

Are tropical lowlands a marginal habitat for macrolichens? Evidence from a field study with *Parmotrema endosulphureum* in Panama

GERHARD ZOTZ^{1,2*}, STEFFEN SCHULTZ³ & STEFANIE ROTTENBERGER³

¹ Botanisches Institut der Universität Basel, Switzerland

² Smithsonian Tropical Research Institute, Balboa, Panama

³ Julius-von-Sachs-Institut für Biowissenschaften der Universität Würzburg, Lehrstuhl für Botanik II, Germany

Submitted: October 1, 2002 · Accepted: October 28, 2002

Summary

There is a striking increase in the abundance of non-vascular organisms (mosses, liverworts, and macrolichens) with altitude in the tropics. The proposed mechanism behind this altitudinal gradient still awaits experimental verification. This study addresses this question using diel (= 24-h) time courses of CO₂ exchange, thallus water relations, and microclimate of the foliose lichen, *Parmotrema endosulphureum*, under natural tropical lowland conditions. In addition, we studied the responses of lichen gas exchange to experimental manipulations of incident light, temperature and thallus water content. Similar to the results of the only other field study on CO₂ exchange in lowland lichens, 24-h carbon gain was strongly limited by nocturnal CO₂ loss: the cumulative dark respiration reached almost 90% of diurnal carbon gain. Our estimates of long-term carbon gain are consistent with direct measurements of growth, and are substantially lower than those for lichens from montane sites in the tropics.

Key words: Barro Colorado Island, dark respiration, lichens, photosynthesis, tropical forests, water content

Introduction

There is a pronounced altitudinal gradient in the abundance of poikilohydric organisms (mosses, liverworts, and macrolichens) in tropical forests (RICHARDS 1984; SIPMAN & HARRIS 1989; APTROOT 1997). Seemingly ideal growth conditions in moist and wet lowland forests make this a surprising observation, and a large number of hypotheses have been put forward to explain this biogeographical pattern (review by FRAHM 1987 and ZOTZ 1999). An hypothesis by RICHARDS (1984) has received particular attention in recent years. It emphasises the importance of high nighttime temperatures in tropical lowlands. Briefly, associated high rates of dark respiration lead to strong nocturnal CO₂ losses in these cryptogams, which cannot be balanced by daytime photosynthesis due to limitations associated with their poikilohydric habit. Consequently, even those species capable of colonising lowland habitats should show rather limited photosynthetic carbon gain and also rather slow growth

(Zotz 1999). Surprisingly, there are very few studies to test this notion. Although there are a number of recent publications on lichen physiology from tropical montane forests (LANGE et al. 1994; ZOTZ et al. 1998; LANGE et al. 2000), there is only a single study with a macrolichen in a natural tropical lowland habitat (ZOTZ & WINTER 1994). The results of this study with the foliose lichen, *Leptogium azureum*, were consistent with RICHARDS' hypothesis: diel (24 h) carbon balances were negative on many days, suggesting that this moist forest is indeed a marginal habitat for this species.

To test whether the *in situ* comportment of *Leptogium azureum* was representative for other co-occurring species of macrolichens, the present study focuses on a different species from the same lowland forest of Barro Colorado Island, *Parmotrema endosulphureum* (Hillm.) Hale. We document on the one hand the *in situ* CO₂-gas exchange and water relations of this foliose species, while also investigating the response of net photosynthesis to controlled changes in temperature,

* **Corresponding author:** Gerhard Zotz, Botanisches Institut der Universität Basel, Schönbeinstrasse 6, CH-4056 Basel, Switzerland, e-mail: gerhard.zotz@unibas.ch

thallus water content, and incident light. Using this information we estimate long-term carbon gain under lowland conditions and compare it with data from montane forests. Our report confirms that lichen carbon gain under lowland and montane conditions differs indeed substantially.

Material and methods

Study site and organism

This study was performed in the Barro Colorado National Monument (BCNM; 9° 10' N, 79° 51' W, c. 30 m a.s.l.), Republic of Panama. The tropical moist forest of this biological reserve receives about 2600 mm of annual precipitation with a pronounced dry season from late December to April. Detailed descriptions of vegetation, climate and ecology are provided by LEIGH et al. (1982) and WINDSOR (1990).

Our study organism, *Parmotrema endosulphureum* (HILLM.) Hale, is a foliose lichen species that is extremely common in the Caribbean region (from Southern USA through Central America and Puerto Rico), but much rarer elsewhere (HALE 1965). In BCNM it is quite frequently found at exposed branches high in the forest canopy or on trees at the shoreline of Lake Gatun such as *Annona glabra* (ZOTZ & SCHLEICHER submitted). All specimens were collected from this tree species. Voucher specimens are deposited in the herbarium of the University of Panama, Republic of Panama and at the University of Würzburg, Germany.

