Chapter 13

Physiological Ecology of Peatland Bryophytes

Tomáš Hájek*
Institute of Botany, Academy of Sciences of the Czech Republic,
Dukelská 135, 379 82 Třeboň, Czech Republic

Faculty of Science, University of South Bohemia, Branišovská 31,
370 05 České Budějovice, Czech Republic

Summary 233
I. Introduction 234
II. Specific Adaptations of Peatland Bryophytes 234
    A. Microtopography Gradients 234
    B. Water and CO_2 Economy 235
    C. Desiccation 240
III. Specific Properties of Peatlands 241
    A. Peat as Carbon Source for Photosynthesis 241
    B. CO_2 Availability in Rich Fens 242
    C. Life in Water-Saturated and Sunny Environment 242
    D. Mineral Nutrition 244
IV. Seasonal Variability of Photosynthesis and Respiration 245
V. Photosynthesis and Production in a Warmer and Richer World 246
VI. Suggestions for Further Research 248
Acknowledgements 248
References 248

Summary

Bryophytes, notably mosses of the genus *Sphagnum*, are significant and essential primary producers in peatlands. Peatland bryophytes face specific physical conditions; they are exposed to direct sunlight, but due to their permanent hydration they do not escape by drying as typical xeric bryophytes of open habitats. Being desiccation avoiders they are actually sensitive to drought. During photosynthesis, hydration increases the diffusion resistance to CO_2, which can be supplied also from respiration in the underlying peat. The distance to the water table affects the degree of hydration, but also influences nutrient availability as mineral nutrients can be carried in capillary water. Consequently, gradients of nutrient and water availability are related in peatlands and their variation in addition to light maintains bryophyte species diversity in peatlands. Habitats with low stress intensity, typically forested peatlands and wet microhabitats of open bogs and fens, host mosses with competitive life strategies, characterized by high rates of photosynthesis, growth and production. In contrast,

---

*Author for correspondence, e-mail: hajek@botany.cas.cz

D.T. Hanson and S.K. Rice (eds.), Photosynthesis in Bryophytes and Early Land Plants, Advances in Photosynthesis and Respiration 37, pp. 233–252, DOI 10.1007/978-94-007-6988-5_13,

mosses inhabiting sun-exposed, nutrient poor microhabitats, typically hummocks, must cope with low water availability and photodamage. Their stress-tolerance/avoidance strategy is reflected by slow photosynthetic and growth rates, and allocation to water holding tissues.

In this chapter, I review the effects of ecologically relevant (stress) factors affecting photosynthesis and growth, especially in *Sphagnum*. Potential consequences of global climate change are also discussed. I mention how the non-uniform experimental conditions used in photosynthetic gas exchange measurements may affect the diffusion resistance to CO_2 and consequent estimates of photosynthesis and evaporation. Suggestions for further research are proposed.

I. Introduction

This chapter deals with bryophyte ecophysiology in temperate to sub-arctic peatlands. These habitats are characterized by the abundance of mosses, which are often the key primary producers. Their biomass undergoes very slow decomposition and thus accumulates as peat. The dominance of mosses and peat accumulation are conditioned by high water level near the surface. If groundwater feeds the peatland surface, minerotrophic fen vegetation develops. The concentration of dissolved ions, particularly calcium and bicarbonate greatly determines the vegetation composition, classifying fens from poor up to extremely rich. If rainwater is the exclusive source of nutrients, namely where the accumulated peat isolates the surface from groundwater, ombrotrophic bog vegetation prevails. The high soil water level in fens and bogs prevents development of dense tree cover so living (peat accumulating) peatlands are often sunny habitats. For bryophytes that dominate the peatland surface, the excess or shortage of water, nutrients and/or light are the main environmental factors limiting photosynthetic light harvesting, CO_2 fixation, growth and production. These limiting factors drive differentiation of ecological niches and consequently bryophyte species diversity in peatlands (Rydin and Jeglum 2006; Vitt and Wieder 2009).

Mosses of the genus *Sphagnum* (peat mosses, sphagna) are the most characteristic representatives of peatlands. Due to their ecological success in these ecosystems, which is based on their unique morphology, physiology and chemistry, they are likely the most successful plant genus in the world, at least in terms of biomass (Clymo and Hayward 1982). It is then not surprising that sphagna have been the subject of intensive research, making them one of the most investigated bryophyte genera. Therefore, the majority of this chapter is devoted to *Sphagnum* ecophysiology.

II. Specific Adaptations of Peatland Bryophytes

A. Microtopography Gradients

Differences in water availability and its chemical composition lead to differentiation not only among bogs and various types of fens, but they also represent the key ecological factors characterizing within-mire differentiation of surface microforms, such as bog pools, wet hollows and carpets, mesophytic lawns, and elevated ombrotrophic hummocks. Species' ecological niches have differentiated along this so-called hummock–hollow gradient. Hummock-forming sphagna usually belong to the section Acutifolia while typical hollow species belong to the section

---

Abbreviations: A – photosynthetic CO_2 assimilation (rate); E – evaporation rate; F_v/F_m – maximum quantum yield of PSII photochemistry; NPQ – non-photochemical quenching of chlorophyll fluorescence; QY PSII – quantum yield of PSII photochemistry; PPFD – photosynthetic photon flux density; PSII – photosystem II; RETR – relative electron transport rate; RH – relative air humidity; WC – water content

Cuspidata. There are general morphological, ecological and physiological differences between sections (Rydin 1993; Rydin et al. 2006). *Sphagnum* species dominating in hollows have a capacity for higher rates of photosynthesis, growth and production. Hollow species, if not limited by drought, may utilize their greater photosynthetic capacity for growth and competition, taking advantage of the relatively rich nutrients and low acidity. Moreover, Cuspidata species also have greater potential to assimilate experimental additions of nitrogen (N) and CO_2 for biomass production (Jauhiainen et al. 1998a, b). In hummocks, however, individual shoots must cooperate in water retention by forming tight cushions and by reducing surface roughness to limit evaporation (Clymo 1973). Individuals that are capable of quicker growth cannot overgrow their neighbors since their growth is regulated by desiccation. This phenomenon is best seen where individual shoots of species from the section Cuspidata penetrate between hummock sphagna, supported by their high capacity of water retention and conduction. They may protrude above the hummock surface only during wet periods but they desiccate quickly during drier periods (Rydin 1985; Rydin and McDonald 1985; Robroek et al. 2007a).

Similarly, Rice et al. (2008) described a principal trade-off between sphagna with higher and lower metabolic cost. High metabolic cost, represented particularly by high investment in water holding capacity, such as in hummock sphagna, is characteristic of species tolerating environmental stress. On the contrary, species with metabolically inexpensive tissue experiencing low stress, such as those in hollows, are capable of efficient photosynthetic and growth rates, having also greater vertical distribution of photosynthesis by allowing deeper light penetration. In addition, Laine et al. (2011) observed typical ruderal life strategy (*sensu* Grime 1977) in *S. fimbriatum* (section Acutifolia). This pioneer species with low competitive but great dispersion potential formed low hummocks on shallow peat in successionally young mires, which are characterized by high water level and nutrient availability. Photosynthetic, growth and production rates of *S. fimbriatum* even exceeded those in hollow species in successionally older mires.

B. Water and CO_2 Economy

Sphagna have a unique competitive strategy among bryophytes. Due to their large capacity to store external capillary water, *Sphagnum* shoots remain photosynthetically active for longer than shoots of other bryophyte groups, particularly in sun-exposed habitats. As a typical trade-off, this competitive advantage brings costs based in great resistance for CO_2 diffusion due to thick water films of external water. Since the C_3 type of moss photosynthesis is not equipped with a CO_2 concentrating mechanism (Bain and Proctor 1980; Raven 1991), the high CO_2 diffusion resistance limits CO_2 fixation by the Calvin–Benson cycle, increasing the need to utilize excess excitation energy.

Sphagnum leaves are unistratose, consisting of a single cell layer. The cells are organized into a mesh of living chlorophyllous cells interposed by larger empty hyaline cells. The hyaline cells form from 60 % (in aquatic habitats) up to 95 % of the leaf volume (Rice 1995; Rice et al. 2008) and are normally filled by capillary water keeping the adjacent chlorophyllous cells turgid. The leaves overlap along the central branch so the spaces between the leaves and branches form another fraction of capillary water. The developing branches in the shoot apex compose the capitulum, which is the growing shoot segment and also the main shoot part exposed to sun and free atmosphere. Below capitula, branches elongate and the leaves senesce if they become too shaded by capitula above; this usually happens at the depth of 1–10 cm below the capitulum surface, depending on the capitulum and shoot bulk density (leaf area index) but it is common that 99.9 % of light is absorbed within top 3 cm (Rice et al. 2008; Robroek et al. 2009; see also Chap. 9).

It is evident that the organization of the *Sphagnum* photosynthetic tissue differs from leaves of tracheophytes, which are arranged above the ground often exposed to turbulent air that reduces the laminar boundary layer and thus the diffusion resistance for CO_2; moreover air-filled leaf mesophyll allows quick CO_2 diffusion to photosynthesizing cells. In contrast, the ground moss cover or its individual leaves are sunk within a thick laminar boundary layer and the water films further reduce CO_2 diffusion by factor of 10^4. As a result, CO_2 availability limits the rate of photosynthetic assimilation of CO_2 (A) in hydrated mosses, particularly sphagna. The CO_2 limitation by diffusive resistance through water films in *Sphagnum* is evidenced by the existence of distinct optimum of water content (WC) for A (see below), by lack of this optimum after sufficient increase of CO_2 availability (Silvola 1990; Jauhiainen and Silvola 1999), and by ^{13}C-enrichment of biomass in water-saturated sphagna caused by low discrimination against $^{13}CO_2$ by diffusion towards Rubisco (Williams and Flanagan 1996; Loisel et al. 2009).

