Growth reconstruction and photosynthesis of aquatic mosses: influence of light, temperature and carbon dioxide at depth

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Summary
1 The mosses Sphagnum subsecundum and Drepanocladus exannulatus dominate the vegetation in the oligotrophic, softwater Lake Grane Langsø, Denmark, even at great depths where light and temperature are low. We used seasonal changes in morphology to reconstruct the annual growth and the longevity of the mosses and measurements of photosynthesis and respiration to evaluate the importance of light, temperature and CO₂ for the growth patterns at depth in the lake.
2 The reconstruction technique revealed that the mosses had a relatively fast growth rate (90–250 mm shoot⁻¹ year⁻¹) and were short lived (0.7–2.9 years). The shoots of both moss species grew faster in deep than in shallow water. Growth experiments in summer confirmed that Sphagnum grew more slowly and decayed more rapidly in shallow than in deep water.
3 Fast growth of mosses in deep waters can be accounted for by lower temperature, extensive CO₂ supersaturation and nutrient enrichment in the hypolimnion during summer stratification. Maximum rate of light-saturated photosynthesis in July was 3.3-fold higher and of dark respiration 1.3-fold lower in Sphagnum from 9.5 m incubated at the ambient 8 °C than in Sphagnum from 0.7 m incubated at 20 °C. The net daily carbon fixation was greater in deep than in shallow water despite the much lower irradiance at depth. Extensive CO₂ supersaturation stimulated photosynthesis several-fold relative to the rates observed in air-saturated water. Tissues of Sphagnum were richer in nitrogen in deep than in shallow water during summer, but the importance of nutrient availability to annual moss growth remains unclear.
4 Reconstruction techniques are recommended for comparative studies on annual and interannual growth patterns of mosses within lakes and among lakes of different altitude, latitude and water chemistry. This information can be based on just a single collection and can therefore include remote sites with adverse climate.

Keywords: Drepanocladus, growth, photosynthesis, reconstruction technique, Sphagnum, water mosses

Introduction
Mosses often dominate the macroscopic vegetation of lakes at the lower depth limit, sometimes mixed with charophytes or higher plants (Hutchinson 1975; Sand-Jensen & Søndergaard 1981; Chambers & Kalff 1985). In temperate regions mosses are particularly abundant in oligotrophic lakes (Raven 1988; Srivastava et al. 1995; Toivonen & Huttunen 1995) and they have expanded their range following lake acidification (Grahn et al. 1974; Grahn 1977; Roelofs 1983; Catling et al. 1986; Raven 1988). Mosses are often the only submerged plants in subpolar and polar lakes where they penetrate to great depths although the lakes are free of ice and snow cover for only 1–3 summer months (Bodin & Nauwerck 1968; Welch & Kalff 1974; Priddle 1980a). These distribution patterns reflect the fact that many aquatic moss species are adapted to low temperature and low pH, have low light and nutrient requirements, and presumably grow and decompose slowly (Bodin & Nauwerck 1968;...
Physico-chemical conditions were examined every two weeks along a vertical depth profile in the deepest part of the regular lake basin. Temperature profiles were measured with a thermistor (±0.1 °C). Dissolved O2 was measured with an O2 probe (Yellow Spring Inst.). Concentrations of total and dissolved N and P were measured on water samples following the methods of Koroleff (1970, 1976). Phytoplankton chlorophyll was measured on filtered samples (Winternans & de Mots 1965). The pH was measured using Radiometer equipment (PHM 82 meter and combined glass electrode GK 2401) particularly suited for poorly buffered water. Dissolved inorganic carbon (DIC) was measured twice during summer stratification on an IRGA-system described by Vermaat & Sand-Jensen (1987).

Irradiance (PAR, 400–700 nm) was estimated at depth using continuous measurements of surface irradiance from a nearby meteorological station, biweekly measurements of Secchi-transparency and relations of Secchi-transparency to the mean vertical attenuation coefficient measured four times during the year. Attenuation of irradiance was measured at 0.5-m depth intervals using a flat, cosine-corrected quantum sensor (Li-Cor 190 PAR). Exponential attenuation in the water column was well characterized by a single attenuation coefficient for the entire water column (Kirk 1983). Monthly estimates of irradiance at depth were obtained assuming that horizontal screening due to surrounding hills was 1% and that loss by surface reflection varied systematically over the year as reported for Grane Langsø by Nygaard (1989).

Reconstruction of moss demography

Two collections of Sphagnum subsecundum coll. and Drepanocladus exannulatus (Günb) Warnstorf (hereafter Sphagnum and Drepanocladus) were made from Grane Langsø around September 1994 and March 1995 (hereafter denoted September and March). Two collections were used to improve the accuracy of the seasonal growth patterns reconstructed from shoot morphology and to test the reliability of the method. The collections were made with a rake. Sphagnum was collected from 0.5, 6, 8 and 10 m and Drepanocladus was collected from 2, 6 and 10 m. At least 30 intact green individuals from each depth were dried under light pressure between sheets of absorbent paper.