At the University of Würzburg, carbon and nitrogen content were analysed with a CHNO-Rapid (Foss Heraeus, Hanau, Germany). The average C content was $45.6 \pm 1.4\%$ (means \pm SE) of dry weight ($n = 3$), and mean nitrogen concentration was $1.1 \pm 0.1\%$ dry weight ($n = 3$).

CO₂-gas exchange measurements

The samples of *P. endosulphureum*, which were collected from branches of *Annona glabra*, were carefully cleaned. Then the thalli were placed in wire-mesh baskets (3.8 cm diameter, 1–1.5 cm height, mesh width 1.6 mm) similar to the standard method used in field measurements of lichen CO₂ exchange (LANGE et al. 1984; LANGE et al. 1994).

Diel courses of net CO₂ exchange under quasi-natural conditions were monitored using a CO₂/H₂O porometer (CQP 130, Walz, Effeltrich, Germany), while response curves of CO₂ exchange under experimentally controlled conditions to changing photosynthetic photon flux density (PFD), temperature, and thallus water content (WC, % dw) were studied with a 'mini-cuvette system' (Walz). In the latter case, artificial illumination was provided by lamps with fibre optics (KL 1500 electronics, Schott Glaswerke, Wiesbaden, Germany). Both systems were open systems and differences in the CO₂ concentration were measured to ± 0.1 ppm with BINOS infrared gas analysers (Rosemount, Hanau, Germany). The absolute CO₂ concentration of the air that was flowing through the systems was determined with an additional BINOS operating in absolute mode. After the measurements, samples were dried

for 4 days at 70°C to determine thallus dry weight (dw). Field measurements were performed near the lake shore, i.e. close to the original growing site of the samples.

Diel courses of CO₂-exchange, thallus water content, incident radiation, and cuvette air-temperature were studied on seven days in the 2001 and 2002 rainy seasons. Three different replicates were used on each occasion, and were exposed to natural conditions at least half a day before the beginning of the experiments. Samples were enclosed in the cuvette of the porometer system in c. 60 min intervals, an individual measurement typically lasting 2 min. The environmental conditions inside the cuvette approximated ambient. Immediately after a measurement the sample fresh weight was determined by weighing wire-mesh baskets plus sample on an electronic digital balance (PM 460, Mettler, Giessen, Germany; accuracy: 1mg). Between measurements samples were horizontally exposed to the ambient conditions near the lake shore on a tray made of wire mesh in ca. 50 cm height.

The response of CO₂ exchange (NP) to different water contents was studied as follows: samples were submerged into distilled water for several minutes, taken out and superficially adherent water was removed by vigorous shaking. Samples were then placed into the cuvette of the 'mini-cuvette system' at 25°C and 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD. Ambient CO₂ concentrations ranged from 350 to 370 $\mu\text{l l}^{-1}$. CO₂ exchange was measured as soon as equilibrium was reached. Then samples were removed, immediately weighed and allowed to dry for a few minutes. Samples were then placed into the cuvette again. This procedure resulted in a stepwise water loss and was continued until no more changes in the relative water content occurred. Measurements were replicated with 8 specimens and with an additional 5 specimens in darkness.

For the study of net CO₂ exchange in relation to changes in PFD samples were moistened by spraying to reach a WC close to the optimum (110–190%), inserted in the cuvette, and illuminated with PFD of ca. 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. PFD was then lowered in small steps until 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and subsequently increased in larger steps to a maximum PFD of ca. 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Each light level was maintained until a steady-state net CO₂ uptake was reached (usually 5–10 min) and then changed to the next level. The samples were weighed before and after the experiment. WG after an experiment was never lower than 80% WC. The PFD response curves were analysed by fitting a 'Smith-function' to the data points of each sample, using STATISTICA software (Statsoft Inc., Tulsa, OK, USA):

$$\text{Equation (1): } NP = \frac{\alpha \cdot PFD}{\sqrt{1 + \frac{(\alpha \cdot PFD)^2}{(PC + r_D)^2}}} - r_D$$

This function allows the determination of α , the initial slope of the curve, NP_{max} , the maximum rate of NP, and R_D , the rate of dark respiration (cf. TENHUNEN et al. 1976).

Finally, we also studied the temperature response of CO₂ exchange (between 10 and 35°C in steps of 5°C). Samples with an initial WC of 200–250% were placed in the cuvette. Once an equilibrium was reached at 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD, the rate of dark respiration was determined. Samples were weighed and re-inserted in the cuvette. This procedure was

repeated three to four times (final WC: 30–50%), and the highest value of NP of such a series was chosen for further analysis. Then the procedure was repeated at a different cuvette temperature. For each temperature five replicates were used.

