Interactive effects of water table and precipitation on net CO₂ assimilation of three co-occurring *Sphagnum* mosses differing in distribution above the water table

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Abstract

Sphagnum cuspidatum, *S. magellanicum* and *S. rubellum* are three co-occurring peat mosses, which naturally have a different distribution along the microtopographical gradient of the surface of peatlands. We set out an experiment to assess the interactive effects of water table (low: -10 cm and high: -1 cm) and precipitation (present or absent) on the CO_2 assimilation and evaporation of these species over a 23-day period. Additionally, we measured which sections of the moss layer were responsible for light absorption and bulk carbon uptake. Thereafter, we investigated how water content affected carbon uptake by the mosses. Our results show that at high water table, CO_2 assimilation of all species gradually increased over time, irrespective of the precipitation. At low water table, net CO_2 assimilation of all species declined over time, with the earliest onset and highest rate of decline for *S. cuspidatum*. Precipitation compensated for reduced water tables and positively affected the carbon uptake of all species. Almost all light absorption occurred in the first centimeter of the *Sphagnum* vegetation and so did net CO_2 assimilation. CO_2 assimilation rate showed species-specific relationships with capitulum water content, with narrow but contrasting optima for *S. cuspidatum* and *S. rubellum*. Assimilation by *S. magellanicum* was constant at a relatively low rate over a broad range of capitulum water contents. Our study indicates that prolonged drought may alter the competitive balance between species, favoring hummock species over hollow species. Moreover, this study shows that precipitation is at least equally important as water table drawdown and should be taken into account in predictions about the fate of peatlands with respect to climate change.

Keywords: climate change, CO₂ assimilation, desiccation, peatlands, photosynthesis, precipitation, raised bogs, recovery, *Sphagnum*, water table

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Introduction

Raised bogs are generally dominated by bryophytes from the genus *Sphagnum* that may reach a cover of 80–100%, thereby substantially contributing to the aboveground biomass production of these ecosystems. Productivity varies among peatland types and regions

and is in the range of $17–380 \, \text{g m}^{-2} \, \text{yr}^{-1}$ (Moore *et al.*, 2002). Additionally, *Sphagnum* mosses influence the hydrological and hydrochemical conditions at the raised bog surface to a high degree (van Breemen, 1995; van der Schaaf, 2002), and thus play an invaluable role in the functioning of this ecosystem. Typically, raised bogs are characterized by a pattern of microtopographical habitats, ranging from wet depressions (hollows) and relatively dry but regularly inundated lawns to dry heights (hummocks). Mosses that occur in the hollows do not posses an efficient mechanism to

transport water to their apical parts. Consequently, they can rely less on capillary water supply (Ingram, 1983), implying increased reliance on precipitation as a source of water. Concomitantly, each microhabitat is occupied by a different set of *Sphagnum* species (Andrus *et al.*, 1983). The relation between the presence of certain *Sphagnum* species and the position along the microto-pographical gradient is likely to be the result of a combination of morphological and physiological characteristics. Several studies have stressed interspecific differences among *Sphagnum* mosses in the efficiency of the external capillary system to conduct water and the ability to hold water. Morphological characteristics may influence the ability to conduct water to the capitula on the one hand and the ability to withstand water loss on the other (Hayward & Clymo, 1982; Titus & Wagner, 1984; Rydin & McDonald, 1985a, b), and in concert affect growth and the sequestration of carbon.

Previously, we studied the effect of prolonged absence of precipitation on the competition between six *Sphagnum* species at different water tables (Robroek *et al.*, 2007a). Interestingly, capitulum water content of species which were grown in mixed cultures in the glasshouse did not differ. Yet, growth differed between competing species, and was generally larger for those species that naturally occur farther from the water table, indicating that these species are more able to cope with drought. These results made us conclude that differences in growth may be explained by different physiological responses (e.g. photosynthesis) to water content. However, other studies on the physiological response of *Sphagnum* to water content have yielded inconsistent and sometimes contrasting data, which may be caused by the differences in methods employed between the studies (for a review, see Rydin, 1993).

Generally, water content in *Sphagnum* is measured in bulk samples. However, for light interception and the concomitant carbon fixation, only the top layer of the *Sphagnum* is likely to be important. There is no consensus in the literature, however, on the thickness of this layer. Titus *et al.* (1983) state that 99% of the carbon fixation in *Sphagnum fallax* and *S. capillifolium* carpets takes place in the upper 5 cm. Light may penetrate only a few centimeters, or even only 1 cm in the case of dense *Sphagnum* carpets, indicating the importance of the carpets density (Wallén *et al.*, 1988; Rydin & Jeglum, 2006).

Habitat preferences of *Sphagnum* species are generally determined by the ability of species to withstand or avoid desiccation (Titus & Wagner, 1984), and therefore, it is expected that hummock species, compared with hollow species, are better to maintain a water content high enough for photosynthesis under periodic drought (i.e. periods without precipitation). As a result, the relative period during which net photosynthesis is positive may be longer for hummock species than for hollow species. Recovery after desiccation may also be important for species performance. Schipperges & Rydin (1998) found hummock species to display a better rate of recovery during several drying and rewetting periods, compared with hollow and lawn species. Strikingly, after complete desiccation, hummock species generally show lower recovery than hollow species (Clymo & Hayward, 1982; Wagner & Titus, 1984; Schipperges & Rydin, 1998). From these results, it was concluded that interspecies differences to avoid desiccation and not the ability to recover from desiccation was important in coping with longer periods of drought.