Both species displayed distinct seasonal growth patterns which allowed us to define a summer and winter season. Sphagnum produced longer (and more) side branches during summer than winter (Fig. 1) and Drepanocladus produced a higher density of side branches along the main shoot axis during summer than winter. For every main shoot of Sphagnum we measured the distance from the shoot apex to each side
Fig. 1. Shoot morphology of *Sphagnum subsecundum* from depths of 0.5 m and 8.0 m in Lake Grane Langsø in September 1994. Summer and winter periods are indicated along the shoot axis.

branches, the length of each side branches, and the dry mass for each centimeter length of shoot. For *Drepanocladus* we modified the procedure slightly by measuring the number of side branches and the dry mass for every 1- or 2-cm length of main shoot.

The overall growth pattern was the same among individual moss shoots in a sample, but total shoot length and annual shoot extension, as well as fine-scale patterns, varied among the 30 replicates, possibly due to natural variability of shoot size and variable position and light availability within the moss carpet. To establish distinct patterns we corrected for interplant variability before attempting to calculate the seasonal growth parameters. We first normalized the total shoot length of every individual shoot to the mean shoot length of all individuals in the sample. For *Sphagnum* we then normalized the length of every side branch on each individual by multiplying by the mean length of all side branches on the 30 shoots and dividing by the mean length of sidebranches on that particular shoot. For *Drepanocladus* we normalized the branch density along the main axis of each individual to the mean branch density of all individuals. After normalization of shoot length and branch length (*Sphagnum*), or shoot length and branch density (*Drepanocladus*), we calculated the mean length and number of side branches (with 95% CL) along the main moss axis from the apex in intervals of 0.5 cm.
(Sphagnum) and 1 or 2 cm (Drepanocladius) measured on each of the 30 replicates.

Normalized graphs were made for average values of all 30 replicate shoots showing length, or number, of side branches along the main axis. For most samples the graphs constructed from samples in September 1994 and March 1995, could be superimposed on each other using maxima or minima as markers implying that the reconstructed unimodal growth patterns are annual (see results). The annual shoot extension can, therefore, be read as the distance between consecutive growth maxima or consecutive growth minima (viz. Duarte et al. 1994). To evaluate the error associated with the reconstructed annual growth, the mean growth rate with 95% CL. was derived by taking three groups of 10 random shoots at each depth and collection. The 10 shoots in each group were normalized to the mean length of the shoots in the group. This procedure gave three graphs from September and three graphs from March for each depth which could be compared in nine combinations. The growth parameters were read from each combination of two graphs and the mean ± 95% CL. was calculated.

The shoot extension from September 1994 to March 1995 was converted from a length to dry mass using measurements of dry weight taken along each moss shoot. At a depth of 0.5 m the Sphagnum shoots were shorter than the annual shoot extension and the dry weight increase was calculated from the mean dry mass per cm of shoot multiplied by the estimated annual shoot extension. Shoot extension and dry weight increase between March and September were found by subtracting the September–March values from the reconstructed annual growth.

**GROWTH EXPERIMENTS IN SITU**

Shoots of Sphagnum were collected from 8 m deep in Grane Langso in February 1995. Unbranched shoot apices 60 mm long were selected and marked with a thin wool thread 30 mm from the apex so that shoot growth at the apex and decomposition at the base could be determined. Twenty individuals were fastened with plastic rings to a nylon net stretched over the upper surface of each of 12 Perspex frames. The frames were anchored to the lake bottom, but kept 0.5 m above moss carpet at the lake bottom by a submerged float, and positioned along two transects such that their depths were 2, 4, 6, 8, 10 and 12 m (one frame per depth per transect). This procedure was chosen to keep the transplants off the moss carpet and, thereby, avoid shading and overgrowth by neighbouring shoots. Initial fresh and dry mass were measured using a further 20 individuals. The incubated plants were retrieved after 2 and 4 months and the lengths from the shoot apex to the thread mark and from the thread to the base were measured together with the fresh and dry mass.

**LABORATORY PHOTOSYNTHESIS EXPERIMENTS**

Sphagnum shoots were collected in July 1995 from 0.7 m water depth at 20 °C in the epilimnion and from 9.5 m at 8 °C in the hypolimnion. Photosynthesis was measured on 20–30 mm long green apices as O2 evolution at ambient temperature and nine irradiances (from 0 to 430 μmol photon m-2 s-1), but constant CO2 supersaturation (about 250 μmol L-1). Photosynthesis was also measured at seven CO2 concentrations (from 0 to 325 μmol L-1) under light saturation (430 μmol photon m-2 s-1).

