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Lichen carbon gain under tropical conditions: water relations and CO$_2$ exchange of three *Leptogium* species of a lower montane rainforest in Panama

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Summary

Diel time courses of microclimate, hydration, and CO$_2$ exchange of *Leptogium azureum*, *L. cyanescens*, and *L. phyllocarpum* (homoiomerous cyanolichens) were measured under quasi-natural conditions at a forest edge of a lower montane, tropical rainforest (Panama). In addition, responses to experimentally controlled water content (WC), photosynthetic photon flux density (PPFD), and temperature were studied for *L. phyllocarpum*. Performance of the *Leptogium* species was compared with two other, but heteromerous, cyanolichens from the same site and treated in earlier publications (*Dictyonema glabratum*, *Sticta tomentosa*).

Net photosynthesis (NP) of *L. phyllocarpum* was adapted to high temperatures with an upper temperature compensation point well above 40°C. The light saturation of NP was highly dependent on WC and occurred at PPFD levels between 100 and 600 µmol m^{-2}s^{-1}. Light compensation point was about 20 µmol m^{-2}s^{-1} and increased with decreasing WC. All three *Leptogium* species suffered from a strong depression of NP at suprasaturating WC, which reduced CO$_2$ assimilation by 55 to more than 80%, compared to the maximum.

Natural NP was controlled by the interplay of thallus hydration and radiation. In contrast to the heteromerous species, high water holding capacity of the gelatinous lichens, especially of *L. phyllocarpum*, shortened the periods of inactivity through desiccation, thus essentially extending the daily time span for photosynthetic activity. However, high WC reduced the rates of CO$_2$ fixation. A rough estimate for *L. azureum* reveals that net photosynthetic carbon gain would be increased by about one third in the absence of suprasaturation depression.

In spite of these limitations, average daily net photosynthetic carbon gain of mature thalli of all three *Leptogium* species was relatively high [between 6.2 and 9 mgC (gC)$^{-1}$d^{-1}, as related to thallus carbon content]. However, a very large portion of assimilated carbon – on average 60 to 90% – was lost again through nocturnal respiration which was stimulated by high night temperatures of the continuously moist thalli. The resulting diel carbon balance amounted from 0.6 to 3.6 mgC (gC)$^{-1}$d^{-1}. Abundance of *Leptogium* species and of other macrolichens was high in the lower montane forest, it was low in warmer lowland rainforests of the same area. Based upon a literature review for lichens under different climate conditions the existing hypothesis is discussed to what extend this phenomenon might be explained through negative carbon balances due to temperature-induced increases in nocturnal respiration.

Key words: Lichen, water content, photosynthesis, carbon gain, rainforest, *Leptogium*

1. Introduction

Tropical rainforests are known for their high lichen diversity (e.g., APTROOT 1997). These humid habitats are particularly rich in cyanolichens which seem to be well adapted to warm and moist conditions. The vast majority of all known lichen species, i.e. about 90%, are phycolichens containing an eucaryotic alga as their primary photobiont, and only about 10% are cyanolichens with cyanobacteria (FRIEDL & BÜDEL 1996).

This proportion is substantially changed in the humid tropics. No general statistical account is available but, in the montane rainforest of the Fortuna watershed in Panama, the site of the present study, almost one half of all of the macrolichens were cyanobacterial species (BÜDEL et al. 2000). In addition, many phycolichens such as *Sticta*, *Lobaria*, and *Pseudocyphellaria* species occur in this area, which have cyanobacteria at least as their secondary photobiont (see JAMES & HENSSEN 1976).

With respect to their water relations, cyanolichens show two different functional life forms. There are the stratified, heteromerous species found in genera like *Sticta* or *Peltigera*, with a relatively thin thallus divided in different layers the structure of which is determined by the mycobiont. In contrast, the photobionts of the homoiomerous species are almost evenly distributed in an unstratified thallus, which consists of a highly swelling slime matrix mainly produced by the *Nostoc*-cyanobiont. At maximal hydration, the water content of such gelatinous, lobate lichens can attain several thousand percent of their dry weight, much more than that of their heteromerous counterparts. Such differences in water holding capacity must affect the overall water economy and, in this respect, the gelatinous life-form apparently is well suited for the tropical habitat (see SIPMAN & HARRIS 1989). In our study area (Fortuna watershed and the Volcan Baru, BÜDEL et al. 2000) almost one third of all of the cyanobacterial species of macrolichens belong to the homoiomerous and gelatinous genera *Leptogium* and *Collema*, the first genus being represented by 13 different species.

In preceding publications we have reported about photosynthetic and respiratory performance of the two heteromerous cyanolichens *Dictyonema glabratum* (LANGE et al. 1994a) and *Sticta tomentosa* (ZOTZ et al. 1998) in their natural environment in the Panamanian montane rainforest. A somewhat surprising result was that these lichens experienced frequent desiccation and became inactivated through dehydration almost every day even under the humid tropical conditions. Their water content was not sufficient to maintain metabolic activity over the dry midday period before the onset of the regular afternoon rain showers. This reduced their photosynthetic carbon gain substantially. The present study reports about CO_2 exchange measurements with three gelatinous *Leptogium* species from the same site and conducted during the same time period. We were especially interested in the significance of the high water holding capacity for photosynthetic production of these species. The results can be compared with the only other known field gas exchange study on a tropical gelatinous lichen conducted with *Leptogium azureum* in a lowland tropical forest in Panama (ZOTZ & WINTER 1994).

2. Materials and methods

2.1. Research site and experimental lichens

The measurements were conducted in September and October 1993 at the Centro de Investigaciones Tropicales Jorge L. Arauz of the Instituto de Recursos Hidráulicos y Electrificación (IRHE). This field station is located in the "Reserva Forestal Fortuna" (Republic of Panama, Cordillera Central, Province of Chiriquí, north east of David, 8° 45′ N, 82° 15′ W; ca. 1100 m a.s.l.). Annual rainfall for the research station (IRHE, unpublished) was 3509 mm and 3113 mm for 1991 and 1992, respectively; monthly precipitation was never less than 100 mm in the 3 years before our measurements. Our study month September 1993 was very wet with ca. 500 mm of rain. Annual mean air temperature in the Fortuna region is between 21 and 22°C (ANONYMOUS 1988).

The forest at Fortuna has an open canopy. Trees are generally 20–30 m tall, but emergents reach up to 40 m. The physiognomic characteristics suggest that the almost virgin forest is a lower montane (premontane) tropical rain forest *sensu strictu* (Grubb 1977). A brief description of the vegetation of the Fortuna area is provided by CAVELIER (1992), and there is a preliminary species list of phanerogamic taxa supplied by ADAMES (1977). The Fortuna Research Station is located on a hill 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 and at the forest edges with higher light-exposure. BÜDEL et al. (2000) list 69 different species of macrolichens for the Fortuna watershed. The more abundant and typical epiphytic genera are *Coccocarpia*, *Coenogonium*, *Dictyonema*, *Heterodermia*, *Hypotrachina*, *Leptogium*, *Lobaria*, *Pseudocyphellaria*, *Sticta*, and *Usnea*. *Stereocaulon* species form a dense vegetation cover on rocks and on open soil.

Leptogium belongs to the family Collemataceae characterized by *Nostoc* photobionts. The thallus lobes, without internal stratification, are wrinkled and papery when dry, but very swollen when wet. Worldwide, the genus is best developed and reaches its greatest abundance in tropical regions, however, it is widely distributed with some species reaching arctic and antarctic regions (GALLOWAY 1985). The following corticolous species were selected for our experiments:

Leptogium phyllocarpum (PERS.) NYL. (Small gorge on east slope below the Research Station, on branches of the shrub *Baccharis pedunculata*.)

This species formed small, orbicular, irregular, confluent, cushion-like thalli of one to several cm in diameter. The small lobes were crowded, somewhat imbricate, crenulate or lacerate and crisp. There were no isidia but apothecia were often numerous and reached 1–2 mm in diameter with reddish-brown to dark-red discs and margins covered with relatively large, lobulate squamules. *Leptogium phyllocarpum* is an epiphyte in subtropical and tropical areas (ZAHLBRUCKNER 1925) and has a pantropical distribution growing predominantly in montane forests and woodlands from 1000 to 3000 m alt. (SWINSCOW & KROG 1988).

Large, old ("mature") samples of this species covered with many apothecia served as the main experimental material for

measuring diel time courses of CO_2 exchange (14 days) as well as for analyzing dependencies of photosynthesis and dark respiration on water content, light and temperature. As a comparison, 4 diel time courses were also obtained with small, young, sterile specimens of *L. phyllocarpum* from the same site, the thalli of which were closely appressed to a branch.

Leptogium cyanescens (RABENH.) KÖRBER (Forest edge, west of the Research Station, on stems of *Heliocarpus* sp.)

The thalli of this species were 5–8 cm in diameter with flat to involute, irregularly wrinkled lobes up to 1 cm across, having overlapping margins. Their upper surface was smooth with dense patches of numerous isidia (see SPECTOR & JENSEN 1977). The thalli were loosely attached to the substrate by scattered tufts of hairs. Apothecia are generally very rare with this species and were lacking in all of our experimental samples. *Leptogium cyanescens* is a cosmopolitan lichen, extensively distributed in temperate, subtropical and tropical regions of the northern and southern hemisphere (see DEGELIUS 1935). – 14 diel time courses were monitored with samples of this species.

Leptogium azureum (SW. ex ACH.) MONT. (On the exposed stem of a single tree within the clearing, immediately near the Research Station.)

Lobes of this species were sinuate and rounded but several centimeters broad so that the total thallus, which could attain almost 10 cm in diameter, made a rather monophyllous impression. It was loosely attached to the bark by short hairs. Upper thallus surface was smooth without any isidia; color of the lobes were distinctly bluish when dry. Apothecia were scattered on most of the individuals, and our experimental samples contained a few of them. *Leptogioum azureum* is a pantropical species, distributed from America and Africa to Asia and New Zealand (WOLSELEY 1991, GALLOWAY 1985). – 7 diel time courses were monitored with samples of this species.

For the CO_2 exchange measurements, the thalli were collected fresh from their open habitats, detached from their substrate and cleaned of adherent mosses and particles. For exposure in the gas exchange cuvettes, the thalli then were fixed in small wire-mesh baskets. Each sample consisted of one individual thallus or of several lobes from different thalli of the same population, giving a total thallus area between 9 and 12 cm².

2.2. Experimental methods

As described in the earlier papers (LANGE et al. 1994a, 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 CO_2 exchange under quasi-natural conditions together with climate parameters, such as air temperature (in the cuvette) and photosynthetically active photon flux density (PPFD), were measured by means of "CO_2/H_2O porometers". The technique utilized, the methods of data evaluation and handling together with general methodological considerations, are explained and discussed in detail by LANGE et al. (1984, 1994b, 1998).

