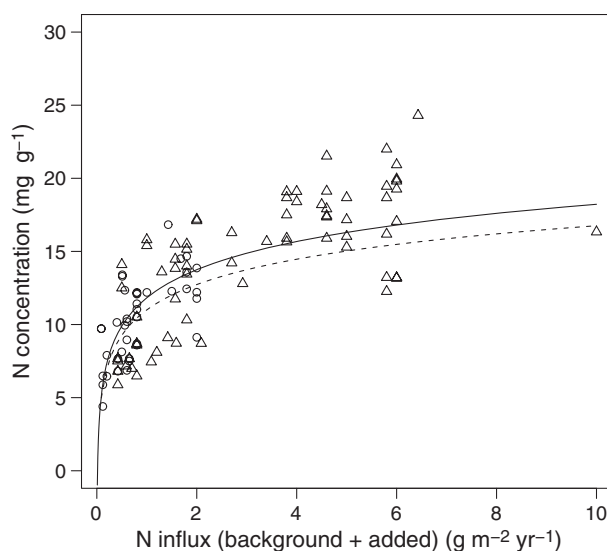

Fig. 1 Relationship between *Sphagnum* nitrogen (N) concentration and sum of background wet deposition and applied N. We included data on *Sphagnum* N concentrations (upper 0–3 cm shoot, DW basis) from both control (circles) and N treatments (triangles) from our dataset (*n* = 109). The solid line indicates the best fit through our data (N concentration = 11.8 + 2.8 × log$_e$(N influx)). The dashed line indicates the relationship reported by Bragazza *et al.* (2005) for *Sphagnum* collected at unfertilized sites and includes an extrapolation beyond the range of collection sites (with a maximum of 2 g N m^{-2} yr^{-1} in background deposition). There is no evidence for N-induced toxicity below *Sphagnum* N concentrations of 20 mg N g^{-1} DW (Granath *et al.*, 2009).
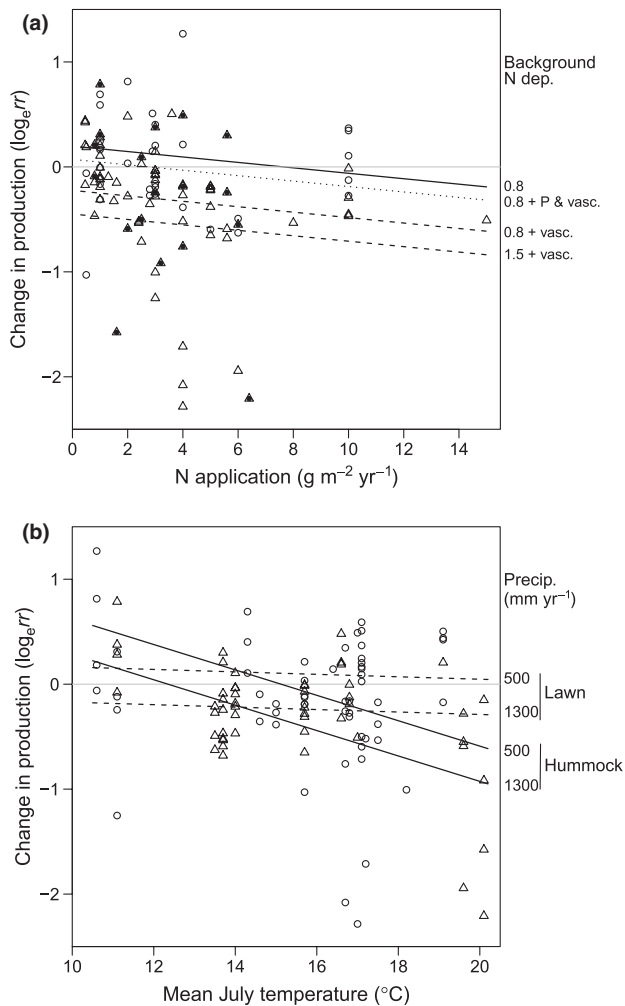
Fig. 2 Modelled response curve of *Sphagnum* production to experimental nitrogen (N) addition (PRODlog$_e$*rr*) as affected by: (a) N-application rate combined with background N deposition (N dep., two rates), without vascular (vasc.) plants and phosphorus (P) addition (solid line, open circles) and with vascular plants alone (open triangles, dashed lines), or in combination with P addition (closed triangles, dotted line), (b) mean July temperature combined with mean annual precipitation (precip., two rates) and height above the water table. Hummock is high (triangles, solid lines) and lawn low (circles, dashed lines). Positive values for the response ratio indicate an increased production relative to the control treatment. For the fitted lines all other variables in the model (Table 1) were set at their average values. Each data point represents one experiment.