The experiments were made in a Hansatech photosynthesis chamber (DW3, 15 mL) illuminated by a tungsten-halogen light source and shaded to the selected irradiances by neutral density filters. The O2-electrode was calibrated in air-saturated and N2-bubbled water of known temperature. Electrode drift was negligible during long-term incubation at constant temperature in air-saturated distilled water. Also, physical O2 exchange through the glass chamber walls was shown to be negligible by incubation in O2-depleted water. Electrode output was recorded on a computer equipped with a Hansatech Interface A/D Board (IF2). Temperature was kept at the preselected level by circulating water through the water jacket surrounding the photosynthesis chamber from a constant temperature water bath.

The experimental water was filtered lake water which was brought to the required CO2 concentration either by passing CO2-stripped atmospheric air through the water or adding small equal amounts of 100 μmol L-1 NaHCO3 and 100 μmol L-1 HCl. The experiment was started with an O2 concentration at around 50% of air saturation and it never exceeded 80% during the incubation. The pH was maintained between 4.8 and 5.0. Concentrations of CO2 calculated from NaHCO3 additions were checked on the IRGA-system.

Plant material was weighed after incubation, freeze-dried and reweighed. Subsamples were ground in a mortar in ethanol. The solution was filtered and chlorophyll a and b were measured spectrophotometrically and calculated according to Wintermans & de Mots (1965). The carbon and nitrogen content was measured on a Carbo-Erla analyser on other subsamples of experimental plants and on 20–30 mm long dried apices of Sphagnum and Drepanocladius collected in September for reconstruction measurements.

**Results**

**PHYSICO-CHEMICAL CONDITIONS**

Grane Langso is a relatively nutrient-poor, transparent lake with a small phytoplankton biomass relative to many others Danish lakes (Table 1). Dissolved inorganic nutrients in the surface waters varied over
Table 1. Summary of chemical characteristics and light climate in the surface water of Lake Grane Langsø during 1994

<table>
<thead>
<tr>
<th>Chemical Characteristic</th>
<th>Mean ± SE</th>
<th>Range</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total N (μmol L⁻¹)</td>
<td>27 ± 2</td>
<td>8-44</td>
<td>19</td>
</tr>
<tr>
<td>NH₃ + NH₄⁺ (μmol L⁻¹)</td>
<td>4 ± 10</td>
<td>0-15</td>
<td>19</td>
</tr>
<tr>
<td>NO₂ + NO₃⁻ (μmol L⁻¹)</td>
<td>6 ± 2</td>
<td>1-20</td>
<td>19</td>
</tr>
<tr>
<td>Total P (μmol L⁻¹)</td>
<td>0.5 ± 0.0</td>
<td>0.3-0.9</td>
<td>19</td>
</tr>
<tr>
<td>Ortho-P (μmol L⁻¹)</td>
<td>0.1 ± 0.0</td>
<td>0.5-0.6</td>
<td>19</td>
</tr>
<tr>
<td>Chlorophyll (μg L⁻¹)</td>
<td>5.0 ± 1.7</td>
<td>1.0-30</td>
<td>19</td>
</tr>
<tr>
<td>Secchi depth (m)</td>
<td>7.2 ± 0.3</td>
<td>5.5-9.5</td>
<td>18</td>
</tr>
<tr>
<td>Attenuation coefficient (m⁻¹)</td>
<td>0.40 ± 0.02</td>
<td>0.30-0.52</td>
<td>18</td>
</tr>
<tr>
<td>pH</td>
<td>5.21 ± 0.07</td>
<td>4.70-5.88</td>
<td>18</td>
</tr>
<tr>
<td>O₂ (μmol L⁻¹), surface</td>
<td>363 ± 7</td>
<td>278-609</td>
<td>120</td>
</tr>
<tr>
<td>O₂ (μmol L⁻¹), 10-12m*</td>
<td>6.5 ± 0.7</td>
<td>0.2-12.5</td>
<td>33</td>
</tr>
</tbody>
</table>

* Hypolimnion during summer stratification

Table 2. Concentrations of CO₂ (μmol L⁻¹) in the water column of Lake Grane Langsø, measured during summer of 1961 (n = 1, Nygaard 1965), 1994 and 1995 (mean, n = 2)

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>1961</th>
<th>1994</th>
<th>1995</th>
</tr>
</thead>
<tbody>
<tr>
<td>9 July</td>
<td>0.0</td>
<td>17.3</td>
<td>17.9</td>
</tr>
<tr>
<td>23 August</td>
<td>20.5</td>
<td>18.4</td>
<td>21.1</td>
</tr>
<tr>
<td>7 July</td>
<td>28.4</td>
<td>13.4</td>
<td>32.1</td>
</tr>
<tr>
<td>22 August</td>
<td>30.5</td>
<td>14.5</td>
<td>16.1</td>
</tr>
<tr>
<td>10</td>
<td>29.9</td>
<td>22.0</td>
<td>21.5</td>
</tr>
<tr>
<td>11</td>
<td>32.9</td>
<td>23.9</td>
<td>91.9</td>
</tr>
<tr>
<td>29.9</td>
<td>203.2</td>
<td>30.5</td>
<td>203.2</td>
</tr>
<tr>
<td>17.9</td>
<td>176.0</td>
<td>30.5</td>
<td>203.2</td>
</tr>
</tbody>
</table>

