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Factors modulating cottongrass seedling growth stimulation to enhanced nitrogen and carbon dioxide: compensatory tradeoffs in leaf dynamics and allocation to meet potassium-limited growth

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Abstract *Eriophorum vaginatum* is a characteristic species of northern peatlands and a keystone plant for cutover bog restoration. Understanding the factors affecting *E. vaginatum* seedling establishment (i.e. growth dynamics and allocation) under global change has practical implications for the management of abandoned mined bogs and restoration of their C-sequestration function. We studied the responses of leaf dynamics, above- and belowground biomass production of establishing seedlings to elevated CO_2 and N. We hypothesised that nutrient factors such as limitation shifts or dilutions would modulate growth stimulation. Elevated CO_2 did not affect biomass, but increased the number of young leaves in spring (+400 %), and the plant vitality (i.e. number of green leaves/total number of leaves) (+3 %), both of which were negatively correlated to $[K^+]$ in surface porewater, suggesting a K-limited production of young leaves. Nutrient ratios in green leaves indicated either N and K co-limitation or K limitation. N addition enhanced the number of tillers (+38 %), green leaves (+18 %), aboveground and belowground biomass (+99, +61 %), leaf mass-to-length ratio (+28 %), and reduced the leaf turnover (−32 %). N addition enhanced N availability and decreased $[K^+]$ in spring surface porewater. Increased tiller and leaf production in July were associated with a doubling in $[K^+]$ in surface porewater suggesting that under enhanced N production is K driven. Both experiments illustrate the importance of tradeoffs in *E. vaginatum* growth between: (1) producing tillers and generating new leaves, (2) maintaining adult leaves and initiating new ones, and (3) investing in basal parts (corms) for storage or in root growth for greater K uptake. The K concentration in surface porewater is thus the single most important factor controlling the growth of *E. vaginatum* seedlings in the regeneration of selected cutover bogs.

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Introduction

Eriophorum vaginatum L., commonly named tussock cottongrass, is one of the most characteristic plants of oligotrophic northern peatlands (Gebauer et al. 1995) and arctic tundra, and is a keystone species for the regeneration of mined peatlands (Kivimäki 2008). Where *E. vaginatum* colonises bare peat, its tillering growth form affects the microclimatic conditions at the soil surface facilitating the regrowth of *Sphagnum*, thus speeding up peatland regeneration (Grosvernier et al. 1995). The regeneration of mined peatland is aimed at: (1) providing habitat for biodiversity, and (2) restoring the C-sequestration function. It is therefore important to understand how global change affects this species. Our focus here is on how elevated CO_2 and N deposition affect *E. vaginatum* seedling establishment.

E. vaginatum has a high production/biomass ratio, because it produces roots annually and has a leaf replacement period of less than 1 year (Bliss 1956). In addition, retranslocation from ageing leaves was shown to account for more than 90 % of P and 85 % of N input into new leaves appearing in early summer, and 100 % for leaves appearing later (Jonasson and Chapin 1985). The unusual vascular system and leaf production dynamics of *E. vaginatum* are therefore highly efficient for recycling nutrients internally and contribute to making this species very competitive in nutrient-poor habitats (Cholewa and Griffith 2004).

The effects of global change on *E. vaginatum* have been studied on adult plants mostly from tundra tussocks as opposed to peatlands. In field-greenhouse studies elevated CO_2 enhanced tillering (Tissue and Oechel 1987; Oechel and Vourlitis 1996), had various effects on biomass (Hunt et al. 1991; Stulen and den Hertog 1993; Oechel and Vourlitis 1996), and had no effect on the root/shoot ratio (Bassirirad et al. 1996). N fertilization enhanced tillering (Goodman and Perkins 1968a; Chapin and Shaver 1996) and above- and belowground biomass (Sullivan et al. 2007), while Shaver et al. (1986) observed a 1-month extension of the growing season for *E. vaginatum* fertilized with NPK. These results suggest that both elevated CO_2 and N stimulate the growth of *E. vaginatum*. Plant nutrient balance, leaf turnover or hydrochemistry may explain potential differences in the specific responses to each treatment, but these aspects were usually not studied in detail, making generalization difficult. Additionally, little is known in general about the establishment, phenology, and biomass allocation of seedlings (Gough 2006) and, to our best knowledge, nothing is known about possible effects of elevated CO_2 or N deposition on this critical early life history phase.

Soil mineral nutrient content has been shown to control the growth of adult *E. vaginatum* plants in the following order: $K \geq P > K$ and P mixture $\geq N > Ca > Mg$ (e.g. Goodman and Perkins 1968a, b), and nutrient ratios in porewater or plant tissue (e.g. N/P, N/K) are useful to determine limitation (Hoosbeek et al. 2002). K is often limiting as it is essential in regulating osmotic/electric potentials, activates enzymes involved in photosynthesis, and is extremely mobile and easily retranslocated from old parts to new growths (Taiz and Zeiger 1998). Yet, under field-enhanced CO_2 or N treatments, plant nutrients commonly experienced dilutions or limitation shifts due to complex environmental and hydrochemical nutrient imbalances with consequences for the ontogenesis and biomass allocation of growing plants (e.g. Johnson et al. 1997; Hoosbeek et al. 2002; van Heerwaarden et al. 2003; Taub and Wang 2008).

We studied, in two experiments, the effects of elevated CO_2 or N wet deposition on *E. vaginatum* seedlings in a regenerating cutover *Sphagnum* peatland. We monitored the hydrochemistry, leaf dynamics and plant nutrient contents in detail. We hypothesised that both treatments would: (1) change the hydrochemistry, (2) generally increase growth limitation by macronutrients and especially K, and (3) change the nutrient balance of seedlings resulting in adaptive increases of leaf turnover, compensatory root growth and/or enhanced storage in the basal part (corm) to meet the needs for expected saturated growth.

Materials and methods

Study site

The study was based on the transplantation of field-collected seedlings of *E. vaginatum* to experimental field plots. The two experiments were carried out in a regenerating ombrotrophic *Sphagnum* bog in the Swiss Jura mountains (Chaux-des-Breuleux, 47°15′N, 6°55′E, alt 1,000 m a.s.l.). The mire had been drained and exploited until 1945. The vegetation cover is mainly a mosaic assemblage of two dominant mosses, *Polytrichum strictum* and *Sphagnum fallax*, growing intricately among *E. vaginatum* tussocks. The average daily temperature in the warmest and coldest months are 15 and −5 °C, respectively. On average, annual precipitation is 1,390 mm; snow covers the site 80–120 days per year. The bulk and wet N deposition rates were estimated at 1.5 and 0.58 g N m^{-2} $year^{-1}$, respectively (NABEL 1995), and no significant changes have occurred since 1997 (NABEL 2009).

Experimental setup

Two 200-m^2 sites (15 m apart) were selected on Chaux-des-Breuleux bog to set up two separate experiments: atmospheric CO_2 enrichment (site A)—elevated, 560 p.p.m. (C+)/ambient, 360 p.p.m. (C−); mineral N addition (site B)—enhanced, added 3 g N m^{-2} year^{-1} (N+)/ambient (N−). There were five random plot replicates within each treatment of each experiment. The first experimental site was equipped with 1-m-diameter miniFACE (free air CO_2 enrichment) rings with 72 venting tubes, supplying either ambient or CO_2-enriched air. The five treatment rings were connected to a pure CO_2 gas inlet that was adjusted automatically on the basis of wind speed and CO_2 concentrations from air continuously measured with an infrared gas analyser in the centre of each plot at 7.5 cm above the moss surface (Miglietta et al. 2001). The five control rings were not connected to the pure CO_2 gas inlet. In the second experimental site, mineral N was applied on four plots (1 × 1.5 m) in six applications during the growing season as a fine spray of a 107 mM aqueous solution of NH_4NO_3 in 2 L of distilled water per plot. We focused on wet N deposition in the form of NO_3^- and NH_4^+, which mainly come from the hydrolyzation of NO_2 and NH_3 gases in the atmospheric water droplets. Control plots received 2 L of distilled water. In order to allow the ecosystem to acclimatize, both treatments were started 1 year prior to both the transplantation of the seedlings and the measurements.

