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Photosynthesis of *Sphagnum fuscum* at long-term raised CO_2 concentrations

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Rate of net photosynthesis in *Sphagnum fuscum* (Schimp.) Klinggr. was measured during long-term (50–122 days), and subsequently during short-term ($^1/_2$ h), exposure to 350, 700, 1 000 or 2 000 ppm CO_2 concentrations. Raised CO_2 concentrations caused a general increase in the rate of net photosynthesis, increasing the rate of photosynthesis at light saturation and causing a given rate of net CO_2 exchange to be reached at lower light fluxes. The relative increase in the rate of net photosynthesis by increasing radiation fluxes was independent of the CO_2 treatment. The rates of net photosynthesis at enhanced CO_2 concentrations gradually decreased compared to rates found with the 350 ppm treatment and this acclimation was also noticed during short-term exposure to all four CO_2 concentrations. At 2 000 ppm of CO_2, the depression of net photosynthesis at high water contents, found at lower CO_2 concentrations, was removed. Observed rates of net photosynthesis indicated that water-use efficiency of *Sphagna* was not coupled with constant long-term CO_2 concentrations.

Keywords: acclimation, carbon dioxide, light flux, moss, peat, water content

INTRODUCTION

The effect of increased CO_2 concentrations on the photosynthesis of vascular plants, especially crop plants, has been widely documented. Many C_3 vascular plants have been found to acclimate to raised CO_2 concentrations: after an initial increase in net CO_2 exchange, a marked decrease has been observed after prolonged exposure (Wong 1979, DeLucia *et al.* 1985, Williams *et al.* 1986). As *Sphagna* usually grow on peat, itself formed by slow decay of the peat mosses, they may be exposed to raised CO_2 concentrations for extended periods, independent of any long-term increase in ambient atmospheric CO_2 concentrations. In short-term experiments in which *Sphagna* have been exposed to raised CO_2 concentrations, a clear increase has been found in net CO_2 exchange (Silvola 1985, 1990). However, despite the areal extent of *Sphagnum*-covered areas in the northern hemisphere, the responses of *Sphagna* to long-term raise of CO_2 concentrations have not been extensively studied.

The light reactions in photosynthesis are mainly dependent on light flux, whereas CO_2 fixation and the formation of carbohydrates take place in temperature-dependent dark reactions. At low temperatures, low rates of dark reactions restrict the processes in photosynthesis and therefore light saturation is reached at a lower radiation flux (*see* Proctor 1978 and the references therein). For *Dicranum majus* Turn. (Silvola 1985) and *Hylocomium splendens* (Hedw.) B.S.G. (Sonesson *et al.* 1992), CO_2 concentrations above ambient concentrations have been found to increase the net CO_2 exchange rates and thus to compensate for low radiant flux. Mosses grown at high radiant flux conditions show a distinct increase in the rate of net photosynthesis at enhanced CO_2 concentrations. For example, doubling the CO_2 concentration from 320 ppm CO_2 while keeping photosynthetically active radiation (PAR) fixed at 500 µmol m^{-2} s^{-1}, doubled the rate of net CO_2 exchange of *D. majus* (Silvola 1985). However, the relationship between radiation flux and net rate of CO_2 exchange in *Sphagna* grown at raised CO_2 concentrations for long periods has not previously been studied.

Sphagna stay wet by upward capillar movement of water but they are unable to control their tissue water content (Titus & Wagner 1984, Rydin & McDonald 1985, Wallén *et al.* 1988) and their CO_2 uptake is more or less controlled by abiotic factors (Nobel 1991). Silvola (1985) observed that, the maximum rate of net photosynthesis in *Sphagnum fuscum* (Schimp.) Klinggr. gradually shifts towards higher water contents with increasing CO_2 concentration and that the typical decrease in CO_2 exchange observed at higher water contents, found at lower CO_2 concentrations, disappears.

The effect of water content on rate of photosynthesis seems to depend greatly on the structure of the moss (Rydin & McDonald 1984, Silvola & Aaltonen 1984, Titus & Wagner 1984, Silvola 1991). Capitulum dry mass in *Sphagnum fuscum* has been found to increase at long-term raised CO_2 concentrations (Jauhiainen *et al.* 1994). Dependence of relative CO_2 exchange rates on capitulum water content may therefore reflect structural differences between *Sphagna* formed at various CO_2 concentrations.