The pH was usually < 5.5 (Table 1) such that DIC was present almost solely as CO₂ (Rebsdorf 1972), which is also the only form of inorganic carbon used during photosynthesis by virtually all moss species tested (Steemann-Nielsen 1960; Bain & Proctor 1980). Detailed CO₂ measurements in Grane Langsø in 1960–61 (Nygaard 1965) showed concentrations in the surface waters from 40 μmol L⁻¹ during winter to 9.1 μmol L⁻¹ during summer and concentrations at 11 m depth up to 287 μmol L⁻¹ during summer stratification. Measurements in July and August 1994–95 showed similar CO₂ profiles to those measured in July and August 1961 (Table 2), and CO₂ concentrations between autumn and spring are also likely to resemble those previously measured. Dissolved O₂ declined in the deeper part of the hypolimnion during summer stratification (Table 1). Oxygen dropped below 60 μmol L⁻¹ at depths exceeding 10.5 m in August–September (data not shown).

Monthly surface irradiance (PAR) varied between 54 mol photon m⁻² in January and 1470 mol photon m⁻² in July. Averages of daily irradiance in January and July ranged between 0.17 and 1.8 mol photon m⁻² at 0.5 m and between 0.06 and 1.8 mol photon m⁻² at 10 m. The cumulative annual irradiance at the different depths from which we collected the mosses is shown in
Table 3. The estimated irradiance at the maximum depth of moss growth at 10.5 m was 121 mol m⁻² year⁻¹, corresponding to about 1.8% of annual surface irradiance.

GROWTH PATTERNS OF MOSSES

Shoots of Sphagnum had clear seasonal growth patterns visible in the morphology of the shoots collected from 6- to 10-m depth (Fig. 3). Irradiances at these depths are low (2.1–9.2% of surface irradiance; Table 3) and moss photosynthesis and growth are thus likely to follow seasonal variations in irradiance. Even the longest plants only represented about 1.5 years growth so that the accuracy of the reconstruction technique declined with time and therefore with distance along the shoot axis as reflected by the wide bars (95% CL) and the presence of data points based on single measurements. Side branches located up to about 40 mm from the apex on shoots collected from 6, 8 and 10 m in September were not fully extended in comparison with their final length which had been attained by March. This pattern accords with Rincon & Grime (1989) who emphasized that much extension growth occurs in autumn. Side branches located close to the apex in the March sample had apparently already reached their final length, which is plausible because the growth rate is slower in winter than in summer, such that cell division and elongation can keep pace.

Shoots of Sphagnum collected at 0.5-m depth were much shorter and growth patterns were more difficult to interpret (Fig. 3). Shoots collected in March had short side branches at the apex and a peak in the length of side branches about 50 mm behind the apex which probably represented the previous midsummer and, thus, a predicted 50-mm extension of shoot length over around eight months. Shoots collected in September did not display a clear peak presumably, because elongation of side branches formed near the apex in summer was incomplete. Assuming that in September shoots elongation had finished in branches over 50 mm behind the apex (as was observed at 6, 8 and 10 m), the lengths of fully extended sidebranches in September shoots, matched those at 120 mm behind the apex in March shoots. An annual shoot extension of 120 mm is more than twice the extension between September and March as also observed at 6, 8 and 10 m.

Shoot growth in Drepanoclados was reconstructed using the density of side branches along the main axis to predict seasonal maxima and minima (Fig. 4). Seasonal patterns were clearly discernible among shoots collected at 2 and 6 m and at 10 m in September.

GROWTH RATES RECONSTRUCTED

Annual shoot growth calculated by the reconstruction technique was significantly less for Sphagnum at 0.5 m (average 120 mm shoot⁻¹) than at 6–10 m (226–251 mm shoot⁻¹, Table 3). Annual increase in dry weight rose significantly from about 18 mg shoot⁻¹ at 0.5 and 6 m to about 27 mg shoot⁻¹ at 8 and 10 m. Mean annual shoot extension increased 1.9-fold between 0.5 and 10 m and shoot length increased 3.5-fold, such that the mean longevity of the moss shoot increased from 0.69 years at 0.5 m to 1.25 years at 10 m. This result does not imply that the moss tissues are fully decomposed after this period of time, but that, on the average, the basal parts of the moss tissues are no longer connected to the green shoot apices, or cannot be retrieved intact from the moss carpet, after this period.

