

Mixing ratio and species affect the use of substrate-derived CO₂ by *Sphagnum*

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Abstract

Question: Can mixing ratio and species affect the use of substrate-derived CO₂ by *Sphagnum*?

Location: Poor fen in south Sweden and greenhouse in Wageningen, The Netherlands.

Methods: Two mixing ratios of *Sphagnum cuspidatum* and *S. magellanicum* were exposed to two levels of CO₂ by pumping CO₂ enriched and non-enriched water through aquaria containing the species mixtures in the greenhouse.

Results: Enhanced CO₂ stimulated the production of *S. cuspidatum*, but only in aquaria co-dominated by *S. magellanicum*, coinciding with higher CO₂ concentrations in the water layer. The denser growing *S. magellanicum* seemed to reduce gas escape from the water, resulting in accumulation of dissolved CO₂. Adding CO₂ did not affect species replacement.

Conclusions: The use of substrate-derived CO₂ for *Sphagnum* production depended on species identity and mixing ratio. The effect of mixing ratio on CO₂ concentrations in the water layer suggests that species composition may affect both the efficiency with which substrate-derived CO₂ is trapped and subsequently used. This could result in hitherto unexplored feedbacks between vegetation composition and gas exchange.

Keywords: Bog; Bryophyte; Carbon production; Gas exchange; Mire; Peatland.

Nomenclature: Daniels & Eddy (1990).

Abbreviations: Peatlands = *Sphagnum* dominated peatlands; Sc = *Sphagnum cuspidatum*; Sm = *Sphagnum magellanicum*.

Introduction

Although *Sphagnum*-dominated peatlands (peatlands) have sequestered atmospheric carbon (C) since the last ice age (Turunen et al. 2001), many peatlands are currently balancing between being sinks or sources for atmospheric C (Heikkinen et al. 2004). Whether a peatland emits or sequesters C is mainly determined by the balance between C evolving from the peat layers and the amount of C fixed by the upper thin layer of living vegetation, mostly made up by mosses from the genus *Sphagnum*. The balance itself seems to depend on succession stage or dominant microform, with moist lawn vegetation showing a higher short-term sequestration rate than wet hollow or relatively dry hummock vegetation (Strack et al. 2006).

The relative abundance of each microform, and concomitantly the dominant *Sphagnum* species, may shift as a result of natural succession as the age of a peatland increases and as a response to climatic change. Under dry conditions a shift usually occurs towards hummock vegetation, whereas under wet conditions a shift towards hollow vegetation is observed (Bragazza 2006). Shifts in these microforms may be reflected in the functioning of the ecosystem such as its surface hydrology or its potential for the sequestration of C (Belyea & Baird 2006). In general, a decrease in water availability favours *Sphagnum* species characteristic for drier microforms (Robroek et al. 2007) and promotes CO₂ production (Strack et al. 2006). To what extent the increased availability of substrate derived CO₂ may be captured and reused by *Sphagnum* is ambiguous and may differ between species. CO₂ has been shown to affect growth of hollow and lawn *Sphagnum* species in monocultures (Riis & Sand-Jensen 1997; Heijmans et al. 2001) but information on how species mixtures respond to enhanced CO₂ is scarce. Mitchell et al.

(2002) showed that CO₂ favoured lawn-species *S. fallax* in competition with *Polytrichum strictum* and Smolders et al. (2001) showed that CO₂ stimulated the formation of structural tissue, allowing emergent lawn species to rise above the water table. The latter would presumably increase their competitive ability relative to hollow species.