Long-term carbon gain

Since measurement dates of diel CO₂ exchange were chosen at random throughout the rainy season, we assumed our data set to be representative for the entire period, and we estimated the annual carbon gain of *Parmotrema endosulphureum* as follows. First, the average diel carbon gain (in $\mu\text{mol CO}_2 \text{ g}_{\text{dw}}^{-1} \text{ d}^{-1}$) was converted to diel C gain [CG_{day} , in $\text{mg C (g C in thallus)}^{-1} \text{ d}^{-1}$] by multiplying it with 10^{-3} (conversion to mmol) times 12 (mol mass of C, conversion to mg C) divided by 0.46 (relative carbon content in thalli). Beginning with a thallus of 1 g dw we then calculated the absolute C gain after n days as $(1 + 0.001 * \text{CG}_{\text{day}})^n - 1$.

Results

Dependency of CO₂ exchange on hydration, light and temperature

Measurements of the net CO₂ exchange (NP) of *P. endosulphureum* at different water contents yielded a typical optimum relationship (Fig. 1). Samples showed substantial variation in their maximum rates of net CO₂

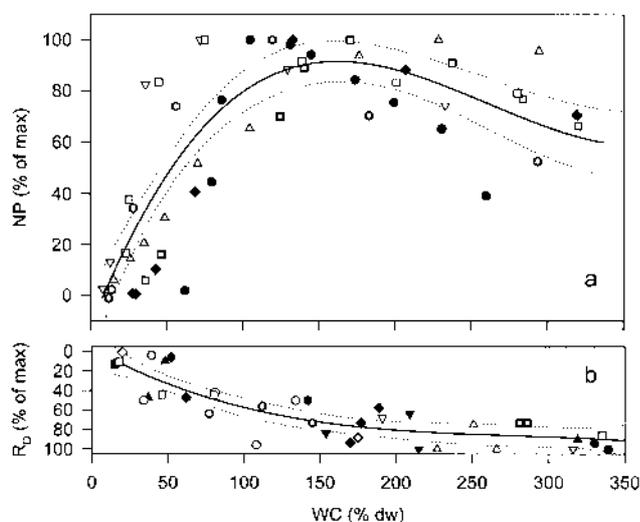


Fig. 1. Effect of changes in the thallus water content on net CO₂ exchange (NP, in % NP_{max}, plot a) and dark respiration (R_D, in % of R_{Dmax}, plot b). Different symbols represent different thalli. Cuvette temperature was 25 °C and PFD was 600 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. The relative humidity inside the cuvette ranged from 90–96%. Solid lines are 3rd degree polynomial regression ($r^2 = 0.68$ and 0.76), dotted lines are 95% confidence intervals. The height of plot a and b is scaled to the absolute values of NP_{max} and R_{Dmax}.

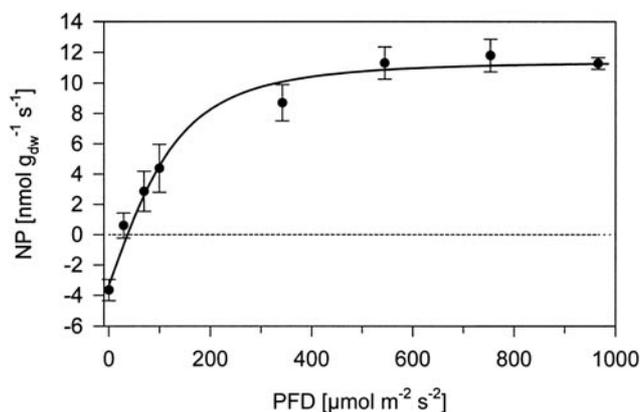


Fig. 2. Light response of net CO₂ exchange (NP, in $\text{nmol CO}_2 \text{ mg}_{\text{dw}}^{-1} \text{ s}^{-1}$) in *Parmotrema endosulphureum*. Data are means \pm SD ($n = 4$). The regression line was computed by fitting a ‘Smith’-function to the original data ($r^2 = 0.99$). Cuvette temperature was 25 °C. Thallus water content (WC, % dw) was in the optimal range of 100–200 % (compare Fig. 1).

