Light responses of mire mosses – a key to survival after water-level drawdown?

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Mosses are important ecosystem engineers in mires. Their existence may be threatened directly or indirectly by anthropogenic drying, which further leads to shading and changed competition conditions via increased arboreal plant cover. Yet, some species are able to acclimate to the changing habitat, while some give way to new colonizers. In the shaded conditions, acclimation or adaptation to low light levels is likely to be a winning strategy to survive. We studied the light responses of photosynthesis and photosynthetic pigment concentrations in mosses from an open mire and its shaded, i.e. drained and forested counterpart. Against our expectations, the *Sphagnum* species found only in the open habitat had lower photosynthetic capacity and maximum quantum yield than those found to grow in the shade. Chlorophyll fluorescence results suggested that photoinhibitory damage to photosystem II is responsible for the low photosynthetic performance of the Sphagna of the open habitat, which were inefficient to utilize any light level. In the shaded habitat, *Sphagnum* mosses showed adaptation to lower light conditions only by possessing a higher chlorophyll content. *Pleurozium schreberi* reached photosynthetic light saturation at half the irradiance level compared to Sphagna. The lack of efficient photoprotection or repair mechanism after photodamage may constrain the success of these species in the open habitat. Thus, the dominant Sphagna in the open pristine conditions seem to be stress tolerant, while the dominants of the shaded drained mire appear to be species capable of maximizing their growth and production to compete in the unstressful conditions in terms of light and desiccation.

Mosses, especially those of the genus *Sphagnum*, are essential ecological agents in mire (peatland) ecosystems: they form the growing media and environment for themselves and other plants as part of their necromass accumulates as peat. There are 250–400 *Sphagnum* species over the world (Shaw 2000), but the few dozens of species that grow in the temperate and boreal zones form a largest part of the total biomass (Vitt 2000). The ecological range of northern *Sphagnum* species covers the large variation of northern mires, from extremely nutrient-poor bogs to rich fens, from open to densely forested habitats, and from wet hollows to dry hummocks.

The large variation in mire vegetation is related to differences in ecohydrology (Wheeler and Proctor 2000, Økland et al. 2001, Bragazza et al. 2005). The most important external factors controlling the succession of mire plant communities are, directly or indirectly, the inflow rate and chemical composition of water, and climatic variations resulting in changes in the ratio between precipitation and evapotranspiration (Gorham 1991). Relatively rapid changes in ecohydrology may be mediated through land-use change, and/or climatic change, which both will lead to lowered water-levels in

northern mires (Gitay et al. 2001), accompanied with dramatic changes in ecosystems functions. As ecological agents, the fate of *Sphagnum* mosses may be a key factor for the mires to retain, for instance, their carbon accumulation function (Strack et al. 2006).

A general trend in the vegetation succession in mires affected by water-level drawdown is an increase in the abundance of arboreal plants (Laine et al. 1995, Vasander et al. 1997, Laiho et al. 2003), which greatly increases the shading of the moss layer. Logically, this would shape the moss community composition in favour of shade-adaptable species although this has not been studied. An opposite pattern has been observed during successional opening of boreal forest; shade-adapted feathermosses were replaced by Sphagna (Fenton and Bergeron 2006, Fenton et al. 2007). We therefore assume that acclimation or adaptation of mire moss dominants to the light conditions is essential for optimizing the photosynthetic, growth and production rates, which are the precursors of success in the competition among similar species utilizing similar resources, and may be a key factor in shaping the moss community in the secondary succession following a persistent water-level drawdown.

The general aim of this paper is to study whether and how the moss dominants respond to their open and shaded mire habitats. We expect that the adaptation or acclimation to low light levels is a strategy to cope in the shaded conditions following a persistent water-level drawdown, i.e. that the mosses will reflect the sun/hade dichotomy (Givnish 1988). In other words, the parameters related to photosynthetic productivity and adaptation to light conditions would form a single gradient, verified by the following general patterns:

1. The dominant mosses of open mires have greater photosynthetic capacity to utilize the higher irradiation of their habitat, than the mosses in the understorey of shaded mires that reach the light saturation of photosynthesis ($PPFD_{95\%}$) under lower irradiation (Givnish 1988). Further, the mosses of open mires have a higher proportion of opened reaction centers (q_P) and higher quantum yield of photosystem II (Φ_{PSII}) under moderate irradiation.
2. Mosses adapted to high light conditions in the open mire should not show symptoms of light-induced stress to their photosynthetic apparatus represented by reduced maximum quantum yield of photosystem II (F_V/F_M) and thus maximum quantum yield of photosynthesis (α).
3. The dominant mosses of shaded mires have higher total chlorophyll content than the mosses of open mires, as found typical for shade-adapted mosses (Marschall and Proctor 2004). They may also show a lower chlorophyll a:b ratio and a higher chlorophyll/carotenoid ratio, even though these indicators of enhanced light harvesting capacity do not necessarily behave consistently among mosses (Marschall and Proctor 2004, Glime 2007).
4. In shaded mires, the shoot segments below capitula do not have a potential to contribute to moss photosynthesis. In open mires, the deeper segments are acclimated to utilize the low levels of light that still seeps down past the capitula, and contribute to photosynthesis.
5. To test our hypotheses, we studied parameters of photosynthesis (P_{max}, α, $PPFD_{95\%}$) and photosystem II (q_P, Φ_{PSII}, F_V/F_M), and photosynthetic pigment concentrations and ratios in mosses from an open fen and its shaded, forested counterpart.

Material and methods

Study site

Our study site was the Lakkasuo mire located in Orivesi, central Finland (61°48′N, 24°19′E, ca 150 m a.s.l.). This raised bog complex offers a unique opportunity to study the long-term effects of water-level drawdown on ecosystem functioning. It contains a large minerotrophic lagg, consisting mostly of oligotrophic fen, about half of which was drained for forestry in 1961. Along the border ditch we can find sites that were initially uniform, but while one part has remained open (pristine, unaffected by the ditch because of the water flow direction), the other part has undergone drainage succession for four decades.

