

Lichen carbon gain under tropical conditions: water relations and CO₂ exchange of *Lobariaceae* species of a lower montane rainforest in Panama

Otto L. LANGE, Burkhard BÜDEL, Angelika MEYER, Hans ZELLNER and Gerhard ZOTZ

Abstract: Diel (24-h) time courses of microclimate, water relations, and CO₂ exchange were measured under quasi-natural conditions at a forest edge in a lower montane, tropical rainforest in Panama for six *Lobariaceae* (*Lobaria crenulata*, *L. dissecta*, *Pseudocyphellaria aurata*, *P. intricata*, *Sticta sublimbata*, *S. weigeli*). Responses to experimentally controlled water content (WC), photosynthetic photon fluence rate (PPFR), and temperature were studied in most detail with *P. aurata*.

Photosynthesis was well adapted to high temperatures, and all species exhibited 'shade plant' characteristics with low light compensation points and low light saturation. *Lobaria* and *Pseudocyphellaria* species suffered from a strong depression of net photosynthesis (NP) at suprasaturating WC; suprasaturation depression was less in cyphellate *Sticta* species.

Photosynthetic capacity correlated with thallus nitrogen concentration, and maximal NP rates of the cyanobacterial *Sticta* species was 4 to 5 times higher than that of the green algal *Lobaria* species. However, high rates of NP were uncommon and brief events under natural conditions; the different environmental factors were rarely optimal at the same time. Similar to earlier observations with other rainforest lichens, NP ceased during the period of highest irradiation on most days due to desiccation. During moist periods low light often limited carbon fixation, and high thallus hydration was often detrimental to NP. In spite of these limitations the maximal daily integrated net photosynthetic carbon income (Σ NP) was quite high especially for the *Sticta* species [17.3 and 24.1 mgC (gC)⁻¹ day⁻¹ for *S. sublimbata* and *S. weigeli*, respectively]. High nocturnal carbon loss, due to high night temperatures and continuous hydration, resulted in frequent negative diel carbon balances (Σ C) in all species. The average nocturnal carbon loss amounted to 83 and 70% Σ NP for *P. aurata* and *P. intricata*, respectively and to 64 and 59% of Σ NP for *S. sublimbata* and *S. weigeli*, respectively. Their average diel Σ C was as high as 3.7 and 5.3 mgC (gC)⁻¹ day⁻¹. In contrast, Σ C were much lower for the other species, it amounted to only 0.18 mgC (gC)⁻¹ day⁻¹ for *L. crenulata*. Thus, the *Sticta* species stood out amongst the species studied for their most successful adaptation of their photosynthetic productivity to the habitat conditions in the lower montane rainforest.

Key words: carbon gain, *Lobariaceae*, Panama, photosynthesis, rainforest, respiration, water content

Introduction

Tropical rainforests are well-known for their high diversity of lichen species (Galloway 1991; Aptroot 1997). In tropical lowlands, crustose species dominate while the proportion of foliose and fruticose lichens increases with altitude attaining a high degree of biomass in the cooler montane zone (Seifriz 1924; Sipman & Harris 1989; Sipman 1989; Zotz 1999). Broad-lobed *Lobariaceae* (*sensu* Tehler 1996) with the three large genera *Lobaria*, *Pseudocyphellaria*,

O. L. Lange, A. Meyer and H. Zellner: Julius-von-Sachs-Institut für Biowissenschaften der Universität Würzburg, Lehrstuhl für Botanik II, Julius-von-Sachs-Platz 3, D-97082 Würzburg, Germany.

B. Büdel: Fachbereich Biologie, Allgemeine Botanik, Universität Kaiserslautern, Postfach 3049, D-67653 Kaiserslautern, Germany.

G. Zotz: Botanisches Institut der Universität Basel, Schönbeinstraße 6, CH-4056 Basel, Switzerland and Smithsonian Tropical Research Institute, Balboa, Panama.

and *Sticta* are frequent and conspicuous colonizers of stems and branches in rain-forest biomes worldwide (Galloway 2001), especially under tropical montane conditions. They represent a notable percentage of the epiphytic biomass of these forests, and nitrogen-fixing genera such as *Pseudocyphellaria* and *Sticta* contribute considerably to the nitrogen-income of the total ecosystem (Forman 1975).

Several studies (such as Rundel *et al.* 1979; Green & Lange 1991; Lange *et al.* 1993; Green *et al.* 1995; Green *et al.* 2002; see also review in Kappen 1988) report ecophysiological adaptations and primary productivity of *Lobariaceae* species in temperate rainforests. However, in spite of a similar importance in the tropics, information about their functional performance in tropical rainforest is extremely scarce. We are only aware of one pertinent publication, on *Sticta tomentosa* (Sw.) Ach. from a tropical montane rainforest in Panama (Zotz *et al.* 1998). At the same site, we studied additional *Lobariaceae* to test the generality of these earlier observations for this important lichen family under tropical conditions.

We selected six of the most abundant representatives of the *Lobariaceae* at this site, two species per genus: *Lobaria crenulata*, *L. dissecta*, and *Pseudocyphellaria aurata* were tripartite chlorolichens (for terminology see Lange & Wagenitz 2003) with green algae as their main photobionts and with *Nostoc* containing internal cephalodia; *Pseudocyphellaria intricata*, *Sticta sublimbata* and *S. weigeli* were bipartite cyanolichens. The *in situ* photosynthetic and respiratory CO₂ exchange of these species, their water relations along with microclimatic conditions were documented, and responses to changes in temperature, incident light, and degree of hydration under controlled conditions were investigated. Data from cyanobacterial *S. tomentosa* (Zotz *et al.* 1998) were used for comparison.