The aim of the present experiment was to investigate the effect of long-term raised CO_2 concentrations on the rate of net photosynthesis of *Sphagnum fuscum* at varying light, temperature and moisture conditions. Possible acclimation of net photosynthesis to the raised CO_2 concentrations was first followed during a long-term exposure period and then after short-term exposure to the range of CO_2 concentrations used in the long-term experiment but with constant light flux and temperature conditions. The possible effects of long-term raised CO_2 concentrations on the rate of net photosynthesis at various water contents in *Sphagna* were studied by subsequently determining the response to all these CO_2 concentrations in short-term exposures.

MATERIALS AND METHODS

Sphagnum fuscum samples were collected at the beginning of the growing season from a *Sphagnum fuscum* pine bog, Ahvensalo mire (62°51´N, 30°53´E), in eastern Finland in May 1989. The sampling site was characterised by low hummocks and scattered small Scots pine (*Pinus sylvestris* L.) trees. Other common species in the ground layer were *Empetrum nigrum* L., *Andromeda polifolia* L. and *Rubus chamaemorus* L., and the bottom layer was dominated by *S. fuscum*, *S. angustifolium* (Russ.) C. Jens. and *S. balticum* (Russ.) C. Jens.

Sections of the surface layer of the *Sphagnum fuscum* carpet (30 × 40 cm, depth 20 cm) were cut, placed into plastic containers and taken to a greenhouse at the University of Joensuu. The water table in the containers was kept at ca. 5 cm below the capitulum level during transportation and for the few days before further handling. Subsamples were taken by pressing an upturned Petri dish (∅15 cm) into the surface of the *Sphagnum* sections and cutting away the uppermost part of the mosses. The Petri dishes containing the shoots were then turned over and the stems cut level with the height of the Petri dish (1.5 cm height). Another dish with four 2 mm diameter holes in the bottom was then placed over the trimmed stems and the whole arrangement turned over again. The first dish was removed to expose the capitula.

The samples were placed in four growth chambers (six samples per chamber) for 100–122 days. The stems were trimmed 1–3 times during the first 50 days by using the procedure described above. The temperature in the chambers was usually some °C higher than the daily summer temperature at the field sampling site, reaching 30°C on some warm days. The chambers received natural sunlight through the transparent plastic walls of the greenhouse and growth chambers. Four CO_2 concentrations in the growth chambers were maintained automatically by a data acquisition system (Hewlett-Packard 3421 A), which directed gas samples from the growth chambers to an absolute infra red gas analyzer (IRGA, Uras 2, Hartmann & Braun) and if needed, regulated the gas flow from a CO_2 source. The applied CO_2 concentrations were: the reference (350 ppm), the doubling scenario (700 ppm), and two highest concentrations (1 000 and 2 000 ppm) selected in order to study response to CO_2 concentrations on a wider scale. The samples were watered daily throughout the experiment by dipping the Petri dishes into deionized water for approximately 5 seconds, excess water draining out through the holes in the bottom of the dish.

For CO_2 exchange measurements, pneumatically regulated trap-type plexi-glass gas exchange chambers, of the shape and size to fit over a Petri dish, were placed over the samples in the growth chambers (*see* Silvola (1985) for a more detailed description of the procedures). The gas exchange chamber was fully closed and an air flow of 60 l h^{-1} was conducted through it for 100 seconds. Net CO_2 exchange rate was measured by a differential IRGA (URAS 2 T, Hartmann & Braun) connected to a data acquisition system (Hewlett-Packard 3052A). Temperatures in the exchange chamber and inside the moss sample, as well as the light flux, were measured during the CO_2-exchange measurement.

The measurements were made after an initial growth period of 50 d. Each day afterwards, two randomly selected samples from each CO_2 chamber that had been watered on the previous day, were placed in the gas exchange chambers (two of them in each growth chamber). After each measurement, the samples were weighed and returned to the same chamber. Weights were used to calculate the water content of the mosses. Natural sunlight was used in the first phase of the experiment. The measurements were carried out for a period of some 70 days.