The rate of A is therefore constrained by shoot WC from both directions: too low WC is accompanied by water loss from hyaline and chlorophyllous cells, turgor loss and inhibition of cellular biochemistry, while excessive water reduces carboxylation in the Calvin–Benson cycle by CO_2 shortage. This indicates that the optimum shoot WC is relatively narrow, representing a state between low and high WC. Fully turgid *Sphagnum* capitula free of capillary water contain about 1.7–2.4 g H_2O g^{-1} of shoot dry mass, depending on the species (Hájek and Beckett 2008), which is the theoretical but unreachable optimum WC for CO_2 diffusion and thus photosynthesis. Published values of optimum WC measured either in the field or laboratory conditions lie in a wide range between 5 and 30 g g^{-1} (Table 13.1).

There are few data on the optimum WC for photosynthesis of non-*Sphagnum* peatland mosses, but the general relationship described above is valid for all poikilohydric plants. Among bryophytes, Polytrichaceae have low water holding capacity that corresponds with their low optimum WC for photosynthesis (below 5 g g^{-1}; Skre and Oechel 1981; Silvola 1991). Their leaves possess lamellae protected by surface waxes from filling the interlamellar spaces with water; lamellae enhance CO_2 exchange by a factor of 6 or more (Proctor 2005). Polytrichaceae may afford maintaining low WC since they have efficient internal conducting tissue (Skre et al. 1983a) and tolerance to desiccation (Proctor et al. 2007a). Therefore they may replace sphagna on high hummocks (*Polytrichum strictum*) or they may form the uppermost moss layer above carpet of *Sphagnum* capitula in forested mires (*P. commune*). Optimum WC of feather mosses in forested mires is clearly lower than that for sphagna, ranging between 3–4 and 6–7 g g^{-1} for *Hylocomium splendens* and *Pleurozium schreberi* respectively (Skre and Oechel 1981; Silvola 1991). On the other hand, variable optimum WC was reported in semiaquatic brown mosses in fens: 16 g g^{-1} in *Calliergon giganteum* and about 5 g g^{-1} in *C. sarmentosum* (*Warnstorfia sarmentosa*) (Ueno and Kanda 2006; Oechel and Collins 1976, respectively).

Most of the variability in the optimum WC for photosynthesis between (and partly also within) the published works originates from incomparable measurement conditions. In *Sphagnum*, capitula usually represent the majority of sample biomass used in CO_2 assimilation measurements. As in the field, the water evaporates predominantly from the capitulum surface so the uppermost leaves lose the capillary water first, being replaced by air. Capitula become relatively well supplied by CO_2 but the chlorophyllous cells have already lost some water. In the field, the moss carpet evaporates water relatively slowly and the lost water is continuously replenished by capillary transport from the deeper water-saturated peat. In a ventilated gas exchange chamber, isolated apical stem segments may dry relatively rapidly, missing the continuous water replenishment. The uppermost layer may dry and become photosynthetically

Table 13.1. Optimum shoot water content (WC) for photosynthetic CO_2 assimilation measured for various Sphagnum species under close-to-ambient CO_2 concentration using various gas-exchange apparatuses.

Water content ($g_{H_2O}\ g_{dm}^{-1}$)	*Sphagnum* species	References
6–10	*S. angustifolium*	Murray et al. (1989)
10–12	*S. angustifolium*	Silvola and Aaltonen (1984)
12–16	*S. angustifolium*	T. Hájek, unpublished (in part Hájek et al. 2009)
7	*S. balticum*	Rydin and McDonald (1985)
9	*S. balticum*	Schipperges and Rydin (1998)
7	*S. capillifolium*	Titus et al. (1983)
9	*S. capillifolium*	Titus and Wagner (1984)
7–10	*S. capillifolium*	Silvola (1991)
≤15	*S. capillifolium*	Gerdol et al. (1996)
11–13	*S. centrale*	Silvola (1991)
14–25	*S. cristatum*	Maseyk et al. (1999)
≥30	*S. cuspidatum*	Robroek et al. (2009)
7–8	*S. cuspidatum*	Schipperges and Rydin (1998)
5	*S. fallax*	Titus et al. (1983)
7	*S. fallax*	Titus and Wagner (1984)
10–17	*S. fallax*	T. Hájek, unpublished (in part Hájek et al. 2009)
≤15	*S. fallax*	Gerdol et al. (1996)
14–22	*S. flexuosum*	T. Hájek, unpublished (in part Hájek et al. 2009)
6	*S. fuscum*	Silvola (1990)
≥7	*S. fuscum*	Rydin and McDonald (1985)
7–9	*S. fuscum*	Silvola and Aaltonen (1984)
8	*S. fuscum*	Schipperges and Rydin (1998)
8–13	*S. fuscum*	Jauhiainen and Silvola (1999)
5–7	*S. magellanicum*	T. Hájek, unpublished (in part Fig. 13.1)
9	*S. magellanicum*	Schipperges and Rydin (1998)
11–13	*S. magellanicum*	Silvola (1991)
12–16	*S. magellanicum*	T. Hájek, unpublished (in part Hájek et al. 2009)
13–25	*S. magellanicum*	T. Hájek, unpublished (in part Hájek et al. 2009)
≤15	*S. magellanicum*	Gerdol et al. (1996)
24–30	*S. magellanicum*	Robroek et al. (2009)
27	*S. magellanicum*	Rudolph (1968)
6–12	*S. papillosum*	T. Hájek, unpublished (in part Fig. 13.2)
8–13	*S. papillosum*	Schipperges and Rydin (1998)
10–20	*S. papillosum*	T. Hájek, unpublished (in part Hájek et al. 2009)
12–21	*S. rubellum*	Robroek et al. (2009)
10–13	*S. russowii*	T. Hájek, unpublished (in part Hájek et al. 2009)
6–8	*S. squarrosum*	Murray et al. (1989)
6–9	*S. subsecundum*	Skre and Oechel (1981)
8	*S. tenellum*	Rydin and McDonald (1985)
7–8	*S. teres*	Van Gaalen et al. (2007)
6–8	*S.* sec. Acutifolia	Williams and Flanagan (1996)

The within-reference variability can be usually attributed to species differences while the contrasting WC optima among references represent various gas exchange set-ups. As a result, measured optimum WC, for example, in *S. magellanicum* may vary as much as between 5 and 30 g g^{-1}

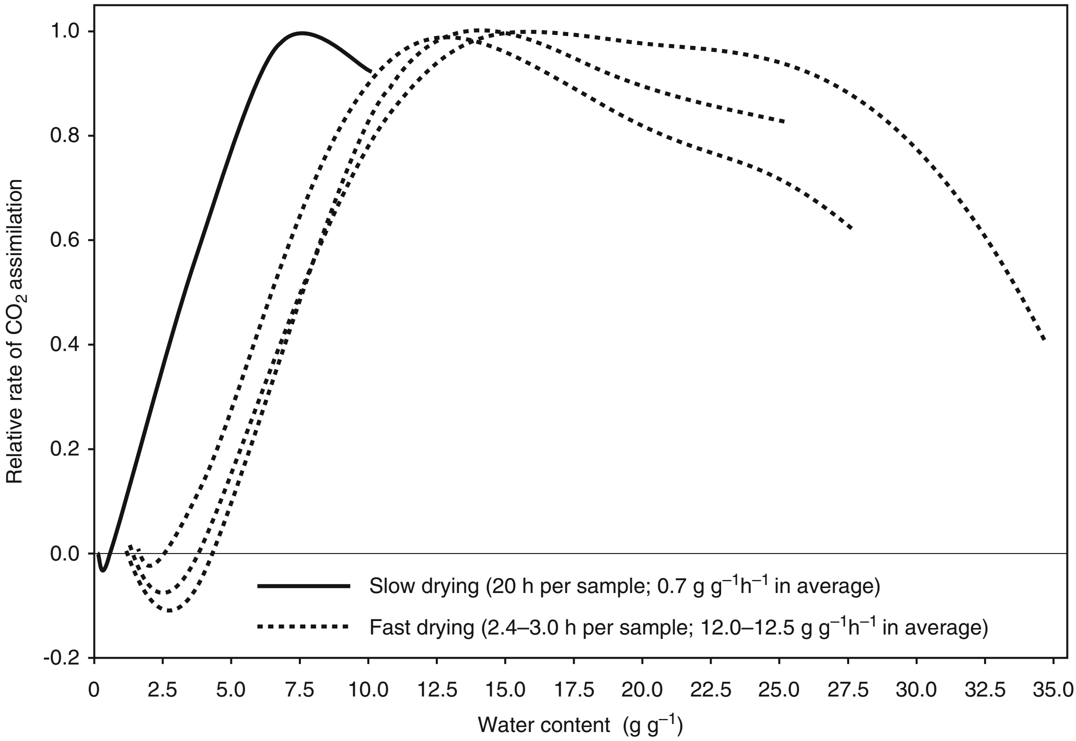

Fig. 13.1. Photosynthetic CO_2 assimilation rate of *Sphagnum magellanicum* capitula (10 mm apical shoot segments) in relation to capitulum water content. Photosynthetic and evaporation rates were continuously measured under saturation irradiance by infra-red gas analyzers (GFS-3000, Heinz Walz GmbH, Germany for low drying and LI-6400, Li-Cor Inc., USA for fast drying) while the samples were desiccated inside the gas-exchange chamber. The water content was then reconstructed using the evaporation data. The example demonstrates that the instrumental set-up may greatly affect the desiccation rate and therefore also the optimum and compensation water content for photosynthesis.

