

A moss “canopy” – Small-scale differences in microclimate and physiological traits in *Tortula ruralis*

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Dedicated to Prof. Dr. Dr. h.c. mult. Otto Ludwig Lange on the occasion of his 80th birthday

Abstract

We studied vertical changes in light regime and water content (WC) in combination with vertical gradients in several physiological response variables, i.e. net CO₂ uptake, chlorophyll content and nitrogen content in the moss species, *Tortula ruralis*. The rate of light attenuation within the moss turf, which was determined with a custom-made optical microprobe system, was strongly dependent on plant WC. Curling movements of the upper leaves associated with the beginning desiccation of the uppermost parts of a turf allowed increased penetration of light to greater depth with decreasing WC. The capacity to fix carbon declined steeply with depth: below ca. 9 mm no net CO₂ uptake occurred, even when removing the shading parts above. The potential rates of photosynthesis in different depths were highly correlated with chlorophyll content, but not nitrogen content.

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Introduction

Photosynthetically active radiation (PAR) drives photosynthetic carbon gain of green plants. Strong vertical gradients in PAR can be recognized not only at different scales, e.g. at the level of entire vegetation units (Torquebiau, 1988) and at the level of individual plants (Pitman, 2000), but also within individual vascular-plant leaves (Evans, 1996; Terashima and Hirotsuka, 1995) or lichen thalli (Dietz et al., 2000), and can be linked directly to physiological responses, e.g. the differentia-

tion of sun or shade leaves within a canopy (Boardman, 1977), allocation patterns of leaf nitrogen (Field, 1983) or distinct profiles of CO₂ fixation through a single leaf (Evans and Vogelmann, 2003; Gould et al., 2002).

The canopies of bryophytes operate at a scale that is intermediate between the leafy canopies of vascular plants and the mesophyll of vascular-plant leaves. Moss leaves are known to vary in their photosynthetic characteristics with distance from the top of a turf, feather moss or cushion (Busby and Whitfield, 1978; Hinshiri and Proctor, 1971), although this relationship may be at least partly confounded with age (Bates, 1979). Surprisingly, few bryological papers have attempted to study several parameters in combination, which would allow to relate directly differences in light

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environment and other parameters to physiological responses: there are mostly studies on particular aspects, i.e. vertical light profiles (Davey and Ellis-Evans, 1996; Van der Hoeven et al., 1993), vertical changes in chlorophyll contents (Gerdol et al., 1994; Löscher et al., 1983), or vertical gradients in the maximum rates of net photosynthesis (Bates, 1979; Busby and Whitfield, 1978). This lack of information motivated the current study, in which we characterize both abiotic gradients (PAR and water content (WC)) and differences in physiological parameters (net CO₂ fixation, chlorophyll and nitrogen content) within the dense turfs of *Tortula ruralis*, a common species in central Europe that is frequently used in physiological studies with mosses.

In view of the usual light gradient within a moss turf, we expected both the potential of photosynthesis and chlorophyll concentrations to show a similarly steep decline with depth. Moreover, similar to the theoretical optimum distribution of nitrogen in the foliage of vascular plants (Field, 1983; Hirose and Werger, 1987), we hypothesized that the nitrogen concentrations should closely track photosynthetic capacity. These expectations, however, were only partly fulfilled.

Material and methods

Plant material

Turfs of *T. ruralis* were collected at the Würzburg University campus growing on a plane surface with pebbles. The plant material was quite homogeneous in height (ca. 20–25 mm) and could easily be removed from the substrate. In all experiments, we arbitrarily distinguished four layers: layer 1 (top 3 mm), layer 2 (3–6 mm), layer 3 (6–9 mm), and layer 4 (>9 mm). All samples intended for gas exchange measurements were cleaned carefully under a dissecting microscope, i.e. tiny pebbles or animals were removed. Care was taken not to alter the structure of the turfs during these procedures.