Changes in climatic and environmental conditions, such as precipitation and water table, have an important effect on the microenvironment in which *Sphagnum* mosses grow, and may affect the competition between co-occurring species. Decreased water tables and increased temperatures are known to have different effects on different *Sphagnum* mosses (Robroek *et al.*, 2007b), yet how prolonged periods without precipitation affect the performance of *Sphagnum* species at different water tables has – to our knowledge – never been assessed. In this study, we set out to test the interactive effects of water table and precipitation on the ability of *Sphagnum* species to assimilate CO₂. First, we nondestructively determined the effects of water table (high or low) and precipitation (present or absent) on the net CO₂ assimilation of *Sphagnum cuspidatum* (hollow), *S. magellanicum* (lawn) and *S. rubellum* (hummock) microcosms. Thereafter, relationships between water content and photosynthesis were assessed destructively. Additionally, for each species, we determined the extent to which light penetrates into the *Sphagnum* carpet and the part of the *Sphagnum* layer that is important for carbon uptake. Finally, interspecific differences in the ability to recover from prolonged drought were investigated.

Methods

Sampling

In September 2006, intact cores (diameter 12.5 cm, depth 11 cm) of *S. cuspidatum* Ehrh. ex Hoffm., *S. magellanicum* Brid. and *S. rubellum* Wilson were collected at Clara bog (53°19′N, 007°58′W), Ireland. A detailed description of this raised bog is given in Schouten (2002). Different species were taken from adjacent (< 25 m) monospecific stands in their natural habitat (i.e. *S. cuspidatum* was taken from microhabitats with a 2–7 cm water table depth beneath the moss surface, *S. magellanicum* at habitats with 4–20 cm and *S. rubellum* at habitats with

9–27 cm water table depth). Care was taken to maintain the natural density of the species, before putting them into pots (hereafter referred to as microcosms). The microcosms were transported to the Netherlands where the sparse vascular plant shoots were clipped to the *Sphagnum* surface.

Experimental setup

At the end of September 2006, two water table treatments, low (10 cm below the *Sphagnum* surface) and high (1 cm below the *Sphagnum* surface), were randomly assigned to the microcosms. These water tables are within the range in which these species naturally occur. From late September 2006 through December 2006, all mosses were kept outdoors, where natural precipitation kept them moist. At the beginning of January 2007, the mosses were transported to a greenhouse (average temperature: 19.4 °C; average relative humidity: 45%), where two precipitation treatments were assigned within each water table treatment: microcosms received either 2 mm day^{-1} (ca. 25 mL day^{-1}) precipitation (cf. Sweeney & Fealy, 2002) or no precipitation at all. We used artificial rainwater solution (a diluted seawater solution based on Garrels & Christ, 1965), which was spread over the capitula, in order to apply the solution evenly over the surface. Vapor pressure deficit based on the glasshouse average temperature and humidity would be ca. 1.25, which falls well within the ranges as published in field studies (Hobbie & Chapin, 1998; Dorrepaal *et al.*, 2004). All treatments were replicated four times, resulting in 48 microcosms. Treatments are abbreviated as follows: high water table without precipitation, HWT−; high water table with precipitation, HWT +; low water table without precipitation, LWT− and low water table with precipitation, LWT +. Precipitation treatments were applied at the end of every day. High water tables were maintained by adding the rainwater solution as described above ≈ 1 cm below the capitulum layer. If a low water table was applied, no extra water was added to the microcosms, by which we mimicked a situation where capillary rise is hampered.

Light intensity was at least 200 µmol m^{-2} s^{-1} [photosynthetic photon flux density (PPFD) of photosynthetically active radiation (PAR, 300–700 nm)], because we supplemented light with high-pressure sodium lamps (12-h period), and increased up to ca. 1000 µmol m^{-2} s^{-1} PPFD during periods of sunshine. The average PAR per day over the experiment was ca. 12 mol quanta m^{-2} day^{-1}. These light conditions are similar to or above the conditions of other peat moss studies (e.g. Jauhiainen & Silvola, 1999; Lindroth *et al.*, 2007; van Gaalen *et al.*, 2007). Moreover, several studies indicate that light saturation of peat mosses for photosynthesis under natural conditions is generally below 350 µmol m^{-2} s^{-1} PPFD (Harley *et al.*, 1989; Maseyk *et al.*, 1999; Riutta *et al.*, 2007).

Measurements

CO_2 assimilation (see below), as well as fresh weight, of all microcosms was measured every 2 days over a 23-day period. After 23 days, all microcosms except LWT− (which were used to measure recovery) were separated into three sections: capitulum layer (0–2 cm), subcapitulum layer (2–4 cm) and bulk layer (4–10/11 cm). A tight-fitting PVC-ring was placed around the layer to be separated, after which a dissection knife was used to horizontally cut into the microcosms. The ring prevented deformation, by disabling pressure possibly exerted on the layer during handling. Per layer, light absorbance was measured by placing the layer on a clean glass plate, under which a quantum sensor (Skye Instruments, Powys, UK) was attached. Light absorbance of the layers was defined as the light intensity under the layer relative to the amount of light at the moss surface (430–530 µmol m^{-2} s^{-1}), correcting for the light absorption by the glass plate. To elucidate each layer's potential contribution to the total microcosm carbon uptake, net CO_2 assimilation was measured per layer just above saturation light intensity (ca. 450 µmol m^{-2} s^{-1}). Light absorption in the capitulum layer was further investigated by further separating this layer into a 0–1 cm and a 1–2 cm layer. Finally, fresh weight : dry weight ratios (fw dw^{-1}) were calculated for all layers.