In autumn, less than 1-year-old *E. vaginatum* seedlings were collected from a bare peat surface of a nearby cut-over *Sphagnum* bog (Bois-des-Lattes, 47°00′N, 6°40′E). Most seedlings had three leaves and three rootlets. In some rare cases (<5 %) any additional leaf or rootlet was cut to harmonize the seedlings. The seedlings were washed with demineralized water, weighed and replanted in sieved (2-mm mesh) steam-sterilised (3.5 h at 124 °C) horticultural *Sphagnum* peat and over-wintered in a greenhouse, where they were watered with demineralized water.

PVC tubes (length 50 cm, diameter 5 cm, with 20 holes of 5 mm diameter perforated in a quincunx) were lined with 35-µm-mesh polyester socks, filled with sieved peat, and inoculated with bog water pooled from both experimental sites. Six tubes were inserted into each plot using a corer so as to narrowly interlock with the vegetation. From a total of 226 collected seedlings, we selected 108 plants of median size and median fresh weight (0.2–0.4 g) and randomly assigned them to the tubes before planting at the end of March [2 experiments × 2 treatments × 4 (N+/N−) or 5 (C+/C−) plots × 6 plants]. Leaves and tillers were counted 12 times during the growing season. At the end of the experiment, the tubes were extracted. The socks were carefully removed to preserve roots before determining the biomass allocation and nutrient contents. As the seedlings had colonized all available space after one growing season (ca. five tillers, 50 leaves, and 50-cm-long roots) we stopped the experiment after one growing season.

Water chemistry and water table depth

The surface water of each plot was sampled using soil moisture samplers (Rhizon, Eijkelkamp, Holland) permanently installed in the peat acrotelm (5 cm depth) and vacuumed bottles (−0.7 bar). The samples were taken in between N additions in April, July and October and were analysed for major cations and anions, dissolved organic C (DOC), dissolved organic N (DON), total soluble N (TN), dissolved inorganic N (DIN), and P following standard protocols (Buurman et al. 1996). The water table depth (wtd) was measured every second week and was defined as the height difference between the mean peat-moss carpet height around each tube and the water level measured in each plot's piezometer.

Leaf dynamics

Every second week all leaves were counted. For a complete description of the leaf assets we selected several univocal variables: number of tillers, total number of leaves, which was further detailed as the number of green leaves, dying brown leaves (still turgescent), dead grey leaves (fully dried out) and young leaves. For a more gradual description of the senescence process we added a category of half-brown leaves for photosynthesising leaves with a dying segment starting from the tip and covering between 25 and 75 % of the blade. This was justified by the fact that a plant might have photosynthetically active leaves, though with only 25 % of the blade's surface being active. Young leaves represented sequentially emerging leaves not yet detached from the shoot base.

Measurements such as leaf number may fail to capture the physiological state or fitness of each plant. Assuming that healthy plants have a higher ratio of green leaves over total number of leaves, we added a vitality index as follows:

$$\begin{aligned}&\text{Vitality index (vitality)}\\&\quad = \text{green leaves}/\text{total number of leaves}\end{aligned} \tag{1}$$

From the set of univocal variables, we also defined four process variables: growth rate, death rate, turnover and residence time at peak biomass, in order to better quantify the changes occurring in the phenology of leaves.

The growth rate of green leaves at time i was defined as:

$$\begin{aligned}&\text{Growth rate}_i\\&\quad = \left(\text{green leaves}_{i+1} - \text{ green leaves}_i\right)/(t_{i+1} - t_i)\end{aligned} \tag{2}$$

The calculations were made for $i = 1,\ldots,12$ time increments. The rate of dead or dying leaves at time i was defined as:

$$\text{Death rate}_i = (\text{dead leaves}_{i+1} - \text{dead leaves}_i)/(t_{i+1} - t_i) \quad (3)$$

where dead leaves = number of dead grey leaves (fully dried out) or number of dying brown leaves (still turgescent). The calculations were made for $i = 1,\ldots,12$ time increments.

We calculated a turnover index based on cumulative rates. We used the same approach as Fitter et al. (1997) who calculated the difference between cumulative births and deaths of roots measured at a certain time interval (equivalent to rates). Thereafter, our turnover index was more explicitly defined as:

$$\text{Turnover index (turnover)} = 1 - \left(\sum \text{growth rate}_i - \sum \text{death rate}_i\right) \quad (4)$$

where $\sum$growth rate$_i$ = cumulative growth rate from $t = 1$ to $t = i$, $\sum$death rate$_i$ = cumulative death rate from $t = 1$ to t = i, for $i = 1,\ldots,12$ time increments. The constant was arbitrarily set to 1 to facilitate the reading, as intuitively the turnover ought to be equal to 1 rather than 0 when $\sum$growth rate = $\sum$death rate.

Finally we determined the residence time of leaves as follows:

$$\text{Residence time } (t_r) \text{ (days)} = \text{green leaves}_i/\text{growth rate}_i = \text{green leaves}_i/\text{death rate}_i \quad (5)$$

Only calculated for i = time at peak biomass, when growth rate$_i$ = death rate$_i$. Unlike leaf turnover, the residence time is calculated at a single time point. The residence time is therefore not the inverse function of the turnover index.

Biomass and allocation

At the end of the experiment, the aboveground part of each plant was cut off, weighed, and separated into dead leaves, green leaves, and from the shoot base an 8-mm basal part representing the corm of one tiller and which was expected to have an important storage function (e.g. Backéus 1985; Cholewa and Griffith 2004). The core of the field-incubated peat, which included the roots, was cut into five 10-cm sections. The roots (dead and live) from each section were carefully extracted from the peat using fine tweezers and a dissecting microscope. The roots were cleaned in alkaline (pH = 8) demineralised water. Fresh and dry weights of all parts and sections as well as each leaf's green proportion (length of the green segment in percent of the total length) were determined.

Plant nutrient content

The living plant parts were pooled for each plot and ball-milled. N was analysed using an elemental analyser (CHN1106; Carlo Erba, Milano, Italy). The remaining subsamples were digested with sulphuric acid, salicylic acid, hydrogen peroxide and selenium and analysed for P by colorimetry. K was measured from the digest with an atomic absorption spectrometer (AA4100; PerkinElmer, USA) following Walinga et al. (1995).

Numerical analyses

The leaf variables were measured repeatedly during the growing season. We first checked for the error associated with time dependence. After having rejected the sphericity assumption among the repeated time components (Mauchly's criterion) from a multivariate ANOVA approach, the variation in repeated measures of leaf variables explained by environmental variables were analysed using a generalised linear mixed-effects model (glmm) approach with a Gaussian distribution family and the identity link function.

We started with a backbone model close to optimal in terms of fixed components defined using a stepwise forward selection with n relevant environmental variables (V_1–V_n) based on the minimisation of the Akaike information criterion. We then added the random error structure by including together the hierarchy (nesting) and repeated time measures (random: ~1|time/treatment/plot, "/" nested within). We use restricted maximum likelihood (REML) for the estimation of random components. We then used the model with the best random error structure to find the optimal fixed components by comparing different models using maximum likelihood. Finally, in Tables 1 and 2, we present the parameter estimates and ±SE of the optimal model by using REML estimation. The generic R formula was: $Y \sim \text{treatment} + \text{time} + \text{treatment} \times \text{time} + V_1 + \cdots + V_n + \text{error (time/treatment/plot)} + \varepsilon_n$. The time was set as a categorical factor. For the best glmm models, we expressed the explained deviances (model-G_2/total-G_2, in percent). The porewater chemistry was used to capture the chemical changes occurring in between two treatments in spring, summer and autumn. The same porewater chemistry data were therefore used as explanatory variables at four successive leaf measurement time points (four in spring, four in summer and four in autumn). For some relevant points in time based on Figs. 1 and 2, selected contrast tests (G-statistic) were made and specified in the text. The leaf variable analyses were performed with R version 2.11.1 (R Development Core Team 2008).

