CO₂ environment, microclimate and photosynthetic characteristics of the moss *Hylocomium splendens* in a subarctic habitat

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Summary. In order to document the natural CO_2 environment of the moss *Hylocomium splendens,* and ascertain whether or not the moss was adapted to this, and its interactions with other microenvironmental factors, two studies were carried out. Firstly, the seasonal variations of CO_2 concentration, photosynthetically active radiation (PAR), tissue water content and temperature were measured in the natural microenvironment of *H. splendens* in a subarctic forest during the summer period (July-September). Secondly, the photosynthetic responses of the species to controlled CO_2 concentrations, PAR, temperature, and hydration were measured in the laboratory. CO_2 concentrations around the upper parts of the plant, when PAR was above the compensation point (30 μmol m^{-2} s^{-1}), were mostly between 400 and 450 ppm. They occasionally increased up to 1143 ppm for short periods. PAR flux densities below saturating light levels for photosynthesis (100 μmol m^{-2} s^{-1}), occurred during 65% (July), 76% (August) and 96% (September) of the hours of the summer period. The temperature optimum of photosynthesis was 20° C: this temperature coincided with PAR above the compensation point during 5%, 6% and 0% of the time in July, August and September, respectively. Optimal hydration of tissues was infrequent. Hence PAR, temperature and water limit CO_2 uptake for most of the growing season. Our data suggest that the higher than normal ambient CO_2 concentration in the immediate environment of the plant counteracts some of the limitations in PAR supply that it experiences in its habitat. This species already experiences concentrations of atmospheric CO_2 predicted to occur over the next 50 years.

Key words: CO_2 environment – Photosynthesis – Microclimate – Moss – *Hylocomium splendens*

During recent years, substantial interest has been focussed on predicting how the expected increase in atmospheric CO_2 concentrations will affect plants. A rise in atmospheric CO_2 has been reported to increase the rate of photosynthesis in many vascular plants (Lemon 1983; Strain and Cure 1985), and most C_3 plants – which constitute 95% of global plant biomass – would probably respond in this way. Atmospheric CO_2 concentrations influence important physiological parameters such as the light compensation point of CO_2 uptake and the quantum yield (Björkman 1981). As CO_2 concentration increases, the light compensation point decreases while the carbon yield per unit of photosynthetically active radiation (PAR) and the water use efficiency of CO_2 uptake (Nobel 1983) increase.

Little is known about the CO_2 related responses of plants that normally grow at high CO_2 levels. Examples are decumbent, prostrate vascular plants and cryptogams which form the bottom layer of plant canopies and are exposed to CO_2 respired by soil organisms (Bazzaz et al. 1969; Silvola 1985). Mosses and lichens often grow close to the ground, with part of their tissue tightly attached to the humus layer from which CO_2 is released at high concentrations as a consequence of below-ground respiratory processes (Heal 1979; Schlentner and Van Cleve 1985; Silvola 1985; Carlyle and Than 1988). Adaptations for utilizing high atmospheric CO_2 levels can therefore, be expected in these plants. Indeed, enhanced CO_2 levels near the soil surface may be an additional reason why many cryptogams grow in the shade of the forest floor. In this humid microclimate, the degree of hydration of thalli may be high enough to enable a positive carbon balance to be maintained at enhanced atmospheric CO_2 concentrations despite a low PAR.

In this paper we will describe the natural microenvironment and laboratory-determined photosynthetic responses of a moss typical of the forests and tundra shrublands in subarctic Fennoscandia, *Hylocomium splendens* B. & S. It has a wide distribution in the northern hemisphere and seems to be particularly abundant in shaded and mesic sites. The following question will

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primarily be addressed: does this moss show adaptations to the interactions between enhanced atmospheric CO_2 levels and the microclimate it experiences in the field?

Materials and methods

Site and plant material

The investigation took place at Abisko in northern Swedish Lapland (68° 20′ N; 18° 45′ E) using plant material from a birch forest site (380 m asl) corresponding to the "Empetrum-Vaccinium myrtillus variant" described in Sonesson and Lundberg (1974). Samples were collected from a site dominated by *H. splendens* in the moss canopy. A *Hylocomium* plant consists of segments/fronds produced sympodially to form a thin vertical axis: each segment represents a specific period of growth, 1 year. Thus the youngest segment, segment *c*, was formed during the current year and segment *c+1* in the previous year. Together, *c* and *c+1* constitute the "top frond", *c+(c+1)*. Segment *c+2* was formed 2 years earlier (cf. Callaghan et al. 1978).