inefficient while the leaves deeper inside the capitula are still water saturated. Experimental settings used for measurements of *A*, such as airflow, speed of the internal chamber fan, or incoming relative air humidity (RH) always affect the heterogeneity in capitulum WC via interlinked factors of evaporation rate (*E*) and the thickness of boundary layer. Anatomical and morphological differences between species/populations from leaf up to the carpet organization level may be obscured by the variation in diffusion resistance due to capillary water (Rice and Giles 1996) or experimental conditions in gas exchange chambers, as also indicated by comparison of species or ecological groups across the literature (Table 13.1). For instance, relatively higher and wide optimum WC of 10–20 g g^{-1} was found when photosynthesis was measured under low RH of incoming air and efficient air mixing inside the chamber (Fig. 13.1). This setup greatly reduced the boundary layer but also greatly increased *E* up to 25 mmol m^{-2} s^{-1} (*i.e.* 1.6 kg m^{-2} h^{-1}!). These conditions led to heterogeneity in capitulum WC. On the other hand, slow air mixing and higher RH of incoming air reduced *E* (3–4 mmol m^{-2} s^{-1}) and shifted the optimum WC of the same species down to 7 g g^{-1} (Fig. 13.1); these values are comparable to those of Williams and Flanagan (1996). Thicker boundary layer is indicated by narrow range of the optimum WC, which is achieved after relatively long times. This complicates routine measurements of *A* under defined conditions such as optimum WC because experimental designs (*e.g.*, number of replicates or treatment levels) are usually limited by the time-consuming photosynthetic measurements. To accelerate the measurements, it is desirable to widen the optimum WC of the sample by tuning the parameters controlling *E* and boundary layer thickness inside the gas-exchange chamber, together with the initial WC of the bryophyte sample.

However, even the lowest *E* occurring inside gas exchange chambers—standardly equipped with air-mixing fan—probably still overestimate the field reality where we can expect slower net water loss due to thicker boundary layers. Data on E from moss cover, unaffected by artificial air mixing are however rare. Bond-Lamberty et al. (2011) measured and modeled *E* of boreal forest; the maximum values (annual means), which were found in sphagna from bogs, did not exceed 0.9 mmol m^{-2} s^{-1}. Evaporation rates of about 0.5 mmol m^{-2} s^{-1} were measured in water-saturated *Sphagnum* cores under RH of 93 %, no air mixing and photosynthetic photon flux density (PPFD) of 500–1,000 µmol m^{-2} s^{-1} (Skre et al. 1983a). Recalculated cumulative evaporation data from greenhouse *Sphagnum* cultivation (Robroek et al. 2007b) showed that the mean half-year *E* for four sphagna are close to 1 mmol m^{-2} s^{-1} at RH ~75 %. In another greenhouse experiment with lower RH (45 %), *E* of hydrated sphagna slightly exceeded 2 mmol m^{-2} s^{-1} (Robroek et al. 2009). Although the last three examples represent artificial conditions, the boundary layer and *E* more likely resemble field conditions more so than those used in gas-exchange experimental chambers where the boundary layer is purposefully minimized.

Nevertheless, the WC of well hydrated apical green shoot segment ranges between 15 and 30 g g^{-1} (*e.g.*, Schipperges and Rydin 1998; Rice et al. 2008) suggesting that field-grown sphagna rather rarely utilize the optimum WC, which is closely connected to desiccation stress (however, *cf.* Williams and Flanagan 1996). In open mires, desiccation sensitive sphagna occupy either wet hollows or form compact hummocks and remain hydrated in the sun where most of the excitation energy from PSII cannot be utilized for CO_2 fixation. Excess excitation generates reactive oxygen species (ROS) and causes uncontrolled photodamage to photosynthetic apparatus. Photorespiration is a significant alternative sink for excessive electrons preventing the over reduction of the photosynthetic electron transport pathway (Wilhelm and Selmar 2011). Photorespiration may reduce net photosynthesis to one half in *Sphagnum* as well as in feather mosses (Skre and Oechel 1981). Beside this, sphagna and other bryophytes of unshaded habitats possess non-saturating electron flow through PSII, where the excess excitation energy is continuously taken from PSII, although the carboxylation/oxidation capacity of Rubisco is already light-saturated (Fig. 13.2). Proctor and Smirnoff (2011) identified molecular oxygen as the electron acceptor at high PPFD (Mehler reaction; see also Chap. 7). Because O_2 is reduced to O_2^- (superoxide), these mosses are also highly tolerant to ROS. The results of Proctor and Smirnoff (2011) stress the importance of Mehler reaction in bryophytes, being probably more of a significant alternative electron sink than in C_3 tracheophytes where it consumes only <10 % of transported electrons (Badger et al. 2000). In *Sphagnum*, the non-saturation electron flow was first reported in sun-grown, brown colored *S. cristatum* while the shade-grown green plants of the same species showed light saturation at PPFD ~200 µmol m^{-2} s^{-1} (Maseyk et al. 1999). Similarly, Laine et al. (2011) revealed the saturation character of *A* relative to RETR, indicating efficient electron flow to alternative sinks in all studied sun-grown species at high light intensities.

Examples of two light response curves measured under contrasting levels of diffusion resistance to CO_2 are demonstrated (Fig. 13.2). Similar course of quantum yield of PSII photochemistry (QY PSII; estimated by chlorophyll fluorescence) and of relative electron transport rate (RETR = QY PSII × PPFD) in the two samples indicates that electron flow is almost unaffected by diffu-

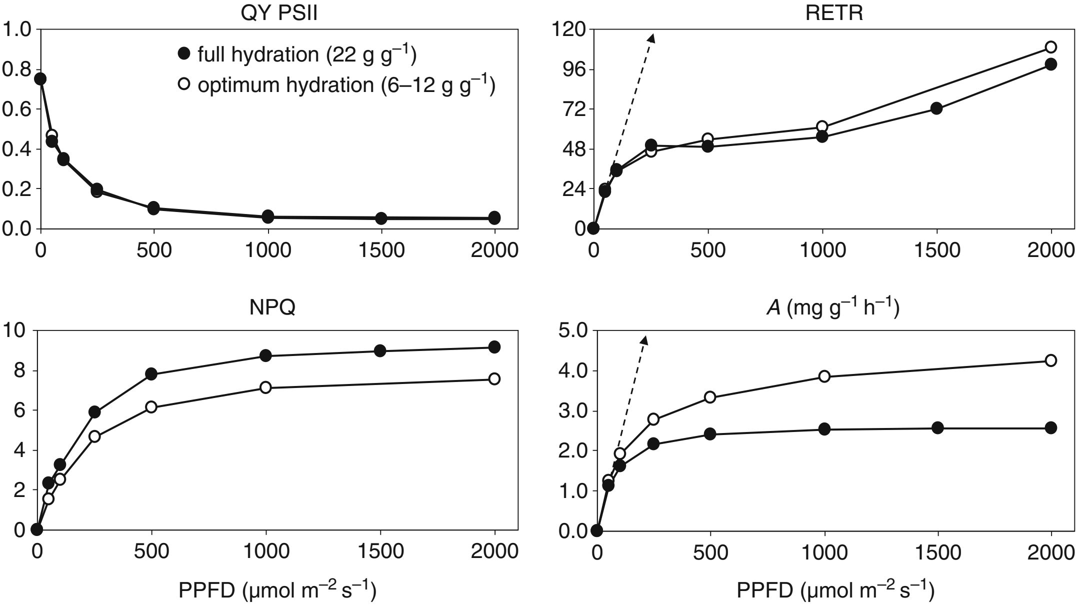

Fig. 13.2. Photosynthetic response of *Sphagnum papillosum* capitula (6 mm) to photosynthetic photon flux density (PPFD) measured under two contrasting levels of diffusion resistance to CO_2. The light curves were measured under full hydration (22 g g^{-1}) and limited sample aeration (high diffusion resistance to CO_2; *closed symbols*), and under optimum hydration (6–12 g g^{-1}) and thorough sample aeration (low diffusion resistance to CO_2; *open symbols*) using GFS-3000 Portable Gas Exchange Fluorescence System (Heinz Walz GmbH, Germany). CO_2 concentration was set to 400 ppm and temperature to 24 °C. *QY PSII* quantum yield of photosystem II photochemistry, *RETR* relative electron transport rate (RETR = QY_PSII × PPFD), *NPQ* non-photochemical quenching of chlorophyll fluorescence, *A* photosynthetic CO_2 assimilation rate. Measurements started in light-acclimated state and finished by dark measurement. Value of QY in the *dark* represents maximum QY PSII (F_v/F_m) after 12-h dark acclimation and the associated NPQ is zero by definition. Means of two replicates are shown. *Dashed arrows* show the rate of photon absorption, illustrating the huge fraction of excess light that the photosynthetic apparatus must cope with (the excess light may be visualized as area included between the light response curve and the *arrow*).

sion resistance to CO_2 but the low diffusion resistance clearly limits *A*. It should be noted that majority of the chlorophyll fluorescence signal comes from the uppermost leaves in capitula and thus the parameters of chlorophyll fluorescence are not as sensitive to CO_2 diffusion as *A*. The RETR become PPFD-saturated at about 500 μmol m^{-2} s^{-1} but then continues to rise with higher light levels, contrary to *A*. The high saturation level of *A*–PPFD curve in the sample with low diffusion resistance to CO_2 results from efficient air-mixing through the canopies of moss capitula. The curve thus integrates CO_2 exchange across the entire 6-mm gradient of light penetration through the sample, resulting in its gradual inflexion and higher estimate of saturation PPFD. The slightly greater NPQ in the sample with high diffusion resistance reflects the greater proportion of heat-dissipated excess excitation energy that could not be taken by photochemistry.

C. Desiccation

Bryophytes as poikilohydric plants generally tolerate some level of cytoplasmic dehydration. Species of xeric habitats are equipped with constitutive desiccation tolerance to survive rapid, irregular and repeated drought, but species of mesic and hydric habitats may afford inducible tolerance by hardening (acclimation; Proctor et al. 2007b).