to the control, leading to positive *Sphagnum* PRODlog$_e$*rr* values for lawn *Sphagnum* without vascular plants, or hummock *Sphagnum* at low temperatures with additional P. By contrast, applying high rates of N generally depressed production relative to the control, resulting in a negative PRODlog$_e$*rr*. The N application rate at which the PRODlog$_e$*rr* shifted to negative was lowered by high background N deposition, high annual precipitation, and the presence of vascular plants. P addition had the opposite effect, alleviating the negative response to N and leading to

higher PRODlog$_e$*rr* (Fig. 2a,b, Table 1). For microhabitats above the water table, an increase in July temperature made *Sphagnum* production more sensitive to adding N, particularly when combined with high precipitation rates, leading to a significant interaction between July temperature and microhabitat (Fig. 2b, Table 1). The temperature effect on PRODlog$_e$*rr* was comparable to an N application rate of almost 4 g N m^{-2} yr^{-1} for each 1°C increase (calculated using nonstandardized model coefficients, Table S2).

Omitting studies with N-application rates beyond realistic deposition rates (> 5 g N m^{-2} yr^{-1}) from the analysis did not change the coefficients in our model (not shown), indicating that our results were not driven by high rates of N application. This further supports our assumption that the *Sphagnum* response to experimental N addition can be used to predict its response to natural atmospheric N deposition, even at more extreme N influx. It also illustrates the importance of factors other than N application rate in explaining the N effect on *Sphagnum* production.

Our main model explained 53% of the heterogeneity in outcomes among the experiments (calculation based on τ^2, see the Description section). Model runs on subsets of the dataset containing individual *Sphagnum* species confirmed the general effects of the explanatory variables, with the exception of July temperature. High July temperatures depressed PRODlog$_e$*rr* of *S. fuscum*, but did not affect *S. magellanicum*. Consequently, we included an interaction effect between July temperature and microhabitat in the main model. Initial model runs without this interaction term, indicated a smaller, but still significant temperature effect on PRODlog$_e$*rr* (not shown).