In this study we focus on the effects of mixing ratio and species on the use of substrate-derived CO₂. We selected the hollow species *S. cuspidatum* and the lawn species *S. magellanicum*. Living *S. cuspidatum* dominates from submerged conditions to 5 cm above the water table in the field, whereas *S. magellanicum* may dominate from 5 cm to 25 cm above the water table (Daniels & Eddy 1990). In line with expectations from Smolders et al. (2001), we expected that *S. magellanicum* would profit more from substrate-derived CO₂ than *S. cuspidatum*. To test this hypothesis we conducted a greenhouse experiment in which we exposed mixtures of *S. magellanicum* and *S. cuspidatum* in two mixing ratios to two levels of CO₂ by pumping CO₂ enriched and non-enriched water through aquaria containing the species mixtures. The mixing ratios represented a situation dominated by *S. cuspidatum* and a situation co-dominated by both species, mimicking a species assemblage of an early and later succession stage. At the start of the experiment, the water level for both mixtures was set at 5 cm below the moss surface, reflecting the position above the water table where *S. magellanicum* is often observed to colonize *S. cuspidatum* vegetation.

Methods

Experimental set-up

In August 2005, cores (0.1 m diameter, 0.1 m depth 0.1 m) of mono-specific *Sphagnum magellanicum* and *S. cuspidatum* stands were cut from a south Swedish poor fen site (56° 51' N, 13° 27' E). The species were collected adjacent to each other at microhabitats with a high water table (ca. 5 cm below the *Sphagnum* surface) and sparse vascular plant cover (< 1 %). The cores were transported to Wageningen and stored for one month at 1 °C in the dark. In September 2005 the peat mosses were randomly assigned to four treatments; two mixing ratios and two CO₂ treatments. An additional five cores per species were used for assessing capitulum density and biomass at the start of the experiment (t_0 , see measurements).

Treatments were assigned as follows. First the cores were divided into halves and quarters, which were subsequently reassembled into mixing ratios: one mixture dominated by *S. cuspidatum* (Sc dominant) and one mixture where both species occupied equal

areas (Sc-Sm co-dominant). The mixtures were divided among aquaria (0.1 m × 0.1 m, height 0.25 m), with ten aquaria per mixture. After an acclimatization period of two weeks, the CO₂ treatment levels were assigned to each mixture, with half of each mixture treatment receiving extra CO₂ and half receiving no extra CO₂. The aquaria were grouped into five replicate blocks in the greenhouse.

The water level in the containers was kept at a fixed level throughout the experiment by means of an outflow in the aquaria. At the beginning of the experiment the water level was set at 5 cm below the *Sphagnum* surface and not adjusted for moss growth. We choose this set-up to mimic the situation in the field where distance to the water table increases with *Sphagnum* height increment. Demineralized water was supplied to the aquaria from ten storage containers (25 l) by means of a peristaltic pump with ten outlets, at such a rate that the water in the aquaria was replaced ca. twice per 24-h period. Four times per week, the flow rate of the aquaria was checked, and adjusted when necessary. Each block had its own two storage containers (one with extra CO₂ and one without extra CO₂), with the two mixture treatments sharing one container and one pump outlet.

CO₂ was applied to the aquaria as a supersaturated water solution similar to Smolders et al. (2001) by passing pure gaseous CO₂ through the demineralized water of the containers designated for the CO₂-aquaria. The water in all containers was covered by a layer (3 cm) of sunflower oil to keep the water in the supersaturated CO₂ containers. The resulting CO₂ concentration in the water was ca. 0.4 mmol.l⁻¹ for the aquaria without extra CO₂ and 1.5 mmol.l⁻¹ for aquaria with extra CO₂ (see Results).

Precipitation (equivalent to 780 mm a year) was simulated once a week by dripping 15 ml artificial rainwater solution (Garrels & Christ 1965) over the *Sphagnum* surface with a syringe. No nutrients were added during the experiment. The experiment lasted from 26.09.2005 to 27.03.2006.

Relative humidity in the greenhouse was set at 70%, temperature varied from 25 °C (day) to 15 °C (night) and natural light was supplemented by high pressure sodium lamps (Philips MASTER SON-T PIA agro 400W E E40 SLV, Luminous flux EM [Lm] 55000) to induce a 12-h photoperiod, using three lamps for 5 m².

Measurements

To test whether the CO₂ treatment resulted in enhanced CO₂ in the aquaria, the concentration of total inorganic carbon (C) as well as the pH of the aquarium-water was measured once a month. Total inorganic carbon was measured colorimetrically. Since the water

pH stayed below 4.2 (4.0 ± 0.04 SE), we assumed that all inorganic carbon was present in the form of CO₂. To check for differences in through-flow and concomitant differences in CO₂ flux between the aquaria, through-flow per aquarium was monitored four times a week.