Two weeks after net CO_2 assimilation of the LWT− mosses had become negative, the mosses were re-wetted. Rainwater solution was added to the microcosms until the water level remained 1 cm below the moss surface. Recovery was assessed by measuring net CO_2 assimilation just before rewetting, as well as 2.5 h, 2, 6 and 16 days after rewetting. Per individual microcosm, recovery was defined as net CO_2 assimilation after rewetting compared with the maximum net CO_2 assimilation of that microcosm. Before these measurements, interstitial water was drained from the pots, in order to be able to compare the measured values with the values as measured during the CO_2 assimilation experiment.

Gas exchange

CO_2 and H_2O exchange was measured in a flow-though gas exchange system, which consisted of 18 L cuvettes made of glass and stainless steel. CO_2 and H_2O partial pressures in the air flowing in were controlled by mixing CO_2 with CO_2-free air by means of flow con-

trollers [CO_2: Brooks Mass Flow Controller (Veenendaal, the Netherlands), type 5850, 0–36 mL min^{-1}; air: type 5851, 0–60 L min^{-1}) and by dehumidifying moistened air at a preset dew point, respectively. For a detailed description of the cuvettes, see Poorter & Welschen (1993). Net assimilation was measured at a light intensity of 410–470 µmol m^{-2} s^{-1} (PAR) and a CO_2 concentration of 360–390 ppm. The light intensity used for the measurement was well above the saturating values for peat moss photosynthesis under natural conditions (e.g. Riutta *et al.*, 2007). It would be useful at this point to note that carbon assimilation measurements, therefore, reflect more a potential C-gain than the actual carbon uptake in the glasshouse. The plants were enclosed in the cuvettes for at least 35 min before the measurements started. Differences in CO_2 and H_2O partial pressures between cuvettes with and without plants were measured using an infrared gas analyzer (LI-6262 CO_2/H_2O analyzer, LI-COR, Inc., Lincoln, NE, USA) in combination with a dew point mirror (General Eastern, Watertown, MA, USA).

Data analysis

Calculations of net CO_2 assimilation and evaporation follow Von Caemmerer & Farquhar (1981). Per species, data on net CO_2 assimilation over time were analyzed using repeated-measures ANOVA (RM-ANOVA), with water table and presence/absence of precipitation as fixed factors. Because significant ($P \leq 0.05$) interactions between water table and precipitation occurred, the separate impact of precipitation was determined in a similar way, but within water table treatment.

Because we only measured carbon assimilation during the periods in which the mosses resided in the cuvettes, at a fixed light intensity, one has to take into account that these values are not true values of day-round performance of total assimilation, but rather a reflection of the physiological status of the mosses at certain points during the experiment. To achieve not only a day-to-day estimate of this parameter but also an indicator of the long-term capacity, we integrated the gas exchange data obtained over the whole experimental period, interpolating for the days between measurements. We present these data as integrated assimilation (A_{int}). Because we found water table × species and water table × precipitation interactions (ANOVA, $P \leq 0.05$), we continued the analysis per water table treatment. Next, per water table, interspecific differences in A_{int} with and without precipitation were analyzed using ANOVA followed by Tukey's *post hoc* tests for species.

Because our LWT− microcosms were in a drying process, and therefore cover a large range of water contents, we could treat the data of these microcosms as continuous. The dependence of net CO_2 assimilation on that water content, expressed as fw dw^{-1}, was concomitantly determined by regression analysis. Quadratic curves were fitted through the data. Additionally, similar analyses were performed on the relationship between the capitulum water contents of the other microcosms (i.e. all microcosms except LWT−) and capitulum CO_2 assimilation.

Light attenuation by the *Sphagnum* layers was first analyzed using analysis of co-variance (ANCOVA). Species and layer were included as fixed factors, and water table and precipitation as co-variables. Light attenuation did not differ between these co-variables. We, therefore, pooled all data and analyzed the effect of species and layer depth using ANOVA. Because significant interactions occurred between species and layer depth ($P \leq 0.001$), the effect of species was analyzed per layer. These data did not always meet the assumptions of equal variances, but ANOVA appears not to be greatly influenced if the assumptions are not met (Heath, 1995). Therefore, we decided to perform our analyses without transformations. Per species, CO_2 assimilation of the different layers was analyzed, using ANCOVA with layer as a fixed factor and water table and precipitation as co-variables. Assimilation data were square root transformed.

Recovery of the dried-out microcosms over time was analyzed using ANOVAR, with species as a fixed factor. Tukey's *post hoc* tests were used to determine the interspecific differences. Not all data met the assumptions of homosphericity. Because Huyn–Feldt conditions were met (Potvin *et al.*, 1990), we were able to base our analysis on corrected degrees of freedom.

Results

Water table, precipitation and species effects on carbon uptake

For all species, effects of water table and precipitation on CO_2 assimilation showed significant interactions (Fig. 1, Table 1). In the microcosms grown at high water table, no effect of precipitation was found. Furthermore, CO_2 assimilation of these microcosms increased during the experiment (Fig. 1, Table 1). At low water table with precipitation, the course of net CO_2 assimilation of *S. magellanicum* and *S. rubellum* was similar to these at high water tables. For *S. cuspidatum*, in comparison, it was higher during the first part of the experiment but lower at the end (Fig. 1). At low water table without precipitation, CO_2 assimilation gradually decreased in all microcosms (Fig. 1), but species differed in their response. Net CO_2 assimilation of *S. cuspidatum* immediately decreased, whereas *S. magellanicum* and
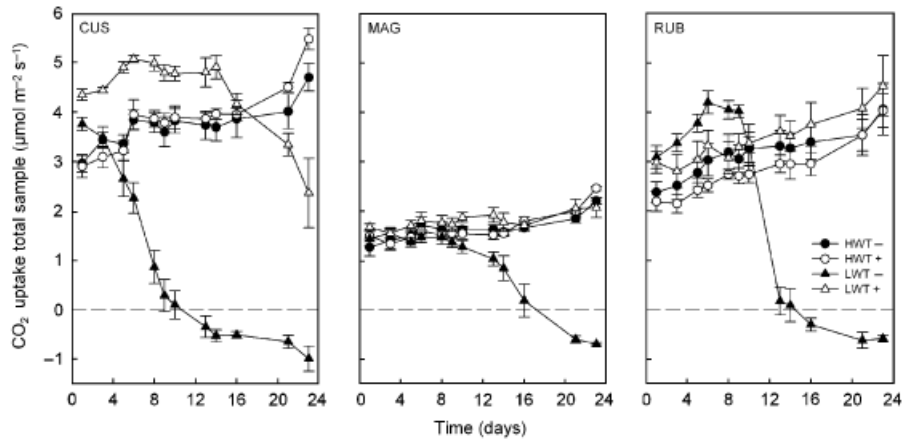
Fig. 1 Relationship between CO_2 assimilation ($\pm$ SEM, $n = 4$) during residence in the experiment cuvettes and time for *Sphagnum cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB) when grown at high water table (HWT) or low water table (LWT) and in the absence ($-$) or presence ($+$) of precipitation. Negative values indicate net CO_2 loss of the microcosms. For statistical values, see Table 1.

