New Phytologist

Heatwave 2003: high summer temperature, rather than experimental fertilization, affects vegetation and CO_2 exchange in an alpine bog

Renato Gerdol, Luca Bragazza and Lisa Brancaleoni

Department of Biology and Evolution, Ferrara University, Corso Ercole I d'Este 32, I 44100 Ferrara, Italy

Author for correspondence:
Renato Gerdol
Tel: +39 (0)532 293775
Fax: +39 (0)532 208561
Email: grn@unife.it

Received: *29 November 2007*
Accepted: *4 February 2008*

Summary

• Nitrogen and phosphorus were added experimentally in a bog in the southern Alps. It was hypothesized that alleviating nutrient limitation will increase vascular plant cover. As a consequence, more carbon will be fixed through higher rates of net ecosystem CO_2 exchange (NEE).

• The vascular cover did increase at the expense of *Sphagnum* mosses. However, such vegetation changes were largely independent of the treatment and were probably triggered by an exceptional heatwave in summer 2003.

• Contrary to the tested hypothesis, NEE was unaffected by the nutrient treatments but was strongly influenced by temperature and water-table depth. In particular, ecosystem respiration in the hot summer of 2003 increased dramatically, presumably owing to enhanced heterotrophic respiration in an increased oxic peat layer.

• At the end of the experiment, the *Sphagnum* cover decreased significantly in the nitrogen-fertilized treatment at hummock microhabitats. In the long term, this will imply a proportionally greater accumulation of vascular litter, more easily decomposable than the recalcitrant *Sphagnum* litter. As a result, rates of carbon fixation may decrease because of stimulated respiration.

Key words: atmospheric nitrogen deposition, climate change, decomposition, gas exchange, nutrient, peat, photosynthesis, respiration.

New Phytologist (2008) **179**: 142–154

doi: 10.1111/j.1469-8137.2008.02429.x

Introduction

Northern bogs are characterized by a sustained imbalance between rates of plant production and decay, which results in the accumulation of partially decomposed organic matter (i.e. peat) (Gorham, 1991; Tolonen & Turunen, 1996). Most of the northern bogs represent long-term sinks for atmospheric CO_2 (Turunen *et al.*, 2002), although carbon (C) flux can vary from a sink to a source in individual years, mostly owing to weather fluctuations (Roulet *et al.*, 2007). Despite rather low CO_2 uptake rates through photosynthesis (Frolking *et al.*, 1998), emission rates of CO_2 from northern peatlands are much slower than photosynthetic CO_2 fixation. Harsh environment, including acidic pH, cold soil temperatures and frequent substrate anoxia, account for slow decay and, hence, low rates of CO_2 emission from peatland surface. However, organic matter decomposition in peatlands is also regulated by litter quality, the latter depending upon intrinsic features of bog plants (Moore & Basiliko, 2006). Bogs are hydrologically ombrotrophic, that is, they are fed exclusively by precipitation, which historically has very low concentrations of dissolved nutrients. As a consequence, bog vegetation is formed of species adapted to cope with extreme nutrient poorness (Aerts *et al.*, 1999).

The vegetation of ombrotrophic bogs consists of two functionally distinct layers, as plants in the two layers use different sources of nutrients. On one hand the moss layer, mostly comprising *Sphagnum* species, depends on nutrients derived from the atmosphere through dry and wet deposition. On the other hand the field layer, including rooting vascular

species of various growth forms, absorbs nutrients derived from the mineralization of the litter (Malmer *et al.*, 1994). Bog plant litter, in general, breaks down slowly because of the low nutrient content in plant tissues. However, rates of bog litter decomposition vary greatly in relation to growth form. In particular, decomposition rates of *Sphagnum* litter always are much slower than those of vascular litter (Bragazza *et al.*, 2007), as *Sphagnum* tissues are rich in recalcitrant phenolics (Verhoeven & Liefveld, 1997; Freeman *et al.*, 2004).

Environmental changes associated with human activities, including both climate warming and increased atmospheric nutrient deposition, are likely to affect the C balance of northern peatlands. However, variations in individual environmental factors can have different, and in some cases contrasting, effects on C incorporation in, and C loss from northern peatlands. For example, higher temperatures are likely to raise net plant productivity but they are also expected to enhance litter decay (Dioumaeva *et al.*, 2002) in bogs. Increased drainage and aeration of peatland surface, as a possible consequence of higher evapotranspiration rates, can reduce both photosynthetic C incorporation and respiratory C loss from living bog plants, especially *Sphagnum* mosses (Gerdol *et al.*, 2007), but they likely promote C loss from the underlying peat layers (Scanlon & Moore, 2000). Increased atmospheric deposition of nutrients, especially nitrogen (N) reduces the capacity of the *Sphagnum* layer to retain N from aerial deposition, thus increasing N availability for vascular root absorption (Heijmans *et al.*, 2002). Consequently, a higher nutrient status in the rooting layer will promote growth of vascular plants, thus altering the competitive balance between *Sphagnum* mosses and vascular plants and, possibly, among vascular species of different growth forms. In particular, higher vascular plant cover can be detrimental to *Sphagnum* because of shading (Hayward & Clymo, 1983). This may eventually lead to changes in the floristic composition of bog ecosystems (Berendse *et al.*, 2001). If the accumulation of recalcitrant *Sphagnum* litter decreases with respect to the accumulation of more easily decomposable vascular litter, this can further increase rates of organic matter decay. However, the effects of increased nutrient input on peat decay are still unclear, with extant studies reporting enhanced (Coulson & Butterfield, 1978), reduced (Rochefort *et al.*, 1990), or unchanged (Tomassen *et al.*, 2004) peat decomposition rates after experimental N addition.

In 2002 we set up an experiment for N and phosphorus (P) addition in an ombrotrophic bog in the south-eastern Alps (North Italy). This bog was chosen for this experiment because total atmospheric N deposition in this region (*c.* 0.8 g m^{-2} yr^{-1}; see Gerdol *et al.*, 2007) probably is close to the threshold at which the N retention capacity of the *Sphagnum* layer is saturated (Gunnarsson & Rydin, 2000; Bragazza *et al.*, 2004). The main goal of the experiment was to test whether the *Sphagnum* layer in the bog still is able to absorb the amended N. If not, the N not retained by *Sphagnum* will be absorbed by vascular plants, thus ameliorating the nutrient status in their tissues. Since previous studies have reported stoichiometric imbalance between N and P in *Sphagnum* tissues as possibly hindering absorption of additional N by *Sphagnum* plants (Bragazza *et al.*, 2004; Limpens *et al.*, 2004), a reduced ability of *Sphagnum* plants to take up N may be counteracted if P is amended together with N.

Our main hypothesis was that increased growth of vascular plants owing to fertilization will, in the short term, enhance rates of CO_2 fixation since these rates are positively correlated with vascular cover (Humphreys *et al.*, 2006; Wilson *et al.*, 2007). We also hypothesized that in the long term the accumulation of vascular litter will accelerate C loss through enhanced heterotrophic respiration, thus counteracting and possibly reversing the short-term trend. We report here on the short-term results of this experiment, corresponding to the years 2002–2005, when the experiment was strongly affected by an unprecedented heatwave in summer 2003. The frequency of extreme climate events, particularly heatwaves, is expected to increase in the alpine region as climate continues to warm (Beniston, 2007). Therefore, the 2003 anomaly represented a sort of natural experiment, which allowed us to explore interactions between nutrient amendment and climate.

Materials and Methods

Study site and experimental design

The study site and the experimental design are described in detail elsewhere (Gerdol *et al.*, 2007). Briefly, the experiment was carried out in a bog located close to San Pellegrino Pass in the Dolomites (North Italy, 46°21′N, 11°44′E; 1800 m above sea level). The vegetation consists of a mosaic of hummocks and lawns. The moss layer is dominated by *Sphagnum fuscum* in hummocks and by a mixture of *Sphagnum russowii*, *Sphagnum fallax* and *Sphagnum magellanicum* in lawns. The field layer comprises vascular species of different growth forms: deciduous shrubs (*Vaccinium myrtillus* and *Vaccinium uliginosum*), evergreen shrubs (*Calluna vulgaris* and *Vaccinium vitis-idaea*), graminoids (mostly *Eriophorum vaginatum*) and forbs (*Potentilla erecta* and *Homogyne alpina*). Plant growth starts a few days after snowmelt, which is usually achieved in late May, and lasts *c.* 100 d (R. Gerdol, pers. obs.). Although snowmelt timing varies to a certain extent from year to year, we conventionally set the growing season as the period 1 June–15 September (Gerdol *et al.*, 2007). The regional climate is cool-temperate and moderately humid, with mean annual temperature of *c.* 3°C and mean total annual precipitation of *c.* 1000 mm (of which *c.* 500 mm falling during the growing season) at 2000 m.