Our study site represented oligotrophic (poor) fen that in its pristine stage was characterized by sedges such as *Carex lasiocarpa* and *C. rostrata*. The dominant *Sphagnum* mosses *S. fallax*, *S. flexuosum* and *S. papillosum* formed an almost continuous carpet. *Sphagnum angustifolium* and *S. magellanicum* were also found but with lower abundances. In the drained part, the volume of the tree stand had increased from close to zero to about 150 m³ ha⁻¹, leading to an estimated photosynthetic photon flux density of 20% reaching the moss surface as compared to that in the open (Mälkönen 1995). The understorey vegetation was dominated by shrubs such as *Vaccinium vitis-idaea* and *Empetrum nigrum*, with *Eriophorum vaginatum* as the only common graminoid. The moss layer was almost continuous also in the drained part, *Pleurozium schreberi*, *S. angustifolium*, *S. magellanicum* and *S. russowii* being the most common species.

Sampling

In September 2004, we sampled the dominant moss species in each part, open and shaded, from monospecific patches (Table 1). Five replicates per species and part were taken. The samples were placed, at natural structure and density, into plastic boxes, $10 \times 10 \times 3$ cm, which where stored closed in the dark at 8°C.

We grouped the species regarding to their successional behaviour following persistent water-level drawdown (Table 1): 1) losers, i.e. lawn species that are adapted only to open conditions and disappear following water-level drawdown; 2) survivors, i.e. hummock species that are present in the

Table 1. The studied species, their sampling sites and response to the persistent water-level drawdown. The bulk density (means±SE) of 10 mm long shoot segments was measured from five replicates.

Species	Habitat	Species group	Bulk density (g dm⁻² cm⁻¹)		
			1st segment	2nd segment	3rd segment
Sphagnum fallax	open	loser	0.82±0.12	0.30±0.02	0.27±0.02
S. flexuosum	open	loser	0.72±0.14	0.34±0.04	0.32±0.04
S. papillosum	open	loser	1.38±0.15	0.77±0.15	0.63±0.08
S. angustifolium	open	survivor	1.19±0.16	0.40±0.06	0.38±0.07
S. magellanicum	open	survivor	1.36±0.21	0.95±0.19	0.90±0.19
S. angustifolium	shaded	survivor	1.23±0.11	0.43±0.02	0.37±0.02
S. magellanicum	shaded	survivor	1.02±0.13	0.46±0.07	0.33±0.06
S. russowii	shaded	winner	1.36±0.20	0.49±0.02	0.39±0.03
Pleurozium schreberi	shaded	winner	0.59±0.05	0.75±0.05	0.74±0.08

open sites and are able to acclimate to the new conditions as well; and 3) winners, i.e. new species that are colonizing the site following water-level drawdown (Laine et al. 1995). We expected the three species groups to differ in their response to light.

Sample treatment

A week after collection, the moss samples were transported to the Univ. of South Bohemia, České Budějovice, Czech Republic, where the laboratory measurements were carried out. Here the samples were kept in a growth chamber during the 10 days before the photosynthetic measurements were started. The measurements took 5 days; thus the last samples were analyzed after 15 days. The photosynthetic photon flux density (PPFD) in the chamber was 220 μmol $m^{-2} s^{-1}$, and the day/night (14/10 h) temperature was 22°C/12°C. To keep the water table at 3 cm below the moss surface we supplied the mosses with artificial rainwater every 3rd day (0.1 mg l^{-1} of Na^+, K^+ and Mg^{2+}, 0.3 mg l^{-1} of Ca^{2+}, NH_4^+ and Cl^- and 1.0 mg l^{-1} of NO_3^- and SO_4^{2-}).

A day before the measurements, subsamples of moss shoots were cut into three 10-mm long segments in order to evaluate the role of subapical segments in photosynthesis of entire shoots. Seven to 31 shoot segments, roughly corresponding to the field shoot density, were reassembled into a mat in plexiglas gas-exchange cuvettes of inner size $3 \times 2 \times 1$ cm. The excess extra-tissue-water was drained out from the moss samples through the mesh bottom of the cuvettes by cellulose strips to minimize the photosynthesis limitation by slow diffusion of CO_2 through water (Titus and Wagner 1984, Schipperges and Rydin 1998). The water content of the *Sphagnum* capitula ranged between 1230–1030% in *S. russowii* and 2070–1920% of dry weight in *S. papillosum* during the measurement period. This content was very close to optimum as showed preliminary measurements of the water content effect on photosynthetic rates of all *Sphagnum* species. One of five replicate sets of each species and site was processed per day.

The remaining moss shoots were counted to obtain the total number of shoots per unit area. Sub-samples of the three shoot segments were oven-dried at 60°C and weighed to obtain the bulk density, i.e. mass per unit volume for each shoot segment. These were used to express the gas-exchange data on a unit-area basis corresponding to the natural densities of the different moss species in the field.

CO₂-exchange measurements

We measured gas exchange with an open system infrared CO_2/H_2O gas analyser with a standard chamber of 3×2 cm, which was modified to measure moss photosynthesis in 1-cm high plexiglass cuvettes. The rapid response of photosynthesis to irradiance was measured under increasing levels of PPFD: 0, 100, 250, 800 and 2000 μmol $m^{-2} s^{-1}$. Artificial light was provided by a built-in LED light source. Chamber temperature was 22°C, the CO_2 concentration in incoming air was 400 ppm and the relative humidity of outgoing air was adjusted to 75%, corresponding to the air flow of 350–700 μmol s^{-1}. One

measurement at each level of PPFD took about 200 s, during which time the CO_2 exchange had been stabilised.

After the measurements, the shoot samples were immediately frozen at $-22°C$, stored and transported for pigment content analysis and after that, the dry weights of samples were determined.

