Photosynthesis and carbon gain of the lichen, *Leptogium azureum*, in a lowland tropical forest

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**Summary**

CO₂ gas exchange and microclimatic conditions of *Leptogium azureum* (Sw. ex ACH.) Mont., a foliose lichen, were investigated in the lowland tropical forest of Barro Colorado Island, Panama. Thalli growing epiphytically in the forest canopy or epilithically on boulders in the understory were studied. Under the prevailing temperature and humidity conditions, thallus water contents were generally high during the night, resulting in high rates of respiration. Daytime net CO₂ uptake was restricted by low light in the understory or by temporary reduction of thallus water content in the canopy. As a consequence, carbon balances were negative on many days. The results of these first field measurements of the CO₂ gas exchange of a tropical lichen support the notion that the low abundance of macrolichens in tropical lowland forests is mainly caused by an unfavourable combination of high temperature and low light.

Keywords: *Leptogium azureum*, lowland rain forest, carbon balance, lichen

1. **Introduction**

In recent years, increasing attention has been paid to the taxonomy and ecology of tropicallichens and bryophytes (Frahm & Gradstein 1990, Galloway 1991, Gradstein et al. 1990, Richards 1984, Wolf 1993), but there are few studies of the causal relationships between observed patterns of abundance and the physiology of these cryptogamic organisms in tropical ecosystems. In tropical lowland forests both bryophyte and lichen species seldom play an important role, whereas in montane forests mosses and lichens are often extremely abundant (Ellenberg 1975, Frahm 1987b, Seifriz 1924). Many hypotheses have been proposed to explain this phenomenon (Frahm 1987a). Richards (1984) suggested that the apparent unsuitability of lowland tropical forests for bryophytes was due to the combination of continuous high temperatures, high relative humidity, and low light intensities. As a consequence, respiratory losses at night would be large and could not be balanced by day-time photosynthesis. Laboratory experiments with several moss and liverwort species yielded the first supporting evidence (Frahm 1987b, 1990). Since bryophytes and lichens — as small, poikilohydric organisms — show many similarities in their physiology and ecology, a similar explanation seems plausible for the altitudinal gradient in the distribution of lichens.

The main goal of this study was to examine whether the proposed patterns of high CO₂ losses at night and low carbon gain during the day would be observed in the natural setting of a lowland tropical forest and whether carbon balances would be correlated with ambient temperature, thallus water content (WC) and light conditions. We used *Leptogium azureum* (Sw. ex ACH.) Mont., a foliose gelatinous lichen species that is widely distributed at lower elevations in tropical America (Dodge 1933). In the semi-evergreen moist forest of Barro Colorado Island, Panama, this species grows epiphytically and epilithically on trunks and boulders in the understory, but is also found on branches high in the canopy. As one of the few more common macrolichens on Barro Colorado Island, *Leptogium azureum*
is an appropriate organism for studying the limitations that lichens experience in their photosynthesis and their carbon gain in this tropical habitat.

2. Materials and methods

Diel gas exchange patterns

The investigations were conducted on Barro Colorado Island (9°10'N, 79°51'W), Republic of Panama. The vegetation of this reserve has been classified as 'tropical moist forest' (HOLDRIDGE et al. 1971) or as 'semievergreen moist tropical forest' (KNIGHT 1975). The average annual rainfall is 2600 mm with a pronounced dry season from mid-December through April. Detailed descriptions of vegetation, climate and ecology can be found in CROAT (1978), LEIGH et al. (1982), and WINDSOR (1990).

CO₂ gas exchange of Leptogium azureum (Sw. ex Ach.) Mont. (Collemataceae) was studied at two different sites between September 1991 and November 1992. Site 1 was in the crown of a kapok tree (Ceiba pentandra (L.) GAERTN., FRUCT. & SEM.), where thalli were growing on branches approximately 35 m above the ground. Site 2 was in the understory, where L. azureum can be frequently found on basaltic boulders.