In situ measurements of CO_2 and microclimate

Diurnal observations of CO_2 concentrations were made by collecting air samples (2 ml) from the moss layer with syringes every hour during each of eight 24-h periods that covered the main part of the growing season, from the beginning of July to the end of September. Collections were taken from under the *c+1* and under the *c+2* segments of the moss. Reference air samples were taken c. 20 cm above the moss surface. On each sampling occasion, ten replicate air samples were taken from different positions in each stratum within an area measuring approximately 10×10 cm. They were injected into an infrared gas analyser (IRGA, ADC 245A, Hoddesdon, UK, in differential mode) within 10 minutes of being collected and the areas of the response curves recorded using an integrator (HP-3396A, Hewlett-Packard, Avondale PA, USA). Ten replicates of a calibration gas, with a CO_2 concentration of 1000 ppm (± 10 ppm accuracy) were injected in a similar way to serve as a reference. A calibration of this method before the experiment showed a linear relationship between measured IRGA response and CO_2 concentration. A linear regression of eight CO_2 concentrations between 200 ppm and 1500 ppm on the integrated response areas gave a good fit with the data ($r^2 = 0.998$; $n = 54$) and showed an average deviation of ppm CO_2 less than 2%.

PAR was measured using a LiCor quantum sensor (LI-190SB, LiCor Inc., Nebraska, USA) at the top segments of the moss. Temperature was measured with copper/constantan thermocouples inserted under the *c+1* (at 0.5–1.0 cm from the surface) and *c+2* (at 2–4 cm) segments of the moss and at 15 cm depth in the moss layer. The sensors were connected to a datalogger (Campbell Scientific Inc. Logan, USA). The logging interval was 20 s and the period of observations lasted from 1 July to 30 September.

Diurnal changes in the water content of the *H. splendens* top frond fraction were measured every hour during each of the eight periods that covered the main part of the growing season. The water content was determined by weighing five cores of moss as follows: five shallow 25 cm² cores of moss, containing approximately the *c+(c+1)* fronds only, were carefully extracted from cushions, positioned on 5 nylon net trays of the same diameter, and replaced in the same holes from which the cores had been taken. The surface of the cores was level with that of the intact moss mat.

The frequency of each of five CO_2 concentration ranges (330–400, 401–450, 451–500, 501–550, >550 ppm) at the segment *c+1* level for each of six PAR classes (0–10, 11–30, 31–50, 51–100, 101–200, >200 μmol m⁻² s⁻¹) was calculated for the whole observation period. It was assumed that the data from the eight 24-h samplings were representative of this period.

Laboratory measurements

Treatment of experimental plants. Well-developed top fronds of the moss were sampled and carefully mixed 1 day before the start of each series of measurements, and kept outdoors in the shade (in aluminium trays covered with polythene film). Prior to the measurements, five specially designed 25-cm² trays made of nylon net to provide a framework to hold the mosses were each covered with 8–10 fronds. The trays were constructed to fit the cuvettes used for the subsequent gas exchange measurements. An effort was made to completely cover the trays while minimizing overlap between the fronds. The plant material was hydrated to a water content of approximately 600–700% of dry weight by mist spraying with distilled water. The trays were then placed in petri dishes in a growth chamber for preconditioning at +15° C and exposed continuously to low PAR (40 μmol m⁻² s⁻¹) for 18 h before measurements were taken. The flow rate of the open differential CO_2 exchange system used was 12 l h⁻¹ and the air in each cuvette was mixed with a fan (Sonesson 1989). Each experiment was completed in 4–5 h, and all experiments were conducted in the same way, starting without irradiance and thereafter successively increasing the light level. A different tray set, comprising five replicate trays of preconditioned plant material, was used for each experiment (i.e. for each treatment of CO_2 concentration and temperature).

Measurements. Different CO_2 concentrations in the air were obtained by mixing CO_2-free air and CO_2 gas using mass flow regulators (Ultraflo, Vacuum General, San Diego, USA). Two different types of measurement were conducted:

In experiment (1) we studied the light response of plants at different CO_2 levels (in 1990). Air was circulated across the net trays containing the plant material. Different PAR levels were obtained using grey filters (Kodak Wratten ND). The light source was a metal halogen lamp (Osram HQI, TS 400W). All measurements were conducted at +15° C using fronds with water contents of approximately 600–700% of dry weight. The degree of hydration was checked after each measurement by weighing. The water content was restored by mist spraying with distilled water.

In experiment (2) we analysed the effect of water content on photosynthesis at seven different temperatures (0–30° C) and at 400 ppm CO_2 using fronds that were completely soaked in distilled water for 30 min prior to measurements. The plants were quickly removed after each measurements, weighed and replaced in the cuvette until the continuously desiccated mosses reached a water content at, or near, the point where the gas exchange ceased. Plant material for this experiment was sampled in late August 1991 from the same site as for experiment 1.

Data evaluation

Second-or third-degree polynomial regression lines were fitted to the data on photosynthesis and water content at different temperatures.