An equation describing the saturation kinetics was fitted into the data on light-response of gross photosynthesis (P_G):

$$P_G = P_N - R_D = \frac{\alpha \times PPFD \times P_{max}}{\sqrt[c]{\alpha^c \times PPFD^c + P_{max}^c}}$$

$$\approx \frac{\alpha \times PPFD \times P_{max}}{\alpha \times PPFD + P_{max}} \quad (1)$$

where P_N and R_D represent measured values of net photosynthesis and dark respiration, respectively; α determines the maximum (apparent) quantum yield of photosynthesis as the initial slope of the curve and P_{max} is photosynthetic capacity, the maximum rate of light-saturated gross photosynthesis. The global value of parameter c (convexity of the light curve) was estimated by fitting the curve to all the data of all species (n = 230). Because it was found to be 0.9, the global value of c = 1.0 was set up and c could be excluded from the equation. We tried also the exponential model applied by Marschall and Proctor (2004), but in our material it resulted in clearly non-random residuals. The model we chose provided both a good fit to our data and a random distribution of residuals.

Although Marschall and Proctor (2004) used a different photosynthetic light response model, their $PPFD_{95\%}$ concept is fully applicable to the model used in this study. Light saturation point of photosynthesis, $PPFD_{95\%}$, was defined as the PPFD where the P_G reaches 95% of P_{max} (Marschall and Proctor 2004). Hence the expression using the model (Eq. 1) and for c = 1 is:

$$PPFD_{95\%} = \frac{0.95}{\sqrt[c]{1 - 0.95^c}} \frac{P_{max}}{\alpha} \approx 19 \frac{P_{max}}{\alpha} \quad (2)$$

P_G will be expressed on a unit-area basis (mg CO_2 m^{-2} h^{-1}) to facilitate ecological inference of the results. It is possible to calculate the rate of photosynthesis based on dry-weight using the bulk density values given in Table 1.

Chlorophyll-fluorescence measurements

We applied the chlorophyll-fluorescence method to quantify the physiological condition of photosystem (PS) II. Chlorophyll fluorescence (ChlF) of each sample was measured just before the gas exchange measurement. ChlF was first measured on dark-adapted (12 min) moss samples in the gas-exchange cuvettes using a kinetic modulated imaging fluorometer. The minimum (dark) ChlF yield (F_0) was obtained using weak flashes of red LEDs and the maximum ChlF yield (F_M) was determined with an 800-ms saturating pulse (halogen lamp, 1800 μmol $m^{-2} s^{-1}$ PPFD). The maximum variable ChlF yield (F_V) was determined as a difference between F_M and F_0. After the dark-adapted measurements, the slow ChlF induction kinetics (Kautsky curve; red-LEDs providing PPFD of 220 μmol $m^{-2} s^{-1}$) was carried out to measure the peak of

ChlF yield at the actinic illumination (F_P), as well as the steady-state, maximum and minimum ChlF yield (F_S, F'_M and F'_0) in the light-adapted state. The ChlF signals of all shoots in the 6-cm^2 cuvette area were visualised, separated, and averaged using FluorCam software.

We present three parameters of ChlF referring to the photochemical processes in PSII: maximum quantum yield of PSII photochemistry [F_V/F_M ratio] is a proportion of quanta absorbed by PSII in dark-adapted mosses. Quantum yield of PSII photochemistry [$\Phi_{PSII} = \Delta F/F'_M = (F'_M - F_S)/F'_M$] is a proportion of quanta absorbed by PSII in mosses adapted to light. Photochemical quenching of variable fluorescence [$q_P = \Delta F/F'_V = (F'_M - F_S)/(F'_M - F'_0)$] quantifies the proportion of opened PSII reaction centres in light-adapted samples.

Analyses of pigment concentrations

Frozen moss samples were ground in 80% (v/v) buffered aqueous acetone (50 mM Na_3PO_4 buffer, pH 7.8). Absorbance at 470, 647, 664 and 750 nm were read on a spectrophotometer. The chlorophyll a, b and total carotenoid concentrations were determined from the equations after Porra et al. (1989).

Statistical analyses

In *Pleurozium schreberi*, the first two shoot segments together formed the fully irradiated top moss layer because of the pleurocarpous, partially horizontal growth form. These segments were therefore considered as the top segments compared with the apical segments of the Sphagna.

We used multilevel models (a.k.a. mixed linear models; Goldstein 1995) to test whether there were differences between species groups, or sites, in the studied variables. Thus we were able to take into account that our data were clustered (replicates within species within site) and the individual observations were not independent in a statistical sense. The total variance in the data was separated into components derived from each level of the data, and binary variables describing the species groups or sites were added to the fixed part of the models to see if they significantly reduced the remaining total variance. These analyses were done using MLwiN ver. 1.1.

Oneway ANOVA, using the general linear models of Statistica ver. 6.0, was applied to detect whether there were differences in *S. angustifolium* and *S. magellanicum* between habitats (these two species were found in both habitats). Twoway ANOVA was applied to detect differences between stem segments in all species. The Tukey's HSD test was performed to compare levels within factors.

We applied principal component analysis (PCA) to study the correlations between different variables and the relationships between different species. We used the parameters of photosynthetic light response, chlorophyll fluorescence and pigment contents as response variables. These were centered and standardized in order to make them comparable. Because PPFD$_{95\%}$ and Chl/Car were combinations of other variables already included, we used them as supplementary variables, i.e. they did not influence the analysis or the resulting ordination diagram. The PCA was done using Canoco for Windows ver. 4.5 (ter Braak and Šmilauer 2002).

Results

Light response of photosynthesis

Photosynthetic capacity, P_{max}, of the top segments decreased in the order: *Sphagnum angustifolium* from the open habitat (O), *S. angustifolium* from the shaded habitat (S), *S. russowii* (S), *Pleurozium schreberi* (S), *S. magellanicum* (S), *S. magellanicum* (O), *S. fallax* (O), *S. flexuosum* (O), *S. papillosum* (O) (Fig. 1). The species, whose distribution was limited to the open habitat, i.e. losers, had a significantly (<0.05) lower P_{max} (190 mg_{CO2} m^{-2} h^{-1} on average) than the survivors (453 mg_{CO2} m^{-2} h^{-1}) and winners (770 mg_{CO2} m^{-2} h^{-1}). *Sphagnum angustifolium* that was growing in both the open and the shaded habitats, had the highest photosynthetic capacity in both. Therefore, although the species in the shaded habitat (winners and survivors) generally reached higher P_{max} than the species in the open (losers and survivors), the difference was not statistically significant.