Lichen samples, in their baskets and kept horizontal, were positioned near the porometer chamber so that they were exposed to an environment of similar illumination and water status as 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 favorable 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. Therefore, we decided to use horizontal exposure for the present study thus allowing a standardized comparison of gas exchange performance between the different co-occurring species. For CO_2 exchange measurements, lichen samples were enclosed every 50–90 min (higher frequency during the day, lower frequency during night) in the porometer cuvette which, internally, approximated the air temperature and light levels of the external environment. Steady-state CO_2 exchange was reached within 1–2 min. Sample weight was determined immediately after each CO_2 exchange measurement to establish actual thallus water content (WC, which was related to thallus dry weight as a percentage). Water drops adhering to the samples were removed before each gas exchange measurement by shaking.

In addition, a "minicuvette system" allowed CO_2 exchange measurements to be made under conditions of exactly controlled temperature, light, and humidity. In addition, a "click-cuvette system", also with artificial illumination, was installed in which air temperature could be maintained near ambient and in which the samples remained enclosed for longer periods of time during continuous CO_2 exchange measurements.

Rates of CO_2 exchange were related to thallus dry weight (4 days at 70 °C), projected thallus area, thallus carbon content (elemental analyzer; CHNO-Rapid, Foss Heraeus, Hanau, FRG; also for thallus nitrogen contents), and chlorophyll *a* content (RONEN & GALUN 1984, ARNON et al. 1974). For statistical analysis, STATISTICA for Windows (Statsoft, Inc. 1995, Tulsa, OK) was used. A WILCOXON Matched Pairs Test was applied for multiple comparisons and values of $P < 0.05$ (corrected by BONFERRONI adjustment) accepted as significant (see Table 3).

2.3. Specific thallus parameters, chlorophyll, carbon and nitrogen contents

Thallus parameters were rather similar for the three experimental species (Table 1). Specific mass was in the same range as for *Sticta tomentosa* (ZOTZ et al. 1998) but substantial higher than for the thin thalli of *Dictyonema glabratum* (LANGE et al. 1994a) from the same site. Area as well as dry weight related chlorophyll content of the *Leptogium* species was relatively high, almost certainly because of their thick, gelatinous thallus structure (note, that projected area is indicated). Thallus carbon content proved to be very similar for all of the species with low variability. Thallus nitrogen content, between 3.9 and 4.9% of dry weight for the *Leptogium* species, is a

Table 1. Thallus specific mass, maximal water content (WC), chlorophyll, carbon and nitrogen content of the experimental lichens (area always means projected area). Characterization of the fertile population for *Leptogium phyllocarpum* (averages ± SD, n = number of samples) and data for the individual samples of diel-course measurements for the other species.

	Specific mass g m^{-2}	Maximal WC % of dry weight	Chl. per dw mg $(g_{dw})^{-1}$	Chl. per area mg m^{-2}	C content % of dry weight	N content % of dry weight
Leptogium phyllocarpum	150.9 ± 50.5 (n = 33)	ca. 2750	1.03 ± 0.33 (n = 39)	147.5 ± 59.0 (n = 33)	45.0 ± 1.9 (n = 78)	4.7 ± 0.6 (n = 78)
Leptogium cyanescens	128.7	ca. 1350	1.71	220.6	43.9	4.9
Leptogium azureum	105.0	ca. 2500	0.96	100.9	47.0	3.9

consequence both of their nitrogen fixing capacity and their possession of a *Nostoc* cyanobiont (GREEN et al. 1980, KELLY & BECKER 1975).

3. Results

3.1. Response of net photosynthesis to degree of hydration

All of the experimental *Leptogium* species suffer from a distinct depression of NP at high thallus hydration. For *L. phyllocarpum* this was confirmed by four different types of experiments. Firstly, a fully saturated thallus sample (after immersion in water for 3 min) was placed in the click cuvette and allowed to dry out very slowly over about 20 hours, its CO_2 exchange being monitored every 2 min (Fig. 1, top; drying process from right to left). Secondly, a similar, fully hydrated sample was placed in the minicuvette and the relative air humidity adjusted to manipulate the water loss rate so that it became dry within 10 h. About every 30 min NP was measured, and subsequently the sample was removed for determination of its water content (Fig. 1, center). Thirdly, all data points of NP at PPFD higher than about light saturation during gas exchange measurements under natural conditions (see Section 3.5) were plotted against WC (Fig. 1, bottom). As a fourth independent data set, the theoretical maximum of WC-dependent NP was derived from SMITH-functions used to describe NP response to light of the lichen (see Section 3.3, Fig. 5, panel D). The response curves obtained by all of the above methods revealed a strong depression of NP at suprasaturating water content which reduced maximal CO_2 fixation by 55% to more than 80% at highest WC and created only a relatively small WC window for optimal NP. Slow experimental drying at different rates led to response patterns qualitatively similar to the situation *in situ*. However, optimal NP seemed to occur at lower WC during field performance, and the optimal range was broader. Most probably this is the result of inhomogenous distribution of water in the gelatinous lichen thallus during quick changes of weather conditions in

the field, a feature already described for *L. puberulum* from maritime Antarctica by SCHLENSOG et al. (1997). Under experimental drying over many hours, water would be expected to equilibrate evenly across the thallus. In contrast, in nature, changes in hydration of the uppermost layers of thallus might well have occurred before larger changes in bulk water-content took place. In addition, differences in thallus temperature might also have increased the scatter of responses during the field measurements (see section 3.4 for a more detailed discussion).

Figure 2 shows NP responses to WC as extracted from the diel time courses of field performance for the other two *Leptogium* species. Again suprasaturation depressed NP under field conditions by about two thirds of maximal rates.

3.2. Initial CO_2 response upon rewetting

Resaturation of lichens after a drying period often results in an initial, transient phase of elevated CO_2 release before steady-state gas exchange is attained. Such a burst ("resaturation respiration"; SMITH & MOLESWORTH 1973) can last for several hours. However, this phenomenon seems to be rather small for *L. phyllocarpum*. To quantify the significance of resaturation respiration, the lichen was kept air-dry for two days, a drought period certainly much longer than the maximum possible for this species under natural conditions. Subsequently, the thalli were submerged in water for 4 min and then immediately inserted in the click-cuvette, their CO_2 exchange being recorded continuously in a dark-light cycle (Fig. 3). For technical reasons, the first reliable measuring point was possible 6 min after the end of the wetting period. At that time, dark respiration was increased only by about 40% in comparison to the following, almost constant rates of respiration. NP increased in an expected fashion due to recovery of the photosynthetic processes and decreasing diffusion resistances as water equilibrated within the thallus (see Section 3.1).
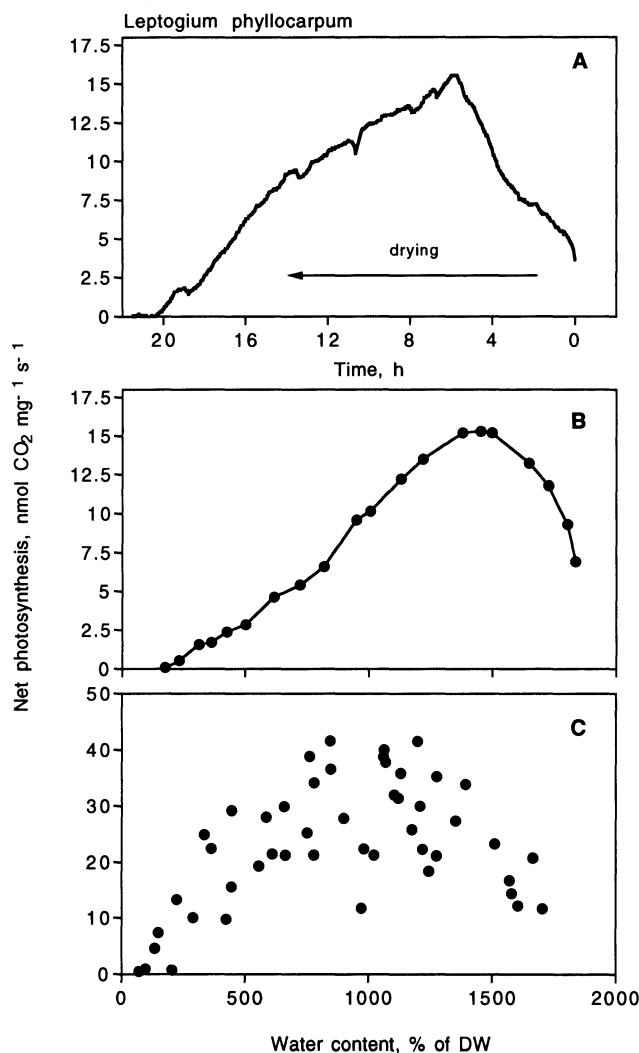
Fig. 1 Changes of chlorophyll-related net photosynthesis of *Leptogium phyllocarpum* with time during drying (A) and related to thallus water content (B, C). A: Drying-down curve with continuous monitoring of CO_2 exchange. The lichen was maximally soaked at time zero (temperature 20–31 °C, 200 µmol m^{-2} s^{-1} PPFD). B: Stepwise drying of initially fully soaked thalli (temperature 20 °C, 150 µmol m^{-2} s^{-1} PPFD). C: Single data points of net photosynthesis versus water content at PPFD > 500 µmol m^{-2} s^{-1} as selected from 14 diel time course measurements of CO_2 exchange under natural conditions (see Fig. 8). Note differences in PPFD which explain differences in NP between A/B and C.
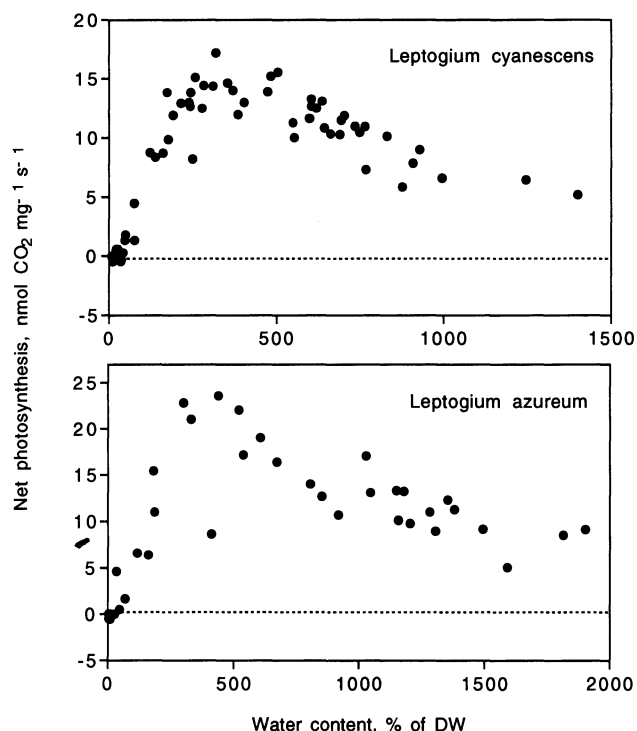

Fig. 2. The dependence of chlorophyll-related net photosynthesis on thallus water content for *Leptogium cyanescens* and *L. azureum*. Single data points of net photosynthesis versus water content at PPFD > 300 (*L. c.*) or > 400 (*L. a.*) µmol m^{-2} s^{-1}, respectively, as selected from, respectively, the 14 (*L. c.*) or 7 (*L. a.*) time course measurements of CO_2 exchange under natural conditions.