The water chemistry data were analysed using the same approach as for the leaf variables, although using a linear mixed-effects model (lmm) (details in the Electronically Supplemental Material, ESM1, 2). The biomass allocation and nutrient content ratios were analysed using a lmm with plots nested within the treatment.

In all models, few outliers were removed based on leverage plots and Cook's distances. For some models (mentioned in Tables 1, 2), response variables needed to be transformed (ranked) prior to testing. Distributions and homeoscedacity of residuals were checked using Q–Q and scatter plots. The treatment effects (in percent) mentioned in the text are significant ($P \leq 0.05$), unless they are explicitly described as trends ($0.05 \leq P \leq 0.1$). The lmm for the water chemistry and biomass allocation were performed with the JMP/SAS 8.0 statistical software (SAS Institute, Cary, USA).

Results

Water chemistry

Average values of wtd and chemistry variables over the growing season are given in Tables ESM1 and 2 for the CO_2 and N experimental sites, respectively. Treatments effects and relevant seasonal patterns (mean ± SE) are detailed hereafter, but these results are not presented or discussed in full detail for concision. Our interest here lies in: (1) the treatment effects on water chemistry, and (2) the correlation of these variables with the response variables in the models.

The strongest changes observed in water chemistry between elevated CO_2 and control plots were increases in DIN (+82 %) which doubled by summer (C− 0.06 ± 0.01, C+ 0.112 ± 0.01 mg L^{-1}) and tripled by autumn, Al^{3+} (+58 %), Mg^{2+} (+31 %), Ca^{2+} (+23 %), Na^{+} (+17 %) and Cl^{-} (+15 %), and decreases in TN (−35 %), DON (−27 %), P (−24 %), K^{+} (−23 %), and DOC (−20 %) (Online resource 1). Water pH was higher in the treated plots. Concentrations of K^{+} strongly decreased by −81 % from spring (C− 1.66 ± 0.45, C+ 1.45 ± 0.34 mg L^{-1}) to summer (C− 0.25 ± 0.05, C+ 0.34 ± 0.05 mg L^{-1}) and decreased further to almost null in autumn (C− 0.04 ± 0.002, C+ 0.06 ± 0.02 mg L^{-1}).

The strongest changes observed in water chemistry under elevated N were increases in TN (+30 %), Mg^{2+} (+29 %), Ca^{2+} (+24 %), DIN (+22 %), Fe^{3+} (+13 %), and Na^{+} (+8 %) and decreases in Al^{3+} (−34 %), P (−27 %), and K^{+} (−26 %) (Online resource 2). Water pH was higher in treated plots as compared to control ones (5.9 ± 0.17 and 5.6 ± 0.25, respectively). In spring, treated plots had 51 % less K^{+} than control plots (N− 0.37 ± 0.18, N+ 0.18 ± 0.07 mg L^{-1}). By summer, while control plots experienced a slight decrease, treated plots experienced a 100 % increase in K^{+}, bringing it back to the control level (N− 0.33 ± 0.06, N+ 0.31 ± 0.07 mg L^{-1}), after which the K^{+} of all plots drastically dropped close to null in autumn (N− 0.05 ± 0.005, N+ 0.09 ± 0.01 mg L^{-1}).

Leaf dynamics

Elevated CO_2 slightly increased the vitality (green leaves/total number of leaves) of seedlings (+3 %), but had no other significant effects on leaf dynamic variables (Table 1). There was also a significant treatment × time effect on vitality, which was at first higher for treated plants, up to 172 % higher in the elevated CO_2 plots in June, and then lower from August onwards (Fig. 1). Vitality dropped in April, then increased until mid-August and finally decreased to its lowest values by November. The significant contrasts in turnover from April to June ($P \leq 0.05$) can be explained by the combination of increasing numbers of green leaves and tillers until the end of July (trends).

The wtd and water chemistry variables (porewater) explained between 2 and 19 % of the deviance in the leaf dynamical models (Table 1). wtd correlated most strongly negatively with the production of leaves, and green leaves, and positively with leaf turnover. The higher pH was associated with lower tillers, half-brown leaves, brown leaves, grey leaves, death rate, and higher production, vitality and growth rate of young leaves. Total N concentration was only negatively correlated with the number of senescing half-brown leaves or dying brown leaves, while DIN concentration was negatively correlated with the production of green leaves and positively correlated with increasing turnover. K concentration was positively correlated with the production of tillers, half-brown leaves, brown leaves, and grey leaves, and negatively correlated with the production of young leaves and vitality. Mg concentration was positively correlated to the number of tillers, leaves, green leaves, half-brown leaves, brown leaves, and negatively correlated with turnover.

The N treatment enhanced the number of leaves, green leaves, tillers, and young leaves, and reduced the number of grey leaves and leaf turnover (Table 2). This latter effect was most marked in summer and faded towards the end of the growing season (Fig. 2).

Several significant treatment × time effects were observed (Table 2). The number of young leaves more than doubled with N addition between August and September. The number of grey leaves was increased between the end of June and mid-August and then reduced in mid-September. Although there were no significant cross-effects, the contrast analyses revealed that during October, the N addition drastically increased the number of half-brown leaves by 142 % and brown leaves by 59 %. The vitality varied during spring and summer, and became higher for N

Table 1 Leaf variable responses (mean ± SE) to elevated atmospheric CO_2 expressed in a summary table of the optimal generalised linear mixed-effect models (glmm) for both fixed and random components

Leaf-variable (unit)	Control (C−)	Treatment (C+)	C+ effect (*df* = 1)		Treat × time (*df* = 10)	Water table depth (*df* = 1)		pH (*df* = 1)		Concentrations in the pore water (mg L^{-1})							
										TN (*df* = 1)		DIN (*df* = 1)		K^+ (*df* = 1)		Mg^{2+} (*df* = 1)	
	Mean ± SE	Mean ± SE	∂C+ (%)	L-R	L-R	Slope	L-R	Slope	L-R	Slope	L-R	Slope	L-R	Slope	L-R	Slope	L-R
Tillers (no.)	5.07 ± 0.31	5.30 ± 0.32	4.6	0.695	8.33	−0.016	15.5***	−1.66	11.2***					1.59	18.9***	8.15	14.7***
Total leaves[a] (no.)	23.5 ± 1.4	24.6 ± 1.34	4.8	0.284	6.17	−0.356	12.2***									111	5.66*
Green leaves[a] (no.)	18.1 ± 1.1	18.4 ± 1.1	1.9	2.45	10.6	−0.444	14.1***					−163	6.01*			147	6.81**
Young leaves (no.)	0.55 ± 0.07	0.60 ± 0.07	9.0	0.319	17.4			0.288	5.23*					−0.408	4.51*		
Half brown leaves (no.)	0.65 ± 0.07	0.76 ± 0.07	17.1	0.016	9.56			−0.708	17.3***	−1.13	9.41**			0.401	11.2***	3.28	8.35**
Brown leaves (no.)	1.24 ± 0.1	1.35 ± 0.13	8.9	0.169	2.62			−0.721	10.6**	−1.33	7.69**			0.538	11.9***	5.85	15.5***
Grey leaves (no.)	4.59 ± 0.4	5.33 ± 0.43	16.1	0.768	13.3			−2.47	18.7***					1.32	9.31**		
Vitality[a] (n.a)	0.74 ± 0.01	0.76 ± 0.01	3.1	3.73*	19.3*			65.8	10.7**					−63.7	17.4***		
Growth rate[a] (no. d^{-1})	0.12 ± 0.02	0.11 ± 0.02	−5.2	0.327	6.45			38.3	3.95*								
Death rate[a] (no. d^{-1})	0.08 ± 0.01	0.10 ± 0.01	20.1	2.01	11.0			−37.4	3.85*								
Turnover[a] (n.a)	0.33 ± 0.05	0.31 ± 0.05	−5.9	0.464	17.7	0.579	16.2***					266	8.82**			−162	4.29*
Residence time[a, b] (*d*)	237 ± 50	233 ± 89	−1.7	2.46	n.a	n.a	n.a	n.a	n.a	n.a	n.a.	n.a	n.a	n.a	n.a	n.a	n.a