Since *Sphagnum* mosses are typical desiccation avoiders, they usually posses only limited or no ability to recover their physiological functions and growth after natural or experimental drying (Abel 1956; Clymo 1973; Wagner and Titus 1984; Schipperges and Rydin 1998; Bragazza 2008). Desiccated *Sphagnum* cells are able to maintain constant QY PSII until they lose turgor (Hájek and Beckett 2008), but exact determination of shoot compensation WC for photosynthesis is similarly problematic as the exact determination of optimum WC (Fig. 13.1) due reasons described above. Within the genus *Sphagnum*, species forming hummocks have greater water holding capacity than those occupying hollows. As a consequence, hollow species became more quickly desiccated in the field in comparison to hummock formers (Wagner and Titus 1984; Rydin 1985). Better recovery of the hollow species after experimental drought was interpreted as a trade-off, *i.e.* that the hollow species lack the avoidance strategy of hummock sphagna (anatomical adaptation), but possess better physiological tolerance to desiccation (Wagner and Titus 1984). This hypothesis has been supported only by single published study (Sagot and Rochefort 1996). By contrast, hummock sphagna showed better recovery of photosynthetic parameters after slow drying in the dark (Hájek and Beckett 2008); however, the desiccation did not proceed by same rates for all species. Subsequent experiments on controlled very slow desiccation of *Sphagnum* capitula supported the hypothesis of Wagner and Titus (1984)—hollow sphagna were able to recover their photosynthesis better after severe desiccation treatment because they have better biochemical hardening to drought during initial phases of protoplast desiccation (T. Hájek and E. Vicherová, unpublished). Application of abscisic acid had comparable effects as acclimation by slow desiccation. Accordingly, only slow desiccation to *Sphagnum* capitula in the field, ensured by capillary contact with hydrated basal stem parts (Schipperges and Rydin 1998), seem to provide sufficient time for the biochemical induction of desiccation tolerance at least down to WC of 0.2 g g^{-1} (Wagner and Titus 1984) or even 0.07 g g^{-1} (Rydin and McDonald 1985), corresponding to WC of *Sphagnum* capitula dried under 80 and 40 % relative air humidity (read from the water sorption curves in Clymo and Hayward 1982).

During desiccation of bryophyte shoots, air replaces water from capillary spaces between leaves and in case of *Sphagnum* also from the interior of hyaline cells. In desiccated *Sphagnum* capitula, reflectance of photosynthetic active radiation increases roughly twofold (Vogelmann and Moss 1993; Harris et al. 2005; Van Gaalen et al. 2007), *i.e.* the excess PSII excitation pressure will decrease. Reflectance in the infrared (water absorption bands) increases even more, notably in the mid-infrared (Vogelmann and Moss 1993; Harris et al. 2005), preventing overheating when evaporative cooling is absent.

III. Specific Properties of Peatlands

A. Peat as Carbon Source for Photosynthesis

Peatland bryophytes are mostly terrestrial plants utilizing atmospheric CO_2 for photosynthesis. Most of the photosynthetically fixed carbon entering the acrotelm, the upper aerobic peat layer in mires, is mineralized back to CO_2 before it reaches catotelm, the deeper water-logged anoxic peat layer. Reducing conditions in the catotelm facilitate methane production. Mire bryophytes form an interface between the soil or water and the atmosphere. The peat-derived gases diffuse upwards through the peat pore water or in air pockets, but they move also internally within central parenchyma of *Sphagnum* stems (Rydin and Clymo 1989). Both pathways were found to represent significant C source for photosynthesis and growth in *Sphagnum* mosses. In the case of hummock forming sphagna in a boreal bog, long-term C refixation could represent about 15–25 % of the total C assimilated (Tolonen et al. 1992) based on analysis of peat profiles for ^{14}C originating from nuclear weapons testing in 1960s. Turetsky and Wieder (1999) estimated that about 5 % of ^{14}C incorporated to living *Sphagnum fuscum* had been refixed within 90 days. Additional, substrate-derived C was found to be indispensable for normal development of *S. magellanicum* shoots in wet conditions supporting C allocation to structural tissues (Smolders et al. 2001).

Hyaline cells in *Sphagnum* leaves provide suitable microhabitat for methanotrophic bacteria. They may oxidize up to 100 % of methane produced in the catotelm (Whalen 2005), leaving CO_2 that can be readily assimilated by neighbouring chlorophyllous cells. Methane-derived CO_2 represents 5–35 % of photosynthetically assimilated CO_2 in many *Sphagnum* species, particularly in aquatic conditions (Raghoebarsing et al. 2005; Kip et al. 2010; Larmola et al. 2010). Liebner et al. (2011) also found the moss–methanotroph associations in "brown" mosses; they estimated that *Scorpidium scorpioides*, a dominant moss in pools of polygonal tundra, obtained as much as 70 % of assimilated CO_2 from methane oxidation.

In summary, peat-derived CO_2 serves as a significant source of C for *A* in peatland mosses, particularly in aquatic habitats. This locally elevated CO_2 may be understood as a kind of compensation for high leaf diffusion resistance to atmospheric CO_2 caused by large content of extracellular capillary water which is typical notably for *Sphagnum* shoots (see above).

B. CO_2 Availability in Rich Fens

In terms of their total area, rich and extremely rich fens represent only a small fraction of the world's peatlands. The plant cover here is strongly influenced by chemistry of groundwater, often running over the surface. Such water is rich in calcium bicarbonate that originates from dissolving of calcium carbonate underground. When the groundwater reaches the surface, the free and bicarbonate-bound CO_2 releases from the water into the atmosphere. This equilibration is accompanied by a pH increase in the fen water (Shotyk 1988). In extremely-rich fens this process may lead to precipitation of calcium carbonate as tufa resulting in the lack of free CO_2 for photosynthesis. Such water chemistry is tolerated by only a few species, typically brown mosses from the family Amblystegiaceae such as *Cratoneuron* or *Scorpidium* species. Although direct uptake of bicarbonate could be a competitive advantage in bryophytes submerged in rich fen water, this adaptation has been only indicated in the aquatic moss *Fontinalis antipyretica* (Peñuelas 1985), and has not been observed in rich fen mosses (Ruttner 1947; Bain and Proctor 1980; see Chap. 12 for further details). There is also no evidence that moss–methanotroph associations facilitate moss growth in such hard waters. Therefore the photosynthesizing moss shoots growing at the groundwater–atmosphere interface assimilate aerial CO_2. Alternatively, CO_2-enriched groundwater provides CO_2 until its concentration becomes equilibrated with the air. After that, CO_2 consumption down to the photosynthetic CO_2 compensation point leads to CO_2 release from bicarbonate followed by carbonate precipitation. Such re-equilibration of CO_2/bicarbonate/carbonate may explain bryophyte growth in nearly stagnant alkaline waters (Bain and Proctor 1980). Active proton extrusion from protoplasts and also cation exchange in the cell walls may acidify the bicarbonate and increase CO_2 concentration near the photosynthesizing shoots. The capacity of these two mechanisms is, however, low when compared to the buffering capacity of the excess hard groundwater.

C. Life in Water-Saturated and Sunny Environment

Bryophyte-dominated peatlands are often treeless due high water levels and associated anoxic conditions in the catotelm. Especially in bogs and partly in fens, *Sphagnum* biomass is the key contributor to the peat formation and thus the lack of trees may be understood as a result of competition between rootless bryophytes and rooting tracheophytes (vascular plants). *Sphagnum* mosses are typical desiccation avoiders, storing large amount of capillary water that prevents drying. In most terrestrial habitats, bryophytes get dry and physiologically inactive in full sunshine, activating their metabolism during wet, *i.e.* mostly cloudy periods. On the other hand, permanent shoot hydration is common in shady habitats. Therefore, the combination of full sunlight irradiance and permanent hydration in *Sphagnum* places demands on efficient photoprotection because the rate of chlorophyll excitation greatly exceeds the capacity for CO_2 fixation.

Synthesis of red or brown cell-wall pigments is the most conspicuous photoprotective mechanism in sun-grown sphagna, while the same species are deep green in the shade (*e.g.*, sun grown *S. capillifolium* and *S. magellanicum* are often red to crimson while *S. teres* and *S. fuscum* are brown). These pigments simply shield those involved in light harvesting (chlorophylls and carotenoids) by reflecting and absorbing part of the photosynthetically active radiation. If the readily-reversible protective mechanisms (notably non-photochemical quenching provided largely by xanthophyll cycle; Bukhov et al. 2001), as well as photochemical quenching by alternative electron sinks such as photorespiration, are insufficient, the photosynthetic apparatus faces photodamage (Raven 2011; Wilhelm and Selmar 2011) resulting in long term depression of chlorophyll excitation and reduction of growth and production. These symptoms were evident in experimentally shaded and unshaded *Sphagnum* in a subarctic mire, as well as under controlled laboratory cultivation of subarctic and temperate *Sphagnum* samples (Murray et al. 1993). Specifically, mosses treated by sun or moderately high PPFD showed impairment of PSII (lowered F_v/F_m) resulting in decreased A and growth; this impairment persisted for the 2-week experimental period. Similar conclusions were provided by a screening of gas exchange and chlorophyll fluorescence parameters in dominant species from pristine (open) and forested (shaded) halves of single boreal poor fen (Hájek et al. 2009); similar patterns were found in *S. cristatum* from New Zealand (Maseyk et al. 1999). Analogously, the uppermost capitulum level of arctic sphagna experiencing 24-h daylight showed substantially reduced F_v/F_m, notably in the late season, in contrast to the subcapitulum shoot level that experienced lower irradiance (Zona et al. 2011).