Sphagnum height increment was measured once a month at eight fixed points per aquarium, with a minimum of three points per species, by measuring the distance of the moss surface to the top of the aquaria. Mean data were calculated to obtain one measurement per species per aquarium. The area covered by the individual *Sphagnum* species was measured on the same day as *Sphagnum* height increment by taking a digital image of the moss surface. For each species, cover was calculated using the graphical programme ImageJ (version 1.34s, Wayne Rasband, National Institute of Health, Bethesda, MD, USA).

At final harvest, the number of capitula per species per aquarium was counted. Subsequently, a minimum of 15 *Sphagnum* individuals per species per aquarium were randomly selected and cut into a top capitulum section (0-1 cm) and a stem section (1-3 cm). Capitulum fresh weight was determined and both capitulum and stem sections were oven dried at 70 °C for 48 h before dry weight was determined. Capitulum water content was expressed as the ratio between fresh and dry weight. Measurement of capitulum water content occurred three days after the last precipitation event. *Sphagnum* production during the experimental period P ($\text{g}\cdot\text{m}^{-2}$) was calculated per species using the capitulum correction method (Clymo 1970), adapted for species mixtures. As such, the formula encompassed stem productivity over the experimental period ($D_{t_x} \times S_{t_x} \times G$) corrected for cover changes ($0.5 \times ((D_{t_x} - D_{t_0}) \times S_{t_x} \times G)$), assuming that half of the cover change during the experimental period resulted in changed stem biomass, and changes in capitulum

biomass over the experimental period ($D_{t_x} \times C_{t_x} - D_{t_0} \times C_{t_0}$), yielding:

$$P = (D_{t_x} \times S_{t_x} \times G) - 0.5 \times ((D_{t_x} - D_{t_0}) \times S_{t_x} \times G) + (D_{t_x} \times C_{t_x} - D_{t_0} \times C_{t_0}) \quad (1)$$

D = no. capitula per m², S = stem dry weight in g per cm stem, G = *Sphagnum* height increment in cm, C = capitulum dry weight in g per capitulum, t_0 = start experiment and t_x = end of the experiment.

Statistical analyses

Data for three aquaria were omitted from all analyses due to infection by the fungal parasite *Tephroclype palustris* (Limpens et al. 2003), leaving a minimum of three replicates per treatment. Remaining data were tested for their normality and equality of variance and, if necessary, transformed by taking their natural logarithm. Treatment effects on CO₂ concentration in aquarium-water were tested for five dates with an ANCOVA with CO₂ treatment, block and mixture as factors and date as a co-variable. ANCOVA was possible because concentrations measured for consecutive dates turned out to be independent from each other. We omitted one sampling date from the analyses to improve equality of variance. *Sphagnum* performance was analysed per mixing ratio with repeated measures ANOVA (height increment, cover change) or ANOVA (production) with CO₂ treatment and species as independent factors. For these analyses, block (which was not significant) was omitted from the models to gain degrees of freedom. Relationships between variables were tested with linear regression.