Vertical light gradients

The light distribution within *T. ruralis* turfs was studied with a custom-made device using a KL 1500 lamp (Schott, Mainz, Germany) as light source delivering a vertical beam. Moss samples were put on the stage of a modified microscope stand, and a fibre optic probe (200 µm diameter) that was connected to a light sensor, and amplifier was moved through the turf starting from the bottom until it reached the top of the sample taking a reading every 0.4 mm. Measurements were replicated up to 15 times on different spots of each of five replicate samples, which were allowed to dry slowly. Before and after each measurement, samples were weighed for later

determination of the WC corresponding to each light determination.

The probe was moved relative to the sensor during these measurements and, consequently, the resulting raw signals had to be corrected. This was achieved by determining the control signals at full light intensity as a function of distance. Subsequently, the PAR readings for each depth inside the moss turf were converted to a percentage of these control values.

Vertical gradients in plant water content (WC)

The WC of mosses and liverworts is routinely given in % dry weight (dw). To quantify possible WC gradients within a moss turf, we soaked turfs of ca. 30 cm² in distilled water, put them on plastic plates and left them to dry under laboratory conditions (air temperature ca. 25 °C, PAR ca. 20 µmol m⁻² s⁻¹, RH ca. 50%) for different periods of time (30 min to several hours). Then, two central subsamples of ca. 5 cm² each were weighed. After cutting the uppermost 3 mm of the first sample, the remaining plant material was weighed again. Repeating this procedure three times yielded estimates for the fresh weight of four layers, the sum of which deviated by less than 5% from the whole turf fresh weight. All five samples were dried for 2 days at 60 °C, and WCs were determined as 100 × (fw–dw)/dw(%). To distinguish the WC of individual layers from that of the intact turf the latter is subsequently called average water content (WC_{avg}).

CO₂ gas exchange measurements

CO₂ exchange as a function of PAR was studied with a total of six samples (diameter: ca. 40 mm; dw: 0.9–1.1 g) using a ‘mini-cuvette system’ (Walz, Effeltrich, Germany). For all CO₂ measurements, we used a BINOS infrared gas analyser (Rosemount, Hanau, Germany) operating in differential mode, which detected differences in the CO₂ concentration to within 0.1 ppm. An additional BINOS in absolute mode was used to determine the CO₂ concentration of the air flowing through the system (380–420 µl l⁻¹). The temperature inside the cuvette was kept at 20 °C, relative humidity ranged from 80% to 95%.

The photosynthetic performance of different layers of a homogeneous patch of *T. ruralis* (area: 60–100 cm²) was assessed by dividing each of the six replicate samples in four parts. One was left intact, from the second to fourth sample the uppermost 3, 6, and 9 mm, respectively, were removed with a razor blade. Samples were put in wire-mesh baskets (3.8 cm diameter, 1–1.5 cm height, 1.6 mm mesh width) and allowed to dry. After rewetting, samples were kept at low light (ca. 30 µmol m⁻² s⁻¹ PAR, temperature 20 °C, WC_{avg} > 400%

dw) for 12 h. Before measurements, samples were transferred to ca. $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR for ca. 10 min to ensure photosynthetic induction. Subsequently, light response curves were determined at a WC_{avg} of 300–400% dw, which represents the optimal range of WC_{avg} (Zotz and Rottenberger, 2001). PAR was increased in 14 steps from 0 to $1430 \mu\text{mol m}^{-2} \text{s}^{-1}$. Each light level was maintained until a constant net CO_2 uptake was reached (ca. 5 min). The samples were weighed before and after the experiment. Finally, all samples were dried for 4 days at 70°C and the CO_2 exchange of the bryophytes related to their dry weight. The light response curves were subsequently fitted following the function given by Smith (1937).

Estimation of the rates of net CO_2 exchange of individual layers

Instantaneous rates of net CO_2 exchange (A) were only directly determined for layer 4 (>9 mm depth), while the A of layer 3 and above were estimated using

$$A_{13} = \frac{A_{13+4}(\text{dw}_{13} + \text{dw}_{14}) - A'_{14} \times \text{dw}_{14}}{\text{dw}_{13}},$$

where A_{13} is A of layer 3, A_{13+4} is the measured A of layer 3 and 4, dw is the dry weight of the respective layer, and A'_{14} is the A of layer 4 corrected for the reduced PAR. The A 's of the remaining two layers were calculated analogously. Light response curves were conducted at a WC_{avg} , which was characterized by a lack of vertical gradients in WC within a moss plant (Fig. 1). Hence no correction was applied for differences in WC between layers.