Annual shoot growth of Drepanoclados (90–248 mm shoot⁻¹) resembled the rates for Sphagnum.
and was about 2.5-fold higher at 6 m than at 2 m in terms of length, while the growth in dry weight was about 2.5-fold higher at 6 m than at 2 and 10 m (Table 3). Mean shoot length also peaked at 6 m. Mean longevity of Drepanocladus shoots ranged from 1.35-2.87 years and exceeded the longevity of Sphagnum shoots.

The 95% CLs associated with calculations of the mean shoot growth were relatively small (3-5% for Sphagnum and 15-24% for Drepanocladus of the
Fig. 4. Density of side branches (number cm$^{-1}$) along the shoot axis of *Drepanoclados exannulatus* collected in (●) September 1994 and (○) March 1995 at 3 depths in Lake Grane Langsø. September shoots from 2 and 6 m were positioned relative to March shoots to ensure that maxima and minima of branch density coincided. Values are means (± 95% CL) of about 30 replicates. Shoot and branch lengths were normalized as described in text.

Mean growth in length. The estimates demonstrate that the reconstruction technique is highly reproducible and that differences in moss growth between shallow and deep water are statistically significant (Table 3).

Shoot growth from September to March was calculated as the shoot length added during this period and estimated over the remaining half-year as the difference from the total annual growth (Table 4). Shoot growth in terms of length or dry weight was...
Table 4. Shoot extension and increase of dry mass on a half-year basis for *Sphagnum subsecundum* and *Drepanocladius exannulatus* collected at depth in Lake Grane Langsø, Denmark. Mean ± 95% CI. *n* is number of shoots examined in September and March. Sept.–Mar. values are Mar.–Sept. values subtracted from annual values in Table 3

<table>
<thead>
<tr>
<th>Shoot extension (mm)</th>
<th>Increase of dry mass (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. subsecundum</em></td>
<td></td>
</tr>
<tr>
<td>0.5 m deep</td>
<td>36 ± 4</td>
</tr>
<tr>
<td>6 m deep</td>
<td>62 ± 15</td>
</tr>
<tr>
<td>8 m deep</td>
<td>107 ± 7</td>
</tr>
<tr>
<td>10 m deep</td>
<td>105 ± 8</td>
</tr>
<tr>
<td><em>D. exannulatus</em></td>
<td></td>
</tr>
<tr>
<td>2 m deep</td>
<td>37 ± 8</td>
</tr>
<tr>
<td>6 m deep</td>
<td>46 ± 11</td>
</tr>
<tr>
<td>10 m deep</td>
<td>0</td>
</tr>
</tbody>
</table>

**Growth Experiments**

Shoots of *Sphagnum* tied to frames located 0.5 m above the moss carpet grew 2.8–4.6 mm week⁻¹ at depths between 4 and 10 m and significantly more slowly (1.7 mm week⁻¹) at 12 m from March to May (Fig. 5). From May to July shoots had died at 2 m, deteriorated at 4 m, and grown 3.7–4.7 mm week⁻¹ between 6- and 12-m depth (Fig. 5). These experiments verify the reliability of the growth rates reconstructed from the shoots located in the natural moss populations, because the annual shoot growth at 6–10 m depth of 226–251 mm (Table 3), distributed evenly over the year, yields weekly rates of 4.3–4.8 mm week⁻¹ corresponding to the direct measurements. Moreover, the reduced growth rates of *Sphagnum* set out in shallow water agree with the reduced growth rates reconstructed from moss shoots collected at 0.5-m depth (Table 3). The rate of shoot decomposition declined with depth in the lake, particularly between late April and late June (Fig. 5), probably due to falling temperatures at depth (Fig. 2).

While experimental shoots increased in length in deep water, they decreased in length, or died, in shallow water. We are hesitant, however, to draw further conclusions from the *in situ* experiments because shoots were located above the moss carpet and are likely to experience smaller supply rates of nutrients and CO₂, which may influence, in particular, the shoots set out in shallow water, because the epilimnion waters get warm and depleted in nutrients over the summer. The hypolimnion experiences lower temperatures and enrichment in nutrients and CO₂ which may benefit moss growth and retard decomposition.

**Photosynthesis Experiments**

Shoots of *Sphagnum* collected in July from 9.5-m depth contained significantly more chlorophyll and nitrogen on a dry weight basis and photosynthesized 3.3-fold faster at both light- and CO₂-saturation than shoots from 0.7-m depth (Tables 5 and 6). Photosynthesis remained several-fold higher in *Sphagnum* shoots from 9.5 m than 0.7 m depth at all irradiances.
Table 5. Photosynthetic variables and parameters, chlorophyll- and N-content of Sphagnum subsecundum collected from depths of 0.7 m and 9.5 m in Lake Grane Langso in July and incubated at ambient temperature (20 and 8 °C, respectively) at a CO₂ concentration of about 250 μmol L⁻¹. The photosynthetic efficiency, compensation point and dark respiration are calculated by linear regression on the four data points located between irradiances 0 and 53 μmol m⁻² s⁻¹. The saturation point is calculated as the irradiance where 90% of the maximum gross production is obtained. Mean ± SD (n = 3). Cases marked with 'a' show significant difference between values from the two depths (t-test, P < 0.05).