Materials and Methods

Research site and experimental lichens

The measurements were made in September and October 1993 at the Centro de Investigaciones

Tropicales Jorge L. Arauz of the Instituto de Recursos Hidráulicos y Electrificación, IRHE ('Reserva Forestal Fortuna', Republic of Panama, Cordillera Central, Province of Chiriquí, north east of David, 8°45'N, 82°15'W; c. 1100 m a.s.l.). Annual rainfall in the area is between 3000 and 4000 mm (IRHE, unpublished); monthly precipitation was never less than 100 mm in the 3 years before our measurements. September 1993 was relatively wet with c. 500 mm of rain. Annual mean air temperature in the Fortuna region is between 21 and 22°C (Anonymous 1988). The tropical climate around Fortuna is considered to be relatively uniform with little seasonal fluctuation. Thus, we may assume that even a limited time period of measurements allow a general characterization of the performance of *Lobariaceae* under the conditions of a montane rainforest.

The forest at Fortuna has an open canopy. Trees are generally 20–30 m tall with emergents reaching up to 40 m. According to its physiognomic characteristics the almost virgin forest is a lower montane (premontane) tropical rainforest *sensu strictu* [Grubb 1977; see also the description of the vegetation of the Fortuna area by Cavelier (1992) and the list of phanerogamic taxa by Adames (1977)]. The Fortuna Research Station is located on a slope at one side of a clearing containing a few small, remnant trees. The surrounding, evergreen forest is rich in cryptogamic epiphytes; lichens are especially abundant at open sites, such as clearings and gaps in the forest, and at the forest edges with higher light exposure. The experimental samples were collected from stems and branches in such open habitats. Büdel *et al.* (2000) list 69 different species of macrolichens for the Fortuna watershed. The more abundant and typical epiphytic genera are *Coccocarpi*, *Coenogonium*, *Dictyonema*, *Heterodermia*, *Hypotrachina*, *Leptogium*, *Lobaria*, *Pseudocyphellaria*, *Sticta*, and *Usnea*.

The following corticolous species were selected for our experiments (for details see Büdel *et al.* 2000):

Lobaria crenulata (Hook. in Kunth) Trev. [syn. *Lobariella crenulata* (Hook. in Kunth) Yoshim.]—chlorolichen. General distribution: Tropical America, New Zealand, Pacific Islands from Easter Island to Hawaii

Lobaria dissecta (Sw.) Racuschel—chlorolichen. Tropical America (Jamaica, Puerto Rico, Mexico).

Pseudocyphellaria aurata (Ach.) Vain.—chlorolichen. Pantropical, cosmopolitan; extending to temperate regions. In Fortuna frequent on stems, branches, and decomposing logs. Fifteen complete diel time courses were monitored with samples of this species, and the present report about response of the lichens has been primarily based upon measurements with this species.

Pseudocyphellaria intricata (Delise) Vain.—cyanolichen. Pantropical, extending to temperate regions.

Sticta sublimbata (J.Steiner) Swinscow et Krog—cyanolichen. Palaeotropical.

Sticta weigeli (Ach.) Vain.—cyanolichen. Pantropical, a wide-spread tropical-subtropical rather polymorphic species. Experimental samples tending to *S. weigeli* var. *xanthotropa* (Krempelh.) Hue.

For the CO₂ exchange measurements, the thalli were collected fresh from their open habitats, detached from

TABLE 1. Concentrations* of chlorophyll (*a+b*), nitrogen, and carbon in the thalli of the experimental species and in two bipartite chlorolichens from the same site for comparison

Species (<i>n</i>)†	Photobiont	Chlorophyll mg (g _{dw}) ⁻¹	Nitrogen % of dw	Carbon % of dw
<i>Lobaria crenulata</i> (2)	tripartite chlorolichen	2.23	2.8	45.2
<i>L. dissecta</i> (2)	tripartite chlorolichen	1.27	3.3	46.9
<i>Pseudocyphellaria aurata</i> (14)	tripartite chlorolichen	2.11 ± 0.50	2.7 ± 0.2	48.6 ± 0.7
<i>P. intricata</i> (2)	bipartite cyanolichen	0.78	2.9	48.3
<i>Sticta sublimbata</i> (6)	bipartite cyanolichen	1.00 ± 0.05	4.5 ± 0.1	45.8 ± 0.3
<i>S. tomentosa</i> (20)	bipartite cyanolichen	0.61 ± 0.22	4.4 ± 0.2	46.9 ± 0.4
<i>S. veigelii</i> (6)	bipartite cyanolichen	0.96 ± 0.18	3.3 ± 0.9	47.1 ± 1.4
<i>Cladonia ceratophylla</i> (4)	bipartite chlorolichen	0.30 ± 0.07	0.32 ± 0.04	44.7 ± 0.11
<i>Usnea rubicunda</i> (6)	bipartite chlorolichen	0.43 ± 0.10	0.46 ± 0.12	45.1 ± 1.2

*mean values, ± 1 SD where appropriate.

†*n*=number of samples.

their substratum and cleaned. For exposure in the gas exchange cuvettes, they were fixed in small wire-mesh baskets. Each sample usually consisted of several lobes from different thalli, thus representing an average performance of the population. Total thallus area of a sample was between 9 and 12 cm².

As expected (Palmqvist *et al.* 2002), thallus nitrogen concentration of the tripartite green algal and the bipartite cyanobacterial *Lobariaceae* was high and around ten times higher than that of the bipartite chlorolichens of the same site (Table 1). Nitrogen-concentration of the *Sticta* species ranged from 3.3 to 4.5% of dry weight (DW). Total chlorophyll concentration (*a+b*) was lowest for the bipartite chlorolichens of the same habitat, although interspecific variation was substantial. Thallus carbon concentration varied from 45.2 to 48.6% of dry weight.