General formula is: leaf variable ~ treatment + time + treatment × time + V_1–V_n + error (time/treatment/plot) + ε_n. For simplification, the very significant Time/treatment/plot and Time factors are not represented here. Time is a categorical factor (as factor)

∂C+ percent treatment effects = $(X_{C+}-X_{C-})/X_{C-} \times 100$ (%), *slopes* estimates for continuous variables, *L–R* likelihood ratio χ^2 (G^2-statistic)

DIN dissolved inorganic N, *TN* total soluble N, *n.a* not applicable

* $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$, *** $P \leq 0.001$

[a] Ranked response variables were used for testing, presented mean values are not transformed

[b] Calculated at peak biomass

Table 2 Leaf variable responses (mean ± SE) to enhanced N addition expressed in a summary table of the optimal glmm for both fixed and random components

Leaf-variable (unit)	Control (N−)	Treatment (N+)	N+ effect ($df = 1$)		Treat × time ($df = 10$)	Water table depth ($df = 1$)		Concentrations in pore water (mg L^{-1})									
								TN ($df = 1$)		DIN ($df = 1$)		K^+ ($df = 1$)		Mg^{2+} ($df = 1$)		Al^{3+} ($df = 1$)	
	Mean ± SE	Mean ± SE	∂N+ (%)	L-R	L-R	Slope	L-R	Slope	L-R	Slope	L-R	Slope	L–R	Slope	L-R	Slope	L-R
Tillers[a] (no.)	3.96 ± 0.306	4.63 ± 0.380	16.8	12.6***				38.1	12.1***			−28.1	17.8***				
Total leaves[a] (no.)	18.0 ± 1.41	20.7 ± 1.66	15.0	16.4***								−17.2	11.1***				
Green leaves[a] (no.)	14.1 ± 1.19	16.6 ± 1.44	17.6	8.63***				27.1	3.73*			−17.1	6.06**	−79.5	0.678		
Young leaves[a] (no.)	0.45 ± 0.07	0.66 ± 0.11	47.3	3.19*	20.2*			37.7	4.68*			−26.9	6.15*				
Half brown leaves[a] (no.)	0.66 ± 0.09	0.73 ± 0.10	10.9	0.861								−27.7	6.04*				
Brown leaves[a] (no.)	1.18 ± 0.13	1.24 ± 0.15	5.1	0.063		−0.211	1.87									138	3.66*
Grey leaves[a] (no.)	2.59 ± 0.24	0.74 ± 0.27	−71.4	7.41**	25.8**	0.247	4.79*					−19.3	4.98*				
Vitality[a] (n.a.)	0.73 ± 0.01	0.74 ± 0.01	2.3	1.65	21.0*							20.7	3.81*	95.6	6.81**		
Growth rate[a] (no. d^{-1})	0.12 ± 0.02	0.15 ± 0.03	19.3	0.012	13.6			36.3	4.09*								
Death rate[a] (no. d^{-1})	0.07 ± 0.01	0.08 ± 0.02	23.5	0.191	21.5*							−24.5	4.48*				
Turnover[a] (n.a)	0.60 ± 0.05	0.41 ± 0.06	−32.3	18.2***		−0.241	4.08*			−104	6.33*	−24.5	4.48*				
Residence time[a, b] (d)	213 ± 14.9	267 ± 21.4	−32.3	1.16	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a

General formula is: leaf variable ~ treatment + time + treatment × time + V_1–V_n + error (time/treatment/plot) + ε_n. The very significant Plot and Time factors are not represented here. Time is a categorical factor (as factor)

∂N+ percent treatment effects = $(X_{N+}-X_{N-})/X_{N-} \times 100$ (%), *slopes* estimates for continuous variables; for other abbreviaitons, see Table 1

* $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$, *** $P \leq 0.001$

[a] Ranked response variables were used for testing, presented mean values are not transformed

[b] Calculated at peak biomass

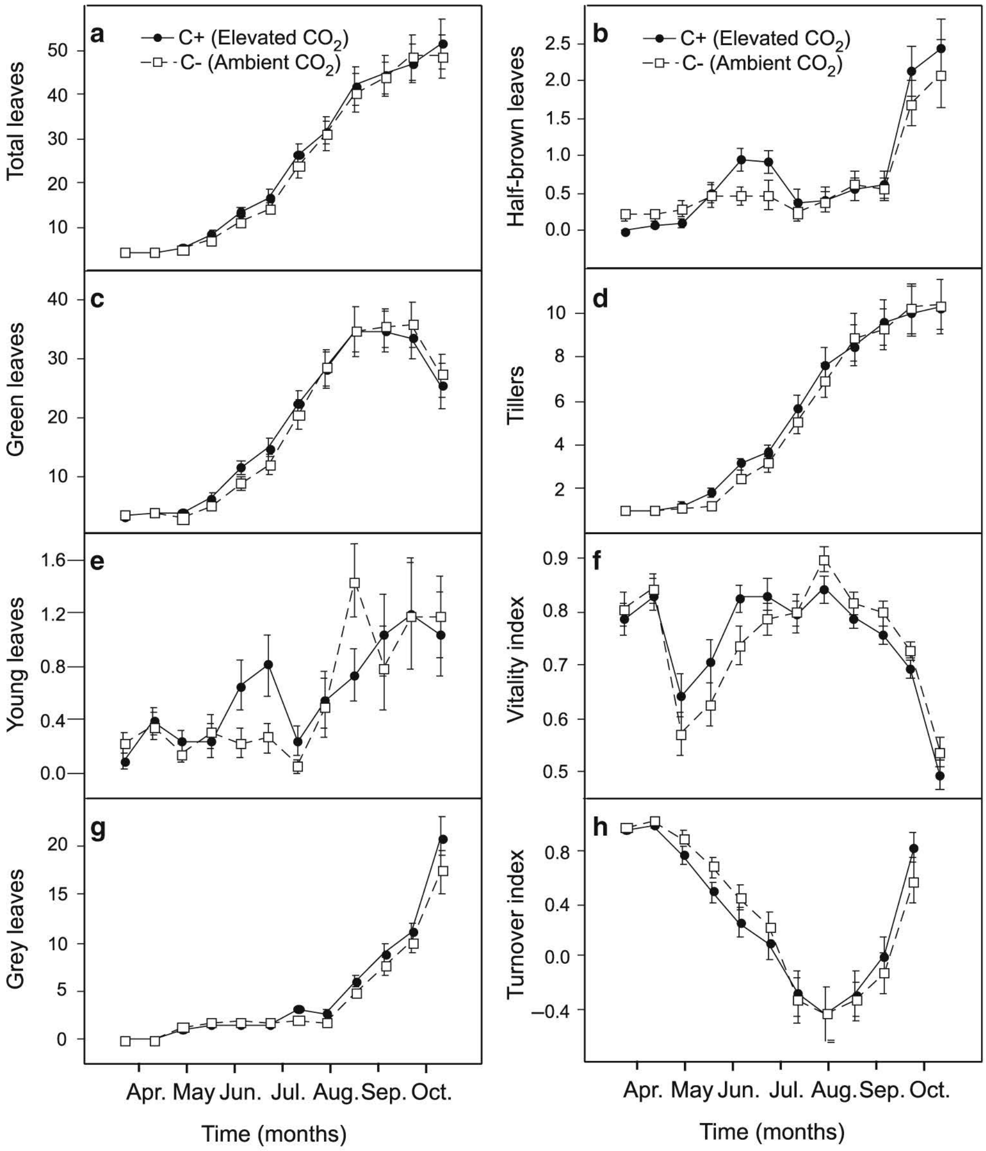

Fig. 1 Leaf variable responses of *Eriophorum vaginatum* seedlings to elevated atmospheric CO$_2$ (*C*+) and control (*C*−) treatments throughout time (mean ± SE), *n*(C+/C−) = 30, with *panels* showing the number of: **a** leaves, **b** half-brown leaves, **c** green leaves, **d** tillers, **e** young leaves, **g** grey leaves, and **f** vitality index (unitless), **h** turnover index (unitless)

treated plants by August. N addition stimulated the growth rate only in July/August (N+ 0.6 leaves day^{-1}, N− 0.4 leaves day^{-1}), whereas the death rate increased exponentially and was enhanced by N addition in September/October. The green proportion of leaves was reduced by −9 % by N addition (N+ 78 %, N− 86 %).