Sixty 1-m^2 plots, 36 in hummocks and 24 in lawns, were set up in late May 2002. The nutrients (N as NH_4NO_3 and P as NaH_2PO_4) were added, in equal amounts, five times in each of the growing seasons 2002–2005 as sprayed solutions simulating small (1 mm) rainy events. The control plots

received the same amount of distilled water. The experimental design was full factorial, with five replicates × two habitats (hummocks and lawns) × six treatments, that is: –N –P (control, no N or P added); –N +P (no N, 1 g P m^{-2} yr^{-1}); LN –P (1 g N m^{-2} yr^{-1}, no P); LN +P (1 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}); HN –P (3 g N m^{-2} yr^{-1}, no P); HN + P (3 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}).

Plant cover

In each plot a 50 cm × 50 cm frame was set up in which the cover of vascular species was assessed nondestructively by the point intercept method (Jonasson, 1988). The percentage cover of mosses (mostly consisting in *Sphagnum* species) was estimated visually within each frame. All estimates of plant cover were performed once in each year, at the peak of the growing season (end July), on a day when the peatland was well hydrated. In 2004 and 2005, in all plots the leaf area index (LAI) was determined on each of the four occasions when CO_2 exchange was measured. The LAI was measured using a ceptometer (AccuPAR LP-80; Decagon, Pullman, WA, USA).

CO_2 exchange

Ecosystem CO_2 exchange Before the beginning of the experiment, three replicate plastic square collars (inner size: 28 × 28 cm) for each treatment were placed in the two habitats (hummocks and lawns), with 36 collars in total. The collars were pushed into the peat after cutting a 5 cm deep slot around the collar edge. Preliminary measurements of ecosystem CO_2 exchange were performed two times during the growing season 2002 (early August and mid September, respectively). However, since in the first experimental season nutrient addition had not yet exerted any effect either on CO_2 exchange (data not shown) or on production rates of *Sphagnum* plants (Gerdol *et al.*, 2007), the CO_2 exchange data of the growing season 2002 were not considered in the statistical computations. In the growing seasons 2003–2005, CO_2 exchange rates were determined four times per season at approximately monthly intervals. On each occasion, water-table depth was measured manually in 10 perforated pipes of which six were in hummocks and four were in lawns. Temperature in the surface (10 cm) peat layer, called soil temperature for brevity, was recorded continuously by a data logger in the growing seasons 2003–2005 (see Gerdol *et al.*, 2007 for details).

All measurements of ecosystem CO_2 exchange were made on clear days, from 10:00 h to 16:00 h, when irradiance was > 1200 μmol photons m^{-2} s^{-1} and, therefore, saturating the photosynthetic capacity of the plant cover (Frolking *et al.*, 1998; Alm *et al.*, 1999). A Plexiglas chamber (basal area 900 cm^2), equipped with a circulation fan and a pressure equilibration tube, was attached to the collar and the height of the chamber above the top of the *Sphagnum* capitula was measured each time in order to obtain the exact volume sampled. The CO_2 concentrations in the chamber were measured with a Li-Cor 800 infrared gas analyser (Li-Cor Instruments, Lincoln, NE, USA), attached by hoses to the chamber wall and connected with a 0.6 cm plastic pipe to the chamber itself in a closed circuit. The CO_2 fluxes were calculated on the basis of changes in headspace CO_2 concentrations with time and expressed as mass of CO_2 exchange per square meter and hour, using the ideal gas law. Change in headspace CO_2 concentration was measured every 15 s until stabilization. In *c.* 95% of the runs stabilization occurred within 2 min. However, air temperature within the chamber never rose more than 3°C above outer air temperature.

In every collar, CO_2 exchange was measured first under ambient light conditions, which corresponds to net ecosystem CO_2 exchange (NEE). In our sign convention, negative values indicate CO_2 uptake by, and positive values CO_2 emission from, the ecosystem. The CO_2 exchange was the measured under darkness, obtained by covering the chamber with a thick, black plastic sheet. This corresponds to CO_2 release and will be called, for brevity, ecosystem respiration (ER). However, CO_2 released from the bog surface has several sources: autotrophic (i.e. plant) respiration, including both respiration of above-ground tissues and root respiration, as well as respiration of living moss tissues; heterotrophic (i.e. microbe) respiration; anaerobic microbial CO_2 production during peat decomposition and CH_4 oxidation by methanotrophs. At the end of the experiment, 24 50 cm × 50 cm additional plots (12 in hummocks and 12 in lawns) were set in areas that had not received any treatment. At the beginning of the growing season 2005 the whole above-ground vascular vegetation as well as the top 5-cm layer of *Sphagnum* mosses, including all below-ground vascular tissues rooting in the surface layer, was clipped in half of these additional plots. On that occasion, connections with the rooting system of plants growing outside the plots were severed using a 40-cm long serrated knife. All regrowth from the cut plant parts was clipped again the day before measurement. The CO_2 release in dark chambers was determined in these additional plots (both clipped and unclipped) two times in the growing season 2005 (mid August and mid September, respectively) during dry climatic conditions. By comparing rates of CO_2 release from clipped and unclipped plots we aimed to assess autotrophic respiration. It is possible that the measurements may be affected by CO_2 emission from residual decomposing roots left in the plot and/or by respiration from some residual connections with deep-rooting plants. Nonetheless, we are confident that the data can be used for obtaining at least a rough estimate of autotrophic respiration vs other sources of CO_2 emission (principally heterotrophic respiration).

Plant net CO_2 exchange At the peak of the growing season 2003, net CO_2 exchange was determined in living plants. The measurements were made on a sunny day that followed 2 d

of moderate precipitation so that the bog surface was well hydrated. However, in that period the bog had experienced high temperatures for several weeks during which the bog surface appeared strongly dehydrated and the moss layer presented a pale brittle aspect.

Net CO_2 exchange was determined on: a current-year shoot for deciduous and evergreen shrubs; the apical green part of a wisp of leaves for graminoids; 8–10 capitula for *Sphagnum*. Forbs were not considered since they occurred only in a small fraction of the plots. Since rates of net CO_2 exchange in bryophytes, including *Sphagnum* mosses, strongly depend on water content, we determined gravimetrically the moss water content (expressed as the fresh weight : dry weight quotient) in five samples of *Sphagnum* mosses harvested close to the sampling plots at each of the two habitats. The mean mass per mass water content (± 1 SE) in *Sphagnum* tissues was 9.2 ± 0.3 in hummocks and 8.9 ± 0.4 in lawns (i.e. close to the optimum for net photosynthesis in *Sphagnum* mosses) (van Gaalen *et al.*, 2007). The measurements were carried out, at ambient CO_2 concentration (360–380 μmol mol^{-1}), full irradiance (1500–2000 μmol photons m^{-2} s^{-1}) and optimum temperature (20–25°C), using an open infrared gas analyser (LCA4; ADC Co., Hoddesdon, UK). The plant material was enclosed in the leaf chamber for *c.* 1 min during which three or four measurements were taken at 15–20 s intervals. The mean of all measurements performed on each sample was treated as a single value. The sign convention for indicating CO_2 uptake in, or emission from, the plants was the same as for ecosystem CO_2 exchange. At the end of each run the material was stored and carried to the laboratory to determine dry weight after oven-drying for 48 h at 70°C. All of the plants used for the gas exchange measurements were located at least 10 cm apart from the point-intercept grid and from the collars used for determining ecosystem CO_2 exchange as well. Although the harvests were reduced at the very minimum, we are aware that this may have somewhat disturbed the canopy. However, we are confident that the disturbance effect did not vary systematically either with habitat or with treatment. However, in order to avoid excessive disturbance, the plant CO_2 exchange was not measured in subsequent years.