Sphagnum N concentration

Adding N increased *Sphagnum* N concentration (Fig. 3a,b, Table 1) relative to the control, leading to positive response ratios (Nlog$_e$*rr*). Nlog$_e$*rr* showed a curvilinear response to N-application rate, suggesting N saturation of the *Sphagnum* tissue or, alternatively, reduced N-uptake efficiency at high N-application rates. Increasing the duration of the experiment intensified the response of *Sphagnum* N concentration (Fig. 3a, Table 1), while an elevated position above the water table (hummocks; Fig. 3b) and a high N dose concentration (Table 1) depressed the response ratio. July temperature, annual precipitation and P addition showed small coefficients with wide credible intervals overlapping zero, indicating they were less important in explaining the N effect on Nlog$_e$*rr* (Table 1). Overall, the explanatory variables explained 61% of the heterogeneity in the outcomes among the experiments. Model runs on subsets of the dataset containing individual *Sphagnum* species confirmed the general effects of the explanatory variables.
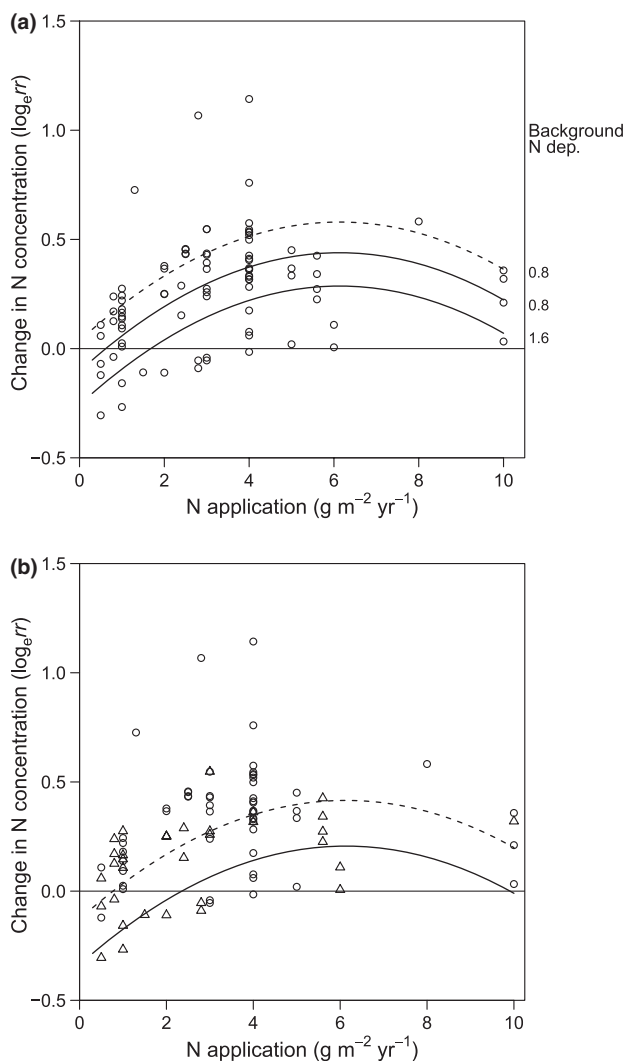
Fig. 4 Relationship between *Sphagnum* production response to experimental nitrogen (N) addition (PRODlog$_e rr$) and *Sphagnum* N concentration for four different scenarios combining low and high (lower and upper quartile of the variables) July temperature and annual precipitation rate. Solid lines, mean July temperature = 13.5°C; dashed line, mean July temperature = 16.5°C. Post-treatment *Sphagnum* N concentration on a dry weight (DW) basis was regarded as a proxy for N loading, which comprises N-application rate, experiment duration and the background N deposition. Positive values for the response ratio indicate an increased production relative to the control treatment.

Fig. 3 Modelled response curve of *Sphagnum* nitrogen (N) concentration (Nlog$_e rr$) to experimental N addition as affected by: (a) N application rate combined with background N deposition (N dep., two rates) and experiment duration (two seasons, solid lines; five seasons, dashed line), (b) height above the water table. Hummocks is high (triangles, solid line) and lawn low (circles, dashed line). Positive values for the response ratio indicate an increased N concentration relative to the control treatment. For the fitted lines, all other variables in the model (Table 1) were set at their average values. Each data point represents one experiment.

Sphagnum N concentration as a predictor of production response?