An estimate of the diurnal *in situ* photosynthetic rates during periods when the CO_2 concentration was higher or lower than 400 ppm was made. Rates were calculated applying the laboratory-determined relationships between photosynthesis and PAR, photosynthesis and CO_2 concentration and photosynthesis and water contents at different temperatures of the moss, to the diurnal PAR, CO_2, water content and temperature data measured in the field during 3 days of the observation period. Values for compensation and PAR saturation points were calculated from the data. We assumed that there was a linear increase/decrease in photosynthetic rates with an increase/decrease in light and CO_2 concentration. The fitted polynomials were used to describe water and temperature relations.

Results

CO₂ environment

The seasonal mean of CO_2 concentration in the field ranged between 350 and 530 ppm at the $c + 1$ segment level and between 370 and 730 ppm at the $c + 2$ segment level (Fig. 1A), with highest concentrations occurring during the peak growing season. The highest mean hourly concentrations, 1143 ppm (SE = 37; n = 10) and 1472 ppm (SE = 52; n = 10) at the $c + 1$ and $c + 2$ segment levels, respectively, occurred on 9 August. These levels were recorded during the morning and afternoon, when PAR at the surface was 57 and 101 µmol m⁻² s⁻¹, respectively. The standard errors of the hourly mean concentrations were usually lower than 10% of the mean but reached 13–15% in a few cases. Except for low values in early August, the CO_2 level of the air 20 cm above the moss surface was about 10% higher than "normal" throughout the observation period, with a maximum of 466 ppm (SE = 62; n = 10) at PAR 44 µmol m⁻² s⁻¹ recorded on the afternoon of 5 July.

Under the top fronds, CO_2 concentrations remained between 330 and 550 ppm for 53% of the time during which PAR was above 30 µmol m⁻² s⁻¹, but for less than 2% of the time during which CO_2 was above 550 ppm and PAR more than 100 µmol m⁻² s⁻¹ (Fig. 2). The most commonly recorded concentrations above the light compensation point ranged between 400 and 450 ppm, i.e. 50–100 ppm above normal ambient air.

Light and temperature climate

PAR flux densities above 30 µmol m⁻² s⁻¹, which approximately correspond to the lowest compensation levels of photosynthesis in *H. splendens* at normal CO_2 concentration, were recorded at the surface of the moss layer for 64%, 52% and 21% of all of the hours during July, August and September, respectively (Fig. 3A). PAR above 100 µmol, corresponding to saturating light levels, was recorded for 35% of the hours of July, 24% of those of August and 4% of those of September. At PAR above 30 µmol m⁻² s⁻¹ the most common temperatures were 12–18° C in July, 10–14° C in August and 6–10° C in September. A temperature of 20° C, which was optimal for photosynthesis, was recorded for 5% of the hours of July, 6% of those of August and 0% of those of September (Fig. 3B).

Temperature response of photosynthesis at different tissue water contents

Net photosynthetic rates increased from approximately 0.5 mg CO_2 g⁻¹ h⁻¹ at a temperature of 0° C up to an optimum of about 1.5 mg CO_2 g⁻¹ h⁻¹ at 20° C (Fig. 4). Optimum water contents for photosynthesis varied between approximately 500% and 700% of dry weights at temperatures between 0° C and 15° C and between 300% and 500% between 20° C and 30° C. There was a large variation in the photosynthetic response, particularly at
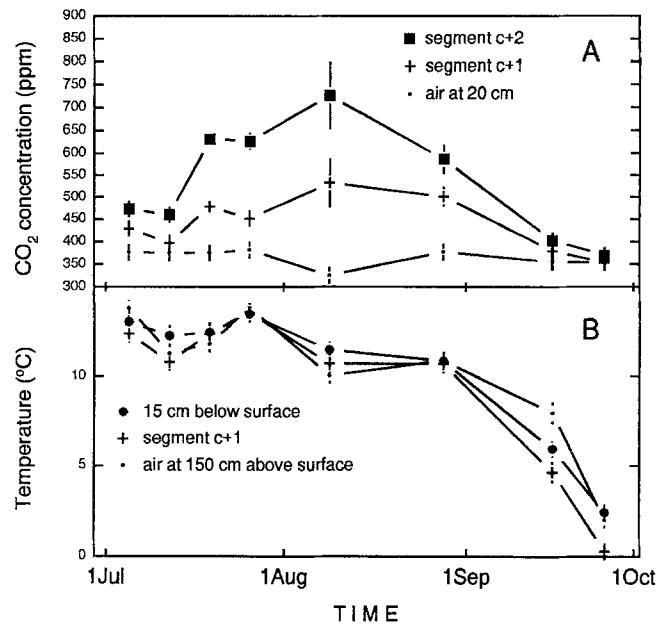
Fig. 1. A Seasonal course of diurnal mean CO_2 concentrations ±SE at PAR higher than 10 µmol m⁻² s⁻¹ at three levels in a moss mat dominated by *Hylocomium splendens*. The segment $c + 1$ and segment $c + 2$ levels of *Hylocomium* are at about 0.5–1 cm and 2–4 cm below the moss surface, respectively. B Mean temperatures at three levels at the same site
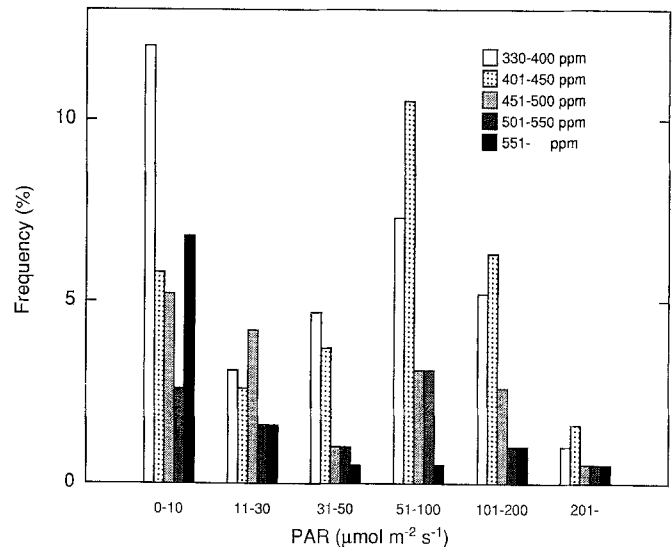