3.3. Light response of net photosynthesis

Net photosynthesis of all three *Leptogium* species showed typical saturation-type light responses with no indication of photoinhibition at the highest irradiation levels either during our experiments or under natural conditions. However, as shown in the previous section, rates achieved at various PPFDs were highly dependent on
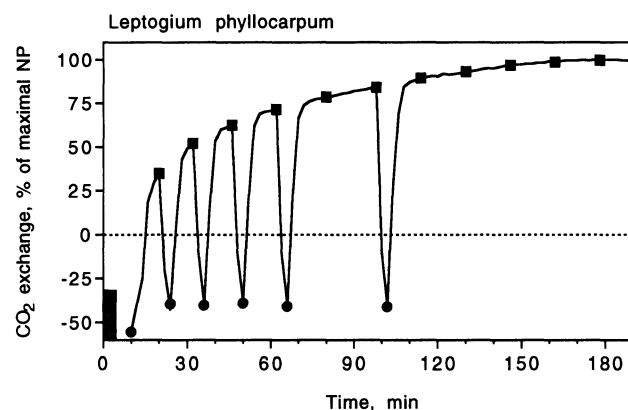

Fig. 3. Recovery of metabolic activity of *Leptogium phyllocarpum* after two days of desiccation. CO_2 exchange was continuously monitored (drawn line, temperature 17–24 °C) when light (300 µmol m^{-2} s^{-1} PPFD) was interrupted by dark phases of 4 min duration. Circles: dark respiration; squares: net photosynthesis when constant readings of CO_2 exchange were attained. The initially dry sample was rewetted at time zero and was kept submersed in water for 4 min (dotted section).
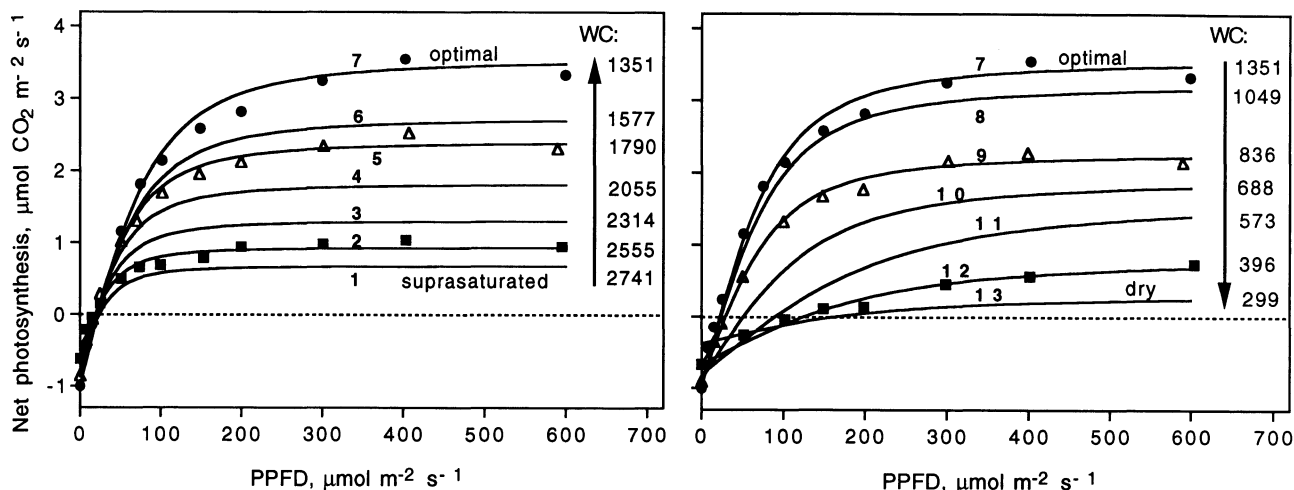
Fig. 4. Response of area-related net photosynthesis to incident photon flux density (PPFD) of *Leptogium phyllocarpum* at different water contents and 20 °C. Curves were fitted by the SMITH-function (see text). Actual data points are given for several examples (curves no. 2, 5, 7, 9, 12); all the other data points show similar levels of fit (r^2 between 0.95 and 0.99). Average water content (WC, in % of dry weight) during generation of each response curve is given at the end of each line. Sequence of numbers and arrows indicate decreasing steps of WC of the thalli. Curve 1 is characteristic of the performance of the lichen at high WC, near water holding capacity. Left panel indicates range of increasing NP during drying from suprasaturation to optimal conditions; right panel indicates decreasing NP from optimal conditions to almost dry sample.

actual water content of the lichens. The interaction between thallus hydration and PPFD-dependent NP was studied in detail for *L. phyllocarpum*. Using the minicuvette system, samples were subjected to stepwise changes in incident PPFD at different levels of WC, and the NP responses were then simulated by SMITH-functions (non-linear regressions; see LANGE et al. 1991, GREEN et al. 1997), which allow calculation of theoretical maximum of NP at saturating PPFD (NP_{max}), light compensation point of CO_2 exchange ($PPFD_{comp}$), apparent quantum yield of CO_2 fixation (Φ, initial slope of light response curve), and light level necessary to saturate NP ($PPFD_{sat}$; defined for 95% of NP_{max}, see LANGE et al. 1991).

Figure 4 shows NP response curves to PPFD at different levels of hydration, and the extracted WC-dependence of the different gas exchange parameters is depicted in Fig. 5. At maximal WC (2741% of dry weight), maximal NP was strongly depressed (Fig. 4, left panel, curve number 1). Suprasaturation of the thallus with water decreased NP at both saturating and limiting PPFD, even near the light-compensation point. Decreasing WC at first increased the level of NP (curve numbers 2 to 7), and maximal rates were achieved at optimal WC of 1351%. The subsequent decrease of NP as WC declined further was obvious (Fig. 4, right panel, curve numbers 8 to 13) until photosynthesis of the desiccated thalli almost ceased. Light saturation of *L. phyllocarpum* was also strongly dependent on thallus hydra-

tion (Fig. 5, panel A). $PPFD_{sat}$ was very low at high degrees of hydration; the suprasaturated thalli needed no more than 110 µmol m^{-2} s^{-1} PPFD to attain maximal rates of NP, and light saturation increased only slightly until the lichen had lost three quarters of its maximal water content. $PPFD_{sat}$ then increased, steeply although maximal NP still was high. In a similar fashion, light compensation point of CO_2 exchange (Fig. 5, B) proved to be rather insensitive to degree of thallus hydration over a large range of high WC. $PPFD_{comp}$ remained around 20 µmol m^{-2} s^{-1} between 2700 and 1050% WC and only at lower WC did $PPFD_{comp}$ increase to more than 150 µmol m^{-2} s^{-1}. At low WC, apparent quantum yield of CO_2 fixation increased with increasing degree of hydration in a similar fashion as NP_{max} (Fig. 5 C, D) and reached its highest value at around 1350% WC, a similar value as needed to reach NP_{max}. This response confirms that, at low water contents, limitation of NP is due to dehydration of the photosynthetic apparatus. In contrast, the decrease of NP_{max} at high WC takes place whilst Φ remains high. This agrees with performance of other lichen species (see LANGE et al. 1996) and allows the conclusion that suprasaturation-depression of NP for *L. phyllocarpum* is also due to lack of CO_2 supply for the photobionts when thallus diffusion resistances for carbon dioxide have increased at high water contents.

No experiments under controlled conditions were carried out for the two other *Leptogium* species. However, some information about light response of their NP
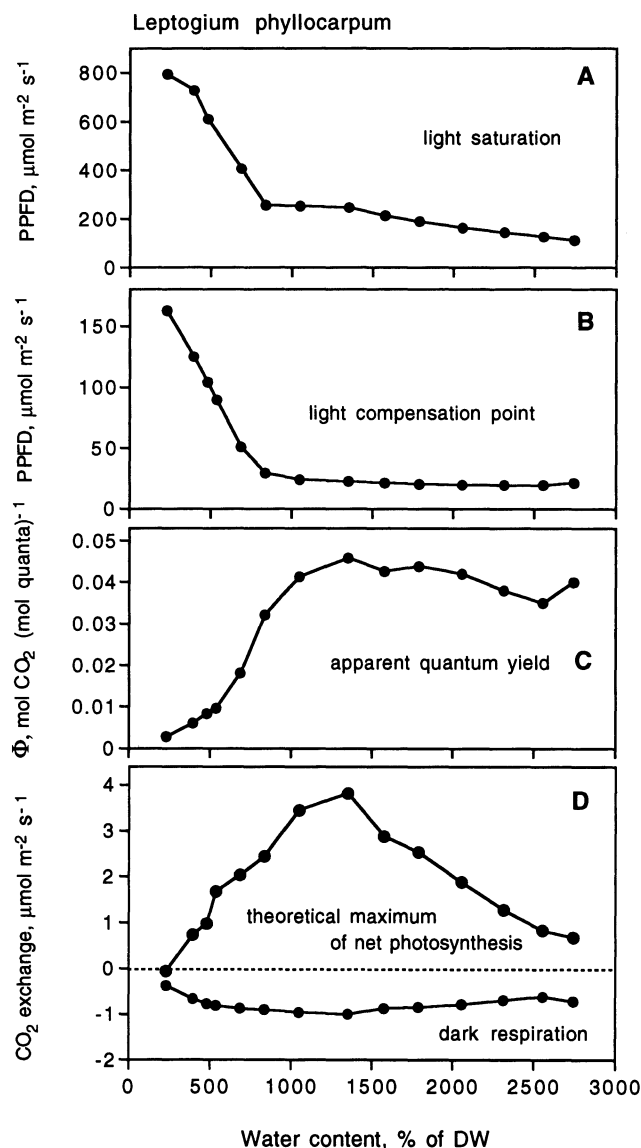
Leptogium phyllocarpum

