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Ecophysiological adaptations of coexisting *Sphagnum* mosses

PhD. thesis

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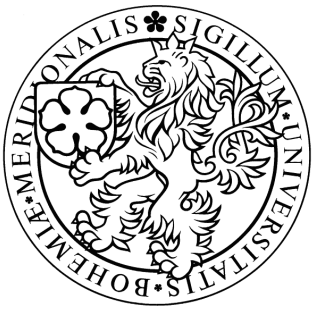

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Annotation

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I studied ecological and physiological adaptations of peat mosses (*Sphagnum* species) coexisting along the environmental gradients in mires. Production, decomposition, water relations, desiccation tolerance and nutrient economy of *Sphagnum* species were evaluates along the hummock–hollow gradient of water table, while the light adaptations were assessed in an open and a forested mire.

Declaration – Prohlášení

I hereby declare that this PhD. thesis has been fully worked out by myself and the named co-authors, and with the use of the cited references.

I declare that in accordance wit the Czech legal code § 47b law No. 111/1998 in its valid version, I consent to the publication of my PhD. thesis (in an edition made by removing marked parts archived by the Faculty of Science) in an electronic way in the public access to the STAG database run by the University of South Bohemia in České Budějovice on its web pages.

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České Budějovice, 31th July 2008

Author contribution statement

Tomáš Hájek, author of this PhD. thesis, is the first author of all four papers (manuscripts) and wrote the substantial part of them. Most of the material and raw data processing as well as most of the statistical analyses were performed by him. Mati Ilomets performed the pigment analyses and Raija Laiho did the mixed models and principal component analysis presented in Study IV.

All co-authors hereby consent to the publication of the papers in the PhD. thesis of Tomáš Hájek and support it by their signatures:

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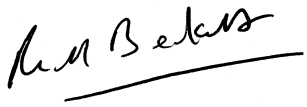

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Contents

General introduction

Peat mosses (*Sphagnum* species, sphagna) have become probably the most successful plant genus over the world, at least in terms of biomass, which accumulates as peat (Clymo and Hayward 1982). Sphagna are also the only bryophytes having direct and significant economic value, based mainly on the high water absorptive capacity and antimicrobial properties of their shoots (Turner 1993; Painter 2003). These features are crucial particularly in *Sphagnum* ecology – in the ability to accumulate biomass and thus to form mires (peatlands). *Sphagnum*-dominated mires have covered extensive areas namely in the boreal zone of the Northern Hemisphere and serve as an important sink and reservoir for global carbon (Gorham 1991), as well as the source of peat, which is used as an important raw material in several branches of industry, agriculture, horticulture as well as in medicine.

A *Sphagnum* story

It is astonishing how such a minute plant, moss, could be so successful, especially when it lacks specialized water-conductive vascular tissues which are assumed to play a key role in the colonization of terrestrial habitats. Many *Sphagnum* species chose an original ecological strategy. Although most of the other bryophytes are adapted to wet and shaded or sunny and dry habitats (e.g., forest understorey vs. rocks), sphagna have taken advantage of both mentioned strategies – life in a sunny and water-saturated environment. Unique morphology and growth habit enable sphagna to avoid desiccation by conducting and retaining extraordinary amounts of water. This allows them to maintain their photosynthesis, cell turgidity and thus the growth also under temporarily dry environmental conditions, analogously to succulents.

Although the productivity of *Sphagnum* mosses is not unusually high, they accumulate peat due to the unusually slow decomposition of their biomass (Clymo 1984). Peat creates water saturated, anoxic, acidic and nutrient poor soil conditions which are unsuitable for rooting plants and often lead to the formation of a treeless, open mire expanse. This is a way how to outcompete trees to ensure full light and avoid desiccation stress.

Sphagnum is therefore referred to as an autogenic ecosystem engineer (sensu Jones at al. 1994), i.e., an organism which uses its own body and physiological processes to modify the availability of resources to other species by creating a new habitat – mire (or peatland) or, more specifically, *Sphagnum* bog. Another engineering activity of certain *Sphagnum* species can be observed on the surfaces of open bogs, which are patterned into a mosaic of elevated and depressed microhabitats, differed by the depth of water-level. Elevated bog hummocks are built by dead shoots, usually of those *Sphagnum* species which are currently growing on the top while other species form wet moss carpets and hollows. The reason why hummock species accumulate more biomass than hollow species does not consist in *Sphagnum* production, which tends to be smaller in hummocks than hollows (Gunnarsson 2005), but rather in the poor litter quality of the hummock sphagna (Johnson and Damman 1991, Belyea 1996). Therefore, *Sphagnum* seems to be responsible also for creating and/or maintaining the so-called hummock-hollow microtopography of bogs.

Niche diversification

Sphagnum-dominated mires represent several types of habitats. Nutrient-poor ombrotrophic bogs on the one side, and rich fens on the opposite side. Forested vs. open mires. Pools, wet hollows and carpets vs. dry hummocks. Such differentiation of environmental conditions enabled *Sphagnum* to evolve into dozens of species – their ecological niches have differentiated along these environmental gradients. Therefore several *Sphagnum* species may coexist in a mire.

The hummock-hollow microtopography is the most characteristic source of niche diversification in mires. The differences in water availability predetermine the species' morphological and ecophysiological adaptations. Briefly, robust and quickly growing shoots of hollow sphagna, belonging mostly to the section Cuspidata, form relatively productive sparse carpets. On the contrary, hummocks are usually formed by densely growing tiny shoots of species from the section Acutifolia, which are characterized by slow growth and smaller production (Gunnarsson 2005; Rydin et al. 2006). The dense growth enables the mosses to perform an effective water management in exposed hummock, i.e., water retention and conduction. Hummock sphagna are therefore referred to as desiccation avoiders, lacking the true desiccation tolerance, an adaptation typical of many bryophytes. On the other hand, hollow species, growing in loose carpets and relying on a high water table, may be subjected to desiccation more often than sphagna in hummocks if the water table draws down during a dry summer.

This corresponds with the observation that sphagna tolerate desiccation better in hollows than in hummocks (Wagner and Titus 1984); however, this statement is not supported by other authors (Clymo 1973; Schipperges and Rydin 1998), probably because of differences in the pre-experimental moss treatment and experimental design.

Nutrient availability is another factor forming distinct gradients over mire habitats. Although ombrotrophic bogs are assumed to be fed exclusively with rainwater, there are also differences in nutrient availability along the hummock–hollow or forested–open mire series. While hummocks are solely ombrotrophic microhabitats, hollows or pools receive also the nutrients which were not retained in hummocks. Moreover, inundated habitats are often rich in N-fixing cyanobacterial communities (Granhall and Selander 1973). Mosses in forested habitats receive also mineral nutrients intercepted by the forest canopy, which may several times increase the nutrient supply as it is evident from the data on rainwater chemistry. Owing to the ombrotrophic character of bogs, *Sphagnum* vegetation has evolved an efficient nutrient retention, particularly by cation adsorption on cation-exchange sites. This allows the mosses to control nutrients entering the top peat layers and thus the availability of nutrients to co-occurring rooted plants taking up particularly the nutrients released from decomposing litter (Malmer et al. 1994).

Aims of the thesis

The general aim of my thesis was to study various aspect of functional ecology of *Sphagnum* species co-occurring in mire ecosystems with respect to the hummock–hollow microtopography. The thesis consists of four original studies:

I. **Habitat and species controls on *Sphagnum* production and decomposition in a bog**
Hájek T. [submitted];

II. **Effect of water content components on desiccation and recovery in *Sphagnum* mosses**
Hájek T. & Beckett R.P. 2008. *Annals of Botany* 101: 165–173;

III. **Mineral nutrient economy in competing species of *Sphagnum* mosses**
Hájek T. & Adamec L. *Ecological Research* DOI: 10.1007/s11284-008-0506-0;

IV. **Light responses of mire mosses – a key to survival after water-level drawdown**
Hájek T., Tuittila E.-S., Ilomets M. & Laiho R. *Oikos*
DOI: 10.1111/j.2008.0030-1299.16528.x.

The first study is focused on *Sphagnum* control in the hummock–hollow microtopography. I asked whether the biomass production of *Sphagnum* species and/or the decomposition of their litter, may contribute to creating and maintaining the microtopography. I hypothesized that the hummock-forming *Sphagnum* species possess mechanisms enhancing peat accumulation forming and maintaining their own microhabitats.

The second study is devoted to water relations in desiccated *Sphagnum* mosses from contrasting microhabitats such as hummocks, hollows, and forest. The question was how water availability influences the desiccation tolerance and subsequent recovery as well as the water relations parameters of moss cells. We tested controversial hypothesis of Wagner and Titus (1984) that hollow sphagna are more desiccation tolerant because they are unable to avoid desiccation as efficiently as the hummock ones.

In the third study, we studied the compartmentalization of mineral nutrients between intracellular and extracellular exchangeable fractions in *Sphagnum* species coexisting along the hummock–hollow microtopography. We tested the hypothesis that the cation compartmentalization in ombrotrophic sphagna follows that in other mosses from minerotrophic habitats. We also asked how closely coexisting species pairs compete for mineral nutrients in mixed patches. We thus tested the contrasting hypotheses that mineral nutrient economy is controlled either by the species (Aulio 1982) or by habitat conditions (e.g., Malmer 1988).

The fourth study presents the light responses of photosynthesis and photosynthetic pigment concentrations in mosses from an open mire and from its shaded, i.e., drained and forested, counterpart. We tested the hypothesis that mosses occupying the open mire are well adapted to the full solar irradiance while the mosses from the shade have characteristics of shade-adapted plants. We expected that the adaptation or acclimation to low irradiance is a strategy to facilitate survival in shaded conditions following a persistent water-level drawdown.

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Sphagnum cuspidatum (greenish, emerging shoots) normally grows in the wettest, inundated microhabitats in bogs of the Bohemian Forest. In autumn 2006, the rainy weather enabled this species to utilize its high growth potential of this species to overgrow *S. majus*, the brown-coloured dominant of wet carpets. However, *S. cuspidatum* has insufficient water-holding capacity to avoid desiccation damage. Therefore its sudden success is only illusive – the emerging shoots get dry and stop their growth during the first sunny days.

Habitat and species controls on *Sphagnum* production and decomposition in a bog

Tomáš Hájek (submitted)

Abstract

I evaluated the production and decomposition characteristics of six dominant *Sphagnum* species in their natural microhabitats distributed along the gradient of water table in an open ombrotrophic bog. The growth in length was much faster in pools and hollows than in hummocks, but the resulting annual production was roughly similar between the microhabitats due to a greater shoot density and consequently higher biomass in hummocks. Although hummocks provided a much higher potential for decomposition than hollows and pools, the *Sphagnum* litter decomposed more slowly in hummocks because of a much poorer litter quality of the hummock sphagna. Thus the hummock *Sphagnum* species possess both principal mechanisms participating in maintaining hummocks above hollows – a sufficient production rate and limited decomposition rate. These mechanisms emphasize the role of *Sphagnum* mosses as autogenic ecosystem engineers controlling also the microhabitat diversification in patterned mires.

Introduction

Sphagnum-dominated peatlands cover large areas in the boreal zone of the Northern Hemisphere. They developed due to long-term accumulation of extremely slowly decomposing plant litter (Clymo 1984). Decay-resistant *Sphagnum* mosses (Coulson & Butterfield 1978) and tissues of vascular plants or animals impregnated with *Sphagnum* leach (Verhoeven and Toth 1995, Painter 1991) undergo only partial decomposition during peat formation. Moreover, the accumulated peat provides such environmental conditions that are unfavourable for communities of microbial decomposers; peat is waterlogged and anoxic, cold, acid, poor in available nutrients and rich in antimicrobial compounds (Johnson and Damman 1993).

The mire surface used to be differentiated into a mosaic of contrasting microhabitats such as elevated hummocks, flat lawns, wet carpets and hollows and water-filled pools. Position of the water table is the main factor constraining the species adaptations and, consequently, species composition in this hummock-hollow gradient (e.g. Rydin 1993, Nordbakken 1996). Generally, robust and rapidly growing shoots of hollow sphagna, belonging mostly to the section Cuspidata, form relatively productive sparse carpets. On the contrary, hummocks are formed by densely growing tiny shoots of species from the section Acutifolia, which are characterized by slow growth and smaller production (Moore 1989, Gunnarson 2005, Rydin et al. 2006). The long-term persistence of the hummock-hollow pattern (Backéus 1972, Svensson 1988, Rydin and Barber 2001) is a consequence of the same rate of vertical peat accumulation below the hummocks and hollows. Peat accumulation is controlled mainly by the biomass production rate (Malmer and Wallén 1999) or its litter quality and thus decomposition rate in these microhabitats (Johnson & Damman 1991, Van Bremen 1995, Belyea 1996).

The water status of the microhabitats strongly influences also the conditions for populations of soil decomposers and, consequently, the litter decomposition. Hummocks provide a higher decomposition potential than waterlogged hollows as measured using the decomposition of standard litters (Farrish and Grigal 1985 and 1988, Santelmann 1992). Reciprocal *Sphagnum* litter transplants, used to separate the effects of the environment and species-characteristic litter quality, showed that the litter quality of typical hollow species, *S. cuspidatum*, exceeds that of typical hummock species, *S. fuscum* (Johnson & Damman 1991, Belyea 1996). These findings promoted a hypothesis that *Sphagnum* litter quality, as an intrinsic, species-controlled factor, is responsible for the initiation and maintenance of the hummock–hollow microtopography.

In the present study, I examine the hypothesis that hummock-forming *Sphagnum* species have mechanisms enabling them to maintain their microhabitats in the hummock-hollow pattern. That means mechanisms enhancing peat accumulation in hummocks, microhabitats characterized by a low growth potential but a high decomposition potential. I investigate the production and decomposition characteristics of six dominant *Sphagnum* species in a bog with a well-developed surface microtopography. The objectives were: (i) to specify the basic production parameters (i.e. biomass, shoot density, annual increment, annual net production) and relationships among them; (ii) to asses the seasonal growth dynamics; (iii) to determine the decomposition rate of *Sphagnum* litter within the six species' microhabitats, (iv) to determine the decomposition potential of species' microhabitats using a standard "litter" (cellulose), (v) to specify the relative *Sphagnum* litter quality by separating the effect of microhabitat, and (vi) to relate the discovered production, decomposition and litter quality to the hummock-hollow dynamics.

Materials and methods

Site description and species

I carried out the experiments in a mountain raised bog Rokytecká slať (49° 01.3' N, 13° 25.1' E; 1115 m a. s. l.) in the Bohemian Forest – Šumava National Park and Biosphere Reserve, Czech Republic. The annual mean air temperature is 3.5 °C, the warmest month is July (12.2 °C). The mean total annual precipitation of 1486 mm is uniformly distributed during the year. Snow cover persists, on average, for 140 days. I performed the study within a 3-ha mire area which consisted of a narrow strip of lagg spruce forest of *Picea abies*, a broader zone of tall *Pinus* × *pseudopumilio* shrubs and large mire expanse. The understorey of the woody mire edge was dominated by dwarf shrubs of *Vaccinium uliginosum* and *V. myrtillus* with *Sphagnum capillifolium* in the moss layer. The treeless mire expanse was covered by lawns of *Eriophorum vaginatum* and *Trichophorum cespitosum*. Some parts were dominated by low shrubs of *Pinus* × *pseudopumilio* with *S. magellanicum*. Other moss species, namely *S. fuscum*, *S. rubellum* and *Polytrichum strictum* built flat hummocks, elevated microhabitats inhabited by the ericaceous dwarf shrubs of *V. uliginosum*, *Andromeda polifolia* and *Oxycoccus palustris*. The slightly sloping mire expanse was patterned into elongated depressions, flarks, which used to be filled with water or seasonally inundated. The shallow flarks and hollows were

inhabited by *S. majus* with *Scheuchzeria palustris* and *Carex limosa*, the deeper flarks and bog pools hosted floating *Sphagnum cuspidatum*. I studied all the *Sphagnum* species listed above in their typical microhabitats (Table 1). The average water table was estimated in all *Sphagnum* microhabitats (Table 1) using the method of PVC tape discoloration (Belyea 1999). Strips of red PVC insulating tape were attached to bamboo stalks and inserted vertically into the peat. The discoloration indicated the depth of occurrence of anoxic conditions, which corresponds particularly with the seasonally high water table (Booth et al. 2005, Navrátilová and Hájek 2005). Based on the mean water table (Table 1), *S. fuscum*, *S. rubellum* and *S. magellanicum* are referred to as hummock sphagna, *S. majus* as a hollow species and *S. cuspidatum* as an aquatic, pool species.

I will discuss the seasonal growth rate dynamics with the respect to seasonal precipitation dynamics (by months). The precipitation data were collected by the Czech Geological Survey at a site located 40 km to the east at 795 m a. s. l. Because of the lower altitude, the absolute precipitation was lower at the meteorological station, but the seasonal dynamics is assumed to be comparable with that at the study site.

Table 1. List of *Sphagnum* species studied in their typical microhabitats and the depth of water table in these microhabitats (means ± s. e.). Different letters in superscript indicate statistical differences (ANOVA, $p < 0.0001$; Tukey HSD test, $\alpha = 0.05$, $n = 13$ to 24).

Sphagnum species	Typical microhabitat	Water table (cm)
fuscum	flat hummocks	18.1 ± 1.2 [a]
rubellum	flat hummocks and lawns	16.1 ± 1.9 [a]
capillifolium	lagg spruce and *Pinus* × *pseudopumilio* forest	43.6 ± 1.3 [b]
magellanicum	lawns below low *Pinus* × *pseudopumilio*	15.5 ± 1.1 [a]
majus	carpets, hollows and shallow flarks	4.1 ± 1.3 [c]
cuspidatum	permanently flooded flarks and pools	0.2 ± 0.1 [c]

Growth and production measurements

In order to estimate seasonal variation in *Sphagnum* growth, I measured the apical increments in length in five periods: Summer 2000 (15 Jun – 28 Aug; 74 days), Autumn 2000 (29 Aug – 28 Oct; 60 days), Spring 2001 (29 Oct 2000 – 9 Jun 2001; 70 days since the snow melted), Summer 2001 (10 Jun – 28 Aug; 79 days) and Autumn 2001 (29 Aug – 30 Oct; 63 days). The spring of 2001 included also the preceding very late autumn and winter, but no growth was assumed to have occurred before spring. I chose three monospecific plots (replicates) of each of the six species. I measured the growth of their shoots

using white thread as a marker, tied around the stem 10 mm below the shoot apices (Clymo 1970). I labelled 15 *Sphagnum* shoots from each plot and inserted them carefully back into the moss vegetation of the same replicates. At the end of each period, I harvested the labelled plants and made new sets of 15 individuals each. The increment was calculated from the new distance of the thread below the shoot apices and the average growth rate was expressed as shoot increment in μm day^{-1} for each season.

After finishing the growth measurements in October 2001, I removed a *Sphagnum* block (50 cm^2 and 4 cm deep) from each investigated plot and determined the *Sphagnum* shoot density and biomass. The shoot density of adult plants was expressed as the shoot number per dm^2 (tiny juveniles lacking differentiated branches were neglected). Few shoots of other *Sphagnum* species were included among those of the dominant species. The *Sphagnum* biomass was determined as the bulk density of the apical 10-mm moss layer (in g m^{-2} cm^{-1}). The biomass of the second 10-mm shoot segment multiplied by the mean annual increment in 2001 (in cm y^{-1}; sum of three measurements) gives the net primary production (NPP in g m^{-2} y^{-1}) (Weltzin et al. 2001). The method of NPP estimation assumes that the biomass of the apical and subapical 10-mm shoot segments is constant in time.

Decomposition measurement

I measured *Sphagnum* and cellulose decomposition rate using litter bags. I collected shoots of the six *Sphagnum* species from their typical microhabitats (Table 1) in May 2000. According to Johnson & Damman (1991), I removed the capitula (about 5 mm of the shoot apices) and dried the next 15 mm shoot segment for 10 days at 24 °C and RH of about 40 %. Subsamples of the air-dried shoots were oven-dried (80 °C, 4 hours) to calculate the oven-dry weight of the air-dried samples.

I sealed 70.0–150.0 mg of air-dried shoots into nylon mesh bags (55 × 55 mm, 0.6-mm mesh with 63% of openings; 50 bags per species). Similarly, I prepared 300 bags with cellulose (squares of ash-free filter paper, 50 × 50 mm, 80 g m^{-2}, one layer). Each *Sphagnum* bag was coupled with a cellulose bag and such bag-pairs (55 × 110 mm) were provided with a nylon thread. I prepared the total of 300 bag-pairs for the six species, ten replicates and five incubation periods. The bags were buried horizontally, about 5 cm below the moss surface of each species in June 2000. The nylon threads were anchored above the moss surface.

I collected a bag-pair of each replicate (60 altogether) at the end of each incubation period (0.4, 1.0, 1.4, 2.0, 2.4 years). In the laboratory, I removed roots and stolons grown into the bags and air-dried and weighted the incubated substrates. Mass loss was expressed as the remaining fraction of the original substrate.

Data processing

I performed the statistics using STATISTICA (StatSoft, Inc., 2006, version 7), unless otherwise indicated. If necessary, the data were normalized (log-transformed) and general linear models ANOVA was used to test the differences within each factor. Tukey's HSD mean separation test compared factor levels. All data are presented without transformation.