Experimental methods

As described in earlier papers (Lange *et al.* 1994; Zotz *et al.* 1998) net photosynthesis (NP) and dark respiration (DR) of the lichens were studied using three different instruments (manufactured by Walz Company, Effeltrich, Germany). Diel courses of CO₂ exchange under quasi-natural conditions together with climate parameters, such as air temperature (in the cuvette) and photosynthetically active photon fluence rate (PPFR), were measured by means of 'CO₂ porometers'. Field methods, data evaluation, and data handling together with general methodological considerations, are explained and discussed in detail by Lange *et al.* (1984, 1994). Lichen samples were positioned horizontally in their baskets near the porometer cuvette with illumination and water status similar to their original, unshaded, natural habitat. At the same site Zotz *et al.* (1998) have documented for *Sticta tomentosa* that photosynthetic performance is strongly dependent on the exposure of the lichen; duration of favourable hydration in combination with incident light level resulted in daily carbon gains being largest for

westerly exposed and lowest for northerly exposed samples. Carbon budgets and periods of activity of horizontally exposed thalli fell well within the performance range of vertically exposed specimens. The horizontal exposure of all samples in the present study allowed a standardized comparison of gas exchange performance between co-occurring species. For *in situ* CO₂ exchange measurements, lichen samples were enclosed every 50–90 min (higher frequency during the day, lower frequency during night) in the porometer cuvette which approximated the air temperature and light levels of the external environment. Steady-state CO₂ exchange was reached within 1–2 min. The sample weight was recorded immediately after each CO₂ exchange measurement to determine thallus water content (WC, in% dry weight).

A 'minicuvette system' allowed CO₂ exchange measurements under controlled temperature, light, and humidity conditions, while continuous CO₂ exchange measurements during longer periods of time were made with a temperature-controlled 'click-cuvette' system, also with artificial illumination.

Rates of CO₂ exchange were related to thallus dry weight (4 days at 70°C), projected thallus area, thallus carbon concentration (elemental analyser; CHNO-Rapid, Foss Heraeus, Hanau, FRG; also for thallus nitrogen determination), and total (*a+b*) chlorophyll concentration (Ronen & Galun 1984).

Results

Dependency of CO₂ exchange on hydration, light, and temperature

All the experimental species showed a more or less extensive suprasaturation depression, i.e. their net photosynthetic CO₂ fixation was reduced at high thallus water content in

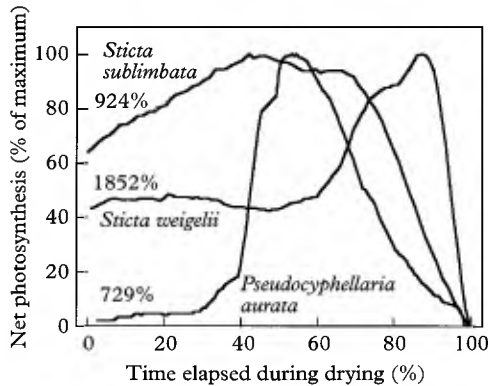


FIG. 1. Time courses of net photosynthesis (percentage of maximum) of three experimental species during drying. The experiment began at maximal thallus water content (time 0, water content indicated in percent of dry weight), and the thalli dried out subsequently until CO_2 -uptake ceased (100% of drying period).

a species-specific fashion. When thalli with maximal WC slowly dehydrated under controlled conditions for 4 to 5 hours, their NP was initially low and increased with decreasing water content until metabolic inactivation at high degrees of desiccation. Figure 1 shows the extremes with lowest (*S. sublimbata*) and highest (*P. aurata*) initial depression to only less than 5 and about 70% of maximum, respectively, and the intermediate response type of *S. weigelii* with c. 45%. The remaining three species had a greater depression than *S. weigelii*. Similar drying-down curves were constructed during which WC of the lichens was determined at regular intervals (results not shown in detail). *Pseudocyphellaria aurata* lost about one third of its maximal water content until CO_2 uptake increased strongly, and maximal rates of NP occurred at between 150 and 200% WC. Suprasaturation depression was no artefact of experimental manipulation, but was common under field conditions: The sample of *P. aurata* displayed in Fig. 1 (maximal WC of 729%) had been collected after a heavy rainstorm from its natural site and was subsequently enclosed in the measuring cuvette. The relationship of *in situ* NP and thallus water content was very similar (Fig. 2). The scatter of data (all readings of 15 days of field measurements

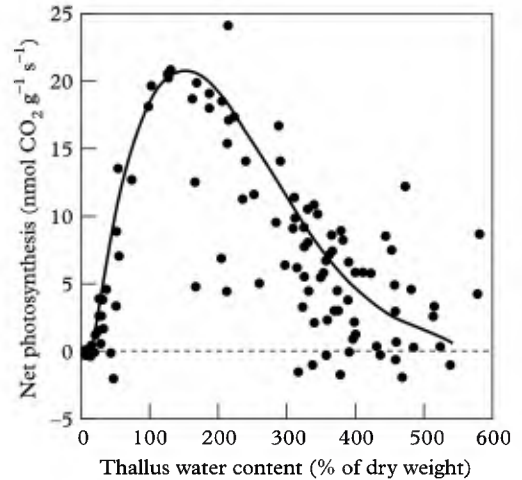


FIG. 2. Net photosynthesis in relation to thallus water content of *Pseudocyphellaria aurata* during daylight ($\text{PPFR} > 15 \mu\text{mol m}^{-2} \text{ s}^{-1}$) under natural conditions on 15 days of recording. All measuring points are plotted which were made when the lichen was metabolically active (polynomial regression).

where $\text{PPFR} > 15 \mu\text{mol m}^{-2} \text{ s}^{-1}$) is due to simultaneous changes in temperature and PPFR.