S. rubellum showed no decrease in the first half of the experiment. For *S. rubellum*, assimilation even increased during this time (Fig. 1). *S. magellanicum* and *S. rubellum* maintained positive net CO_2 assimilation values for a longer period than *S. cuspidatum* (Fig. 1, Table 2).

Integrated potential assimilation over the experimental period (A_{int}) at a high water table was highest for *S. cuspidatum* and lowest for *S. magellanicum*, and did not differ between the precipitation treatments (Fig. 2). Strikingly, A_{int} at low water table with precipitation was similar to that at high water tables (ANOVA, $P > 0.05$); *S. magellanicum* assimilation was again lowest (Tukey HSD, $P < 0.05$). However, at low water table, the effect of precipitation differed among species ($F = 24.9$, $P < 0.001$). For all species, A_{int} was lower when the mosses did not receive precipitation; the effect however was largest for *S. cuspidatum* (Fig. 2).

Carbon uptake in relation to water content and light penetration

Over the course of the experiment, the total water content of the microcosms exposed to low water tables without precipitation decreased, which may have affected net CO_2 assimilation. Therefore, we examined the relation between the total water content and net assimilation (Fig. 3a). Net CO_2 assimilation of *S. cuspidatum* was high at high water contents but rapidly decreased with decreasing microcosm water content. *S. magellanicum* and *S. rubellum* both showed optimum assimilation within the water content range given, with the optimum of *S. rubellum* occurring at lower total water contents than *S. magellanicum* (Fig. 3a). The response of net CO_2 assimilation to capitulum water content differs from the response of the total sample, especially at the lower range of water contents (Fig. 3a and b). This difference

is unlikely to be due to different treatments, because both sets of data cover a wide range of water contents. The difference probably reflects the large effect of the photosynthetic nonactive layers on the assimilation rates. It is clear that there are interspecific differences in the response of CO_2 uptake to capitulum water content. *S. magellanicum* assimilation was not significantly affected by water content, whereas there was an optimum water content for *S. cuspidatum*. Net CO_2 assimilation of *S. rubellum* increased with decreasing water content, though the water content may not have been low enough (due to the absence of the LWT– microcosm data) to find the optimum capitulum water content for this species.

For all three *Sphagnum* species, more than 97% of the light was absorbed in the first centimeter of the vegetation (Table 3). Minor interspecific differences were found, with absorption in this layer being highest in *S. rubellum* and lowest in the less dense growing *S. cuspidatum* (Table 3). Approximately 0.1–2% of the light could reach the layer below the first centimeter, but deeper than 2 cm all light had been absorbed. Visual inspection showed that hardly any chlorophyll was present below a depth of 2 cm, highlighting the importance of the capitulum section. This was further demonstrated by the result that all net carbon uptake took place in the capitulum layer (Fig. 4). Even at the relatively high light intensity used in this experiment, CO_2 assimilation was negative in the subcapitulum and the bulk layer of all species (Fig. 4), indicating that total respiration exceeded potential photosynthesis. Differences in carbon dissimilation between the subcapitulum and bulk layer may not only be caused by differences in photosynthetically active material, but rather by the larger volume of respiring peat material in the bulk layer. At low water tables, CO_2 assimilation in the bulk

Table 1 Between- and within-subject effects of RM-ANOVA of the overall analysis (upper table) and analyses per water table (bottom two tables) to test the effect of water table (WT), precipitation and their interactive effects on CO_2 assimilation over 23 subsequent days of three *Sphagnum* mosses. Values in bold indicate significant P-values ($P < 0.05$)