I used mostly linear regressions to test the relationship between the characteristics variables and water table. I analyzed the *Sphagnum* growth rate by hierarchical ANOVA with interactions. The model expression was: $GrowthRate = Species + Season + Season \times Species + Plot(Species)$.

I expressed the relative rates of *Sphagnum* (k_S) and cellulose (k_C) decomposition as the parameter k of the negative simple exponential model $R_t = e^{-kt}$, where R_t is fraction of the remaining *Sphagnum* (R_S) or cellulose (R_C) in time t (cf., Wieder and Lang 1982). I used the simple exponential model because it facilitates the comparison between litter types and the environment. I estimated k_S and k_C by fitting the model to all 50 values of remaining litter per substrate and species. I tested k_S and k_C for statistically significant differences between all six species with Extra sum-of-squares F-Test using Prism for Windows (GraphPad, Inc., 2007, version 5). Therefore I used the Bonferroni correction to reduce the standard α-level of 0.05 by a factor of 15. Cellulose decomposition rates characterized the decomposition potential of the species' microhabitats. For quantifying relative litter quality of *Sphagnum*, I standardised k_S by k_C ($Q_S = k_S\, k_C^{-1}$) and plotted k_S against k_C to visualize Q_S as a slope. To test Q_S for statistical differences I calculated it for each pair of litter bags and tested it using nested analysis of covariance: $\log(R_S+1.5)\ \log(R_C+1.5)^{-1} = Species + Plot(Species) + Period$, where *Period* was a covariate. The constant 1.5 ensures the dividing by a positive, non-zero divisor. To test if k changed during the litter exposition, I calculated k_S and k_C values for all samples and exposition times (k_t): $k_t = -\log(R_t + 0.001)\ t^{-1}$; the constant 0.001 makes it possible to take the logarithm of immeasurable low R_t values of cellulose. The model of repeated measures ANOVA was: $k_t = Species + Period + Species \times Period$; *Period* was the repeated measures factor (5 levels).

Results

Production characteristics

Covers of the six *Sphagnum* species differed greatly in shoot density and consequently in their biomass (Table 2). These parameters correlated with the position of *Sphagnum* apices above the water table (Table 1), i.e., along the gradient from pools and hollows to hummocks (Fig. 1). *S. capillifolium* was excluded from Fig. 1 because it grew in the lagg forest, out of the hummock–hollow patterning of the open part. Although the sparsely growing aquatic species *S. cuspidatum* had the lowest shoot density and biomass, it had clearly the highest apical increment in 2001; however, due to low biomass, it had a lower net primary production than the other species (although this difference was not statistically significant). *S. majus*, occupying wet hollows, behaved similarly but less markedly. On the contrary, the densely growing hummock species *S. fuscum*, *S. rubellum* and also *S. magellanicum* had small annual increment but, thanks to their higher biomass, a higher NPP than the two species from wet habitats (Fig. 1). *S. capillifolium* shared the characteristics of the species of both contrasting microhabitats (Table 2).

Table 2. Production characteristics of *Sphagnum* covers determined at the end of the vegetation season of 2001 (means ± s.e.). Values with different letters in superscript within columns differed (ANOVA, Tukey's HSD test, $\alpha = 0.05$, $n = 3$).

Sphagnum species	Shoot density (dm^{-2})	Biomass ($g\ m^{-2}\ cm^{-1}$)	Increment ($mm\ y^{-1}$)	Net production ($g\ m^{-2}\ y^{-1}$)
ANOVA *p*-level	0.0002	0.0062	< 0.0001	0.52
fuscum	1023 ± 205 ^{a}	444 ± 64 ^{a}	12.4 ± 0.4 ^{a}	365 ± 58
rubellum	607 ± 103 ^{ab}	304 ± 46 ^{ab}	14.3 ± 2.6 ^{a}	229 ± 17
capillifolium	464 ± 140 ^{bc}	204 ± 56 ^{b}	27.3 ± 5.3 ^{ab}	310 ± 122
magellanicum	385 ± 76 ^{bc}	303 ± 65 ^{ab}	14.0 ± 3.5 ^{a}	251 ± 35
majus	211 ± 26 ^{bc}	207 ± 63 ^{b}	41.1 ± 4.1 ^{b}	242 ± 60
cuspidatum	97 ± 42 ^{c}	104 ± 61 ^{b}	91.9 ± 13.4 ^{c}	199 ± 116

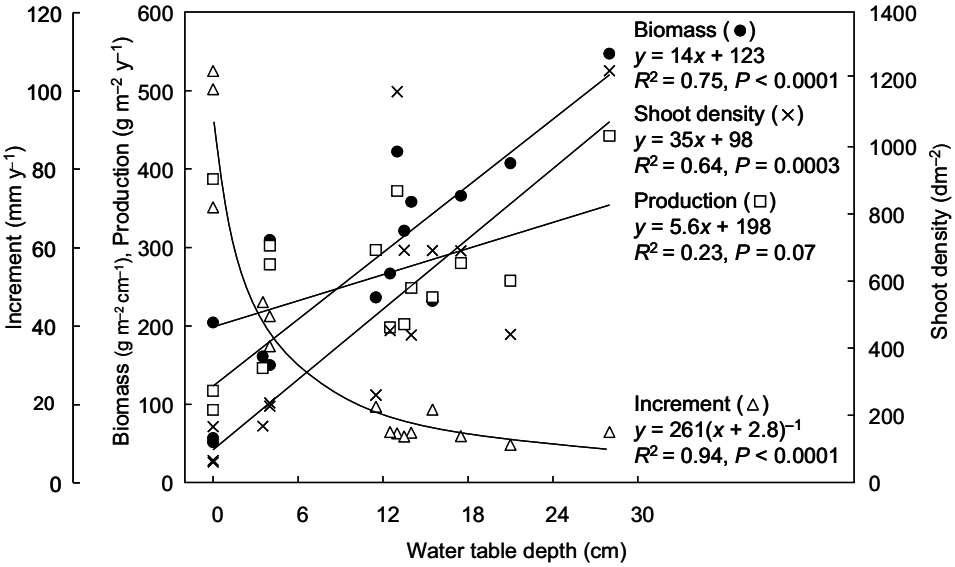

Fig. 1. Production characteristics of five *Sphagnum* species (three sites per species) along the gradient of water table depth, which represents the hummock-hollow gradient (Table 1).

Seasonal variability of growth rate

S. majus and *S. cuspidatum*, species of water-saturated habitats had the same seasonal dynamics of growth rate. They grew fastest in the summers and slowly in the autumns (Fig. 2). The two typical hummock species, *S. fuscum* and *S. rubellum*, had different seasonal growth dynamics. They grew slowly in summer 2000 but 1.5–2 times as fast in the autumn and 2–4 times as fast in summer 2002. *S. magellanicum* had a similar growth dynamics as the species of wet habitats while *S. capillifolium* grew like the hummock species, which was indicated by the strong increase in growth rate between the summers of 2000 and 2001.

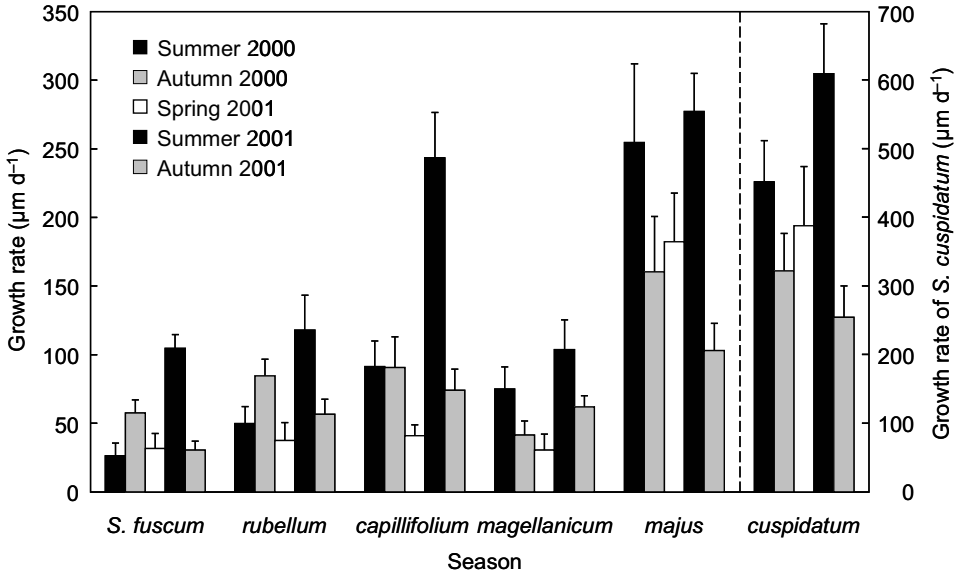

Fig. 2. Seasonal dynamics of growth rate in six *Sphagnum* species. Error bars denote 95% confidence intervals (n = 19 to 44).

Decomposition

The course of decomposition of *Sphagnum* litters and, especially, of cellulose greatly varied within the species groups (Fig 3). But the slopes of the negative simple exponential models of *Sphagnum* and cellulose decomposition (k_C and k_S) expressed well the mean relative decomposition rates as single values which could be statistically tested (Fig. 4 and Table 3). Cellulose decomposed rapidly in the drier habitats of hummocks and, particularly, in *S. magellanicum* where no remaining cellulose litter was often recorded even after the first year. Both *Sphagnum* and cellulose were decomposed most slowly in pools with *S. cuspidatum*, the only habitat where *Sphagnum* litter decomposed almost as fast as cellulose. Hollows showed a relatively low decomposition potential, but the litter of *S. majus* was decomposed at the highest rate among the sphagna. The forested habitat of *S. capillifolium* had a transitional character in terms of both k_C and k_S.

In comparison with cellulose, the relative decomposition rate of *Sphagnum* litters was not constant during the whole exposure period. It decreased after the first year to about a half of that found in the fifth month in all species ($p < 0001$; Fig 5), indicating that the fresh litter contained a significantly large fraction of a labile organic matter.

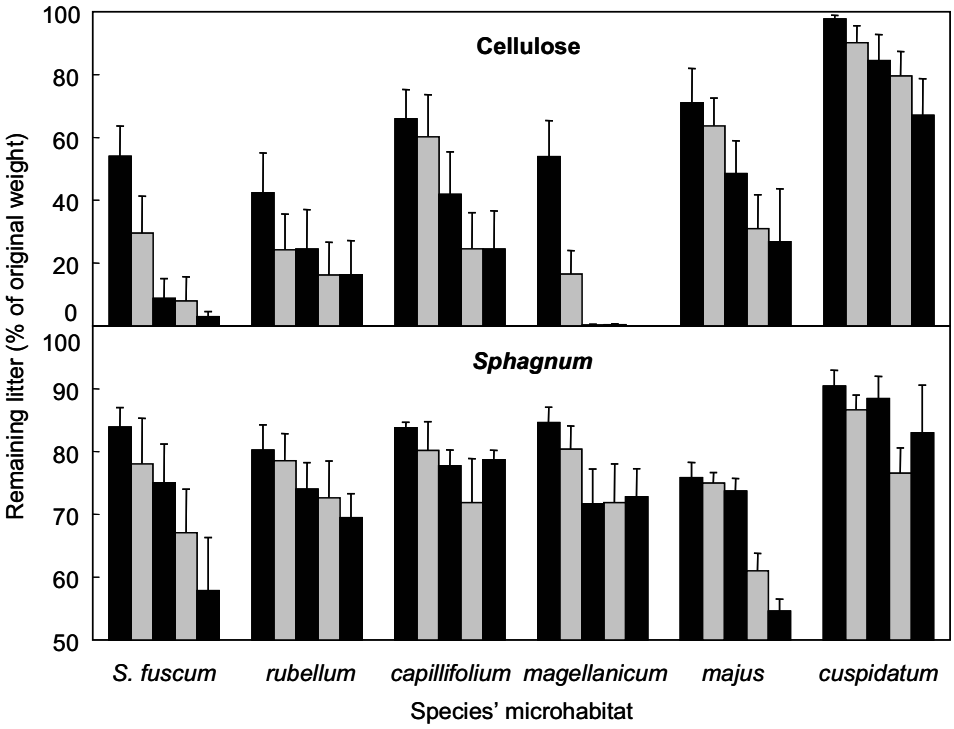

Fig. 3. Course of decomposition of six *Sphagnum* species and cellulose in microhabitats of those species (mean ± s.e., n = 7 to 10). The grouped columns indicate five incubation periods (from the left: 0.4, 1.0, 1.4, 2.0 and 2.4 years).

Sphagnum litter quality

The relative decomposition rate of *Sphagnum* divided by that of cellulose gave an estimate of the relative *Sphagnum* litter quality, expressed in % of k_C (Table 3 and Fig. 4). There was a steep increase in *Sphagnum* litter quality from the species of elevated habitats towards those of wet habitats.

Table 3. Relative rates of decomposition (*k*; parameter of the negative exponential model of decomposition) of *Sphagnum* and cellulose in six *Sphagnum* microhabitats. Relative litter quality (Q_L) of *Sphagnum* was expressed as *Sphagnum k* in % of cellulose *k*. Data of the cation exchange capacity (CEC, means ± s.e., $n = 5$) were estimated in 2005 (Hájek and Adamec 2008) in mosses from the same microhabitats where the growth and decomposition measurements were conducted. Values in columns with different letters differed (Extra sum-of-squares F-Tests, $\alpha = 0.0033$ and ANOVA, Tukey's HSD test, $\alpha = 0.05$ in case of Q_L and CEC). See Materials and Methods for details.

Sphagnum species	*Sphagnum k* (k_S)	Cellulose *k* (k_C)	*Sphagnum* Q_L $k_S\,k_C^{-1}$ (%)	CEC µeq g^{-1} d.w.
ANOVA *p*-level			< 0.0001	< 0.0001
fuscum	0.22 ^{ac}	1.42 ^{a}	16 ^{ab}	918 ± 9 ^{a}
rubellum	0.18 ^{abc}	1.31 ^{ab}	14 ^{a}	860 ± 20 ^{b}
capillifolium	0.15 ^{ab}	0.64 ^{bc}	24 ^{b}	859 ± 10 ^{b}
magellanicum	0.18 ^{ab}	1.80 ^{a}	10 ^{a}	831 ± 10 ^{b}
majus	0.26 ^{c}	0.55 ^{c}	48 ^{c}	461 ± 9 ^{c}
cuspidatum	0.11 ^{b}	0.13 ^{d}	86 ^{d}	469 ± 12 ^{c}

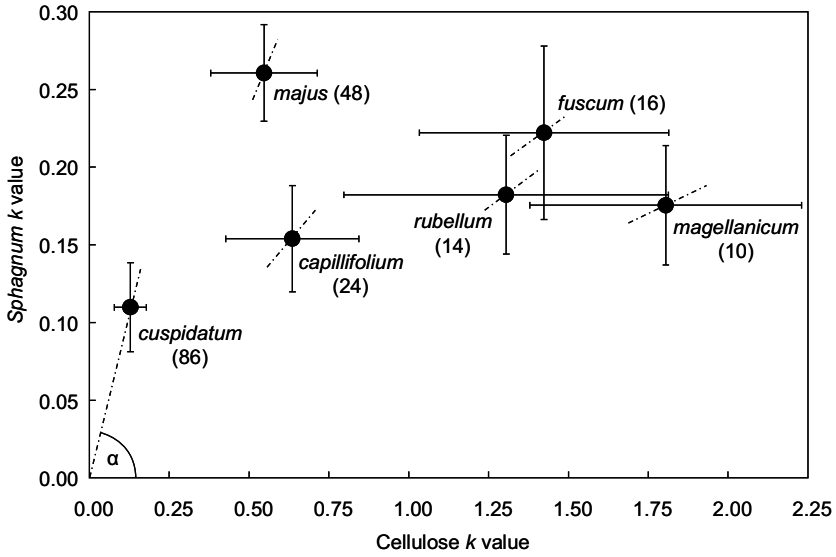

Fig. 4. Relative rates of decomposition (*k*; parameter of the negative exponential model of decomposition) of six *Sphagnum* species plotted against those of cellulose in the six *Sphagnum* microhabitats. The model was fitted to five successive measurements of remaining litter in ten replicates (n = 44 to 50). Relative litter quality of *Sphagnum* was expressed as *Sphagnum k* in % of cellulose *k* (numbers in parentheses) and is shown as a slope (tg α) by the dash-and-dot lines. Error bars indicate 95% confidence intervals.

Discussion

Growth and production

Our results deviated from the general pattern of *Sphagnum* production along the hummock-hollow gradient. Hollow species of the section Cuspidata are, globally, about 1.9 times as productive as hummock species of the section Acutifolia with the mean NPP of 200 g m^{-2} y^{-1} (Gunnarsson 2005). Moore (1989) reviewed the literature and constructed a simple linear model of *Sphagnum* NPP as a function of mean annual temperature. According to this model, the expected NPP of my hummock and hollow sphagna is 195 and 300 g m^{-2} y^{-1}, respectively (at the mean annual temperature of 3.5 °C). Inspite of the large variation in the NPP of the species studied, it is obvious that hollows and pools were not more productive than hummocks. Moreover, the typical hummock species *S. fuscum* had the highest NPP while *S. cuspidatum*, which was observed to be generally the most productive hollow species (Gunnarsson 2005), had the lowest NPP, comparable to the NPP expected for hummock species (Moore 1989, Gunnarsson 2005). Nevertheless, a higher or equal *Sphagnum* NPP in hummocks compared to hollows has been reported from fens (Bartsch and Moore 1985, Rochefort et al. 1990, Vitt 1990). The mean NPP of *S. magellanicum* lawns in this study closely corresponded with the general NPP of lawns and this species (Gunnarsson 2005).

Water availability is a more (Luken 1985, Moore 1989, Gerdol 1995, Weltzin et al. 2001, Gunnarsson 2005) or less (Robroek et al. 2007) important environmental factor promoting *Sphagnum* growth and NPP. The hollow species *S. majus* showed the same seasonal growth dynamics (Fig. 2) as the permanently aquatic *S. cuspidatum*. This indicates that *S. majus* did not experience a summer drought period (cf., Luken 1985, Moore 1989) and that other factors than water limitation were responsible for differences in *Sphagnum* growth. Summer growth of those species was probably enhanced by a generally higher summer temperature and longer photoperiod than in the spring or autumn. On the contrary, the other sphagna of elevated habitats may have been limited by lack of water, as indicated by the clear differences in the growth rates of all six species during the two summer seasons, and the differences in the distribution of precipitation. Summer 2000 was poor in precipitation in July (2.8× less than in 2001) but rich in August (2.4× more; data not shown). Rainy periods are, however, accompanied by a poorer irradiance, which protects the sun-exposed *Sphagnum* mosses from photoinhibition and a resulting significantly reduced growth rate (Murray et al. 1993). Radiation frost often occurs at the study site

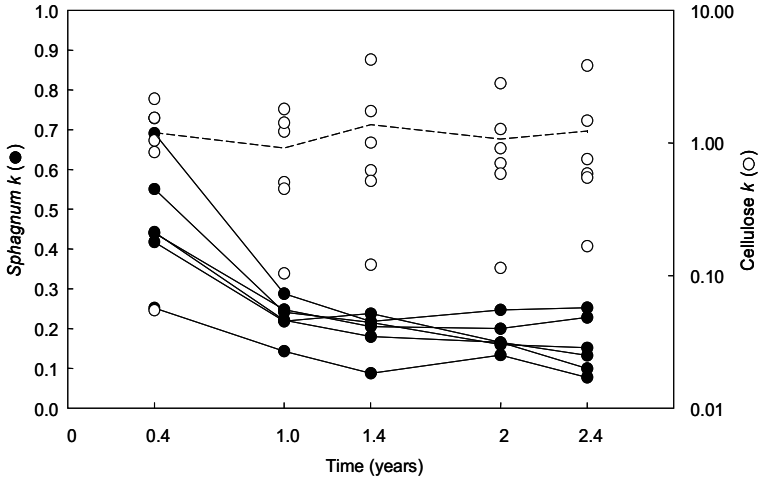

Fig. 5. Relative rates of decomposition (*k*; parameter of the negative exponential model of decomposition) of *Sphagnum* and cellulose in six *Sphagnum* microhabitats calculated separately for each of the five exposure periods (n = 10). The parameter k was constant during cellulose decomposition (dashed line, $p = 0.17$) but decreased within the first year of exposure in *Sphagnum* litters (solid lines, $p < 0.0001$, repeated measure ANOVA).

also during summer. Rainy periods could also reduce the inhibitory effect of low night temperatures on the photosynthetic apparatus and growth (Rudolph et al. 1977, Gerdol 1995, Gerdol et al. 1998).