Maximum quantum yield of photosynthesis, α, increased systematically from losers to survivors and winners in the top segments (Table 2). It was also significantly lower in the open than in the shaded habitat ($p < 0.001$).

Photosynthesis of the top-segments of all *Sphagnum* species reached the light saturation point, PPFD$_{95\%}$, in a much higher light intensity than *Pleurozium* (Table 2). Therefore the PPFD$_{95\%}$ of the winners and in the shaded habitat was significantly lower than that of the other groups and the open. However, the PPFD$_{95\%}$ was almost constant in *Sphagnum* capitula of all species, on average 2124 ± 86 (SE) μmol m^{-2} s^{-1}.

Sphagnum angustifolium and *S. magellanicum*, the two survivors, differed in their response to the habitat (Fig. 1). P_{max} and α were about 13% lower in *S. angustifolium* in the shaded habitat ($p = 0.12$), while in *S. magellanicum* they were 41% higher ($p = 0.10$).

Chlorophyll fluorescence

The maximum quantum yield of PSII photochemistry, F_V/F_M, was very variable between species but without significant differences between species groups or habitats (Fig. 1). In the *Sphagnum* capitula, the F_V/F_M usually varied between 0.60 and 0.75, but was below 0.50 in *S. papillosum* and *S. magellanicum* from the open habitat.

Quantum efficiency of PSII photochemistry, Φ_{PSII}, tended to be lower in the losers and in the open; however, the difference was not significant. The proportion of opened reaction centers in PSII, expressed by q_P, was similar between species, and no significant differences were found between species groups or habitats (Fig. 1).
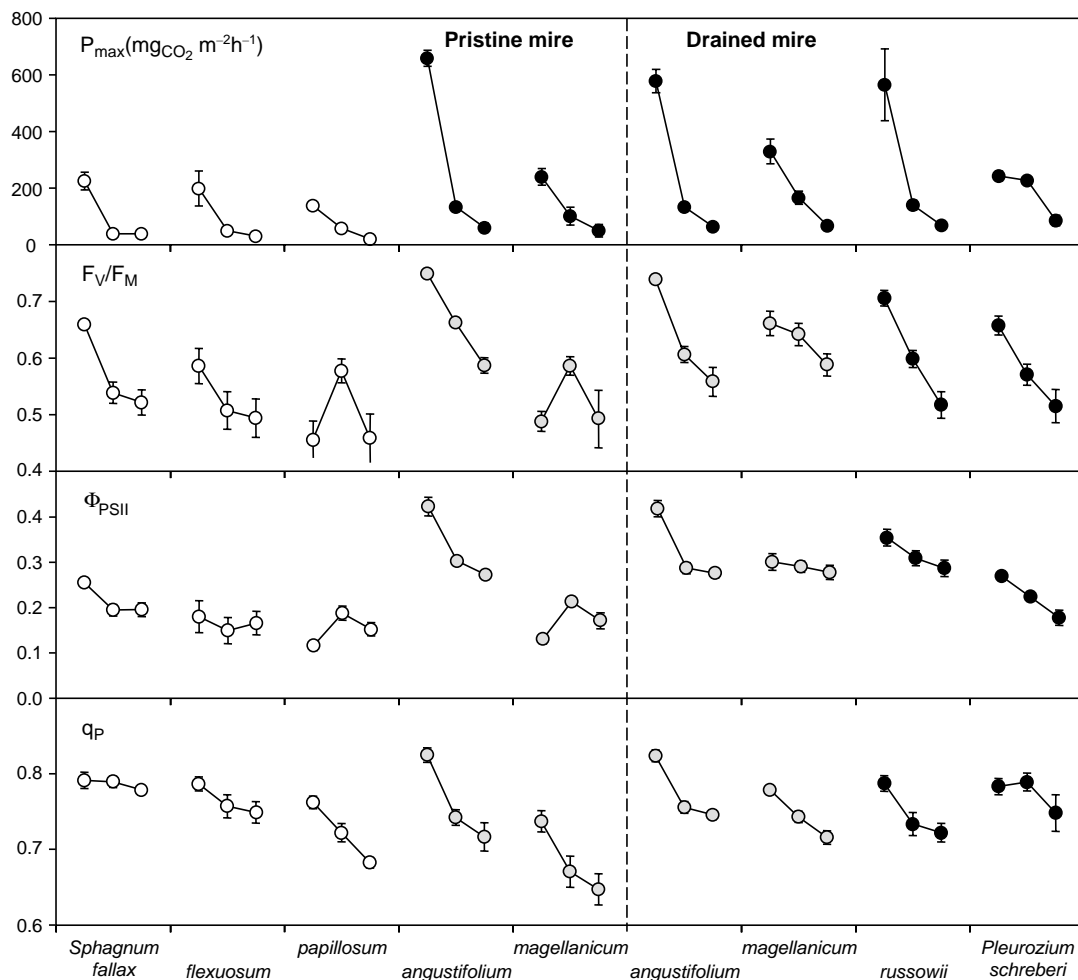
Figure 1. Maximum rate of photosynthesis (P_{max}) and chlorophyll-fluorescence parameters of the studied mosses. The triplets of connected circles represent the 10-mm shoot segments; the leftmost is the top segment. White, grey and black symbols denote the species groups: losers, survivors and winners, respectively. Actinic light PPFD of 220 $\mu mol\ m^{-2}\ s^{-1}$ was used for measurement of Φ_{PSII} and q_P. Means $\pm$ SE, n = 5.

Pigment contents

The total chlorophyll (Chl) content in the top segments (Fig. 2) was significantly lowest in losers and was generally lower in the open than in the shaded habitat, even though the difference was not significant. The Chl a/b ratio and carotenoid (Car) content were clearly the highest in *Pleurozium* and similar in all Sphagna (Fig. 2); consequently, Chl/Car ratio was the lowest in *Pleurozium*.