Water chemistry variables (porewater) explained 4–10 % of the deviance in the N addition experiment (Table 2). The production of dead grey leaves and the turnover were respectively positively and negatively correlated to wtd. The production of tillers, young leaves, green leaves, and the growth rate were positively correlated to TN concentration. Leaf turnover was negatively correlated to DIN concentration. The number of tillers, leaves, young leaves, green leaves, half-brown leaves, and grey leaves as well as the death rate and turnover were all negatively correlated to K$^+$ concentration while vitality was positively correlated to K$^+$ and Mg^{2+} concentrations. The number of brown leaves was positively correlated to Al concentration.

Biomass and plant nutrient content

The total biomass of the seedlings reached 320 mg at the end of the growing season on average across all treatments and was divided into the leaves (130 mg), the basal part (corm) (90 mg) and the roots (100 mg). Thus the biomass of the corm was almost equal to the total root biomass. Comparatively, the brown leaves and grey leaves

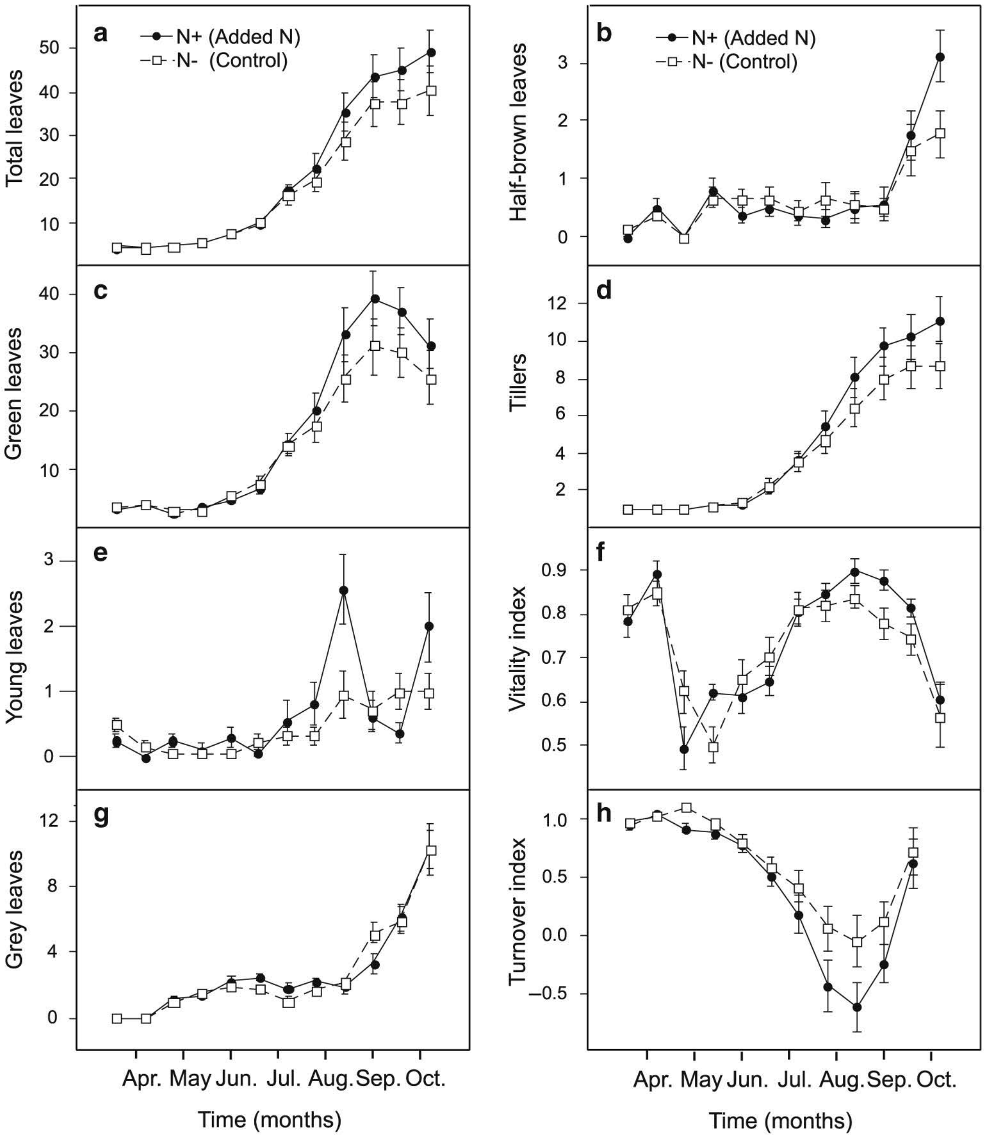

Fig. 2 Leaf variable responses to enhanced N deposition (*N*+) and control (*N*−) treatments throughout time (mean ± SE); *n*(N+/N−) = 24, with *panels* showing the number of: **a** total leaves, **b** half-brown leaves, **c** green leaves, **d** tillers, **e** young leaves, **g** grey leaves, and **f** vitality index (unitless), **h** turnover index (unitless)

represented 71 % of the green leaves biomass (70 mg). The root biomass in the uppermost section (0–10 cm) represented 60 % of the total root biomass. Total biomass of the seedlings was strongly correlated to the number of tillers per plant (Fig. 3).

CO_2 addition did not affect the plant biomass allocation to any plant part (data not shown). N and P contents in green leaves were lower in plants grown under elevated CO_2, but there was no difference for K, N/P and N/K ratios (Fig. 4).

N addition strongly enhanced total plant biomass, aboveground biomass, dead leaves, green leaves, biomass of the basal part, belowground biomass, root biomass at 10–20 and 40–50 cm depths (Table 3). The mass-to-length ratio was 28 % higher in treated plants, while the root/shoot ratio was not significantly affected. The contents of P and K in green leaves were lower in the plants exposed to the elevated N treatment (Fig. 4), and N/P and N/K ratios were therefore higher.

Discussion

Leaf dynamics and models

CO_2 experiment

In agreement with our hypothesis, we found positive CO_2 treatment and treatment × time effects on the vitality,

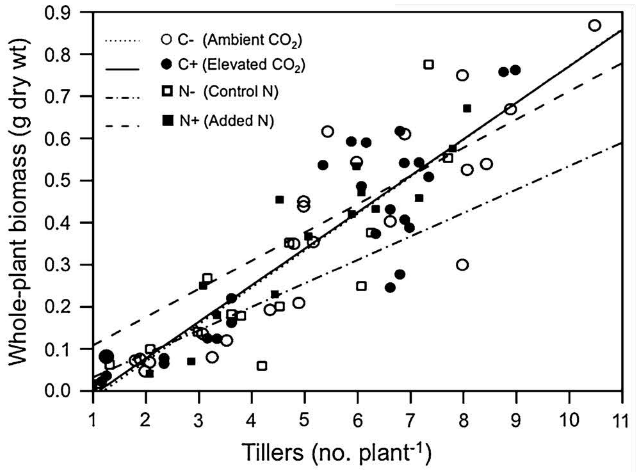

Fig. 3 Linear regressions between the whole-plant biomass (g dry weight) and the number of tillers per plant, n(C+/C−) = 30, n(N+/N−) = 24, $N+$ biomass (g) = 0.029 + 0.071 × no. tillers, $N-$ biomass (g) = −0.038 +0.059 × no. tillers, $C+/C-$ biomass (g) = −0.018 + 0.085 × no. tillers, all $r^2 > 0.8$ and $P < 0.001$