Hydration-dependent changes in NP clearly also determines also the shape of light response of the experimental lichens. This is shown in Fig. 3 for the two species *P. aurata* and *S. sublimbata*. NP was plotted against experimentally changed PPFR under otherwise controlled conditions at three ranges of thallus water content. Light saturated NP is highest under medium, near optimal water content (B), it decreased with higher, supraoptimal (A) as well as with lower, suboptimal WC (C). Quantum yield was almost unaffected by WC, i.e. the initial slopes of the light response curves were almost identical for each species. A depression of quantum use efficiency could only be observed at low WC (e.g., *S. sublimbata*, Fig. 3B, curve iii). The light compensation point of CO_2 exchange could be extracted from the measurements *in situ*. For all of the *Lobariaceae* studied it was relatively low with 12 to 40 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFR. According to the light response curves under controlled conditions (Fig. 3) it amounted to 12.0 ± 2.3 (mean \pm SD, $n=4$) for *P. aurata*

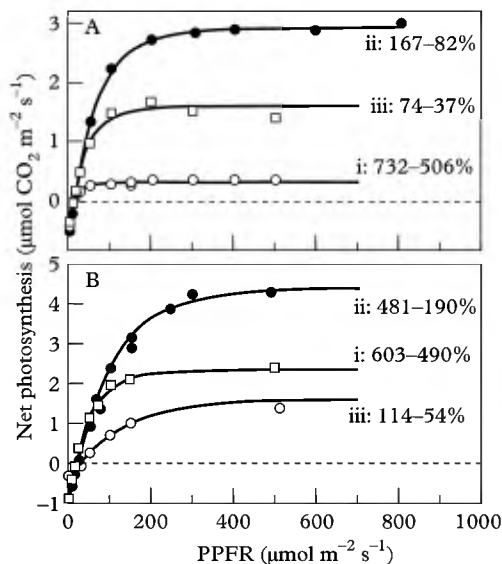


FIG. 3. The response of net photosynthesis to incident PPFR of *Pseudocyphellaria aurata* (A panel) and *Sticta sublimbata* (B panel) at different water contents (WC, 20°C). Curves were fitted by the Smith-function (see Lange *et al.* 1991). Each response curve is annotated with the initial and final WC (percent of dry weight) during its experimental generation. Curve ii: optimal range of WC, i: supraoptimal, ii: suboptimal hydration.

and to $23.5 \pm 4.0 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFR for *S. sublimbata* at near optimal temperatures of 20°C. Light saturation (defined as lowest PPFR which results in 90% of the theoretical maximum of NP as determined with the Smith-model, see Lange *et al.* 1991) was attained between 150 and 300 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFR in the optimal range of WC and at 20°C; it usually increased at very low thallus water content. On the other hand, light saturation substantially decreased when lichens were suprasaturated. For example, it was only 57 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFR for *P. aurata* at high WC (Fig. 3A, curve i).

Temperature dependency of CO_2 exchange was studied using *P. aurata*. Figure 4 shows the result of six experimental runs with thalli of this species in the optimal range of WC. At 150 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFR, near optimal NP was around 20°C, and the upper temperature compensation point of CO_2 exchange was between 35 and 40°C. No detailed studies have been possible on

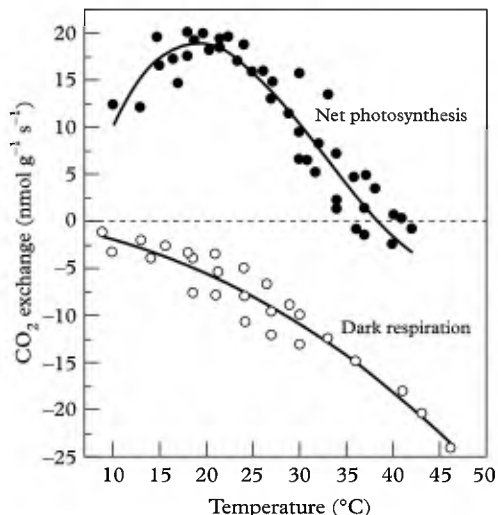


FIG. 4. The dependence on temperature of net photosynthesis and dark respiration of *Pseudocyphellaria aurata* at 150 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFR and in the optimal range of thallus hydration.

temperature responses of the other experimental species. However, spot checks reveal similar ranges of performance (data not shown; see Zotz *et al.* 1998 for *S. tomentosus*).

Natural diel courses of CO_2 exchange, water content, and microclimate

Continuous measurements (24 h) of CO_2 exchange, thallus water content, and microclimate were conducted *in situ* for 15 days (*P. aurata*), 9 (*P. intricata*), 8 (*S. sublimbata*, *S. weigeli*), or 5 days (*L. crenulata*), respectively. For *L. dissecta* only spot check measurements are available. The most detailed results with *P. aurata* are shown in Fig. 5.

Typically, there was fog in the early morning followed by a period of high PPFR with low and variable cloud cover. On most days, there was a distinct period of clear sky with PPFR exceeding 2000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ around noon. Overcast sky and rainstorms of different duration and intensity characterized the afternoon. An exception was 18 September with rain throughout the day. Night temperatures were rather uniform at 17°C to 20°C. Apart from the drier period