Litter decomposition and litter quality

For the sake of simplification, I consider the *Sphagnum* and cellulose mass loss from the litter bags as decomposition losses due to microbial respiration. According to the resuts of Coulson and Butterfield (1978) I assume negligible losses of solid particles due to mesh size, soil fauna and leaching of water-soluble organic compounds. The substantial mass loss in all *Sphagnum* litters during the first five moths (Fig. 3, Fig. 5) may be attributed to easily metabolized organic compounds (Johnson and Damman 1993, Limpens and Berendse 2003) and relatively high nitrogen (N) and particularly phosphorus (P) contents in the green subapical shoot segments used in this study than in the brown dead segments (Hájek and Adamec 2008). The relative decomposition rate of *Sphagnum* became stabilized after the first five months and most of the interspecific differences disappeared (Fig. 5); such ‘aging’ of green *Sphagnum* litter was observed also by Limpens and Berende (2003). Therefore the fitted

constant of the simple exponential model tends to underestimate the *Sphagnum* litter remaining at the later stages of decomposition (Yu et al. 2001). Nevertheless, the simple exponential model is indispensable when the parameter comparisons are required and are sufficient for short-term studies.

Cellulose, free of mineral nutrients and readily available carbon, was decomposed at a constant relative rate. The decomposition potential of microhabitats was evaluated as the cellulose decomposition rate. Although cellulose is often used in field decomposition studies it is not so in studies of bog microtopography. Consistently with the present study, Farrish and Grigal (1985, 1988) found about three times higher cellulose loss from hummocks than from hollows in a bog after a year. Santelmann (1992) observed a similar pattern only if the water table was within 5 cm of the bog surface, but failed to find differences between hummocks and hollows if the water table was below 5 cm in the hollows. Differences in the position of the water table seem to be responsible for large differences in decomposition potential between microhabitats at the study site. Permanently aerated and still water-saturated (from the viewpoint of water potential) soil conditions make the hummocks more favourable microhabitats for decomposition than the hollows and pools, which are flooded either permanently or temporarily (i.e., limited by oxygen diffusion; see also Clymo 1965, Johnson and Damman 1991, Belyea 1996, Moore et al. 2007). The lagg forest had the lowest decomposition potential, although the soil was well aerated but protected against desiccation. This fact can be explained by lower mean daily temperatures in the lagg. I observed that snow cover persisted there by several weeks longer than it did in the open mire expanse.

Most studies compared litter decomposition of *Sphagnum* in its species' original microhabitats. Mass losses of hummock sphagna are generally half of those of hollow species (Johnson and Damman 1993 for review) or even less (Moore and Basiliko 2006). Also the present study showed that the hollow species *Sphagnum majus* had the fastest relative decomposition rate; but it was only by about 15–70 % faster than that of the species of elevated microhabitats and by almost 250 % faster than that of the aquatic *S. cuspidatum*. Such a comparison, however, does not enable us to separate the effects of the plant litter chemistry from those of the environment. Johnson and Damman (1991) and Belyea (1996) used therefore litter of two and four species, respectively, transplanted between contrasting microhabitats. Their results pointed to the role of litter quality – all the hummock species were intrinsically more decay-resistant than the hollow one, *S. cuspidatum*, used in both studies. I used a similar method but replaced the reciprocal transplants by cellulose as a standard substrate and expressed the

relative litter quality of *Sphagnum* as a single value (where cellulose = 100 %). Such an evaluation of the litter quality allows us to make direct comparisons between any litters under the assumption that the plant litter and cellulose decomposition is controlled by the same factors. Thus the relative litter quality of the hummock sphagna was significantly lower than that of the hollow species *S. majus* and particularly *S. cuspidatum* from pools.

Regulation of *Sphagnum* litter quality

The source of differences in the litter quality of *Sphagnum* can be sought among the factors controlling *Sphagnum* litter decomposition: deficiency of mineral nutrients under ombrotrophic conditions, and the content of decay-inhibiting and decay-resistant compounds (Johnson and Damman 1993). Important interspecific differences existed in the litter nutrient contents of (Hájek and Adamec 2008). *S. capillifolium*, which grew in the lagg forest, received also the nutrients intercepted by dry deposition in the forest canopy. This explains the relatively high contents of N, some cations and particularly P in this species, which also had the highest relative litter quality among the species of elevated microhabitats. Although the aquatic *S. cuspidatum* decomposed the most slowly, its litter quality was about twofold in comparison with the hollow *S. majus*. *S. cuspidatum* also had an about twofold N and quadruple P content, probably thanks to the rich cyanobacterial flora found in floating mats of this species at the study site (Lederer and Soukupová 2002). Enhanced N (Limpens and Berendse 2003) and P (Hogg et al. 1994) contents were found to stimulate the decomposition of *Sphagnum* litter. Nutrient contents, however, do not explain the differences in the litter quality between the hummock and hollow species.

Cation exchange capacity (CEC) of *Sphagnum* shoots was found to be closely related to the content of uronic acid in cell wall hemicelluloses, which is higher in hummock sphagna than in hollow ones (Clymo 1963, Spearing 1972). Painter (1991) suggested that uronic acids are responsible for the well-known decay-inhibiting properties of *Sphagnum* litter, although the mechanism has not yet been fully understood (Ballance et al. 2008). Johnson and Damman (1993) searched the literature and compared data on uronic acid content of five *Sphagnum* species with data of mass loss of the same species but taken from other studies. They found a weak negative correlation between the content of uronic acids and mass loss. The mean relative litter quality presented in this study correlated negatively with the mean CEC (Table 3) across the six *Sphagnum* species ($r = -0.88$, $p = 0.021$, $n = 6$). Thus the uronic acids may be responsible for the variation in litter quality of hummock and hollow species.

Hummock–hollow dynamics

The development and maintenance of the bog-surface patterning was subjected to discussions and investigations during the whole 20th century (Zobel 1988 for a review). Although Zobel listed also several abiotic mechanisms, the long-term persistence of the hummock–hollow pattern (Backéus 1972, Svensson 1988, Malmer and Wallén 1999, Rydin and Barber 2001) is assumed to be under the control of biological mechanisms such as litter production (Malmer and Wallén 1999) or decomposition (Johnson and Damman 1991, Moore 1991, van Breemen 1995, Belyea 1996).

It is therefore obvious that the long-term persistence of the bog microtopography must result from equal rates of volumetric peat accumulation across the hummock–hollow pattern. Peat formation is thus generally the function of the ratio between biomass production and decomposition. In the present study, the *Sphagnum* primary production was generally the same in all microhabitats, with the tendency to be slightly higher in hummock. This resulted from the high shoot density forming the high biomass of the compact hummock cushions, despite the smaller annual increment in these species. The biomass of the hummock sphagna had a poorer litter quality. Therefore it decomposed slightly more slowly than hollow species, despite of the much greater decomposition potential in hummocks. This summarization shows that hummock species possess both principal mechanisms participating in maintaining hummocks above hollows – a sufficient production rate and limited decomposition rate. The former is connected with species' growth pattern (shoot density and biomass), the latter with the species' litter quality. These properties provide the hummock sphagna with the exclusivity to control the persistence of their own microhabitat, in which they avoid competition with species restricted to wet microhabitats (Rydin 1993). Such a vertical niche separation allows different species to coexist at the mire surface.

The presented data of production and decomposition are based on short-term experiments; an estimation of the final rate of peat formation and accumulation is therefore impossible. Nevertheless, these trends emphasize the role of *Sphagnum* mosses as autogenic ecosystem engineers (sensu Jones at al. 1994) controlling not only the bog development but also the microhabitat diversification in patterned mires.

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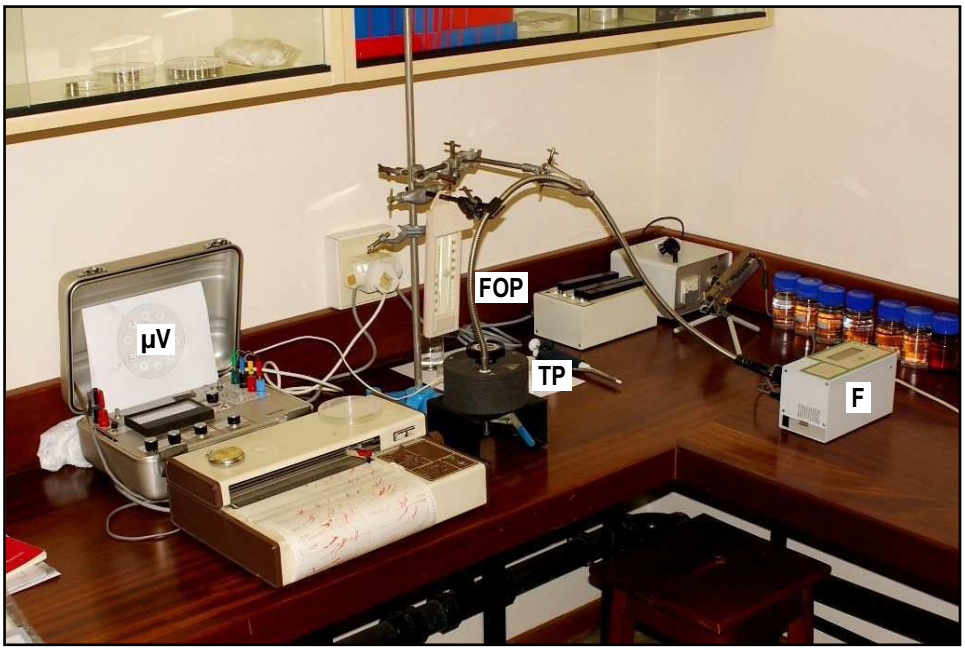

Simultaneous determination of water potential and chlorophyll fluorescence parameters in moss samples. Moss shoots were placed in the ten-sample Decagon SC-10A thermocouple psychrometer (TP), linked to a Wescor HR-33T microvoltmeter (µV). Chlorophyll fluorescence was measured using Hansatech FMS2 modulated fluorimeter (F). The fibre-optic probe (FOP) was inserted tightly into the loading aperture of the thermocouple psychrometer using a specially manufactured adapter. This enabled us to measure chlorophyll fluorescence in completely dark-relaxed samples immediately after the water potential measurement.

Effect of water content components on desiccation and recovery in *Sphagnum* mosses

Hájek T. & Beckett R. P. (*Annals of Botany* 101: 165–173, 2008)

Abstract

• *Background and Aims* We measured the basic parameters of water relations in *Sphagnum* mosses. We then tested the relationship of these parameters to the photosynthetic response to desiccation, and the ecology of these mosses.

• *Methods* The water relations parameters of six *Sphagnum* species (mosses typical of wet habitats) and *Atrichum androgynum* (a typical, more mesophytic, moss) were calculated from pressure–volume isotherms. Photosynthetic properties during and after moderate desiccation were monitored by chlorophyll fluorescence.

• *Key Results* When desiccated, the hummock forming species *S. fuscum* and *S. magellanicum* lost more water before turgor started dropping than other sphagna inhabiting less exposed habitats (73 % compared to 56 % on average). Osmotic potentials at full turgor were similar in all species with an average value of –1.1 MPa. Hummock sphagna had clearly more rigid cell walls than species of wet habitats ($\varepsilon = 3.55$ compared to 1.93 MPa). As a result, their chlorophyllous cells lost turgor at higher relative water contents (RWC) than species of wet habitats (0.61 compared to 0.46) and at less negative osmotic potentials (–2.28 compared to –3.00 MPa). During drying, Φ_{PSII} started declining earlier in hummock species (at RWC of 0.65 compared to 0.44), and F_v/F_m behaved similarly. Compared to other species, hummock sphagna desiccated to –20 MPa or –40 MPa recovered more completely after rehydration. *A. androgynum* responded to desiccation similarly to hummock sphagna suggesting that their desiccation tolerance may have a similar physiological basis.

• *Conclusion* Assuming a fixed rate of desiccation, the higher water holding capacities of hummock sphagna will allow them to continue metabolism for longer than other species. While this could be viewed as a form of "desiccation avoidance", hummock species also recover faster than other species during rehydration, suggesting that they have higher inherent tolerance. This may help them to persist in drought-exposed hummocks. By contrast, species growing in wet habitats lack such strong avoidance and tolerance mechanisms. However, their turgor maintenance mechanisms, for example more elastic cell walls, enable them to continue metabolizing longer as their water contents fall to the turgor loss point.

Introduction

Peat mosses (genus *Sphagnum*) have the unique ability to modify their environment by forming peat when they die. Decay is inhibited by unfavourable soil conditions, and low quality *Sphagnum* litter accumulates. The resulting marshy conditions favour the continued growth of *Sphagnum*. *Sphagnum* species have arrangements of shoots, branches and leaves that enable them to conduct and retain water efficiently. Their tissues consist of large dead empty cells perforated by pores. Such cells in the leaves are termed "hyaline", and occupy a substantially larger volume than the living chorophyllose cells. Thus in *Sphagnum* the external, capillary water fraction considerably exceeds the cytoplasmic (symplast) water fraction held within the fully turgid cells. In addition, apoplastic water, water firmly bound within cell walls, comprises a third fraction (Dilks and Proctor, 1979). This unusual cellular structure makes it difficult to determine the basic water parameters of peat mosses, and perhaps not surprisingly surveys of mosses have not included *Sphagnum* species (e.g. Proctor *et al*., 1998; Proctor, 1999). However, providing that proper precautions are taken, thermocouple psychrometry can be used to carry out pressure–volume (PV) curves, even with "difficult" mosses such as *Sphagnum*. From these curves, all of the basic parameters of water relations can be determined. The first aim of the work presented here was to estimate these parameters for a range of *Sphagnum* species. We also compared our results with data obtained using the same techniques with the more desiccation tolerant moss *Atrichum androgynum*, and also with data in the literature for other mosses and liverworts.

Sphagna are generally assumed to be desiccation intolerant mosses, which avoid desiccation by storing water (Green, 1968; Shipperges and Rydin, 1998). In *Sphagnum*-dominated peatlands, various characteristic *Sphagnum* species grow along a vertical "hummock-hollow" gradient (Rydin, 1993). It has been suggested that species originating from wet hollows show better recovery after desiccation than species from drier hummocks (Wagner and Titus, 1984). This paradox was explained as a trade-off between desiccation resistance by avoidance, i.e. high water holding capacity in compact hummocks and true desiccation tolerance, developed in sparsely growing hollow species that lose water and dry quickly in dry periods. Although it was later concluded that there are no general differences in the extent of desiccation tolerance between hummock and hollow species (Rydin *et al.*, 2006), the physiological mechanisms responsible for unequal desiccation tolerance among *Sphagnum* species are unknown. The second aim of this study was to compare water-relation parameters and the response of photosynthesis to desiccation in

Sphagnum species coexisting along the hummock-hollow gradient, and to test if these parameters can explain their different ecological niches.

Materials and Methods

Plant material

Four *Sphagnum* species were collected from open parts of the peatbog Mrtvý luh in the Šumava National Park, Czech Republic. In this peatbog, *S. fuscum* tends to form elevated hummocks, while *S. magellanicum* forms rather lower flattish hummocks; for convenience both species are referred to as hummock species in this study. In contrast, *S. cuspidatum* and *S. tenellum* are typically hollow species, occupying wet depressions between hummocks. *S. girgensohnii* typically occupies understorey habitats. Material was collected from *Pinus sylvestris* forest surrounding Purkrabský pond in Třeboňsko Landscape Protected Area, Czech Republic. *Atrichum androgynum* was collected from the understorey of Afromontane forest dominated by *Podocarpus* at Ferncliffe, Pietermaritzburg, Republic of South Africa. All mosses were collected hydrated, transported in the dark and then kept in a growth chamber at 20 °C, relative humidity of 100 % and photosynthetic photon flux density (PPFD) of 50 μmol m^{-2} s^{-1} for at least six weeks.

Water potential (ψ) determination

Apical 6-mm shoot segments of each species were washed in distilled water and thoroughly blotted using paper towelling until they released almost no water. They were then quickly placed in five steel cups and transferred to the ten-sample thermocouple psychrometer (Decagon SC-10A; Decagon Devices, Pullman, USA) linked to a Wescor HR-33T microvoltmeter (Wescor Electronics, Logan, USA). After equilibration for 8 to 16 h (or 4 h for *A. androgynum*) the water potential (ψ) of moss samples was measured, together with deionised water and two standard solutions. Moss samples were then allowed to lose about 5–20 % of their water (more in the beginning at high external water content) and allowed to equilibrate again. Measurements were repeated until water potential fell to about –10 MPa. After that, the cups were placed in desiccator over 2 M NaCl solutions for 25 h to equilibrate mosses to a water potential of –20 MPa. Samples were kept in the dark during the

experimental period of about 10 d (3 d for *A. androgynum*). Raw estimates of ψ were corrected to standard temperature of 20 °C.

Calculation of the parameters of water relations

PV curves were plotted as the reciprocal of ψ against 1–RWC_u (relative water content uncorrected for external water; $RWC_u = 1$ in blotted moss); an example is presented in Fig. 1. The PV curve was linear at low ψ, where turgor does not contribute to ψ. The apoplastic water fraction was calculated as 1–*x*-intercept of the extrapolated linear portion of the PV curve and recalculated to apoplastic WC (water content in g g^{-1} of dry weight). Turgor potential (ψ_p) was calculated as the difference of the extrapolated linear portion and the actual curve, and was plotted as a function of WC. With increasing WC, ψ_p increased almost linearly above the turgor loss point (TLP) to full turgor (FT), a maximum where the RWC (RWC_u corrected for the external water) is stated to be 1 (cf. Beckett, 1997). Turgor potential was plotted as a function of RWC and the gradient of a linear regression fitted to ψ_p between RWC at TLP (RWC_{TLP}) and FT used to quantify elasticity modulus of cell walls (ε). Osmotic potential (ψ_π) at FT ($\psi_{\pi s}$) was calculated as *y*-intercept of the linear portion of the PV curve. The WC above FT was assumed to be external, while the WC at FT after subtracting apoplastic WC was assumed to be symplastic. In practice, mosses had very slightly negative water potentials at FT (probably samples were not equilibrated completely) and as a result the estimates of maximum ψ_p (i.e. at those at FT) were slightly less than $\psi_{\pi s}$ (theoretically, $\psi_p = -\psi_\pi$ at FT). For convenience, estimates of ψ_p at full turgor were adjusted according to the value of $-\psi_{\pi s}$.

Chlorophyll fluorescence measurements

During the construction of the PV curve by slow desiccation in the thermocouple psychrometer, the state of photosynthetic apparatus was studied by measuring chlorophyll fluorescence using modulated fluorimeter (FMS2; Hansatech Instruments, King's Lynn, UK). The fibre-optic probe was inserted tightly into the loading aperture of the thermocouple psychrometer using a specially manufactured adapter. This enabled us to measure chlorophyll fluorescence in completely dark-relaxed samples immediately after the water potential measurement. After F_o and F_m measurements, an actinic light at a PPFD of 22 µmol m^{-2} s^{-1} was switched on and F_s and F'_m were recorded after 210 s. A low actinic light intensity was selected to prevent photodamage in dark desiccated samples. F_v/F_m and Φ_{PSII} were calculated following Maxwell and Johnson

(2000). Fluorescence was measured after each ψ determination in experimental samples and also in three fully hydrated control samples. The hydrated controls allowed us to adjust the chlorophyll fluorescence parameters according to changes that occurred as a result of acclimation to the dark conditions. This procedure had only a minimal effect on the parameters during the first stages of external water loss. We rehydrated the moss samples after storage for 25-h at a ψ of –20 MPa in the dark, and measured fluorescence after 15 min and at selected intervals during rehydration for 4 d. Another five replicates of all species were equilibrated over 1 M NaCl (ψ = –5 MPa) for 60 h and then over saturated NaCl solution at ψ of – 40 MPa. After 48 h, the samples were rewetted and F_v/F_m recovery measured after 4 d.

Chlorophyll fluorescence parameters

Chlorophyll fluorescence parameters (F, i.e. F_v/F_m and Φ_{PSII}) were measured in desiccating mosses during construction of the PV curve, and plotted against WC. The resulting curve could be described by the function $F = (F_{max} \times WC \times a)/(F_{max}^{c} + WC^{c} \times a^{c})^{(1/c)}$, where F_{max} is the unstressed maximum parameter value, a is the slope of the parameter decrease at low WC and c expresses sharpness of the curve when the parameter started to fall. The WC when F_v/F_m or Φ_{PSII} started to fall was calculated as a WC at $0.95F_{max}$, and osmotic potentials at these points were calculated. Moss dark recovery after rehydration following desiccation was expressed as a percentage of the original (F_{max}) value following rehydration for 15 min and 4 d.

Statistical analyses

Data were analysed using STATISTICA version 7.1 (StatSoft, Inc., USA). All the measurements were done using five replicates per species. One-way GLM ANOVAs were carried out to test species for differences in parameters followed by Tukey's HSD test to determine the significant differences between species means. Linear regressions were run to test statistical significance of selected parameter correlations. We applied principal component analysis (PCA) using Canoco for Windows 4.5 (Lepš and Šmilauer, 2003) to show the correlations between different water-relation and chlorophyll fluorescence parameters and their relationships to moss species. The species data were centred and standardized in order to make the variables comparable.