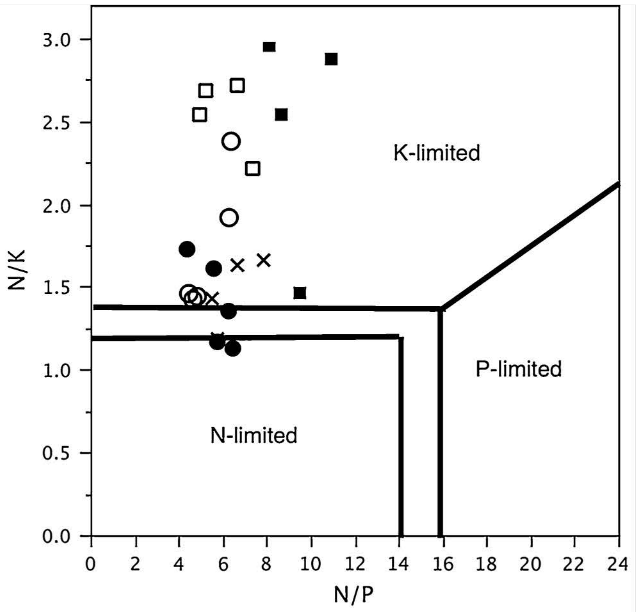

Fig. 4 N/K versus N/P nutrient content ratios in green leaves for different treatments measured at final harvest. Plants were pooled for each plot. *Solid circles* (n = 5) C+, *open circles* (n = 5) C−, *solid squares* (n = 5) N+, *open squares* (n = 4) N−, *crosses* adult plants (n = 3). Limits between areas of N, P and K limitations and data on adult plant leaves from our site as from Hoosbeek et al. (2002)

which was higher from May to July (Table 1; Fig. 1). In addition, the treatment induced a fourfold increase in young leaves in May and June. The reduced turnover of treated plants during that time is due to the fact that newly produced tillers hold fewer leaves than older ones; new tillers sequentially generate leaves in cohorts of three new leaves, whereas older ones could support from six to seven green leaves. Conversely, the reduction of vitality after July is due both to a slight death rate increase (i.e. passage of June's higher number of half-brown leaves into the grey leaves' pool), followed by a 50 % reduction of the emergence of young leaves in August. However, contrary to our hypothesis and to previous observations made on adult plants we did not find any enhancement of tillering (Tissue and Oechel 1987) nor of any other specific part (Rogers and Runion 1994) in response to elevated CO$_2$. Independently from treatment effects and implicit relationships to pH, our models show that the production of tillers or green leaves increase with rising water table. Tiller production is predicted by positive relationships with the K$^+$ and Mg^{2+} concentrations in the porewater, while the production of young leaves and the greater vitality are negatively related to K$^+$ concentration only, suggesting that the production of young leaves is more K$^+$ limited than that of tillers.

We expressed the nutrient contents of green leaves on a N/K versus N/P scatter plot using the same thresholds as were used for adult plants growing on our site (Hoosbeek et al. 2002; Fig. 4). The position of the seedling samples in the scatter plot suggests that they are far from being P limited, seedlings are either co-limited by N and K or K limited with no significant differences between treatment and control. The porewater chemistry data suggest that the marked, but transient, increase in the number of young leaves may be supported by the doubling in DIN in summer, and is stopped soon after due to the overall K$^+$ concentration drop in summer and autumn. The nutrient content of green leaves at the end of the season may be the imprint of that late K$^+$ overruling limitation.

N experiment

N addition enhances tillering throughout the growing season; by the time of the final harvest the number of tillers was as much as 38 % greater (17 % overall). This steady enhancement, together with the sharp threefold increase in the number of young leaves from July until August, was responsible for the subsequent increase in the number of leaves and green leaves (Fig. 2). The greater production of the number of green leaves relative to the total number of leaves enhanced the vitality index in the second half of the growing season. Whilst the growth rate was higher in the N treatment between June 27 and August 29, the death rate remained unaffected. The outcome was an increased green leaves pool and therefore an overall 32 % reduction in turnover, its lowest point being recorded on August 29.

Enhanced tillering due to N fertilization has been reported for adult *E. vaginatum* (Goodman and Perkins 1968a; Chapin and Shaver 1996), and for other graminoids (Noble and Miller 1979; Shaver and Chapin 1980). In the context of cutover bog regeneration, increased tillering of

Table 3 Biomass allocation responses (mean ± SE) to N addition treatment expressed in a linear model summary table

Plant part	Unit	Control (N−)	Treatment (N+)	N+ effect (*df* = 1)	
		Mean ± SE	Mean ± SE	∂N+ (%)	*F*-ratio
A. Whole plant	mg dry wt	180 ± 45	350 ± 41	90	6.92*
B. Aboveground	mg dry wt	130 ± 32	250 ± 29	99	7.61*
Dead leaves	mg dry wt	19 ± 7.6	46 ± 6.9	136	6.15*
Green leaves	mg dry wt	54 ± 14	95 ± 12	75	4.73*
Basal parts	mg dry wt	52 ± 12.9	110 ± 12	109	9.9**
C. Belowground	mg dry wt	57 ± 14	98 ± 12	61	4.58*
Roots 0–10 cm	mg dry wt	37 ± 9.1	59 ± 8.3	61	2.91
Roots 10–20 cm	mg dry wt	4.8 ± 1.6	9.5 ± 1.5	98	5.33*
Roots 20–30 cm	mg dry wt	4.8 ± 1.4	8.1 ± 1.3	68	3.03
Roots 30–40 cm	mg dry wt	5.6 ± 1.9	10 ± 1.7	83	2.74
Roots 40–50 cm	mg dry wt	4.6 ± 2.1	10 ± 1.8	126	4.23*
D. Root/shoot ratio	n.a	3.60 ± 0.81	2.70 ± 0.75	−26	0.434
E. Mass/length ratio[a]	$g\ cm^{-1}$	0.76 ± 0.058	0.97 ± 0.054	28	5.62*
F. Green proportion[b]	%	86 ± 1.9	78 ± 1.8	−9	8.28**

$\partial N+$ Percent treatment effects $[(X_{N+}-X_{N-})/X_{N-} \times 100\ (\%)]$

* $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$

[a] Leaves' mass-to-length ratio

[b] Length of the green segment compared to total leaf length in %; the significant plot treatment effect ($df = 6$) is not shown in this table

seedlings may, in the mid term, influence: (1) shading of lower growing plants such as *Sphagnum* mosses, (2) nutrient availability and growth response of inter-tussock species, (3) microtopography. In this regard, two parallel experiments conducted on our site already confirmed that enhanced N deposition favoured the height growth of *Polytrichum strictum* to the detriment of *Sphagnum fallax* (Mitchell et al. 2002) and that the competition was shifted in favour of vascular plants as compared to peat moss (Berendse et al. 2001).

During September and October, the death rate of N-treated plants was enhanced and caused the turnover to rise to almost the control level. This late acceleration, together with higher number of half-brown leaves, indicates that the treatment was not only enhancing the number of green leaves during summer, but also accelerating their senescence in autumn. The outcome of these antagonist effects still resulted in a 20 % increase in the number of green leaves at the time of final harvest (Fig. 2). It is interesting to note that the green leaves' peak (growth rate = death rate) was simultaneously reached for both treated and control plants, despite the difference in growth and death rates. This accelerated senescence is in line with the growth-limiting effect brought by a higher N supply (Aerts et al. 1992).

Leaf residence time was <1 year in both treated and control plants (N+ 267 days, N− 213 days), in agreement with previous studies for adult plants (Vasander 1982; Jonasson and Chapin 1985). This implies that the turnover reduction observed for treated seedlings will negatively feedback on nutrient cycling. N recycling by means of litter fall has been shown to represent as much as 220 % of the annual mineral N import through precipitation in peatlands of the French Massif Central (Francez 1995). As N uptake of *E. vaginatum* is usually higher than its N mineralization, the total flux circulating in the system is proportional to the mineralization (Damman 1978; Francez 1995). However, as *E. vaginatum* is able to take up amino acids (Schimel and Chapin 1996), N does not necessarily need to be mineralized prior to uptake. Nevertheless, a reduction in litter production, relative to the phytomass will down-regulate mineralization, although this imperatively needs to be related to qualitative and synecological aspects of litter. It is tempting, for instance, to hypothesize that under light-limiting (shading) and space-limiting conditions, higher atmospheric N inputs will: (1) globally decrease N turnover without changing the community structure, and/or (2) induce a better exploitation of space and increase the phytomass by different means (specific plant composition, morphological changes, symbioses, etc.).