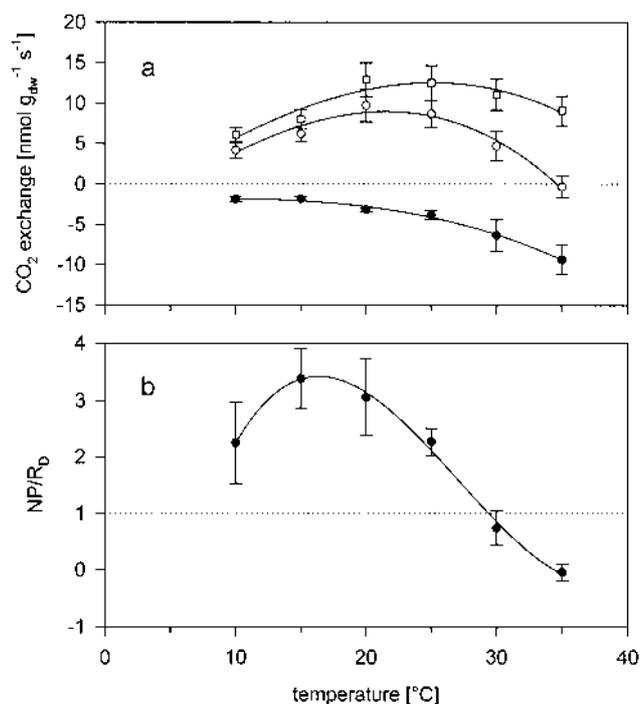


Fig. 3. a: Net photosynthesis (NP, open circles), dark respiration (R_D, closed circles) and estimated gross photosynthesis (GP, open squares) in relation to temperature at optimal water content (PFD = 600 $\mu\text{mol m}^{-2} \text{ s}^{-1}$). b: Ratio of net photosynthesis to dark respiration as a function of temperature. All data are means \pm SE, $n = 5$. Regression lines are 3rd degree polynomial functions with r^2 between 0.96–0.99. The dotted lines indicate, respectively, zero gas exchange and unity of NP/R_D.

uptake ($16.2 \pm 2.9 \text{ nmol g}_{\text{dw}}^{-1} \text{ s}^{-1}$, mean \pm SE, $n = 8$, range $5.0\text{--}26.4 \text{ nmol g}_{\text{dw}}^{-1} \text{ s}^{-1}$). Thus, for reasons of clarity, normalised values are depicted. There was a rather broad optimal range of NP from c. 100–200% WC; higher thallus WC only lead to a slight depression of CO_2 uptake. Maximum rates of dark respiration averaged $5.6 \pm 0.8 \text{ nmol g}_{\text{dw}}^{-1} \text{ s}^{-1}$ (mean \pm SE, $n = 5$). R_D was rather stable at $\text{WC} > 200\%$, but decreased at lower WC: no measurable respiration was observed at $\text{WC} < 15\%$. The dependency of NP on light is shown in Fig. 2 for four different samples. Dark respiration rates averaged

$3.4 \text{ nmol g}_{\text{dw}}^{-1} \text{ s}^{-1}$, corresponding to about a third of the maximum rate of net CO_2 uptake (mean NP_{max} : $11.5 \text{ nmol g}_{\text{dw}}^{-1} \text{ s}^{-1}$). The light compensation point was reached at $35 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PFD, light saturation of net CO_2 uptake (95% NP_{max}) at about $330 \text{ m}^{-2} \text{ s}^{-1}$ PFD. The temperature response of the CO_2 exchange is shown in Fig. 3. Net photosynthesis is clearly adapted to high temperatures with an optimum between $20\text{--}25^\circ\text{C}$ and an upper temperature compensation point of about 35°C . Dark respiration increased steadily with temperature from $1.8 \text{ nmol g}_{\text{dw}}^{-1} \text{ s}^{-1}$ at 10°C to $9.4 \text{ nmol g}_{\text{dw}}^{-1} \text{ s}^{-1}$