Fig. 5. Photosynthetic parameters of NP response to light of *Leptogium phyllocarpum* as dependent on thallus water content (extracted from data set and SMITH-regressions as depicted in Fig. 4, see text). A: light saturation ($PPFD_{sat}$); B: light compensation point ($PPFD_{comp}$); C: apparent quantum yield of CO_2 fixation (Φ); D: theoretical maximum of net photosynthesis as calculated from SMITH-function, and dark respiration.
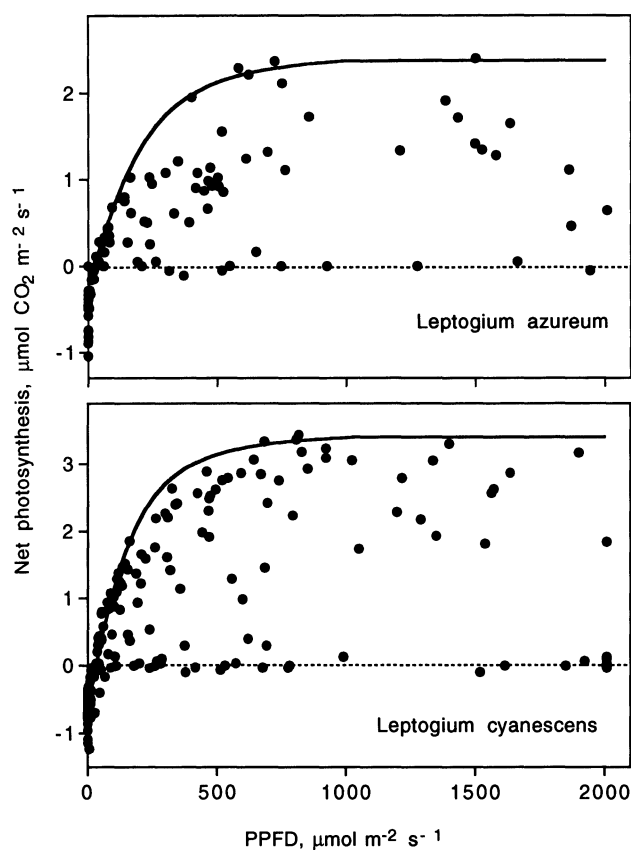

Fig. 6. Response of area-related net photosynthesis to incident photon flux density (PPFD) of *Leptogium azureum* and *L. cyanescens*. Single data points extracted from the 7 (*L. a.*) or 14 (*L. c.*), respectively, diel time course measurements of CO_2 exchange under natural conditions. The drawn line characterizes the envelope curve.

can be derived from Fig. 6, where all gas exchange values obtained under natural conditions (see section 3.5) for *L. azureum* and *L. cyanescens* are plotted against concomitant PPFD. The envelope curves represent the light responses under most favorable combinations of hydration and temperature for the range of incident light that had occurred under field conditions. The scatter of data points below the envelope curves is mainly due to limitation of NP by sub- or supraoptimal WC, through

short-term after-effects of desiccation, or as a temperature effect. The $PPFD_{sat}$ of both species, between 500 and 600 µmol m^{-2} s^{-1} PPFD, seems to be higher than that found for *L. phyllocarpum* under optimal WC. The light-compensation point for *L. azureum* (21 µmol m^{-2} s^{-1} PPFD, calculated from the SMITH-functions) is almost identical with that found for *L. phyllocarpum* under controlled conditions, but $PPFD_{comp}$ was higher for *L. cyanescens* (33 µmol m^{-2} s^{-1}).

3.4. Temperature response of photosynthesis and respiration

Using the minicuvette system, samples of *L. phyllocarpum* were subjected to stepwise changes in temperature (increasing and decreasing sequences), and dark respiration and net photosynthesis were recorded under momentary steady-state conditions. The intention was to maintain WC within its optimal range for NP during
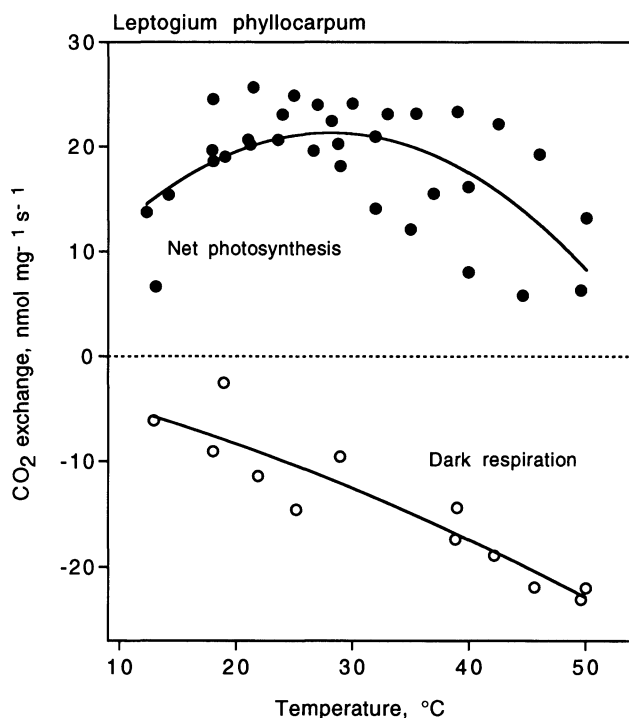
Fig. 7. Dependence of chlorophyll-related net photosynthesis (closed symbols) and dark respiration (open symbols) on cuvette air temperature for 4 different samples of *Leptogium phyllocarpum* at 300 μmol m^{-2} s^{-1} PPFD.

these experiments, but this proved difficult due to rapid drying of the thalli. As a result the lichens had to be rehydrated from time to time and this is one reason for a large scatter in the temperature responses (Fig. 7). Air temperature was controlled inside the cuvette but, due to evaporative cooling, differences between air and thallus temperature occurred which became larger as temperatures increased. A thin thermocouple was inserted in the thallus during measurement which showed maximal deviation of more than 6 K between air and the coolest parts of the transpiring lichen. Conspicuous temperature gradients within the thick gelatinous lichen did not allow a clear definition of thallus temperature. Thus, these technical problems introduce a considerable error when the response of *L. phyllocarpum* is related to air temperature (Fig. 7). However, even with these shortcomings, our results suggest that this species is highly adapted to warm conditions. Net photosynthesis was near-optimal for a broad range centred on 30 °C, and considerable CO$_2$ fixation (almost 40% of the maximum) was still possible at air temperatures around 50 °C, corresponding to thallus temperatures substantially above 40 °C. In addition, lichens may display transiently increased respiration rates as temperature is increased which may require hours to reach a lower steady-state (see SUNDBERG et al. 1999). This feature

would possibly conceal an even higher capacity of NP at high temperatures which would occur after longer time periods of temperature adaptation.

It should be stressed that the potential of *L. phyllocarpum* for carbon gain at elevated temperatures was coupled with a high heat resistance in general. The experimental treatments during which the lichen was exposed for more than 1 h to air temperatures between 42 and 50 °C under fully hydrated conditions did not cause any recognizable damage. At the end of one of these experiments temperature was lowered to 20 °C and the lichen immediately returned to its original high rates of NP which then remained constant for at least several hours.