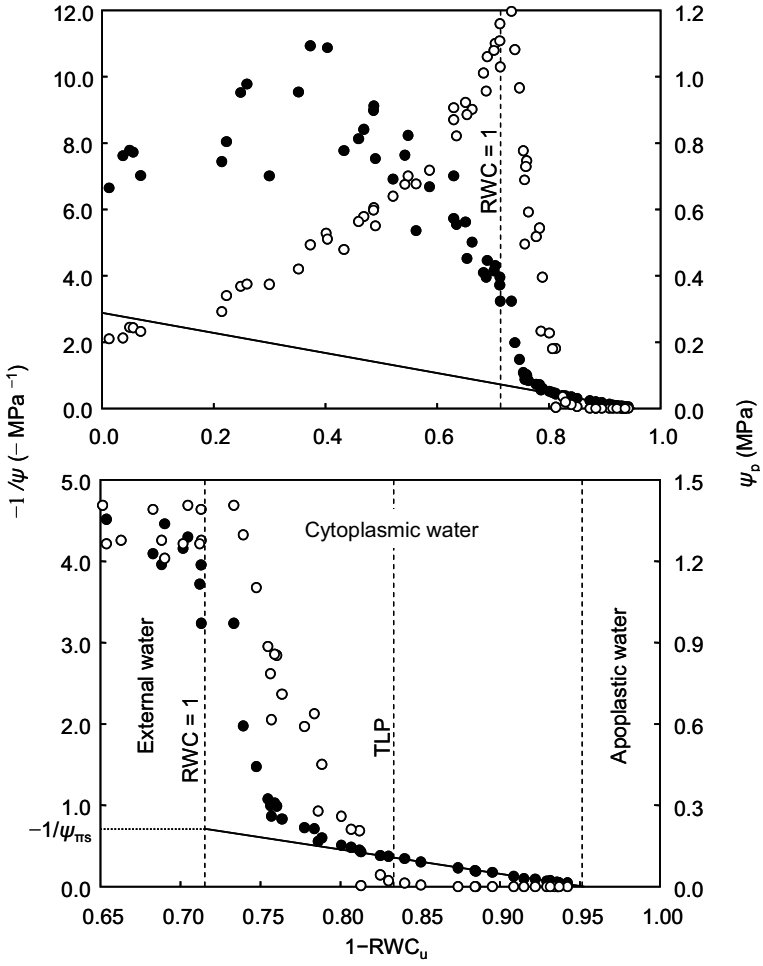

Fig. 1. Representative pressure–volume curve of *Sphagnum fuscum*, i.e. reciprocal of water potential ($-1/\psi$, solid circles) plotted against relative water content, uncorrected for the presence of external water (RWC_u). Turgor pressure (ψ_p, empty circles) was first plotted as the difference of the extrapolated linear portion (osmotic potential, ψ_π, solid line) and the actual pressure–volume curve. The peak of ψ_p is assumed to correspond to the point at which external water has evaporated, i.e. RWC = 1. The lower plot shows the same pressure–volume curve at the turgor pressure decrease zone in detail. The *y*-intercept of the extrapolated ψ_π at RWC = 1 shown in the lower plot denotes $1/\psi_\pi$ at full turgor ($\psi_{\pi s}$). At full turgor ψ should be approximately zero and therefore, as predicted, this value was almost the same as the reciprocal of maximum ψ_p (see Materials and Methods for full details). Data from five replicates are presented.

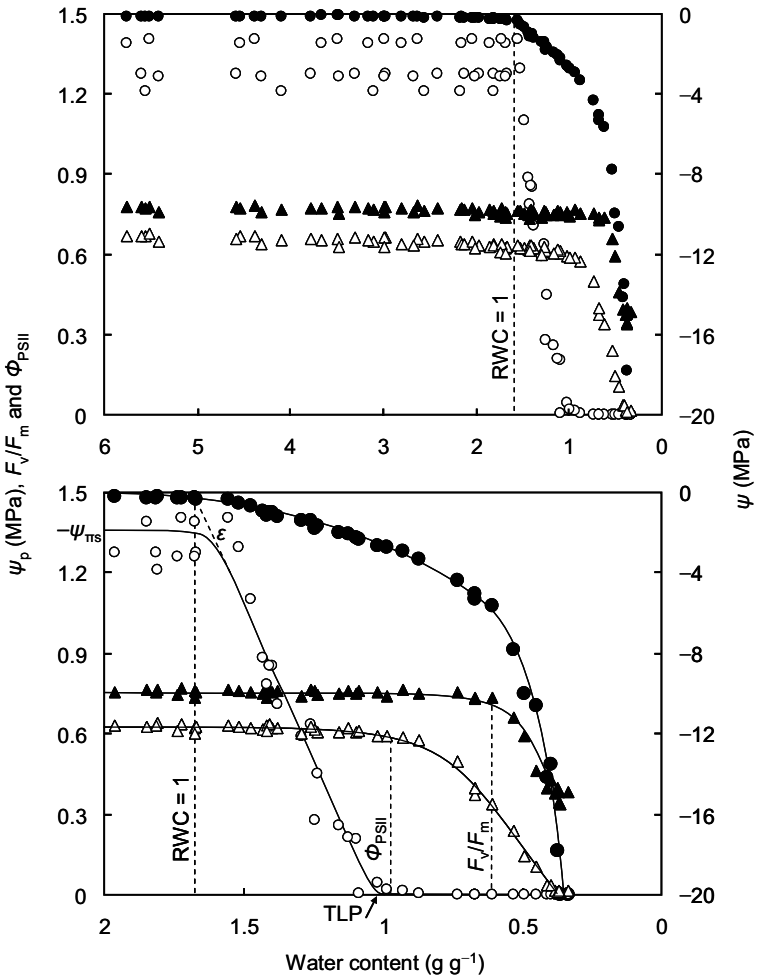

Fig. 2. Representative plot of water potential (solid circles), turgor pressure (empty circles), F_v/F_m (full triangles) and Φ_{PSII} (empty triangles) against decreasing water content recorded during slow dark desiccation of *Sphagnum fuscum* (five replicates). The lower plot shows the same curves in the range where turgor is reduced. Lines are drawn by hand. Dashed lines show water contents of F_v/F_m and Φ_{PSII} decrease points, relative water content (RWC) value of 1 when the turgor pressure starts do decline and turgor loss point (TLP). The elasticity modulus of cell walls (ε) was calculated as the slope of turgor pressure decrease fitted by linear regression.

Table 1. Parameters of water relations and chlorophyll fluorescence in mosses. Percentages are related to the values measured in fresh (original) material. Means of five replicates ± s.d. are given. Different letters indicate significant differences between species in the parameter ($p < 0.05$; Tukey's HSD test). See text for an explanation of the meaning of the parameters.

	Atrichum androgynum	*Sphagnum cuspidatum*	*Sphagnum fuscum*	*Sphagnum girgensohnii*	*Sphagnum magellanicum*	*Sphagnum tenellum*
Total WC (g g^{-1})	2.15 ± 0.07^{a}	4.21 ± 0.24^{b}	5.57 ± 0.13^{c}	5.08 ± 0.22^{d}	7.74 ± 0.32^{e}	5.84 ± 0.31^{c}
External WC (g g^{-1})	0.06 ± 0.05^{a}	2.29 ± 0.18^{b}	3.89 ± 0.15^{c}	2.68 ± 0.24^{b}	5.96 ± 0.31^{d}	3.73 ± 0.3^{c}
Apoplastic WC (g g^{-1})	0.14 ± 0.02^{a}	0.24 ± 0.01^{bd}	0.27 ± 0.02^{bc}	0.26 ± 0.02^{bcd}	0.29 ± 0.01^{c}	0.23 ± 0.02^{d}
WC at RWC=1 (g g^{-1})	2.09 ± 0.07^{a}	1.91 ± 0.09^{ad}	1.68 ± 0.09^{bd}	2.40 ± 0.09^{c}	1.78 ± 0.18^{d}	2.11 ± 0.03^{a}
$-\psi_{\pi s}$ (MPa)	1.05 ± 0.03^{a}	1.08 ± 0.08^{a}	1.31 ± 0.09^{b}	0.98 ± 0.09^{a}	1.12 ± 0.13^{a}	1.09 ± 0.10^{a}
RWC_{TLP}	0.77 ± 0.03^{a}	0.62 ± 0.05^{b}	0.61 ± 0.04^{b}	0.36 ± 0.05^{c}	0.61 ± 0.07^{b}	0.41 ± 0.06^{c}
$-\psi_{\pi}$ at TLP (MPa)	1.40 ± 0.05^{a}	1.94 ± 0.29^{a}	2.44 ± 0.14^{ab}	3.58 ± 0.95^{b}	2.11 ± 0.33^{a}	3.48 ± 1.32^{b}
ε (MPa)	4.02 ± 0.51^{a}	2.79 ± 0.24^{b}	3.68 ± 0.45^{a}	1.40 ± 0.24^{c}	3.42 ± 0.58^{ab}	1.61 ± 0.05^{c}
RWC at F_v/F_m decrease	0.53 ± 0.08^{a}	0.31 ± 0.01^{bc}	0.37 ± 0.03^{bd}	0.28 ± 0.01^{c}	0.42 ± 0.03^{d}	0.32 ± 0.02^{bc}
RWC at Φ_{PSII} decrease	0.65 ± 0.06^{ac}	0.44 ± 0.03^{b}	0.59 ± 0.04^{a}	0.44 ± 0.01^{b}	0.70 ± 0.07^{c}	0.43 ± 0.02^{b}
$-\psi_{\pi}$ at F_v/F_m decrease (MPa)	2.22 ± 0.56^{a}	5.11 ± 0.50^{b}	5.39 ± 0.53^{b}	4.84 ± 0.62^{b}	3.70 ± 0.31^{c}	4.80 ± 0.37^{b}
$-\psi_{\pi}$ at Φ_{PSII} decrease (MPa)	1.73 ± 0.22^{a}	2.99 ± 0.22^{b}	2.61 ± 0.10^{c}	2.46 ± 0.14^{c}	1.81 ± 0.14^{a}	3.17 ± 0.25^{b}
F_v/F_m at $\psi = -20$ MPa (%)	82 ± 0.5^{a}	68 ± 0.9^{b}	45 ± 0.6^{c}	58 ± 0.3^{d}	59 ± 0.9^{d}	5.4 ± 0.1^{e}
F_v/F_m recov. after $\psi = -20$ MPa (%)	98 ± 1.2^{ab}	97 ± 0.5^{ab}	99 ± 0.4^{b}	94 ± 1.2^{ac}	97 ± 1.3^{ab}	90 ± 4.8^{c}
Φ_{PSII} recov. after $\psi = -20$ MPa (%)	98 ± 1.2^{a}	95 ± 0.6^{ab}	98 ± 0.6^{a}	92 ± 1.3^{bd}	105 ± 1.7^{c}	90 ± 4.8^{d}
F_v/F_m recov. after $\psi = -40$ MPa (%)	94 ± 0.9^{a}	5.2 ± 3.4^{b}	66 ± 7.8^{c}	11 ± 1.6^{bd}	80 ± 7.2^{ac}	32 ± 16^{e}

Results

Basic parameters of water relations

Table 1 presents 16 parameters of water relations in *Sphagnum* species and *Atrichum androgynum*. Fig. 2 shows some typical results for *S. fuscum*. The blotted *Sphagnum* shoots contained a high volume of external water (2.3 to 6.0 g g^{-1}). During drying, the presence of this external water meant that ψ remained close to zero until the minimum WC at which plants were still at full turgor. After further water loss, ψ and ψ_p rapidly declined. By contrast, *A. androgynum* contained a very small volume of external water, and ψ (and ψ_p) declined immediately during desiccation (data not shown). The *x*-intercept of the linear part of the PV curves did not change when the value of WC corresponding to a ψ of –20 MPa was included. *Sphagnum* shoots did not change their architecture when the turgor was lost. When rewetted, they absorbed the water within a minute. By contrast, *A. androgynum* leaves rolled up during drying, and needed several minutes to rehydrate completely when rewetted.

PCA (Fig. 3) revealed correlations between the parameters of water relations, and relationships between species and parameters. The separation of the first principal component axis, which explained 51 % of the total variation, is mainly controlled by TLP-related parameters. The second axis explained 22 % of the total variation. Allocation of species' centroids in the PCA distinguished between parameters showing general differences between *A. androgynum* and all sphagna, and parameters forming gradients within *Sphagnum*. The latter parameters were able to separate hummock species (*S. fuscum* and *S. magellanicum*) from species growing in hollows (*S. tenellum*) and *S. girgensohnii* from a forest floor habitat. *S. cuspidatum* displayed an intermediate character for many of the parameters. In *S. fuscum* and *S. magellanicum*, turgor pressure started to fall later (lower WC at RWC = 1) but was lost early (high RWC_{TLP}). In addition, the maximum ψ_p (equivalent to $-\psi_{\pi s}$) was significantly higher in *S. fuscum*. All these factors are linked to higher cell wall rigidity (elastic modulus, ε) in the two hummock species.

All sphagna differed from *A. androgynum* not only by having a high volume of the external water, but also by having almost double the volume of apoplastic water. The volume of external water was positively correlated with the apoplastic water fraction within *Sphagnum* ($P = 0.002$, $n = 25$).

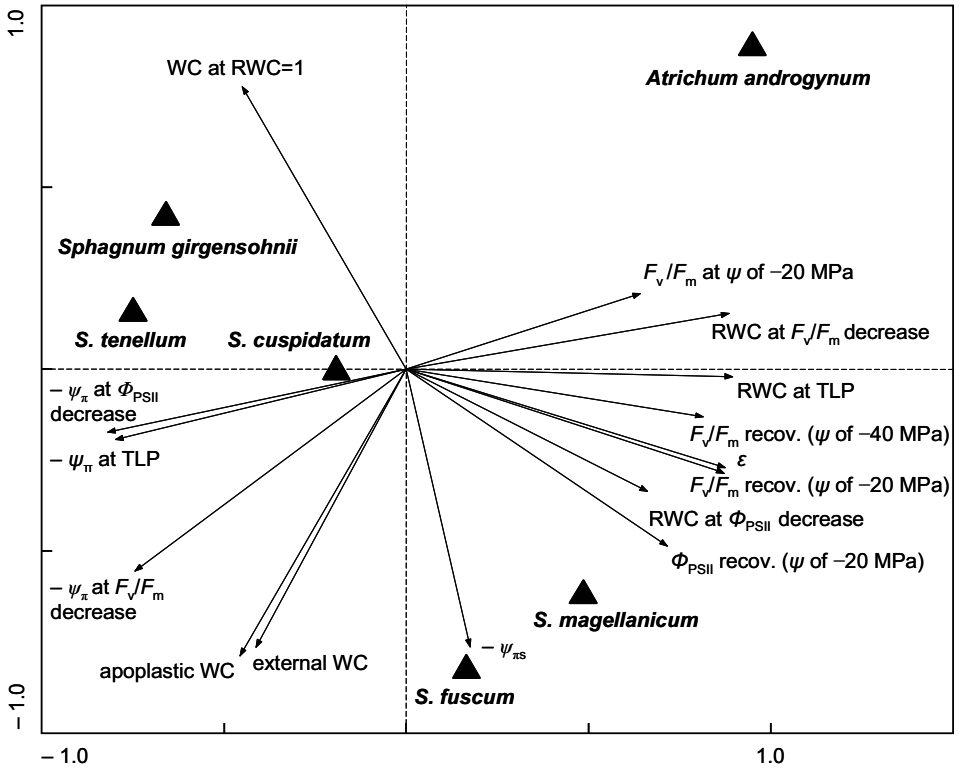

Fig. 3. Result of principal component analysis of 15 water relation parameters displaying correlations among the parameters. Centroids of moss species are projected onto these correlations. See text for parameter explanations.

Response of the photosynthetic apparatus to desiccation

During drying, the photosynthetic activity (Φ_{PSII}) started to decline at values of RWC or ψ_π close those corresponding to the TLP (Table 1). By contrast, the potential efficiency of relaxed photosystem (PS) II, F_v/F_m, only started to decline at lower tissue water contents, typically when all turgor was lost (Fig. 2). Comparing results from all the *Sphagnum* species showed that the RWCs at which both fluorescence parameters decreased were correlated with RWC_{TLP} (linear regressions, $P < 0.0001$, $n = 30$). While Φ_{PSII} has already disappeared at $\psi = -20$ MPa, F_v/F_m fell only to 80 % in *A. androgynum*, to 68-45 % in most sphagna but to almost zero in *S. tenellum* (Fig. 4). Such relatively high values of F_v/F_m were a consequence of decreased F_o in desiccated samples (data not shown).

In general, species in which photosynthetic parameters began falling early during desiccation to –20 MPa (Table 1) recovered more completely during rehydration (Fig. 4). This was especially true for F_v/F_m. Here, long-term recovery after 4 d was strongly correlated with the value of ψ corresponding to the point at which Φ_{PSII} started falling ($P < 0.0001$, $n = 30$ for all species and replicates). Similarly, following exposure to –40 MPa, the ability of F_v/F_m to recover after rehydration for 4 d, was strongly correlated to the values of ψ when Φ_{PSII} started falling ($P = 0.009$, $n = 6$ means). The ability of mosses to display short-time recovery (within 15 min or 1 h) correlated very closely with the values of F_v/F_m at $\psi = –20$ MPa ($r = 0.94$ and 0.96 for F_v/F_m and Φ_{PSII} recovery, respectively).

Relationship between water relations parameters, photosynthesis and ecology

PCA analysis of the parameters presented in Table 1 separated the more desiccation-tolerant species on the right hand side, specifically the hummock species *S. fuscum* and *S. magellanicum* and particularly *A. androgynum* (Fig. 3). These species also displayed much better recovery of F_v/F_m following exposure to $\psi = –40$ MPa (Fig. 4) than the sphagna inhabiting hollows (*S. cuspidatum* and *S. tenellum*) and wet forest floor (*S. girgensohnii*). Although osmotic potential at full turgor and osmotic potential at TLP were not correlated ($P = 0.55$, $n = 30$), desiccation tolerance was associated with low WC at FT (and more negative $\psi_{\pi s}$) and high RWC_{TLP} (and less negative ψ_π). A decrease in the amount of water lost between FT and TLP in more desiccation-tolerant species was a consequence of higher ε. Therefore, ε was closely correlated to the recovery of F_v/F_m and Φ_{PSII} after rewetting ($P < 0.0001$, $n = 30$).

Discussion

It is well known that sphagna hold substantial volume of water within dead hyaline cells, outside the protoplasts. This is the first study to use PV analyses in *Sphagnum* to estimate first the amount of external water, and second the water-relation parameters of living chlorophyllous cells, such as water content, maximum turgor pressure or cell wall modulus of elasticity. By measuring these parameters the physiological condition of the moss (here the condition of the photosynthetic apparatus) could be assessed at precisely known water contents and water potentials.

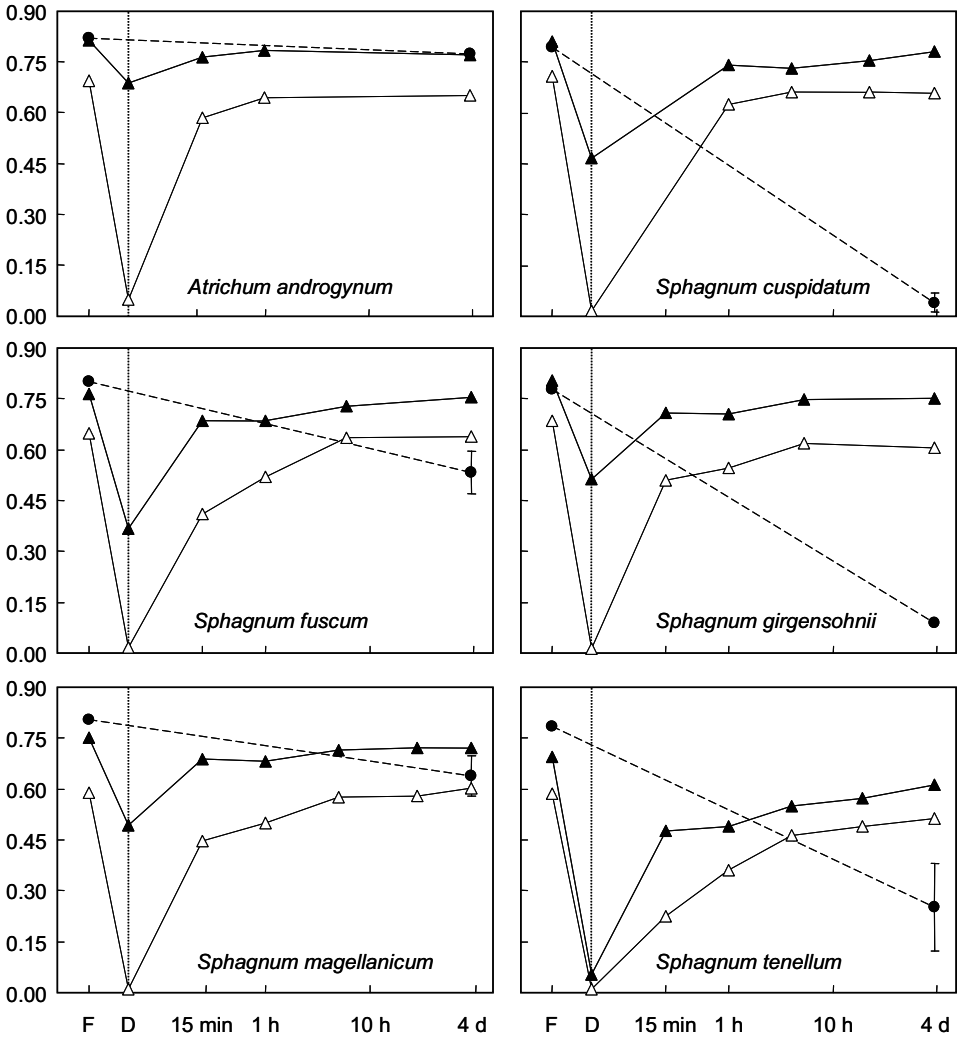

Fig. 4. Dynamics of the recovery of F_v/F_m (solid symbols) and Φ_{PSII} (empty symbols) following rewetting of samples previously dried to a water potential of –20 MPa (triangles connected with solid lines) and –40 MPa (circles connected with dashed lines). Values measured in fresh (F) and dried mosses (D) are also shown. Vertical dotted lines denote sample rewetting; recovery time on *x*-axis to the right from this line is log-scaled. Absolute values of parameters are means of five replicates, standard deviations are presented only after –40 MPa treatment (they are negligible in other cases).