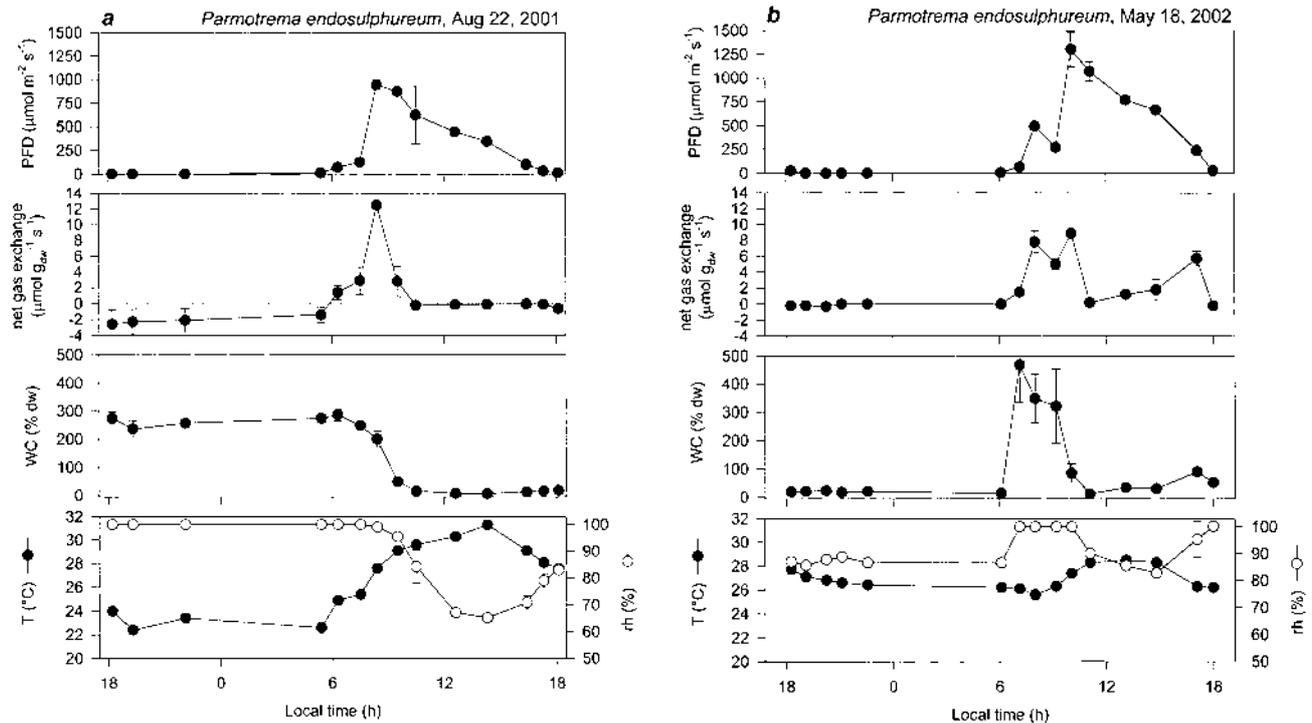


Fig. 4 a, b: Two representative diel courses of incident photon flux density (PFD, $\mu\text{mol m}^{-2} \text{ s}^{-1}$, upper panel), net CO_2 exchange (NP, $\text{nmol CO}_2 \text{ g}_{\text{dw}}^{-1} \text{ s}^{-1}$, second panel), thallus water content (WC, % dw, third panel), and cuvette air-temperature and relative humidity (T, $^\circ\text{C}$, and rh, %, bottom panel) for *Parmotrema endosulphureum*. Sudden increases of WC on May 18, 2002 indicate rain events. Integrals of NP and PFD are given in Table 1.

Table 1. Integrals of diel carbon exchange, nocturnal CO_2 loss and incident photon flux density on seven days in the 2001 and 2002 rainy seasons. Data are means \pm SE ($n = 3$). The average diel carbon budget was $11.9 \pm 58.6 \text{ mmol g}_{\text{dw}}^{-1} \text{ d}^{-1}$, the average nocturnal CO_2 loss was $90.3 \pm 54.9 \mu\text{mol g}_{\text{dw}}^{-1} \text{ 12 h}^{-1}$.

Day	Diel carbon balance ($\mu\text{mol g}_{\text{dw}}^{-1} \text{ d}^{-1}$)	Nocturnal CO_2 loss ($\mu\text{mol g}_{\text{dw}}^{-1} \text{ 12 h}^{-1}$)	Integrated PFD ($\text{mol m}^{-2} \text{ d}^{-1}$)
18. Aug 01	-2.9 ± 5.9	-157.9 ± 23.7	11.0 ± 2.7
22. Aug 01	-11.2 ± 35.9	-70.9 ± 8.6	17.0 ± 2.2
04. Dez 01	15 ± 6.7	-142.5 ± 13.8	15.5 ± 1.7
07. Jan 02	12.7 ± 11.3	-100.2 ± 12.8	20.3 ± 2.1
15. Mai 02	-14.8 ± 13.4	-42.6 ± 9.1	39.4 ± 1.2
16. Mai 02	-50.9 ± 13.6	-114.2 ± 31.2	38.7 ± 2.6
18. Mai 02	135.1 ± 9.4	-3.7 ± 2.6	24.7 ± 1.7

at 35°C. The ratio between net photosynthesis and R_D was optimal at 15°C with an average of 3.4 and reached unity at about 30°C.