As most explanatory variables that affected production affected *Sphagnum* N concentration even more, we tested how well we could predict N effects on production by using *Sphagnum* N concentration as an explanatory variable. We simplified our model by replacing the three predictors quantifying N loading (application rate, experiment duration and background N deposition) with the *Sphagnum* N
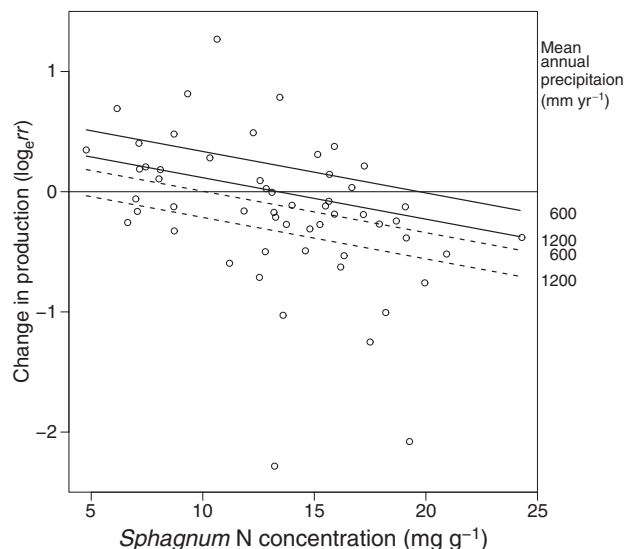
concentration in the N-treated plots. Doing this also accounted for the effects of N dose concentration and P addition, since they are largely mediated through the *Sphagnum* N concentration (Limpens *et al.*, 2004). For the simplified model, we used a data subset containing 55 experiments with values for both production and N concentration. The smaller dataset reduced the number of predictors we could include. Since the subset mainly included long-term experiments, in which vascular plants were seldom removed, we did not include presence of vascular plants in this model. Additionally, we left out the interaction between microhabitat and temperature, but kept temperature and precipitation, as these predictors explained the greater heterogeneity between experiments. Consequently, our simplified model only included temperature, precipitation and *Sphagnum* N concentration in the N-treated plots as explanatory variables.

In the simplified model, tissue N concentration was a strong predictor for the effect of N application, showing a positive effect on production at low N concentrations but negative at higher values (Fig. 4, Table 1). Increases in July temperature or annual precipitation exacerbated the negative N effect, leading to lower PRODlog$_e rr$ values for the same N concentration. For example, the model predicted depressed production relative to the control above tissue N

concentrations of 10 mg g^{-1} DW for an average July temperature of 16.5°C and a mean annual precipitation of 600 mm (Fig. 4, Table 1). The simplified model explained 59% of the heterogeneity among experimental outcomes in this data subset. Our main model, containing eight covariates, explained 58% when run for the same subset. The accuracy with which the simplified model could predict an increase (positive PRODlog$_e$rr) or decrease (negative PRODlog$_e$rr) in production after N fertilization was assessed with the leave-one-out procedure (see the Description section). The simplified model predicted correctly in 75% of the experiments, with many of the wrongly predicted data points close to zero. Using the coefficients of the simplified model presented in Table 1 gave an accuracy of 76%.

Model checking

There were no indications of bias in our dataset related to sample size. Sampling variance of PRODlog$_e$rr peaked in a few experiments with strongly negative effect sizes (PRODlog$_e$rr < −1.5) compared with the rest of the data set (six experiments, Fig. S1c). Some extremes are expected, as disturbance of a natural ecosystem may generate large variation. Residual analyses of the main models for PRODlog$_e$rr and Nlog$_e$rr showed no patterns (not shown), but the six experiments were largely overestimated in the main PRODlog$_e$rr model. These experiments were associated with high sample variances compared with the other experiments. We found no other common factors – the concentration, the form, the frequency in which N was applied, or extreme summer drought – that set these experiments apart; none of these explained the low PRODlog$_e$rr. Excluding the data points did not affect the results, except for two terms: the interaction between July temperature × microhabitat and the mean annual precipitation. Although both remained significant predictors, their standardized regression coefficients changed from −0.53 to −0.30 (July temperature × microhabitat) and from −0.30 to −0.17 (annual precipitation). When the interaction term, July temperature × microhabitat, was omitted from the model, temperature remained an important predictor (coefficient and upper and lower interval limits: −0.17, (0.00, −0.37).

Predictive model checking showed that the main features of the data were captured by the PRODlog$_e$rr and the Nlog$_e$rr models: the minimum and maximum values as well as the standard deviation of the replicated data sets did not differ significantly from the original data. Furthermore, the 95% interval coverage of the coefficients given by the replicated data sets covered the point estimates in the main models in 94–96% of the cases. In view of the above, the models showed a reasonable fit and gave robust results.