<table>
<thead>
<tr>
<th>Depth</th>
<th>Pₛ</th>
<th>α</th>
<th>Iₛ</th>
<th>IₛΑ</th>
<th>69 ± 50</th>
<th>16.5 ± 0.9a</th>
<th>1.88</th>
<th>2.45 ± 0.02a</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.7 m</td>
<td>125 ± 44</td>
<td>2.8 ± 0.3</td>
<td>30.0 ± 6.1a</td>
<td>120</td>
<td>180</td>
<td>53 ± 22</td>
<td>27.6 ± 1.5</td>
<td>1.87</td>
</tr>
</tbody>
</table>

Pₛ, photosynthetic rate (μmol O₂ g⁻¹ DW h⁻¹); α, photosynthetic efficiency (μmol O₂ g⁻¹ DW h⁻¹ ((μmol m⁻² s⁻¹))⁻¹); Iₛ, compensation point (μmol m⁻² s⁻¹); IₛΑ, saturation point (μmol m⁻² s⁻¹); rate of O₂ dark uptake (μmol O₂ g⁻¹ DW h⁻¹); Chl. (a + b) (mg g DW); Chl.a/Chl.b; N-content (% DW).

Table 6. Photosynthetic variables and parameters of Sphagnum subsecundum collected from 0.7 m and 9.5 m in Lake Grane Langso in July and incubated at ambient temperature, light saturation and varying CO₂ concentrations. The carbon affinity, compensation point and O₂ consumption at zero CO₂ are calculated by linear regression on the four data points located between 0 and 50 μmol CO₂ L⁻¹. The saturation point is calculated as the CO₂ concentration where 90% of the maximum gross production is obtained. Mean ± SD (n = 3).

<table>
<thead>
<tr>
<th>Depth</th>
<th>Pₛ</th>
<th>A_c</th>
<th>CP</th>
<th>SP</th>
<th>C(O₂)₀</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.7 m</td>
<td>77 ± 16</td>
<td>19 ± 1.3</td>
<td>13.3 ± 0.6</td>
<td>80</td>
<td>25.6 ± 19.4</td>
</tr>
<tr>
<td>9.5 m</td>
<td>256*</td>
<td>2.5 ± 1.9</td>
<td>7.8 ± 4.2</td>
<td>190</td>
<td>15.3 ± 3.4</td>
</tr>
</tbody>
</table>

Pₛ, photosynthetic rate (μmol O₂ g⁻¹ DW h⁻¹); A_c, carbon affinity (μmol O₂ g⁻¹ DW h⁻¹(μmol CO₂ L⁻¹)⁻¹); CP, compensation point (μmol CO₂ L⁻¹); SP, saturation point (μmol CO₂ L⁻¹); C(O₂)₀, O₂ consumption at zero CO₂ (μmol O₂ g⁻¹ DW h⁻¹).

*The mean photosynthesis rate at the two highest CO₂ concentrations.

(Fig. 6). The light compensation point was 7.3 μmol photon m⁻² s⁻¹ in shoots from 9.5 m and much higher at 30 μmol m⁻² s⁻¹ in shoots from 0.7 m, because the former shoots had higher photosynthetic efficiency (initial slope of photosynthesis versus irradiance) and slightly lower dark respiration (Table 5). Dark respiration was also lower relative to maximum photosynthesis in shoots from 9.5 than 0.7 m reflecting, in part, the lower ambient (and experimental) temperature (8 vs. 20 °C).

Higher photosynthetic capacity in shoots from 9.5 m than 0.7 m depth was also observed in the dependence of photosynthesis on CO₂ concentration (Fig. 7). Shoots from 9.5 m had a slightly steeper initial slope of photosynthesis versus CO₂ concentration and had lower CO₂ compensations points than shoots from 0.7 m (Fig. 7, Table 6).

The daily net oxygen evolution in July was estimated for unshaded 20–30 mm long apices of Sphagnum located at 0.7 and 9.5 m water depth in Grane Langsø assuming that the photosynthesis-irradiance relationship (Fig. 6). The light compensation point was 7.3 μmol photon m⁻² s⁻¹ in shoots from 9.5 m and much higher at 30 μmol m⁻² s⁻¹ in shoots from 0.7 m, because the former shoots had higher photosynthetic efficiency (initial slope of photosynthesis versus irradiance) and slightly lower dark respiration (Table 5). Dark respiration was also lower relative to maximum photosynthesis in shoots from 9.5 than 0.7 m reflecting, in part, the lower ambient (and experimental) temperature (8 vs. 20 °C).