Fig. 2. Frequency distributions of CO_2 concentration classes at the top segment level of *Hylocomium* in 6 PAR classes. Based on primary data (Fig. 1A and 3A)

25° C and 30° C. The coefficients of determination (r^2; Zar 1984) were: 0°, 0.81; 5° C, 0.65; 10° C, 0.55; 15° C, 0.60; 20° C, 0.80; 25° C, 0.23; 30° C, 0.18; (n = 28–51).

Light response of photosynthesis at CO₂ concentrations of 350 ppm

Saturating PAR was measured between 80 and 120 µmol m⁻² s⁻¹ during most of the season (Fig. 5A–E). Com-
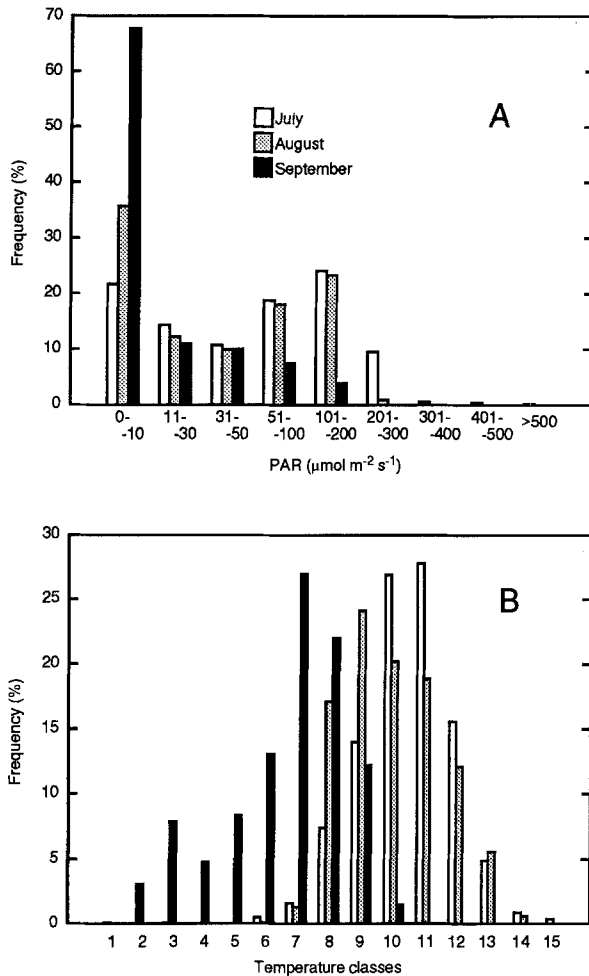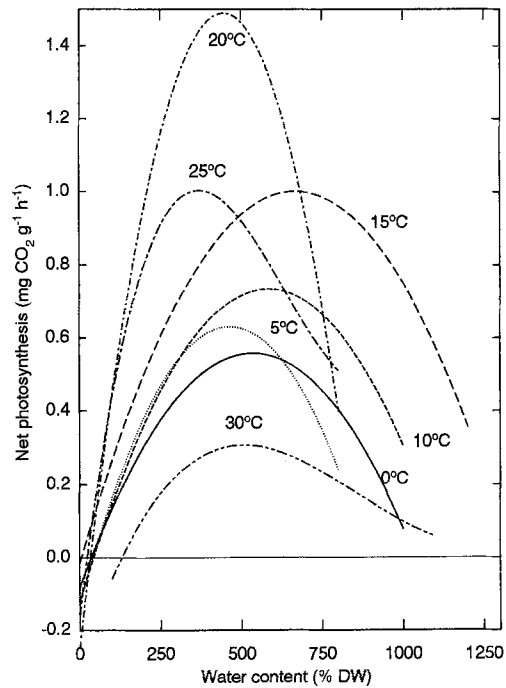
Fig. 3. A Frequency distributions of photon flux densities (PAR μmol m^{-2} s^{-1}) in 1990 at the surface of a *Hylocomium* moss mat. **B** Frequency distributions of temperatures under the $c+1$ segment of the moss at PAR > 30 μmol m^{-2} s^{-1}. Temperature (°C) classes are: $1 = < -4.0$; $2 = -4.0$ to -2.0; $3 = -2.1$–0.0; $4 = 0.1$–2.0; $5 = 2.1$–4.0; $6 = 4.1$–6.0; $7 = 6.1$–8.0; $8 = 8.1$–10.0; $9 = 10.1$–12.0; $10 = 12.1$–14.0; $11 = 14.1$–16.0; $12 = 16.1$–18.0; $13 = 18.1$–20.0; $14 = 20.1$–22.0; $15 = > 22.0$