Discussion

Our most important result is the interaction of N deposition with climatic factors, such as precipitation and temperature, on *Sphagnum* production. This result is particularly important given that most peatlands are situated at high latitudes where the largest increases in atmospheric temperatures have been observed (Hansen *et al.*, 2006) and further strong increases in temperature and shifting precipitation patterns (IPCC, 2007) are expected. N-deposition rates at the northernmost remote sites, such as in northern Canada and Siberia are still very low, and are not rising fast, while deposition rates at more southern locations are high and rising faster or stabilizing at high values, as in the Netherlands (Holland *et al.*, 2005; Galloway *et al.*, 2008). As even a small temperature increase offset the positive effect of N application on *Sphagnum* production at low N loading (Figs 2b, 4), our results indicate that current rates of N deposition in warmer conditions will strongly inhibit C sequestration in *Sphagnum*-dominated vegetation. This would not only be a result of the accelerated decomposition of peat associated with higher temperatures (Dorrepaal *et al.*, 2009), but also through depressed production of the main peat former *Sphagnum*. Initially we assumed that, at constant N loading, an elevation in temperature (Xia & Wan, 2008; Breeuwer *et al.*, 2009) and increase in precipitation (Robroek *et al.*, 2009) would dilute the plant N content by stimulating biomass production, thus postponing negative effects associated with high tissue N concentration (Limpens *et al.*, 2006). However, the opposite was found. Why elevated temperature and high precipitation should make *Sphagnum* production more sensitive to N is poorly understood and urgently needs to be elucidated, as interactions between temperature, precipitation and N deposition may accelerate changes in vegetation composition and associated effects on C sequestration potential (Dise, 2009). The temperature sensitivity might be explained at different scales, making interpretation of our results difficult. It is generally assumed that, at the plant-leaf scale increases in N enhance (vascular) plant respiration relatively more than gross photosynthesis (Anten *et al.*, 2000), leading to curvilinear relationships between production and N application (Salemaa *et al.*, 2008). The same holds for temperature: when temperature rises, respiration increases more than gross photosynthesis (Harley *et al.*, 1989). The combination of high N and high temperature could thus result in a lower PRODlog$_e$rr than assumed from N loading alone. Alternatively, the reduction in PRODlog$_e$rr could be mediated through other factors, such as water stress (Van der Heijden *et al.*, 2000; Bragazza, 2008) at the plant scale, or through intensified biotic interactions (Wiedermann *et al.*, 2007) or increased N mineralization in the underlying peat (Weltzin *et al.*, 2000)

at the community level. The sensitivity of the N effect to mean annual precipitation is even more unexpected than the temperature effect. As mosses are poikilohydric plants (Proctor, 2000), their photosynthetic activity is often limited by water. Indeed, Gunnarsson (2005) reported a positive correlation between mean annual precipitation and *Sphagnum* production. This suggests optimal growing conditions if precipitation is high, in marked contrast to our result. A similar, poorly explained, negative interaction between precipitation and N fertilization has been reported for vascular plant productivity in wetlands in a meta-analysis by LeBauer & Treseder (2008). The authors contributed this effect to limitation of production by elements other than N, and by increasingly anoxic conditions. Although this would explain an absence of an N effect on production, it does not help us understand a greater negative effect with increasing precipitation. It should be noted that the correlations with temperature and precipitation are not necessarily causal relationships. Other factors might be correlated with these variables and experimental work is needed to further explore the relationships we found.

The strong sensitivity of the N effect to explanatory variables other than N-application rate shows that the effects of N deposition cannot be accurately predicted from experimental N addition by focusing on N-application rates alone. One way is to calculate the cumulative N flux into the ecosystem (Dupré *et al.*, 2010); another is to focus on the extent to which the vegetation or ecosystem has been loaded, or saturated, by N (Berendse *et al.*, 2001). We showed for *Sphagnum* that the production response could be well predicted using only tissue N concentration, temperature and precipitation. Whether changes in *Sphagnum* N concentration can also be used to predict changes in production outside fertilization experiments remains to be tested.