After 100 days from the start of exposure of samples to the long-term CO_2 treatment, a new procedure for measuring rate of net photosynthesis was used. In this second phase of the experiment the samples were placed in a Bioklim 2.6 growth chamber (Kryo-service, Helsinki), after watering and weighing, and exposed to short-term cycles of each of the same CO_2 concentrations as used in the first phase of the study. The exposure to each of the four CO_2 concentrations lasted ca. $^1/_2$ h, during which the net photosynthesis measurement were made as described above. The four CO_2 concentrations were cycled consecutively in the growth chamber for 3 days during which the samples progressively dried out. The weight of the sample after each measurement was recorded and the oven dry weight determined after the 3 days of measurement. Constant light flux (340 µmol m^{-2} s^{-1} PAR) and temperature (22°C) were maintained throughout this phase of the experiment.

When studying the net photosynthesis at various light fluxes during exposure to the four long-term CO_2 concentrations, non-linear regression analysis was used. Analysis of variance was applied to the data to study the acclimation of net photosynthesis to long-term CO_2 concentrations and net photosynthesis at various water contents. For these statistical analyses, SPSS for Windows (©SPSS Inc.), release 6.1, was used.

RESULTS AND DISCUSSION

Photosynthesis in long-term CO_2 exposure

Within the light fluxes of the experiment (0–1 000 µmol m^{-2} s^{-1} PAR), net CO_2 exchange rates of *S. fuscum* exposed to raised long-term CO_2 concentrations increased by 16%–125% compared to the samples grown in the reference CO_2 concentration (350 ppm) (Fig. 1). The highest increase in the net rate of photosynthesis, about doubling at the radiation flux of 100 µmol m^{-2} s^{-1} PAR, was found for samples grown between adjacent CO_2 treatment concentrations 350 and 700 ppm. Differences in the net rate of photosynthesis between the three highest CO_2 concentration treatments were 5%–19%. At light fluxes up to 400 µmol m^{-2} s^{-1} PAR, the non-linear regression model suggested somewhat higher net photosynthesis for samples grown at 1 000 ppm compared to samples exposed to 2 000 ppm CO_2 (Fig. 1). As the rate of net CO_2 exchange was enhanced at relatively low radiation fluxes, especially at the two lowest CO_2 concentrations, more effective carbon exchange may be expected also in moss stands under field conditions. According to the simulation of field CO_2 concentrations by Silvola (1985), the increase in CO_2 exchange may be as high as 6.3% in *Sphagnum fuscum* in the actual prevailing CO_2 concentrations as compared to 320 ppm.

At 350 ppm CO_2, the highest net rate of photosynthesis according to the model was 215 mg CO_2 m^{-2} h^{-1}. Due to form of the model used, net photosynthesis reaches saturation level very slowly as a function of light flux. In practice, maximum net CO_2 exchange was estimated to take place at radiation fluxes < 400 µmol m^{-2} s^{-1} PAR at 350 ppm CO_2 (*see* Fig. 1). Although much higher light fluxes occur during the growing season (Johansson & Linder 1980, Silvola 1985), these are only occasional and radiation usually remains below the light saturation level for *Sphagnum fuscum* photosynthesis in the normally occurring ambient CO_2 concentration. The highest net rate of photosynthesis in samples grown at 700 or 1 000 ppm CO_2 treatments, estimated by the fitted non-linear regression model, were 518 and 624 mg CO_2 m^{-2} h^{-1}, respectively (Table 1). Net photosynthesis saturation in the 2 000 ppm CO_2 treatment was expected to be 675 mg CO_2 m^{-2} h^{-1}, while