The two experimental sites were somewhat different with, on average, 4 cm lower water tables at the N+/N− site. This may further disconnect the gravity water from the biologically active acrotelm. Accordingly, the pH values were overall higher and further enhanced by the relatively alkaline NH_4NO_3 1:1 (mole/mole) addition compared to rainwater. Moreover, because of the comparatively drier conditions, the easily leachable NH_4^+ may not be leached away and instead remain concentrated in the acrotelm, and this would explain the higher values of TN and DIN under elevated N. The abundant supply of available N in turn allowed, K^+ concentration increase in treated plots and the generally increasing K^+ concentration (back to control levels in summer), to stimulate the growth of seedlings. This suppression in K limitation may have reduced leaf turnover by 32 %.

In support of this interpretation, the N/K versus N/P scatter plot (Fig. 4) shows that seedlings in the N+/N− plots were neither N limited nor P limited and that seedlings were more K limited in N+ than in N− plots. The luxury production was therefore mainly K driven. Yet, K-limiting conditions emerged between summer and autumn as the K^+ concentration in porewater progressively declined by 78 % and became on average 2–3 times lower in this experimental site as compared to the C+/C experimental site.

The positive relationship between vitality and the Mg^{2+} concentration in porewater was expected, since Mg is an important constituent of chlorophyll and ATP mostly found in green leaves. Finally, the positive treatment-independent relationship between the Al^{3+} concentration and brown leaves may relate to its toxicity (Taiz and Zeiger 1998). The abundance of alumino-tolerant Ericaceae in the site is also in line with this.

Biomass and plant nutrient content

CO_2 experiment

The CO_2 treatment only affected the vitality of plants. In the literature, both positive and negative responses to enhanced atmospheric CO_2 concentrations were observed for arctic plants, although the root biomass was expected to increase in arctic vegetation in response to elevated CO_2 (Oechel and Vourlitis 1996). Moreover, in a review, 87 % of the studies showed root biomass increases regardless of the species or conditions (Rogers and Runion 1994). Our study differs from others in two aspects: we worked on seedlings, and these were growing in non-P-limiting conditions. Thereafter, the absence of growth stimulation by CO_2 may be due to several factors, which are discussed hereafter:

1. C losses through respiration and exudation. A hypothetical C overflow induced by the treatment may be consumed by plant respiration and root exudation (Farrar 1985; Lambers and Atkin 1995). The CO_2-enhanced bacterial biomass observed in our plots agrees with this (Mitchell et al. 2003).
2. Down-regulation of photosynthesis. Some authors reported a reduced N requirement under elevated CO_2 (Tissue and Oechel 1987) due to diminished activity of RuBP carboxylase (Conroy 1992; Körner 1995), whereas the P uptake capacity remained unchanged (Conroy 1992; Bassirirad et al. 1996). This mechanism can lead to P limitation (Tamm et al. 1954; Goodman and Perkins 1968b). In our case, the aboveground nutrient contents in seedlings indicate an N and K colimitation rather than P limitation (Fig. 4).
3. End-product limitation. Photosynthesis is not an independent driver of growth and is controlled to match the sink demand (Körner 1995). Under nutrient-limited conditions, end-product inhibition through starch accumulation was shown to reduce the photosynthesis capacity in *E. vaginatum* (e.g. Wulff and Strain 1982; Oechel and Vourlitis 1996).

N experiment

N addition clearly stimulates the growth of seedlings: the whole plant by 90 %, the aboveground part by 99 %, the belowground part by 60 %, especially root biomass at 10–20 and 40–50 cm depth (Table 3). This parallels the changes found in the leaf variables although these effects are weaker than on biomass, because treated plants have 28 % higher leaf mass-to-lengths ratios. Additionally, the enhanced senescence occurring at the final harvest was confirmed by the higher necromass (136 %) and the reduced green portion of leaves (−9 %).

In previous studies based on adult plants, N fertilization commonly enhanced the growth of vascular plants including *E. vaginatum* (Tamm 1954; Shaver and Chapin 1980; Shaver et al. 1986). Moreover, biomass increases were mostly due to enhanced tillering (Shaver and Chapin 1980; Shaver et al. 1986). In agreement with this, we found a strong relationship between total biomass and the number of tillers per plant. Furthermore, the slope of this regression was 20 % steeper for N-treated plants as compared to control plants (overall $r^2 = 0.944$, $P < 0.0001$; Fig. 3). This contrasts with a 3-year field experiment where photosynthesis and tillering of adult plants were stimulated, but biomass was not (Chapin and Shaver 1996). In the long term, graminoids with high production/biomass (P/B) ratios showed large positive responses to nutrient addition compared to evergreen shrubs (Bliss 1956; Jonasson and Chapin 1985; van Wijk et al. 2004). In our study, the seedlings presented high P/B ratios, fast leaf replacements, and accordingly were strongly affected.

Under K limitation, roots are expected to exhibit compensatory growth for greater K uptake to meet plant growth. The unchanged root/shoot ratio suggests that the K^+ concentrations in the porewater had just begun to become limiting (e.g. Wein 1973; Stulen and Den Hertog 1993). This implies that the seedlings were coping with K^+ shortage appearing towards the end of season solely by augmenting the nutrient retranslocation from declining green leaves into young leaves and tillers. Precisely, both were strongly increasing by the end of the growing season and coupled with strong increases in half-brown, brown leaves and a reduction of the leaves' green proportions.

Synthesis

This study of *E. vaginatum* seedlings shows that just as tradeoffs exist for biomass allocation due to altered nutrient balances, there are also tradeoffs between: (1) producing tillers and generating new leaves, (2) maintaining adult leaves and initiating new ones, and (3) retranslocating from leaves or exhibiting root compensatory growth for greater K uptake to meet plant growth.

Independent from any of the treatments, the existence of enhanced leaf production coupled with a higher leaf death rate emphasizes the primary role of retranslocation in the availability of nutrients: a consequence of sequential leaf development, and an important mechanism enabling *E. vaginatum* to maintain dominance in nutrient-poor ecosystems. Our data confirm this for seedlings, a critical, but rarely studied life stage of these plants.

This study illustrates the importance of considering the growth dynamics in treatment experiments. These types of investigations are virtually absent from the literature or made in artificial environments. Temporary changes in the shoot budget, brought about by bursts of growth in fits and starts, have the potential to modify the whole community structure.

From the lack of root compensatory growth and enhanced leaf turnover during K-limiting conditions, we hypothesise that most of the compensatory root growth of seedlings takes place after the growing season, when leaves die back. In other terms, under N addition, we will expect to find the strong positive growth benefit backed up and carried forward by belowground production or stored in its overwintering form, the corm, the short underground stem that serves as a storage organ and is shown to represent approximately one-third of the total plant biomass at the end of the growing season.

Finally, with respect to the regeneration of cutover bogs, these mainly K-driven changes are expected to favour the spread of *E. vaginatum* seedlings, and diminish the nutrient and light availability to inter-tussock species. As *E. vaginatum* is a keystone species for the reestablishment of *Sphagnum* mosses leading to the restoration of the C sequestering function of cutover bogs, understanding which factors affect the establishment of its seedling has practical implications for the management of abandoned mined bogs.

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Conflict of interest The authors declare that they have no conflict of interest and that experiments comply with the current laws of Switzerland.