The key mechanism causing the N-induced decline in *Sphagnum* production remains uncertain: the strong predictive value of *Sphagnum* N concentration in combination with the alleviating, albeit tentative, effect of adding P suggests physiological stress associated with nutrient imbalance (Bragazza *et al.*, 2004; Carfrae *et al.*, 2007; Arróniz-Crespo *et al.*, 2008). Experimental evidence for N-induced physiological stress in *Sphagnum* is scarce and damage to the photosynthetic apparatus does not seem to occur below concentrations of 20 mg N g^{-1} DW (Granath *et al.*, 2009). This argues for a more important role for biotic interactions (Manning *et al.*, 2006), such as sensitivity to pests or pathogens (Wiedermann *et al.*, 2007) and enhanced competition with microalgae (Gilbert *et al.*, 1998), other mosses (Mitchell *et al.*, 2002) or vascular plants (Heijmans *et al.*, 2002). Indeed, our results indicate that *Sphagnum* production with vascular plants present was more sensitive to adding N than *Sphagnum* with vascular plants removed. Since most fertilization experiments used

plots with maximum vascular plant covers of 25% in their first year, the results suggest negative effects at covers well below the 70% which has been suggested to be the lowest cover of dwarf shrub vegetation at which *Sphagnum* production becomes limited by light (Hayward & Clymo, 1983; Malmer *et al.*, 2003). It is likely that factors other than light interception by the canopy dominate the *Sphagnum* production response at these sparse vascular plant covers, such as increased litter production (Limpens *et al.*, 2006), interception of snow or dry N deposition (Dorrepaal *et al.*, 2003; Limpens *et al.*, 2004), or microclimatic effects (Grosvernier *et al.*, 1995). In light of their potential impact on the *Sphagnum* production response, the nature of biotic interactions requires attention in future fertilization experiments.

The degree of explained heterogeneity among experimental outcomes in our main models (53–61%, Table 1) is very high when compared with other meta-analysis studies, using similar methods (leBauer & Treseder, 2008), presumably because we restricted our analysis to the response of one genus, *Sphagnum,* growing in peatlands. Nevertheless the unexplained 47–39% in combination with the relatively small effect size of N-application rate in comparison to the other covariates suggests that the *Sphagnum* production response to N addition is also subject to factors outside our analyses. Potential candidates, for which data were not available for every study, are the water availability in the upper moss layer (Gerdol *et al.*, 2007), accurate values for total background N deposition (Boring *et al.*, 1988) and cover of vascular plants instead of presence–absence data.

Conclusion

Adding N depressed *Sphagnum* production at high N loading. The magnitude of the decline was related to *Sphagnum* N concentration, indicating negative effects associated with N saturation. The presence of vascular plants and absence of P addition accentuated the detrimental N effects, indicating intensified biotic interactions and altered nutrient stochiometry with N loading, respectively. Increased mean annual precipitation and elevated July temperature (for moss growing well above the water table on hummocks) made *Sphagnum* more sensitive to N deposition: an increase of 1°C in mean July temperature or 300 mm annual precipitation was equivalent to the negative effect of adding 4 g N m^{-2} yr^{-1}. The unexpected negative interacting effects of climatic factors indicate an important gap in our current understanding of the mechanisms by which N affects *Sphagnum* production. Our results suggest that current rates of N deposition in a warmer world will strongly inhibit C sequestration in *Sphagnum*-dominated vegetation, not only through the accelerated peat decomposition associated with higher temperatures, but also through depressed production of the main peat former *Sphagnum*.

Acknowledgements

We are indebted to Dr John Stevens for his statistical advice on meta-regressions and anonymous referees for improving the quality of the manuscript. We thank Uppsala University and Wageningen University for facilitating contact between the lead authors. Finally, a warm thanks to all researchers who worked on the N fertilization experiments included in this meta-analyses: without their work, ours would not have been possible.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Scatterplots of effect size vs sample size and sample variance for *Sphagnum* production (a, c), and N concentration (b, d).

Table S1 Data file with overview of data sources and explanatory variables

Table S2 Results of the Bayes linear models with PRODlog$_e$rr and Nlog$_e$rr with *nonstandardized* coefficients and the range and SD for the continuous explanatory variables

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