3.5. Natural diel courses of carbon dioxide exchange and thallus water content

Continuous measurements of CO$_2$ exchange, thallus water content, and microclimate were recorded *in situ* for all three species for 14 days (*L. cyanescens*, *L. phyllocarpum*) or 7 days (*L. azureum*), respectively. As an example, 14 diel courses are depicted in Fig. 8 for *L. phyllocarpum*. Weather conditions over night were characterized by showers, often together with thunderstorms, and by fog in the morning hours. Subsequently, on most days, there was a distinct period with a clear sky and full sunlight reaching more than 2000 μmol m^{-2} s^{-1} PPFD around noon. Much lower PPFD occurred during the afternoons due to increasing cloud cover and rainstorms which were normally heavy and of variable duration. Night temperatures were uniform, between 17 °C and 20 °C, and only once falling to 16 °C; whilst daily maximal air temperatures could reach more than 35 °C. With exception of the dry period around noon, relative humidity stayed high, between 90 and 100%, for most of the time. As a consequence of these typical tropical weather conditions, the water content of the lichen thalli underwent pronounced diel changes. During the whole night thalli were so wet that continuous dark respiration occurred. At sunrise, the lichens were always well hydrated so that, before noon, net photosynthesis responded to incident light although suprasaturation usually limited CO$_2$ fixation at first. Maximal NP was attained late in the morning at high light when substantial water loss had taken place. Subsequently, on most of the days, further decrease in WC resulted in reduced NP which sometimes reached the moisture compensation point. Afternoon rain showers then rehydrated the thalli. However, this produced only lower rates of CO$_2$ fixation due to thallus suprasaturation and PPFD which was usually well below light saturation. In general, the other two experimental species responded in a similar fashion. However, water holding capacity of *L. cyanescens* was lower than that of *L. phyllocarpum*, and *L. azureum*
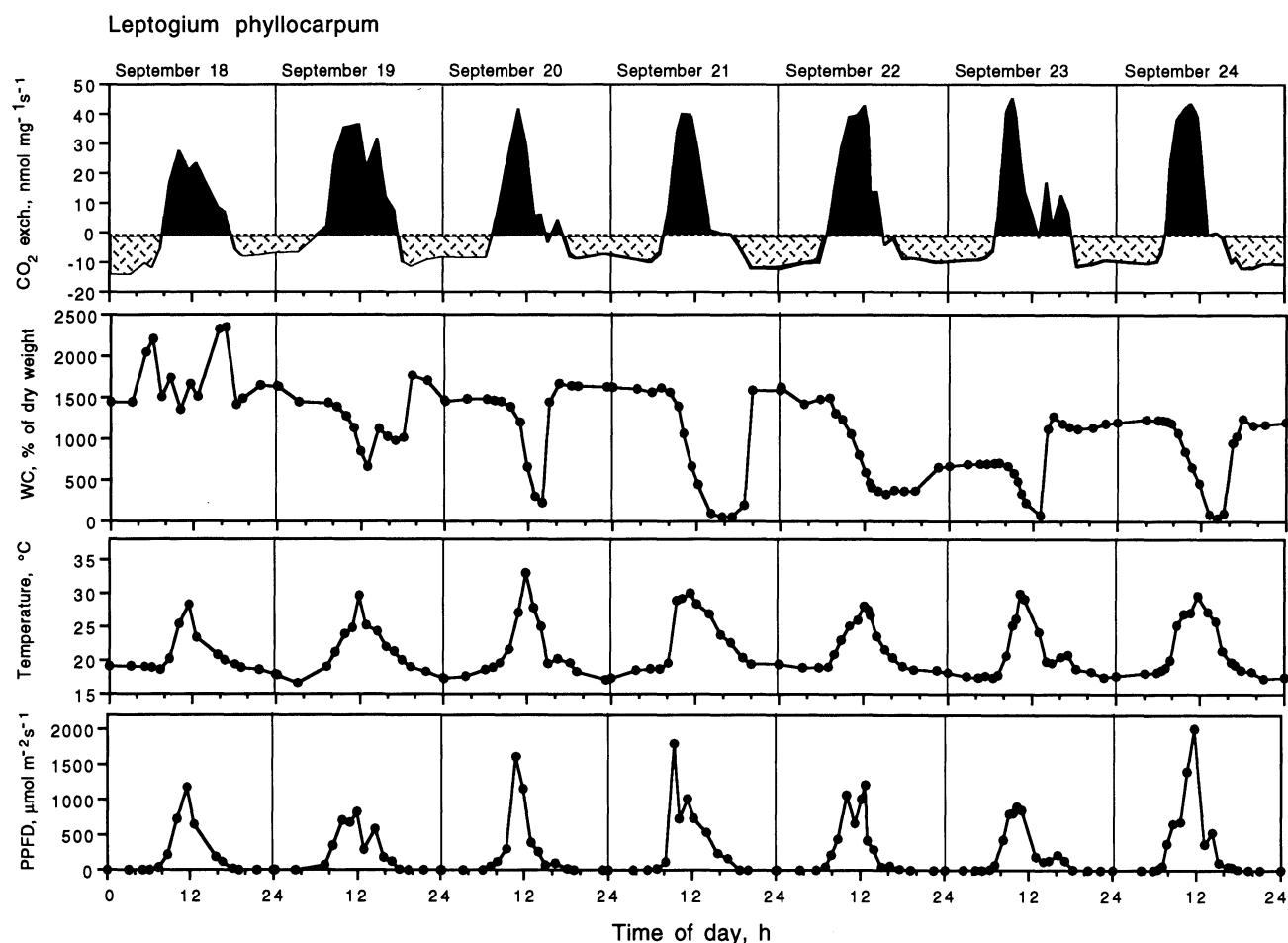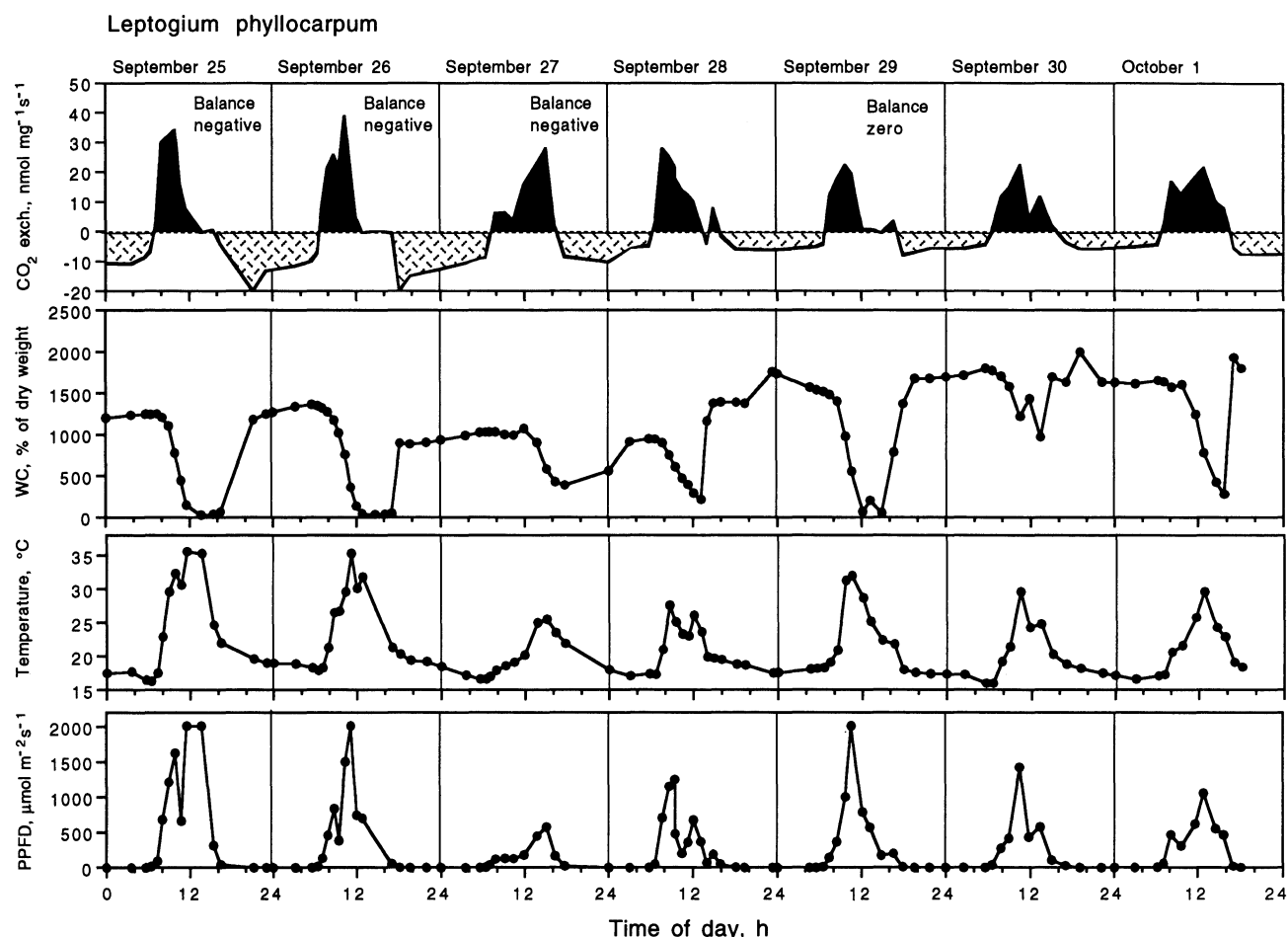
Leptogium phyllocarpum

Fig. 8. Diel time courses of chlorophyll-related CO_2 exchange (upper panel, CO_2 uptake black, CO_2 release hatched), water bottom panel) for *Leptogium phyllocarpum* from September 18 to October 1, 1993. Single porometer-readings are indicated by

Table 2. Maximal rates of CO_2 exchange under natural conditions for *Leptogium* species, *Dictyonema glabratum* and *Sticta tomentosa* from the same site (see LANGE et al. 1994a, ZOTZ et al. 1998). Numbers of days of measurements are indicated.

	Maximal net photosynthesis, CO_2 fixation related to				Mean dark respiration during night with maximal carbon loss. CO_2 release related to	
	Dry weight nmol $g^{-1}\,s^{-1}$	Area μmol $m^{-2}s^{-1}$	Chlorophyll nmol $mg^{-1}s^{-1}$	Carbon nmol $(gC)^{-1}s^{-1}$	Dry weight nmol $g^{-1}s^{-1}$	Carbon nmol $(gC)^{-1}s^{-1}$
Leptogium cyanescens (14 days)	29.5	3.8	17.2	67.6	5.4	12.4
Leptogium phyllocarpum fertile (14 days)	28.0	6.2	45.2	63.2	8.3	17.9
Leptogium azureum (8 days)	22.6	2.4	23.6	48.0	8.2	17.5
Leptogium phyllocarpum young and sterile (4 days)	46.2	8.1	29.7	103.3	6.6	14.8
Dictyonema glabratum (14 days)	116.7	7.9	69.7	254.5	12.4	27.1
Sticta tomentosa (9 days)	56.9	5.6	45.2	120.8	6.3	13.4

Leptogium phyllocarpum

content (WC, second panel), cuvette air-temperature (third panel), and incident photosynthetic photon flux density (PPFD, dots, data points at 0 h or 24 h are generated by interpolation.

seemed to respond more quickly when drying and re-hydrating.

In Table 2, maximal rates of CO_2 exchange under natural conditions of the three *Leptogium* species are listed together with those of the two heteromerous cyanolichens from the same site which were studied at the same time (LANGE et al. 1994a, ZOTZ et al. 1998). With exception of the young, sterile thalli of *L. phyllocarpum*, dry weight related maximal NP was surprisingly similar for the three *Leptogium* species, and this was also true for their carbon related NP. Due to large differences in specific mass and chlorophyll content (see Table 1), area and chlorophyll related maximal rates differed substantially between the three species, highest rates being

Table 3. Average diel time periods of metabolic activity during the measuring period (September 18 – October 1). Significant differences within columns are indicated by different letters (WILCOXON Matched Pairs Test, P < 0.05, see Methods).

	Activity during the day, in % of 24 hours			Activity during daylight hours, in % of daylight (12 h 18 min)		
	Metabolic activity	Respiratory activity	Photosynthetic activity	Metabolic activity	Respiratory activity	Photosynthetic activity
Dictyonema glabratum	83.5[a]	57.4[a,b]	26.1[a]	67.7[a]	16.8[a,b]	50.9[a]
Leptogium cyanescens	86.7[a]	56.5[a]	30.2[a,b]	74.1[b]	15.2[a]	58.9[a,b]
Leptogium phyllocarpum	94.3[b]	60.9[b]	33.4[b]	89.0[b]	23.8[b]	65.2[b]

attained by the fertile thalli of *L. phyllocarpum*. Four diel courses of CO_2 exchange measurements are also available for a sterile thallus of the latter species. Apparently as a transient ontogenetic situation and certainly due to lack of massive apothecia, it showed much higher rates of dry weight, area and carbon related maximal NP. In comparison with the mature *Leptogium* samples, the basidiolichen *D. glabratum* was much more active with four times higher dry weight and carbon related maximal NP rates. *Sticta tomentosa* also had higher maximal rates when related to dry weight and carbon-content. In order to compare the maximal respiratory activity, mean DR rates of the different species during the night with maximal CO_2 loss were calculated (Table 2). This procedure was necessary because high but short peaks of CO_2 release could occur as the result of respiratory bursts during resaturation (see ZOTZ et al. 1998) which would upset comparisons using single data points. These mean maximal, dry weight or carbon related respiratory rates were very similar for all of the *Leptogium* species and for *S. tomentosa*. Only *D. glabratum* stood out also in this respect with substantially higher rates.

When the diel patterns of CO_2 exchange of the *Leptogium* species with high water holding capacity are compared with the thalli of *D. glabratum*, distinct differences became obvious with respect to the time periods of metabolic activity. As an example, September 24 (Fig. 9, right panel) was a day with early fog and drizzling rain in the early morning hours. It cleared up at about 9 a.m. and incident PPFD was high at noon. This dry and hot midday period was terminated by a strong rain storm which began at 15:15 h. NP of all of the well hydrated lichens *L. phyllocarpum*, *L. cyanescens*, and *D. glabratum* increased steeply after sunrise whilst their water content decreased. *Dictyonema glabratum* reached its NP maximum at 8:30 h. However, one hour later its WC was already lower than 45% and CO_2 exchange of the dry thallus ended after less than 3 hours of photosynthetic carbon gain. In contrast, the gelatinous *L. phyllocarpum* continued photosynthesis for more than 6 hours. Its NP ceased when thallus WC fell to around 84% at 13:00 h. The kinetics of water loss by the two lichens were almost identical (Fig. 9, center panel) – but the higher initial water content of *L. phyllocarpum* allowed a much longer period of activity. *Leptogium cyanescens* had both intermediate water holding capacity and performance pattern. Afternoon showers resulted in a second, though highly light-limited, peak of NP at 16:30 h for *D. glabratum* and *L. cyanescens*. For *L. phyllocarpum* WC remained too low, so that only respiratory metabolism occurred. The advantage of higher water content and thus longer time periods of photosynthetic activity for the *Leptogium* species was also obvious on September 19 (Fig. 9, left panel). Photo-

synthetic carbon gain ended for *D. glabratum* by noon due to desiccation and rehydration by another rain shower at about 2 p.m. generated a second high peak of NP. *Leptogium cyanescens* also dried and ceased net photosynthetic CO_2 uptake around noon. However, the gelatinous structure of its thallus retarded water uptake, so that its second afternoon peak of NP was much smaller than that of *D. glabratum*. Initial, pre-dawn WC of *L. phyllocarpum* was almost twice as high as that of both of the other species. This was sufficient to allow continuous metabolic activity by this species through the total day with only a small depression of NP in the early afternoon.