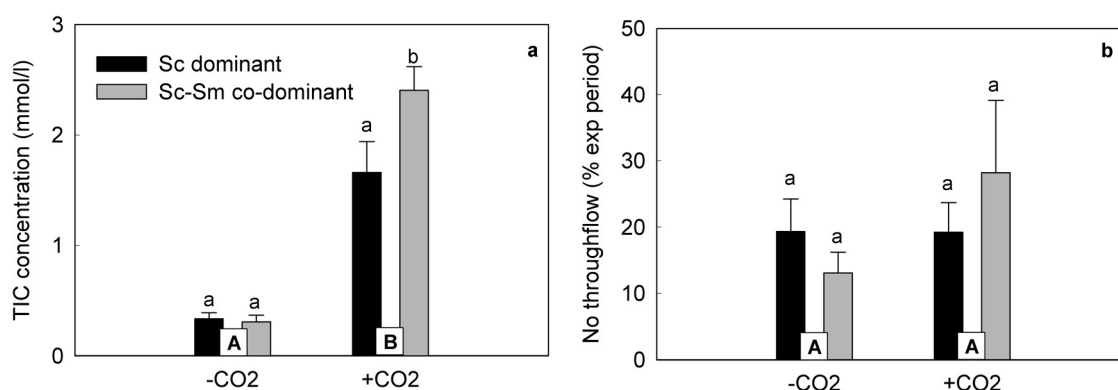


Fig. 1.a. The concentration of total inorganic carbon in the aquarium water over the experimental period (mean + 1 SE) per CO₂ treatment and mixture. Sc = *Sphagnum cuspidatum*; Sm = *Sphagnum magellanicum*. Different letters indicate significant (ANCOVA, $P < 0.05$) differences between the CO₂ treatments (capitals) or mixtures (lower case). **b.** The number of days without through-flow in the aquaria (mean + 1 SE) per CO₂ treatment per mixture. Treatments had no significant effect (ANOVA, $P > 0.05$).

Results

CO₂ concentration

The two CO₂ treatments differed in their CO₂ concentrations of the aquarium water (Fig. 1a, $F_{1,14} = 126$, $P < 0.001$); aquaria receiving CO₂ enriched water had CO₂ concentrations above 0.7 mmol.l⁻¹, a value indicated as limit for vigorous *Sphagnum* (Smolders et al. 2001). In contrast, CO₂ concentrations in the aquaria receiving demineralized water stayed below this value with a mean of 0.4 mmol.l⁻¹ (Fig. 1a). The CO₂ treatment resulted in a pH difference of ca. 0.2 units between the aquaria with (pH = 4.00 ± 0.04) and without extra CO₂ (pH = 4.19 ± 0.04) and fell within the range reported for field conditions. Although values above 1 mmol.l⁻¹ CO₂ are seldom reached at purely ombrotrophic sites, concentrations may reach several mmol.l⁻¹ at more minerotrophic (micro) sites, where acidic rainwater comes into contact with water of minerotrophic origin (Smolders et al. 2001).

Surprisingly, mixing ratio affected the CO₂ concentration (but not pH) in the aquaria receiving CO₂; Sc-dominated aquaria had lower CO₂ concentrations than Sc-Sm co-dominated aquaria ($F_{1,12} = 8.7$, $P < 0.05$). This mixture effect was significant for most of the six measurement dates (data not shown) and seemed related to the area covered by *S. magellanicum*. Out of the three dates at which we performed both CO₂ and area measurements, one date (December 2005) showed a significant positive linear relationship between CO₂ concentration and area of *S. magellanicum* ($R^2 = 0.54$, $P = 0.01$), one date (early March 2006) showed no relationship at all and the last date (late March) again showed a positive linear relationship, albeit a weak one ($R^2 = 0.27$, $P = 0.07$). Flow rate, or the rate at which water, and thus CO₂

Table 1. ANOVA testing the effects of CO₂ treatment and species on *Sphagnum* production over the experimental period per mixing ratio. Sc = *S. cuspidatum*; Sm = *S. magellanicum*.

Source of variation	Sc dominant			Sc-Sm co-dominant		
	df	F	P	df	F	P
CO ₂	1	0.20	0.66	1	6.14	0.03
Species	1	0.34	0.57	1	0.01	0.92
CO ₂ * Species	1	<0.01	0.96	1	1.87	0.19
Error	14			14		

for the high CO₂-treatment, was applied to the aquaria did not seem affected by the treatments, although Sc-Sm co-dominated aquaria with CO₂ did seem to have more days during which through-flow was obstructed than the other treatments (Fig. 1b).