These results indicate that F_v/F_m is a sensitive indicator of light stress in peatland mosses, which is also true for other bryophytes. Bukhov et al. (2001) concluded that the F_v/F_m of moss gametophytes does not exceed 0.80 and suggested that this was due to photoinhibition, *i.e.* heat dissipation of excess excitation energy in damaged PSII. This indicates that mosses are generally incapable of the rapid and/or full photoacclimation of PSII known from tracheophytes whose sun leaves reach $F_v/F_m > 0.80$ within minutes after darkening. Instead, F_v/F_m in sun sphagna may remain below 0.60 after 12–20 min of dark acclimation (Hájek et al. 2009; Laine et al. 2011), but shade sphagna may regularly exceed the value of 0.80 after overnight dark acclimation as observed in many species from boreal spruce mires in Southern Finland (T. Hájek, unpublished). This result suggests that mosses do not possess a kind of constitutive photoinhibition since their PSII is capable of full shade acclimation. Permanent F_v/F_m reduction in the sun may be also considered as an acclimation mechanism of avoiding excess excitation when the fast-reversible dissipation mechanisms are insufficient (Štroch et al. 2004). Since the photoinhibitory components of non-photochemical quenching are slowly reversible and very heterogenous, the length of the dark acclimation period for F_v/F_m should be indicated when the parameter values are compared and interpreted, especially in bryophytes.

Thus, the shady forest floor seems to be a favorable habitat in terms of low light and also low evaporation rate. Moreover, the understory rainwater is substantially enriched by nutrients deposited in and leached out of the forest canopy. These nutrients can then be readily taken up by nutrient-limited mosses (Tamm 1964). Low nutrients, particularly nitrogen in *Sphagnum* tissue are hypothesized to be responsible for the inability of photoacclimation to high light conditions (Murray et al. 1993). Close correlation between mass-based shoot N content and maximum quantum efficiency of *A*, a good indicator of light stress, has been reported for bryophytes (Waite and Sack 2010). Direct experimental evidence supporting the hypothesis of Murray et al. (1993) is however missing.

In summary, forested peatlands are relatively unstressful habitats for bryophytes in terms of light, water, and nutrients. This allows them to maximize their photosynthesis, photosynthate allocation to growth, and production, which is necessary for efficient competition. Sphagnum mats in nutrient-rich sparsely forested peatlands are thus one of the most productive peatland habitats (Brock and Bregman 1989). On the other hand, sphagna in open peatlands do not seem to maximize their photosynthetic and biomass production. They have already suppressed their vascular competitors (van Breemen 1995). Therefore they can afford the reduction of light acquisition efficiency in PSII protecting their photosynthetic apparatus against more severe damage that may result from over excitation.

D. Mineral Nutrition

Peatlands have typically slow biomass mineralization rates resulting in low nutrient availability in the soil; these nutrients are however utilized preferentially by rooting tracheophytes (Malmer et al. 1994). Especially in bogs, bryophytes must rely rather on efficient nutrient acquisition from atmospheric deposition and nutrient recycling from senescent shoots. Numerous recent studies question the effect of anthropogenically raised atmospheric concentrations and deposition of nutrients, particularly nitrogen, on peatland ecosystems (Limpens et al. 2011). Despite nutrient-poor characteristics of peatlands, production of most *Sphagnum* populations is currently not N-limited, except some remote sites with very low (but probably still not pre-industrial) atmospheric deposition of biologically active N (reviewed by Limpens et al. 2006, 2011; Wieder 2006). Consequently, (co-)limitation with other nutrients results, notably phosphorus (P) and potassium (K) (Bragazza et al. 2004; Limpens et al. 2011). Only few studies investigated the effect of N availability on *Sphagnum* photosynthesis. Foliar N content correlates well with net photosynthesis in tracheophytes (Wright et al. 2004), but perhaps less in bryophytes (Waite and Sack 2010) including *Sphagnum* capitula (but not whole canopies; Rice et al. 2008). Maximum *A* and in part also F_v/F_m increased with tissue N and chlorophyll contents along the North–South gradient of increasing background wet N deposition across N–W Europe (Granath et al. 2009a). Specifically, *A* increased 3–6 times from low deposition rates of 0.3 up to 1.1 or 1.4 g N m^{-2} year^{-1} depending on species, but production showed only weak, if any, trend across Europe. In another study, *A* in *Sphagnum* decreased with artificial N oversaturation of 6–23 g N m^{-2} year^{-1} (van der Heijden et al. 2000). Correspondingly, moderate experimental N deposition of 1.5 g N m^{-2} year^{-1} resulted in greater *A* (but not F_v/F_m) than under deposition of 0.2 and 3.0 g N m^{-2} year^{-1} in *S. balticum* (Granath et al. 2009b, 2012). However, *A* (but neither F_v/F_m nor production) of *S. fallax* and *S. fuscum* benefited from experimental N deposition up to 5.6 g N m^{-2} year^{-1} (Granath et al. 2012), resulting in the capitulum N content about 1.3 %. Above this optimum N content, *Sphagnum* production generally decreases, perhaps due to shifted nutrient stoichiometry (Limpens et al. 2011); the optimum capitulum N content was about 1.3 % which is in a good agreement with the general limit for sphagna above which the production decreases (Limpens et al. 2011; see also Granath et al. 2012). *Sphagnum magellanicum* in Patagonian bogs receives only about 0.1 g N m^{-2} year^{-1} in precipitation. When the mosses were experimentally overloaded by 4 g N m^{-2} year^{-1}, their capitulum responded by doubled N (1.5 %) and chlorophyll contents but *A* and production of entire moss carpets did not change at all due to strong P limitation (Fritz et al. 2012). Even though the combined N and P treatment stimulated *A* and especially production, P failed to alleviate the stress imposed by excess N.

As mentioned above, Murray et al. (1993) hypothesized that generally low N availability to mire sphagna may limit PSII recovery from photoinhibition. Nitrogen may significantly limit the PSII recovery in areas of very low N deposition, which has been indicated by low F_v/F_m in such conditions (Granath et al. 2009a; Hájek et al. 2009). On the other hand, experimental shading (60 % reduction of PPFD) of four *Sphagnum* species in an open Central-European mountain bog had only a negligible effect on the relatively high $F_v/F_{m;}$ during the whole year (increased from 0.71 to 0.72), although the total wet N deposition did not exceed 0.5 g N m^{-2} $year^{-1}$ and capitulum N content did not differ from that in Murray et al. (1993) (T. Hájek and E. Vicherová unpublished data). Interspecific differences in the ability to recover the PSII efficiency may be also important; in a boreal mire with low N deposition, *S. angustifolium* and *S. magellanicum* dominated in both open and shaded habitats, but only *S. magellanicum* exhibited strong and long-term reduction of F_v/F_m and *A* in the open, while these parameters did not differ between habitats in *S. angustifolium* (Hájek et al. 2009).

In sites with non-limiting N deposition, ammonium was found to accumulate in *Sphagnum* cells where it is considered to directly inhibit the moss physiology (Limpens and Berendse 2003). Although cytosolic ammonium *per se* was, however, not found to be toxic to plants, its inhibitory action to photosynthesis is diverse and complex (Britto and Kronzucker 2002). Among other mechanisms, ammonium was found to reduce non-photochemical dissipation of excitation energy by xanthophyll cycle pigments, the key photoprotective mechanism in plants. This reduction may be compensated by alternative photochemical processes of energy dissipation such as photorespiration and O_2 reduction via Mehler reaction (Britto and Kronzucker 2002). The latter mechanism is particularly efficient in sun growing bryophytes including sphagna (Proctor and Smirnoff 2011). On the other hand, high ammonium availability may be accompanied by an increase in chlorophyll content (Tomassen et al. 2003; Bonnett et al. 2010; Fritz et al. 2012; but cf. Rudolph and Voigt 1986), which may further increase chlorophyll excitation and risk of photodamage.

IV. Seasonal Variability of Photosynthesis and Respiration

Optimum conditions for growth and production often occur in spring (Gaberščik and Martinčič 1987; Brock and Bregman 1989) when the supply of water exceeds evaporation, where summer production can be limited by drought. A second growth optimum may come in late summer/autumn (Johansson and Linder 1980; Lindholm 1990; Asada et al. 2003). In general, moisture distribution is a key factor explaining seasonal variability in *Sphagnum* growth (Backéus 1988), particularly in hollows, which host species with low water retention capacity (Asada et al. 2003). Hulme and Blyth (1982) found that wetter bog microhabitats have a longer growth season for *Sphagnum* species. Thus, aquatic conditions allowed whole-year growth in *S. cuspidatum*, while sphagna on flat hummocks or sphagna transplanted from these hummocks to pools grew only for about 6 months in the temperate climate of South Scotland. The last finding emphasizes species control on the length of growth season. Corresponding with the contrasting ecological strategies of hummock and hollow sphagna described above, hollow species maximize their growth and competitive ability also by maximizing the length of their growth season.

Seasonal patterns of *Sphagnum* photosynthesis and production rates are, however, not always correlated. Gaberščik and

Martinčič (1987) measured the greatest photosynthetic and dark respiration rates as well as highest chlorophyll contents of *S. papillosum* in summer, peaking in early August, after the period of maximum growth and production. Similarly, Skre and Oechel (1981) reported a gradual increase in net photosynthetic rates of *Sphagnum* and other spruce mire mosses to a maximum in August, but dark respiration did not follow this seasonal pattern. The model of Williams and Flanagan (1998) revealed that maximum carboxylation rate by Rubisco in *Sphagnum* peaks in summer while the dark respiration was again stable. This seasonal pattern of *A*, respiration, and growth could be explained by seasonality in resource allocation. There is specific allocation to photosynthetic capacity in summer. In the late season, photosynthates may be stored in capitula as lipids (Karunen and Salin 1982) or carbohydrates (monosaccharides and reserve polysaccharides; Skre et al. 1983b); the carbohydrates also provide osmotic protection to survive forthcoming freeze. In the spring, the photosynthetic apparatus is still acclimated to winter dormancy. The low efficiency in light harvesting and CO_2 fixation may be compensated by utilization of the capitulum storage accumulated in previous autumn. This corresponds with the finding of Backéus (1988) who revealed that the water availability in August is a good predictor of *Sphagnum* growth for the next year. Moreover, the reduced *A* may be compensated by efficient C translocation from senescent shoot segments to the capitula (Rydin and Clymo 1989).