	S. cuspidatum				S. magellanicum				S. rubellum			
Source	df	MS	F	P	df	MS	F	P	df.	MS	F	P
Overall												
Between subjects												
Water table (WT)	1	69.24	46.53	**≤ 0.001**	1	4.22	8.72	0.012	1	2.69	0.96	0.347
Precipitation (Prec.)	1	158.06	106.22	**≤ 0.001**	1	9.08	18.76	**≤ 0.001**	1	12.34	4.39	0.058
WT × Prec.	1	143.34	96.33	**≤ 0.001**	1	8.38	17.32	**≤ 0.001**	1	35.88	12.76	**0.004**
Error	12	1.49			12	0.48			12	2.81		
Within subjects												
Time	4.6	3.68	11.9	**≤ 0.001**	6.2	0.18	2.72	0.018	4.4	4.3	17.19	**≤ 0.001**
Time × WT	4.6	25.19	81.39	**≤ 0.001**	6.2	2.32	34.44	**≤ 0.001**	4.4	14.7	58.57	**≤ 0.001**
Time × Prec.	4.6	7.18	23.2	**≤ 0.001**	6.2	1.65	24.49	**≤ 0.001**	4.4	15.8	62.86	**≤ 0.001**
Time × WT × Prec.	4.6	5.32	17.21	**≤ 0.001**	6.2	1.01	15.01	**≤ 0.001**	4.4	14.4	57.40	**≤ 0.001**
Error (Time)	55				74.2	0.07			52.4	0.25		
High water table												
Between subjects												
Precipitation (Prec.)	1	0.18	0.1	0.763	1	0.01	0.02	0.894	1	3.07	1.11	0.333
Error	6	1.81			6	0.37			6	2.77		
Within subjects												
Time	8.7	3.42	41.63	**≤ 0.001**	5.8	1.13	32.57	**≤ 0.001**	3.3	6.53	25.89	**≤ 0.001**
Time × Prec.	8.7	0.19	2.28	0.032	5.8	0.07	2.14	0.075	3.3	0.13	0.50	0.702
Error (Time)	52.4	0.08			34.8	0.04			19.8	0.25		
Low water table												
Between subjects												
Precipitation (Prec.)	1	301.22	258.48	**≤ 0.001**	1	17.46	28.99	**≤ 0.01**	1	45.15	15.83	**≤ 0.01**
Error	6	1.17			6	0.6			6	2.85		
Within subjects												
Time	3.6	28.85	48.34	**≤ 0.001**	6.6	1.36	14.15	**≤ 0.001**	4.8	12.88	45.19	**≤ 0.001**
Time × Prec.	3.6	15.67	26.26	**≤ 0.001**	6.6	2.44	25.32	**≤ 0.001**	4.8	24.48	96.46	**≤ 0.001**
Error (Time)	21.3	0.6			39.5	0.1			28.8	0.29		

Table 2 Time period (mean ± SEM, $n = 4$) per species in which we found net CO_2 uptake for the LWT− microcosms (see also Fig. 1)

Time period (days) of positive CO_2 assimilation

	Mean ± SEM
S. cuspidatum	10.1 ± 1.1 a
S. magellanicum	16.8 ± 0.9 b
S. rubellum	14.1 ± 0.8 b

section and subcapitulum section showed less negative values for *S. cuspidatum* ($F = 12.7$, $P \leq 0.001$) and *S. rubellum* ($F = 16.5$, $P \leq 0.001$; Fig. 4).

Besides light availability, the water conditions in the capitulum layer also determined the CO_2 assimilation potential (Fig. 3b). We found that in most cases, the water content of the subcapitulum and bulk section was higher than the capitulum water content, especially when the microcosms were grown at low water table (Fig. 5). In mosses, evaporation is not actively regulated, but is nevertheless a strong indicator of net CO_2 assimilation (Fig. 6). The slope of the relationship between evaporation and CO_2 uptake indicates the water use efficiency (WUE = mmol carbon fixed/mol water lost) of the species. WUE was found to be lowest for *S. magellanicum* (1.17 ± 0.06), which showed lowest assimilation over the course of the experiment. WUE of *S. cuspidatum* (2.69 ± 0.15) and *S. rubellum* (2.66 ± 0.13) was more than a factor 2 higher.

Recovery after drought

The ability of *Sphagnum* mosses to recover from desiccation may be an important factor that determines the competition between mosses. In the first hours after rewetting, CO_2 assimilation of all the microcosms

grown at low water table without precipitation became even more negative (Fig. 7). After this first response, recovery started, but even 6 days after rewetting, all species showed negative values of CO_2 assimilation. The recovery was particularly slow for *S. magellanicum* ($F = 10.7$, $P \leq 0.01$). CO_2 assimilation was positive 16 days after rewetting for all species ($F = 0.3$, $P = 0.8$) and varied from 15% (*S. magellanicum*) to 18% (*S. cuspidatum*) and 22% (*S. rubellum*) of the maximum.
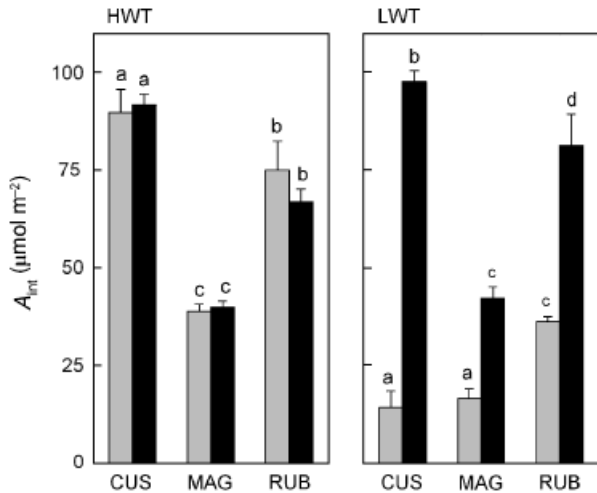