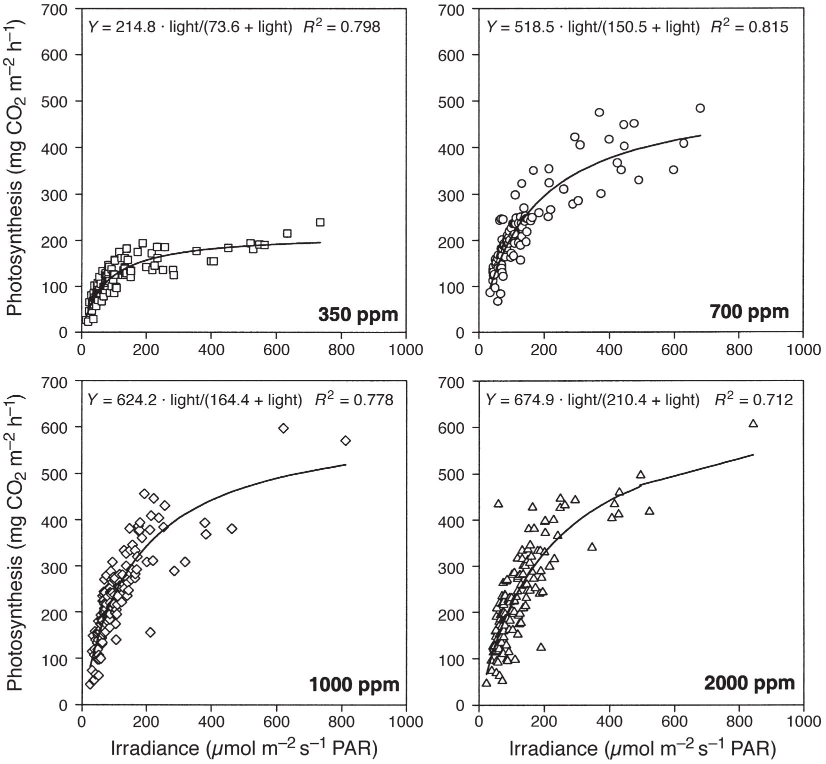

Fig. 1. Net rate of photosynthesis of *Sphagnum fuscum* at the four CO_2 concentrations at which the plants were grown (350, 700, 1 000 or 2 000 ppm). Open symbols represent measured net photosynthesis and the line is the fitted curve (*see* Table 1).

saturation would have taken place at a light flux beyond the maximum used in the experiment (Table 1 and Fig. 1). The net rates of photosynthesis measured in growth chambers may be slightly different than in field conditions because of greater vigour of chamber-grown material (Harley *et al.* 1989). However, altered growing conditions are not likely to affect the relative differences in the photosynthetic response at various CO_2 concentrations.

Table 1. *Sphagnum fuscum* net photosynthesis regression models. The data are fitted to hyperbolic curves of the form $Y = Q \times \text{light}/(K + \text{light})$, where Q = net rate of photosynthesis under light saturation and K = radiation flux at the point where half of the light saturation, is achieved in net photosynthesis. Estimates for parameters K and Q, their asymptotic SE and R^2-goodness of fit are presented. Data include measurements at 18–25°C, < 2 200% dry weight water content and irradiation 0–1 000 μmol m^{-2} s^{-1} PAR.

CO_2 concentration (ppm)	Parameter	Estimate	Asymptotic	
			SE	R^2
350	*K*	73.6	6.6	0.798
	Q	214.8	7.6	
700	*K*	150.5	13.4	0.815
	Q	518.5	22.4	
1 000	*K*	164.4	16.1	0.778
	Q	624.2	33.7	
2 000	*K*	210.4	25.8	0.712
	Q	674.9	47.4	

The ratio between estimated net rate of photosynthesis at the radiation flux where half of the theoretical maximum of net photosynthesis is reached (*K*) and rate of net photosynthesis at saturation (*Q*) were compared between the four CO_2 treatments. The largest difference in the ratio K:Q between the four CO_2 concentrations was only 0.9%, which indicated that the relative changes in the rate of net photosynthesis over radiation fluxes were independent of available CO_2 concentration. Silvola (1985) has made a similar observation about the net photosynthesis of *Dicranum majus* grown at somewhat lower light fluxes and CO_2 concentrations. The light level where half of the theoretical maximum net photosynthesis was reached (*K*) was displaced towards higher radiation fluxes; most notably between CO_2 concentrations of 350 ppm and 700 ppm, and between 1 000 ppm and 2 000 ppm, respectively (Table 1).

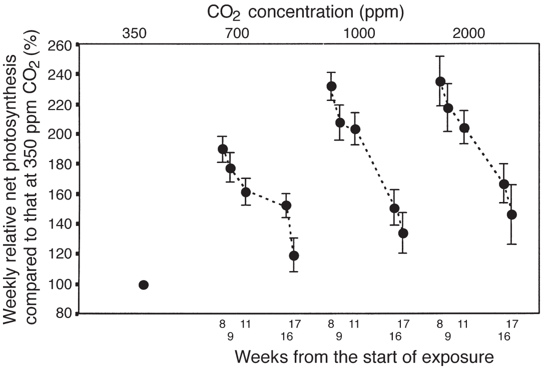

Fig. 2. Weekly relative rate of net photosynthesis at four long-term CO_2 concentrations (%) compared to that at 350 ppm CO_2 (100%) in *Sphagnum fuscum* at various times from the start of exposure. All measurements of photosynthesis at each week have been pooled across all the radiation fluxes, temperatures and water contents. Mean ± SE presented.