Table 2. Maximum quantum yield of photosynthesis (α) and light saturation point ($PPFD_{95\%}$) in the top segments of the studied mosses. Means $\pm$ SE of five replicates.

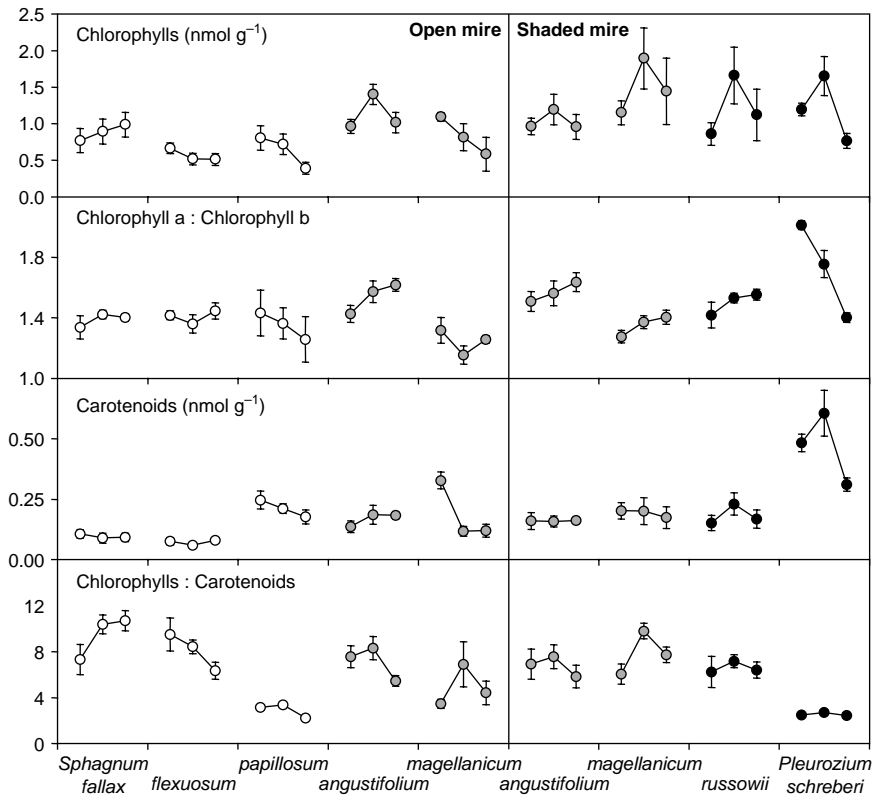| Species	Habitat	Species group	α ($g_{CO2}\ mol_{PPFD}^{-1}$)	$PPFD_{95\%}$ ($\mu mol\ m^{-2}\ s^{-1}$)
Sphagnum fallax	open	loser	0.628 ± 0.148	2107 ± 147
S. flexuosum	open	loser	0.489 ± 0.141	2287 ± 225
S. papillosum	open	loser	0.333 ± 0.064	2603 ± 354
S. angustifolium	open	survivor	1.759 ± 0.188	2151 ± 240
S. magellanicum	open	survivor	0.776 ± 0.223	1956 ± 268
S. angustifolium	shaded	survivor	1.587 ± 0.180	2043 ± 180
S. magellanicum	shaded	survivor	1.018 ± 0.146	1906 ± 343
S. russowii	shaded	winner	1.605 ± 0.319	1942 ± 164
Pleurozium schreberi	shaded	winner	2.547 ± 0.296	1076 ± 66
	open		0.797	2219
	shaded		1.689	1742
		loser	0.483	2319
		survivor	1.285	2014
		winner	2.076	1509

Figure 2. Chlorophyll and carotenoid parameters of the studied mosses. The triplets of connected circles represent the 10-mm shoot segments; the leftmost is the top segment. White, grey and black symbols denote the species groups: losers, survivors and winners, respectively. Means $\pm$ SE, n = 5.

Relationships between the parameters of photosynthesis, chlorophyll fluorescence and pigment contents

The ratio between P_{max} and α was almost constant in the top segments of Sphagna (Fig. 3), thus by definition (Eq. 2) the $PPFD_{95\%}$ varied only little as well. A similar but less distinct pattern was found in the 2nd and 3rd segments ($P_{max} = 125\alpha + 114$, p = 0.020 and $P_{max} = 72\alpha + 114$, p = 0.006, respectively; data not shown). Although *Pleurozium* has very different shoot characteristics and lower $PPFD_{95\%}$, it exhibited similar but much less distinguished P_{max} dependency on α (Fig. 3).

The markedly reduced efficiency of PSII, indicated by low F_V/F_M in *S. papillosum*, *S. magellanicum* and *S. flexuosum* from open habitat, was associated with low α (Fig. 4). Also in *P. schreberi*, F_V/F_M was related to α although the level of F_V/F_M was relatively lower at high levels of α.

Principal component analysis revealed two strong gradients in the top segment data (Fig. 5). The main gradient was related to the photosynthetic capacity and parameters describing the efficiencies of photosynthesis and PSII. This 'productivity and efficiency gradient', which explained 39% of total variation among mosses, separated the winners and survivors from the losers as well as the mosses of the shaded habitat from those of the open. The second gradient separated *Pleurozium schreberi* with the highest pigment contents and the lowest light saturation point from all

Sphagna. The losers, survivors and winners were distinctly grouped along this 'light-adaptation gradient', which explained 26% of the total variation. In comparison to all Sphagna, *Pleurozium* was clearly a shade plant.

The role of subapical segments

There was a steep gradient in P_{max} from the apical to the 3rd shoot segment in all *Sphagnum* species (Fig. 1) indicating low contribution of the 2nd and 3rd segments to overall carbon assimilation. It was relatively highest in the two *Sphagnum* mosses belonging to section *Sphagnum*, *S. magellanicum* and *S. papillosum*; their P_{max} of the second segment was about half of the first one. In the pleurocarpous *P. schreberi*, P_{max} of the 1st and 2nd segments was similar. Similarly to P_{max}, F_V/F_M decreased abruptly from top segments downwards in all species except, again, *S. papillosum* and *S. magellanicum* from the open habitat (Fig. 1). In these two exceptional cases, the highest F_V/F_M values were found in the 2nd segment while the values for capitula were similar to those of the 3rd segments.