Fig. 2 Integrated potential assimilation (A_{int}) over the experimental period ($\pm$ SEM, $n = 4$) of *Sphagnum cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB) at high water table (HWT) and low water table (LWT), and without (gray bars) and with (black bars) precipitation. Because we found significant interactions with water level (ANOVA, $P < 0.001$), data were further analyzed per water level treatment. Different letters indicate significant differences (ANOVA, $P < 0.05$).
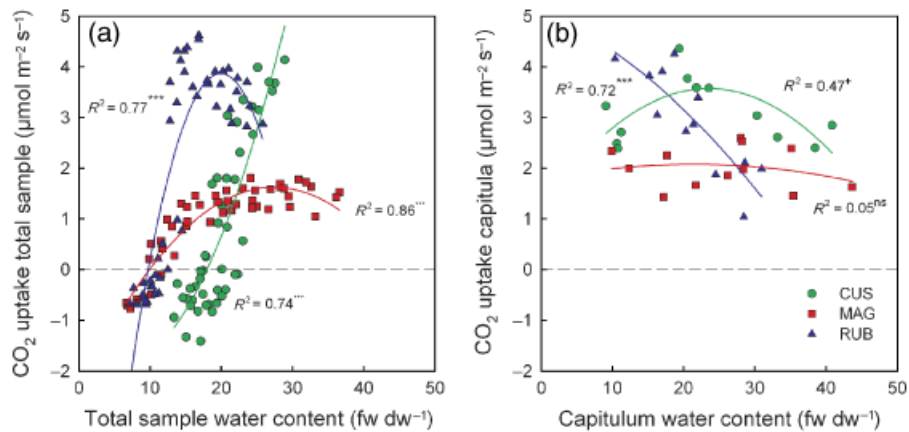
Discussion

Water table, precipitation and species effects on carbon uptake

The absence of precipitation resulted in decreased net CO_2 assimilation only when water tables were low (Fig. 1). At high water tables, the absence of precipitation did not result in decreased CO_2 assimilation, presumably because the water content of these samples was not affected by additional precipitation (i.e. extra water by precipitation was lost by means of an overflow that prevented the water table to become higher than the desired level). Interestingly, assimilation of all mosses that were grown at high water levels increased during the experiment. Similarly, assimilation of the drought-resistant species *S. magellanicum* and *S. rubellum* (Hayward & Clymo, 1983; Titus & Wagner, 1984) increased at low water table, but only with precipitation. The increase in assimilation may be explained by the rise of the capitula of the *Sphagnum* mosses above the water

Table 3 Light attenuation profile of the microcosms

Layer	Species		
	CUS	MAG	RUB
0	100	100	100
0–1 cm	2.3 ± 0.17 a	0.8 ± 0.14 b	0.1 ± 0.07 c
1–2 cm	0.1 ± 0.01 a	0 b	0 b
2–4 cm	0	0	0
4–11 cm	0	0	0

Data represents the percentage of light that can reach the next *Sphagnum* layer. Different letters indicate interspecific differences (ANOVA, $P \leq 0.05$) per layer.
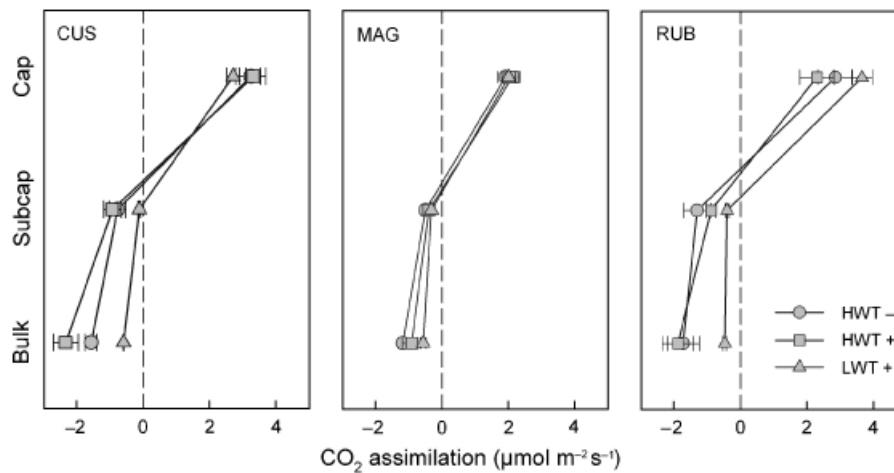

Fig. 3 (a) Relationship between CO_2 assimilation and water content of the microcosm for *Sphagnum cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB) grown at low water tables without precipitation (LWT−). (b) Relationship between net CO_2 assimilation of the capitulum section and the capitulum water content. Per species, quadratic curves were fitted through the data. ns, non significant; +, $P \leq 0.1$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

Fig. 4 CO_2 assimilation of the different layers [Cap: capitulum (0–2 cm), Subcap: 2–4 cm and Bulk: 4–10/11 cm] per *Sphagnum* species: *S. cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB). Measurements were performed at high light intensities, 430–530 μmol m^{-2} s^{-1}. HWT, high water table; LWT, low water table; $+/-$, presence/absence of precipitation. Carbon uptake was highest in the capitulum layer for all species (ANOVA, $P \leq 0.001$).

table due to growth during the experiment. As a result, the layer of water surrounding the photosynthetic active cells decreases, thereby favoring CO_2 exchange (Clymo & Hayward, 1982; Silvola & Aaltonen, 1984). Alternatively, the mosses may have gradually acclimated physiologically to the experimental light and temperature conditions (Titus *et al.*, 1983), which were better than the conditions before the experiment. If this is the case, this potential acclimation only seems to play a role when environmental conditions are favorable, while our results show that the negative effect of drying far exceeds the potentially positive effect of acclimation.