Nutrients

At the peak of the growing seasons 2003–2005, a very small amount (*c.* 200 mg) of young living plant parts (*Sphagnum* capitula, defined as the top 1 cm segments) and current-year leaves of vascular species of all growth forms was harvested at each of the 60 plots. About 50 mg of plant material, previously oven-dried for 48 h at 40°C and powdered with a mill, was digested in 3 ml of H_2SO_4 at 420°C for determination of total N concentrations, by the blue-indophenol method, and total P concentration, by the molybdovanadate method, using in both cases a continuous flow autoanalyser (FlowSys; Systea, Anagni, Italy). Subsamples of the plant material were oven-dried at 105°C for 24 h in order to detect mass loss from 40°C to 105°C.

Computations and statistical analyses

At each plot, percentage change was calculated in the cover of the moss layer as follows: ((Cover 2005 – Cover 2002)/Cover 2002) × 100. Similarly, percentage change was calculated in the number of intercepts of vascular plants as follows: ((Intercepts 2005 – Intercepts 2002)/Intercepts 2002) × 100. The data of percentage changes in moss cover and number of vascular intercepts, respectively, were statistically analysed by two separate three-way factorial ANOVAs with habitat, N addition and P addition as fixed factors.

In order to analyse periodic variations in rates of ecosystem CO_2 exchange in relation to environmental factors, two separate ANCOVAs (for NEE and ER, respectively) were carried out. Water-table depth (with each plot being assigned the water-depth recorded at the closest pipe), LAI and temperature were the continuous predictors; year and season (the latter henceforth called, for clarity, month) were the categorical predictors. The LAI values for the growing season 2003 were estimated based on regression coefficients against point intercepts calculated in 2004 and 2005. The variables were entered stepwise in the analysis with a $P = 0.05$ threshold at each step. The effects of nutrient addition on rates of ecosystem CO_2 exchange were assessed by two-way factorial ANOVAs with N addition and P addition as fixed factors. The ANOVAs for both NEE and ER were run separately for each combination of habitat × year × month.

The data for ER in clipped vs unclipped plots were statistically analysed by a three-way factorial ANOVA with treatment, habitat and month as fixed factors. The data for plant net CO_2 exchange were statistically analysed by a four-way factorial ANOVA with habitat, N addition, P addition and plant type (i.e. *Sphagnum* vs vascular plants) as fixed factors.

The data for nutrient concentrations in the vegetation were subjected to two separate four-way factorial ANOVAs (for N concentration and P concentration, respectively) with habitat, N addition, P addition and year as fixed factors.

Since percentage data obviously were not normally distributed, they were arcsin-transformed before statistical computations. All other variables were checked for normality of distribution by the Kolmogorov–Smirnov test. In most (*c.* 90%) cases the normality assumption was fulfilled. The remainder were log-transformed before analysis. However, in no cases did the statistical tests performed on the transformed variables differ from the ones performed on the original data. Therefore, the results of statistical analyses performed on the untransformed data are presented. When appropriate, LSD *post hoc* tests were used to assess significance of differences among treatments. All statistical computations were performed using the package STATISTICA (Release 6; StatSoft Inc., Tulsa, OK, USA).

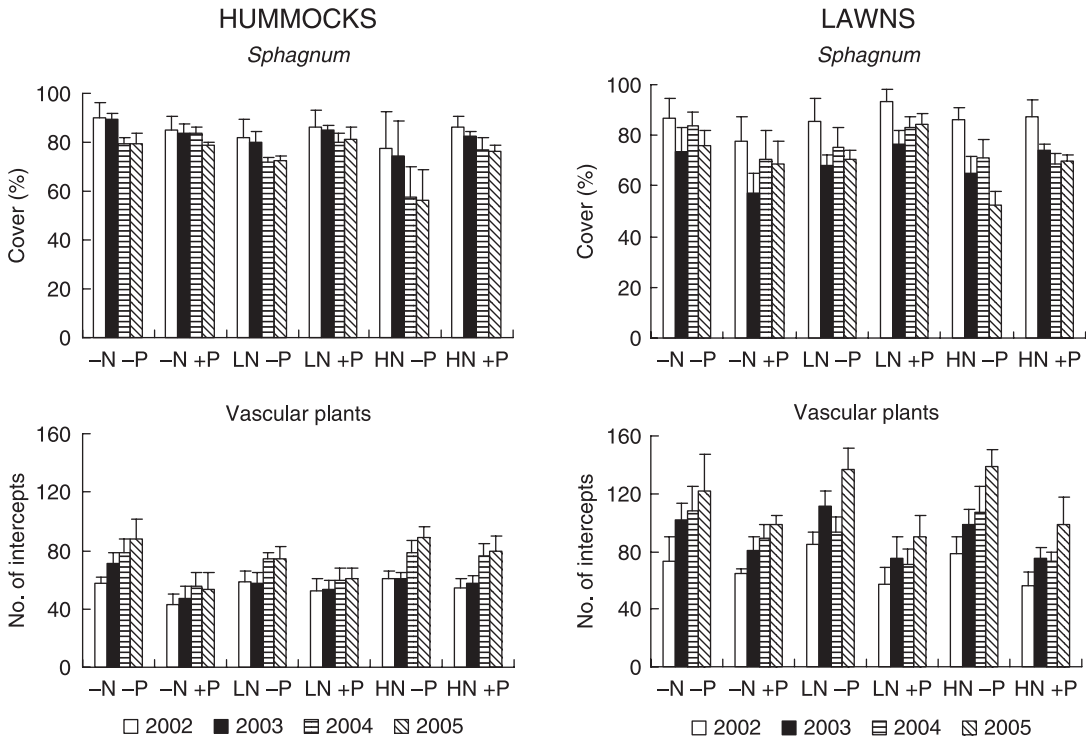

Fig. 1 Mean (+ 1 SE) percentage cover of *Sphagnum* mosses and mean (+ 1 SE) number of intercepts of vascular plants in two bog habitats treated by adding nitrogen (N) and phosphorus (P): –N –P (control, no N or P added); –N +P (no N, 1 g P m^{-2} yr^{-1}); LN –P (1 g N m^{-2} yr^{-1}, no P); LN +P (1 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}); HN –P (3 g N m^{-2} yr^{-1}, no P); HN +P (3 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}). From 2002 to 2005, *Sphagnum* cover decreased and vascular cover increased significantly independent of the treatments.

	Air temperature (°C)	Precipitation (mm)	Soil temperature (°C)
2003	14.1	461	13.9 (4.0–25.1)
2004	12.1	531	12.2 (3.4–21.5)
2005	11.5	284	12.0 (2.5–21.8)

Table 1 Mean air temperature, precipitation and soil temperature (range in parenthesis) in the growing seasons 2003–2005

Results

Environmental variables

There are no climatic records available for the study site. However, data acquired at a meteorological station located *c.* 4 km far from the bog, at almost the same altitude (1770 m), showed that the growing season 2003 was very hot, while mean air temperatures in the growing seasons 2004 and 2005 were at least 2°C lower (Table 1). Total precipitation was close to the regional average in the growing seasons 2003 and 2004 but much lower in the growing season 2005 (Table 1).

Mean soil temperature was higher in the growing season 2003 than in the growing seasons 2004 and 2005. In particular, maximum soil temperature was *c.* 3°C higher in 2003 (Table 1). The water table was closer to the bog surface, and fluctuated less, in the growing season 2004, when precipitation was rather abundant and temperature was intermediate (Table 1). Water-table depth was greater, and fluctuated much more, both in the dry growing season 2005 and in the hot growing season 2003. In the latter the water table achieved maximum depth, especially in July, even if precipitation was normal (Table 1).