References

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

Backéus I (1985) Aboveground production and growth dynamics of vascular bog plants in Central Sweden. Acta Phytogeogr Suec 74:1–98

Bassirirad H, Tissue DT, Reynolds JF, Chapin FS III (1996) Response of *Eriophorum vaginatum* to CO_2 enrichment at different temperatures: effects on growth, root respiration and PO_4^{3-} uptake kinetics. New Phytol 133:423–430

Berendse F, Rydin H, van Breemen N, Buttler A, Heijmans M, Hoosbeek MR, Lee J, Mitchell EAD, Saarnio S, Vasander H, Wallen B (2001) C sequestration is influenced by competitive shifts among plant species in *Sphagnum* bogs at elevated atmospheric CO_2 and N deposition. Glob Change Biol 7:591–598

Bliss LC (1956) A comparison of plant development in microenvironments of arctic and alpine plants. Ecol Monogr 26:303–337

Buurman P, van Lagen B, Velthorst EJ (1996) Manual for soil and water analysis. Backhuys, Leiden

Chapin FS III, Shaver GR (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. Ecology 77:822–840

Cholewa E, Griffith M (2004) The unusual vascular structure of the corm of *Eriophorum vaginatum*: implications for efficient retranslocation of nutrients. J Exp Bot 55:731–741

Conroy JP (1992) Influence of elevated atmospheric CO_2 concentrations on plant nutrition. Aust J Bot 40:445–456

Damman AWH (1978) Distribution and movement of elements in ombrotrophic peat bogs. Oikos 30:481–495

Farrar JF (1985) The respiratory source of CO_2. Plant Cell Environ 8:427–438

Fitter AH, Graves JD, Wolfenden J, Self GK, Brown TK, Bogie D, Mansfield TA (1997) Root production and turnover and carbon budgets of two contrasting grasslands under ambient and elevated atmospheric carbon dioxide concentrations. New Phytol 137:247–255

Francez AJ (1995) Carbon and nitrogen dynamics in *Carex-rostrata*, *Eriophorum-vaginatum* and *Calluna-vulgaris* in *Sphagnum* peat of the Forez mountains (France). Can J Bot 73:121–129

Gebauer RLE, Tenhunen JD, Reynolds JF (1995) Soil aeration in relation to soil physical properties, nitrogen availability, and root characteristics within an arctic watershed. Plant Soil 178:37–48

Goodman GT, Perkins DF (1968a) The role of mineral nutrients in *Eriophorum* communities. III. Growth response to added inorganic elements in two *E. vaginatum* communities. J Ecol 56: 667–683

Goodman GT, Perkins DF (1968b) The role of mineral nutrients in *Eriophorum* communities. IV. Potassium supply as a limiting factor in an *E. vaginatum* community. J Ecol 56:685–696

Gough L (2006) Neighbour effects on germination, survival, and growth in two arctic tundra plant communities. Ecography 29:44–56

Grosvernier P, Matthey Y, Buttler A (1995) Microclimate and physical properties of peat: new clues to the understanding of bog restoration process. In: Wheeler B, Shaw S, Foyt W, Robertson A (eds) The restoration of temperate wetlands. Wiley, Chichester, pp 437–445

Hoosbeek M, van Bremen N, Vasander H, Buttler A, Berendse F (2002) Potassium limits potential growth of bog vegetation under elevated atmospheric CO_2 and N deposition. Glob Change Biol 8:1130–1138

Hunt R, Hand DW, Hannah MA, Neal AM (1991) Response to CO_2 enrichment in 27 herbaceous species. Funct Ecol 5:410–421

Johnson DW, Ball JT, Walker RF (1997) Effects of CO_2 and nitrogen fertilization on vegetation and soil nutrient content in juvenile ponderosa pine. Plant Soil 190:29–40

Jonasson S, Chapin FS III (1985) Significance of sequential leaf development for nutrient balance of the cotton sedge, *Eriophorum vaginatum* L. Oecologia 67:511–518

Kivimäki SK (2008) Carbon sink function of sedge and *Sphagnum* patches in a restored cut-away peatland: increased functional diversity leads to higher production. J Appl Ecol 45:921–929

Körner C (1995) Biodiversity and CO_2: global change is under way. Gaia 4:234–243

Lambers H, Atkin O (1995) Regulation of carbon metabolism in roots. In: Madore MA, Lucas WJ (eds) Carbon partitioning and source-sink interactions in plants. The American Society of Plant Physiologists, Rockville, pp 226–238

Miglietta F, Hoosbeek MR, Foot J, Gigon F, Heijmans M, Peressotti A, Saarinen T, van Breemen N, Wallén B (2001) Spatial and temporal performance of the MiniFace (free Air CO_2 enrichment) system on bog ecosystems in northern and central Europe. Environ Monit Assess 66:107–127

Mitchell AED, Buttler A, Grosvernier P, Rydin H, Siegenthaler A, Gobat JM (2002) Contrasted effects of increased N and CO_2 levels on two keystone species in peatlands restoration and implications for global change. J Ecol 90:529–533

Mitchell EAD, Gilbert D, Buttler A, Amblard C, Grosvernier P, Gobat JM (2003) Structure of microbial communities in *Sphagnum* peatlands and effect of atmospheric carbon dioxide enrichment. Microb Ecol 46:187–199

NABEL (1995) Air Pollution 1994. Measurements made by the national survey network of atmospheric pollutants. Federal Service for Environment, Forest and Landscape, Bern

NABEL (2009) Air Pollution 2008. Measurements made by the national survey network of atmospheric pollutants. Federal Service for Environment, Forest and Landscape, Bern

Noble JC, Miller PC (1979) The population biology of plants with clonal growth. The morphology and structural demography of *Carex arenaria*. J Ecol 62:151–177

Oechel WC, Vourlitis GL (1996) Direct effects of elevated CO_2 on arctic plant and ecosystem function. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, pp 163–176

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. URL http://www.R-project.org

Rogers HH, Runion GB (1994) Plant responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. Environ Pollut 83:155–189

Schimel JP, Chapin FS III (1996) Tundra plant uptake of amino acid and NH_4^+ nitrogen in situ: plants compete well for amino acid N. Ecology 77:2142–2147

Shaver GR, Chapin FS III (1980) Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61:662–675

Shaver GR, Chapin FS III, Gartner BL (1986) Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. J Bryology 74:257–278

Stulen I, Den Hertog J (1993) Root growth and functioning under atmospheric CO_2 enrichment. Vegetatio 104(105):99–115

Sullivan PF, Sommerkorn M, Rueth HM, Nadelhoffer KJ, Saver GR, Welker JM (2007) Climate and species affect fine root production with long-term fertilization in acidic tussock tundra near Toolik Lake, Alaska. Oecologia 153:643–652

Taiz L, Zeiger E (1998) Plant physiology. Sinauer, Sunderland

Tamm CO (1954) Some observations on the nutrient turn-over in a bog community dominated by *Eriophorum vaginatum* L. Oikos 5:189–194

Taub DR, Wang XZ (2008) Why are nitrogen concentrations in plant tissues lower under elevated CO2? A critical examination of the hypotheses. J Integr Plant Biol 50:1365–1374

Tissue DT, Oechel WC (1987) Response of *Eriophorum vaginatum* to elevated CO_2 and temperature in the Alaskan tussock tundra. Ecology 68:401–410

van Heerwaarden LM, Toet S, Aerts R (2003) Nitrogen and phosphorus resorption efficiency and proficiency in six sub-arctic bog species after 4 years of nitrogen fertilization. J Ecol 91:1060–1070

van Wijk MT, Clemmensen KE, Shaver GR, Williams M, Callaghan TV, Chapin FS, Cornelissen JHC, Gough L, Hobbie SE, Jonasson S, Lee JA, Michelsen A, Press MC, Richardson SJ, Rueth H (2004) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. Glob Change Biol 10:105–123

Vasander H (1982) Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Ann Bot Fenn 19:103–125

Walinga I, van der Lee JJ, Houba VJG, Van Vark W, Novozamsky I (1995) Plant analysis manual. Kluwer, Dordrecht

Wein RW (1973) Biological flora of the British Isles. J Ecol 61:601–613

Wulff RD, Strain BR (1982) Effects of CO_2 enrichment on growth and photosynthesis in *Desmodium paniculatum*. Can J Bot 60:1084–1109