Induction of winter dormancy in sphagna may be independently triggered by both short photoperiod (Li and Glime 1991; Gerdol 1995) and chilling, *i.e.* low night temperature of about 5 °C and lower (Gerdol 1995; Gerdol et al. 1998). Chilling seems to induce rapid degradation of chlorophylls (Gerdol et al. 1994) accompanied by synthesis of sphagnorubins, red cell-wall anthocyanin-derived flavonoid pigments (Rudolph et al. 1977; Rudolph and Jöhnk 1982), produced perhaps by all species. Gerdol et al. (1998) observed no reduction in chlorophylls, but great reduction in photosynthetic rate and growth after low night temperatures of 5 °C. This indicates that the induction of dormancy in the light-harvesting apparatus probably requires lower temperatures than the reactions involved in *A*. Seasonal changes in chlorophylls and sphagnorubins are important in reduction of excess excitation that cannot be utilized for C fixation since biochemical processes are more temperature dependent than the light harvesting. Sphagnorubins, which are also synthesized in sun conditions without chilling (Rudolph et al. 1977), acts partly as a shield reflecting red (photosynthetically active) radiation and partly as a heater absorbing photosynthetically inactive radiation. The quantitative importance of both effects is however unknown. Moreover, sphagnorubins seem to be synthesized also under other stress conditions, such as nutrient imbalance (Li et al. 1993).

V. Photosynthesis and Production in a Warmer and Richer World

The most discussed global climate-related environmental changes are increases in temperature, atmospheric CO_2 concentration, nutrient deposition, UV irradiance, and irregularity of water supply. Much interest is currently being focused on peatlands and their C balance since these habitats are likely to be greatly impacted due to their distribution in colder and (thus) wetter parts of the world, to their primary production being nutrient limited, and to their production showing CO_2 limitation.

Short-term increases of air CO_2 concentration lead to temporarily proportional increases of photosynthetic rates in *Sphagnum* mosses (Silvola 1985), but over a few days (van der Heijden et al. 2000) or months (Jauhiainen and Silvola 1999) photosynthesis is down-regulated so final *A* only slightly exceed the original ones. Relatively high N fertilization and elevated CO_2 stimulated half-year production of *Sphagnum fallax* taken from minerotrophic fen (van der Heijden et al. 2000); bog sphagna, however, did not respond to elevated CO_2 for 3 years, although the experimental sites were distributed along the gradient of aerial N deposition across N–W Europe (Hoosbeek et al. 2001). Their analysis of nutrient stoichiometry revealed that K and partly also P limited the production under elevated CO_2.

Depending on species and initial temperatures, increased temperature may stimulate or reduce production of peatland bryophytes through several pathways such as direct physiological response or indirect effects like drought stress (due to increased evaporation or reduced water holding capacity of the new biomass), increased nutrient availability (due to enhanced mineralization of organic matter), expansion of vascular or bryophyte competitors or pathogen infection. Although the optimum temperature for net A varies during the growth season (Gaberščik and Martinčič 1987), the summer optimum temperature seems to be relatively high (20 °C), even in tundra and taiga ecosystems (Harley et al. 1989; Skre and Oechel 1981, respectively). Studies linking direct photosynthetic responses to elevated temperature with indirect growth and production responses are, however, absent. For example, high temperature stress alone (36 and 43 °C) temporarily reduced F_v/F_m and net A in two fully hydrated hummock sphagna under moderate PPFD (Gerdol and Vicentini 2011); however such heat stress is usually accompanied by drought and high PPFD in the field, conditions that may be already lethal (Bragazza 2008). Thus, the indirect impacts of increased temperature such as desiccation or competitive pressure can be considered as the threat to peatland bryophytes, whereas the (slightly) increased temperature *per se* may have rather positive effect on A, growth and production (Gerdol 1995; Dorrepaal et al. 2003), notably in colder zones. Increased temperature in warmer zones, accompanied by elevated N deposition rates is, however, detrimental to *Sphagnum* production due to imbalanced nutrient stoichiometry (Limpens et al. 2011) or risk of desiccation due to reduced water retention capacity (Manninen et al. 2011).

The effects of UV radiation on bryophytes, including sphagna have been recently reviewed elsewhere (see also Chap. 7). Briefly, neither current nor expected elevated fluxes of UV radiation seem to have substantial effects on A, pigments content (chlorophylls, carotenoids, UV-absorbing compounds), and biomass production in *Sphagnum*. Sphagna seem to be equipped with inherent UV protection rather than with prompt repair mechanisms. The protection may be provided by UV-B absorbing phenolic compounds fixed within cell-walls, namely lignin-like polymers and flavonoid pigments. Although this hypothesis has not been tested in *Sphagnum* yet, the cell-wall pigments were found to provide efficient UV-screen in Antarctic bryophytes (Chap. 7). Nonetheless, UV radiation may become harmful in combination with other stress factors associated with climate change such as severe desiccation.

Desiccation stress is currently becoming more frequent under ongoing climatic change, which is characterized by irregularity in seasonal distribution of precipitation. Robroek et al. (2009) emphasized that lack of precipitation, rather than a low water table *per se*, inhibits A in *Sphagnum*, particularly in hollow more than in hummock species. Bragazza (2008) documented extensive and permanent die off in hummock sphagna following a spell of hot and dry weather in Italian Alps.

In summary, most of the individual factors representing climate change such as realistically elevated temperature, CO_2, UV radiation or N supply do not have direct and substantial negative effects on peatland bryophytes, represented by several *Sphagnum* species, at least in terms of photosynthesis and biomass production. Current levels of biologically active N and CO_2 considerably exceed pre-industrial levels. Therefore species' response to our current 'control' levels may obscure the effect of the experimentally increased levels. Water availability is perhaps the most variable and most significant environmental factor limiting photosynthesis and production in the field conditions. It can be expected that drought, when metabolic activity including repair mechanisms is retarded, will be intensified by stress induced by climate change and exacerbated by excess PPFD.

VI. Suggestions for Further Research

This review pointed out several questions that deserve further interest. For example, there are only indications that the recovery of PSII from photoinhibition is limited by low N availability in traditionally nutrient deficient peatlands. The general question remains, what is the nutrient control on light harvesting and CO_2 assimilation in peatland bryophytes in field conditions?

We have quite good overview of how moss shoot WC retards diffusion of atmospheric CO_2 (and its assimilation) in individual experimental measuring set-ups. But how does it work in the field? We need a model for field CO_2 exchange that includes conductance to water vapor and CO_2 within the natural moss cover, taking into account also laminar boundary layer thickness (wind speed, surface roughness), CO_2 source (air and peat-derived) or water pressure deficit.

We have almost no data on the combined effects of desiccation stress and other stress factors (high PPFD, nutrient availability, heat or elevated UV radiation and ozone concentration) on photosynthesis and growth in peatland bryophytes. Generally high sensitivity of *Sphagnum* to desiccation combined with exclusively inducible desiccation tolerance has been a barrier to deeper experimental work on this topic. The high sensitivity, however, has a potential to affect these bryophytes differently than in the more desiccation tolerant species of mesic and xeric habitats. The induction of *Sphagnum* desiccation tolerance, when technically mastered, may open new experimental possibilities.

Sphagnorubins, the cell-wall pigments, are synthesized under several stress conditions, but their expected ecophysiological significance (reflection of photosynthetically active radiation, absorption of other wavelengths including UV) has not been subjected to specific experimental testing. Moreover, the synthesis of these flavonoid pigments—secondary metabolites—may interact with the current increase in N availability mediated through phenylalanine pools, an amino acid that is the primary resource for sphagnorubin synthesis (Tutschek 1982; Chap. 7).

This review also revealed how the ecophysiological research of brown mosses—in comparison with sphagna—is neglected although they are key species in nutrient rich peatlands. They are tightly connected with the relatively alkaline groundwater rich in calcium and bicarbonate, which may lead up to precipitation of calcium carbonate. Such water chemistry represents a stress factor that may interact with other abovementioned abiotic stress factors typical for sun-exposed peatland habitats.

Acknowledgements

I am grateful to the editors for helpful comments and language correction. This work was supported by long-term research development project no. RVO 67985939 (Academy of Sciences of the Czech Republic) and grant GAP505/10/0638 (The Czech Science Foundation).

