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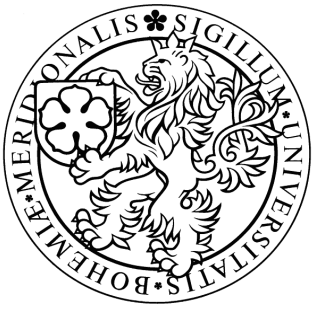

Ecophysiological adaptations of coexisting *Sphagnum* mosses

PhD. thesis

(shortened electronic version)

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Annotation

Hájek T. 2008. *Ecophysiological adaptations of coexisting* Sphagnum *mosses*. PhD. thesis. University of South Bohemia, Faculty of Science, České Budějovice, Czech Republic, 98 pp.

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.

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Tomáš Hájek

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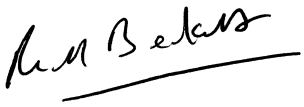
Author contribution statement

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:

Lubomír Adamec



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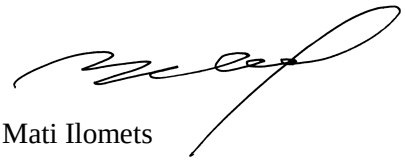

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I gratefully acknowledge the personal support by the Department of Ecosystems Biology and Department of Plant Physiology of the Faculty of Science, University of South Bohemia in České Budějovice and the Department of Functional Ecology of the Institute of Botany, Academy of Sciences of the Czech Republic at Třeboň. My sincere thanks are due to Dr. Jan Květ, supervisor of my PhD. thesis, and to my co-authors for their patience with my writing. Special thanks are due to my family and my colleagues and friends for making my student's life nicer and easier.

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

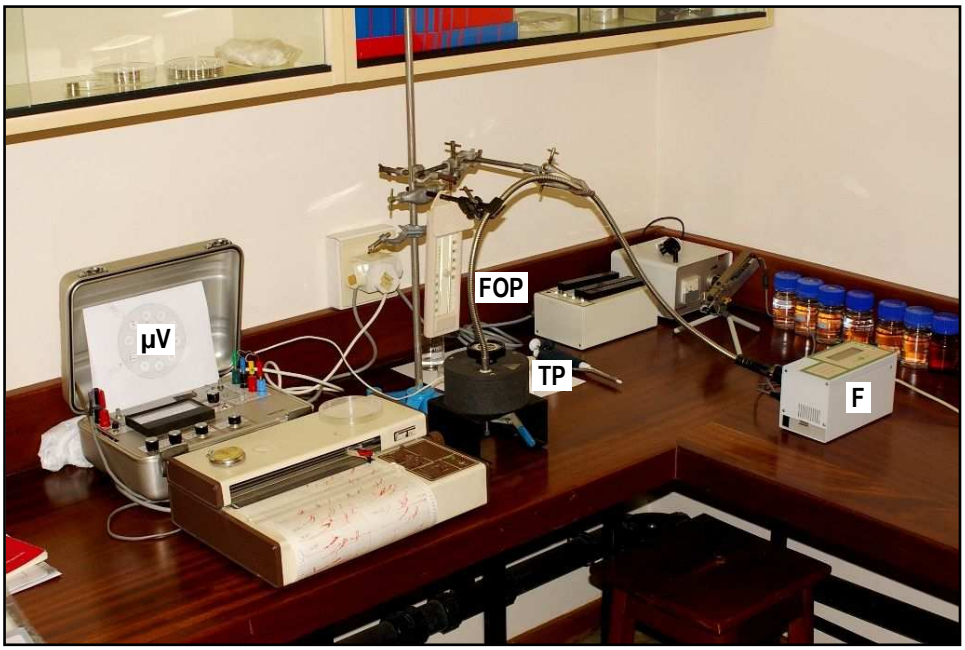
I evaluated the production and decomposition characteristics of six dominant *Sphagnum* species in their natural microhabitats distributed along the gradient of water table in an open ombrotrophic bog. The growth in length was much faster in pools and hollows than in hummocks, but the resulting annual 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.