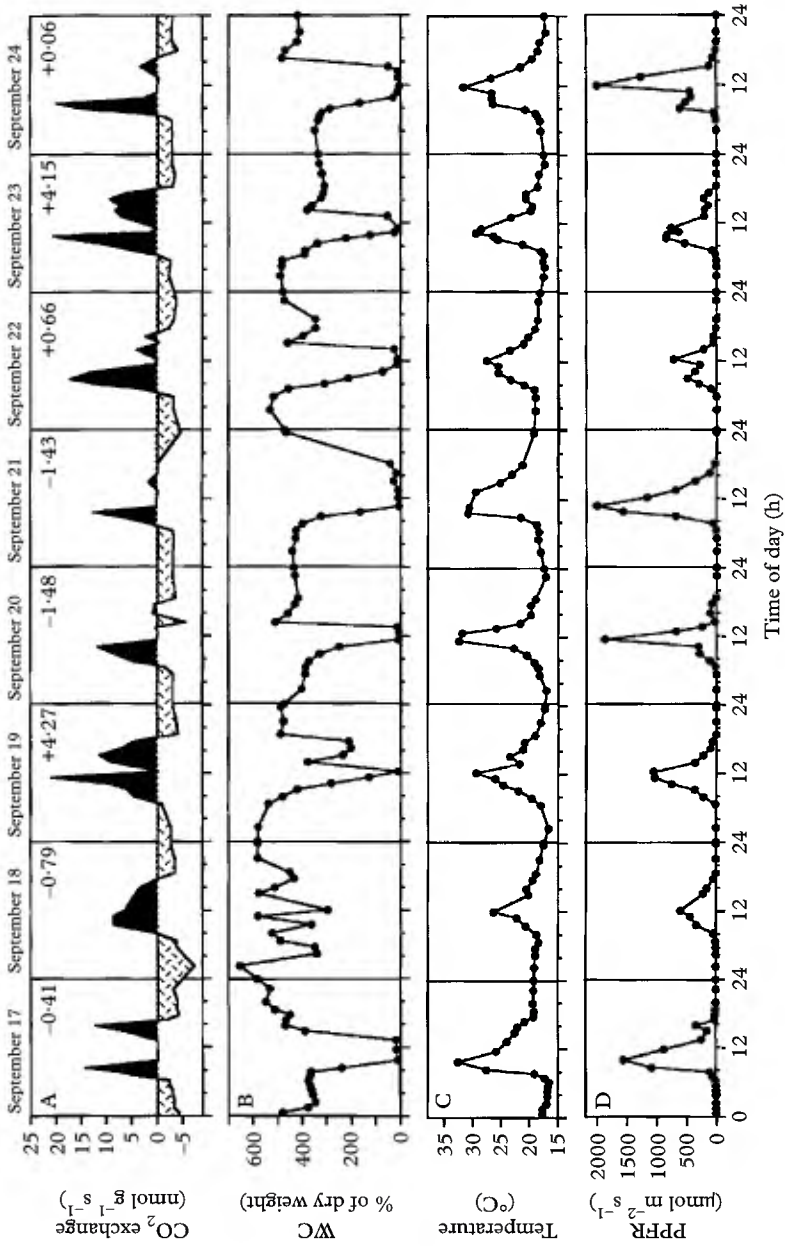


FIG. 5.

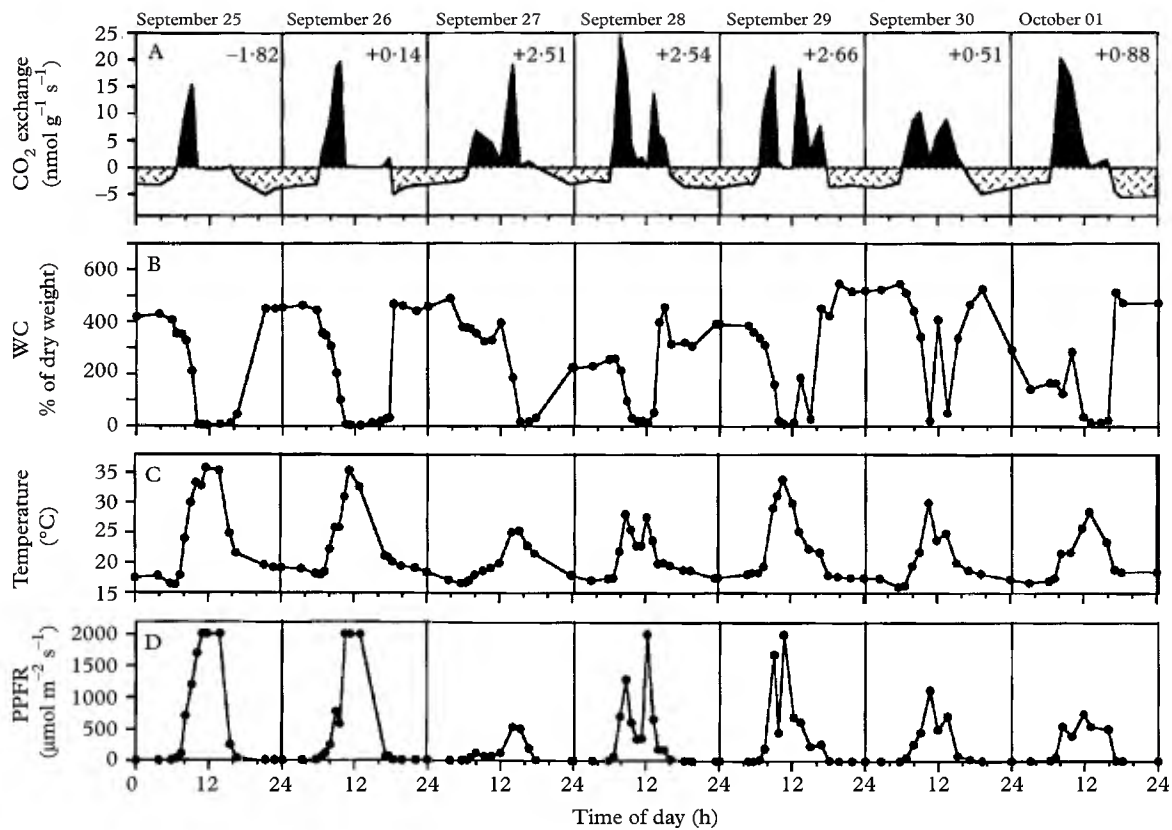
FIG. 5. *continued.*

FIG. 5. Diel time courses for *Pseudocyphellaria aurata* under natural conditions, from 17 September through 1 October 1993. A, dry weight-related CO₂ exchange (CO₂ uptake black, CO₂ release hatched; numbers indicate integrated diel carbon balance in mgC (gC)⁻¹ day⁻¹); B, water content (WC); C, cuvette air-temperature; D, incident photon fluence rate (PPFR). Single porometer-readings are indicated by filled circles, data points at 0 or 24 h are generated by interpolation.