References

Abel WO (1956) Die Austrocknungsresistenz der Laubmoose. Sitzungsberichte. Österreichische Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse, Abt. I 165:619–707

Asada T, Warner BG, Banner A (2003) Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia, Canada. Bryologist 106:516–527

Backéus I (1988) Weather variables as predictors of *Sphagnum* growth on a bog. Holarct Ecol 11:146–150

Badger MR, von Caemmerer S, Ruuska S, Nakano H (2000) Electron flow to oxygen in higher plants and algae: rates and control of direct photoreduction

(Mehler reaction) and Rubisco oxygenase. Philos Trans R Soc Lond B Biol Sci 355:1433–1445

Bain JT, Proctor MCF (1980) The requirement of aquatic bryophytes for free CO_2 as an inorganic carbon source: some experimental evidence. New Phytol 86:393–400

Bond-Lamberty B, Gower ST, Amiro B, Ewers BE (2011) Measurement and modeling of bryophyte evaporation in a boreal forest chronosequence. Ecohydrology 4:26–35

Bonnett SAF, Ostle N, Freeman C (2010) Short-term effect of deep shade and enhanced nitrogen supply on *Sphagnum capillifolium* morphophysiology. Plant Ecol 207:347–358

Bragazza L (2008) A climatic threshold triggers the die-off of peat mosses during an extreme heat wave. Glob Change Biol 14:2688–2695

Bragazza L, Tahvanainen T, Kutnar L, Rydin H, Limpens J, Hájek M, Grosvernier P, Hájek T, Hájková P, Hansen I, Iacumin P, Gerdol R (2004) Nutritional constraints in ombrotrophic *Sphagnum* plants under increasing atmospheric nitrogen depositions in Europe. New Phytol 163:609–616

Britto DT, Kronzucker HJ (2002) NH_4^+ toxicity in higher plants: a critical review. J Plant Physiol 159:567–584

Brock TCM, Bregman R (1989) Periodicity in growth, productivity, nutrient content and decomposition of *Sphagnum recurvum* var. mucronatum in a fen woodland. Oecologia 80:44–52

Bukhov NG, Heber U, Wiese C, Shuvalov VA (2001) Energy dissipation in photosynthesis: does the quenching of chlorophyll fluorescence originate from antenna complexes of photosystem II or from the reaction center? Planta 212:749–758

Clymo RS (1973) The growth of *Sphagnum*: some effects of environment. J Ecol 61:849–869

Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In: Smith AJE (ed) Bryophyte ecology. Chapman and Hall, New York, pp 229–289

Dorrepaal E, Aerts R, Cornelissen JHC, Callaghan TV, van Logtestijn RSP (2003) Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. Glob Change Biol 10:93–104

Fritz C, van Dijk G, Smolders AJ, Pancotto VA, Elzenga TJ, Roelofs JG, Grootjans AP (2012) Nutrient additions in pristine Patagonian *Sphagnum* bog vegetation: can phosphorus addition alleviate (the effects of) increased nitrogen loads. Plant Biol 14:491–499

Gaberščik A, Martinčič A (1987) Seasonal dynamics of net photosynthesis and productivity of *Sphagnum papillosum*. Lindbergia 13:105–110

Gerdol R (1995) The growth dynamics of *Sphagnum* based on field measurements in a temperate bog and on laboratory cultures. J Ecol 83:431–437

Gerdol R, Vicentini R (2011) Response to heat stress of populations of two *Sphagnum* species from alpine bogs at different altitudes. Environ Exp Bot 74:22–30

Gerdol R, Bonora A, Poli F (1994) The vertical pattern of pigment concentrations in chloroplasts of *Sphagnum capillifolium*. Bryologist 97:158–161

Gerdol R, Bonora A, Gualandri R, Pancaldi S (1996) CO_2 exchange, photosynthetic pigment composition, and cell ultrastructure of *Sphagnum* mosses during dehydration and subsequent rehydration. Can J Bot 74:726–734

Gerdol R, Bonora A, Marchesini R, Gualandri R, Pancaldi S (1998) Growth response of *Sphagnum capillifolium* to nighttime temperature and nutrient level: mechanisms and implications for global change. Arct Alp Res 30:388–395

Granath G, Strengbom J, Breeuwer A, Heijmans MMPD, Berendse F, Rydin H (2009a) Photosynthetic performance in *Sphagnum* transplanted along a latitudinal nitrogen deposition gradient. Oecologia 159:705–715

Granath G, Weidermann MM, Strengbom J (2009b) Physiological responses to nitrogen and sulphur addition and raised temperature in *Sphagnum balticum*. Oecologia 161:481–490

Granath G, Strengbom J, Rydin H (2012) Direct physiological effects of nitrogen on *Sphagnum*: a greenhouse experiment. Funct Ecol 26:353–364

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Hájek T, Beckett RP (2008) Effect of water content components on desiccation and recovery in *Sphagnum* mosses. Ann Bot 101:165–173

Hájek T, Tuittila E-S, Ilomets M, Laiho R (2009) Light responses of mire mosses – a key to survival after water-level drawdown? Oikos 118:240–250

Harley PC, Tenhunen JD, Murray KJ, Beyers J (1989) Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. Oecologia 79:251–259

Harris A, Bryant RG, Baird AJ (2005) Detecting near-surface moisture stress in *Sphagnum* spp. Remote Sens Environ 97:371–381

Hoosbeek MR, van Breemen N, Berendse F, Grosvernier P, Vasander H, Wallén B (2001) Limited effect of increased atmospheric CO_2 concentration on ombrotrophic bog vegetation. New Phytol 150:459–463

Hulme PD, Blyth AW (1982) The annual growth period of some *Sphagnum* species on the Silver Flowe National Nature Reserve, south-west Scotland. J Bryol 12:287–291

Jauhiainen J, Silvola J (1999) Photosynthesis of *Sphagnum fuscum* at long-term raised CO_2 concentrations. Ann Bot Fennici 36:11–19

Jauhiainen J, Silvola J, Vasander H (1998a) Effects of increased carbon dioxide and nitrogen supply on mosses. In: Bates JW, Ashton NW, Duckett JG (eds) Bryology for the twenty-first century. Maney Publishing and the British Bryological Society, Leeds, pp 343–360

Jauhiainen J, Wallén B, Malmer N (1998b) Potential $^{15}NH_4{}^{15}NO_3$ uptake in seven *Sphagnum* species. New Phytol 138:287–293

Johansson LG, Linder S (1980) Photosynthesis of *Sphagnum* in different microhabitats on a subarctic mire. In: Sonesson M (ed) Ecology of a subarctic mire, Ecological bulletins, 30. Swedish Natural Science Research Council, Stockholm, pp 181–190

Karunen P, Salin M (1982) Seasonal changes in lipids of photosynthetically active and senescent parts of *Sphagnum fuscum*. Lindbergia 8:35–44

Kip N, van Winden JF, Pan Y, Bodrossy L, Reichart G-J, Smolders AJP, Jetten MSM, Damste JSS, Op den Camp HJM (2010) Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. Nat Geosci 3:617–621

Laine A, Juurola E, Hájek T, Tuittila E-S (2011) *Sphagnum* growth and ecophysiology during mire succession. Oecologia 167:1115–1125

Larmola T, Tuittila E-S, Tiirola M, Nykäne H, Martikainen JP, Yrjälä K, Tuomivirta T, Fritze H (2010) The role of *Sphagnum* mosses in the methane cycling of a boreal mire. Ecology 91:2356–2365

Li Y, Glime JM (1991) Growth response of two *Sphagnum* species to photoperiod. Can J Bot 69: 2643–2646

Li Y, Glime JM, Drummer TD (1993) Effects of phosphorous on the growth of *Sphagnum magellanicum* Brid. and *S. papillosum* Lindb. Lindbergia 18:25–30

Liebner S, Zeyer J, Wagner D, Schubert C, Pfeiffer E-M, Knoblauch C (2011) Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra. J Ecol 99:914–922

Limpens J, Berendse F (2003) Growth reduction of *Sphagnum magellanicum* subjected to high nitrogen deposition: the role of amino acid nitrogen concentration. Oecologia 135:339–345

Limpens J, Heijmans MMPD, Berendse F (2006) The nitrogen cycle in boreal peatlands. In: Wieder RK, Vitt DH (eds) Boreal peatland ecosystems, vol 188, Ecological studies. Springer, Berlin/Heidelberg, pp 195–230

Limpens J, Granath G, Gunnarsson U, Aerts R, Bayley S, Bragazza L, Bubier J, Buttler A, van den Berg LJL, Francez A-J, Gerdol R, Grosvernier P, Heijmans MMPD, Hoosbeek MR, Hotes S, Ilomets M, Leith I, Mitchell EAD, Moore T, Nilsson MB, Nordbakken JF, Rochefort L, Rydin H, Sheppard LJ, Thormann M, Wiedermann MM, Williams BL, Xu B (2011) Climatic modifiers of the response to N deposition in peat-forming *Sphagnum* mosses: a meta-analysis. New Phytol 191:496–507

Lindholm T (1990) Growth dynamics of the peat moss *Sphagnum fuscum* on hummocks on a raised bog in southern Finland. Ann Bot Fennici 27:67–78

Loisel J, Garneau M, Hélie J-F (2009) Modern *Sphagnum* $\delta^{13}C$ signatures follow a surface moisture gradient in two boreal peat bogs, James Bay lowlands, Québec. J Quart Sci 24:209–214

Malmer N, Svensson BM, Wallén B (1994) Interactions between Sphagnum mosses and field layer vascular plants in the development of peat forming systems. Folia Geobot Phytotaxon 29:483–496

Manninen S, Woods C, Leith ID, Sheppard LJ (2011) Physiological and morphological effects of long-term ammonium or nitrate deposition on green and red (shade and open grown) *Sphagnum capillifolium*. Environ Exp Bot 72:140–148

Maseyk KS, Green TGA, Klinac D (1999) Photosynthetic responses of New Zealand *Sphagnum* species. N Z J Bot 37:155–165

Murray KJ, Harley PC, Beyers J, Walz H, Tenhunen JT (1989) Water content effects on the photosynthetic response of Sphagnum mosses from the foothills of the Philip Smith Mountains, Alaska. Oecologia 79:244–250

Murray KJ, Tenhunen JD, Nowak RS (1993) Photoinhibition as a control on photosynthesis and production of *Sphagnum* mosses. Oecologia 96:200–207

Oechel WC, Collins NJ (1976) Comparative CO_2 exchange patterns in mosses from two tundra habitats at Barrow, Alaska. Can J Bot 54:1355–1369

Peñuelas J (1985) HCO_3^- as an exogenous carbon source for aquatic bryophytes *Fontinalis antipyretica* and *Fissidens grandifrons*. J Exp Bot 36:441–448