The patterns in pigment parameters along the shoot gradient varied among the species (Fig. 2). In the shade and *S. angustifolium* from the open, i.e. in species with the highest photosynthetic capacity, the apical segment contained less chlorophyll then the second one. Unlike in Sphagna, the Chl a/b ratio in *Pleurozium* decreased steeply along the shoot gradient.
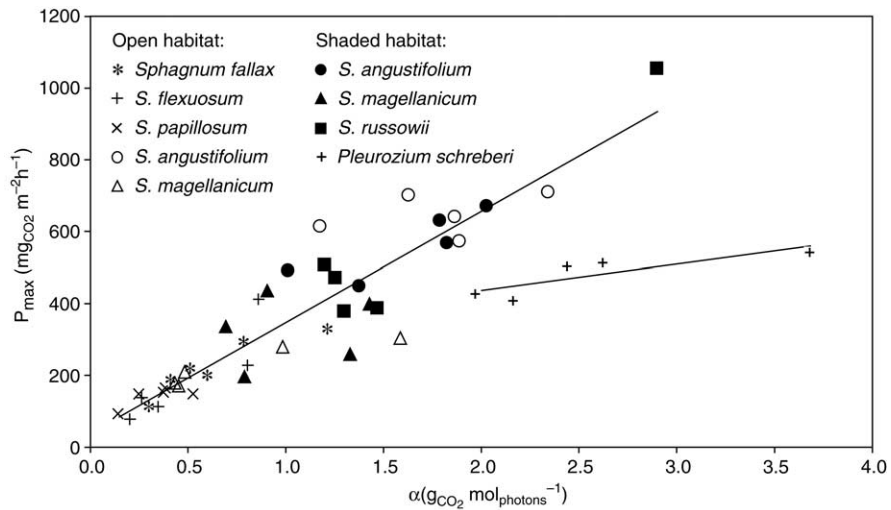
Figure 3. Relationship between the maximum quantum yield of photosynthesis (α) and light-saturated gross photosynthesis (P_{max}) in the top-segments of the studied mosses. Regression model for Sphagna: $P_{max} = 329\alpha + 44$ [$r^2 = 0.85$, n = 41], and for *Pleurozium*: $P_{max} = 78\alpha + 307$ [$r^2 = 0.70$, n = 5].

Discussion

Sun and shade adaptations

Our study showed a clear existence of two independent gradients: 'productivity and efficiency' and 'light-adaptation'. In contrast to our expectation, we found that the parameters related to photosynthetic productivity and adaptation to light conditions did not show clear correlation. The losers, i.e. *Sphagnum* species found only in the open part of the fen were inefficient in utilizing any light level in comparison to survivors and winners, i.e. species occurring in the shaded part. Moreover, there were no differences in the light saturation point of photosynthesis ($PPFD_{95\%}$) between Sphagna.

The relatively high $PPFD_{95\%}$ measured in our Sphagna (Titus and Wagner 1984, Harley et al. 1989, Maseyk et al. 1999) largely resulted from the cuvette design we used for the photosynthetic measurements. The open-bottom (mesh-covered) cuvette provided an efficient gas exchange between the inner space of the sample and the measured air above and below the sample. Consequently, we were in practice measuring the gas-exchange of the whole moss 'micro-canopies' instead of individual leaves or the upper leaf layer of the *Sphagnum* mat as has usually been the case. Thus in our material the initial, light-limited part of the light curve was longer, at the expense of the CO_2-limited part (as the inner shaded leaves become saturated under higher external PPFD), and also the curve inflexion was more flat and occurred at higher PPFD. Such a reduction in
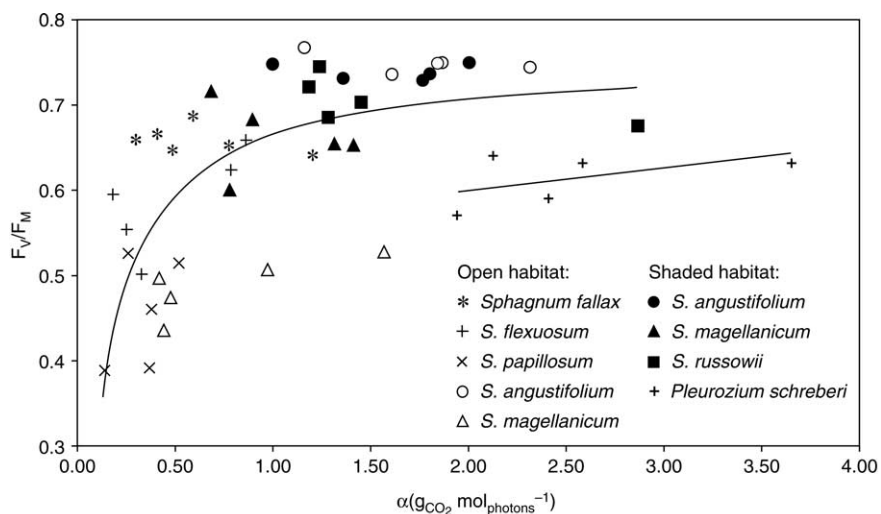