Sphagnum production

Sphagnum production over the experimental period (roughly equivalent to one growing season in length) was strongly variable, ranging from 93 to 662 g.m⁻² for *S. cuspidatum* and from 108 to 588 g.m⁻² for *S. magellanicum*. Both highest values were found for the Sc-Sm co-dominated aquaria receiving extra CO₂ (Fig. 2). Despite the high variability, the mean productivity of *S. cuspidatum* and *S. magellanicum* was close to the 350 and 250 g.m⁻².a⁻¹ respectively reported for the field (Gunnarsson 2005). The low productivity of *S. cuspidatum* in the Sc-Sm co-dominated aquaria without CO₂ was an exception to the above. Adding CO₂ increased *Sphagnum* production, but only in the Sc-Sm co-dominated aquaria (Table 1). The CO₂ effect on production was mainly due to increased production of *S. cuspidatum* (Fig. 2).

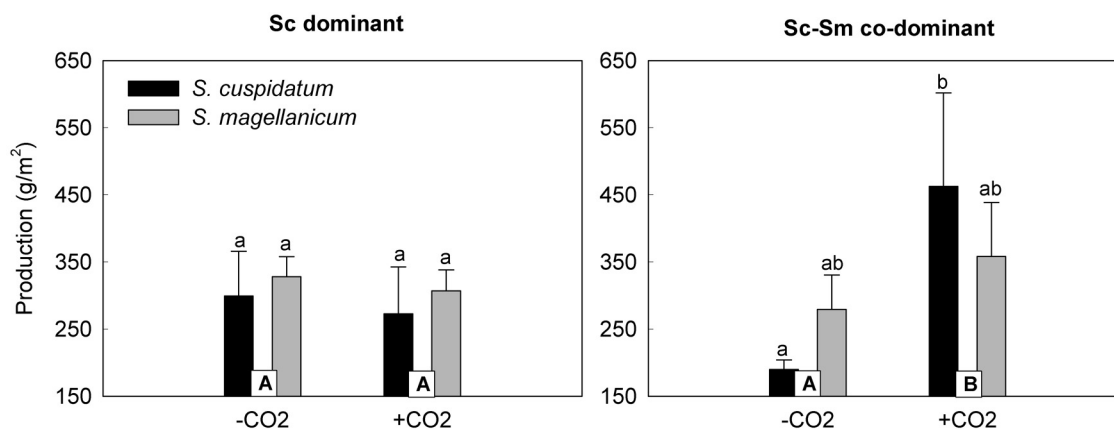


Fig. 2. *Sphagnum* production (mean + 1 SE) per CO₂ treatment per species per mixing ratio. Sc = *Sphagnum cuspidatum*; Sm = *Sphagnum magellanicum*. Different letters indicate a significant difference between the CO₂ treatments (capitals) or between CO₂ treatment-species combinations within mixtures (lower case). For details on statistics, see Table 1.