Plant cover

From 2002 to 2005 the cover of *Sphagnum* mosses decreased on average by 13.6% while that of vascular plants, as estimated by the number of intercepts, increased by 54.4% (Fig. 1). The *Sphagnum* cover decreased to the same extent in both habitats (Table 2), while the vascular cover increased more (70.8%) in lawns compared with hummocks (38.1%). The effects of nutrient addition on percentage changes in plant cover were overall modest, with only N addition accelerating the decline in *Sphagnum* cover in the HN treatments (23.5%; Table 2). Such a decline was weakly ($P = 0.09$) counteracted by P

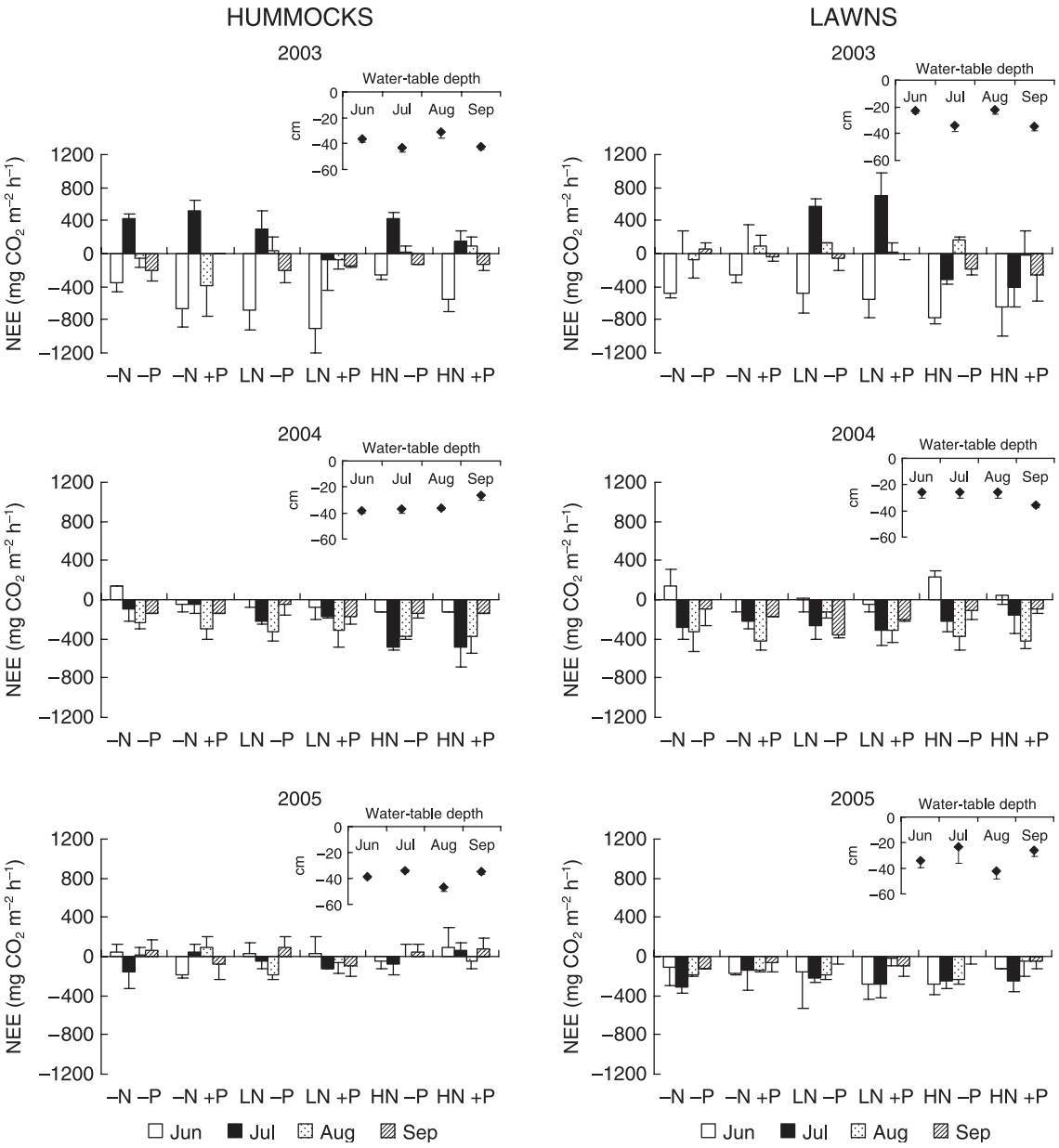

Fig. 2 Mean (+ 1 SE) rates of net ecosystem CO_2 exchange (NEE) in the growing seasons 2003–2005 from two bog habitats treated by adding nitrogen (N) and phosphorus (P): –N –P (control, no N or P added); –N +P (no N, 1 g P m^{-2} yr^{-1}); LN –P (1 g N m^{-2} yr^{-1}, no P); LN +P (1 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}); HN –P (3 g N m^{-2} yr^{-1}, no P); HN +P (3 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}). Negative values indicate CO_2 fixation; positive values indicate CO_2 efflux. There were no significant effects of nutrient addition. The mean (+ 1 SE) water-table depth on each sampling date is shown in the insets.

addition, since *Sphagnum* cover decreased somewhat less when P was amended together with N (Fig. 1).

The LAI in 2004 and 2005 was close to zero at the beginning of the growing season, increased rapidly in June and peaked at the end of July. Then, it remained almost unchanged in August and decreased by *c.* 20% in September (data not shown). The peak-season LAI ranged between 0.25 and 1.85 in hummocks, and between 0.35 and 2.25 in lawns. The LAI was positively correlated with total number of vascular plant intercepts both in 2004 ($r = 0.59$; $n = 60$; $P < 0.001$) and in 2005 ($r = 0.54$; $n = 60$; $P < 0.001$).

Ecosystem CO_2 exchange

Instantaneous rates of NEE were strongly influenced both by water-table depth and by temperature, but were unaffected by

	Sphagnum cover	Vascular intercepts
Habitat	1.01 (1)	**11.54 (1)****
Nitrogen (N) addition	**3.50 (2)***	0.26 (2)
Phosphorus (P) addition	2.99 (1)	0.21 (1)
Habitat × N addition	0.15 (2)	0.49 (2)
Habitat × P addition	0.09 (1)	0.24 (1)
N addition × P addition	0.78 (2)	0.09 (2)
Habitat × N addition × P addition	0.04 (2)	0.50 (2)

Habitat, N addition and P addition were the fixed factors.
Significant values are in bold type: *$P < 0.05$; **$P < 0.01$.

Table 2 *F* values (df in parentheses) obtained from three-way ANOVAs of percentage variations in *Sphagnum* moss cover and number of vascular plant intercepts from 2002 to 2005

Table 3 Synthesis of the statistics for the stepwise ANCOVAs of net ecosystem CO_2 exchange (NEE) and ecosystem respiration (ER)

	NEE	ER
Water-table depth	12.26 (1)***	4.25 (1)*
Leaf area index (LAI)	–	–
Temperature	7.52 (1)**	7.86 (1)**
Year	–	7.22 (2)**
Month	7.98 (3)***	23.37 (3)***
Year × month	14.50 (6)***	25.06 (6)***
r^2	*0.36****	*0.46****

Only significant *F* values (df in parentheses) are shown, for the variables retained at the last step of the analysis. Multiple r^2 are in italics.
Water-table depth, LAI and temperature were the continuous predictors; year and month were the categorical predictors.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

LAI (Table 3). Indeed, there was less CO_2 uptake when temperature was higher and/or water-table was deeper. The NEE was most negative in 2004, when there was net CO_2 uptake in all months (Fig. 2) and least negative in 2003, but there were no significant among-year differences in rates of NEE (Table 3). By contrast, NEE did vary significantly with month, with overall most negative values in June. There was a significant year × month interaction, especially because of the positive NEE values, indicating net loss of CO_2, recorded at most of the plots in July and August 2003 (Fig. 2). The NEE was unaffected by the nutrient amendments. However, NEE was weakly ($P < 0.10$) enhanced by adding N at high level in the lawns in July 2003 and in the hummocks in July and August 2004 (Fig. 2).

The ER also was strongly influenced by water-table depth and temperature, but not by LAI, with greater CO_2 emission at high temperatures and greater water-table depth (Table 3). It varied significantly with year and with month as well (Table 3). Indeed, rates of CO_2 emission were overall highest in 2003 and in July (Fig. 3). However, ER was particularly high in June and August 2003, which resulted in a significant year × month interaction (Table 3, Fig. 3). Unlike NEE, ER was affected to a certain extent by nutrient amendment, especially towards the end of the experimental period. The observed pattern, however, was rather variable, since N addition stimulated ER in the hummocks in July 2005 and in the lawns in September 2004. Conversely, P addition had no effects on ER in the hummocks, reduced ER in the lawns in September 2004 but increased ER in the lawns in September 2005 (Fig. 3).