Before the experimental treatments, all mosses were kept at high water tables in order to create identical,
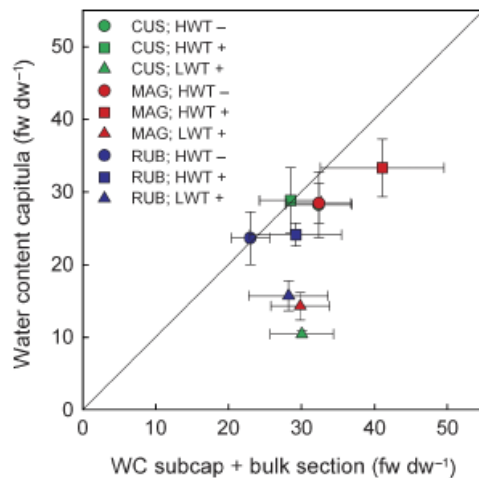

Fig. 5 Relationship between capitulum water content and the water content of the underlying layers (subcapitulum and bulk section). Values are means ($\pm$ SEM, $n = 4$). The solid line indicates a one-to-one relationship.

saturated, total water contents. Only in *S. cuspidatum* grown at a low water table during the experiment, the presence of precipitation was not sufficient to maintain net CO_2 assimilation for a prolonged period. Net CO_2 assimilation of *S. cuspidatum*, however, was relatively high for a short period (Fig. 1). Interestingly, a similar response was observed for *S. rubellum* but then without precipitation (Fig. 1). At the beginning of the desiccation process, the diffusion-hampering water film (Rice & Giles, 1996) on the *Sphagnum* leaves disappears, which may cause the increase in assimilation in *S. cuspidatum* and *S. rubellum*. The photosynthesizing cells of *S. magellanicum* are embedded in large hyaline cells and are therefore less affected by the evaporation of the water film on the leaves. Progressive desiccation, however, may lead to a decrease in net CO_2 assimilation. In concert, the absence of precipitation results in large water loss by *S. cuspidatum*, resulting in decreased assimilation. *S. rubellum* is much better in holding water than *S. cuspidatum*, resulting in prolonged high assimilation rates. Concurrently, without precipitation, the slower drying of this species may have resulted in an initial increase in assimilation because of more optimal conditions. The period during which CO_2 assimilation is positive is relatively short for *S. cuspidatum*. This period is larger for *S. magellanicum* than for *S. rubellum*, but does not significantly differ between these species. The absolute decline, however, seems much slower for *S. magellanicum* (Fig. 1). These differences may be caused by the interspecific differences in water holding capacity (Wagner & Titus, 1984).

Integrated potential assimilation (A_{int}) is lowest for *S. magellanicum*. In the case of low water tables and absence of precipitation, potential carbon uptake was
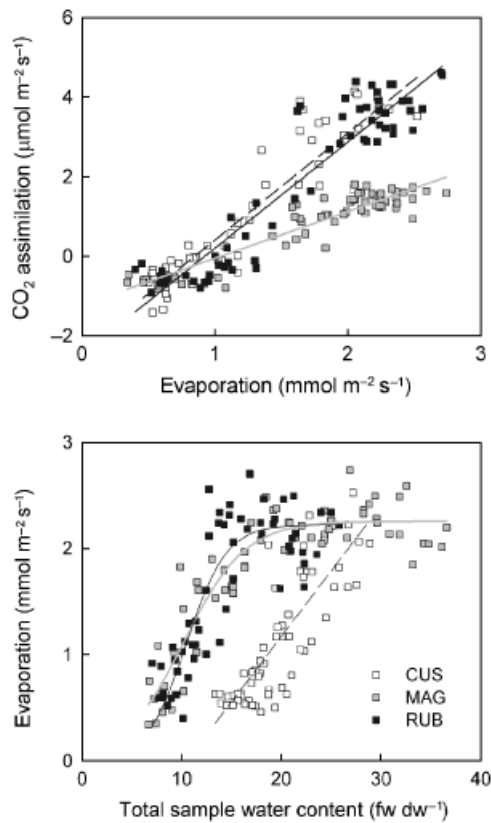
Fig. 6 (a) Relationships between evaporation and CO_2 assimilation of *Sphagnum cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB) grown at low water table without precipitation (LWT−) for 24 days. All relationships were highly significant: CUS: $R^2 = 0.85$, $F = 336.9$, $P < 0.001$; MAG: $R^2 = 0.85$, $F = 331.9$, $P < 0.001$; RUB: $R^2 = 0.88$, $F = 425.0$, $P < 0.001$. (b) Relationships between total sample water content and evaporation of CUS, MAG and RUB grown at LWT− for 24 days.

reduced for all species, yet uptake of *S. cuspidatum* was reduced more than that of the other two species (Fig. 2). These results stress the importance of taking species composition and changes therein into account when assessing changes in carbon budgets as a response to climate change, as they highly influence *Sphagnum* CO_2 assimilation.

Carbon uptake in relation to water content and light penetration

Net CO_2 uptake as a response to the water content of the total microcosm is more or less in accordance with that of the low water table treatment curves without precipitation (Figs 1 and 3a). We show that species differ in their response to total water content (Fig. 3a) but also to capitulum water content (Fig. 3b), although the specific responses toward total and capitulum water content diverge somewhat. The difference in response may be
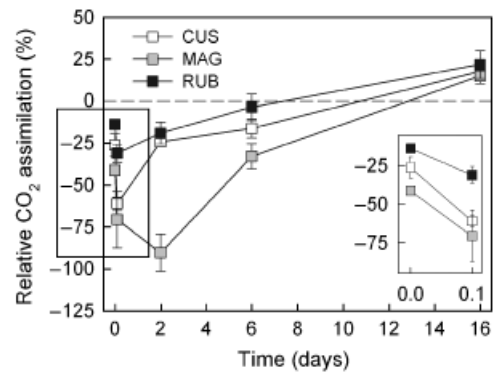

Fig. 7 Response of *Sphagnum cuspidatum* (CUS), *S. magellanicum* (MAG) and *S. rubellum* (RUB) to rewetting after a 14-day period in which CO_2 assimilation was negative, expressed as the percentage of CO_2 assimilation related to the maximum assimilation measured before the drought treatment. The inset figure corresponds to the first 2.5 h (≈ 0.1 day) after rewetting.