Fig. 4. Net photosynthesis of *Hylocomium splendens*, $c + (c+1)$, in relation to water content and temperature of tissues. Measurements were taken at a CO_2 concentration of 400 ppm. *Curves* are second- or third-degree polynomial regression lines fitted to the data. Coefficients of determination (r^2) are: 0° C, 0.81; 5° C, 0.65; 10° C, 0.55; 15° C, 0.60; 20° C, 0.80; 25° C, 0.23; 30° C, 0.18. $n = 28$–51

pensation points varied between approximately 30 and 100 μmol m^{-2} s^{-1} during the season but no statistically significant differences were found. The late autumn value applies to the c segment alone, which was nearly fully developed by that time, whereas the earlier values were measured in the top fronds, consisting of tissue formed during both the current and previous year $[c + (c+1)]$. Photosynthetic rates of the youngest tissue, c, were quite low in late autumn and segment $c+1$ had a negative carbon balance at all light levels. The quantum yields, QYs, showed no consistent seasonal trend.

Light response of photosynthesis at different CO_2 concentrations

The lowest and highest responses of photosynthesis of the top frond fraction, $c + (c+1)$, were obtained at 200 ppm and 1000 ppm CO_2, respectively, when sat-

urated with PAR and optimally hydrated during the peak growing season and early autumn. The differences in photosynthetic rates were 2–3 fold between 350 and 600 ppm and 3–4 fold between 350 and 1000 ppm. The response at 1700 ppm was about 25–50% lower than that at 1000 ppm and similar to that at 600 ppm (Fig. 5A–C).

No reduction in photosynthetic rates was obtained at 1700 ppm in current-year tissue, c, in late autumn. The photosynthetic rate was negligible at 350 ppm, ca 1.5 mg g^{-1} h^{-1} at 600 ppm, 4 mg g^{-1} h^{-1} at 1000 ppm and 4.8 mg g^{-1} h^{-1} at 1700 ppm, which was the highest rate observed. In the $c+1$ segment, CO_2 exchange was slightly positive at 600 and 1000 ppm, but negative at 350 and 1700 ppm (Fig. 5D–E).

The light compensation point tended to decrease as the CO_2 concentration increased, although most of the differences were not statistically significant. The QY varied with the CO_2 concentration, although not in a systematic way.