The ER in the additional unfertilized plots did not differ with habitat ($F_{1,40} = 0.26$; $P = 0.61$) and was unaffected by clipping ($F_{1,40} = 0.88$; $P = 0.35$). In other words, autotrophic respiration accounted for a negligible part of ecosystem CO_2 emission in dry periods. The ER in the additional plots was significantly ($F_{1,40} = 4.79$; $P = 0.03$) greater in August than in September. However, in both months the rates of CO_2 emission from the additional plots were very similar to the overall rates of CO_2 emission from the treatment plots (August 2005: 222 ± 20 mg CO_2 m^{-2} h^{-1} in the treatment plots vs 233 ± 20 mg CO_2 m^{-2} h^{-1} in the additional plots; September 2005: 205 ± 20 mg CO_2 m^{-2} h^{-1} in the treatment plots vs 177 ± 16 mg CO_2 m^{-2} h^{-1} in the additional plots).

Plant net CO_2 exchange

At the peak of the growing season 2003, the rates of net CO_2 exchange in living plants were not influenced by N addition ($F_{2,237} = 1.65$; $P = 0.19$) or P addition ($F_{1,237} = 0.48$; $P = 0.49$). Net CO_2 exchange varied greatly in the two plant types ($F_{1,237} = 918.87$; $P < 0.001$), with *Sphagnum* plants in the moss layer emitting CO_2 and vascular plants in the field layer taking up CO_2, independent of the treatment (Fig. 4). Overall, the rates of net CO_2 exchange did not vary significantly in relation to habitat. However, *Sphagnum* mosses presented lower rates of CO_2 emission in hummocks, compared with lawns (Fig. 4).

Nutrients

The N and P concentrations in the plant biomass (Figs 5, 6) varied strongly with habitat and with year. Indeed, N concentration ($F_{1,72} = 28.02$; $P < 0.001$) and P concentration ($F_{1,72} = 90.30$; $P < 0.001$) were higher in lawns. The N

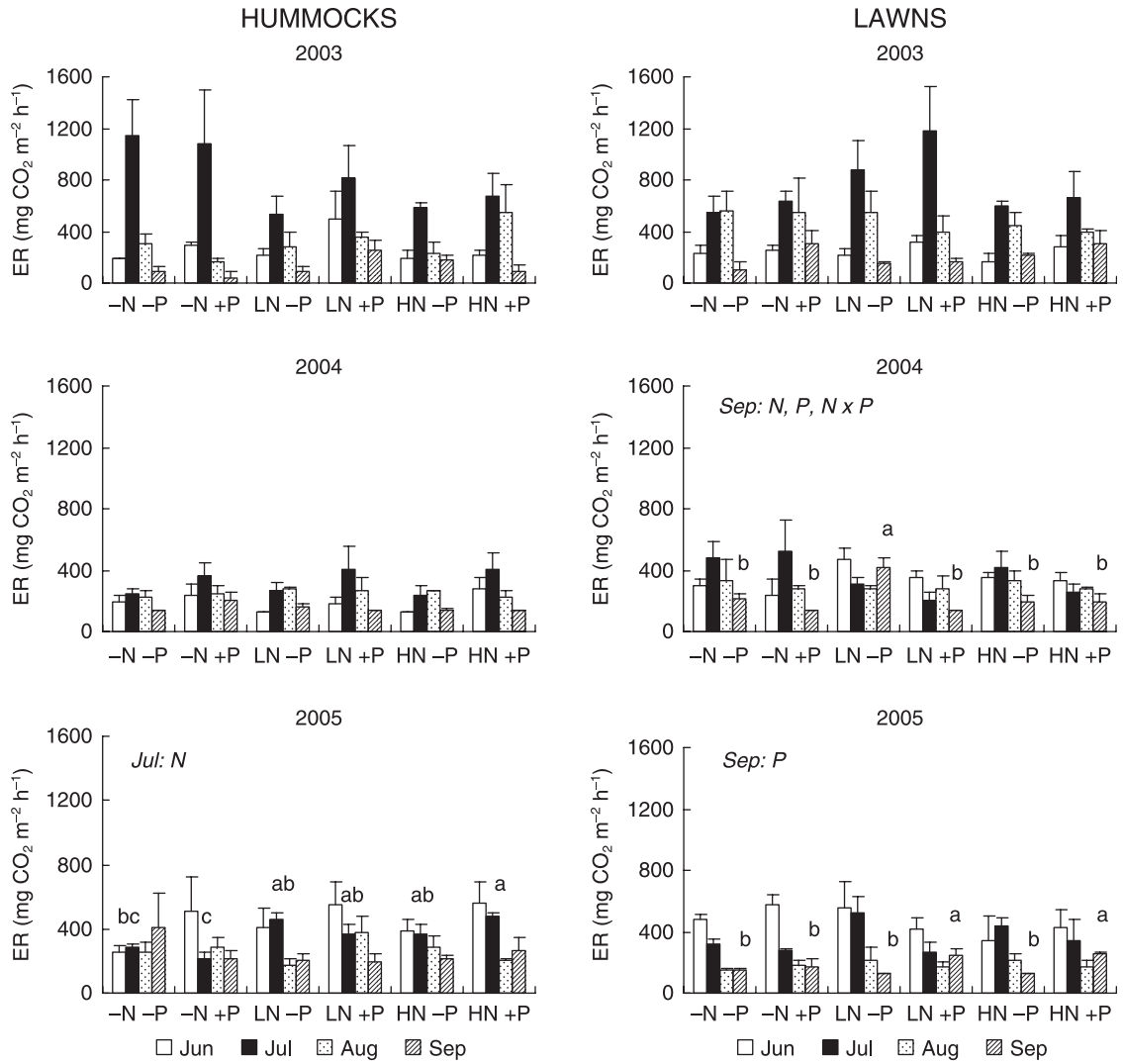

Fig. 3 Mean (+ 1 SE) rates of ecosystem respiration (ER) in the growing seasons 2003–2005 from two bog habitats treated by adding nitrogen (N) and phosphorus (P): –N –P (control, no N or P added); –N +P (no N, 1 g P m^{-2} yr^{-1}); LN –P (1 g N m^{-2} yr^{-1}, no P); LN +P (1 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}); HN –P (3 g N m^{-2} yr^{-1}, no P); HN +P (3 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}). Significant ($P < 0.05$) effects of N addition and/or P addition are summarized at the top of the panels (for example, July: N in the 2005 hummock panel indicates a significant effect of N addition on hummock ER in July 2005). In the case of significant main effects and/or interactions, different letters on the columns indicate significant ($P < 0.05$) differences among the means.

concentration ($F_{1,72} = 50.37$; $P < 0.001$) and P concentration ($F_{1,72} = 18.68$; $P < 0.001$) were both ranked as follows with respect to year: 2003 < 2005 < 2004. Adding N significantly ($F_{2,72} = 13.39$; $P < 0.001$) raised N concentration while adding P significantly ($F_{1,72} = 66.96$; $P < 0.001$) raised P concentration in plant biomass (Figs 5, 6). There were no significant interactions between N addition or P addition and habitat. However, the differences in nutrient concentrations among the treatments became sharp, especially for P, only in 2005 (Figs 5, 6).

The average rates of NEE and ER in each of the 3 yr (2003–2005) were poorly correlated with N and P concentrations in the plant biomass. In particular, there were no significant correlations at all both in the hot year (2003) and in the dry year (2005). However, ER in the humid temperate year 2004 was positively correlated with N concentration in the plant biomass ($r = 0.35$; $n = 36$; $P < 0.04$).