The influence of differences in structure-dependent water holding capacity for the daily duration of metabolic activity is summarized in Fig. 10 for those species for which 14 measurement days were available. All of the three species depicted were well hydrated with respiratory activity during the nights. However, during the day, *D. glabratum* became desiccated on 13 of the 14 days and, in one extreme case, it was inactivated and dry for one third of the day. In contrast, *L. phyllocarpum* experienced only 5 days during which its metabolism was interrupted by dehydration and then only much shorter time periods than its heteromerous counterpart. As an average, over all days of the measuring period, total duration of metabolic and photosynthetic activity per day, as well as per daylight hours, lasted significantly longer for *L. phyllocarpum* than for *D. glabratum* (Table 3). *Leptogium cyanescens* showed an intermediate performance but it was still active longer during the day than *D. glabratum*.

3.6. Lichen carbon balance

Integrated diurnal net photosynthetic carbon gain by *L. phyllocarpum* during the 14 days of continuous measurements ranged between 13.7 and 6.2 with an average of 9.3 mgC $(gC)^{-1}$ d^{-1} (Table 4). In spite of relatively low light intensities (integrated daily PPFD 16.5 mol $m^{-2}d^{-1}$), highest integrated CO_2 uptake [September 19; 13.7 mgC $(gC)^{-1}$ d^{-1}] was possible because of a relatively constant, moderate level of hydration (average WC of 1095% during daylight hours), when both suprasaturation and severe desiccation were avoided because of drizzle rain and a thin fog layer. The day with the lowest integrated CO_2 uptake [September 25; 6.2 mgC $(gC)^{-1}d^{-1}$] was very bright (integrated PPFD 40.0 mol m^{-2} d^{-1}), and the lichen thalli were already dry at noon and remained so until the next shower took place at sunset (average WC during daylight hours of 562%). Low daily carbon gain also occurred on days when the lichen thallus was suprasaturated for longer periods of the daylight period.
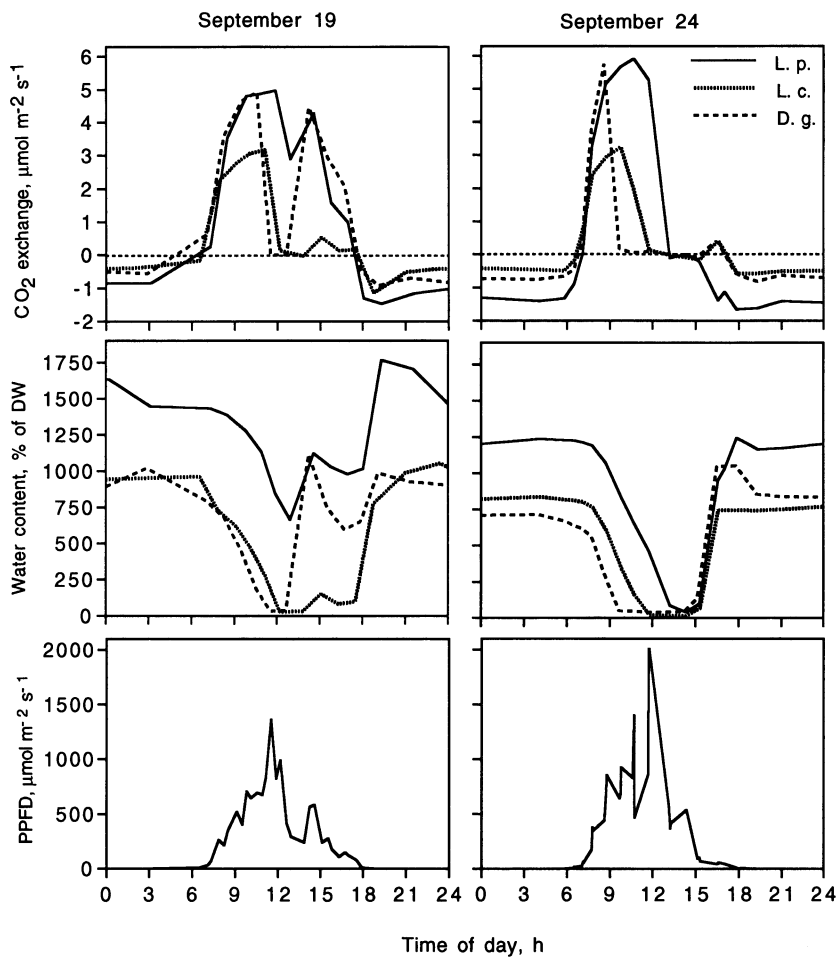
Fig. 9. Diel time courses of area-related CO_2 exchange (upper panel) and thallus water content (center panel) for *Leptogium phyllocarpum* (*L. p.*), *L. cyanescens* (*L. c.*), and *Dictyonema glabratum* (*D. g.*) on September 19 and 24, 1993. Bottom panel: incident photon flux density (PPFD).

Table 4. Integrated carbon gain, loss, and diel (24 h) balance under natural conditions. Numbers of days of measurements used for the averages are indicated.

|	Net photosynthetic carbon gain mgC $(gC)^{-1}d^{-1}$		Respiratory carbon loss mgC $(gC)^{-1}d^{-1}$		Diel carbon loss as % of carbon gain	Diel balance mgC $(gC)^{-1}d^{-1}$ mmol CO_2 $m^{-2}d^{-1}$ μmol CO_2 $g_{dw}^{-1}d^{-1}$		
	Maximum	Average	Maximum	Average	Average	Maximum	Minimum	Average
Leptogium phyllocarpum adult, fertile (14 days)	13.7	9.3	−9.6	−7.2	77.4	8.9 77.5 343	−3.3 −29.1 −129	2.1 15.6 77.5
Leptogium phyllocarpum juvenile, sterile (4 days)	24.6	15.7	−8.2	−7.4	47.1	18.4 120 688	3.9 25.1 144	8.3 53.6 307
Leptogium cyanescens (14 days)	13.1	8.97	−7.0	−5.4	60.2	8.1 37.7 293	−0.27 −1.3 −9.8	3.57 18.1 140
Leptogium azureum (8 days)	9.9	6.2	−9.7	−5.5	88.7	5.1 19.8 198	−6.1 −25.1 −238	0.7 2.59 24.7
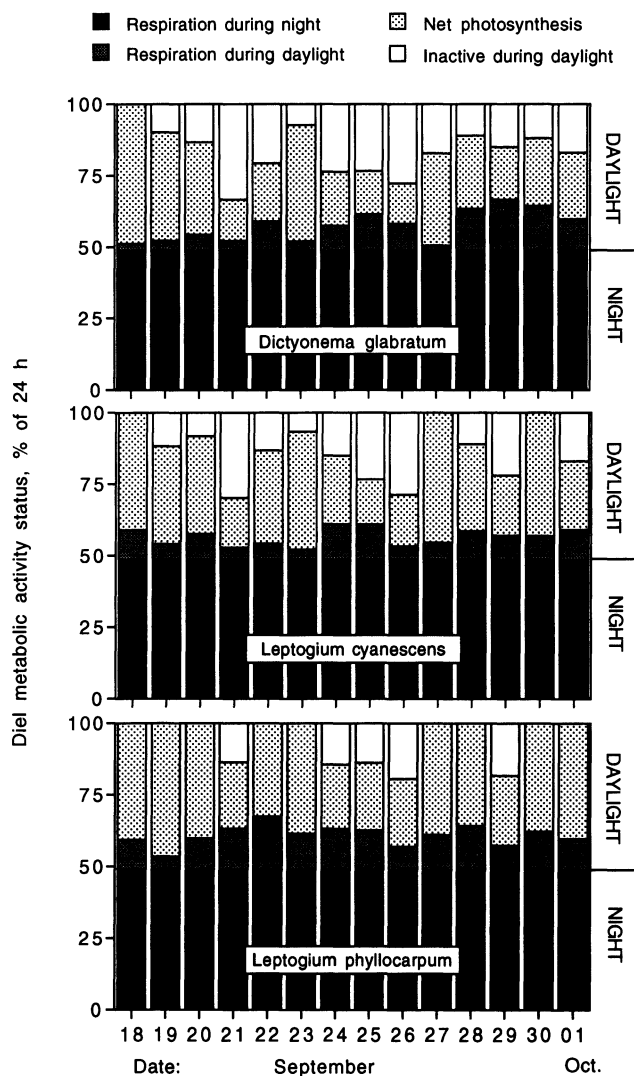
Fig. 10. Daily duration of activity as a proportion (%) of 24 h for *Leptogium phyllocarpum*, *L. cyanescens*, and *Dictyonema glabratum* during the measurement period from September 18 through October 1, 1993. Average daily dark period (PPFD $\leq 1\ \mu mol\ m^{-2}\ s^{-1}$) lasted for 11 h 42 min (NIGHT), PPFD was >1 $\mu mol\ m^{-2}\ s^{-1}$ for 12 h 18 min (DAY). Dark columns: respiratory activity in the dark or in the light; dotted columns: positive net photosynthetic activity; white columns: metabolic inactivity due to desiccation. There were no inactive periods during the night.

Throughout every night during our measuring period, the thalli of *L. phyllocarpum* were always hydrated to an extent that allowed respiratory activity without limitation by water shortage (see respiration response curve, Fig. 5 D). Night temperatures were relatively constant, the highest integrated respiratory daily carbon loss being 9.6 and the lowest 4.9 mgC $(gC)^{-1}\ d^{-1}$ with an average of 7.2 mgC $(gC)^{-1}\ d^{-1}$ (Table 4).

Diel carbon balance was calculated as the integrated diurnal net photosynthetic carbon gain minus integrated respiratory carbon loss. Even though *L. phyllocarpum* fixed carbon effectively, it was still not sufficient on all days to compensate for the extremely high nocturnal respiratory losses. There were three days where the diel carbon balance was negative, and a nil balance occurred on one day (see Fig. 8). In the extreme case (Sept. 25) respiratory carbon loss amounted to 154% of photosynthetic carbon gain. Integration over the total measuring period of 14 diel courses revealed that, *L. phyllocarpum* respired 77.3% of its carbon income from net photosynthesis.