Proctor MCF (2005) Why do Polytrichaceae have lamellae? J Bryol 27:219–227

Proctor MCF, Smirnoff N (2011) Ecophysiology of photosynthesis in bryophytes: major roles for oxygen photoreduction and non-photochemical quenching? Physiol Plant 141:130–140

Proctor MCF, Ligrone R, Duckett JG (2007a) Desiccation tolerance in the moss *Polytrichum formosum*: physiological and fine-structural changes during desiccation and recovery. Ann Bot 99:75–93

Proctor MCF, Oliver MJ, Wood AJ, Alpert P, Stark LR, Cleavitt NL, Mishler BD (2007b) Desiccation-tolerance in bryophytes: a review. Bryologist 110:595–621

Raghoebarsing AA, Smolders AJP, Schmid MC, Rijpstra WI, Wolters-Arts M, Derkens J, Jetten MSM, Schouten S, Sinninghe Damste JS, Lamers LPM, Roelofs JGM, Op den Camp HJM, Strous M (2005) Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. Nature 436:1153–1156

Raven JA (1991) Implications of inorganic carbon utilization: ecology, evolution, and geochemistry. Can J Bot 69:908–924

Raven JA (2011) The cost of photoinhibition. Physiol Plant 142:87–104

Rice SK (1995) Patterns of allocation and growth in aquatic *Sphagnum* species. Can J Bot 73:349–359

Rice SK, Giles L (1996) The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in *Sphagnum*. Plant Cell Environ 19:118–124

Rice SK, Aclander L, Hanson DT (2008) Do bryophyte shoot systems function like vascular plant leaves or canopies? Functional trait relationships in *Sphagnum* mosses (Sphagnaceae). Am J Bot 95:1366–1374

Robroek BJM, Limpens J, Breeuwer A, van Ruijven J, Schouten MGC (2007a) Precipitation determines the persistence of hollow *Sphagnum* species on hummocks. Wetlands 27:979–986

Robroek BJM, Limpens J, Breeuwer A, Schouten MGC (2007b) Effects of water level and temperature on performance of four *Sphagnum* mosses. Plant Ecol 190:97–107

Robroek BJM, Schouten MGC, Limpens J, Berendse F, Poorter H (2009) Interactive effects of water table and precipitation on net CO_2 assimilation of three co-occurring *Sphagnum* mosses differing in distribution above the water table. Glob Change Biol 15:680–691

Rudolph H (1968) Gaswechselmessungen an *Sphagnum magellanicum*. Ein Beitrag zur Membranochromie der Sphagnen (III). Planta 79:35–43

Rudolph H, Jöhnk A (1982) Physiological aspects of phenolic compounds in the cell walls of Sphagna. J Hattori Bot Lab 53:195–203

Rudolph H, Voigt JU (1986) Effects of NH_4^+-N and NO_3^--N on growth and metabolism of *Sphagnum magellanicum*. Physiol Plant 66:339–343

Rudolph H, Kabsch U, Schmidt-Stohn G (1977) Änderungen des Chloroplastenpigment-Spiegels bei *Sphagnum magellanicum* im Verlauf der Synthese von Sphagnorubin und anderer membranochromer Pigmente. Z Pflanzenphysiol 82:107–116

Ruttner F (1947) Zur Frage der Karbonatassimilation der Wasserpflanzen. I. Teil: Die beiden Haupttypen der Kohlenstoffaufnahme. Ost Bot Z 94:265–294

Rydin H (1985) Effect of water level on desiccation of *Sphagnum* in relation to surrounding Sphagna. Oikos 45:374–379

Rydin H (1993) Mechanisms of interactions among *Sphagnum* species along water level gradients. Adv Bryol 5:153–185

Rydin H, Clymo RS (1989) Transport of carbon and phosphorus compounds about *Sphagnum*. Proc R Soc Lond B 237:63–84

Rydin H, Jeglum JK (2006) The biology of peatlands. Oxford University Press, New York

Rydin H, McDonald AJS (1985) Photosynthesis in *Sphagnum* at different water contents. J Bryol 13:579–584

Rydin H, Gunnarsson U, Sundberg S (2006) The role of *Sphagnum* in peatland development and persistence. In: Wieder RK, Vitt DH (eds) Boreal peatland ecosystems, vol 188, Ecological studies. Springer, Berlin/Heidelberg, pp 49–65

Sagot C, Rochefort L (1996) Tolérance des sphaignes à la dessiccation. Cryptogam Bryol Lichénol 17:171–183

Schipperges B, Rydin H (1998) Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytol 148:677–684

Shotyk W (1988) Review of the inorganic geochemistry of peats and peatland waters. Earth Sci Rev 25:95–176

Silvola J (1985) CO_2 dependence of photosynthesis in certain forest and peat mosses and simulated photosynthesis at various actual and hypothetical CO_2 concentrations. Lindbergia 11:86–93

Silvola J (1990) Combined effects of varying water content and CO_2 concentration on photosynthesis in *Sphagnum fuscum*. Holarctic Ecol 13:224–228

Silvola J (1991) Moisture dependence of CO_2 exchange and its recovery after drying in certain boreal forest and peat mosses. Lindbergia 17:5–10

Silvola J, Aaltonen H (1984) Water content and photosynthesis in the peat mosses *Sphagnum fuscum* and *S. angustifolium*. Ann Bot Fennici 21:1–6

Skre O, Oechel WC (1981) Moss functioning in different taiga ecosystems in interior Alaska. I. Seasonal, phenotypic, and drought effects on photosynthesis and response patterns. Oecologia 48:50–59

Skre O, Oechel WC, Miller PM (1983a) Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. Can J For Resour 13:860–868

Skre O, Oechel WC, Miller PM (1983b) Patterns of translocation of carbon in four common moss species in a black spruce *Picea mariana* dominated forest in interior Alaska. Can J For Resour 16:869–878

Smolders AJP, Tomassen HBM, Pijnappel H, Lamers LPM, Roelofs JGM (2001) Substrate-derived CO_2 is important in the development of *Sphagnum* spp. New Phytol 152:325–332

Štroch M, Špunda V, Kurasová I (2004) Non-radiative dissipation of absorbed excitation energy within photosynthetic apparatus of higher plants. Photosynthetica 42:323–337

Tamm CO (1964) Growth of *Hylocomium splendens* in relation to tree canopy. Bryologist 67:423–426

Titus JE, Wagner DJ (1984) Carbon balance for two *Sphagnum* mosses: water balance resolves a physiological paradox. Ecology 65:1765–1774

Titus JE, Wagner DJ, Stephens MD (1983) Contrasting water relations of photosynthesis for two *Sphagnum* mosses. Ecology 64:1109–1115

Tolonen K, Possnert G, Jungner H, Sonninen E, Alm J (1992) High resolution ^{14}C dating of surface peat using the AMS technique. Suo 43:271–276

Tomassen HBM, Smolders AJP, Lamers LPM, Roelofs JGM (2003) Stimulated growth of *Betula pubescens* and *Molinia caerulea* on ombrotrophic bogs: role of high levels of atmospheric nitrogen deposition. J Ecol 91:357–370

Turetsky MR, Wieder RK (1999) Boreal bog *Sphagnum* refixes soil-produced and respired $^{14}CO_2$. Ecoscience 6:587–591

Tutschek R (1982) An evaluation of phenylpropanoid metabolism during cold-induced sphagnorubin synthesis in *Sphagnum magellanicum* BRID. Planta 155:301–306

Ueno T, Kanda H (2006) Photosynthetic response of the arctic semi-aquatic moss *Calliergon giganteum* to water content. Aquat Bot 85:241–243

van Breemen N (1995) How *Sphagnum* bogs down other plants. Trends Ecol Evol 10:270–275

van der Heijden E, Verbeek SK, Kuiper PJC (2000) Elevated atmospheric CO_2 and increased nitrogen deposition: effects on C and N metabolism and growth of peat moss *Sphagnum recurvum* P. Beauv. var. mucronatum (Russ.) Warnst. Glob Change Biol 6:201–212

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

Vitt DH, Wieder RK (2009) The structure and function of bryophyte-dominated peatlands. In: Goffinet B, Shaw AJ (eds) Bryophyte biology, 2nd edn. Cambridge University Press, Cambridge, pp 357–392

Vogelmann JE, Moss DM (1993) Spectral reflectance measurements in the genus *Sphagnum*. Remote Sens Environ 45:273–279

Wagner DJ, Titus JE (1984) Comparative desiccation tolerance of two *Sphagnum* mosses. Oecologia 62: 182–187

Waite M, Sack L (2010) How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. New Phytol 185:156–172

Whalen SC (2005) Biogeochemistry of methane exchange between natural wetlands and the atmosphere. Environ Eng Sci 22:73–94

Wieder RK (2006) Primary production in boreal peatlands. In: Wieder RK, Vitt DH (eds) Boreal peatland ecosystems, vol 188, Ecological studies. Springer, Berlin/Heidelberg, pp 145–164

Wilhelm C, Selmar D (2011) Energy dissipation is an essential mechanism to sustain the viability of plants: the physiological limits of improved photosynthesis. J Plant Physiol 168:79–87

Williams TG, Flanagan LB (1996) Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and $C^{18}O^{16}O$ in *Pleurozium* and *Sphagnum*. Oecologia 108: 38–46

Williams TG, Flanagan LB (1998) Measuring and modelling environmental influences on photosynthetic gas exchange in *Sphagnum* and *Pleurozium*. Plant Cell Environ 21:555–564

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin FS, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas E, Villar R (2004) The world-wide leaf economics spectrum. Nature 428:821–827

Zona D, Oechel WC, Richards JH, Hastings S, Kopetz I, Ikawa H, Oberbauer S (2011) Light stress avoidance mechanisms in a *Sphagnum*-dominated wet coastal Arctic tundra ecosystem in Alaska. Ecology 92:633–644