Vliv stanoviště a druhu na produkci a rozklad rašeliníků na vrchovišti

Tomáš Hájek (podáno k opublikování)

Shrnutí

Měřil jsem produkční a dekompoziční charakteristiky šesti dominantních druhů rašeliníků v jejich přirozených mikrostanovištích, rozložených podél gradientu hladiny podzemní vody na bezlesém ombrotrofním vrchovišti. Délkový přírůstek rašeliníků bych mnohem větší v jezírkách a šlencích než v bultech, ale výsledná roční produkce byla u všech mikrobiotopů podobná, protože bultové druhy měly větší hustotu lodyžek, a tudíž i větší biomasu. Ačkoli bulty utvářely mnohem vhodnější prostředí pro dekompozici než jezírka a šlenky, rašeliníky se v bultech rozkládaly pomaleji díky mnohem menší kvalitě opadu. Bultové druhy jsou tak vybaveny oběma základními mechanismy, které se podílejí na udržení bultů nad šlenky – mají dostatečnou rychlost produkce a omezenou rychlost dekompozice. Tyto mechanismy zdůrazňují roli rašeliníků coby autogenních ekosystémových inženýrů (edifikátorů), které řídí i rozrůzňování mikrostanovišť na strukturovaných rašeliništích.



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 five *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 (ε = 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.

Vliv vodního režimu rašeliníků na jejich vysýchání a následnou regeneraci

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

Spoluautorský podíl T. Hájka na publikaci: 85 %

Shrnutí

- *Úvod a cíle* Měřili jsme základní parametry vodního režimu rašeliníků. Poté jsme sledovali vztah těchto parametrů k fotosyntetické reakci na vysýchání a k ekologii těchto mechů.
- *Metody* Ze změřené závislosti vodního potenciálu na obsahu vody jsme vypočítali parametry vodního režimu pěti druhů rašeliníků (charakteristických mechů vlhkých stanovišť) a *Atrichum androgynum* (typického mezofytního mechu). Metodou fluorescence chlorofylu jsme sledovali fotosyntetické vlastnosti při vysýchání.
- *Hlavní výsledky* Než buňky začaly během vysýchání ztrácet turgor, bultové druhy rašeliníků *S. fuscum* a *S. magellanicum* ztratily více vody, než rašeliníky obývající méně exponovaná stanoviště (průměrně 73 % v porovnání s 56 %). Osmotické potenciály byly při plném turgoru u všech druhů podobné (průměrně –1.1 MPa). Bultové rašeliníky měly výrazně pevnější buněčné stěny než druhy vlhkých stanovišť (ε = 3.55 v porovnání s 1.93 MPa). Proto jejich živé buňky ztratily turgor při vyšším relativním obsahu vody (RWC) a méně záporném osmotickém potenciálu (–2.28 v porovnání s –3.00 MPa) než u druhů vlhkých mikrostanovišť (0.61 v porovnání s 0.46). Parametr Φ_{PSII} začal klesat během vysýchání dříve u bultových druhů (při RWC 0.65 v porovnání s 0.44); F_v/F_m se choval podobně. V porovnání s ostatními druhy, bultové rašeliníky, vysušené při –20 MPa nebo –40 MPa, ožívaly po ovlhčení lépe. Druh *A. androgynum* reagoval na vysušení podobně jako bultové rašeliníky, což naznačuje, že jejich tolerance k vysýchání může mít podobnou fyziologickou podstatu.
- *Závěry* Za předpokladu stejné rychlosti vysýchání, větší vodní retenční kapacita umožňuje bultovým rašeliníkům udržet metabolizmus po delší dobu než ostatní druhy. To můžeme považovat za způsob, kterým lze vyschnutí předcházet. Bultové druhy však dokáží po ovlhčení regenerovat rychleji, což napovídá na jejich lepší toleranci k vysušení. Oba tyto mechanismy jim tak mohou pomoci přežít v bultech vystavených vysýchání. Naopak druhy obývající vlhká stanoviště postrádají tak účinné prostředky předcházení a tolerance k vysýchání. Avšak jejich mechanismy pro uchování turgoru, jako jsou pružnější buněčné stěny, jim umožňují udržet metabolizmus déle, než obsah vody poklesne k bodu ztráty turgoru.

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

Hájek T. & Adamec L. (*Ecological Research*,
DOI: 10.1007/s11284-008-0506-0)

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.