Cellular location of water in *Sphagnum*

Total water contents of fully saturated mosses tend to be higher in hummock than hollow species (Table 1). Using thermocouple psychrometry, it is possible to divide the total water content of *Sphagnum* into three fractions. The first fraction comprises the "external water" in Table 1, and varied between 54% of total water in *S. cuspidatum* to 77% in *S. megellanicum*. This proportion was generally higher in hummock species. External water can probably be divided into two sub-fractions, first excess water held in capillary spaces between branches and leaves that remains after blotting the moss, and second water in the hyaline cells. The diameter of the pores in the hyaline cells determines the ψ at which the water meniscus in the pore breaks and the cells become air filled. For example, the meniscus will collapse in a cell with a pore size of 8 µm when ψ falls to –19 kPa (Clymo and Hayward, 1982). These subfractions cannot be distinguished by psychrometry, but it seems to be reasonable to assume that most of the water was in the hyaline cells in our blotted samples. Once desiccation removes all the water from the hyaline cells, mosses start losing water in the second fraction, corresponding to cytoplasmic water in the chlorophyllous cells. Loss of this water is accompanied by a rapid decline in ψ (Fig. 2). The third fraction of water is the apoplastic water, water bound within cell walls. This can be calculated from the interception of the extrapolation of the linear part of the PV curve with the *x*-axis. Apoplastic water varied from 3.7 to 6.5% of the total, and was generally lower in the hummock species (Table 1). However, because they contained more water in total, hummock species contained more apoplastic water per unit dry weight. A possible explanation for this is that hummock sphagna tend to have higher contents of cell wall uronic acids, and these can readily bind water (Clymo, 1963; Spearing 1972; Clymo and Hayward, 1982). Previous works on mosses and liverworts (Proctor *et al*., 1998; Proctor, 1999) disputed the reliability of this approach of estimating apoplastic water applied on data measured down to ψ = –6 MPa and suggested to include vapour equilibration at lower ψ. Our data indicated that the ψ measurements down to –10 MPa are sufficient for precise and reliable estimates of apoplastic WC because the additional sample equilibration at ψ = –20 MPa did not change the estimates of basic water parameters. Radin (1983) has suggested that low apoplastic WC may represent a turgor maintenance mechanism, because it can reduce RWC_{TLP}. However, in the sphagna tested here these two variables were not correlated, and the significance of the observed variations in apoplastic water contents remains unclear. However, thermocouple psychrometry has for the first time allowed us to accurately divide the cellular water of sphagna into its various fractions.

Cell wall modulus of elasticity

Increased $\psi_{\pi s}$ (osmotic adjustment) and decreased ε (i. e. cell wall rigidity) are other mechanisms maintaining turgor to lower RWC (Radin, 1983). In *S. fuscum*, $\psi_{\pi s}$ was lower (more negative) than in the other species. However, despite this, *S. fuscum* reached the TLP at a high RWC. In mosses, however, $\psi_{\pi s}$ is generally not related to habitat conditions (Proctor *et al*., 1998; Proctor, 1999), although Beckett (1995) found that more desiccation tolerant lichens from drier habitats tended to have lower $\psi_{\pi s}$. By contrast, there are clear differences in ε between species and habitat types. Cell walls in *A. androgynum* and hummock sphagna were more rigid (had high ε) and so were not able to maintain turgor to such low RWC as *S. girgensohnii* and *S. tenellum*. The elasticity modulus was the most important parameter that controlled RWC_{TLP}. We cannot directly compare directly the absolute values of ε with that presented in literature, because we used a linear fit (Fig. 2) to ψ_p, which assumes constant ε between full turgidity and TLP. Nevertheless the published values of ε (Proctor *et al*., 1998; Proctor, 1999) are correlated well with those recalculated as a simple ratio of the published values of $-\psi_{\pi s}$ (equivalent to maximum turgor) and [1 – RWC_{TLP}] ($r = 0.88$). Such comparison showed low ε in all sphagna, notably *S. girgensohnii* and *S. tenellum*, comparable to Proctor's thalloid liverworts *Conocephalum conicum* or *Dumortiera hirsuta*. In these liverworts, low ε causes turgor loss at a RWC of about 0.6. In *S. girgensohnii* and *S. tenellum*, similarly low values of ε in combination with high external water resulted in RWC_{TLP} at values lower than those recorded in any moss, liverwort or lichens (Beckett, 1995 and 1997; Proctor *et al*., 1998; Proctor, 1999). Assuming that positive turgor is needed for cell division, the implication is that during a desiccation event *S. girgensohnii* and *S. tenellum* can continue growing for longer than other mosses, liverwort and lichens.

Response of the photosynthetic apparatus to desiccation

Complete turgor loss was accompanied by decrease in photosynthetic activity, measured as Φ_{PSII}, while F_v/F_m, which is independent of subsequent CO_2 assimilation, remained unchanged up to even lower RWC.

Photosynthetic activity, measured as Φ_{PSII}, only started to decline when almost all turgor was lost (Table 1). Interestingly, results presented here differ from those of Csintalan *et al*. (1999) and Proctor *et al.* (2007). These authors reported that chlorophyll fluorescence parameters start to decline together with ψ_p during the desiccation of mosses. However, we quantifed ψ_p and RWC_{TLP} using a more

accurate method. Relatively high values of F_v/F_m in the dry state (Fig. 4) were a consequence of quenching of basal chlorophyll fluorescence F_o, which serves as a photoprotective heat dissipation mechanism in PSII reaction centres and is inherent to poikilohydric autotrophs (Heber *et al*., 2006a, b).

In general, sphagna that lost quickly their turgor during drying due to higher ε also lost photosynthetic activity quickly (i.e. *A. androgynum* and the hummock sphagna), but also showed better dark recovery of F_v/F_m and Φ_{PSII}. By contrast, *S. tenellum* and *S. girgensohnii* with the most elastic cell walls maintained turgor pressure down to very low ψ_π but their rates of long and short-term recovery of F_v/F_m and Φ_{PSII} showed that they were more damaged. In bryophytes, recovery from desiccation seems to depend on inherent desiccation tolerance, rather than mechanisms repairing damaged structures; however, more than one constitutive and also inducible protectants seem to play important roles (Rascio and Rocca, 2005; Oliver *et al.*, 2005). In the work presented here, rehydration following dehydration was in the dark, and therefore was not affected by light-induced damage. Other workers have suggested that recovery under these conditions does not require protein resynthesis (Proctor and Smirnoff, 2000; Proctor *et al.*, 2007). Therefore the desiccation tolerance displayed by the mosses used here probably represents a kind of constitutive adaptation, a physical rearrangement of cellular structures after rewetting, as has been described recently in *Polytrichum formosum* (Proctor *et al.*, 2007). This species is taxonomically related and ecologically and physiologically similar to *A. androgynum*. *Polytrichum* responded to desiccation in a similar way to *A. androgynum* and hummock sphagna, suggesting that their desiccation tolerance may have similar physiological bases.

Desiccation in *Sphagnum* ecology

Results of the present study clearly showed that desiccation tolerance is greater in hummock species than those that grow in hollows (Fig. 4), as would be intuitively predicted. The differences in the sensitivity of sphagna from contrasting habitats to the ecologically probable water pressure deficits used here suggest that desiccation tolerance may be an important factor in *Sphagnum* ecology. While two earlier studies have reported that hummock sphagna display less desiccation tolerance than those growing in hollows, these studies may have used inappropriate desiccation protocols or collection methods. Wagner and Titus (1984) tested survival and recovery of photosynthesis in one hummock and one hollow species, *S. capillifolium* and *S. fallax,* respectively. The latter species showed much better desiccation tolerance after being dried to WC of 0.2 g g^{-1}

for 5 d. However, this amount of water corresponds to less water than even the apoplastic WC of the *Sphagnum* species used in the present study and probably corresponds to $\psi < -50$ MPa. Sagot and Rochefort (1996) oven dried individuals of six *Sphagnum* species for 48 h at 30 °C. While only *S. fallax* appeared to survive, the ecological relevance of such fast and severe drying is uncertain.

A further possible reason for the differences between our results and those of earlier studies relate to the way the mosses were collected. Beckett *et al*. (2005) showed that partial dehydration before severe desiccation significantly increased the rate of recovery of Φ_{PSII} in *A. androgynum*; abscisic acid served as a signal for induction of desiccation tolerance. For the material used in this study, the *Sphagnum* samples were collected during humid period, and were unlikely to be affected by drought. After collection, our mosses were stored for several weeks under moderate temperatures, low light intensities, and water saturated conditions. This would remove any previous environmental effects that would tend to increase desiccation tolerance. However, earlier workers appear not to have used a period of "de-acclimation" before their experiments, and their results may have been influenced by weather conditions before collection. *E.g.*, the samples of Wagner and Titus (1984) had apparently experienced severe desiccation before collection from the field. Results presented here show that hummock species have greater desiccation tolerance, which is inherent, not induced by a previous desiccation event. This is also consistent with their ecology. Desiccation tolerance can help to hummock-forming *Sphagnum* species to outgrow the competition of other sphagna that normally grow in water-saturated environment and so enable them to persist in their own drought-exposed microhabitat, the hummock. In the hummock, hollow species are excluded due to their inability not only to avoid but also to tolerate desiccation.

Conclusions

From an ecological point of view, it is possible to consider *Sphagnum* mosses as succulents. They could be viewed as classical "drought avoiders", avoiding desiccation by storing large volume of water. However, unlike true succulents, their water is not cytoplasmic but rather stored in dead hyaline cells. The result of containing such water is that turgor only starts dropping at low WCs. Also, unlike succulents, they have moderate tolerance of low tissue water contents. Although the desiccation avoidance is often contrasted with physiological tolerance, our results suggested that hummock sphagna have both mechanisms, even if tolerance is restricted to moderate levels of desiccation stress. To survive

on exposed hummocks, they "store" i.e. retain externally more water than typical hollow species, and if they dry their photosynthesis recovers and more completely. Use of thermocouple psychrometry has for the first time allowed us to accurately estimate the amount of water associated with a thallus that is "stored" in different species. By contrast, sphagna that grow in less exposed habitats, such as hollows and forest floor, only very rarely dry out. In these species, the absence of metabolically expensive desiccation tolerance mechanisms, but never-the-less an ability to maintain positive turgor and photosynthesis down to low water contents may optimise their growth rates, which are generally higher than in hummock forming sphagna (Rydin *et al.*, 2006).

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❧

Sphagnum magellanicum (red capitula) contained only 40 % of intracellular nitrogen (N) when it occurred together with *S. angustifolium* (green capitula). This may result from a lower intracellular uptake rate of NH_4^+ and NO_3^- in *S. magellanicum* (also by about 40 %), indicating unequal competition for N, a limiting nutrient in N-unpolluted bogs.

Mineral nutrient economy in competing species of *Sphagnum* mosses

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Abstract

Bog vegetation, which is dominated by *Sphagnum* mosses, depends exclusively on aerial deposition of mineral nutrients. We studied how the main mineral nutrients are distributed between intracellular and extracellular exchangeable fractions and along the vertical physiological gradient of shoot age in seven *Sphagnum* species occupying contrasting bog microhabitats. While the *Sphagnum* exchangeable cation content decreased generally in the order $Ca^{2+} \geq K^{+}$, Na^{+}, $Mg^{2+} > Al^{3+} > NH_4^{+}$, intracellular element content decreased in the order N > K > Na, Mg, P, Ca, Al. Calcium occurred mainly in the exchangeable form while Mg, Na and particularly K, Al and N occurred inside cells. Hummock species with a higher cation exchange capacity (CEC) accumulated more exchangeable Ca^{2+}, while the hollow species with a lower CEC accumulated more exchangeable Na^{+}, particularly in dead shoot segments. Intracellular N and P, but not metallic elements, were consistently lower in dead shoot segments, indicating the possibility of N and P reutilization from senescing segments. The greatest variation in tissue nutrient content and distribution was between species from contrasting microhabitats. The greatest variation within microhabitats was between the dissimilar species *S. angustifolium* and *S. magellanicum*. The latter species had the intracellular N content about 40% lower than other species, including even this species when grown alone. This indicates unequal competition for N, which can lead to outcompeting of *S. magellanicum* from mixed patches. We assume that efficient cation exchange enables *Sphagnum* vegetation to retain immediately the cationic nutrients from rainwater. This may represent an important mechanism of temporal extension of mineral nutrient availability to subsequent slow intracellular nutrient uptake.

Introduction

Ombrotrophic (rain-fed) bogs are peatlands in which the surface layers are hydrologically isolated from the surrounding landscape. Therefore, the bog plants receive mineral nutrients exclusively from both wet and dry atmospheric deposition. *Sphagnum* mosses play a major role in the fixation of carbon and mineral nutrients in bogs, the latter due to the ability of whole moss plants to take up nutrients. Sphagna are thus allowed to control nutrients entering the top soil. These traits are an important advantage in the competition with rooting vascular plants in such nutrient-poor habitats as ombrotrophic bogs (Malmer et al. 1994; Aldous 2002b).

The mechanisms of nutrient transport and uptake at the plant–water interface are generally the same in both vascular plants and mosses. Cell walls of the root tip and the moss leaf have an acidic character – they release protons from exchange sites, mostly carboxylic groups of uronic acid (Knight et al. 1961). Therefore, they become negatively charged and ready to form electrostatic interactions with cations. The cation exchange is an extracellular, passive process in which cations (including protons) compete for an exchange site. Although the physiological role of cation exchange in mosses (or plants generally) has never been exactly established (Dainty and Richter 1993), it can be regarded as a concentrating mechanism improving the availability of cations for their further intracellular uptake mediated by specific transport sites (Bates 1989; Büscher et al. 1990; Wells and Brown 1990).

Several authors have reported that shoots of *Sphagnum* species, living or dead, have an unusually high cation exchange capacity (CEC), i.e., capacity to bind a cation in a solution at a given pH and concentration of that cation, in comparison with other plants (Anschütz and Gessner 1954; Clymo 1963; Brehm 1968). *Sphagnum* species or ecotypes occupying elevated bog hummocks have a higher CEC than those growing in lower-situated and wet microhabitats such as carpets and particularly hollows (Clymo 1963; Spearing 1972). Regardless of the role of CEC in plants generally, the high CEC enables sphagna to maintain efficient cation exchange in bogs, notably in *Sphagnum* hummocks, although the CEC is reduced by strongly acidic conditions due to reduced dissociation of the ion-exchanger in the cell walls.

Although many studies have dealt with mineral nutrients, particularly tissue cation content, in several *Sphagnum* species (e.g., Pakarinen 1978, 1981; Aulio 1980, 1982; Lembrechts and Vanderborght 1985; Malmer 1988; Malmer et al. 1992; Wojtuń 1994; Kempter and Frenzel 2007) none of them has distinguished

between the extracellular exchangeable and intracellular pools of cations. Yet, the two main compartments prefer different cations in *Sphagnum* (Brehm 1968) and in other mosses (Brown and Buck 1979; Bates 1982; Koedam and Büscher 1982; Bates 1987, 1992; Wells and Brown 1996; Brown and Brūmelis 1996; Bates 1997; Brūmelis and Brown 1997; Brūmelis et al. 2000). Thus, the aim of our study is to quantify the cation compartmentalization along the vertical physiological gradient of shoot age in six *Sphagnum* species from contrasting bog microhabitats. We test the hypothesis, proposed by Malmer (1993), that also in *Sphagnum* the polyvalent cations (Ca^{2+}, Mg^{2+}, and Al^{3+}) accumulate predominantly on the extracellular ion exchangers and in older shoot segments with reduced protoplasts, while the monovalent K^+ and NH_4^+ ions do not accumulate on exchangers but are mainly taken up into cells and also reutilized from old segments. Due to the small physiological importance of sodium in plants, we suppose that exchangeable Na^+ prevails in sphagna. We determined the intracellular N and P content along the physiological gradient of shoot age to find the degree of potential N and P reutilization from older shoot segments as an important ecological trait of mineral nutrient economy.

The second aim is to study cation compartmentalization in three pairs of *Sphagnum* species which coexist closely and for long periods in hummocks, lawns, and hollows. We test two contrasting hypotheses, namely that the mineral nutrient content of *Sphagnum* mosses is controlled either by moss species (Aulio 1982), or by growth pattern and habitat conditions (e.g., Pakarinen 1978; Malmer 1988; Malmer et al. 1992).

Materials and Methods

Plant material collection

We collected the *Sphagnum* mosses from an ombrotrophic raised bog Rokytecká slať (Bohemian Forest – Šumava National Park and Biosphere Reserve, Czech Republic, 49° 01.4' N, 13° 25.1' E, 1115 m a. s. l.) in October, at the end of the 2005 and 2006 growing seasons. The bog consists of a strip of Norway spruce (*Picea abies*) and bog-pine (*Pinus* × *pseudopumilio*) lagg forest (transition between mineral soil and bog peat) surrounding a large treeless mire expanse differentiated into the vertical hummock–hollow pattern.

We used polyethylene gloves to separate bunches of entire shoots from moss cushions or mats. In 2005, we chose six *Sphagnum* species dominating

contrasting microhabitats: *S. cuspidatum* floating in bog pools and inundated elongated depressions oriented perpendicularly to the slope (flarks); *S. majus* from wet flarks and hollows; *S. magellanicum* from lawns and low flat hummocks; *S. rubellum* and *S. fuscum* from elevated hummocks; and *S. capillifolium* from the lagg forest. In 2006, we collected three pairs of *Sphagnum* species co-occurring in mixed cushions: *S. cuspidatum* and *S. majus* in wet flarks, *S. angustifolium* and *S. magellanicum* in low hummocks and lawns, and *S. rubellum* and *S. fuscum* from elevated hummocks. We collected five replicates (*Sphagnum* cushions) per species or species pair. The minimum distance between replicate samples was 2 m. Moist samples were stored in polyethylene bags.

Sample preparation

We took the samples to the laboratory, stored them at 5 °C, and processed them within two days. We divided each shoot into four segments representing their physiological state: (i) capitulum (apical segment, 3–8 mm long), (ii) subapical segment (10 mm), (iii) last living segment (10 mm) beginning 13–35 mm below the apex (90 mm in *S. cuspidatum*), and (iv) dead segment (10–20 mm). We left an at least 5–mm gap between the last two segments. We distinguished between the third and fourth segment according to the green colour. Where this feature failed (dark samples of *S. fuscum* and *S. rubellum*) we used imaging fluorometer (FluorCam, Photon System Instruments Ltd., Czech Republic) to visualize the chlorophyll content by the method of chlorophyll *a* fluorescence. We verified the reliability of this method earlier on green shoots of *Sphagnum capillifolium* – the variable chlorophyll fluorescence of dark-adapted shoots decreased abruptly where the green shoot colour turned pale-yellow, which indicates chlorophyll breakdown and cell death. In the case of *S. fuscum,* we obtained only three segments (the second and third ones were identical). In 2006, we studied only capitula and dead (first and fourth) segments. Based on shoot apical growth measured in the 2000 and 2001 seasons (unpublished data), the apical segments were 2–4 months old (3 weeks in *S. cuspidatum*) followed by segments not older than one year. The age of dead segments was very uniform across the species (1.4–1.9 years).

Analyses of mineral nutrient content

We washed all the samples in distilled water for 5 min, in order to remove mineral nutrients occurring in the external water located between leaves and

within hyaline cells which are opened by pores and serve as water reservoir. Then we squeezed the excess water and placed the samples (1–2 g of fresh weight, FW) into closeable bottles, added 40 ml of 20 mM HCl, and shook thoroughly for 90 s (after Clymo 1963; Brehm 1968, and Büscher et al. 1990). The eluates were analyzed for the contents of K^+, Na^+, Ca^{2+} and Mg^{2+}; in the case of the 2005 samples, also NH_4^+, and in 2006 also Al^{3+} were analyzed. These eluted cations were supposed to be the extracellular, exchangeable fraction bound by anionic exchange site located on the cell-wall surface. We expressed the total exchangeable metal content in milliequivalents per gram dry weight. After the elution, we washed the samples in distilled water, oven-dried at 80 °C, weighed, and analyzed the subsamples (about 1–3 mg each) for the intracellular content of the cations listed above (after mineralization with nitric acid), of phosphorus (perchloric acid), and of organic nitrogen (sulphuric acid). The elements in the tissue after the acidic elution are referred to as the intracellular, unexchangeable fraction located within chlorophyllous cells. We assume the organic N represents the total N content. Contents of organic nitrogen (mineralized to NH_4^+) as NH_4^+, and phosphorus were analyzed colorimetrically by flow injection analysis (Foss Tecator AB, Sweden) and the metal cations by atomic absorption spectrometry (Varian Inc., Australia).