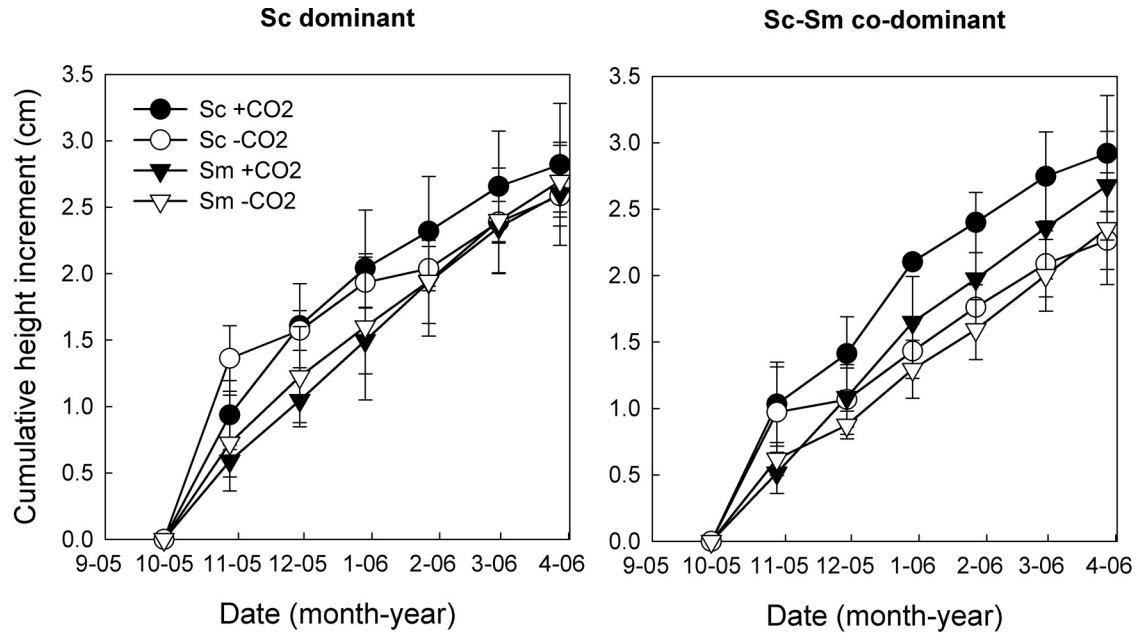


Fig. 3. Cumulative *Sphagnum* height increment (mean \pm 1 SE) per species per CO₂ treatment per mixture. Sc = *Sphagnum cuspidatum*; Sm = *Sphagnum magellanicum*. The treatments had no significant effect on height increment (RM ANOVA, Table 2).

Sphagnum growth

Sphagnum height increment was not affected by mixing ratio or species (Fig. 3, Table 2). In the Sc-dominated aquaria adding CO₂ had no effect, whereas in the Sc-Sm co-dominated aquaria CO₂ seemed to enhance height increment of both species, in particular *S. cuspidatum*, albeit not significantly ($P = 0.13$, Table 2).

For *S. magellanicum* part of the increase in height increment coincided with changes in morphology, particularly of the stem; *S. magellanicum* stem dry weight decreased linearly with height increment irrespective of

CO₂ treatment or mixing ratio ($R^2 = 0.24$, $P = 0.016$), indicating etiolation. For *S. cuspidatum* no such relationship was found.

At the end of the experiment the capitulum water content (expressed as fresh weight: dry weight) of *S. magellanicum* ranged from 18-38, exceeding that of *S. cuspidatum* which ranged from 9-18 (data not shown). Capitulum water content of both species showed a similar linear decrease with cumulative height increment and, concomitantly, distance to the water table (ANCOVA, species $F_1 = 138$, $P < 0.001$, cumulative growth $F_1 = 11$, $P < 0.01$, species \times cumulative growth: ns).

Table 2. Repeated measures ANOVA testing the effects of CO₂ treatment and species on cumulative *Sphagnum* height increment per mixing ratio. Sc = *Sphagnum cuspidatum*; Sm = *Sphagnum magellanicum*. * Degrees of freedom were adjusted by Huynh-Feldt epsilon.

Source of variation	Sc dominant			Sc-Sm co-dominant		
	df	F	P	df	F	P
Between subject effects						
CO ₂	1	<0.01	0.99	1	2.63	0.13
Species	1	1.00	0.33	1	1.31	0.27
CO ₂ *Species	1	0.09	0.77	1	0.29	0.60
Error	14			13		
Within subject effects						
time	2.8*	107	<0.001	2.7*	95	<0.001
time * CO ₂	2.8*	0.61	0.60	2.7*	1.80	0.18
time*CO ₂ *Species	2.8*	0.39	0.75	2.7*	0.11	0.94
Error (time)	39*			35*		

Table 3. Repeated measures ANOVA testing the effects of CO₂ treatment on the changes in *S. magellanicum* cover per mixing ratio. Sc = *Sphagnum cuspidatum*; Sm = *Sphagnum magellanicum*. * Degrees of freedom were adjusted by Huynh-Feldt epsilon.