Diel courses of *in situ* CO₂ exchange and water content

The seven study days encompassed much of the environmental variation given during the rainy season on BCNM, from rather bright days with almost no rain (May 15, 2002) to completely overcast days with frequent precipitation (Aug 18, 2001). On all days but one (May 18, 2002), lichens were hydrated and metabolically active during the entire night (due to precipitation on the preceding day) with mean CO₂ losses of 90.3 $\mu\text{mol g}_{\text{dw}}^{-1} 12 \text{ h}^{-1}$ (Table 1). CO₂ exchange during the subsequent light period was unimodal on four of the seven study days, with CO₂ uptake ending around noon due to desiccation of the thalli (Fig. 4a). On the three remaining days a bimodal pattern was observed (Fig. 4b), because thalli were re-moistened by rain in the early afternoon. The resulting 24 h carbon balances were mostly around zero (Table 1), with two exceptions: a quite negative carbon balance on May 16, 2002 was caused by rather high rates of dark respiration and a comparatively short period of CO₂ uptake before noon (data not shown). On the other extreme, diel carbon gain reached 135.1 $\mu\text{mol g}_{\text{dw}}^{-1} \text{ d}^{-1}$ on May 18, 2002, when CO₂ losses at night were the lowest of all study days due to very low hydration of the thalli (WC 20–30%), and brief rainfall just at dawn and again in the afternoon allowed for re-wetting of the thalli and substantial CO₂ uptake during most of the light period (Table 1, Fig. 4b).

Long-term carbon gain

Based on the average diel CO₂ gain of 11.9 $\mu\text{mol g}_{\text{dw}}^{-1} \text{ d}^{-1}$, which corresponds to a daily carbon gain of 0.31 mg C (g C in thallus)⁻¹ d⁻¹, we calculated an annual carbon gain of 120 mg C (g C)⁻¹ yr⁻¹ or 12.0 % of initial carbon content for *Parmotrema endosulphureum*. However, in this calculation the approximately 4 month dry season (WINDSOR 1990) was included. Assuming a very low metabolic activity with a balanced budget for this period, we arrived at an annual carbon gain of 80 mg C (g C)⁻¹ yr⁻¹.

Discussion

Similar to the only other foliose lichen species studied *in situ* in tropical lowlands (ZOTZ & WINTER 1994), *Parmotrema endosulphureum* frequently experienced negative carbon budgets in 24-h courses of CO₂ gas

exchange. However, in contrast to that earlier study, the average carbon budget of the seven study days was slightly positive (11.9 $\mu\text{mol g}_{\text{dw}}^{-1} \text{ d}^{-1}$ or 0.31 mg C (g C)⁻¹ d⁻¹, Table 1, Fig. 4). Although this number should be interpreted with caution due to our limited data base and the substantial variation in carbon gain between days (Table 1), the emerging pattern is certainly consistent with RICHARDS' (1984) hypothesis: net carbon gain in lowland macrolichens is precariously close to zero, while almost all values of diel carbon gain reported from montane habitats are higher by at least an order of magnitude. For example, LANGE et al. (1994) report diel carbon balance of 6.2 mg C (g C)⁻¹ d⁻¹ for *Dictyonema glabratum*, ZOTZ et al. (1998) 5.4 mg C (g C)⁻¹ d⁻¹ for *Sticta tomentosa*, and LANGE et al. (2000) 3.6 mg C (g C)⁻¹ d⁻¹ and 2.1 mg C (g C)⁻¹ d⁻¹ for *Leptogium cyanescens* and *L. phyllocarpum*, respectively. Even in the species with the lowest value reported to date from a montane growing site in the tropics, *Leptogium azureum* (LANGE et al. 2000), diel carbon gain was more than twice that of *P. endosulphureum*. It is informative to compare the average diel carbon gain documented for *P. endosulphureum* under tropical lowland conditions with that from habitats that are not conducive to rapid growth. Values reported for hot deserts (*Ramalina maciformis*: 0.1–0.4 mg C (g C)⁻¹ d⁻¹ KAPPEN et al. 1980) or cold Antarctica (0.1 mg C (g C)⁻¹ d⁻¹, KAPPEN 1985) are similar to our results.

The extrapolation from these short-term gas exchange measurements to annual carbon budgets is problematic for a number of reasons. For example, (1) our study days may not be representative for the entire year, (2) leaching of assimilates may occur, particularly during drying-rewetting cycles (PRUSSIA & KILLINGBECK 1991), and (3) assimilates may not be available for growth because of limited lateral transfer (e.g. BENCH et al.) or due to other non-growth related functions (cf. HILL 1981). Given these uncertainties, it is remarkable how well our estimate of annual carbon gain in *P. endosulphureum* (c. 80 mg C (g C)⁻¹ yr⁻¹ or 8% of initial carbon content) agrees with direct measurements of growth in this species (ZOTZ & SCHLEICHER submitted). In that research, growth was studied in 35 thalli of *P. endosulphureum* occurring naturally in the canopy of *Annona glabra* on BCNM. The determined annual growth rates of 17.6 ± 11% of the initial thallus dry mass differ only by a factor of two from our estimates. Calculating the approximate average daily carbon budget in the rainy season necessary to reach the observed annual growth (in the absence of leaching) yields 25.3 $\mu\text{mol g}_{\text{dw}}^{-1} \text{ d}^{-1}$. There are a number of possible explanations for this difference in annual growth estimates obtained by different methods. First, although we tried to simulate the environmental conditions given in *Annona glabra* at our measurement site, conditions in this tree may be actual-