Determination of CEC

We determined the CEC as the amount of exchangeable NH_4^+ at pH of 7.2 in samples saturated with NH_4^+ (Spearing 1972). First, we sealed subsamples (70 mg) of the oven-dried material of the apical and fourth segments of *Sphagnum* mosses into polyester mesh bags (mesh size 150 μm) and hydrated them in distilled water under intermittent vacuum (to remove air bubbles) for 3 h. Then, we immersed all 60 bags into 2 litres of 0.5 M ammonium acetate for 5 min. The pH of the shaken solution containing the bags was set to 7.2 by adding ammonia. After the saturation, all the bags were washed several times in a large volume of distilled water for 1 h. The exchangeable ammonium ions were then eluted with 1 M KCl for 15 min. The eluate was diluted eight times and analyzed for NH_4^+ as above.

Atmospheric nutrient deposition

Data on the aerial atmospheric deposition of the studied nutrients were provided by the Czech Hydrometeorological Institute. We averaged data from two monitoring sites (Lake Plešné and Lake Čertovo, 41 km SE and 41 km NW

apart, respectively) at an altitude similar to that of our study site. We compared the deposition data with the mean nutrient contents in *S. fuscum* and *S. rubellum*, the representatives of hummocks as purely ombrotrophic microhabitat, using the "moss enrichment factor", i.e. the ratio between the element concentration in the moss and that in precipitation (Malmer et al. 1992).

Statistical analyses

We performed all statistical tests using STATISTICA software, version 7.1 (StatSoft Inc., USA). We analyzed the data on element content using ANOVA: one-way repeated-measures ANOVA (or t-test for dependent samples in the case of comparing two segments) to test the differences between segments of different age within each species, between species within each segment of a certain age, and between species within each habitat in the case of data of 2006. Hierarchical ANOVA was applied to test the data of 2005 for differences between the species in the element content among the segments (interaction species × segment): element_content = species + segment + replicate (habitat) + species × segment. To test the differences between habitats (2006 data) we applied hierarchical ANOVA to each segment: element_content = species (habitat) + habitat + replicate (habitat). We used the factorial hierarchical ANOVA to test whether the habitats differed in their element content among segments (interaction habitat × segment): element_content = species (habitat) + habitat + segment + replicate (habitat) + habitat × segment. The nested parameter 'replicate' was always the random factor.

To visualize the correlations between different cation contents, compartments, and shoot segments and their relationships to moss species, we used the principal component analysis (PCA) using Canoco for Windows 4.5 (Lepš and Šmilauer 2003). The data were centred and standardized in order to make the variables comparable.

Results

Cation compartmentalization

Compartmentalization of the metallic cations showed a similar pattern across the species, habitats and shoot segments. In general, the extracellular exchange sites of *Sphagnum* species were occupied by cations in the following approximate

order (moles per unit moss DW are always shown): $Ca^{2+} \geq K^{+} > Na^{+} = Mg^{2+} > NH_4^{+}$ in 2005 (Table 1) and $Ca^{2+} > Mg^{2+} = K^{+} = Na^{+} > Al^{3+}$ in 2006 (Table 2). The exchangeable NH_4^{+} content was below the analytical detection limit; it is therefore assumed to be zero and is not shown in Table 1. The exchangeable contents of all four elements were, however, generally very variable both between the species within each shoot segment and, except for Na^{+}, between the segments within each species. Thus, any generalization is ambiguous. The intracellular, unexchangeable metal content decreased in the general order: K >> Na ≥ Mg ≥ Ca = Al in both years (Tables 1 and 2). The proportion of exchangeable to total cation content (Fig. 1) was always highest for Ca^{2+} (75% on average) followed by Mg^{2+} (35%), Na^{+} (18%), K^{+} (11%), and Al^{3+} (7%).

PCA (Fig. 2) revealed relationships between element contents in both compartments. In the samples of 2005, the first principal component axis explained 30% of the total variation and was related to the intracellular element contents. The second axis (27%) was dominated by exchangeable element contents and the third axis (22%; not shown in the PCA diagram) by intracellular contents of Ca and exchangeable Na^{+}, and CEC. There was no general relationship between the exchangeable and intracellular contents of K and Na within all *Sphagnum* species, while this correlation was positive for Ca in both segments (0.88 for the apical and 0.66 for the dead one, $P < 0.0001$, $n = 30$) and negative for Mg in the dead segments ($R = –0.57$, $P = 0.001$).

Table 1. Exchangeable and intracellular element content, the total exchangeable metal cation content (TEM^{+}), and cation exchange capacity (CEC) in six *Sphagnum* species representing six bog microhabitats (samples collected in 2005). Means ± s.e., $n = 5$. Superscripts denote P values of one-way, repeated-measures ANOVA, testing the differences between shoot segments within each species: $^{\#}P < 0.001$; $^{+}P < 0.01$; $^{*}P < 0.05$; $^{n}P > 0.05$. P values given in separate lines denote statistical difference between species within segments (one-way ANOVA) and between segments (factorial hierarchical ANOVA): *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; n.s. $P > 0.05$.

Table 2. Exchangeable and intracellular element content, the total exchangeable metal cation content (TEM^{+}), and cation exchange capacity (CEC) in three pairs of *Sphagnum* species representing dominant bog microhabitats (hummock, lawn, hollow; samples collected in 2006). Means ± s.e., $n = 5$. Superscripts denote P values of the t-test for dependent samples testing the differences between shoot segments within each species: $^{\#}P < 0.001$; $^{+}P < 0.01$; $^{*}P < 0.05$; $^{n}P > 0.05$. P values given in separate line denote statistical difference within the group specified in parentheses (nested ANOVA): *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; n.s. $P > 0.05$.

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Table 1, part 1	Exchangeable content (μmol g^{-1} d.w.)				TEM^{+}	CEC
Species	K^{+}	Na^{+}	Ca^{2+}	Mg^{2+}	(μeq g^{-1})	(μeq g^{-1})
	Apical shoot segment (1st – capitulum)					
S. fuscum	5.2±1.6^{n}	1.1±0.5^{n}	24.7±0.9*	6.5±0.6^{n}	69±2*	868±14*
S. rubellum	9.1±2.4*	2.8±1.1^{n}	21.2±2.4^{+}	4.4±0.5^{+}	63±6$^{\#}$	834±16*
S. capillifolium	46.1±6.8^{+}	3.7±0.7^{n}	36.1±2.4^{+}	7.5±1.1^{n}	137±11^{n}	820 ±6^{+}
S. magellanicum	31.3±5.1*	7.9±3.2^{n}	24.0±1.7^{+}	5.0±0.7^{n}	97±12^{n}	807±3^{n}
S. majus	3.5±0.8^{n}	2.1±1.0^{+}	11.3±0.9^{+}	0.4±0.1$^{\#}$	29±3$^{\#}$	443±3^{n}
S. cuspidatum	31.9±4.1^{n}	15.5±6.3^{n}	18.4±0.8*	5.5±1.2$^{\#}$	95±7*	465±8^{n}
P (species)	***	*	***	***	***	***
	Subapical shoot segment (2nd)					
S. fuscum						
S. rubellum						
S. capillifolium						
S. magellanicum						
S. majus						
S. cuspidatum						
P (species)						
	Last living shoot segment (3rd)					
S. fuscum						
S. rubellum						
S. capillifolium						
S. magellanicum						
S. majus						
S. cuspidatum						
P (species)						
	Dead (brown) shoot segment (4th)					
S. fuscum	6.1±1.4	2.1±0.3	31.7±2.6	8.4±1.2	88±7	918±9
S. rubellum	2.5±0.4	0.8±0.2	33.0±3.2	8.3±0.3	86±7	860±20
S. capillifolium	7.0±1.5	4.4±0.7	49.8±3.8	8.8±1.0	129±10	859±10
S. magellanicum	10.2±1.8	2.5±0.5	30.1±1.1	6.1±0.6	85±4	831±10
S. majus	6.6±1.7	12.2±2.2	18.1±0.8	10.7±0.7	76±4	461±9
S. cuspidatum	26.1±5.0	30.3±9.9	34.6±5.2	15.5±1.1	157±19	469±12
P (species)	***	***	***	*	***	***
	All shoot segments					
P (segment)	***	n.s	***	***	***	***
P (spec × segm)	***	n.s	*	***	***	*

Table 1, part 2	Intracellular element content (µmol g^{-1} d.w.)					
Species	K^+	Na^+	Ca^{2+}	Mg^{2+}	N	P
	Apical shoot segment (1st – capitulum)					
S. fuscum	85±5*	20.1±1.7^{n}	7.3±0.7^{n}	14.6±1.0^{n}	761±105^{n}	10.8±1.5^{+}
S. rubellum	88±5$^{\#}$	25.4±4.5^{n}	9.6±1.4^{n}	14.2±1.0*	954±106$^{\#}$	9.6±0.8$^{\#}$
S. capillifolium	112±3^{+}	20.7±1.9^{+}	13.7±1.7^{n}	19.9±1.8^{n}	1047±100$_{+}$	19.0±2.1$^{\#}$
S. magellanicum	92±4$^{\#}$	22.3±4.1^{+}	7.7±0.6*	16.9±1.0^{n}	801±47$^{\#}$	9.1±1.1$^{\#}$
S. majus	98±8$^{\#}$	25.9±2.2*	3.4±0.3*	16.3±0.8*	558±12$^{\#}$	7.5±1.2^{+}
S. cuspidatum	179±9$^{\#}$	31.2±3.9*	3.8±0.3$^{\#}$	44.9±2.2$^{\#}$	1332±100$_{\#}$	28.6±4.7$^{\#}$
P (species)	***	n.s.	***	***	***	***
	Subapical shoot segment (2nd)					
S. fuscum	87±5	29.8±4.0	7.3±0.3	13.6±0.8	540±47	8.6±0.8
S. rubellum	69±4	25.9±5.3	9.5±2.0	15.2±1.1	788±33	9.0±1.0
S. capillifolium	120±12	19.2±2.2	15.0±3.0	24.3±1.7	970±46	16.1±2.6
S. magellanicum	113±6	13.6±0.7	5.7±0.8	15.9±0.3	920±80	9.0±0.8
S. majus	147±18	25.3±2.6	3.8±0.9	14.3±1.4	764±66	7.9±0.6
S. cuspidatum	259±35	43.9±11.5	3.0±0.3	51.1±3.9	1390±120	26.4±5.6
P (species)	***	*	***	***	***	***
	Last living shoot segment (3rd)					
S. fuscum						
S. rubellum	66±4	29.8±5.0	6.2±0.5	17.0±2.0	798±25	7.4±0.3
S. capillifolium	93±10	22.5±1.7	15.8±3.5	24.1±1.3	836±35	11.3±0.6
S. magellanicum	92±7	18.3±3.8	4.3±0.2	15.2±1.5	708±83	7.7±0.3
S. majus	108±9	52.7±2.8	1.9±0.3	17.8±2.4	468±22	6.6±0.3
S. cuspidatum	149±22	96.6±31.9	2.0±0.2	23.3±2.7	866±51	16.4±1.6
P (species)	*	*	***	n.s.	***	***
	Dead (brown) shoot segment (4th)					
S. fuscum	64±6	25.7±2.3	6.8±0.4	13.1±3.2	506±41	3.5±0.4
S. rubellum	47±3	28.7±1.7	7.3±1.0	11.2±1.1	520±52	2.7±0.2
S. capillifolium	62±10	41.9±5.5	14.1±3.4	20.9±2.9	559±61	7.0±1.0
S. magellanicum	64±10	36.5±4.2	6.6±0.7	18.0±1.3	420±54	2.9±0.3
S. majus	32±8	59.5±19.7	2.3±0.2	7.9±1.7	372±34	3.1±0.6
S. cuspidatum	28±7	29.1±5.5	2.2±0.3	6.4±0.6	646±69	7.8±1.0
P (species)	n.s.	n.s.	***	*	**	***
	All shoot segments					
P (segment)	***	*	n.s.	***	***	***
P (spec × segm)	***	**	n.s.	***	***	**

Table 2, part 1	Exchangeable element content (µmol g^{-1} d.w.)					TEM^{+}	CEC
Species (habitat)	K^{+}	Na^{+}	Ca^{2+}	Mg^{2+}	Al^{3+} (*10^{3})	(µeq g^{-1})	(µeq g^{-1})
Apical shoot segment (capitulum)							
S. fuscum	3.3±0.7*	2.5±0.4^{+}	17.4±1.6*	4.4±0.8*	87±17*	49.6±5.4$^{\#}$	952±5*
S. rubellum	5.4±1.2*	2.2±0.3^{+}	19.9±1.8^{+}	5.6±0.5*	143±38^{n}	59.2±4.0^{+}	928±24^{+}
P (hummock sp.)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S. angustifolium	1.8±0.1*	1.7±0.4$^{\#}$	15.5±2.1^{+}	6.6±1.4^{n}	41±10*	47.6±7.0^{+}	614±10$^{\#}$
S. magellanicum	3.1±0.1^{+}	1.8±0.2*	16.9±3.0*	6.3±1.4^{n}	76±36^{+}	51.6±8.2^{+}	767±11^{n}
P (lawn species)	***	n.s.	n.s.	n.s.	n.s.	n.s.	***
S. cuspidatum	6.6±2.0*	2.9±0.4^{+}	7.3±0.6*	3.5±0.2^{+}	654±172*	33.1±3.1$^{\#}$	531±8^{+}
S. majus	5.3±1.3^{n}	2.8±0.3$^{\#}$	7.2±0.4^{+}	4.1±0.3^{+}	315±57$^{\#}$	31.7±1.7$^{\#}$	499±17^{+}
P (hollow species)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P (spec(habitat))	n.s.	n.s.	n.s.	n.s.	*	n.s.	***
P (habitats)	n.s.	n.s.	**	n.s.	***	*	***
Dead (brown) shoot segment							
S. fuscum	5.1±0.4	5.2±0.5	27.2±3.4	7.6±1.5	228±31	80.5±7.5	875±15
S. rubellum	8.3±1.3	4.8±0.4	30.4±3.1	8.2±1.3	255±31	91.2±7.1	788±18
P (hummock sp.)	*	n.s.	n.s.	n.s.	n.s.	n.s.	**
S. angustifolium	6.0±0.9	4.0±0.3	26.8±3.6	7.0±0.7	561±121	79.4±8.2	776±17
S. magellanicum	10.2±0.9	3.6±0.4	22.9±3.4	7.0±0.8	879±146	76.2±5.9	827±16
P (lawn species)	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S. cuspidatum	10.9±1.9	11.3±1.4	18.5±2.9	9.4±0.7	1127±15	81.3±8.0	617±10
S. majus	8.8±2.3	9.4±0.8	15.8±1.3	9.1±0.8	1199±73	71.5±4.9	651±8
P (hollow species)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*
P (spec(habitat))	***	*	**	n.s.	n.s.	*	***
P (habitats)	n.s.	***	*	n.s.	***	n.s.	***
All shoot segments							
P (habitat)	n.s.	***	*	n.s.	***	n.s.	***
P (segment)	***	***	***	***	***	***	***
P (habit. × segm.)	*	***	n.s.	***	***	**	***

Table 2, part 2	Intracellular element content (µmol g^{-1} d.w.)						
Species (habitat)	K^+	Na^+	Ca^{2+}	Mg^{2+}	Al^{3+}	N	P
				Apical shoot segment (capitulum)			
S. fuscum	107±7^n	13.3±5.0^n	9.6±1.3^n	13.6±1.0^n	4.3±1.6*	974±100^n	11.3±1.2*
S. rubellum	106±10^n	10.0±2.2^n	10.7±1.8^n	9.9±0.9^n	7.5±1.6^n	828±72$^+$	10.9±0.8$^+$
P (hummock sp.)	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.
S. angustifolium	89±12*	17.3±4.1^n	6.4±1.0^n	10.2±0.5^n	7.0±0.6^n	864±28^n	12.6±0.9*
S. magellanicum	81±6*	13.0±4^n	7.5±1.2^n	15.9±1.6^n	10.2±3.1^n	494±33^n	12.0±0.9*
P (lawn species)	n.s.	n.s.	n.s.	*	n.s.	***	n.s.
S. cuspidatum	138±14^n	29.8±8.3^n	5.1±1.1^n	9.2±1.5^n	11.8±2.0^n	895±43$^+$	13.1±1.6$^+$
S. majus	117±15^n	17±7.6^n	3.0±0.2^n	8.2±1.1^n	8.5±1.3^n	833±71$^+$	12.0±1.4$^+$
P (hollow species)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P (spec(habitat))	n.s.	n.s.	n.s.	**	n.s.	**	n.s.
P (habitats)	*	n.s.	**	*	n.s.	*	n.s.
				Dead (brown) shoot segment			
S. fuscum	94±7	17.2±1.8	10.3±1.5	12.6±1.8	8.3±1.1	683±30	7.5±0.7
S. rubellum	84±12	11.0±1.9	10.5±1.9	9.4±1	4.0±0.5	463±48	6.6±0.4
P (hummock sp.)	n.s.	*	n.s.	n.s.	**	**	n.s.
S. angustifolium	72±13	7.7±1.2	6.9±1.3	8.8±0.9	7.9±2.5	733±49	7.0±0.4
S. magellanicum	143±17	16.7±2.6	11.8±2.5	14.3±1.8	9.7±1.6	507±42	8.1±0.1
P (lawn species)	*	*	n.s.	*	n.s.	**	*
S. cuspidatum	142±10	63.3±18.5	4.5±0.7	14.2±2.8	5.6±1.9	469±58	5.9±0.7
S. majus	90±22	44.5±5.6	4.7±1.3	7.3±0.8	8.7±3.4	522±54	6.6±0.6
P (hollow species)	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.
P (spec(habitat))	**	n.s.	n.s.	*	n.s.	***	*
P (habitats)	n.s.	***	*	n.s.	n.s.	n.s.	n.s.
				All shoot segments			
P (habitat)	n.s.	***	**	n.s.	n.s.	n.s.	n.s.
P (segment)	n.s.	*	n.s.	n.s.	n.s.	***	***
P (habit. × segm.)	n.s.	**	n.s.	n.s.	n.s.	***	*

In the samples of 2006, the intracellular N and P contents formed the main gradient (32% of the explained total variation; Fig. 2; see also Table 2), while the intracellular cation contents dominated the second (23%) and third (12%, not shown) axis. Exchangeable cation contents correlated with both, the first and second axis. The exchangeable and intracellular contents in the apical segments correlated only for K and Ca (R = 0.62 and 0.76, $P < 0.0001$, $n = 30$) and in the dead segments for K, Na and Ca (R = 0.57, 0.73, and 0.48, $P = 0.001$, $P < 0.0001$, and $P = 0.008$, respectively).

Variation between species and microhabitats

The six species studied in 2005, which represented six bog microhabitats, were allocated in the PCA diagram (Fig. 2) along the second principal component axis representing the exchangeable cation content. The highest content of exchangeable and intracellular cations was in the apical segments of *S. capillifolium*, the only species collected from the lagg forest understorey. *S. capillifolium* contrasted with the only hollow species, *S. majus*, which was poor in exchangeable cations and also had a low CEC. The other species of elevated microhabitats (*S. fuscum*, *S. rubellum*, and *S. magellanicum*) were generally similar in nutrient contents and were located between the two extremes close to the centre of the PCA diagram. *S. cuspidatum*, collected from bog pools, differed from all other species on the third principal axis (not shown) in its high content of exchangeable monovalent cations in the dead segments (Fig. 1, Tables 1, 2).

The allocation of species and microhabitats, studied in 2006, clearly followed the second principal axis in the PCA diagram. The hollow species contrasted with the hummock ones by a low CEC and exchangeable and intracellular Ca content, but a high exchangeable Al^{3+} content. Although the lawn species tended to have an intermediate character, they were closer to the hummock ones in most of the characteristics. The greatest interspecific variation within microhabitats was in the lawns (Table 2). Here, the N-poor *S. magellanicum* with a high CEC bound more exchangeable K^{+} and retained higher metallic element and P contents in the dead segments.

Element content along the physiological gradient

In 2005, we determined the intracellular content of six elements in four shoot segments – according to their physiological status (Table 1). The N, P, K, and Mg contents highly significantly correlated with one another across all species and segments (R = 0.79–0.92, $P < 0.0001$, $n = 23$ mean values of five

independent replicates per species and shoot segment), while they showed no relation to the Ca and Na contents. Ca and Na correlated negatively with each other ($R = –0.42$, $P = 0.048$). Only Na, but not Ca, accumulated in dead cells. The N, P, and K contents were the highest in the capitula and/or in the subapical segments and were always the lowest in the dead segments; the last living segments approached the nutrient contents of the apical segments. The contents of N, P, and K are thus well explained by the physiological status of the plant parts. *S. capillifolium*, the only species collected from the lagg forest understorey, accumulated more Ca and Mg within the whole shoot than the other species ($P < 0.001$), while the two species of wet habitats, *S. majus* and *S. cuspidatum*, accumulated less Ca than the other species ($P = 0.017$). The floating *S. cuspidatum* accumulated more N, P, K, and Mg in its apical and subapical segments than the other species, but it lost most of K and Mg from the ageing segments. In 2006, the vertical physiological polarity between the apical and dead segments was much less distinct. Only the N and P, but not the metallic element contents, were lower in the dead segments and only Na accumulated there.