Source of variation	Sc dominant			Sc-Sm co-dominant		
	df	F	P	df	F	P
Between subject effects						
Intercept	1	4.95	0.06	1	4.79	0.07
CO ₂	1	0.04	0.85	1	3.66	0.10
Error	7			6		
Within subject effects						
time	1	4.63	0.04	3.1*	2.39	0.06
time*CO ₂	1	0.12	0.86	3.1*	1.28	0.31
Error	12*			19*		

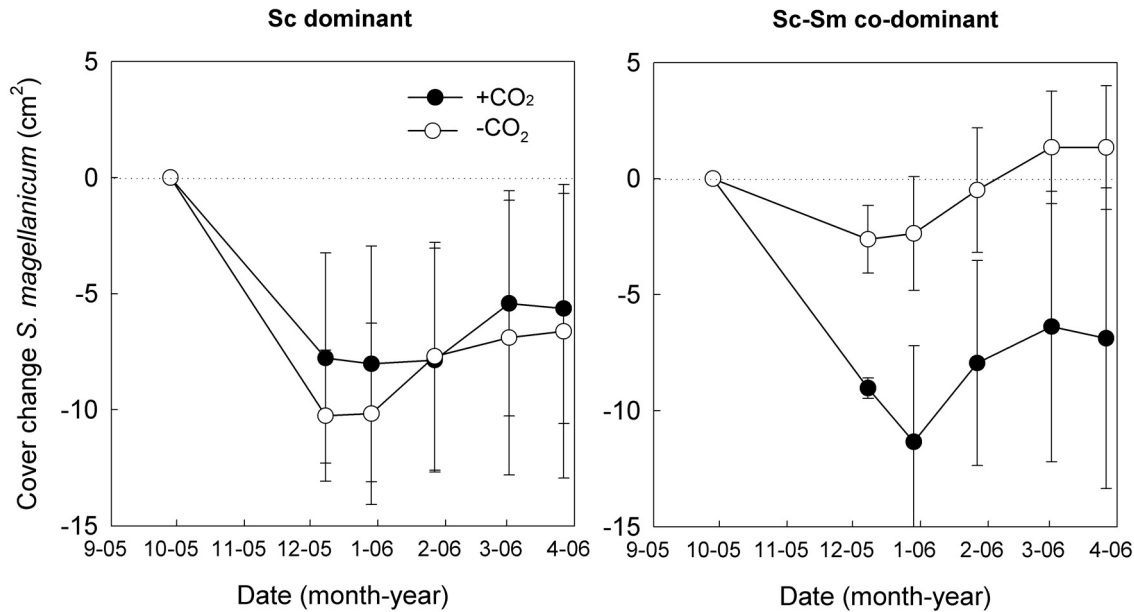


Fig. 4. Changes in *S. magellanicum* cover (mean \pm 1 SE) per CO₂ treatment per mixture. Note: Changes in *S. cuspidatum* cover are the reverse of those for *S. magellanicum*, the sum of cover changes being zero. Treatments did not affect cover at final harvest (RM ANOVA, Table 3).

Sphagnum cover

In the first three months of the experiment, *S. magellanicum* cover decreased sharply in favour of *S. cuspidatum* which expanded in all treatments except for the Sc-Sm co-dominated aquaria without extra CO₂ (Fig. 4). In the latter treatment hardly any changes in cover occurred. The observed initial decrease in *S. magellanicum* cover was a function of the difference in height increment between the species sharing an aquarium ($R^2 = 0.51$, $P < 0.001$). In the second half of the experiment, *S. magellanicum* recovered at the cost of *S. cuspidatum* irrespective of treatment, although adding CO₂ retarded this recovery in the Sc-Sm co-dominated aquaria, albeit not significantly ($P = 0.10$, Table 3).

Discussion

Species

The effect of adding CO₂ differed between species and mixing ratio. Adding CO₂ significantly increased production of *S. cuspidatum* in Sc-Sm co-dominated aquaria, but not in Sc-dominated aquaria, suggesting an effect of the moss carpet structure on CO₂ availability (see next section). Elevated dissolved CO₂ did not stimulate *S. magellanicum* more than *S. cuspidatum* (Figs. 3, 4) disproving our hypothesis and contrasting with the expectations of Smolders et al. (2001) that elevated

dissolved CO₂ supply would increase the competitive advantage of lawn species over hollow species. Our results indicate, instead, that *S. cuspidatum* is likely to profit more from enhanced CO₂ than *S. magellanicum*, annulling the competitive advantage. The absence of a significant CO₂ effect on *S. magellanicum* in our study could be a result of differences in water level and/or CO₂ available for photosynthesis. As we used a water level of 5 cm or more below the capitula (1 cm in Smolders et al. 2001), the concomitantly lower capitulum water content could have reduced the photosynthetic response of *Sphagnum* to elevated CO₂ (Silvola 1990). In addition, the deeper water levels may have reduced the CO₂ concentration at the capitulum level, as evolving gas had more room to mix with the atmosphere.