Discussion

Changes in vegetation

While we hypothesized that any vegetation changes would be triggered by nutrient addition, our results demonstrate that the observed changes in plant cover were largely independent of the experimental manipulations. Indeed, adding nutrients had a very modest effect on the vegetation in the short term,

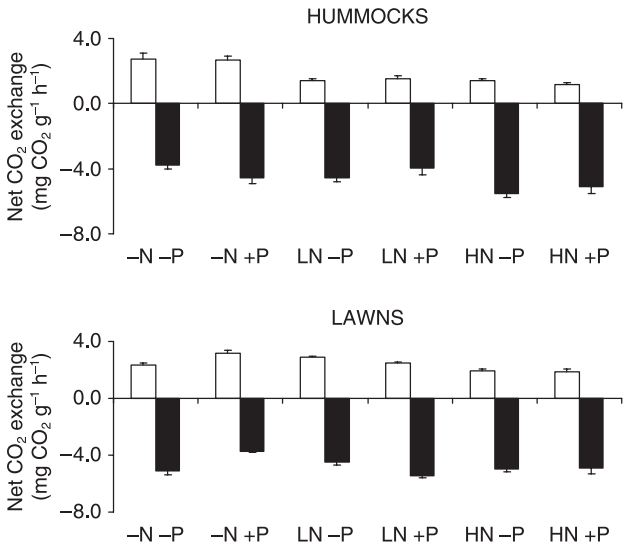

Fig. 4 Mean (+ 1 SE) rates of net CO_2 exchange at the peak of the growing season 2003 in plants of the two functional layers (moss layer, *Sphagnum* (open bars); field layer, vascular plants (closed bars)) in two bog habitats treated by adding nitrogen (N) and phosphorus (P): –N –P (control, no N or P added); –N +P (no N, 1 g P m^{-2} yr^{-1}); LN –P (1 g N m^{-2} yr^{-1}, no P); LN +P (1 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}); HN –P (3 g N m^{-2} yr^{-1}, no P); HN +P (3 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}). There were no significant effects of nutrient addition.

with N addition only slightly accelerating the decline in *Sphagnum* cover. However, the plant cover in our bog changed considerably during the experimental period. The main changes consisted in the expansion of vascular plants and the concomitant decline in cover of *Sphagnum* mosses. Ongoing changes in bog vegetation have been recorded in several studies. For example, Nordbakken (2001) observed increased cover of dwarf shrubs accompanied by decreased cover of *Sphagnum* mosses at an ombrotrophic bog in south-eastern Norway after five moderately dry years. Similarly, Gunnarsson *et al.* (2002) reported higher frequency of vascular species typical of dry microhabitats, when reinvestigating the vegetation of a bog in southern Sweden after 40 yr of natural development. In both studies the authors did not provide a mechanistic explanation of the observed dynamical pattern. However, they argued that surface dryness *per se* and/or a consequent increase in mineralization rates are suitable to promote growth of vascular plants at the expense of *Sphagnum* mosses. We also could not disentangle the role of drought and nutrients, in the absence of data on nutrient availability in the surface peat that were outside the scope of our study, since this would have implied destructive sampling in plots designed for long-term monitoring.

We cannot rule out the hypothesis that the vegetation in our bog was already changing before the onset of the experiment. However, one of us (R. G.) did visit the bog several times since 1981 and did not observe any visible changes in the vegetation until 2003, when increased vascular cover became apparent all over the bog. Therefore, we feel confident to state that during our experiment the vegetation changed at a much faster pace than in the previous two decades even in the absence of any treatment. The expansion of vascular plants in the growing season 2003 may have been promoted by reduced *Sphagnum* growth since competition between vascular plants and *Sphagnum* mosses plays a major role in structuring bog vegetation (Malmer *et al.*, 2003). Indeed, production of *Sphagnum* mosses in the hot growing season 2003 was *c.* 50% lower than the average (Gerdol *et al.*, 2007). Another explanation for the vegetation dynamics documented during our experiment may reside in accelerated nutrient mineralization during the prolonged hot periods in 2003. Interestingly, peak concentrations of inorganic N in surface waters have been recorded during summer 2003 at a subalpine catchment in the north-western Alps (Rogora & Mosello, 2007). Increased nutrient availability resulting from faster mineralization rates may, furthermore, account for vascular growth acceleration persisting during the more normal years 2004 and 2005, when no reduction in *Sphagnum* growth was observed (Gerdol *et al.*, 2007).

CO_2 exchange

A complex interplay of temperature and water-table depth played a major role in controlling CO_2 exchange in the bog. Climatic fluctuations are a well-known cause of interannual variability in CO_2 exchange rates at peatland surface (Roulet *et al.*, 2007). In particular, there is consistent evidence of reduced NEE and increased ER during years with low precipitation at bogs in several geographic locations such as northern Europe (Alm *et al.*, 1999), North America (Shurpali *et al.*, 1995; Roulet *et al.*, 2007) and the Alps (Bortoluzzi *et al.*, 2006). An interesting result of our study is the reduced CO_2 uptake found in summer 2003 when the bog experienced high air and soil temperature but overall normal precipitation. This contrasts with the general trend observed in central-western Europe where drought, owing to very low precipitation, rather than heat stress, accounted for a dramatic reduction in gross production but also in respiration, at a broad range of forest ecosystems (Reichstein *et al.*, 2007). In our bog, the summer 2003 climate anomaly implied both a reduction in NEE and an increase in ER. Less CO_2 uptake was primarily determined by reduced rates of net photosynthesis in *Sphagnum* mosses, which experienced net CO_2 release, especially when the moss layer was rapidly rehydrated after drying out (Gerdol *et al.*, 1996). Although we documented that pattern only once in the season (Fig. 4), it presumably occurred several times in summer 2003, when precipitation mostly consisted of heavy showers followed by rather long periods of clear weather with high potential for evapotranspiration in the atmosphere. Laboratory experiments have also demonstrated a negative effect of drying and wetting cycles on *Sphagnum* production (McNeil & Waddington, 2003).

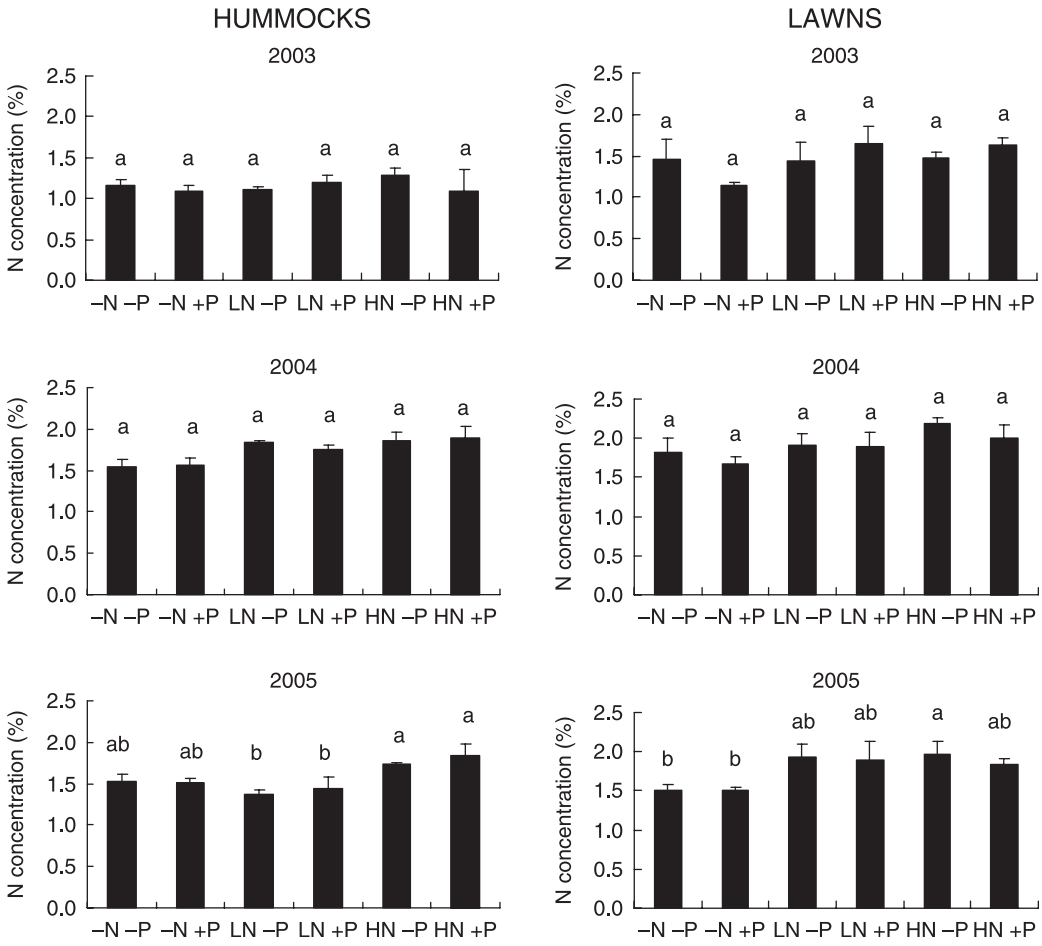

Fig. 5 Mean (+ 1 SE) nitrogen (N) concentrations in plant biomass in two bog habitats treated by adding nitrogen (N) and phosphorus (P): –N –P (control, no N or P added); –N +P (no N, 1 g P m^{-2} yr^{-1}); LN –P (1 g N m^{-2} yr^{-1}, no P); LN +P (1 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}); HN –P (3 g N m^{-2} yr^{-1}, no P); HN +P (3 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}). Within each panel, different letters indicate significant ($P < 0.05$) differences among the means.