Diurnal water contents

There was a large variation in diurnal water contents related to variations in temperature, PAR and precipitation (Fig. 6). Two examples: During the dry period of 26/27 July, water content between 0600 hours and 2000 hours was 10–90% of dry weight, CO_2 concentration was 400–500 ppm, temperature 12–18° C and PAR 60–240 μmol m^{-2} h^{-1}. During the wet period of 9/10
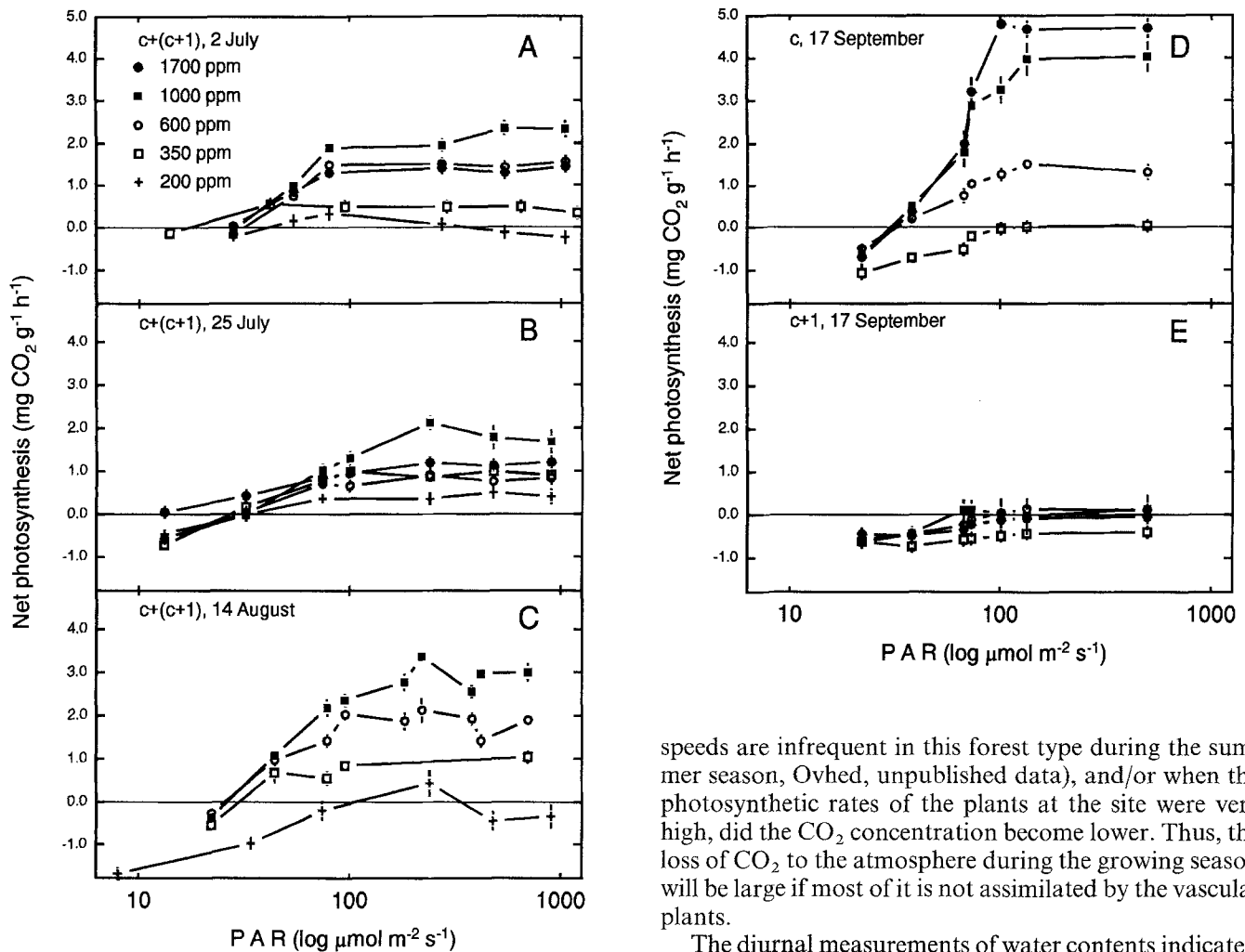
Fig. 5A–E. Net photosynthetic rates of the top segments of *Hylocomium splendens* measured at +15° C and optimal tissue hydration and at different PAR and CO_2 concentrations. Means ± SE, $n = 5$

August, water content between 1300 hours and 1800 hours was 300–400% when the mean CO_2 concentration was 300–750 ppm, temperature 11–13° C and PAR 100–150 μmol m^{-2} h^{-1}. After 1900 hours hydration was higher but PAR less than 30 μmol m^{-2} h^{-1}.

Discussion

In the field, the mean diurnal CO_2 concentration of the air 20 cm above the moss mat was higher than normal. This agrees with the results of measurements in a drained peatland in southeastern Finland (62° 30' N) by Silvola (1985). He found a nocturnal CO_2 concentration of up to 450–600 ppm at the surface of the moss carpet. The concentration decreased to about 320 ppm at noon and throughout the afternoon. The higher than ambient CO_2 concentrations found in this study indicate that the flux from the soil was high enough to more than compensate for the dilution effects due to air convection and diffusion in the sheltered forest site, and uptake by photosynthesis. Only at wind speeds higher than 0.5 m/s (such wind

speeds are infrequent in this forest type during the summer season, Ovhed, unpublished data), and/or when the photosynthetic rates of the plants at the site were very high, did the CO_2 concentration become lower. Thus, the loss of CO_2 to the atmosphere during the growing season will be large if most of it is not assimilated by the vascular plants.

The diurnal measurements of water contents indicated that optimal hydration is very infrequent. Even if the moss is optimally hydrated, light in particular would limit photosynthesis during most of the growing season. Thus it would operate under limiting PAR for 65% of the time in July, 76% of that in August and 96% of that in September.