We compared the exchangeable cation contents in the two contrasting shoot segments – an apical and a dead one. The dead segments contained more exchangeable Ca^{2+} and Mg^{2+} than the apical ones in both 2005 and 2006 seasons and also Al^{3+} accumulated more in the dead segments (Tables 1 and 2). The monovalent cations, however, behaved inconsistently. They prevailed at the exchange sites of the dead segments in 2006, but they concentrated in the capitula in many cases in 2005. The ratio of exchangeable to total cation contents was significantly higher in the dead segments for a half of the species and cations (Fig. 1).

Relationship between element accumulation and availability

Annual deposition (in mmol m^{-2} y^{-1}) of the studied cations decreased in the order of $NH_4^+ >> Na^+ > Ca^{2+} > K^+ > Mg^{2+} >> Al^{3+}$ in both seasons (Table 3). As opposed to the other elements, the high ammonium deposition, zero exchangeable N, and high intracellular N content demonstrate efficient N uptake by the mosses. Similarly, when comparing the moss enrichment factors (Table 3), the capitula showed an efficient intracellular accumulation of deposited K, Al and, to a certain extent, also Mg. In contrast, *Sphagnum* capitula retained a small amount of deposited Na (intracellular) and Ca^{2+} (exchangeable).

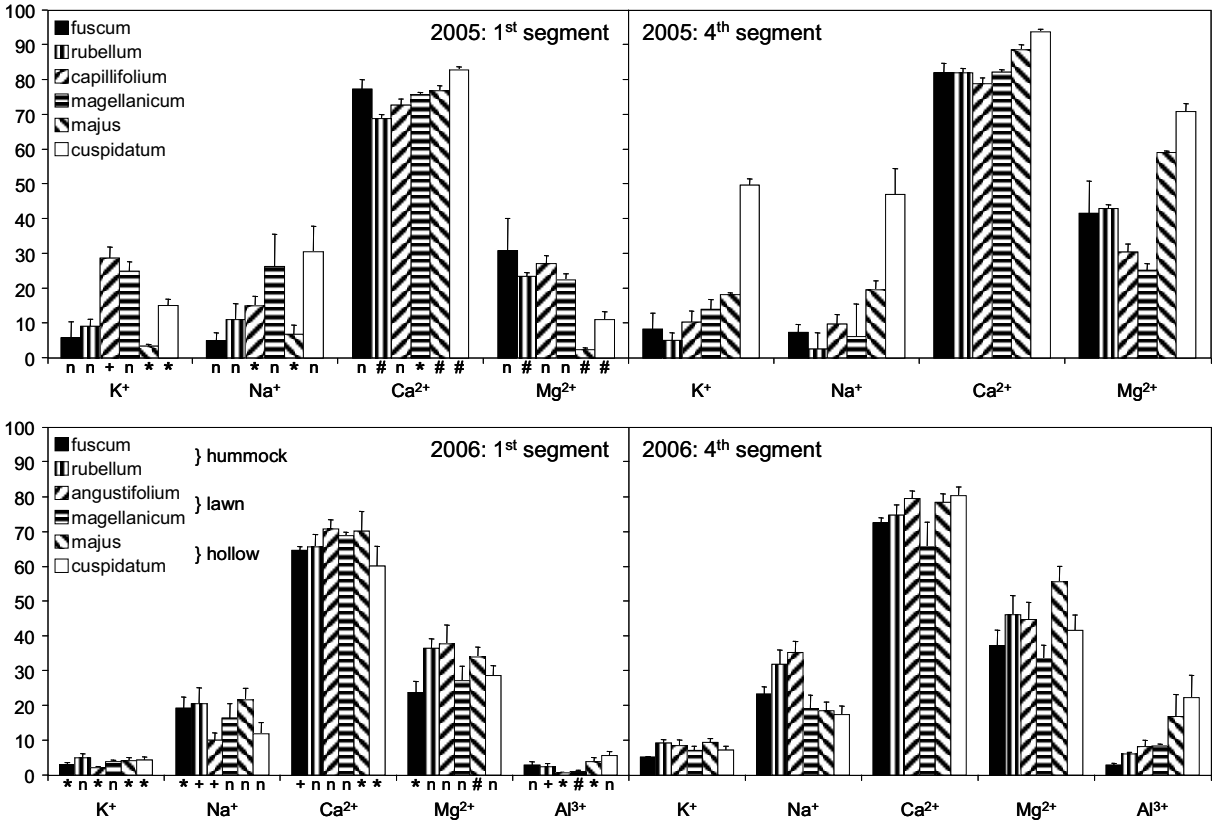

Fig. 1. Exchangeable cation fraction (in %) from the total cation pool in apical (1st) and dead (4th) shoot segments. Symbols below the columns of the segments denote *p* values of the t-test for dependent samples testing the differences between shoot segments: $^{\#}P < 0.001$; $^{+}0.01 < P < 0.001$; $^{*}0.05 < P < 0.01$; $^{n}P > 0.05$. *P* values given in separate line denote statistical difference within groups (one-way and nested ANOVA): *** $P < 0.001$; ** $0.01 < P < 0.001$; * $0.05 < P < 0.01$; n.s. $P > 0.05$.

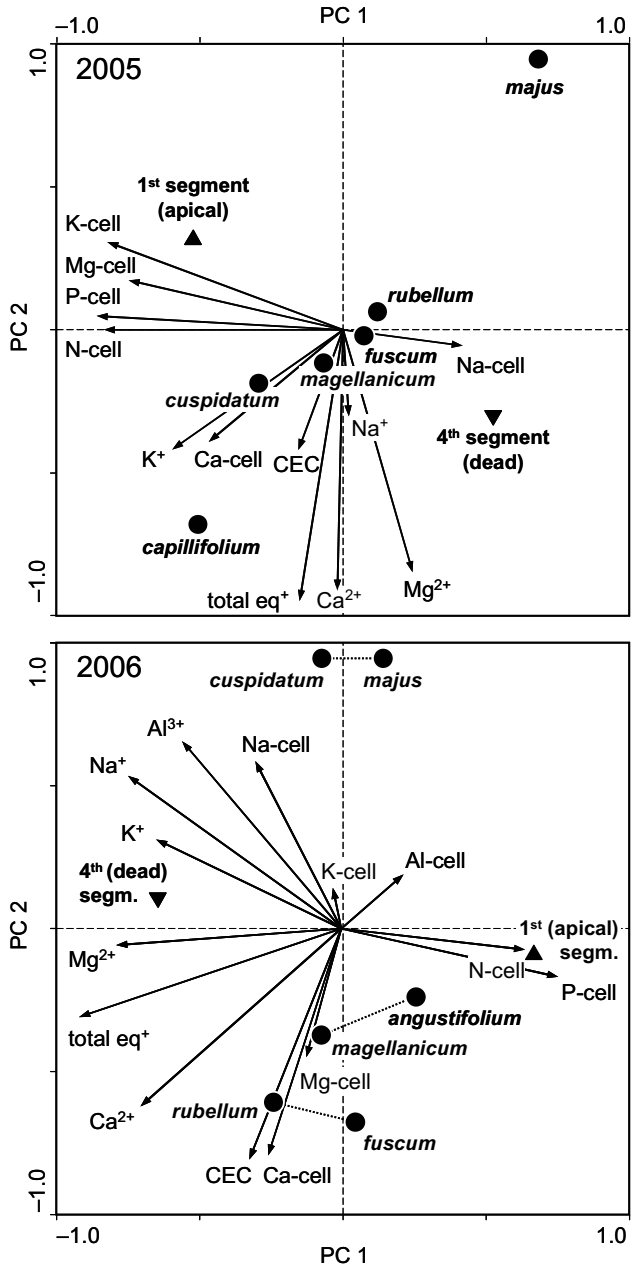

Fig. 2. PCA ordination diagrams (based on data of 2005 and 2006) displaying correlations between element contents located within cells (-cell) and in exchangeable form (marked by + as cations), total exchangeable cation equivalents (total eq^{+}), and potential cation exchange capacity (CEC). Centroids of shoot segments and moss species are projected onto these correlations. Pairs of the connected species belong to the same microhabitat.

Table 3. Annual wet deposition of the studied elements at the sampling site and mean exchangeable and intracellular contents of these elements in apical segments (capitula) of the hummock species *Sphagnum fuscum* and *S. rubellum* (derived from Table 2; $n = 10$). The enrichment factor is a ratio between element content in the moss and element concentration in precipitation. Different superscript letters denote statistical differences between elements at $\alpha = 0.05$ (ANOVA, Tukey's HSD Test; $n = 10$).

Year	Precipitation (mm)	Conduct. ($\mu S\ cm^{-1}$)	pH	K	Na	Ca	Mg	Al	NH_4-N	NO_3-N	N-tot
				Annual deposition (mmol $m^{-2}\ y^{-1}$)							
2005	1284	18.9	4.8	2.7	8.2	5.8	1.3	0.26	23.0	7.4	30.3
2006	1560	12.8	5.1	3.5	9.9	5.5	1.6	0.33	33.7	8.6	42.3
Year	Compartment			*Sphagnum* element content ($\mu mol\ g^{-1}$ d.w.) in hummocks							
2005	Exchangeable			7.2	1.9	22.9	5.4		0.0		
	Intracellular			86.3	22.7	8.5	14.4				857
2006	Exchangeable			4.3	2.4	18.6	5.0	0.12			
	Intracellular			106.3	11.7	10.2	11.8	5.87			901
	Compartment			*Sphagnum* enrichment factor in hummocks ($l\ g^{-1}$)							
Mean	Exchangeable			2.7^{a}	0.3^{b}	5.2^{c}	5.0^{c}	0.5^{b}	0.0^{d}		
	Intracellular			44.5^{a}	2.7^{b}	2.4^{b}	12.6^{c}	28.4^{d}			34.8^{d}
	Total			47.2^{a}	3.0^{b}	7.6^{b}	17.6^{c}	28.0^{d}			

Discussion

Cation compartmentalization

Mosses are characterized by the lack of a thick cuticle as opposed to vascular plants. Therefore, they can utilize their large shoot surface area and its fixed negative charge in cell walls for effective exchange and uptake of cations into cells. This study is the first attempt to separate the exchangeable extracellular and intracellular cation fractions in *Sphagnum* mosses occurring in contrasting microhabitats of a bog (cf., e.g., Malmer 1993). The exchangeable cation content in the moss and cation concentration in external (pore) water are directed towards electrochemical equilibrium; they are regulated by several processes:

(i) cation supply by aerial deposition;
(ii) cation transport from mineral substrate and translocation from senescent tissues;
(iii) cation uptake into cytoplasm;
(iv) cation leakage from cytoplasm;
(v) cation affinity to exchange sites.

In *Sphagnum* mosses from an ombrotrophic bog, the aerial deposition can be assumed to be the same in species growing in the open parts; only *S. capillifolium* received also nutrients intercepted by the lagg forest canopy as indicated by high exchangeable and intracellular contents of K and Ca in the apical segment. Mosses are capable of an effective mineral nutrient transport from the substrate (Bates and Farmer 1990) but no nutrient transport from mineral substrate is assumed in ombrotrophic bogs. Only the nutrients released from decaying biomass in the upper, aerated peat layer (acrotelm) can move upwards. However, the hollow species receive also nutrients washed out from hummocks, and species growing in pools (*S. cuspidatum* in 2005) also receive nutrients from deep peat layers. Desiccation of the living moss usually causes cation leakage from cell cytoplasm during which most of the effused Mg^{2+} (Brown and Buck 1979) or K^+ (Brown and Brūmelis 1996) is retained on the exchange sites and reutilized during the recovery after rewetting (Bates 1997). Cation transport to the cytoplasm is the only process actively regulated by moss cells. Although ammonium ion was the dominant cation in rainwater, it was absent in the exchangeable form in our study. It indicates that the cation exchange is not a process competing with the intracellular uptake of NH_4^+. This seems to be true also for K^+, which has a very similar affinity to the *Sphagnum* cation exchanger as NH_4^+ (Breuer and Melzer 1990), but has a 10 times lower

deposition. A very low concentration of NH_4^+ tracer in mire ground water was found by Williams at al. (1999) in two weeks after the tracer application to a *Sphagnum* vegetation; this points out that *Sphagnum* has efficient N retention (up to 100%; Williams et al. 1999; Li and Vitt 1997), exclusively by intracellular uptake.

Assuming the identical character of the cell-wall cation exchanger among our sphagna, the cation affinity to the exchanger generally correlates with its valency, hydrated atomic radius, and concentration in the ambient water solution (Bates 2000). But it also strongly depends on relative cation concentrations in the solution and the degree of exchanger dissociation (pH). These relationships were described in details by Dainty and Richter (1993).

Generally, our results of exchangeable and intracellular K, Ca and Mg contents in *Sphagnum* apical segments are very similar to the only one published result for *Sphagnum* (*S. magellanicum*, Brehm 1968). Our sphagna also showed a similar pattern of cation compartmentalization to that in other mosses from minerotrophic habitats, in which the relative exchangeable cation contents also decrease in the order $Ca^{2+} > Mg^{2+} > K^+$ (Brown and Buck 1979; Bates 1987; Wells and Brown 1990, 1996; Brown and Brūmelis 1996; Brūmelis and Brown 1997; Brūmelis et al. 2000). The upper values of the intracellular Ca and Mg contents in our sphagna (Tables 1, 2) were similar to the mean values found in six of 20 studied non-*Sphagnum* moss species from minerotrophic habitats (17–24 and 13–29 μmol g^{-1} d.w. for Ca and Mg) and the mean intracellular K content was even the same (Brown and Buck 1979; Bates 1987; Brown and Brūmelis 1996; Wells and Brown 1996). Our sphagna differed strikingly from the 20 moss species by low contents of exchangeable Ca^{2+} and partly also Mg^{2+} but not K^+. The affinity of K^+ to the cell-wall exchanger could be enhanced in *Sphagnum* by a low content of competing polyvalents and low pH (cf. Dainty and Richter 1993). Assuming that sphagna have a lower cytoplasm volume in the entire tissue volume than other mosses (having large empty hyaline cells), the intracellular content of Ca and Mg was roughly the same in ombrotrophic *Sphagnum* and minerotrophic mosses and the intracellular content of K was even higher. By contrast, *S. magellanicum* collected from a bog situated 10 km away from sea (Brehm 1968) contained 2–5 times as much intracellular Na and about 10 times as much exchangeable Na^+ as our *S. magellanicum*. Despite its low physiological demand and functions, Na is taken up into the cells where it accumulates and obviously has an osmotic function. On the other hand, increased deposition of Mg in this maritime bog led to the accumulation of exchangeable Mg^{2+} while the intracellular content remained similar to our values, although Mg is an important macronutrient. Despite no need of Al in

plant cells, at least 94% of the total Al represented the intracellular fraction while only up to 6% of Al^{3+} was bound in exchangeable form.

Although significant differences existed between our sphagna, the intracellular cation content was of the same order of magnitude in species from environments of contrasting cation availability. Thus, the differences of the total metallic cation content are determined rather by the pool of exchangeable cations. Although Ca^{2+} was not the dominant metallic cation in the total cation income (Table 3) as compared to various mineral soils (Büscher et al. 1990), it was the dominant exchangeable cation in most cases, like in the other mosses mentioned above. Only the hollow species *S. majus* (both years) and *S. cuspidatum* (2006) contained little exchangeable Ca^{2+} (and also Mg^{2+}), probably due to a lower cell wall charge density (represented by low CEC), which reduces the binding of polyvalent cations in favour of monovalents (Dainty and Richter 1993). Exchangeable monovalents, particularly Na^{+}, accumulated in dead segments of the preferentially hollow and pool species *S. cuspidatum* and *S. majus*, probably also because they had not been retained as efficiently as bivalents in hummocks.

Element contents along the physiological gradient and nutrient reutilization

The results showed a considerable year-to-year variability in the exchangeable cation content in the apical segment and a smaller variability in the dead one. The spatial variability between replicates was relatively small. This indicates that the exchangeable cation pool of the upper shoot is more susceptible to environmental factors. The higher total exchangeable cation content in the apical segment in 2005 could result from a 2–3 times higher precipitation (and thus nutrient deposition; data not shown) during each of the three months before sampling in 2005 than in 2006. On the other hand, Malmer (1988) showed that there was no correlation between K, Ca and Mg annual wet deposition and the total element content in Scandinavian sphagna.

The intracellular N, P and, in 2005, also K, accumulated significantly in upper segments. Because the exchangeable content of these elements was low or negligible (Fig. 1) the results are comparable and consistent with the total contents reported by other authors (Pakarinen 1978; Malmer 1988). The lower content of these macronutrients in the dead segments indicates their possible translocation to the upper segments. Rydin and Clymo (1989) observed an internal upward translocation of C and P through the *Sphagnum* "stem". Aldous (2002a) found that the upward N translocation was an important basis for N retention in the field, particularly in such a relatively N-unpolluted area as was our collection site, where the annual N deposition of 0.5 g m^{-2} y^{-1} was limiting

for *Sphagnum* growth (Table 3; cf. Bragazza et al. 2004). The intracellular element contents along the vertical physiological gradient could be affected by a temporal variation in the nutrient deposition and the subsequent uptake. This can be a reason for an absence of a pattern in the vertical distribution of metallic elements; only Na accumulated in the dead segments. Although our results do not enable us to estimate accurately the proportion of N and P reutilized from senescing shoot segments upwards to the apical segments (Tables 1, 2), this proportion was only 0–50% (36% in average) for N and 32–72% (54 in average) for P in our sphagna. Vascular plants inhabiting nutrient-poor bogs and fens reutilize N more efficiently (40–50%) but their P reutilization (50–60%) is roughly the same as in our sphagna (Aerts et al. 1999).

Species and habitat controls on shoot nutrient content

The results separated our species into four groups according to their microhabitat: forest, hummock + lawn, hollow, and aquatic species (Fig 2). The most conspicuous differences in shoot nutrient characteristics were found in *S. cuspidatum* submerged in pools (2005) and occupying wet hollows (2006). Submerged form of this species hosted a rich algal microflora (Lederer and Soukupová 2002), which can significantly increase N input by cyanobacterial N fixation, particularly in the given microhabitat (Granhall and Selander 1973). The smallest interspecific differences in nutrient characteristics of the shoots were found in hummocks and also in hollows which were dominated by species pairs of closely related species belonging to the sections Acutifolia (hummocks) and Cuspidata (hollows). In these habitats, the environmental conditions determined the *Sphagnum* nutrient content, consistently with the results of Malmer (1988) and Malmer et al. (1992).

The environmental conditions of contrasting mire microhabitats are, however, highly specific and enable the selection of species according to their adaptations. Thus, the morphologically and ecophysiologically similar species occupying the same microhabitat use to be also taxonomically related. Lawns were, however, dominated by the unrelated species *S. magellanicum* (sec. Sphagnum) and *S. angustifolium* (sec. Cuspidata). *S. angustifolium*, which prefers wetter microhabitats in boreal mires, had low CEC, like the other species of this section. Thus, CEC in *Sphagnum* do not reflect only the position above the water level. However, the low CEC seemed to affect only the exchangeable K^+, but not the polyvalents. The much lower N content in *S. magellanicum* than in *S. angustifolium* (by about 40%) can result from a lower intracellular uptake rate of NH_4^+ and NO_3^- in *S. magellanicum* (also by about 40%) than in species of the

section Cuspidata (Jauhiainen et al. 1998). We found that N content of *S. magellanicum* in 2005 was similar to that in the hummock and hollow species in both 2005 and 2006. Thus, *S. angustifolium* seems to overplay *S. magellanicum* in the competition for N. This leads to the decrease of the N:P ratio to 19 (based on weight content) in *S. magellanicum* and stronger N limitation, which occurs at the N:P ratio < 30 in sphagna (Bragazza et al. 2004). In the other species, P limitation could take place (N:P = 31–39) accompanied by possible K co-limitation in *S. angustifolium* (cf. Bragazza et al. 2004).

From the long-term view, the enhanced N acquisition by *S. angustifolium* may either represent a mechanism enabling its coexistence with *S. magellanicum*, or may lead up to outcompeting of *S. magellanicum*. *S. magellanicum* has a higher water-holding capacity, which is necessary for surviving of scattered individuals of *S. angustifolium* with a lower water-holding capacity (cf. Rydin 1986). The slower growth of N-limited *S. magellanicum* will result in slower peat accumulation. The water table will rise closer to the moss surface and favour *S. angustifolium*, which will not be further limited by water availability. Probably, this outcompetition of *S. magellanicum* by a species of wetter haitats will further be promoted if the atmospheric N deposition increases, as pointed out by Twenhöven (1992).

The role of cation exchange in *Sphagnum*

Many authors have proposed several roles of the unusually high CEC of *Sphagnum* in its biology. Dainty and Richter (1993) concluded that the main role of the cation exchanger could be proton production to acidify bog water and, thus, suppress vascular plant competitors. The acidity also suppresses microbial decomposers and, moreover, the high CEC can limit the availability of essential cations for the decomposers in peat (Thomas and Pearce 2004); both properties thus participate in bog formation.