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curves measured at 250 \text{mM} \text{CO}_2 \text{L}^{-1} (\text{Fig. 6}) represented the field situation and using mean hourly surface irradiances over the day in July to estimate the time course of photosynthesis at the two depths. The daily net oxygen evolution was 1.5 \text{mmol O}_2 \text{g}^{-1} \text{DW} at 0.7 \text{m} and 1.6 \text{mmol O}_2 \text{g}^{-1} \text{DW} at 9.5 \text{m} depth. With typical molar quotients between \text{O}_2 and \text{CO}_2 during metabolism (1.2 \text{mol O}_2 \text{per mol CO}_2; \text{Langdon 1988}) and between carbon and dry weight in the moss biomass (34.6 \text{mmol C g}^{-1} \text{DW}; \text{Table 2}) the daily carbon fixation was 0.035 \text{mole C (mol cell C)}^{-1} \text{day}^{-1} at 0.7 \text{m} and 0.039 \text{mole C (mol cell C)}^{-1} \text{day}^{-1} at 9.5 \text{m}. These estimates are subject to considerable uncertainty. Because experimental \text{CO}_2 supply rates to shoots probably exceeded natural levels in shallow water, but not in deep water (\text{Table 2}), however, the estimates support the notion that summer growth rates of \text{Sphagnum} are higher in deep than in shallow water. If \text{Sphagnum} shoots located at the depth limit at 10.5 \text{m} are assumed to have the same acclimation of photosynthesis to irradiance as the shoots retrieved from 9.5 \text{m}, the daily net oxygen evolution is 0.9 \text{mmol O}_2 \text{g}^{-1} \text{DW}. For an unaltered light acclimatization the compensation point for the daily metabolism of \text{Sphagnum} in July is located at 1.3\% of surface irradiance (0.6 \text{mol photon m}^{-2} \text{day}^{-1}).

Discussion

RECONSTRUCTION OF MOSS GROWTH

Seasonal changes in shoot morphology of \text{Sphagnum} and \text{Drepanocladus} allow the reconstruction of annual growth and estimation of growth rates and longevity of the moss shoots in their natural habitat within the moss carpet. The technique presented is rapid and reliable and can be based on a single collection, although the accuracy was improved by two collections half a year apart. The technique cannot however detect short-term growth patterns, due to the lack of more well-defined markers within the year, or the interannual patterns, because shoots were too short lived.

Carbon and oxygen cycling within a lake can be strongly influenced by the population dynamics of the abundant mosses (Welch & Kalff 1974; Bates 1992; Srivastava et al. 1995), especially since the reconstruction study demonstrates that the mosses grow quite rapidly (about 200 mm shoot \text{year}^{-1}) even at 10 \text{m} water depth where there is only \approx 2.1\% of surface irradiance and the green tissue lives for only 5–7 months (not shown). The notion of deep-water mosses as slow-growing organisms of high longevity and low photosynthetic capacity (Bodin & Nauwerck 1968) does not therefore apply to the populations in Grane Langsø. The deep-water populations of the charophyte, \text{Nitella flexilis} which formerly existed in Grane Langsø also had high photosynthetic capacity, and biomass turnover rates of less than one year (Nygaard & Sand-Jensen 1981). They were also responsible for maintaining a fully-oxygenated hypolimnion which the mosses present today cannot do as they do not cover the deepest parts of the lake.

The reconstruction technique was limited in this study by the need for normalization among individuals. It would be even more suitable for longer lived mosses which display clearer morphological separations between summer and winter (cf. Callaghan et al. 1978), as annual growth more easily could be measured on individual shoots and its variability assessed. Such conditions are expected in arctic lakes with winters of permanent darkness and summers of continuous daylight (e.g. Schindler et al. 1974). Arctic mosses are also likely to contain imprints from several years enabling both annual and interannual growth rates to be analysed and related to changes in environmental variables with depth and between years. Our unpublished analysis of mosses from 4 to 14 m depth in Char Lake, Arctic Canada, do indeed show distinct annual growth cycles representing the past 10 years with shoot growth rates of 9–15 mm year\textsuperscript{-1}, 10–20-fold lower than those measured in Grane Langsø. Comparisons of moss populations from lakes at different latitudes and at different depths within lakes could, therefore, be used to investigate the environmental regulation and internal coupling of growth and longevity of aquatic mosses. The same approach has been used successfully in studies of arctic dwarf shrubs (Havström et al. 1995) and tropical and temperate seagrasses (Duarte et al. 1994).

REGULATION OF MOSS GROWTH

We expected moss growth in Grane Langsø to decrease with depth along with the decline of irradiance from about 75\% of surface irradiance at 0.5 m to 2.1\% at 10 m. The growth in shoot length estimated from both the reconstruction technique (Table 3) and in situ experiments (Fig. 5) showed that this was not the case. Both moss species grew more slowly in shallow water at high irradiance and \text{Sphagnum} attained the fastest growth in terms of dry weight at 8 m and \text{Drepanocladus} the fastest growth at 6 m.