The gas exchange measurements followed the method of LANGE et al. (1984), which is routinely used in field measurements of CO₂ exchange of lichens (e.g. BRUNS-STRENGE & LANGE 1991, LANGE et al. 1991). We used a CO₂/H₂O-Porometer (CQP 130, Walz, Effeltrich, FRG) in continuous open flow mode. The porometer head contained a small cuvette, which was closed with a thin polyethylene foil. This foil reflected up to 9% of incident radiation and absorbed about 1%. External temperature and relative humidity were tracked inside the cuvette, but the dew point of the air entering the gas exchange chamber was kept below ambient when air relative humidity was close to 100% to avoid condensation inside the cuvette. Outside air was led through the cuvette and the CO₂ exchange of enclosed lichen samples was determined with an infrared gas analyser (BINOS 100, Rosemount, Hanau, Germany) according to the gas differential procedure. The CO₂ content of the air stream was determined with another infrared gas analyser operating in the absolute mode (BINOS 100). Before entering the gas analyser, measuring and reference air streams were led through Peltier-controlled water-vapour traps to avoid errors in the CO₂ measurements from differences in water vapour partial pressure. Simultaneously, air temperature, air relative humidity, and photosynthetical photon flux density (PPFD) incident to the lichen were recorded.

One day before measurements, entire thalli (between 0.1 and 0.2 g dry weight) were removed from their substrate, freed of any liverworts growing on them and other organic material under a stereo-microscope, and fixed in a wire-mesh tray in their natural position. The tray was placed at the original site of growth. With two exceptions (September 6 and September 7, 1991), 3–4 replicate samples were used.

In regular intervals, the samples were introduced with their tray into the cuvette, which was located in close proximity to the natural growing site of the lichens. Individual measurements were finished after 2 to 5 minutes. Immediately after a measurement, samples were weighed. In the understory an electronic digital balance (Sartorius Handly H 110, Sartorius, Göttingen, Germany) with an accuracy of 0.1 mg was used. At the canopy site we had to use a balance with lower precision (Sartorius Portable PT 120, Sartorius, Göttingen, Germany; accuracy: 10 mg), which introduced an error of up to 10–20%, when determining low water contents. After weighing, the tray with the sample was put in its natural environment until the next gas exchange measurements.

The relationship of CO₂ exchange rates and thallus water content was analysed as follows. Thalli were submerged in rain water and superficially adherent droplets removed by vigorous shaking. Samples were enclosed in the cuvette at 27–28°C and PPFDs of 0,25, or 110 μmol m⁻² s⁻¹, respectively. Ambient CO₂ concentration ranged from 345–355 μmol l⁻¹. CO₂ exchange was measured as soon as steady-state conditions had been attained. After weighing and a short time outside the cuvette, CO₂ exchange was again determined. This procedure resulted in a stepwise water loss and was continued until no further changes in relative water content were observed.

After the gas exchange measurements, thalli were dried for 48 h at 105°C. Water content and gas exchange were related to the dry weight of the thalli. Ground samples were analysed at the University of Würzburg (Germany) using a CHN-O Element Analyser (Haereus, Hanau, Germany) and an ICP Spectrometer JY 70 Plus (ISA, München, Germany).

To measure the pH-value of the bark of the host tree C. pentandra, small pieces of the outer 0.2 mm of the bark (ca. 0.5 g) were immersed in 5 ml deionised water overnight. After filtration pH was measured with a pH-electrode. For the determination of mineral element contents samples of the outer 2 mm of the bark of C. pentandra were collected, dried, ground, and analysed as described above for lichen samples.

3. Results

3.1. Description of the microhabitat

The bark of the host tree C. pentandra is deeply grooved. In Table 1 its chemical composition is given and compared to the mineral element content of the lichen thalli. Most mineral elements were markedly higher in the lichen thalli. The bark was slightly acidic (pH-value: 5.3 ± 0.2; n = 3).

The lichens at the canopy site received significantly more light (0.94 mol m⁻² d⁻¹, n = 4) than those
in the understory (0.52 mol m\(^{-2}\) d\(^{-1}\), Table 2). On a 12-h-day the average PPFD in the understory averaged 12 \(\mu\text{mol m}^{-2}\text{d}^{-1}\) compared to 22 \(\mu\text{mol m}^{-2}\text{d}^{-1}\) in the canopy.

The sites also differed in the CO\(_2\) concentration of the air (Fig. 1). Compared to the canopy, CO\(_2\) in the understory was up to 70 \(\mu\text{l l}^{-1}\) higher and daily fluctuations were much more pronounced. At the canopy site the CO\(_2\) concentration in the immediate vicinity of the thalli and in the air used during the gas exchange measurements was compared. Air from underneath the lichen thalli was consistently higher in CO\(_2\) than the surrounding air (Fig. 1).

### Table 1. Mineral element contents (in % and \(\mu\text{g g}^{-1}\), respectively) of lichen thalli of *Leptogium azureum* \((n = 6)\), and of the outer 2 mm of the bark of *Ceiba pentandra* \((n = 3)\), where the lichens were growing. Data are means ± SD.