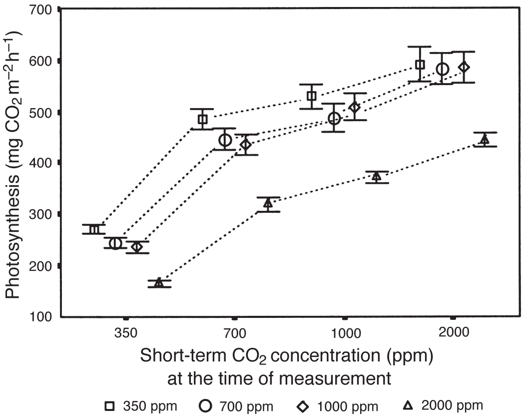

Fig. 3. Rate of net photosynthesis of *Sphagnum fuscum* at four short-term CO_2 concentrations. Before the short-term exposures, samples were grown at four long-term CO_2 concentrations for 100–122 days (indicated by different symbols). Temperature 22°C, radiation flux 340 μmol m^{-2} s^{-1} PAR and water content 800%–2 000% DM. Mean ± SE presented.

Acclimation of photosynthesis

The rate of net CO_2 exchange at increased CO_2 clearly declined with time of exposure, relative to that observed in the 350 ppm CO_2 reference treatment (Fig. 2). Just after the measurements started (50 d) after start of experiment, the net rate of photosynthesis at 700 ppm CO_2 was nearly twice as high as the rate at 350 ppm and the relative rates at 1 000 and 2 000 ppm CO_2 were even higher. However, 17 weeks after the start of exposure, CO_2 exchange rates at enhanced CO_2 concentrations were only ca. 20%–40% higher than at 350 ppm (Fig. 2). It is also worth noticing that between the start and the end of exposure of mosses to a constant CO_2 concentration of 350 ppm the net photosynthesis did not differ significantly (F = 0.1967 in one-way ANOVA and Tukey B-test with 0.050 significance level, $n = 84$).

Short-term exposure of samples to any CO_2 concentration higher than the long-term CO_2 concentration clearly increased the rate of net photosynthesis. In contrast, a comparable decrease was found in net photosynthesis at CO_2 concentrations below the long-term CO_2 concentration (Fig. 3). Independently of the former long-term CO_2 concentration, the greatest difference in net photosynthesis resulting from short-term exposure to raised CO_2 was found between measurements recorded at 350 ppm and 700 ppm CO_2 ($F = 0.0000$ in one-way ANOVA and Tukey B-test with 0.050 significance level, $n = 15$), although distinct differences in the rates of net CO_2 exchange were also found between the higher CO_2 concentrations (Fig. 3).

Independently of the short-term CO_2 concentration applied, the lowest rate of net photosynthesis was associated with the samples grown in long-term exposure at 2 000 ppm CO_2 and the highest rate of net CO_2 exchange was associated with the samples grown in the long-term 350 ppm CO_2 treatment. Net photosynthesis of samples grown at long-term 700 ppm and 1 000 ppm CO_2 treatments fell between values of the other two long-term CO_2 treatments. The photosynthetic rates of mosses grown in 2 000 ppm CO_2 were so low that even if measured at this CO_2 concentration, the net photosynthesis was about the same as for mosses grown in long-term exposure at 700 or 1 000 ppm CO_2 and measured at 700 ppm CO_2 (Fig. 3). Sonesson *et al.* (1996) found that the apparent photosynthetic efficiency of *Hylocomium splendens* grown at 600 ppm CO_2 concentration was 16% lower than that in samples grown at ambient (350 ppm) CO_2 concentration.