Several factors probably contribute to the continued growth of the mosses at low light in the cold bottom waters. The worldwide dominance of mosses in lakes of cold regions and at depth within lakes (Frantz & Cordone 1967; Priddle 1980a; McIntire et al. 1994) suggest that many species are well-adapted to growth and survival under low light and low temperature. Mosses also dominate many cold and low-light terrestrial habitats and the species concerned have low temperature and light requirements in growth experiments (Atanasiu 1971; Priddle 1980b; Furness & Grime 1982). The cold hypolimnion of lakes can offer a metabolic advantage by reducing the rate of maintenance respiration (Salisbury & Ross 1985), and this advantage is most significant when

photosynthesis is light limited (Markager & Sand-Jensen 1994). For Sphagnum in Grane Langsø this suggestion is supported by the lower respiration rate of shoots from 9.5 m incubated at 8 °C than shoots from 0.7 m incubated at 20 °C (Table 5). The reduced dark respiration at depth is even more striking considering that light-saturated photosynthesis was 3.3-fold higher at 9.5 ˚C than at 0.7 ˚C and that maximum photosynthesis and respiration usually change in concert (Markager & Sand-Jensen 1994). On a daily basis in July dark respiration of Sphagnum is estimated to consume 47% of gross photosynthesis in mosses at 0.7 m but only 37% of gross photosynthesis at 9.5 m, despite the much lower irradiance there. These estimates reflect the fact that respiratory losses are important to moss metabolism: reduction of respiration by physiological acclimation and exposure to low temperature at very low irradiances should improve growth and survival as proposed in previous studies of deep-water mosses and charophytes (Pridde 1980b; Nygaard & Sand-Jensen 1981). Further reduction of dark respiration relative to that presented here for Sphagnum at 8 °C can be expected at lower temperatures in colder habitats or seasons. Dark respiration of mosses at 2–3 °C in maritime Antarctic lakes (Pridde 1980b) and Esthwaite Water, England during winter (Maberly 1985a) are only about 3 μmol O₂ g⁻¹ DW h⁻¹ and special precautions, not yet attempted, are needed for unbiased measurements of these low rates.

The hypolimnion offers much higher CO₂ concentrations to moss photosynthesis than the epilimnion. Photosynthesis of Sphagnum is markedly stimulated by CO₂ supersaturation (Fig. 7); this is an aspect considered by Maberly (1985a,b) in work on Fontinalis, but overlooked in most earlier field studies. If the CO₂ concentrations measured at depth through the water column in Grane Langsø (Table 2) are used to represent in situ conditions, maximum photosynthesis of Sphagnum would be 8-fold higher at 9.5 m than at 0.7 m. The CO₂ concentration within the moss carpet is not known, and is probably variable with time and depth (e.g. Maberly 1985b). In the well-mixed waters at shallow depth moss cover is thin and CO₂ accumulation among the mosses is presumably small. In the thick carpet at depth decaying mosses are more abundant than living mosses and greater CO₂ accumulation is anticipated and should be enhanced by the overall CO₂ accumulation in the hypolimnion. Thus, CO₂ should facilitate moss photosynthesis at greater depths and restrict photosynthesis and growth in shallow waters (cf. Table 3 and Fig. 3).

The hypolimnion is also richer in dissolved nutrients than surface waters. Sphagnum apices collected from 9.5 m in July contained higher tissue concentrations of nitrogen than mosses from 0.7 m (Table 5) which may contribute to higher photosynthesis and summer growth in deep waters. Shoot apices of Sphagnum and Drepanocladium received 121 mol photon m⁻² year⁻¹ (about 1.8% of surface irradiance) at the approximate lower depth limit of the moss carpet at 10.5 m in Grane Langsø. This annual irradiance resembles that of 148 mol m⁻², which according to continuous in situ measurements, reached Nitella flexilis on the lake bottom when it was rather more transparent in the 1950s (Nygaard & Sand-Jensen 1981). Similar irradiances are received by mosses and charophytes at their limits in the cold hypolimnion of other transparent temperate lakes (Welch & Kalff 1974; Pridde 1980a, Sand-Jensen & Madsen 1991). In more turbid lakes the depth limits are often located in the warmer epilimnion and higher irradiances may then be required (Middelboe & Markager 1997), but in highly transparent lakes, such as Lake Tahoe, California (Frantz & Cordone 1967) and Crater Lake, Oregon (McIntire et al. 1994) mosses may grow at up to 120 m depth where the temperature is 4 °C and the light only 0.1–0.2% of surface irradiance. Differences in temperature and CO₂ availability, as well as differences in light requirements among species, may therefore influence the minimum light requirement to sustain growth and survival at depth in lakes.

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References


Rebsdorf, A. (1972) *The carbon dioxide system in freshwater*. A set of tables for easy computation of total carbon dioxide and other components of the carbon dioxide system. *Freshwater Biological Laboratory*, University of Copenhagen.


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