<table>
<thead>
<tr>
<th>Element</th>
<th><em>L. azureum</em> (thallus)</th>
<th><em>C. pentandra</em> (bark)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C (%)</td>
<td>42.0 ± 0.34</td>
<td>52.5 ± 0.1</td>
</tr>
<tr>
<td>N (%)</td>
<td>3.7 ± 0.17</td>
<td>0.42 ± 0.02</td>
</tr>
<tr>
<td>Ca (%)</td>
<td>1.01 ± 0.14</td>
<td>2.06 ± 0.03</td>
</tr>
<tr>
<td>P</td>
<td>2060 ± 166</td>
<td>135 ± 6</td>
</tr>
<tr>
<td>K</td>
<td>8.348 ± 6.30</td>
<td>298 ± 34</td>
</tr>
<tr>
<td>S</td>
<td>2.640 ± 97</td>
<td>278 ± 2</td>
</tr>
<tr>
<td>Mg</td>
<td>2.548 ± 123</td>
<td>262 ± 4.7</td>
</tr>
<tr>
<td>Na</td>
<td>1072 ± 609</td>
<td>241 ± 310</td>
</tr>
<tr>
<td>Fe</td>
<td>2092 ± 382</td>
<td>23 ± 0.4</td>
</tr>
<tr>
<td>Zn</td>
<td>2752 ± 1719</td>
<td>4 ± 0.8</td>
</tr>
<tr>
<td>Al</td>
<td>1821 ± 184.7</td>
<td>32 ± 0.6</td>
</tr>
<tr>
<td>Mn</td>
<td>61 ± 8.1</td>
<td>7 ± 0.1</td>
</tr>
<tr>
<td>Cu</td>
<td>29 ± 3.6</td>
<td>10 ± 0.4</td>
</tr>
</tbody>
</table>

3.2. Response of net CO\(_2\) exchange to thallus water content and PPFD

Figure 2 shows changes in the net CO\(_2\) gas exchange of *Leptogium azureum* with different water contents (WC). In the dark (Fig. 2a), respiratory CO\(_2\) loss increased up to a WC of approximately 500—600%, reaching approximately 8 nmol [g d. wt]\(^{-1}\) s\(^{-1}\) at a temperature of 27°C. Higher WCs did not lead to a further increase in respiration. Net CO\(_2\) uptake (A) was studied at PPFDs of 25 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) (Fig. 2b) and 110 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) (Fig. 2c), respectively. Highest rates (A\(_{\text{max}}\)) were also observed at about 600%, but A decreased with lower and higher WC. A\(_{\text{max}}\) was 4.8 nmol [g d. wt]\(^{-1}\) s\(^{-1}\) at 25 \(\mu\text{mol photons m}^{-2}\text{s}^{-1}\) and 14.8 nmol [g d. wt]\(^{-1}\) s\(^{-1}\) at 110 \(\mu\text{mol photons m}^{-2}\text{s}^{-1}\), respectively. The highest single rate of net CO\(_2\) uptake (17.5 nmol [g d. wt] \(\mu\text{l}^{-1}\)) was obtained during two spot measurements at 350 \(\mu\text{mol photons m}^{-2}\text{s}^{-1}\) (air temperature: 27°C, WC: 500%).

3.3. In situ measurements of net CO\(_2\) exchange

**Canopy.** Figure 3 provides four examples of diel courses of net CO\(_2\) exchange, thallus water content and environmental variables at the study site in the canopy. The study site was beneath the crown of a hemiepiphytic *Clusia uvitana* and was shaded by this plant and the leaves of the host tree. Consequently, PPFD was rather low for most parts of the day (< 50 \(\mu\text{mol m}^{-2}\text{s}^{-1}\)), but increased to up to
350 μmol m\(^{-2}\) s\(^{-1}\) during brief lightflecks. Air temperatures (\(T_a\)) averaged about 25°C at night, and regularly increased to more than 30°C in the early afternoon. During the wet season air relative humidity invariably reached 100% at night, but occasionally decreased to 70% around noon.