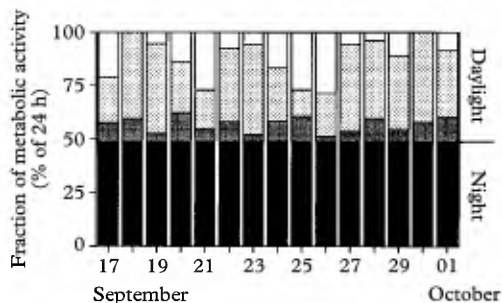


Fig. 6. Diel duration of metabolic activity as a proportion (percent) of 24 h for *Pseudocyphellaria aurata* during the measurement period. Average daily dark period (PPFR $\leq 1 \mu\text{mol m}^{-2} \text{s}^{-1}$) lasted for 11 h 42 min (NIGHT), PPFR was $>1 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 12 h 18 min (DAYLIGHT). ■: respiration during night; ▒: respiration during daylight; □: net photosynthesis; ▨: inactive during daylight.

around noon, relative humidity stayed between 90 and 100%. These weather conditions, which are typical for a lower montane tropical rainforest, were associated with pronounced diel changes in thallus water contents (Fig. 5). At night the sample was always so wet that continuous dark respiration occurred. In the morning, the lichen was well hydrated so that NP followed incident PPFR although suprasaturation usually limited CO_2 fixation initially. Subsequently, a further decrease in WC resulted in desiccation and reduced or suppressed NP. Afternoon rain then rehydrated the thalli. However, NP remained low due to thallus suprasaturation and low PPFR. Despite humid-tropical conditions, field water relations were decisive for carbon gain in these lichens by limiting NP through suboptimal and supraoptimal hydration (compare Fig. 2). The moisture compensation point was reached at least briefly on almost all days. Thallus water content often dropped below 10% (of dry weight), and in extreme cases, the sample desiccated to 4% WC. The inactive period could last for almost 7 hours (Fig. 6). Respiratory carbon loss was not restricted to the night (where it occurred continuously), but was also found during daylight time (with PPFR $>1 \mu\text{mol m}^{-2} \text{s}^{-1}$). This covered periods at dusk and dawn when PPFR was below the light

compensation point, short bursts of resaturation respiration, or times of heavy water suprasaturation.

In general, the other experimental species responded in a similar fashion. In addition to the specific photosynthetic and respiratory capacity of the lichens, differences in patterns were due to different water relations and to their different responses to thallus suprasaturation. The latter phenomenon is illustrated by one example (Fig. 7). On 20 September, high light and favourable thallus WC enabled a short peak of high NP in all species until total desiccation occurred around noon. Between 2 and 3 p.m. a short but heavy rainstorm saturated all thalli, with subsequent changing cloud cover and PPFR exceeding $100 \mu\text{mol m}^{-2} \text{s}^{-1}$. Three species responded with a small afternoon peak of NP (arrows). High respiratory activity and suprasaturation depression did not allow any carbon gain during this phase of the day in the other three species. The resulting diel carbon balance was positive in *P. intricata* and the two *Sticta* species, but negative in *P. aurata* and the two *Lobaria* species.

Maximal rates of CO_2 exchange and carbon balance

The highest rates of NP under controlled conditions with near-optimal WC, saturating light and favourable temperature were between 25 and $30 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ in *P. aurata* thalli. *In situ* rates were slightly lower with 8.7 to $24.1 \text{ nmol g}^{-1} \text{ s}^{-1}$ during the 15 days of measurements (Fig. 5). The maximal rate occurred in the early morning of 28 September, when WC was within the optimal range of around 200% for several hours. At 20.5°C temperature was optimal as well, and with $706 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFR light was above saturation. However, this favourable combination lasted only for a short time and increasing radiation quickly desiccated the lichen. The six species differed substantially in their photosynthetic capacity (NP_{max}), i.e. in the maximal rates achieved under similar natural conditions (Table 2). Dry weight

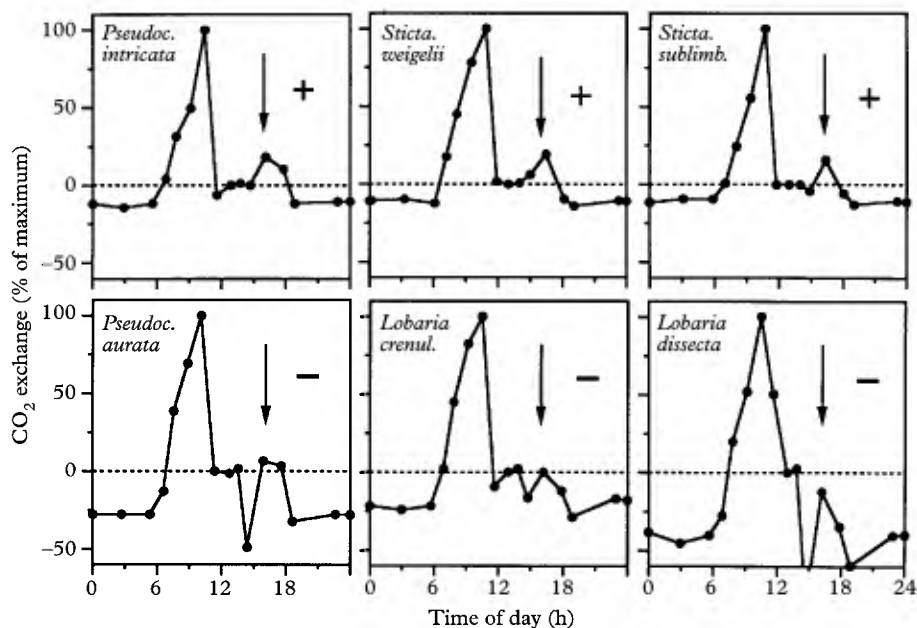


FIG. 7. Diel time courses of CO₂ exchange (in percent of daily maximum) of all experimental species on 20 September. Arrows indicate afternoon peak of photosynthesis (see text); samples had a positive (+) or negative (–) diel carbon balance.