Contrary to our main hypothesis NEE was poorly influenced by vascular cover, presumably because any possible contribution of vascular plants to NEE was overruled by strongly varying rates of net CO_2 exchange in *Sphagnum* mosses. However, we are unable to quantify the relative contribution of the different CO_2 emission sources. A recent study reported a somewhat higher contribution of autotrophic respiration compared with heterotrophic respiration from a well-hydrated peatland (Crow & Wieder, 2005). However, data from our experiment suggest that autotrophic respiration, especially that of dominant *Sphagnum* mosses, is strongly reduced during dry periods (Gerdol *et al.*, 2007). Measurements of CO_2 emission after clipping living plant parts, including the green tissues of *Sphagnum* mosses, also suggest heterotrophic respiration to account for the bulk of ER in dry periods. A likely explanation of the observed pattern is enhanced heterotrophic respiration when the oxic layer is deepened as a result of aridity.

The lack of consistent effects of nutrient addition on CO_2 exchange supports the results of previous research, reporting overall poor effects of experimental fertilization on gas exchange in peatlands (Saarnio *et al.*, 2003; Keller *et al.*, 2005) and, in some occasions, contrasting response patterns between short-term and mid-term observations (Keller *et al.*, 2006; Bubier *et al.*, 2007) or between laboratory experiments and field investigations (Basiliko *et al.*, 2006). However, at the end of the experiment we did observe a weak stimulation of CO_2 efflux from N-fertilized hummocks (Fig. 3). This may represent a sign that in the nutrient poorest (hummock) microhabitat decomposition rates start accelerating, probably in response to a faster accumulation of vascular litter, compared with recalcitrant *Sphagnum* litter, in the N-fertilized treatments. If so, such an effect is expected to become stronger in the long term (Aerts *et al.*, 2006; Bragazza & Freeman, 2007). An alternative explanation, namely a direct stimulation of the microbial community by increased nutrient availability in the soil solutions, is quite improbable for two main reasons. First, bog microbes are highly adapted to the litter chemistry of bog species, so that the chemical features of the litter, rather

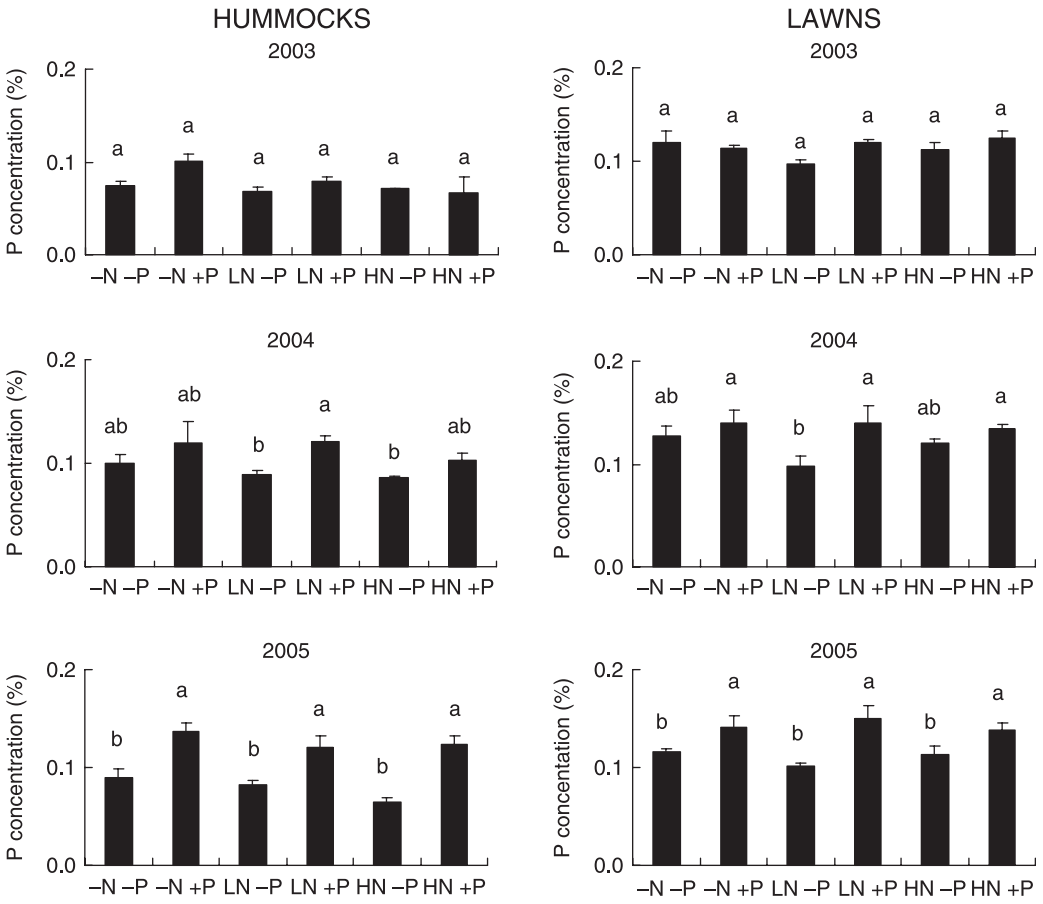

Fig. 6 Mean (+ 1 SE) phosphorus (P) concentrations in plant biomass in two bog habitats treated by adding nitrogen (N) and P: –N –P (control, no N or P added); –N +P (no N, 1 g P m^{-2} yr^{-1}); LN –P (1 g N m^{-2} yr^{-1}, no P); LN +P (1 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}); HN –P (3 g N m^{-2} yr^{-1}, no P); HN +P (3 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}). Within each panel, different letters indicate significant ($P < 0.05$) differences among the means.

than the nutrient status of the substrate, are the main factor accounting for decomposition rates in bogs (Bragazza *et al.*, 2007). Second, adding N as mineral compounds may even reduce CO_2 efflux from peat by inhibiting the CH_4-oxidizing capacity of methanotrophs (Kravchenko, 2002; but see Blodau *et al.*, 2007).

Conclusions

During our experiment, an extreme climate event influenced the bog ecosystem to a much greater extent than our experimental manipulation of nutrient inputs. In particular, a heatwave in summer 2003 triggered the expansion of vascular plants at the expense of *Sphagnum* mosses. Although largely obscured by the summer 2003 climate anomaly, a weak effect of fertilization could nonetheless be observed at the end of our experiment, when *Sphagnum* cover in hummocks declined somewhat more in the N-fertilized treatments, which slightly stimulated ER. A possible explanation is a faster accumulation of vascular litter richer in nutrients compared with recalcitrant nutrient-poor *Sphagnum* litter. If so, this may eventually limit rates of peat accumulation.

Acknowledgements

This research was supported by a grant of Ferrara University to R. Gerdol. We thank the Municipality of Moena for giving us the permission to carry out the field study. Dr A. Petraglia assisted during the field work and Dr R. Marchesini carried out the chemical analyses. Both are kindly acknowledged. We thank Tim Moore and two anonymous reviewers for their constructive criticism on a previous version of the paper.

References

Aerts R, van Logtenstijn RSP, Karlsson PS. 2006. Nitrogen supply differentially affects litter decomposition rates and nitrogen dynamics of sub-arctic bog species. *Oecologia* **146**: 652–658.

Aerts R, Verhoeven JTA, Whigham DF. 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology* **80**: 2170–2181.

Alm J, Schulman L, Walden J, Nykänen H, Martikainen PJ, Silvola J. 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. *Ecology* **80**: 161–174.