It was expected that the QYs would change in a manner similar to that in C_3 plants in general, i.e. that the QYs would increase with increasing CO_2 concentration (Björkman 1981). Although there was a large variation in our data set, nothing in it seems to oppose such a general trend.

The light saturation and compensation levels of the current-year segment, *c*, which does not complete development until late autumn, appear to be poorly compatible with the ambient CO_2 concentration and PAR at that time of the season. Thus, after mid-September, the CO_2 level of the moss layer was lower than 400 ppm and decreasing, and the corresponding compensation point of segment *c* was approximately 100 μmol m^{-2} s^{-1} although the diurnal frequency of PAR above 100 μmol m^{-2} s^{-1} was only 4% of the time. A similar compensation level was also measured in early summer (June) when PAR higher than 100 μmol m^{-2} s^{-1} was recorded more than 50% of the time (unpublished data), and the CO_2 concentration in the moss layer was increasing. Segment *c* seems, therefore, to be adapted to the environ-
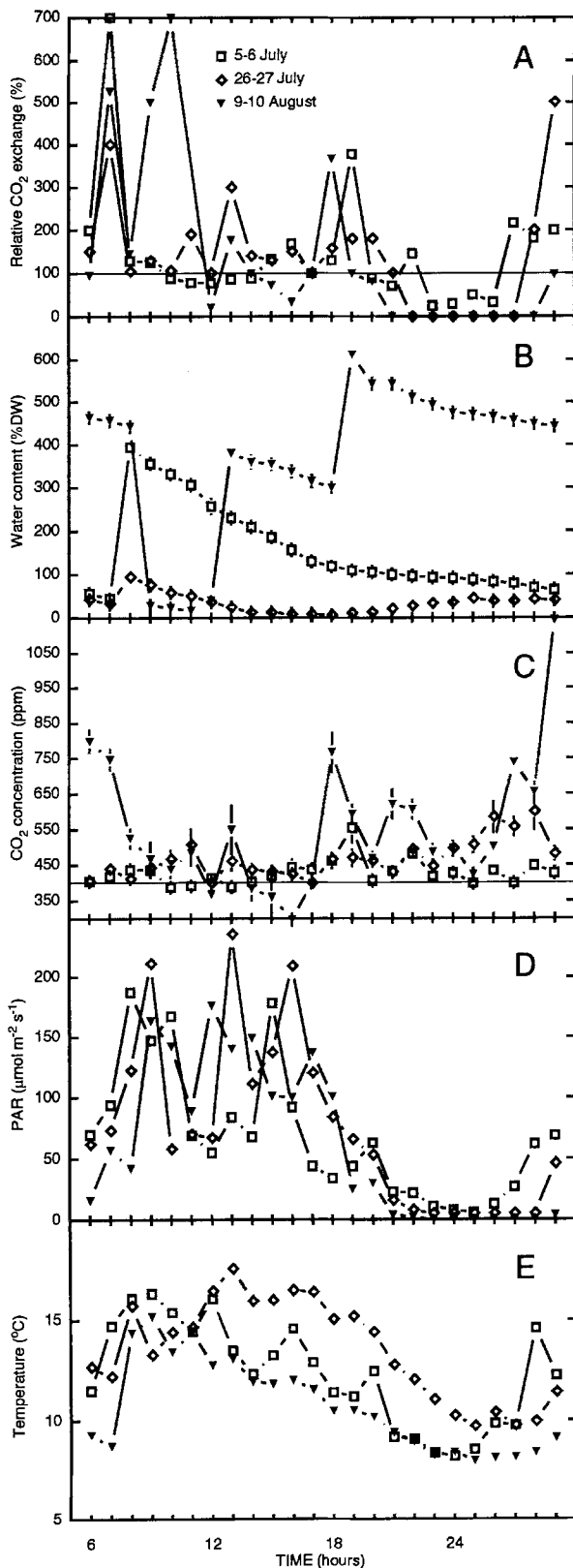
Fig. 6A–E. Diurnal relative net CO_2 exchange rates (rates at 400 ppm are 100%) simulated for *Hylocomium splendens* **A** in field conditions of ambient CO_2 concentrations in excess of 400 ppm, **B** based on data for water contents, **C** CO_2 concentration, **D** PAR and **E** temperature of tissues measured *in situ* during three periods. The simulations are also based on the laboratory data shown in Figs. 4 and 5A–C

mental conditions in spring and early summer of the subsequent season.