ly more conducive to carbon gain. For example, as suggested by ZOTZ & WINTER (1994), CO₂ concentrations immediately adjacent to the bark are probably considerably higher than in the gas exchange cuvette. Secondly, the handling of the lichen specimens during gas exchange measurements may lead to faster desiccation during the day: samples in wire-mesh baskets desiccate faster than neighboring thalli, which are naturally attached to the bark of *Annona glabra* (SCHULTZ & ZOTZ, unpubl. observation). Overall, however, the two different approaches to estimate annual carbon gain yielded surprisingly similar results.

A comparison with estimates of annual carbon gain from non-tropical habitats is complicated by differences in computation. In many cases, yearly estimates are derived from diel carbon budgets by simple multiplication with 365 days, which results in substantially lower numbers (e.g. LANGE et al. 1998). In spite of this problem, a pattern begins to emerge with lichens from tropical montane forests being among the most productive on earth, and lowland species in the lower third of the spectrum (compare review in LANGE et al. 1998). This rather limited productivity is not due to a low potential for carbon gain (see Figs. 1–3), but caused by relatively high dark respiration (for a global comparison see LANGE et al. 2000). The cumulative nocturnal CO₂ loss of almost 90% of daytime NP during the 7 days of this study (Table 1) is only rivaled by another report from tropical lowlands (ZOTZ & WINTER 1994) and one from maritime Antarctica (SANCHO et al. 1997).

Maximum rates of net CO₂ uptake during diel courses (Fig. 4) and under controlled conditions (Figs. 1–3) ranged from c. 11–16 nmol g_{dw}⁻¹ s⁻¹, hence were mid-range compared to those reported in the older literature (2–32 nmol g_{dw}⁻¹ s⁻¹, reviewed in GREEN & LANGE 1994). Most values of NP_{max} of lichens from tropical montane habitats are considerably higher, e.g., c. 60 nmol g_{dw}⁻¹ s⁻¹ (*Dictyonema glabratum*, LANGE et al. 1994) or c. 50 nmol g_{dw}⁻¹ s⁻¹ (*Sticta tomentosa*, ZOTZ et al. 1998). Not surprisingly, the rates of dark respiration in these montane species also exceeded those of *P. endosulphureum*, but only about twofold. Finally, the temperature response of NP differed between the species from lowland and montane habitats (Fig. 3, LANGE et al. 1994; ZOTZ et al. 1998): between 10 and 30 °C, R_D increased much less in *P. endosulphureum* (Q₁₀ c. 1.9) than in *Dictyonema glabratum* (Q₁₀ c. 2.5) and *Sticta tomentosa* (Q₁₀ c. 2.3). Whether this observation reflects a general difference in temperature response remains to be shown.

In conclusion, our study lends credit to the hypothesis proposed by RICHARDS (1984): while carbon gain under tropical montane conditions is very high, lichens in the lowlands can hardly compensate nocturnal CO₂ losses by carbon gain during the day.

Acknowledgements

The research was supported by the Deutsche Forschungsgemeinschaft. Prof. B. Büdel, Kaiserslautern, kindly identified the lichen species. Thanks also to Prof. O. L. Lange, Würzburg, for critically reading an earlier version of the manuscript.