Carbon gain of *L. cyanescens* was similar to that of *L. phyllocarpum*. However, its integrated respiratory carbon loss was smaller and amounted to only about 60% of net photosynthesis (Table 4). This provided a higher average daily production when related to carbon or dry weight. Due to differences in specific mass and in pigment content, relativities between these two species changed when carbon gain was calculated on thallus chlorophyll content or on thallus area. *Leptogium azureum* was the species with the lowest production. Its average integrated daily carbon balance amounted only to 0.7 mgC $(gC)^{-1}\ d^{-1}$. This was mainly due to the extremely unfavorable balance between carbon gain and carbon loss: almost 90% of carbon income of this species was respired again.

The relative proportions of the mycobiont and the cyanobiont within the lichen thallus seem to play an important role in carbon balance of these lichens, especially with respect to the ratio between income and respiratory loss of assimilates. This view was supported by diel measurements with the young sample of *L. phyllocarpum*. In contrast to the mature thalli, which were covered with massive apothecia, this specimen was sterile and consisted of a uniform layer of appressed thallus with an 80% higher area-related chlorophyll content. As listed in Table 4, its maximal and average integrated daily carbon gain was much higher than with all of the other *Leptogium* samples. At similar levels of respiratory losses, on average only 47.4% of carbon photosynthesized during the daylight hours were lost again by nocturnal respiration. Daily carbon balance of this young sample was several times higher than that of the mature sample of *L. phyllocarpum*.

4. Discussion

A large proportion of the lichens in the montane tropical rainforest of our study site are of homoiomerous structure with gelatinous thalli that have a high water holding capacity. We posed the question about possible adaptive features of this growth-form. Our measurements of

natural diel time courses of CO_2 exchange with the heteromerous cyanolichens *Dictyonema glabratum* (LANGE et al. 1994 a) and *Sticta tomentosa* (ZOTZ et al. 1998) had shown that their thalli dried out frequently in unshaded habitats even under humid-tropical conditions. The same was true for most of the other heteromerous cyanobacterial and green algal macrolichens that we studied (unpublished results) as well as for bryophytes (ZOTZ et al. 1997). Brief periods of very strong solar radiation around noon together with high water vapor pressure gradients at elevated temperature levels resulted in high water loss and complete desiccation of the thalli. The homoiomeric structure of the thallus could not totally avoid this problem but it did at least substantially alleviate it. Because of their high water holding capacity which extended their period of metabolic activity, gelatinous species were much less affected by rainless periods. A comparison of two *Leptogium* species and the heteromerous *D. glabratum*, studied under identical conditions continuously for 14 days, clearly showed this advantage (Table 3, Fig. 10). Similar properties of the homoiomerous structure have been discussed for quite different habitats: for *Leptogium puberulum* in maritime Antarctica (KAPPEN et al. 1987, SCHLENSOG et al. 1997), and for *Collema cristatum* under central European conditions (LANGE 2000).

Maximal rates of NP for the co-occurring mature thalli of all three *Leptogium* species (as related to area, chlorophyll, dry weight, and carbon content) were lower than those found for *D. glabratum* and, with exception of area-related NP, also those of *S. tomentosa* (Table 2). Nevertheless, their photosynthetic capacity was still in the upper range of maximal rates known for other lichen species from other climatic regions (KAPPEN 1988). However, during the diurnal time courses such maximal rates were rarely observed (see Fig. 8). Low incident light was certainly one limiting factor since light saturation levels for the lichens were relatively high

(Figs. 4, 6). In addition, the degree of hydration reduced photosynthetic activity (see Figs. 1, 2), either occasionally from desiccation which could result in metabolic dormancy or from high WCs which also depressed NP substantially (Figs. 1, 2). The latter, as also found by GREEN et al. (1995), seemed to be of importance for lichen productivity but its impact needed to be exactly quantified.

In order to get an impression of how deleterious suprasaturation was to productivity we calculated a rough estimate for *L. azureum*, the species in which the effect of high WC on CO_2 uptake was greatest. In Fig. 2 (bottom), all data points for NP as dependent on WC and which were measured at PPFD higher than 300 µmol m^{-2} s^{-1} PPFD are plotted for 7 days under natural conditions. The selected threshold of light intensity was almost saturating for the lichen. In the optimal range of hydration, which was defined between 250 and 650% WC and which is represented in Fig. 2 by 7 data points, average NP amounted to 81.4% of the absolute maximum attained by this species (even when one unexplainable, extreme value below 40% is included). 13 measurements (with an average of 14.7% of maximal NP) took place at WCs below, and 18 (with an average of 49.1% of maximal NP) at WCs above the optimal range. Based on the frequency of readings, each data point represents a lichen activity period of about 1 h 14 min. Extrapolating from the data using this time period it is possible to make an estimate of the lichen's daily photosynthetic yield as dependent on its water status. Table 5 shows that incident PPFD on the lichen was higher than 300 µmol m^{-2} s^{-1} on average for about half of the hours of daylight. During this period of ca. 6 h, the lichen assimilated 98% of its total carbon gain during daylight (carbon losses at low light have been included in this calculation). However, the lichen photosynthesized under optimal conditions of hydration (and almost light saturated), for only about 1 hour per day

Table 5. Impact of high thallus water content on photosynthetic production of *Leptogium azureum* as extracted from 7 diel time course measurements. Indicated are daily averages of length of different time periods during daylight hours and of net photosynthetic CO_2 gain during these periods.

	Length h.min	Average CO_2 gain µmol CO_2 $(gC)^{-1}$	Average CO_2 gain related (%) to time period when PPFD > 300 µmol m^{-2} s^{-1}
Total daily light period	12.18	472	
Total daily time period when light was higher than 300 µmol $m^{-2}s^{-1}$ PPFD	06.14	463	100
Time period (PPFD > 300 µmol $m^{-2}s^{-1}$ when WC was below optimal range	02.08	55	11.9
Time period (PPFD > 300 µmol $m^{-2}s^{-1}$) when WC was above optimal range	02.57	247	53.3
Time period (PPFD > 300 µmol $m^{-2}s^{-1}$) when WC was within optimal range	01.09	161	34.8

and, for about 3 hours, photosynthesis took place when the thalli were suprasaturated. During this time, when CO_2 uptake was substantially suppressed due to high thallus WC, NP yielded 53.3% of the total carbon gain that would have occurred under light saturation. In the absence of this reduction the lichen would have been able to photosynthesize during these 3 hours per day with the same rates as it did under optimal WC, then the mean daily net photosynthetic carbon gain would increase by 34%. When making this calculation, the influence of temperature on NP during the diurnal courses and shorttime fluctuations in PPFD could not be included. In addition, only the impact of suprasaturation at high light was taken into account; the gain would be even greater if the low light periods could also have been considered. This estimate shows that production of L. azureum is considerably reduced by the adverse effects of suprasaturation. Reduction in productivity through suprasaturation (data not shown in detail) was smaller for the other two Leptogium species, but it was substantial in both cases.

Despite the depression of NP due to suprasaturation, daily net photosynthetic carbon gain (i.e. integrated NP per day) of the Leptogium species was still high (Table 4). In the extreme case, the young thalli of L. phyllocarpum assimilated in one day almost 2.5% of its total thallus carbon content. Maximal daily net photosynthetic carbon gain of the mature lichens was around 1% with an average gain of between 0.62 and 0.93%. These values are much higher than those reported from lichens in non-tropical habitats (see LANGE et al. 1998 and literature cited there). This ability of all of the Leptogium species to rapidly fix CO_2 was mainly the result of their high water holding capacity which allowed long periods of activity even under high light intensity in their open habitat. The broad temperature range of optimal NP, which was demonstrated for L. phyllocarpum (Fig. 7), seemed to be another favorable adaptation of these cyanolichens for their tropical habitat allowing photosynthesis almost without limitation due to excessively low or high temperatures. The upper temperature compensation point, substantially above 40 °C, also seems to be exceptional in comparison to lichens from other climatic regions (see KAPPEN 1988). Similar values are known from other cyanolichens of the same site (LANGE et al. 1994a) and from Peltula species growing on inselbergs in North Transvaal (BÜDEL, unpublished). The high heat resistance of L. phyllocarpum is remarkable, since it is known that other species already suffer from irreversible heat damage to their hydrated thalli at much lower temperatures (LANGE 1953, JENSEN et al. 1997).

However, only a small portion of the high net photosynthetic carbon income of these lichens was available for growth. The largest part of the assimilated CO_2 was lost again by nocturnal respiration, so that the diel (24 h) carbon balance of the mature thalli, on average, amounted to low values between 0.26% and 0.06% of their thallus carbon content. In the extreme case, L. azureum lost almost 90% of its assimilated carbon by respiratory processes. Nevertheless, even the small proportion of assimilates that remained was apparently still sufficient for favorable biomass production and continued existence of all three of the Leptogium species studied at open sites in the premontane rainforest.