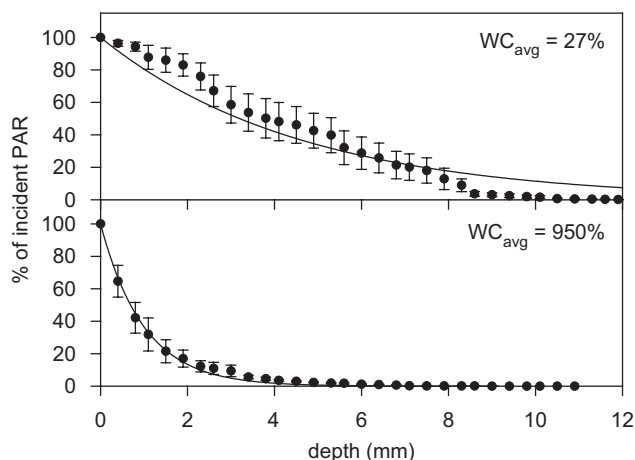


Fig. 1. Attenuation of incident light with increasing depth in a moss turf for two different water contents (WC_{avg}) (data are means \pm SE, $n = 10$). The regression lines are $I = I_0 \exp(-k_{\text{depth}})$, with $I_0 = 100$; $r^2 = 0.94$ and 0.99 , respectively (see also Table 1).

Miscellaneous measurements

Plant nitrogen contents were determined at the University of Würzburg with a CHNO-Rapid (Foss Heraeus, Hanau, Germany), while chlorophyll contents were analysed with an HPLC.

Data analysis

Statistical analysis was carried out with STATISTICA software (STATISTICA 5.1, StatSoft Inc., Tulsa, OK, USA). We often used non-parametric statistics due to low sample size and/or skewed distributions (Sokal and Rohlf, 1995). If not stated otherwise, means are accompanied by ± 1 SE as a measure of variance.

Results

Light attenuation by a moss turf was strongly influenced by plant WC. As shown in Fig. 1 and Table 1, the decrease in PAR with depth could be adequately expressed following the Lambert–Beer law of light extinction as

$$I = I_0 \exp(-k_{\text{depth}}),$$

where I_0 is the incident photon irradiance on top of a turf; it was set to 100. The fit between regression model and measured data improved with increasing WC_{avg} (Table 1). In turfs with low WC_{avg} , e.g. 30–60% dw, about 50% of incident radiation reached as far as 3 mm into the plant (Fig. 1; Table 1), at high WC_{avg}

Table 1. Changes in the proportion of incident light reaching different depths of a moss turf as a function of plant water content (WC_{avg})

| WC_{avg} means \pm SE | 3 mm | 6 mm | 9 mm | k -values | r^2 |
|--|------|------|------|-------------|-------|
| 27 \pm 5 | 52.7 | 27.9 | 14.7 | 0.213 | 0.94 |
| 53 \pm 3 | 49.4 | 24.7 | 12.3 | 0.233 | 0.93 |
| 83 \pm 5 | 39.2 | 15.7 | 6.2 | 0.309 | 0.90 |
| 114 \pm 4 | 29.0 | 8.4 | 2.4 | 0.413 | 0.88 |
| 148 \pm 6 | 27.1 | 7.3 | 2.0 | 0.435 | 0.95 |
| 184 \pm 6 | 14.3 | 2.0 | 0.29 | 0.646 | 0.93 |
| 232 \pm 6 | 14.7 | 2.1 | 0.31 | 0.639 | 0.99 |
| 273 \pm 8 | 11.3 | 1.3 | 0.14 | 0.727 | 0.97 |
| 326 \pm 7 | 2.9 | 0.08 | 0 | 1.179 | 0.99 |
| 375 \pm 8 | 5.7 | 0.33 | 0.01 | 0.956 | 0.99 |
| 429 \pm 7 | 10.8 | 1.16 | 0.12 | 0.742 | 0.97 |
| 471 \pm 10 | 4.7 | 0.22 | 0.01 | 1.018 | 0.98 |
| 621 \pm 11 | 5.3 | 0.28 | 0.01 | 0.978 | 0.92 |
| 1126 \pm 21 | 4.8 | 0.23 | 0.01 | 1.014 | 0.99 |