Hospodaření konkurujících si rašeliníků s minerálními živinami

Hájek T. & Adamec L. (*Ecological Research*,
DOI: 10.1007/s11284-008-0506-0)

Spoluautorský podíl T. Hájka na publikaci: 70 %

Shrnutí

Vrchovištní vegetace, hojně zastoupená rašeliníky, je co do příjmu minerálních živin závislá pouze na atmosférickém spadu. Studovali jsme, jak jsou minerální živiny rozmístěny mezi vněbuněčnou (iontově vyměnitelnou) a vnitrobuněčnou složku a podél vertikálního fyziologického gradientu stáří stélky u sedmi druhů rašeliníků, které obývají odlišná vrchovištní mikrostanoviště. Zatímco obsah vyměnitelných kationtů klesal obecně v pořadí $Ca^{2+} \geq K^{+}$, Na^{+}, $Mg^{2+} > Al^{3+} > NH_4^{+}$, vnitrobuněčný obsah prvků klesal v pořadí N > K > Na, Mg, P, Ca, Al. Vápník se vyskytoval především ve vyměnitelné formě, zatímco Mg, Na a zejména K, Al a N uvnitř buněk. Bultové druhy s větší kationtovou výměnnou kapacitou (CEC) hromadily více vyměnitelného Ca^{2+}, zatímco šlenkové druhy s menší CEC hromadily více Na^{+}, zejména v odumřelých částech stélky. Vnitrobuněčný obsah N a P, ale nikoli kovových prvků, byl obecně menší v odumřelých částech stélky, což napovídá na možnost reutilizace N a P z odumírajících stélek. Největší variabilita v obsahu a rozložení živin byla mezi druhy odlišných mikrostanovišť. Největší variabilita uvnitř mikrostanovišť byla mezi nepodobnými druhy *S. angustifolium* a *S. magellanicum*. Druh *S. magellanicum* zde měl asi o 40% menší vnitrobuněčný obsah N než ostatní druhy, včetně tohoto druhu rostoucího samostatně. To je příznakem nerovnoměrné konkurence o N, která může vést až ke konkurenčnímu vyloučení *S. magellanicum* ze smíšených porostů. Předpokládáme, že účinná kationtová výměna umožňuje porostu rašeliníku okamžitě zadržet živiny ve formě kationtů obsažené ve srážkové vodě. To může být významný způsob, jak prodloužit dobu, po kterou jsou minerální živiny dostupné pro pomalý vnitrobuněčný příjem.

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?

Hájek T., Tuittila E.-S., Ilomets M. & Laiho R. (*Oikos*, DOI: 10.1111/j.2008.0030-1299.16528.x)

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.

Odpověď rašeliništních mechů na ozářenost – – klíč k přežití po snížení hladiny vody?

Hájek T., Tuittila E.-S., Ilomets M. & Laiho R. (*Oikos*, DOI: 10.1111/j.2008.0030-1299.16528.x)

Spoluautorský podíl T. Hájka na publikaci: 60 %

Shrnutí

Mechy hrají na rašeliništích významnou roli ekosystémových inženýrů. Člověk může jejich přítomnost přímo nebo nepřímo ohrozit vysoušením, které pak vede k zástinu a nárůstu pokryvnosti konkurujících dřevin. Některé druhy se pak měnícímu se prostředí dokáží přizpůsobit, zatímco jiné ustoupí novým kolonizátorům. V zástinu může být aklimace a adaptace na nízkou ozářenost vítěznou strategií pro přežití. U mechů z otevřeného rašeliniště a jeho zastíněného, tedy odvodněného a zalesněného protějšku jsme studovali odpověď fotosyntézy na ozářenost a obsahy fotosyntetických pigmentů. Oproti našemu očekáván měly rašeliníky, které obývaly pouze otevřené stanoviště, menší fotosyntetickou kapacitu a maximální kvantový výtěžek fotosyntézy než druhy rostoucí ve stínu. Výsledky fluorescence chlorofylu naznačují, že za malou fotosyntetickou výkonnost rašeliníků z otevřeného stanoviště je zodpovědné fotoinhibiční poškození fotosystému II; mechy tak nedokázaly účinně využít ozářenost jakékoli intenzity. Jedinou adaptací k nízké ozářenosti, kterou měly rašeliníky v zastíněném stanovišti, byl vyšší obsah chlorofylu. V porovnání s rašeliníky dosahovala fotosyntéza *Pleurozium schreberi* světelného nasycení při poloviční hodnotě ozářenosti. Chybějící účinná ochrana proti nadměrné ozářenosti nebo opravný mechanismus po poškození může omezovat úspěch těchto druhů v otevřeném stanovišti. Rašeliníky převládající na otevřeném nenarušeném rašeliništi se tak jeví jako druhy tolerující stres, zatímco druhy typické pro zastíněné odvodněné rašeliniště dokáží maximalizovat svůj růst a produkci, aby konkurenčně obstály v prostředí, které není stresující co do intenzity ozářenosti a vysýchání.

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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