High nocturnal respiratory carbon losses due to continuous hydration at high temperatures throughout the dark period seem to be a characteristic feature for lichens of tropical rain forests (see LANGE et al. 1994a, ZOTZ et al. 1998). Nocturnal losses would increase even more at higher temperatures. A hypothesis was put forward initially for mosses (RICHARDS 1984, FRAHM 1990) and later extended to macrolichens (ZOTZ & WINTER 1994, see also GREEN & LANGE 1994) that the inability of daytime photosynthesis to balance such high respiratory losses might be responsible for the apparent unsuitability of extreme warm-humid, lowland tropical rainforests for these poikilohydric organisms (see LARCHER & VARESCHI 1988). A comparison with data from the literature seems to support this view. In Fig. 11, nocturnal respiratory carbon loss as related to diurnal net photosynthetic carbon gain is depicted for lichens from different habitats. The data available are very heterogeneous in terms of methodology and especially with respect to the length of measuring period suitable for integration. However, the material allows us to tentatively identify a pattern (see legend of Fig. 11 for detailed references). The most complete data sets for annual respiratory carbon loss and NP are available from an open habitat in Germany (Botanical Garden, Würzburg). The integration of continuous monitoring of CO_2 exchange by the epilithic Lecanora muralis (14; see numbers in Fig. 11) over an entire year resulted in respiratory carbon loss of 56.7% of daytime NP. Under similar conditions, the gelatinous Collema cristatum (15) showed higher, the green algal soil lichen Squamarina lentigera (13) and the foliose-fruticose Cladonia convoluta (12) lower losses. Based on a model derived from extensive field measurements, a similar value is reported for the lichen Ramalina maciformis in the Negev Desert (16; 57%). The coastal fog zone of the Namib Desert is much drier with respect to rain precipitation, and lichen activation takes place exclusively through fog, dew, and high humidity. This results in relatively low respiratory losses of 39.7% (Lecidella crystallina, 11), which have been estimated by extrapolation from 12 monitored diel courses. With a range of values between 37.6% and 13.7%, carbon losses for arctic tundra lichens (4–10) are still smaller, their nocturnal respiration being low due to low temperatures and short nights.
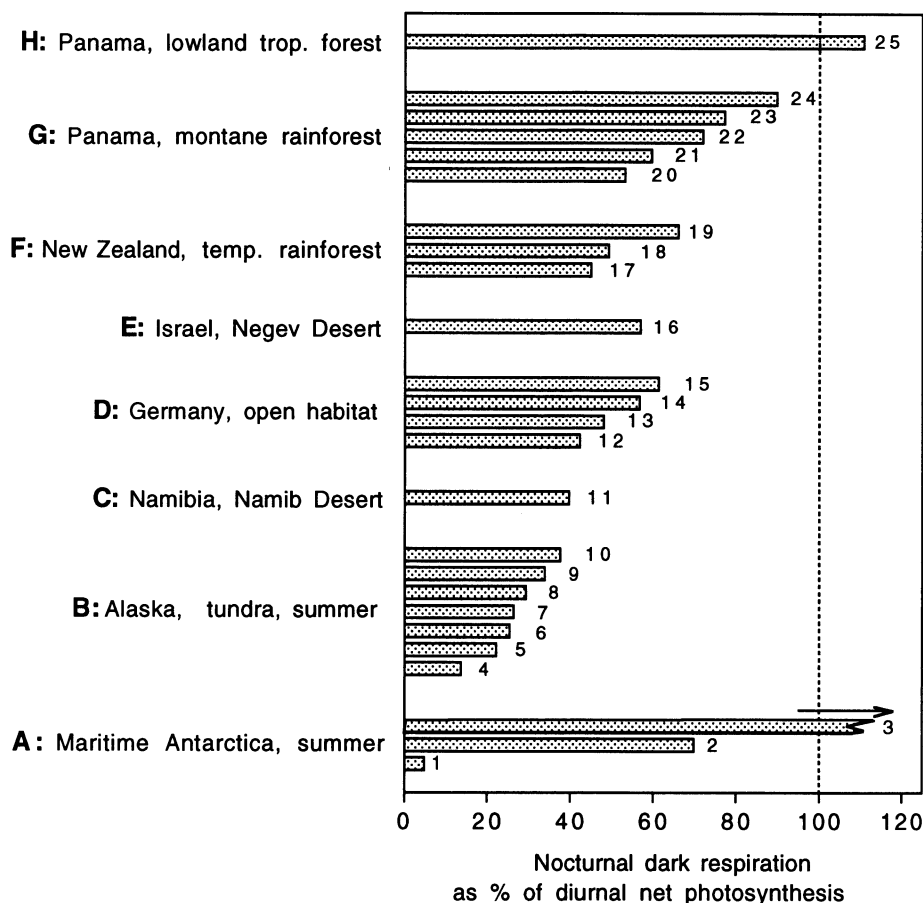
Fig. 11. Nocturnal respiratory carbon losses as percent of diurnal net photosynthetic carbon gain under natural conditions for a selection of lichen species from different habitats (figures behind the species names indicate number of diel courses used for integration). **A** 1: *Usnea fasciata* TORR. [KAPPEN & REDON (1987), simulation based on field data for typical summer conditions in the antarctic summer]. 2: *Usnea antarctica* DU RIETZ (5) [SCHROETER, unpubl., see SCHROETER (1991)]. 3: *Umbilicaria nylanderiana* (ZAHLBR.) H. MAGN. (13), value attaining 173% [SCHROETER, unpubl., see SANCHO et al. (1997), measuring days distributed over 3 summer months; see text for explanation of dark respiration >100%]. **B** 4: *Dactylina arctica* (RICHARDS.) NYL. (26), 5: *Cetraria cucullata* (BELL.) ACH. (24), 6: *Thamnolia vermicularis* (SW.) ACH. ex SCHAER. (24), 7: *Stereocaulon alpinum* LAUR. (24), 8: *Masonhalea richardsonii* (HOOK.) KÄRNEF. (26), 9: *Peltigera aphthosa* (L.) WILLD. (26), 10: *P. malacea* (ACH.) FUNCK (19) [Data from LANGE et al. (1998), measurement days spread over the summer growth period]. **C** 11: *Lecidella crystallina* VÉZDA et WIRTH (12) [Data from LANGE et al. (1994b)]. **D** 12: *Cladonia convoluta* (LAM.) ANDERS (101), 13: *Squamarina lentigera* (WEBER) POELT (108), 14: *Lecanora muralis* (SCHREBER) RABENH. (365, total year), 15: *Collema cristatum* (L.) WEBER ex WIGG. (113) [Unpublished data from continuous gas exchange measurements, see LANGE & GREEN (1997)]. **E** 16: *Ramalina maciformis* (DEL.) BORY (70) [KAPPEN et al. (1979), annual production-model based upon field measurements]. **F** 17: *Cladia aggregata* (SW.) NYL. (3), 18: *Collema laeve* J. D. HOOK. et TAYLOR (8), 19: *Pseudocyphellaria faveolata* (DELISE) MALME (8) [Data from GREEN et al. (1995)]. **G** 20: *Sticta tomentosa* (SWARTZ) ACH. (9) [ZOTZ et al. (1998)]. 21: *Leptogium cyanescens* (14) [present study]. 22: *Dictyonema glabratum* (SPRENGEL) D. HAWKSW. (14) [LANGE et al. (1994a)]. 23: *Leptogium phyllocarpum* (14), 24: *L. azureum* (7) [present study]. **H** 25: *L. azureum* (13) [ZOTZ & WINTER (1994), see text for explanation of dark respiration >100%].

However, these numbers are only representative for the summer growing period and no data are available for CO_2 exchange of these species during the winter period, when additional respiratory metabolism might take place. During the summer in continental Antarctica when there is light for 24 hours, only positive net photosynthesis and 0% respiratory loss was measured for *Umbilicaria aprina* (SCHROETER et al. 1994). Other lichens, in the maritime Antarctica, can have either negligible or substantial higher carbon loss during the summer months, as shown for *Usnea fasciata* (1) and *U. antarctica* (2), but these species also experience additional respiratory carbon losses during the dark winter period (see SCHROETER et al. 1997). However, there are also

species which suffer from an extremely unfavorable carbon budget even during the maritime antarctic summer period. SANCHO et al. (1997) report on the photosynthetic performance of three cosmopolitan species which had a highly negative carbon balance during the summer season, because of the disproportionately high dark respiration rates (respiratory losses > 100%). One species, *Umbilicaria nylanderiana*, is shown in Fig. 11 (3), respiratory losses of the two other species are still higher. These species must achieve positive carbon gain during other periods of the year because they continue to survive. Nevertheless, the measurements made during the summer demonstrated that carbon balance is crucial for these cosmopolitan species at the extreme southern limit of their distribution.

The same seems to be true for the other extreme, marginal habitat of macrolichens, the lowland tropical forest. In contrast to tropical montane habitats, *Leptogium* species are very rare in lowland tropical forests in Panama (see BÜDEL et al. 2000). *Leptogium azureum* is one of the few relatively common macrolichens under such conditions on Barro Colorado Island: ZOTZ & WINTER (1994) studied CO_2 exchange of this species on 13 days in the wet and 2 days in the dry season and found a negative carbon balance on many days. Integrated over all the monitored diel courses, respiratory CO_2 loss exceeded photosynthetic CO_2 gain (25, Fig. 11) for lichens in the crown of trees as well as on basaltic boulders in the understory. Like the measurements made in the maritime Antarctica by SANCHO et al. (1997), this study can not have encompassed the whole range of climatic conditions for *L. azureum*, which must experience periods with a better carbon balance (if we exclude the possibility of heterotrophic carbon gain about which nothing is known). The coincidence of lichen performance in these two extreme and marginal habitats is striking. Under moist-cold antarctic as well as under moist-warm tropical conditions the existence of the lichens seems to be endangered and eventually limited through negative carbon balances when respiratory losses surpass photosynthetic gains – this taking place at a much higher level of absolute CO_2 exchange rates in the tropics than in Antarctica.

Our measurements in the montane rain forest have shown that overall production of *L. azureum* was mainly limited by depression of CO_2 fixation during periods of suprasaturation and by high nocturnal respiratory rates. It is easily conceivable that increase in carbon loss, possibly enhanced by longer periods of dryness in combination with low light, might further reduce carbon balance until a critical limit is approached, as is clear from the measurements of ZOTZ & WINTER (1994). The importance of night temperatures can also be deduced from performance of lichens of the cooler temperate rain forest in New Zealand (17–19). There a gelatinous species, *Collema laeve* (18), respired only 49.2% of its NP at an average night temperature well below 10°C, a much lower percentage carbon loss in comparison with the tropical species (20–24).

These results are in accordance with the hypothesis by RICHARDS (1984) and ZOTZ & WINTER (1994) that a temperature-related increase in nocturnal respiration limits the existence of poikilohydric organisms, including macrolichens, in lowland tropical rainforests. Importantly, Fig. 11 shows that there is no simple linkage between photosynthetic carbon gain and respiratory carbon loss for individual lichens under different environmental conditions. This suggests that lichens are lacking coordinated control of the source-sink relationships for assimilates in their thallus or that such a control is at least very limited. Thus, it seems quite conceivable that disproportionately high dark respiration, most probably generated by the mycobiont, might become a danger for existence of the symbiotic unit. However, mitochondrial respiration is a rather dynamic process with adaptive properties (see PRECHT et al. 1973, SUNDBERG et al. 1998) and short-term responses of respiration to increased temperature may give a misleading impression about long-term processes. LARCHER & VARESCHI (1988) found some homeostatic adjustment of respiratory metabolism to the prevailing temperature regime for *Dictyonema glabratum* from contrasting habitats in the Venezuelan Andes. Additional, detailed studies on the acclimation potential of lichens, especially tropical lichens, are urgently needed. This includes comparative studies of temperature-dependence of respiratory metabolism of individual samples from montane and lowland habitats. Transplanting experiments will be necessary to finally explain differences in abundance of macrolichens between the cooler and the warmer formations of moist tropical habitats. If RICHARDS' hypothesis can be confirmed, the mystery remains to be explained why crustose foliicolous and crustose corticolous lichens, in contrast to macrolichens, are often quite abundant and diverse in tropical lowland forests.

determinations of the *Leptogium* species. We highly appreciate the help of PD Dr. B. SCHROETER (Kiel) who kindly supplied us with unpublished data about carbon balances of antarctic lichens. We thank Ms. DORIS FALTENBACHER-WERNER, Ms. WILMA SAMFAß, and Mr. GERHARD RADERMACHER for their assistance with evaluation and handling of data, and Prof. Dr. A. GREEN (Hamilton, New Zealand) for critically reading the manuscript.

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