References

- APROOT, A. (1997): Lichen biodiversity in Papua New Guinea, with the report of 173 species on one tree. – *Bibl. Lichenol.* **68**: 203–213.
- BENCH, G.; CLARK, B. M.; MANGELSON, N. F.; CLAIR, L. L. S.; REES, L. B.; GRANT, P. G. & SOUTHON, J. R. (2002): Use of ¹⁴C/C ratios to provide insights into the magnitude of carbon turnover in the crustose saxicolous lichen *Caloplaca trachyphylla*. – *Lichenologist* **34**: 169–180.
- FRAHM, J.-P. (1987): Which factors control the growth of epiphytic bryophytes in tropical rainforests? – *Symp. Biol. Hung.* **35**: 639–648.
- GREEN, T. G. A. & LANGE, O. L. (1994): Photosynthesis in poikilohydric plants: a comparison of lichens and bryophytes. In: SCHULZE, E.-D. & CALDWELL, M. M. (eds.): *Ecophysiology of photosynthesis*. *Ecol. Stud.* 100, pp. 319–341. Springer, Berlin Heidelberg New York.
- HALE, M. E. (1965): A monograph of *Parmelia* Subgenus *Amphigymnia*. – *Contrib. US Natl. Herbarium* **36**: 193–358.
- HILL, D. J. (1981): The growth of lichens with special references to the modelling of circular thalli. – *Lichenologist* **13**: 265–287.
- KAPPEN, L. (1985): Water relations and net photosynthesis of *Usnea*. A comparison between *Usnea fasciata* (maritime Antarctic) and *Usnea sulphurea* (continental Antarctic). In: BROWN, D. H. (ed.) *Lichen physiology and cell biology*, pp. 41–46. Plenum Press, New York.
- KAPPEN, L.; LANGE, O. L.; SCHULZE, E.-D.; BUSCHBOM, U. & EVENARI, M. (1980): Ecophysiological investigations on lichens in the Negev desert. VII. The influence of the habitat exposure on dew imbibition and photosynthetic productivity. – *Flora* **169**: 216–229.
- LANGE, O. L.; BEYSCHLAG, W.; MEYER, A. & TENHUNEN, J. D. (1984): Determination of photosynthetic capacity of lichens in the field – a method for measurement of light response curves at saturating CO₂ concentration. – *Flora* **175**: 283–293.
- LANGE, O. L.; BÜDEL, B.; ZELLNER, H.; ZOTZ, G. & MEYER, A. (1994): Field measurements of water relations and CO₂ exchange of the tropical, cyanobacterial basidiolichen *Dictyonema glabratum* in a Panamanian rainforest. – *Bot. Acta* **107**: 279–290.
- LANGE, O. L.; HAHN, S. C.; MEYER, A. & TENHUNEN, J. D. (1998): Upland tundra in the foothills of the Brooks Range, Alaska, U.S.A.: lichen long-term photosynthetic CO₂ uptake and net carbon gain. – *Arct. Alp. Res.* **30**: 252–261.
- LANGE, O. L.; BÜDEL, B.; MEYER, A.; ZELLNER, H. & ZOTZ,

- G. (2000): Lichen carbon gain under tropical conditions: water relations and CO₂ exchange of three *Leptogium* species of a lower montane rain forest in Panama. – *Flora* **195**: 172–190.
- LEIGH, E. G., JR.; RAND, A. S. & WINDSOR, D. M. (Eds., 1982): The ecology of a tropical forest. Seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C.
- PRUSSIA, C. M. & KILLINGBECK, K. T. (1991): Concentrations of ten elements in two common foliose lichens: leachability, seasonality, and the influence of rock and tree bark substrates. – *Bryologist* **94**: 135–142.
- RICHARDS, P. W. (1984): The ecology of tropical forest bryophytes. In: SCHUSTER, R. M. (ed.) *New Manual of Bryology 2. The Hattori Botanical Laboratory, Nichinan*, 1233–1270.
- SANCHO, L. G.; PINTADO, A.; VALLADARES, F.; SCHROETER, B. & SCHLENSOG, M. (1997): Photosynthetic performance of cosmopolitan lichens in the maritime Antarctic. – *Bibl. Lichenol.* **67**: 197–210.
- SIPMAN, H. J. M. & HARRIS, R. C. (1989): Lichens. In: LIETH, H., & WERGER, M. J. A. (eds.): *Tropical Rain Forest Ecosystems (Biogeographical and Ecological Studies)*. Ecosystems of the world **14B**, pp. 303–309. Elsevier, Amsterdam.
- TENHUNEN, J. D.; WEBER, J. A.; YOCUM, C. S. & GATES, D. M. (1976): Development of a photosynthesis model with an emphasis on ecological application. II. Analysis of a data set describing the P_M surface. – *Oecologia* **26**: 101–119.
- WINDSOR, D. M. (1990): Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panamá. Smithsonian Institution, Washington.
- ZOTZ, G. (1999): Altitudinal changes in diversity and abundance of non-vascular epiphytes in the tropics – an eco-physiological explanation. – *Selbyana* **20**: 256–260.
- ZOTZ, G. & SCHLEICHER, T. (2003): Growth and survival of the foliose lichen, *Parmotrema endosulphureum*, on the tree, *Annona glabra*. – *Ecotropica*, submitted.
- ZOTZ, G. & WINTER, K. (1994): Photosynthesis and carbon gain of the lichen, *Leptogium azureum*, in a lowland tropical forest. – *Flora* **189**: 179–186.
- ZOTZ, G.; BÜDEL, B.; MEYER, A.; ZELLNER, H. & LANGE, O. L. (1998): *In situ* studies of water relations and CO₂ exchange of the tropical macrolichen, *Sticta tomentosa*. – *New Phytol.* **139**: 525–535.