TABLE 2. Maximum rates of net photosynthesis under natural conditions [in relation to thallus dry weight, thallus area, and concentrations of chlorophyll (a b), and carbon] for the experimental lichens and for *Sticta tomentosa* (after Zotz et al. 1998)

Species	Maximum rates of net photosynthesis			
	dry weight nmol g ⁻¹ s ⁻¹	area μmol m ⁻² s ⁻¹	chlorophyll nmol mg ⁻¹ s ⁻¹	carbon nmol g ⁻¹ s ⁻¹
<i>Lobaria crenulata</i>	11.1	2.0	8.7	23.6
<i>L. dissecta</i>	14.2	2.9	6.4	31.4
<i>Pseudocyphellaria aurata</i>	24.1	4.2	13.6	50.2
<i>P. intricata</i>	29.1	2.8	41.2	60.3
<i>Sticta sublimbata</i>	49.4	5.9	51.1	107.4
<i>S. weigelii</i>	53.5	4.9	69.7	118.3
<i>Sticta tomentosa</i>	61.5	5.8	48.8	130.5

and carbon related maximal rates in NP were five times higher for *S. tomentosa* than for *L. crenulata*. Area-related NP varied threefold. Certainly, morphological and anatomical features that affect water holding capacity and water loss might have influenced the maximal rates of NP attained under field conditions. However, it seems that physiological characteristics as

well were decisive parameters which determined maximal rates of NP. This is indicated by the significant correlation between thallus nitrogen concentration (averages for the species) and dry-weight related NP_{max} ($r=0.74$). The bipartite cyanolichens of the genus *Sticta* had high nitrogen concentration and high maximal NP in contrast to the tripartite chlorolichens of the genera

Pseudocyphellaria and *Lobaria* with lower maximal rates (see Tables 1 & 2).

Linear interpolation between consecutive data points of the *in situ* measurements was used to estimate integrated net photosynthetic carbon income (Σ NP), respiratory carbon loss (Σ DR), and carbon balance (Σ C). Since respiration always was high during the relatively warm and continuously wet nights, diel Σ C was negative on 5 out of 15 days for *P. aurata*, i.e. diurnal photosynthesis could not compensate for mainly nocturnal carbon release (Fig. 5). Averaged over the 15 measuring days, Σ DR amounted to 82.6% of Σ NP (Table 3). Nevertheless, the average diel Σ C for this species was $0.83 \text{ mgC (gC)}^{-1} \text{ d}^{-1}$ which means that on average 0.83‰ of its thallus carbon content was added per day. For the congeneric cyanolichen *P. intricata* we found an average diel Σ C of 1.74‰ during 9 study days, which was mainly due to its higher photosynthetic capacity. In agreement with their high maximal rates of NP, both *Sticta* species stood out by their much higher production. Their average diel Σ DR ($n=8$) was only 63.8 and 59.1% of their carbon income, respectively. *Sticta weigeli* gained an average diel Σ C of 5.3‰, and *S. tomentosa* achieved an almost identical productivity (Zotz *et al.* 1998).

Discussion

The two *Sticta* species in this study have the potential for very high carbon gain as previously reported for *Sticta tomentosa* (Zotz *et al.* 1998). Absolute maxima of area-related NP under natural conditions of 4.9 and 5.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *S. weigeli* and *S. sublimbata*, respectively, rival the rates of light-saturated leaf photosynthesis of some Panamanian rainforest trees (Zotz & Winter 1996). Of the lichen species studied in the Fortuna rainforest, only the cyanobacterial basidiolichen *Dictyonema glabratum* (Spreng.) Hawskw. stands out with an even higher NP_{max} of 7.2 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Maximal NP rates of the four other *Lobariaceae* species, however, were substantial lower. Thallus bulk nitrogen concentration and photosynthetic capacity were significantly

correlated, although Palmqvist *et al.* (2002) have shown that the fraction of N which is invested in chlorophyll *a* is a better predictor of potential lichen photosynthesis.

In spite of the high photosynthetic potential, high rates of NP were observed only for short periods during the diel courses in nature (Fig. 5): in other words, the different environmental factors were rarely near optimal at the same time. Temperature seemed to be the least important factor in limiting NP because *in situ* temperatures were mostly within the rather broad optimal range for CO_2 uptake. Although photosynthesis of all species was saturated at relatively low PPFR (Fig. 3), low light often limited carbon gain. This was especially true in the afternoon, when thalli became rehydrated but the sky was overcast during and after the rainstorm. Thallus desiccation was an even more important parameter limiting productivity. Within the 15 measuring days with *P. aurata*, desiccation of the thallus during the daylight hours was almost invariably observed around midday. On average, *P. aurata* was dry and fully inactivated for 2 h 54 min every day (Fig. 6). At the other extreme, high WC, i.e. suprasaturation, also depressed net photosynthesis, but this depression affected the *Lobaria* and *Pseudocyphellaria* species more than the *Sticta* species. It became obvious *in situ* as well as under controlled conditions. This suggests that the genus *Sticta* may be favoured by its cyphellae that promote thallus CO_2 exchange (experimentally shown by Snelgar & Green 1980). However, special experiments under controlled conditions with more species would be necessary to prove the role of cyphellae in ameliorating impact of suprasaturation depression.

High rates of nocturnal respiration due to continuous hydration at warm temperatures is characteristic for lichens of tropical rainforests, and excessive nocturnal carbon loss frequently results in a negative diel carbon balance (Table 3). This suggests the existence of substantial pools of stored carbohydrates in thalli sufficient to support respiration for at least a limited period of unfavourable conditions with no net fixation

TABLE 3. Integrated diel (24 h) carbon-related carbon income, loss, and balance under natural conditions. Numbers of days of measurement used for integrations and averages are indicated

Species (days of measurement)	Σ NP, Diel net photosynthetic carbon income $\text{mgC (gC)}^{-1} \text{d}^{-1}$		Σ DR, Diel respiratory carbon loss $\text{mgC (gC)}^{-1} \text{d}^{-1}$		Σ C, Diel carbon balance $\text{mgC (gC)}^{-1} \text{d}^{-1}$	Σ DR in relation to Σ NP %
	Maximum	Average	Maximum	Average	Average	All days integrated
<i>Lobaria crenulata</i> (5 days)	4.71	2.90	-3.02	-2.72	0.18	93.7
<i>Pseudocyphellaria aurata</i> (15 days)	7.41	4.78	-5.30	-3.95	0.83	82.6
<i>P. intricata</i> (9 days)	8.10	5.85	-5.53	-4.11	1.74	70.3
<i>Sticta sublimbata</i> (8 days)	17.29	10.24	-7.19	-6.53	3.70	63.8
<i>S. weigeli</i> (8 days)	24.12	12.96	-10.27	-7.66	5.30	59.1