Van der Heijden *et al.* (1998) found marked increase in quantities of non-structural carbohydrates in *Sphagnum papillosum* Lindb. and *S. balticum* grown at doubled CO_2 concentrations relative to normal ambient levels. Furthermore, they found that increase explained ca. 10%–25% of the shoot dry mass increase at raised CO_2. Although increased shoot unit dry masses at raised CO_2 is observed in some *Sphagnum* species, the response in dry mass production remains surprisingly low (Jauhiainen *et al.* 1994, 1997, 1998, van der Heijden *et al.* 1998). For vascular plant species, one of the consequences of reduced photosynthetic rates related to raised CO_2 concentrations is an increased amount of carbohydrates in leaves (Cave *et al.* 1981, DeLucia *et al.* 1985). It may therefore be that the low response by dry mass production to raised CO_2 we observed in *Sphagna* (Jauhiainen *et al.* 1994, 1997, 1998) is also due to an increased content of carbohydrates in the photosynthetically active tissues, thus leading to lowered sensitivity of net photosynthesis to available CO_2 concentration.

In some vascular plant species, resource limitation, e.g., by nutrients, has been found to be associated with the decline in CO_2 uptake rates during long-term exposure to enhanced CO_2 concentrations (Williams *et al.* 1986, Tissue *et al.* 1993, Sage 1994). The nutrient content of the samples was not determined, but in a similar experiment with *Sphagnum fuscum*, the tissue N and P concentrations did not vary with CO_2 concentration treatments (unpublished data). Therefore, the gradual decrease in net photosynthesis of *S. fuscum* grown at raised CO_2 concentrations is not likely to be due to nutrient deficiency. In vascular plants, decreased rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) activity has been found in samples grown at increased CO_2 concentrations (Wong 1979, Vu *et al.* 1987, Sage *et al.* 1989, Yelle *et al.* 1989, Ziska *et al.* 1991, Tissue *et al.* 1993). Rubisco activity was not measured in this study and the role of this enzyme, responsible for CO_2 fixation, in explaining of the results, remains unknown.

Photosynthesis at different water contents

Following exposure to 350 ppm CO_2, the rate of net photosynthesis of the *Sphagna* increased with increasing water content but decreased when the water content went above an optimal range, ~ 800%–1 400% DM (per cent of dry mass; Fig. 4). These findings are in agreement with the results of earlier studies (Silvola & Aaltonen 1984, Silvola 1990, 1991). The reduction in rate of photosynthesis at high water contents has been shown to be due to slow diffusion rates of CO_2 at the ambient CO_2 concentration (Stålfelt 1937, Grace & Marks 1978, Proctor 1978, Lange & Matthes 1981, Alpert & Oechel 1985, Proctor *et al.* 1992). At 700 and 1 000 ppm CO_2, the optimal water content for photosynthesis was ca. 1 000%–1 600% DM and 1 000%–1 800% DM respectively, i.e. the range of optimal water contents for photosynthesis shifted to higher and wider limits with increasing CO_2 concentrations, which also agrees with the observation by Silvola (1990; *see* also Fig. 4). At the 2 000 ppm CO_2 concentration, the highest rates of net photosynthesis were reached at a water content of ca. 1 200% DM and did not decrease markedly with increased moisture (Fig. 4). Thus, by increasing the CO_2 concentration strongly enough, the partial pressure of the CO_2 in the photosynthetically active tissue is increased so much that the mosses are enabled to continue photosynthesizing at high rates even when the tissue is water-saturated.

The changes in shoot density, dry masses of shoot, length increment and dry mass production have been found to be, for the most part, independent of each other at various CO_2 concentrations (Jauhiainen *et al.* 1994, 1997, 1998, van der Heijden *et al.* 1998). However, long-term exposure to raised CO_2 has been found to increase the capitulum dry mass of many *Sphagnum* spp., including *S. fuscum* (Jauhiainen *et al.* 1994, 1998). It has also been shown that the relationship between net photosynthesis and water content varies among species due to differences in structure (Silvola & Aaltonen 1984, Titus & Wagner 1984, Rydin & McDonald 1985, Silvola 1991). Differences in net photosynthesis at raised CO_2 concentrations and at various water contents might therefore be due to structural differences between *S. fuscum* formed at each of the four long-term CO_2 concentrations. However, the water use efficiency of net photosynthesis of *S. fuscum* was not adapted to long-term CO_2 concentration as the net rates of photosynthesis at increased moisture were quite uniform between *Sphagna* formerly grown at any of these four CO_2 concentrations (Fig. 4). Among the various long-term CO_2 exposure treatments, the only statistically significant differences in rates of net photosynthesis were associated with