Basiliko N, Moore TR, Jeannotte R, Bubier JL. 2006. Nutrient input and carbon and microbial dynamics in an ombrotrophic bog. *Geomicrobiology Journal* **23**: 531–543.

Beniston M. 2007. Linking extreme climate events and economic impacts: examples from the Swiss Alps. *Energy Policy* **35**: 5384–5392.

Berendse F, van Breemen N, Rydin H, Buttler A, Heijmans M, Hoosbeek MR, Lee JA, Mitchell E, Saarinen T, Vasander 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 Biology* 7: 591–598.

Blodau C, Roulet NT, Heitmann T, Stewart H, Beer J, Lafleur P, Moore TR 2007. Belowground carbon turnover in a temperate ombrotrophic bog. *Global Biogeochemical Cycles* **21**: GB1021, doi: 10.1029/2005GB002659.

Bortoluzzi E, Epron D, Siegenthaler A, Gilbert D, Buttler A. 2006. Carbon balance of a European mountain bog at contrasting stages of regeneration. *New Phytologist* **172**: 708–718.

Bragazza L, Freeman C. 2007. High nitrogen availability reduces polyphenol content in *Sphagnum* peat. *Science of the Total Environment* **377**: 439–443.

Bragazza L, Siffi C, Iacumin P, Gerdol R. 2007. Mass loss and nutrient release during litter decay in peatland: the role of microbial adaptability to litter chemistry. *Soil Biology & Biochemistry* **39**: 257–267.

Bragazza L, Tahvanainen T, Kutnar L, Rydin H, Limpens J, Hájek M, Grosvernier P, Hájek T, Hajkova P, Hansen I *et al.* 2004. Nutritional constraints in ombrotrophic *Sphagnum* plants under increasing atmospheric nitrogen depositions in Europe. *New Phytologist* **163**: 609–616.

Bubier JL, Moore TR, Bledzki LA. 2007. Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Global Change Biology* **13**: 1168–1186.

Coulson JC, Butterfield J. 1978. An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. *Journal of Ecology* **66**: 631–650.

Crow SE, Wieder RK. 2005. Sources of CO_2 emission from a northern peatland: root respiration, exudation, and decomposition. *Ecology* **86**: 1825–1834.

Dioumaeva I, Trumbore S, Schuur EAG, Goulden ML, Litvak M, Hirsch AI. 2002. Decomposition of peat from upland boreal forest: temperature dependence and sources of respired carbon. *Journal of Geophysical Research-Atmospheres* **107**: 8222, doi: 10.1029/2001JD000848.

Freeman C, Ostle NJ, Fenner N, Kang H. 2004. A regulatory role of phenol oxidase during decomposition in peatlands. *Soil Biology & Biochemistry* **36**: 1663–1667.

Frolking SS, Bubier JL, Moore TR, Ball T, Bellisario LM, Bhardwaj A, Carroll P, Crill PM, Lafleur PM, McCaughey JH *et al.* 1998. Relationship between ecosystem productivity and photosynthetically active radiation from northern peatlands. *Global Biogeochemical Cycles* **12**: 115–126.

van Gaalen KE, Flanagan LB, Peddle DR. 2007. Photosynthesis, chlorophyll fluorescence and spectral reflectance in *Sphagnum* moss at varying water contents. *Oecologia* **153**: 19–28.

Gerdol R, Bonora A, Gualandri R, Pancaldi S. 1996. CO_2 exchange, photosynthetic pigment composition, and cell ultrastructure of *Sphagnum* mosses during dehydration and subsequent rehydration. *Canadian Journal of Botany* 74: 726–734.

Gerdol R, Petraglia A, Bragazza L, Iacumin P, Brancaleoni L. 2007. Nitrogen deposition interacts with climate in affecting production and decomposition rates in *Sphagnum* mosses. *Global Change Biology* **13**: 1–12.

Gorham E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* **1**: 182–195.

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

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

Hayward PM, Clymo RS. 1983. The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water table depth. *Journal of Ecology* **71**: 845–863.

Heijmans MMPD, Klees H, De Visser W, Berendse F. 2002. Effects of increased N deposition on the distribution of ^{15}N-labelled N between *Sphagnum* and vascular plants. *Ecosystems* **5**: 500–508.

Humphreys ER, Lafleur PM, Flanagan LB, Hedstrom N, Syed KH, Glenn AJ, Granger R. 2006. Summer carbon dioxide and water vapor fluxes across a range of northern peatlands. *Journal of Geophysical Research* **111**: G04011, doi: 1029/2005JG000111.

Jonasson S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. *Oikos* **63**: 420–429.

Keller JK, Bauers AK, Bridgham SD, Kellogg LE, Iversen CM. 2006. Nutrient control of microbial carbon cycling along an ombrotrophic–minerotrophic peatland gradient. *Journal of Geophysical Research* **111**: G03006, doi: 10.1029/2005JG000152.

Keller JK, Bridgham SD, Chapin CT, Iversen CM. 2005. Limited effects of six year of fertilization on carbon mineralization dynamics in a Minnesota fen. *Soil Biology & Biochemistry* **37**: 1197–1204.

Kravchenko IK. 2002. Methane oxidation in boreal peat soils treated with various nitrogen compounds. *Plant and Soil* **242**: 157–162.

Limpens J, Berendse F, Klees H. 2004. How phosphorus availability affects the impact of nitrogen deposition on *Sphagnum* and vascular plants in bogs. *Ecosystems* 7: 793–804.

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

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

McNeil P, Waddington JM. 2003. Moisture controls of *Sphagnum* growth and CO_2 exchange on a cutover bog. *Journal of Applied Ecology* **40**: 354–367.

Moore TR, Basiliko N. 2006. Decomposition in boreal peatlands. In: Wieder RK, Vitt DH, eds. *Boreal Peatland Ecosystems*. Ecological Studies 188. Berlin-Heidelberg, Germany: Springer, 125–143.

Nordbakken JF. 2001. Fine-scale five year vegetation change in boreal bog vegetation. *Journal of Vegetation Science* **12**: 771–778.

Reichstein M, Ciais P, Papale D, Valentini R, Running S, Viovy N, Cramer W, Granier A, Ogée J, Allard V *et al.* 2007. Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. *Global Change Biology* **13**: 634–651.

Rochefort L, Vitt DH, Bayley SE. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology* **71**: 1986–2000.

Rogora M, Mosello R. 2007. Climate as a confounding factor in the response of surface water to nitrogen deposition in an area south of the Alps. *Applied Geochemistry* **22**: 1122–1128.

Roulet NT, Lafleur PM, Richard PJH, Moore TR, Humphreys ER, Bubier J. 2007. Contemporary carbon balance and late Holocene carbon accumulation in a northern peatlands. *Global Change Biology* **13**: 397–411.

Saarnio S, Järviö S, Saarinen T, Vasander H, Silvola J. 2003. Minor changes in vegetation and carbon gas balance in a boreal mire under a raised CO_2 or NH_4NO_3 supply. *Ecosystems* **6**: 46–60.

Scanlon D, Moore T. 2000. Carbon dioxide production from peatland soil profiles: the influence of temperature, oxic/anoxic conditions and substrate. *Soil Science* **165**: 153–160.

Shurpali NJ, Verma SB, Kim J, Arkebauer TJ. 1995. Carbon dioxide exchange in a peatland ecosystem. *Journal of Geophysical Research* **100**: 14319–14326.

Tolonen K, Turunen J. 1996. Accumulation rates of carbon in mires in Finland and implications for climate change. *Holocene* **6**: 171–178.

Tomassen HBM, Smolders AJP, Limpens J, Lamers LPM, Roelofs JGM. 2004. Expansion of invasive species on ombrotrophic bogs: desiccation or high N deposition? *Journal of Applied Ecology* **41**: 139–150.

Turunen J, Tomppo E, Tolonen K, Reinikainen A. 2002. Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions. *The Holocene* **12**: 69–80.

Verhoeven JTA, Liefveld WM. 1997. The ecological significance of organochemical compounds in *Sphagnum*. *Acta Botanica Neerlandica* **46**: 117–130.

Wilson D, Alm J, Riutta T, Laine J, Byrne KA, Farrell EP, Tuittila ES. 2007. A high resolution green area index for modelling the seasonal dynamics of CO_2 exchange in peatland vascular plant communities. *Plant Ecology* **190**: 37–51.