Consistent with the high variability of rainfall, RH, \(T_a\), and PPFD, the thallus water content (WC) varied widely even in the wet season (Fig. 3a–c). It ranged from up to 900% during and after rainstorms to as low as 50%. The night of the first time course (September 16–17, 1991; Fig. 3a) was characterized by a very high WC due to a heavy rainstorm during the preceding day. Respiration rates were very high, reaching 4.8 nmol [g d. wt\(^{-1}\) s\(^{-1}\)]. Concomitantly, a WC of about 50% in the early morning permitted maximum use of the incident radiation (Fig. 2). PPFD exceeded 50 μmol m\(^{-2}\) s\(^{-1}\) and simultaneous net rates of \(CO_2\) uptake 15 nmol [g d. wt\(^{-1}\) s\(^{-1}\)]. Declining WC due to decreasing air relative humidity (RH) and increasing air temperature limited this period of net \(CO_2\) uptake to the morning hours; the moisture compensation point was reached around noon. A rainstorm in the early afternoon of September 17 led to a renewed saturation of the thalli with water (Fig. 3a). Since PPFD had simultaneously decreased, this caused a strong loss of \(CO_2\) with rates of up to 5.5 nmol [g d. wt\(^{-1}\) s\(^{-1}\)].

The second day (October 20, 1991; Fig. 3b) was preceded by a rainless day. WC was much lower as were respiration rates. Low WC, however, also impeded photosynthetic carbon gain during the day. Significant net \(CO_2\) uptake was restricted to a period of 4 h in the morning. Later during the day even a strong lightfleck (190 μmol photons m\(^{-2}\) s\(^{-1}\) at 11:00 h) resulted in no detectable response in assimilation rates.

The third day (October 26, 1991; Fig. 3c) was rather similar, but because of the lower WC \(CO_2\) gas exchange was reduced even further. Net \(CO_2\) uptake was restricted to 3 h with a highest rate of 2.7 nmol [g d. wt\(^{-1}\) s\(^{-1}\)] at 08:30 h. Similar to September 17 (Fig. 2a) and another day (September 27, 1991; data not shown), re-wetting by a rainstorm led to considerable respiration in the late afternoon.

In the early dry season (January 24, 1992; Fig. 3d), WC remained very low throughout day and night (50–70%). The net rates of respiration (\(R_o\)) ranged from -1.5 to -0.5 nmol [g d. wt\(^{-1}\) s\(^{-1}\)] at night. During most of the day, there was no net \(CO_2\) exchange detectable, although on the previous day (January 23)

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**Fig. 2.** Response of net \(CO_2\) exchange of *Leptogium azureum* to changing thallus water content. PPFD was 0.25, 110 μmol m\(^{-2}\) s\(^{-1}\), respectively. Temperature inside the cuvette was 27–28°C, air relative humidity 91–99%, and the absolute \(CO_2\) concentration 345–355 μl l\(^{-1}\). Different symbols are used for different thalli \((n = 5)\).

**Fig. 3.** Diel courses of microclimatic conditions and lichen responses at the canopy site on three days in the wet season and one day in the dry season (January 24), respectively. Shown are data from one of 3–4 replicas. PPFD, photosynthetic photon flux density; A, net rate of \(CO_2\) exchange; \(T_a\), air temperature; RH, air relative humidity; WC, thallus water content. Dotted lines indicate zero net \(CO_2\) exchange, net \(CO_2\) uptake is positive and \(CO_2\) release negative. The 24-h carbon budgets are given in parenthesis. Periods of rainfall are indicated by triplet hatch-marks in the WC panels.

**Fig. 4.** Diel courses of microclimatic conditions at the understory site and lichen responses on four days in the wet season. For further explanation see figure 3.
Canopy

- Sept 17, 1991
  (5.2 \text{ mmol g d wt}^{-1} \text{ d}^{-1})
- Oct 20, 1991
  (-16.9 \text{ mmol g d wt}^{-1} \text{ d}^{-1})
- Oct 26, 1991
  (-98.2 \text{ mmol g d wt}^{-1} \text{ d}^{-1})
- Jan 24, 1992
  (-29.1 \text{ mmol g d wt}^{-1} \text{ d}^{-1})

Understory

- Nov 6, 1992
  (-39 \text{ mmol g d wt}^{-1} \text{ d}^{-1})
- Nov 14, 1992
  (+4 \text{ mmol g d wt}^{-1} \text{ d}^{-1})
- Nov 19, 1992
  (+65 \text{ mmol g d wt}^{-1} \text{ d}^{-1})
- Nov 20, 1992
  (+15 \text{ mmol g d wt}^{-1} \text{ d}^{-1})
maximum rates of 1.5 nmol [g d. wt]⁻¹ s⁻¹ were observed for short periods.