Given are the results of measurements (compare Fig. 2) for 14 different WC_{avg} for depths of 3–9 mm (in % of incident PAR), the values of k of the function $I = I_0 \exp(-k_{\text{depth}})$, and the r^2 of these regressions; $n = 5$ turfs.

Table 2. Differences in chlorophyll and nitrogen contents as a function of the depth within a moss turf

| | Biomass (% total) | Chlorophyll | | | Nitrogen | |
|------------|----------------------|----------------------------------|----------------------|---------|----------------------------------|----------|
| | | mg g ⁻¹ _{dw} | Chl <i>a/b</i> ratio | % Total | mg g ⁻¹ _{dw} | % Total |
| Total turf | | 1.8 ± 0.22 | 1.7 ± 0.04 | 100 | 2.3 ± 0.1 | 100 |
| < 3 mm | 18 ± 2 | 3.6 ± 0.17 ^a | 1.7 ± 0.01 | 47 ± 2 | 3.2 ± 0.1 ^a | 24 ± 1.0 |
| 3–6 mm | 13 ± 3 | 2.1 ± 0.13 ^b | 1.8 ± 0.06 | 19 ± 2 | 2.5 ± 0.1 ^{bd} | 13 ± 0.4 |
| 6–9 mm | 11 ± 4 | 1.4 ± 0.10 ^c | 1.8 ± 0.08 | 11 ± 5 | 2.2 ± 0.1 ^{cd} | 10 ± 0.5 |
| > 9 mm | 58 ± 10 | 0.6 ± 0.12 ^d | 1.8 ± 0.06 | 23 ± 10 | 2.3 ± 0.1 ^d | 53 ± 1.2 |

Given are total chlorophyll concentrations, Chl *a/b* ratios, proportion of total chlorophyll content in a given layer of total content, nitrogen concentration and proportion of total nitrogen content in a layer. Data are means ± SE ($n = 5$). Different letters indicate significant between-layer differences (Friedman ANOVA, post hoc Nemenyi test; $p < 0.05$).

(e.g. > 600% dm) this value had decreased by 1 order of magnitude. Light attenuation did not increase linearly with WC_{avg} over the entire range. While the lowest value of k of about 0.2 was indeed found in almost dry turfs, k increased continuously only up to a WC_{avg} of ca. 300% with no further increase with higher WCs (Table 1).

The WC within a turf was rather homogeneous in plants with a $WC_{avg} > 300\%$, while there were strong gradients at lower WC_{avg} (Fig. 2). Here, the WC of the uppermost layers was consistently lower than those of lower strata. In particular between 100% and 200% dm, these differences were substantial. For example, at 135% WC_{avg} , we observed an almost five-fold difference in WC between lowest and uppermost layer.

Chlorophyll concentrations decreased significantly with depth (Friedman ANOVA, $p < 0.01$; Table 2), while chlorophyll *a/b* ratios did not vary (Friedman ANOVA, $p > 0.05$). Nitrogen content was highest in the uppermost layer, but differences between the three lower layers were again not significant (Nemenyi test, $p > 0.05$). Notably, when expressed as the proportion of total plant nitrogen content, layer 4 held more than half of the overall nitrogen content, i.e. $53 \pm 1\%$.