Figure 4. Relationship between the maximum quantum yield of photosynthesis (α) and maximum quantum yield of photosystem II photochemistry (F_V/F_M) in the top-segments of the studied mosses.
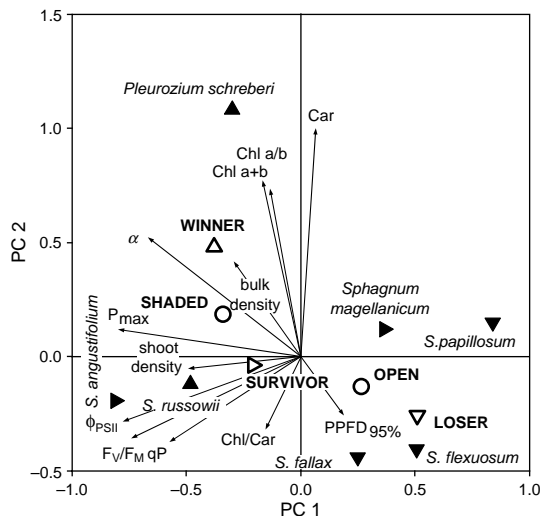
Figure 5. Ordination diagram (PCA) displaying correlations among the measured variables of photosynthetic light response (P_{max}, α, $PPFD_{95\%}$), chlorophyll fluorescence (F_V/F_M, Φ_{PSII}, q_P), and pigment content (Chl a+b, Car) and ratios (Chl a/b, Chl/Car). $PPFD_{95\%}$ and Chl/Car are included as supplementary variables.

the CO_2 diffusion resistance also ensured that the measured photosynthetic rates of *Sphagnum* mats were not significantly influenced by differences in their water holding capacity, expected in Sphagna adapted to contrasting water availability (Titus and Wagner 1984).

Total chlorophyll content, increasing towards the winners of the shaded habitat, was the only parameter reflecting the concept of sun and shade plants. The other indicators of biochemical adaptation to light conditions, i.e. Chl a/b, total carotenoid content and Chl/Car ratio, showed no clear differences between the species groups. Chl a/b ratio and total carotenoids in the Sphagna did not correlate with light conditions, in line with earlier works on mosses (Deora and Chaudhary 1991 in Glime 2007, Marschall and Proctor 2004). The concept of sun and shade plants , which was developed with and for the leaves of vascular plants (Givnish 1988, Larcher 2003, p. 115) does not seem to be fully coherent for mosses; they show corresponding patterns to some extent but there is substantially more variation (Lovelock and Robinson 2002, Marschall and Proctor 2004). Water availability can be an important source of this variability in mosses as exemplified by Ueno et al. (2006). Sun grown moss *Sanionia uncinata* exhibited characteristics of shade plants in dry habitats and those of sun plants in wet habitats. This paradox is based on the short period of photosynthetic activity during and after rain or dew when the PPFD levels are low. After that, the metabolism gets inactivated during desiccation in sunshine. This strategy is inherent to many moss species and can disturb the concept of sun/shade plants in that case.

The role of subapical segments in photosynthesis of entire shoots

The potential contribution of the 2nd and 3rd shoot segments to the total photosynthetic rate of *Sphagnum*

patches was in most cases several fold lower than the contribution of capitula. In natural stands, the realized contribution is likely to be even less because $\sim 95\%$ of PPFD is absorbed in the 1–2 cm of a *Sphagnum* carpet, which corresponds to our 1st segment (Clymo and Hayward 1982). Although the older segments below the capitula live in deep shade, their photosynthetic apparatus generally did not show acclimation to shade. Contrary to other species, the second segments of *S. papillosum* and *S. magellanicum* from the open habitat were able to recover when shaded by growing capitula, as indicated by increased F_V/F_M and Φ_{PSII}. Therefore their subapical segments are more likely to contribute noticeably to their realized gross photosynthesis under full sunlight conditions, but this is mainly due to the very low photosynthetic capacity of the apical segments of these species.

Low photosynthetic capacity in losers

The photosynthetic capacity was clearly related to the maximum quantum yield of photosynthesis, α, in all *Sphagnum* mosses. The broad range of mean α and narrow range of $PPFD_{95\%}$ logically resulted in a broad span of P_{max} (cf. Eq. 2). Such large interspecific variability of P_{max} is typical for Sphagna occupying contrasting habitats (Titus and Wagner 1984, Harley et al. 1989, Maseyk et al. 1999). Generally, α has been found to be a constant parameter in unstressed leaves/plants along the sun-shade gradient (Givnish 1988). However, in our study most of the Sphagna from the open habitat showed lower α than those from the shaded part. Similarly, Maseyk et al. (1999) found three times lower α and P_{max} in *S. cristatum* from an open than shade habitat. Coxson and Mackey (1990) observed diurnal oscillations of photosynthesis in the subalpine sun-grown moss *Pohlia wahlenbergii*, which exhibited late-afternoon depressions of P_{max} and α, not associated with chlorophyll destruction. These examples and our results indicate that full sunlight can induce apparent stress to the photosynthetic apparatus even in hydrated mosses when growing in sunny habitats.

Maximum quantum yield of photosynthesis (α) is measured under light-limiting conditions, i.e. low irradiances when no other factor (CO_2, RUBISCO, mineral nutrients, etc.) limits photosynthetic rate. Reduced α and P_{max} therefore indicate reduced amount of functioning PSII reaction centers (RC) and such damage is considered to be a primary effect of photoinhibition (Powles 1984, Björkman and Demmig 1987).

Our results of CO_2 exchange are supported by the chlorophyll fluorescence results. Close relationship between maximum quantum yields of photosynthesis (α) and that of PSII (F_V/F_M) indicates that the low rate of photosynthesis in the open sites, particularly in *S. papillosum* and *S. magellanicum*, is primarily due to damage in PSII-antennae complex, not in the following light-independent processes. Close linear correlation between almost equal reductions in F_V/F_M and α has been shown in both laboratory (Björkman and Demmig 1987) and field studies (Werner et al. 2001). Our data show that the relationship between α and F_V/F_M (Fig. 4) is close only in the range of low α.

In general, the P_{max} values that we obtained for the apical segments were realistic in comparison to those presented earlier for *Sphagnum* and *Pleurozium* (Williams and Flanagan 1998, McNeil and Waddington 2003). The low P_{max} values of the dominants in the open were actually at the same level as what has been measured in the field for the same moss community (Riutta et al. 2007). This suggests that our results were not an artefact caused by the storing period, transport and laboratory conditions. The temperature during the measurements corresponded to the optimum temperature for P_{max} in the field conditions (Riutta et al. 2007). The samples were collected in September, in the end of unusually wet growth season; therefore the desiccation-induced stress is out of the question.