**Understory.** In contrast to the canopy, air temperatures at the understory site varied little during the course of 24 h (Fig. 4). Temperatures at night were similar to the canopy study site (ca. 24–25°C), but maximum temperatures during the day were much lower (about 27°C). Diel fluctuations in relative humidity were also lower. The air was saturated with water vapour for most of the day, and minimum RH rarely fell below 90%. Incident radiation never reached levels found at the canopy site. On most days PPFD did not exceed 30 μmol m⁻² s⁻¹.

Thallus water contents were generally higher in the understory (mostly between 500 and 800%) and, consequently, so were respiratory CO₂ losses (Figs 2 and 4). During the night of the first measuring period (November 6, 1992; Fig. 4a) Rₚ exceeded 3 nmol [g d. wt]⁻¹ s⁻¹. High WCs during the day permitted the full use of incident PPFD for photosynthetic carbon gain; during a lightfleck of 50 μmol m⁻² s⁻¹ at 10:30 h the instantaneous rate of net CO₂ uptake exceeded 10 nmol [g d. wt]⁻¹ s⁻¹. On 8 of the 9 days studied WC decreased only slowly during the daytime, probably due to the high RH and relatively low air temperatures. These high WCs permitted net CO₂ uptake for longer periods than in the canopy site, e.g. for up to 10 h on November 19, 1992 (Fig. 4c). On a windy day without rain WC decreased below 200% in the understory (Fig. 4d) and net carbon gain was obviously restricted by the low WCs of the thalli (compare November 19 and November 20 in Fig. 4).

**Diel carbon budget.** Integration of the time courses of net CO₂ exchange yielded negative 24-h balances (A₂₄h) for 7 of the 13 days studied in the wet season (4 days in the canopy, 9 days in the understory). Variation in A₂₄h was large across replicas (data not shown) and across individual days. Due to some days with very negative carbon budgets, the average A₂₄h of the 13 days was negative at both study sites (Table 2). Nocturnal CO₂ loss was higher in the understory, where WCs were generally higher than in the canopy (Table 2). Diurnal carbon gain was also significantly higher in the understory, although daily integrated PPFD was more than 45% lower.

In the dry season gas exchange was only studied in the canopy. The 24-h carbon balance was negative on both January 23 (−45 μmol [g d. wt]⁻¹ d⁻¹) and January 24, 1992 (−50 μmol [g d. wt]⁻¹ d⁻¹).

### Table 2. Integrals of gas exchange parameters and microclimatic variables of *Leptogium azureum* in the wet season. PPFD, photosynthetic photon flux density; Aₜ, diurnal carbon balance; Rₚ, nocturnal carbon balance; A₂₄h, diel carbon balance; WCnight, mean thallus water content at night. Data are means ± SD. Differences between sites are significant if p < 0.05.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Canopy</th>
<th>Understory</th>
<th>p (t-test)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PPFD (mol m⁻² d⁻¹)</td>
<td>0.94 ± 0.43</td>
<td>0.52 ± 0.06</td>
<td>0.01</td>
</tr>
<tr>
<td>Aₜ (μmol [g d. wt]⁻¹ 12 h⁻¹)</td>
<td>24.2 ± 40.4</td>
<td>118.5 ± 60.9</td>
<td>0.02</td>
</tr>
<tr>
<td>Rₚ (μmol [g d. wt]⁻¹ 12 h⁻¹)</td>
<td>−77.1 ± 33.6</td>
<td>−131.2 ± 41.0</td>
<td>0.04</td>
</tr>
<tr>
<td>A₂₄h (μmol [g d. wt]⁻¹ d⁻¹)</td>
<td>−52.8 ± 32.4</td>
<td>−12.6 ± 90.9</td>
<td>0.41</td>
</tr>
<tr>
<td>WCnight (%)</td>
<td>393 ± 310</td>
<td>525 ± 230</td>
<td>0.40</td>
</tr>
</tbody>
</table>