Entire turfs reached maximum net assimilation rates of $7.9 \pm 4.5 \text{ nmol g}_{dw}^{-1} \text{ s}^{-1}$ (means ± S.D., $n = 5$). Estimating the individual contributions of the four layers to this integrated rate, as described in material and methods, revealed substantial differences (Fig. 3A), which were consistent with the observed variation in chlorophyll and nitrogen contents. The correlation between A and the two parameters, however, was only significant in the case of chlorophyll (Pearson product moment correlation, $n = 4$, $r = 0.98$, $p < 0.05$). The estimated light-saturated assimilation rate of the uppermost layer at WC_{avg} of ca. 350% ($36.3 \text{ nmol g}_{dw}^{-1} \text{ s}^{-1}$) was more than 50% higher than that of the second layer ($23.2 \text{ nmol g}_{dw}^{-1} \text{ s}^{-1}$) and more than twice that of the third layer ($17.6 \text{ nmol g}_{dw}^{-1} \text{ s}^{-1}$). Even the fourth layer responded to an increase in PAR, but there A never reached the compensation point. The upper three layers had rather similar light compensation points ($6\text{--}8 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR), but differed in saturating

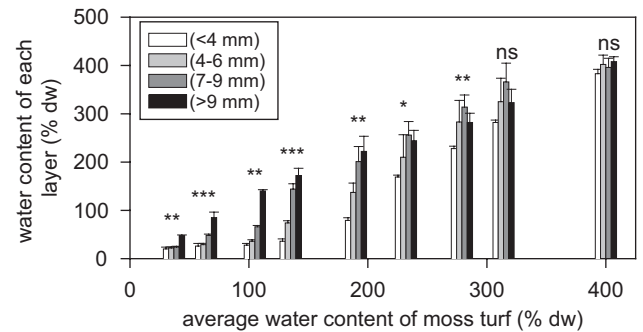


Fig. 2. Water contents of different layers within a turf as a function of the average water content of the turf (WC_{avg}). Given are means ± SE ($n = 5\text{--}7$) for four layers. Significant differences between layers of the same WC_{avg} are indicated by stars (Friedman ANOVA, * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns: not significant).

PAR (defined as PAR that allows 90% of maximum A): A in the uppermost layer saturated at almost twice the PAR (ca. $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR) compared to the subsequent two layers (ca. $350 \mu\text{mol m}^{-2} \text{ s}^{-1}$).

In the intact turf, however, lower layers experience very different light regimes. Correcting for the reduced light availability with depth at the given WC (Fig. 2; Table 1), the differences between layers were much more pronounced (Fig. 3B). Apart from the top 3 mm, only the second layer achieved positive rates of A , increasing linearly with incident PAR to reach up to 40% of those of the top layer at light saturation ($1400 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR).

Discussion

This study documents pronounced gradients in PAR and WC as well as in physiological response variables such as CO_2 gas exchange rates, and chlorophyll and nitrogen contents inside *T. ruralis* turfs. The light extinction coefficients of entire turfs were strongly dependent on the WC (Fig. 2; Table 1). This finding is consistent with an earlier report that compared the light