Cation-exchange processes of plant tissue are often assumed to affect intracellular ion uptake. Mosses growing on acidic substrates have lower CEC than neutrocline taxa, thus avoiding binding of aluminium, which is highly mobile under acidic conditions (Büscher et al. 1990). Al^{3+} toxicity is unlikely in ombrotrophic *Sphagnum* mosses but due to high CEC, they are limited to acidic conditions to avoid excessive binding (condensation) of Ca^{2+} which arises already from pH > 5 (Clymo 1973; Dainty and Richter 1993). The excessive binding of polyvalents may act as a barrier against exchange and intracellular uptake of other cations (cf., Wells and Brown 1990; Mautsoe and Beckett 1996). Nevertheless, these processes need more experimental evidence.

The bog acidity diminishes the dissociation of the cation exchanger and, therefore, the apparent CEC. Thus, high CEC is also necessary for maintaining efficient retention of cations supplied by rainwater. Aldous (2002b) reported that vascular plants received < 1% of N recently added by wet deposition. Such a partitioning of nutrient resources between mosses (utilizing nutrients from atmospheric deposition) and vascular plants (utilizing nutrients by peat mineralization) gives *Sphagnum* mosses competitive advantage (Malmer et al. 1994) and allows their coexistence.

We expect that the cation exchange enhances the intracellular cation uptake by the following mechanism. Rainwater has a higher pH (4.8–5.1; Table 3) than water in our *Sphagnum* habitats (< 4.2 in pools, Lederer and Soukupová 2002, and most probably close to 3.5 in hummocks, Clymo 1963). During rain, the cations supplied will be immediately exchanged for H^+. This will acidify the solution in moss habitat, but the rainwater itself will have a counteracting effect. After rain, evaporation will concentrate the solution among *Sphagnum* apices. This will again acidify the solution, and cations will be eluted from the cell-wall exchangers and become available for the intracellular uptake. Also, the active H^+ efflux, counterbalancing ion transport into the cell (Raven et al. 1998), will acidify the solution. The active intracellular uptake is, in comparison with the cation exchange, a slow biochemical process (cf. Jauhiainen et al. 1998). Efficient cation retention by cation exchange may represent an important mechanism for temporal extension of mineral nutrient availability for their intracellular uptake in nutrient-limited *Sphagnum* habitats.

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❧

Colourful *Sphagnum* samples collected from a pristine mire, i.e., an open and sunny habitat, and from its drained, i.e., forested and shaded counterpart. The dark colours (crimson, yellow-brown or green-brown) belong to sphagna from the open mire (*S. magellanicum*, *S. papillosum*, *S. fallax* or *S. flexuosum*), while the green-red capitula of *S. magellanicum* and *S. russowii* were collected in the shade. It is surprising that *S. angustifolium* was bright green in both habitats having also the highest photosynthetic capacity while the dark, sun-grown sphagna showed symptoms of light-induced stress.

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

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Abstract

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.

Introduction

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 (cf., 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 (e.g., 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 (cf., e.g., 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, cf. 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.

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.

Materials 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* Ehrh. and *C. rostrata*. The dominant *Sphagnum* mosses *S. fallax* (Klinggr.) Klinggr., *S. flexuosum* Dozy & Molk. and *S. papillosum* H. Lindb. formed an almost continuous carpet. *Sphagnum angustifolium* (C. Jens. ex Russ.) C. Jens. and *S. magellanicum* Brid. 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 m^3 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* L. and *Empetrum nigrum* L., with *Eriophorum vaginatum* L. as the only common graminoid. The moss layer was almost continuous also in the drained part, *Pleurozium schreberi* (Brid.) Mitt., *S. angustifolium*, *S. magellanicum*, and *S. russowii* Warnst. 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 × 10 × 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): i) *losers*, i.e. lawn species that are adapted only to open conditions and disappear following water-level drawdown; ii) *survivors*, i.e. hummock species that are present in the open sites and are able to acclimate to the new conditions as well; and iii) *winners*, i.e. new species that are colonizing the site following water-level drawdown (cf., e.g., Laine et al. 1995). We expected the three species groups to differ in their response to light.

Table 1. The studied species, their sampling sites and response to the persistent water-level drawdown. The bulk density (means ± s.e.) of 10 mm long shoot segments was measured from 5 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

Sample treatment

A week after collection, the moss samples were transported to the University 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 hours) 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 × 2 × 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 (e.g., 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 d.w. 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.

CO_2-exchange measurements

We measured gas exchange with an open system infrared CO_2/H_2O gas analyser (LI-6400, Li-Cor Inc., USA) 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 built-in LED light source LI-6400-02. 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, e.g., 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} (cf., Marschall and Proctor 2004). Hence the expression using the model (equation 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 (FluorCam, Photon System Instruments Ltd., Czech Republic). 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 CADAS 100 spectrophotometer (Bruno Lange, Düsseldorf, Germany). 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; e.g., 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 1.1.

One-way ANOVA, using the general linear models of STATISTICA 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). Two-way 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 4.5 (ter Braak and Šmilauer 2002).

Results

Light response of photosynthesis

Photosynthetic capacity, P_{max}, of the top segments decreased in the order: *S. angustifolium* from the open habitat (O), *S. angustifolium* from the shaded habitat (S), *S. russowii* (S), *P. 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 ($p < 0.05$) 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 $mg_{CO2}\ m^{-2}\ h^{-1}$). *S. 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 (s.e.) $\mu mol\ m^{-2}\ s^{-1}$.

S. 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 ($p = 0.10$).

Table 2. Maximum quantum yield of photosynthesis (α) and light saturation point ($PPFD_{95\%}$) in the top segments of the studied mosses. Means ± s.e. of 5 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

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).

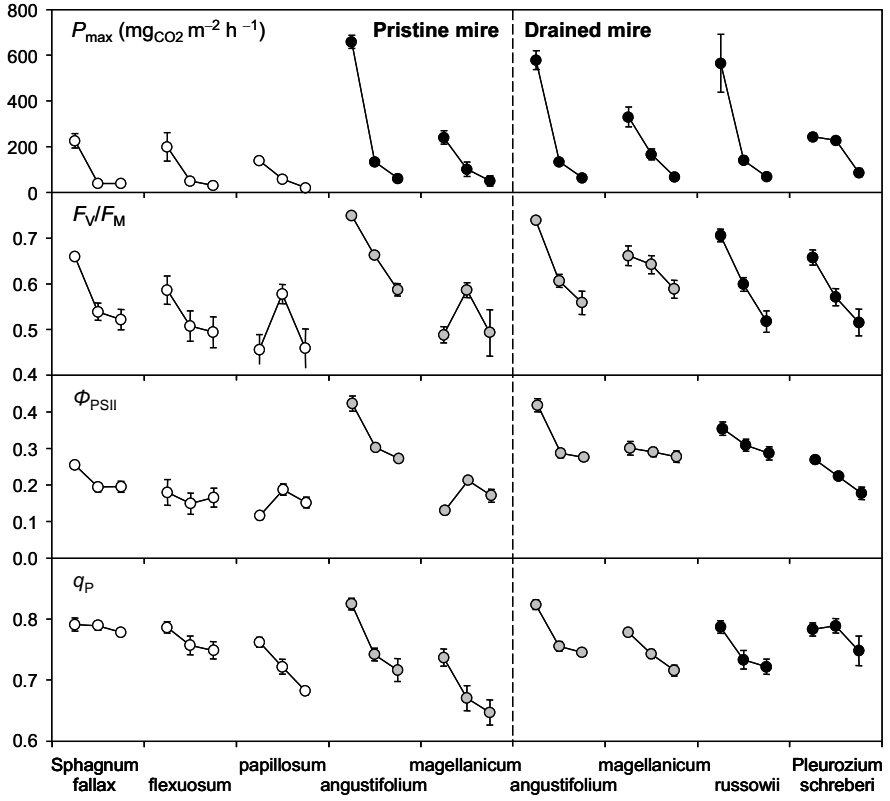

Fig. 1. Maximum rate of photosynthesis (P_{max}) and chlorophyll-fluorescence parameters of the studied mosses. The triplets of connected circles represent the 10-mm shoot segments; the leftmost is the top segment. White, grey and black symbols denote the species groups: losers, survivors and winners, respectively. Actinic light PPFD of 220 µmol m^{-2} s^{-1} was used for measurement of Φ_{PSII} and q_P. Means ± s.e., $n = 5$.

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*.

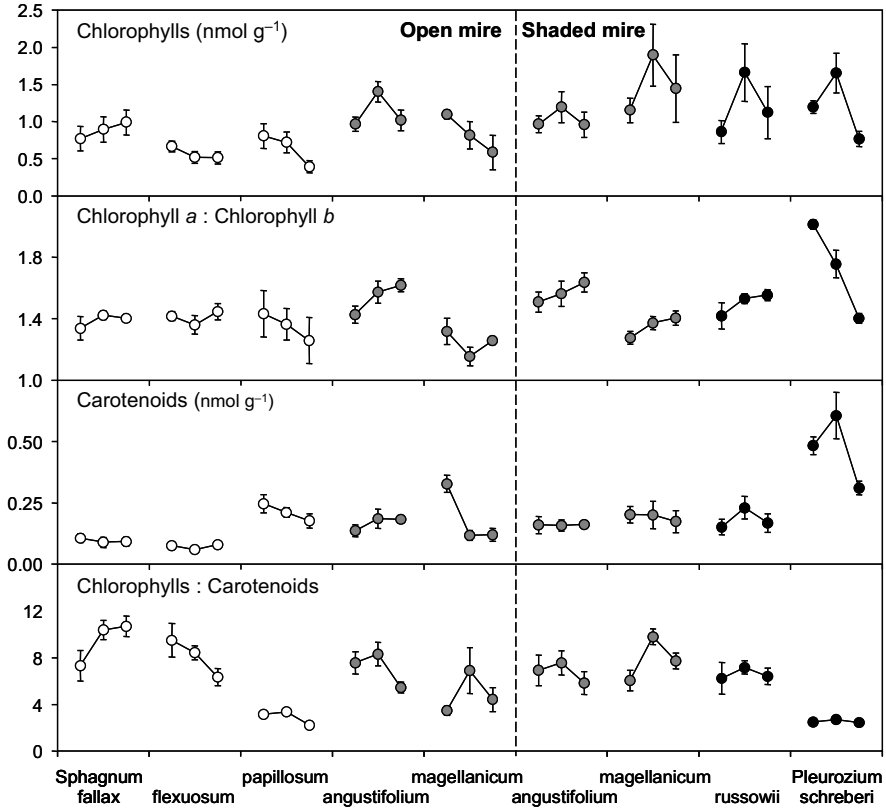

Fig. 2. Chlorophyll and carotenoid parameters of the studied mosses. The triplets of connected circles represent the 10-mm shoot segments; the leftmost is the top segment. White, grey and black symbols denote the species groups: losers, survivors and winners, respectively. Means ± s.e., $n = 5$.

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 (equation 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).

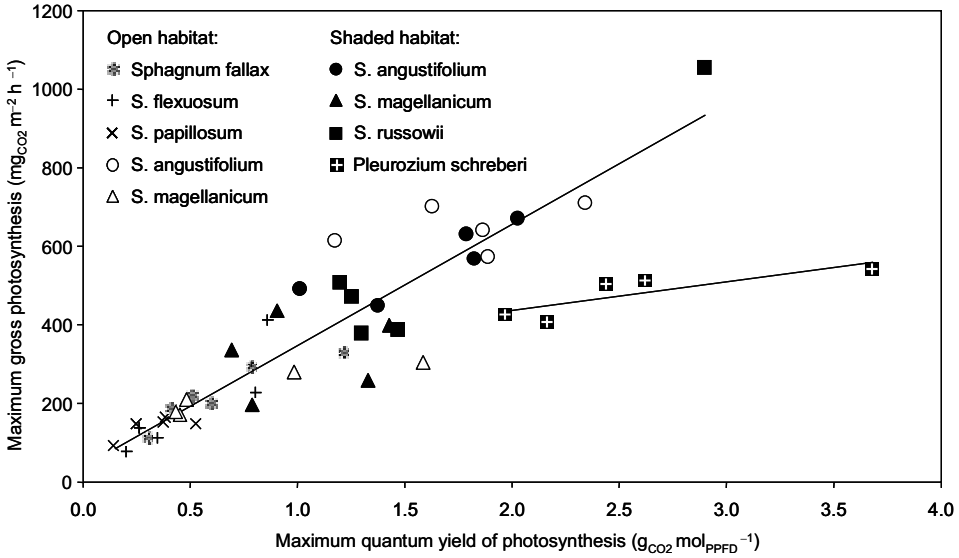

Fig. 3. Relationship between the maximum quantum yield of photosynthesis (α) and light-saturated gross photosynthesis in the top-segments of the studied mosses. Regression model for sphagna: $P_{max} = 329\alpha + 44$ [$r^2 = 0.85$, $n = 41$], and for *Pleurozium*: $P_{max} = 78\alpha + 307$ [$r^2 = 0.70$, $n = 5$].

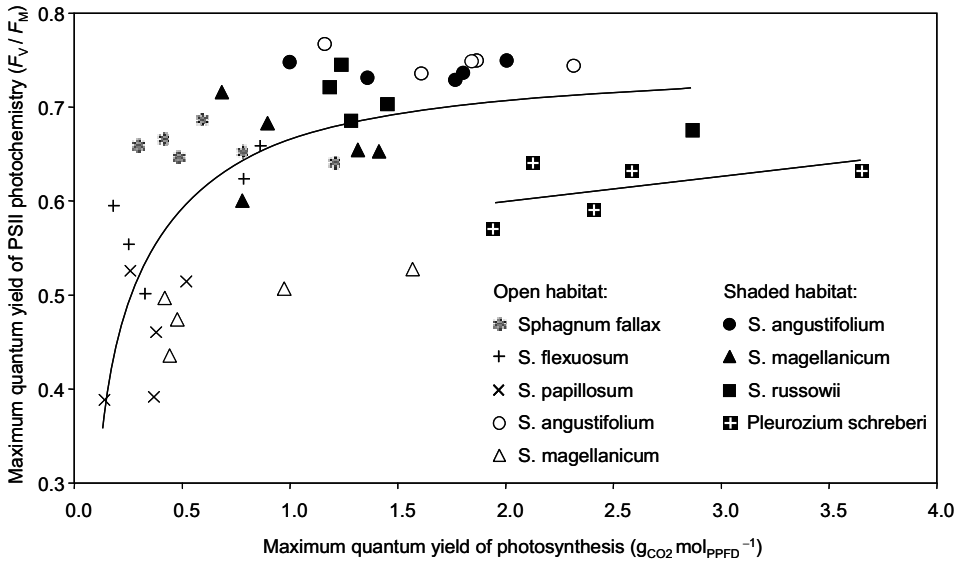

Fig. 4. Relationship between the maximum quantum yield of photosynthesis (α) and maximum quantum yield of photosystem II (F_V/F_M) in the top-segments of the studied mosses.

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 *Pleurozium 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.

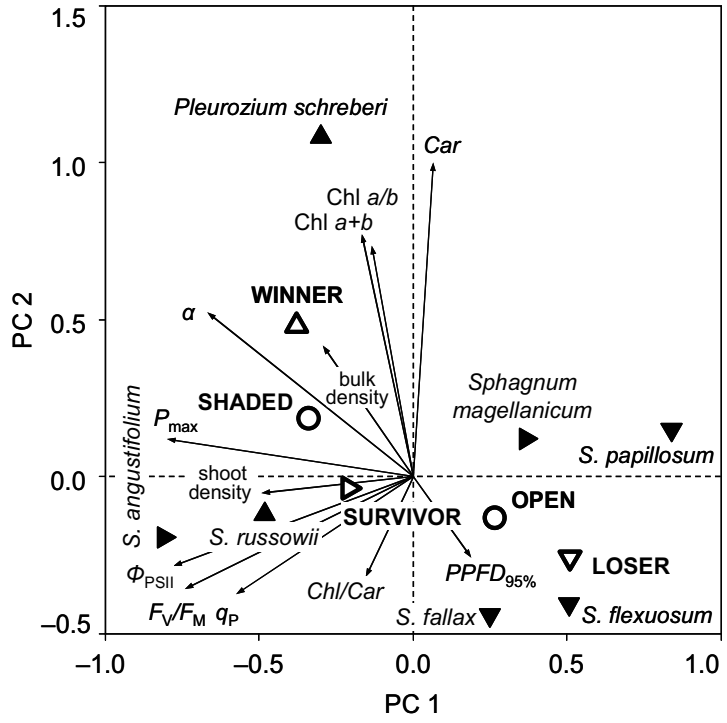

Fig. 5. Ordination diagrams (PCA) displaying correlations among the measured variables of photosynthetic light response (P_{max}, α, $PPFD_{95\%}$), chlorophyll fluorescence (F_V/F_M, Φ_{PSII}, q_P), and pigment content (*Chl a+b*, *Car*) and ratios (*Chl a/b*, *Chl/Car*). $PPFD_{95\%}$ and *Chl/Car* are included as supplementary variables.

The 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 *Pleurozium 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.

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 (cf., e.g., 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 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 (cf., 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 (Marschall and Proctor 2004, Deora and Chaudhary 1991 in Glime 2007). The concept of sun and shade plants , which was developed with and for the leaves of vascular plants (e.g., 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 (e.g., 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 ~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. equation 2). Such large interspecific variability of P_{max} is typical for sphagna occupying contrasting habitats (e.g., 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 (e.g., 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* (e.g., 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 photodamage 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 (e.g., 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 photoprotective 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 photoinhibition (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 *Pleurozium schreberi*.

An unanswered question concerning *Sphagnum 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 (e.g., 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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❧

Conclusions

General summary

Three of the four presented studies are devoted to the adaptations of *Sphagnum* species coexisting along the vertical hummock–hollow gradient, which results in a rich species diversity in ombrotrophic bogs. Species forming elevated microhabitats, generally hummock sphagna, have evolved morphological, production, chemical, physiological and nutritional adaptations enabling them to build and maintain their own microhabitats.

In contrast to the water-saturated hollows and pools, the well-aerated hummocks represent a suitable environment for the activity of microbial decomposers (**Study I**). Therefore the *Sphagnum* species building and inhabiting hummocks have mechanisms that enable them to maintain sufficient peat accumulation. They form dense cushions with high biomass resulting in a similar net production as that in hollows and pools. The chemical composition makes the litter of hummock-forming sphagna more resistant to decomposition than that of the species occupying hollows and pools (**Study I**). Although the shoots of hummock species are better desiccation avoiders having a greater water-retention capacity, they possess also a better inherent tolerance of desiccation (**Study II**). This adaptation may help them to survive unexpected periods of drought in exposed hummocks. Since the mineral nutrition is restricted exclusively to aerial deposition in hummocks, hummock sphagna have developed an efficient mechanism of nutrient retention based on an about doubled content of cation-exchanging sites on their cell wall surfaces in comparison with species of wet microhabitats (**Study III**). So, their intracellular nutrient contents do not differ substantially from those in other mosses inhabiting mineral soils. Moreover, the high content of these carboxylic exchangers may explain the poor litter quality in hummock sphagna (**Study I**).

On the larger scale of the entire mire, the ecosystem engineering activity of *Sphagnum* species often leads to the exclusion of tree cover. The resulting full sun irradiance induces stress and damage to the photosynthetic apparatus in most of the *Sphagnum* species of the open, pristine habitat. But it is not so in the shaded forested mire parts, which were drained in the past (**Study IV**). Thus, the *Sphagnum* dominants of open habitats seem to tolerate the excessive irradiance

stress, while sphagna of shaded mire habitats appear to be better competitors capable of utilizing their photosynthetic capacity to maximize growth and production.

The tolerance and avoidance of environmental stresses represent ecophysiological adaptations as the essential consequence of the *Sphagnum*-mediated ecosystem changes. The studies presented here show how the *Sphagnum* species dominating open mires, particularly in hummocks, cope with and benefit from the severe conditions in terms of water and nutrient deficiency but under excessive irradiance.

Perspectives

All the studies presented raise further questions for future research. What are the chemical compounds responsible for the low litter quality in hummock species and sphagna at all? There is an indication that the low litter quality can be linked with the high cation exchange capacity, important for efficient retention of air-born nutrients. But what is the role of cation exchange in the nutrient uptake into the protoplast? This seemingly elementary process has never been exactly established. Its understanding may elucidate also the toxicity of excessive mineral nutrients in species from ombrotrophic and oligotrophic habitats or, e.g., the calcium tolerance of certain *Sphagnum* species in fens, one of the most rapidly disappearing habitats in Europe.

The results of the previous studies on desiccation tolerance in *Sphagnum* species are hardly interpretable because of the unknown or heterogeneous history of the samples studied, particularly in terms of a possible drought hardening of some of the species compared. We compared mosses adapted to permanent full hydration but what is the potential for drought acclimation in species from contrasting habitats? Since it is rather impossible to precisely control or even measure the water status of the intact moss, a laboratory experiment employing, e.g., polyethylene glycol solution may represent a well-handled approach exactly controlling the intensity of water stress.

The light-induced damage to the photosynthetic apparatus may result from the impact of many other stress factors such as the nutrient, temperature or CO_2 limitations in open mires. A detailed experimental study is needed to clarify this phenomenon with possible consequences for oncoming or expected both local and global environmental changes.

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