The depression of photosynthesis at high CO_2 concentration after mid-September was evident in the old tissue of the top frond, $c + 1$, but not the current-year segment, c. The relative increase of photosynthetic rate from 1000 ppm to 1700 ppm in segment c was reduced in relation to that from 350 to 1000 ppm, however, indicating a limiting effect at high CO_2 levels. Concentrations as high as 1700 ppm CO_2 were not recorded during the growing season but were measured during late winter (March) under snow at the moss surface (Sonesson et al. unpublished). The inactivity of segment $c + 1$ is probably a late autumn phenomenon only. The $c + 2$ segments showed a positive carbon balance during early July similar to that of the top frond although at a lower level. This decreased to only respiration in August and September (unpublished data). Since in July-August the c segment has only 10–13% of the total biomass of the top frond in a bud-like structure, most of the photosynthetic response should then apply to the $c + 1$ segment (unpublished data).

There was a difference between the measured temperature optimum of photosynthesis and temperatures in the field. While photosynthesis was highest at 20° C in the top fronds collected in late August, the most frequent temperatures in the field were 6–10° lower in August and 10–14° lower in September. Such discrepancies between measured temperature optima and *in situ* temperatures have been observed several times in both vascular plants and cryptogams (Lange and Kappen 1972; Collins 1977; Proctor 1982; Kappen 1988; Sonesson et al. 1992).

Although our simple model simulates the response of photosynthesis to CO_2 concentrations in the field based on an incomplete response matrix of driving variables it indicates the great effects on photosynthesis of hydration and light supply, besides that of CO_2 level (Fig. 6).

Diurnal increase in photosynthetic rates at low water contents during 26/27 July was assumed to mainly relate to a decrease in the negative CO_2 balance due to high CO_2 concentration. Drought, in particular, would limit the growth of this moss in subarctic environments owing to low precipitation (Sonesson 1989). However, this may be compensated for, at least partly, by an increased "water content efficiency" (WCE) at enhanced CO_2 levels (Dubé and Sonesson, unpublished). Thus doubling the CO_2 concentration at near optimal water content of the tissue will double the CO_2 uptake without any change in transpiration rates. Unlike vascular plants with stomatal control of the water use efficiency, mosses do not adjust CO_2 entry into the fronds since they do not regulate transpiration in order to match photosynthesis to environmental conditions (Nobel 1991). How drought and low water content of the tissues would affect WCE and diffusion resistance to CO_2 remains to be answered, however, and points to one of the major weaknesses of the model. Apart from studies on liverworts with a complex anatomy and with thick cuticula (Marchantiaceae; Green and Snelgar 1982), little seems to be known of this relationship in bryophytes.

Leaves of mosses, such as *H. splendens*, are usually one or a few cells thick, with only a thin cuticula (Hébant

1977; Proctor 1982). Consequently, the internal resistance to CO_2 in the assimilating tissue of this moss should be low. Proctor (1982) maintained that the diffusion resistance of terrestrial bryophytes is probably rarely, if ever, high enough to influence photosynthesis. Despite the lack of significant diffusional barriers, *H. splendens* shows a strong response to increasing CO_2 supply at least in the range 600–1000 ppm. This indicates a physiological adjustment in this species to utilize high CO_2 levels in naturally CO_2-enriched environments.

It has been shown that the increase in photosynthesis due to experimentally enhanced CO_2 is usually only temporary in C_3 plants. Thus photosynthesis eventually decreases as a result of CO_2 being limited by, for example, a nutrient deficiency or a decrease in the transport of carbohydrates from their formation sites (Melillo et al. 1990). Callaghan et al. (1978) did not find any physiological connections between the segments of *H. splendens* that would allow such translocation, however. Tissue and Oechel (1987) found that the photosynthetic rate decreased nearly 50% in a tundra population of *Eriophorum vaginatum* after it was exposed for 10 days to air with a CO_2 level twice the normal concentration. Nothing is known about the response of mosses in this regard. However, results from the higher plants suggest that any model of photosynthetic response of these cryptogams to enhanced CO_2 in the field must incorporate the time of exposure of the tissue to CO_2 before realistic predictions of the results of possible higher CO_2 concentrations in the future can be made (Silvola 1985). Since extreme, high CO_2 levels in the canopy occurred only sporadically, acclimation of photosynthesis may not be as strong as under continuous exposure to high levels of CO_2. It was evident that the duration of the optimal combinations of PAR, CO_2 levels and water contents of the moss necessary to maximize photosynthetic yield is short.

Conclusions

Hylocomium splendens has higher light compensation points of photosynthesis at 350 ppm than forest plants usually have (Lieth 1960). It experiences ambient CO_2 concentrations higher than "normal" and its potential to utilize these is high, in contrast to its low potential to utilize CO_2 concentrations of 350 ppm. A high CO_2 level in the microenvironment may be necessary for species such as *H. splendens* to maintain a positive carbon balance because of limiting water and light. By contrast a "normal" CO_2 level would probably result in a substantial reduction in CO_2 gain.

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