of carbon. Frequent negative diel carbon balances, however, are not restricted to tropical habitats but seem to be a general feature of lichens. The temperate epilithic lichen *Lecanora muralis* (Schreber) Rabenh., for example, was metabolically active on 274 days of the year and had a negative carbon balance on 69 days, i.e. 25% of the time. Nevertheless its annual carbon balance proved to be rather substantial and amounted to 20.7% of thallus carbon content (Lange 2003a, b). This contrasts with the excessive nocturnal carbon loss under tropical conditions that reduces lichen productivity to a degree that carbon balance may actually limit their occurrence (Lange *et al.* 2000). This is especially true for macrolichens in lowland rainforests (Zotz & Winter 1994; Zotz 1999) and suggests that acclimation of lichen metabolism to high temperatures is rather limited.

Total respiration in the two *Pseudocyphellaria* species amounted to 70.3 and 82.6% of their photosynthetic income, respectively. Proportional CO₂ losses were lowest in the two members of the genus *Sticta* with 63.8 and 59.1% for *S. sublimbata* and *S. weigeli*, respectively. *Sticta tomentosa* respired even less of its carbon income under similar conditions (53.3%; Zotz *et al.* 1998). These latter figures resemble those of temperate zone lichens: *Lecanora muralis* had an average annual ΣDR of 57% of its ΣNP in central Europe (Lange 2003a, b).

On average, *P. aurata* was dry for 12% of the day (24 h), it respired for 8.2% during daylight hours, and it respired for 48.8% during the night. Thus, it experienced only 31%, i.e. 7 h 26 min of net photosynthetic carbon gain per day (Fig. 6). Nevertheless, the resulting carbon gain could be as high as 7.41‰ day⁻¹ of its thallus carbon content on its most favourable day (Table 3). On one third of the measuring days its diel carbon balance became negative, but the average diel ΣC still amounted to 0.83 mgC (gC)⁻¹ day⁻¹. Our information on the performance of the two *Lobaria* species, especially of *L. dissecta*, is more limited. Diel ΣC of *L. crenulata* was surprisingly low, however, this estimation is based on 5 diel time courses

only. Suprasaturation depression of gas exchange and high respiratory carbon loss strongly reduced ΣC of the *Lobaria* species—even on days when the *Sticta* species maintained positive carbon balances. *Sticta weigeli*, the most productive species studied, had a maximal daily ΣNP of 24.1‰ day⁻¹ carbon, and an average diel carbon balance of 5.3 mgC (gC)⁻¹ day⁻¹ (5.3‰). This was almost identical with the results of *S. tomentosa* and considerably higher than most known estimated from other lichen species (Zotz *et al.* 1998). Only two species from the same site showed higher averages of diel ΣC: the basidiolichen *Dictyonema glabratum* (6.2‰ day⁻¹; Lange *et al.* 1994) and juvenile, sterile thalli of the gelatinous *Leptogium phyllocarpum* (Pers.) Nyl. (8.3‰ day⁻¹, Lange *et al.* 2000).

Conclusions

A mixture of adaptations and apparent lack of adaptations to their rainforest environment determined the photosynthetic performance of the lichens studied, and this mixture determined their specific performance. Large differences existed in the photosynthetic capacity of the seven *Lobariaceae*, and all three *Stictas* attained remarkably high dry-weight related rates of NP, up to five times higher than the *Lobaria* species. The strong correlation of NP_{max} to thallus nitrogen concentration highlights the advantage of a cyanobacterial photobiont. Higher metabolic activity necessarily results in higher rates of mitochondrial respiration. However, higher ΣDR of the *Sticta* species was more than compensated for by higher ΣNP so that the ratio of ΣNP to ΣDR was much higher in *Sticta* species than in the *Lobaria* species or the green algal *Pseudocyphellaria* species. It might well be that possession of a cyanobacterial photobiont may be an important feature promoting growth in areas with relatively high nocturnal temperatures such as in tropical forests.

Environmental conditions that supported full photosynthetic capacity in all species studied, occurred rarely and were brief. Very

low light limited productivity substantially during those times of the day when water content of the thalli was favourable. However, low light compensation points and low degrees of light saturation characterized the lichens as 'shade plants', with little species-specific variation. The same is true in respect to the temperature dependence of photosynthesis which does not seem to be limiting productivity. However, it is a surprising result of this and our previous studies that, even under moist-tropical conditions, water content is the most important limiting factor for carbon gain for the *Lobariaceae* and the other lichens and mosses at the same site (Lange *et al.* 1994, 2000; Zotz *et al.* 1997, 1998) Almost every day, the thalli dry out around noon so that they are inactive during the time period of highest PPFR. On the other hand, suprasaturation of the thalli impacts effectively net photosynthesis which can lead to a substantial reduction of potential carbon gain. The *Lobaria* and *Pseudocyphellaria* species suffered greatly from surplus of water. In contrast, the two *Sticta* species were able to reduce suprasaturation depression of their CO₂ exchange, possibly due to their cyphellae. This capability improved the carbon gain of these cyanolichens too, so that their ΣC was substantially higher than that of the green algal *Lobaria* and of the tripartite green algal *Pseudocyphellaria* species.

The limited data of the present study conducted with only six species during a relatively short period of time do not allow firm conclusions about generic differences in photosynthetic productivity. Nevertheless more than 50 complete diel courses of CO₂ exchange *in situ* in combination with experimental results under controlled conditions clearly point to a graduated adaptation of the three *Lobariaceae* genera to the habitat conditions of a montane tropical rainforest.

The work was supported by the Deutsche Forschungsgemeinschaft. We thank the staff of the Smithsonian Tropical Research Institute (Balboa, Panama) for assistance and support, and we acknowledge the hospitality of the Instituto de Recursos Hidráulicos y Electrificación (David, Panama). We thank Wilma Samfaß and Gerhard Radermacher for their assistance with evaluation and handling of data.

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