The high performance of *S. cuspidatum* above the water table is surprising since, in the field, substantial patches of hollow species are rarely found further than 5 cm from the water table (Rydin 1985). Perhaps the frequent precipitation events, in combination with the sheltered growing conditions, enabled *S. cuspidatum* to maintain its capitulum water content at a level close to optimal for photosynthesis throughout the experimental period (fresh weight: dry weight ratio 5-10; Titus et al. 1983; Rydin & Mc Donald 1985; Schipperges & Rydin 1998). The same conditions presumably resulted in a supra optimal capitulum water content for *S. magellanicum*, which neared optimal water content at the end of the experiment. The latter is reflected by the gradual recovery of the *S. magellanicum* cover during the sec-

ond half of the experiment (Fig. 4). As such, our results further stress the importance of water availability as the main driver behind the succession from hollow to lawn species.

Mixing ratio

Mixing ratio affected the concentration of CO₂ measured in the aquaria (Fig. 1a). Since this mixture effect was absent from the aquaria receiving no CO₂, it seems reasonable to assume that it is either related to differences in CO₂ supply or to differences in the evolution rate of the CO₂ present. Since the rate of through-flow, and thus the amount of CO₂ supplied with the oversaturated water, did not differ between the mixtures, and was even slightly lower in the Sm-dominated aquaria (Fig. 1b), the first explanation seems inadequate. Perhaps the speed by which the dissolved CO₂ evolved from the oversaturated water and escaped from the aquaria was affected by the structure of the overlying *Sphagnum* carpet. It has been shown that differences in soil structure and pore geometry (Vogel 2000; Tuli et al. 2005), as well as water filled pore space, may affect flow rates of gasses. On this basis it seems reasonable to assume that, for the surface layer, the denser growing *S. magellanicum* may hamper escape of gaseous CO₂ to the atmosphere more than the looser growing *S. cuspidatum*. Furthermore, the higher volume of water present in the *S. magellanicum* capitula may have acted as an extra barrier to gas escape. This would reduce gas evolution from water so that gaseous CO₂ could accumulate within the *Sphagnum* carpet, explaining the higher concentrations of dissolved CO₂ in the Sm-dominated aquaria. Although the above explanation must be treated with due caution, it could point to hitherto unexpected feedbacks between the species composition and structure of a *Sphagnum* carpet. The latter could affect the degree in which *Sphagnum* re-uses CO₂ from deeper lying peat layers and thereby the gas efflux to the atmosphere. The above would tie in well with observations of Robroek et al. (2007), who reported effects of species area and peat structure on the capitulum water content: both results suggest feedbacks between species area, carpet structure and abiotic conditions.

Conclusions

The effects of mixing ratio and species on the concentration of CO₂ in the water layer and its subsequent use for *Sphagnum* production, suggest that species identity and their spatial configuration may affect the efficiency with which substrate-derived CO₂ is trapped and subsequently used. This could result in hitherto unexplored feedbacks between vegetation composition, soil physical structure and gas exchange. Consequences

for *Sphagnum* ecology could be that once the patch size of a lawn species surrounded by hollow species reaches a certain critical area at which it can maintain its own water, and possibly also gas economy, it may create a positive feedback consolidating its own position, and promoting expansion. Consequences for surface gas exchange could be that areas dominated by hollow species would show a more variable flux than areas dominated by lawn or hummock species. Research targeted at measuring gas concentrations below, as well as gas exchange from different species and patch sizes, could elucidate much of the above.

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