Photoinhibition

Photoinhibition refers to the basically unavoidable light-dependent damage (photodamage) to PSII, which occurs under any light intensity in all oxygen evolving autotrophs. Apparent photoinhibition arises when the rate of photo-damage exceeds the rate of repair. Generally lower F_V/F_M values found in bryophytes suggest the presence of more intensive photoinhibition than in vascular plants since the F_V/F_M in bryophytes do not exceed 0.8, the typical value for unstressed leaves of vascular plants (Bukhov et al. 2001); this was also the case in our study. Accordingly, Murray et al. (1993) showed a long-lasting (>2 weeks) negative effect of even moderately high PPFD (800 μmol m^{-2} s^{-1}) on F_V/F_M and gas-exchange in *S. angustifolium* and, in turn, a quick (days) positive effect of shading on the growth of *S. magellanicum*.

Photoinhibitory damage usually arises when the plant is subjected to excessive light stress combined with another stress factor. Nutrient and CO_2 availability may be such stress factors in our study. Other common factors such as drought, high or freezing temperatures or possible factors like cold-dark storage are not feasible as discussed above. Nitrogen (N) limitation in *Sphagnum* mosses occurs in peatlands subjected to low N deposition (Vitt et al. 2003, Bragazza et al. 2004). Because the repair of photodamage is based on protein resynthesis, N availability can affect the rate of the repair and thus the extent of photoinhibition (Huang et al. 2004). High CO_2 diffusion resistance due to a large content of external water (Titus and Wagner 1984, Schipperges and Rydin 1998, Maseyk et al. 1999) may also induce damage due to Calvin cycle deceleration (Takahashi and Murata 2005, Nishiyama et al. 2006). These aspects require special research in the future with a consideration to different nutrient and water availability in the open and shaded mire.

It is important to note that photoinhibition is sometimes also referred to as a photoprotective processes preventing photodamage by controlled thermal energy dissipation (Choudhury and Behera 2001). Xanthophyll cycle pigments in PSII antennae serve as an efficient, quickly inducible and reversible mechanism of non-photochemical quenching, NPQ (Demmig-Adams and Adams 1996, Bukhov et al. 2001). In this work, it would be errorneous to calculate NPQ values due to the different levels of damage indicated by differences in the dark-adapted values of F_V/F_M (Maxwell and Johnson 2000). Because the xanthophyll cycle-based photoprotection is reversible within minutes in the dark, the low F_V/F_M values obtained after 12 min of dark-adaptation imply a damage to PSII.

In addition, some *Sphagnum* species produce another pigment, sphagnorubin, a cell wall-located flavonoid. Its photoprotective function is indicated by the dark crimson colour of *S. magellanicum* from the open mire while the shade mosses were only reddish-green. Night chilling (+0.5°C), especially when coupled with low N availability, can accelerate sphagnorubin synthesis but also degradation of chlorophyll a (Rudolph et al. 1977, Rudolph and Voigt 1986) as denoted the low values of Chl a and Chl a/b in comparison to *S. angustifolium* which does not synthesizes sphagnorubin. However, neither the shield effect of sphagnorubin nor the decreased Chl a content can explain the reduced F_V/F_M since the effect on F_0 and F_M will be proportionally the same. This indicates that the photo-protective role of sphagnorubin is not sufficient.

Ecological consequences

It seems obvious that the losers in the secondary succession following a persistent water-level drawdown, i.e. Sphagna adapted only to the open conditions, are not exclusively sun plants; they have lower photosynthetic capacity than the others due to suffering from long-term, chronic photo-inhibition (sensu Osmond and Grace 1995). They remain restricted to the open mire either because they can not tolerate the water-level drawdown as such, or get by with the competition that follows.

Sphagnum species having their highest abundance (realized niche) in drier conditions are generally able to grow as well or even better in wetter conditions than what prevails in their natural habitat (fundamental niche) (Rydin 1993, Mulligan and Gignac 2001). Therefore it is unlikely that the high water level in open sites would directly be an excluding factor for the winners, *S. russowii* and *Pleurozium schreberi*. Instead, they may not tolerate the stressful conditions of full light.

Pleurozium has an advantage over Sphagna as it can utilize moderate PPFD, typical in sparse forests, more efficiently. This indicates that even Sphagna from the shade are not well adapted to their light conditions, as compared with *Pleurozium*. This is consistent with the findings of Fenton and Bergeron (2006) and Fenton et al. (2007), that Sphagna do not occur in dense boreal forests but they follow the increase of light availability during succession, replacing feather mosses such as *P. schreberi*.

An unanswered question concerning *S. angustifolium* remains: which features maintain it to be the most photosynthetically productive species in contrasting, open and shaded habitats? Manipulative experiments on photosynthesis, light protective mechanisms and environmental inhibitors of PSII repair are needed, at least in the survivor species.

Conclusions

As autogenic ecosystem engineers, *Sphagnum* mosses compete with other plants by forming a stressful environment in open mires (van Breemen 1995). As a cost, such competition leads to increased light-induced stress. Being desiccation avoiders, Sphagna cannot escape the light stress by drying out, rolling up their shoots or leaves and becoming inactive like other bryophytes in drier habitats (Proctor and Tuba 2002); they must remain metabolically active. Nevertheless, under the reduced competition in the open mires, Sphagna can afford a less efficient photosynthesis and slow growth. Rapid height growth over the stand of peers would further involve a backward regulation by desiccation related to exposition. Hence, *Sphagnum* life strategy in the open conditions seems to be based on stress tolerance. In the shade, the conditions are less stressful in terms of light and evaporation, but the mosses need successfully compete for space and resources, not only among themselves but also with vascular plants. Therefore, higher photosynthesis resulting in higher growth gives more advantage in the shaded conditions, where the strategy of *Sphagnum*, as well as *Pleurozium*, seems to be maximization of production to compete.

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