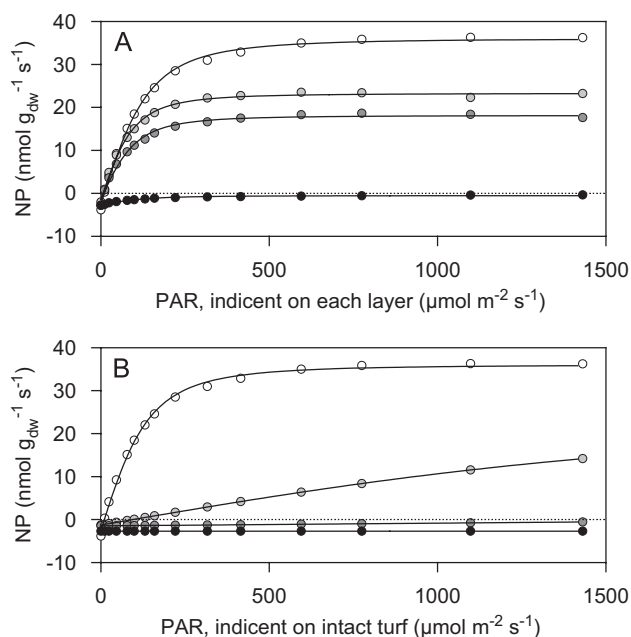


Fig. 3. The response of net CO_2 exchange A of four moss layers to changes in PAR. Data are means of five replications. Curves were fitted using the Smith-function ($r^2 > 0.99$ in all cases). Different colours indicate different layers: Layer 1, white; layer 2, light grey; layer 3, dark grey and layer 4, black. The upper panel (A) relates A and incident light for each layer, with the upper layers removed. The lower panel (B) relates A to incident light for the intact turf. Conditions were: temperature, 20°C ; WC_{avg} , 300–350%.

climate within a number of Antarctic moss species in the wet and in the dry state (Davey and Ellis-Evans, 1996). At lower average WCs, light penetrated to increasing depths in *T. ruralis* because the upper leaves are the first to dry and curl around the stems. These hygroscopic movements may partly solve the seeming puzzle that lower layers of a turf show the capacity for positive carbon gain (Fig. 3A), although very little PAR actually penetrates down to this depth in intact turfs at higher WCs (Fig. 3B). As suggested previously by Davey and Ellis-Evans (1996), deeper layers receive increased levels of PAR during each drying cycle which transiently allows positive CO_2 uptake rates in the depth of intact turfs until the entire moss is desiccated. The same argument applies to gradients in chlorophyll contents, which were highly correlated with the maximum CO_2 uptake rates of each layer. The distribution of nitrogen content, however, did not match our expectations. First, the nitrogen concentrations in the uppermost layer were only slightly higher than those in the remaining moss body (Table 2); second, most of the total nitrogen pool was found in the lowermost portion of the turfs, which never showed any net uptake of CO_2 (Fig. 3A). Symplastic translocation of assimilates and nutrients has been demonstrated both in endohydric and ecto-

hydric bryophytes (Alpert, 1989; Bates and Bakken, 1998; Eckstein and Karlsson, 1999), but interspecific differences in the degree of internal redistribution of nutrients are pronounced (Bates, 1997). The reason that the allocation pattern of N within these turfs does not match theoretical expectations (Kull, 2002) may be that the potential for translocation is rather limited in this particular ectohydric species, that nitrogen is not in short supply at this particular growing site in an urban environment, or that nitrogen is used for other ends than photosynthesis. In addition, many bryophytes show obligate or facultative associations with nitrogen-fixing cyanobacteria (During and Van Tooren, 1990), which could also confound the relationship between nitrogen content and photosynthetic function of the moss. Since we neither analysed the particular forms of nitrogen nor the presence of cyanobacteria, we can only speculate at the moment as to the reasons for this discrepancy.

Cornelissen et al. (2007) proposed that internal tissue N concentrations of the entire vegetative bryophyte shoot could be a shortcut for multi-species screenings of potential relative growth rates in biogeochemical studies. However, our results showing that the largest proportion of N is actually found in non-productive tissue (Table 2) do not lend support to this notion. The problem which parts of a moss are living and should thus be included in gas exchange/growth measurements is difficult to solve, and the inclusion of varying proportions of “green” and/or “brown”, yet living, plant material may explain to some extent discrepancies in the reported gas exchange rates for bryophytes in general and, in particular, for the species of this study (Meenks et al., 1991; Tuba, 1987; Tuba et al., 1998; see also Zotz and Rottenberger, 2001). Finally, our findings highlight the problem of using the analysis of chlorophyll fluorescence as a quantitative surrogate for gas exchange measurements in bryophytes and lichens (see also Green et al., 1998), partly because fluorescence measurements only relate to the uppermost layers of a moss cushion or turf, while gas exchange measurements integrate over the entire gametophyte. Without doubt, fluorescence measurements can provide valuable insight into the physiology of bryophytes (e.g. Marschall and Proctor, 2004) but the results should be used with caution when it comes to the prediction of C fluxes and growth.

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