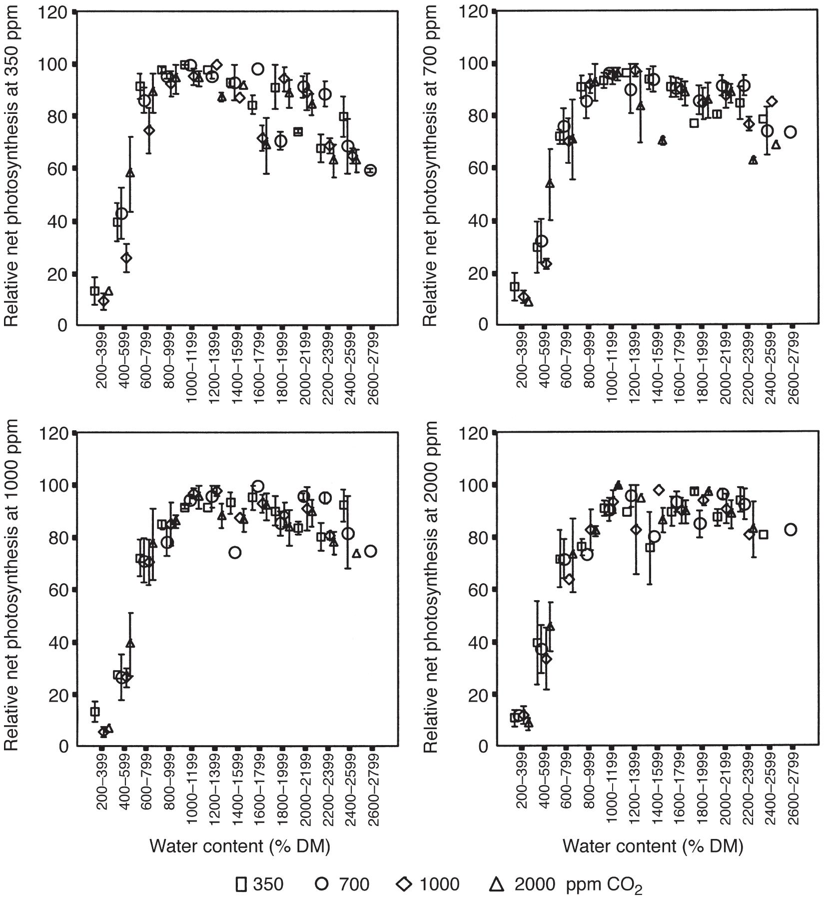

Fig. 4. Relative rate of net photosynthesis (% of maximum) of *Sphagnum fuscum* at various water contents (% DM) in short-term exposures to four CO_2 concentrations. Samples were first grown at 350, 700, 1 000 or 2 000 ppm CO_2 for 100–122 days (indicated by different symbols). Temperature 22°C and radiation flux 340 μmol m^{-2} s^{-1} PAR. Mean ± SE presented.

the 350 ppm and 2 000 ppm CO_2 treatments when the water content was 1 800% DM or higher.

Higher air temperatures and a longer growing season are predicted at northern latitudes in the future as a result of climatic warming (Gorham 1991). Some scenarios predict warmer and drier summers, which may lead to a lowering of water tables (Manabe & Wetherald 1986, Mitchell 1989), and therefore increased decomposition of the peat and subsequent emissions of CO_2 (Moore & Knowles 1989, Freeman *et al.* 1993, Laine *et al.* 1996). Thus, although the rate of photosynthesis of *Sphagnum fuscum* may be somewhat enhanced at raised CO_2 concentrations, the results of this study indicate that the effect of increasing CO_2 concentrations would be counteracted by the negative effect of lowering of the water-table on moss water content, leading to lowered photosynthesis. Negative effects of lowering of tissue water content on photosynthetic rate and dry mass production has been shown also in other studies (e.g., Silvola & Aaltonen 1984, Rydin & McDonald 1985, Lindholm 1990).

In conclusion, the instantaneous rate of net photosynthesis in *Sphagnum fuscum* was shown to clearly increase when exposed to raised CO_2 concentrations, though the response was somewhat lowered after prolonged exposure. At increased CO_2 concentrations, we show that the rate of net photosynthesis is greater at higher light fluxes and that the maximal rate of photosynthesis occurs at higher water contents. However, it appears that the net photosynthesis of *S. fuscum* is not able to adapt to long-term raised CO_2 concentrations to such an extent that it affects the sensitivity of net photosynthesis to various water contents.

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