n = 4

3.4. Dependence of net CO₂ exchange on environmental parameters

During the day, net CO₂ exchange in the understory mostly depend on PPFD (Fig. 5a). On all nine days studied, the correlation between PPFD (< 50 μmol m⁻² s⁻¹) and net CO₂ uptake was highly significant (r² between 0.56 and 0.86, p < 0.001). In the wet season, thalli rarely dehydrated strongly enough to impede photosynthetic carbon gain. In contrast, in the canopy site, a strong correlation between PPFD and A was only given on one of the four days (September 17, 1991; r² = 0.67, p < 0.001); on the three other days A and PPFD were not significantly correlated (Fig. 5b) or the correlation was very weak (October 26, 1991, r² = 0.2, p < 0.05). Low relative humidity, high air temperature and high wind speeds led to a fast loss of water even in the wet season and a consequent reduction in net CO₂ uptake due to low WC (Figs 2 and 3). In the dry season, at continuously low thallus water contents, no correlation between A and PPFD was observed (p > 0.6; Fig. 5c). From the 11 days with significant regressions we estimated the light compensation point. It ranged from 3 to 13 μmol m⁻² s⁻¹ and averaged 7.4 ± 3.1 μmol m⁻² s⁻¹ (n = 11). Daily integrated PPFD and nocturnal WC were good predictors of diel carbon gain of *Leptogium*
**4. Discussion**

This report presents the first field measurements of the gas exchange of a tropical rain-forest lichen. A negative carbon balance on 7 out of 13 days in the wet season strongly suggests that the lowland forest of Barro Colorado Island is a marginal site for *Leptogium azureum*. This result supports the suggestion of Richards (1984), that lichens and bryophytes may often be unable to reach a positive carbon balance in lowland tropical forests and that this explains observed altitudinal gradients in species richness and abundance.

Richards (1984) proposed that high temperatures lead to a large respiratory CO$_2$ loss at night, while daytime photosynthetic CO$_2$ uptake is restricted by low light. This pattern could clearly be observed in *Leptogium azureum* in the understory (Figs. 4 and 5a). WCs around 600% caused high R$_D$ at night. The same high WCs would have also permitted high rates of CO$_2$ uptake during the day, but PPFD was strongly limiting. In the canopy light intensities were higher, but suboptimal and supraoptimal water contents reduced net CO$_2$ uptake (Figs. 2 and 3; Kershaw 1985, Lange et al. 1993). Net CO$_2$ uptake in the canopy was often severely hampered by low WC even in the wet season. In the tree crown, strong winds, relatively low RH and relatively high temperatures (Fig. 3) caused a quick decrease in WC during the early hours of the day, which stopped any further carbon gain (Fig. 3). The days of our study were not exceptionally dry; long-term monitoring of RH in a similar height in the canopy near our study site shows that RH at noon averages 80% during the rainy season (Windsor 1990). Low WCs would minimize respiratory losses in the following night, but rainfall is most probable in the early afternoon (Windsor 1990) and thalli were frequently rewetted before dusk (Fig. 3a, c). Because of the low PPFD during and after these rainstorms the proportion of a 24-h period when lichens released CO$_2$ was substantially prolonged on these days (Fig. 3a, c).

The light compensation point (LCP) of *Leptogium azureum* was 7 µmol m$^{-2}$ s$^{-1}$ (Fig. 5). This is much lower than the LCP found in lichen species of open environments like deserts, tundras or grasslands (Hahn et al. 1989, Hahn et al. 1993, Lange et al. 1991), but considerably higher than in a species like *Pseudocyphelalaria dissimilis*, a lichen growing in the deep shade of a temperate rain-forest (Green et al. 1991). The LCP of *Leptogium azureum* (7 µmol m$^{-2}$ s$^{-1}$) is only slightly lower than the average PPFD in the understory (12 µmol m$^{-2}$ s$^{-1}$). Thus the margin for carbon gain is very small. In forests with an abundance of lichens and mosses like tropical montane rain-forests or temperate rain-forests, 24-h fluctuations in temperature are much more pronounced than on Barro Colorado Island. In these cases R$_D$ and LCP are therefore comparatively low even at high thallus water contents and net CO$_2$ uptake is possible at much lower PPFD (Green et al. 1991, Green & Lange 1991).

Our study, representing 13 days in the wet and 2 days in the dry season, does not encompass the whole variability of diel patterns in thallus water contents and gas exchange and does not allow
long-term estimates of carbon gain. As in other field studies, manipulation of the thalli for gas exchange measurement inevitably introduces a certain error by changing the particular microclimate of the lichen. At the growing site press to the bark lichen thalli experience higher CO2 concentrations (Fig. 1), and possibly higher humidities. Also, light intensities were slightly lower in the cuvette (see materials and methods). All these changes will tend to decrease duration and magnitude of net CO2 uptake so that we probably somewhat underestimated the daytime carbon gain. Given the fact, however, that out of a total of 15 randomly chosen days there were more days with a negative than with a positive carbon balance we suppose that the long-term carbon gain of Leptogium azureum is small and that growth in this habitat is slow. Obviously, long-term measurements of CO2 exchange and growth are necessary to verify this prognosis.

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