caused by the role of the capitulum layer in the carbon uptake of the *Sphagnum* carpet. Because light is essential for photosynthesis, the top layer of the *Sphagnum* vegetation is responsible for the bulk of the carbon uptake. Despite small interspecific differences in light absorption by the first centimeter of the capitulum layer (Table 3), it is clear that no light penetrates deeper than 2 cm in any of the species. Moreover, our results parallel the suggestion already made by Rydin & Jeglum (2006) that photosynthesis is most likely restricted to the upper centimeter. Consequently, when assessing the influence of water content on the net assimilation rate, capitulum water content, not the water content of the total sample, may be the most important differentiating factor (Fig. 4). Generally, capitulum water content is lower than the water content of the underlying layers, especially for *Sphagnum* grown at low water table (Fig. 5). At high water table, the water content of the capitulum section was expected to be close to saturation. From our data, however, it becomes evident that in the capitula, water lost by evaporation is not totally replaced by capillary transport. Because mosses cannot regulate water loss by evaporation, evaporation rates more or less indicate capitulum moisture content. Thus, the capitulum section of the microcosms was drier compared with the underlying sections, even at a high water table (Fig. 5). At low water tables, this effect is even stronger.

Interestingly, net CO_2 assimilation is well correlated to the amount of evaporation (Fig. 6), which may indicate that within the WC range applied here, water content of the top layer (i.e. capitulum water content) strongly determines CO_2 uptake, despite the absence of stomata in *Sphagnum*. The efficiency in water use (WUE) is lowest for *S. magellanicum*, which probably reflects its low capacity for carbon uptake. In the literature, no

consensus exists with respect to differences in the response of photosynthesis to capitulum water content between the functional groups of peat mosses (i.e. hummock, lawn, hollow) (see Rydin, 1985, 1993). From our results, we deduce that interspecific differences in assimilation rates in response to capitulum water content can affect the competitive strength between species. The low water contents in our experiment are clearly beneficial for *S. rubellum*, a true hummock species. *S. magellanicum*, which covers a broad niche along the hydrological gradient, seems hardly affected by capitulum water content, whereas *S. cuspidatum*, a true hollow species, shows a decrease in CO$_2$ assimilation when capitulum water contents become too high or too low. Moreover, our results indicate that the WUEs of *S. cuspidatum* and *S. rubellum* are very high at a low range of water content, whereas *S. magellanicum* is less conservative with its water, but can perform relatively well over a large range of water contents.

Recovery after drought

All *Sphagnum* species recovered from desiccation, but the time span in which species are allowed to recover from drought seems crucial (Fig. 7) and may explain why earlier studies (in which this time span was more short) failed to find recovery after prolonged drought (Silvola, 1991; Schipperges & Rydin, 1998). All species exhibited increased respiration rates shortly after rewetting, which has been reported earlier (e.g. Silvola, 1991; Schipperges & Rydin, 1998; McNeil & Waddington, 2003). This 'resaturation respiration' may be the result of increased microbial activity due to leakage of cell contents from damaged cells (Gupta, 1977; Gerdol *et al.*, 1996), but may also be caused by increased respiration of the mosses themselves, which is associated with the recovery of their damaged tissue. *S. magellanicum* appears to be more affected by desiccation than the other two species, as its initially increased respiration diminishes much slower than in the other species, yet recovery after 2 weeks was similar for all three. The initial strong respiration of the *S. magellanicum* microcosms may have large implications when assessing the long-term carbon budget of raised bogs.

Implications of environmental changes

Palaeobotanical records show that the overall cover of peat mosses on bogs can change over time as a response to changes in climate conditions such as temperature, precipitation and solar radiation (e.g. Svensson, 1988; Mauquoy *et al.*, 2001, 2002). Climate change-induced water table drawdown may affect the performance of peat mosses, but hitherto it remained uncertain whether this was caused by the direct effects of water table drawdown or by the effects of prolonged periods without precipitation. We show that frequent precipitation is important for the long-term carbon uptake of *Sphagnum* mosses. Frequent precipitation can even compensate for the negative effect of water table drawdown. Precipitation directly affects capitulum water content (Robroek *et al.*, 2007c), where most of the CO$_2$ uptake takes place. Yet, we found interspecific differences in the relation between net CO$_2$ assimilation and capitulum water content, which related to the niche along the water table gradient on which these species naturally occur. *S. cuspidatum* assimilation can be very high in a narrow range of hydrological conditions. Similarly, *S. rubellum* performs very well under a narrow, but relatively dry, range of hydrological conditions. *S. magellanicum* assimilation, on the other hand, is relatively low, but the species performs over a broad range of environmental conditions. All mosses were able to recover from desiccation in the long term, but carbon loss during the dry period was largest for *S. magellanicum*. Prolonged water table drawdown may alter the competitive balance between species, which concomitantly may change the species composition of the raised bog, favoring hummock species over hollow species. This study shows that changes in the patterns of precipitation are at least equally important as changes in water table and should be taken into account in predictions about the fate of peatlands in being carbon sinks or sources with respect to climate change.

Conclusions

In this study, we show that lack of precipitation, rather than a low water table per se, negatively affects CO$_2$ uptake of *Sphagnum*, with *S. cuspidatum* suffering more than *S. magellanicum* and *S. rubellum*. Capitulum water content is an important factor determining carbon assimilation, but the photosynthetic response to water content differs between species. Recovery after drought was slow, and 2 weeks after resumed precipitation treatment, carbon assimilation was still marginal, stressing the strong impact of drought on the carbon budget of raised bogs. Additionally, interspecific differences in the response to drought may impact upon the distribution of peat mosses along the surface of peatlands, which may have an effect on the future carbon balance in peatlands.

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