In situ studies of water relations and CO_2 exchange of the tropical macrolichen, *Sticta tomentosa*

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SUMMARY

Diel (24-h) time courses of CO_2 exchange, water relations, and microclimate of the foliose lichen, *Sticta tomentosa* (Swartz) Ach., and responses to experimentally manipulated conditions were measured at a forest edge in a lower montane rainforest in Panama.

Similar to earlier observations on two other rain forest lichens, daily desiccation suppressed net photosynthesis (NP) during the period when irradiation was highest. Not surprisingly, the light response curves of NP showed saturation at rather low light levels. Rehydration was associated with an initial resaturation burst of short duration, which could be demonstrated both under natural conditions and experimentally. This additional loss of CO_2 seems too low to be ecologically relevant. Moreover, high thallus hydration was also detrimental to NP: at maximum water content net CO_2 uptake was depressed by $> 50 \%$. Although NP was well adapted to the prevailing high temperatures, the latter also stimulated dark respiration. On average, almost 60% of the diurnal carbon gain was lost during the night.

In spite of these limitations, the integrated 24-h C gain was quite high, on average 0.5% of the thallus C content. Whilst these figures were determined for horizontally exposed samples, we also assessed the role of different exposures on photosynthetic performance. Diel C gain was highest under conditions of semi-shade (westerly exposure), which allowed long periods of activity, whilst much higher irradiance at other exposures could not be utilized for photosynthetic production: easterly exposed thalli dried out even faster than horizontally exposed samples.

Key words: Lichen, rain forest, water content, photosynthesis, resaturation respiration, Panama.

INTRODUCTION

Tropical forests harbour a large number of lichen species. Together with other poikilohydric organisms, like mosses and liverworts, they can account for a considerable biomass in the tree tops, in particular in montane regions (Sipman & Harris, 1989; Gradstein, 1992). However, our knowledge of the ecophysiology of tropical lichens under natural conditions is extremely limited. To date, there are only two recent reports about the *in situ* gas exchange

of tropical lichens, both foliose species. One study focused on *Leptogium azureum* in the lowland forest of Barro Colorado Island, Panama (Zotz & Winter, 1994), whilst in another the physiological responses of the basidiolichen *Dictyonema glabrata* in a montane forest in the Fortuna watershed in Panama were investigated by Lange *et al.* (1994*a*). A somewhat surprising result of both studies was the frequency of low thallus water contents and its importance for daily C gain. Although growing under humid (Barro Colorado Island) or even very humid conditions (Fortuna watershed), the lichen thalli dried out almost every day. Therefore, positive CO_2 uptake was not only impeded for up to several hours almost every day, but after-effects of desiccation further decreased the possible C gain when rewetted by the next rainstorm (Lange *et al.*, 1994*a*). Another

common observation was rather frequent negative 24-h C budgets, apparently a result of relatively high respiration rates associated with the high night-time temperatures, especially in lowland forests (Zotz & Winter, 1994).

We selected a foliose lichen species with a cyanobacterial photobiont, *Sticta tomentosa*, to test the idea that the observations described above were representative of other co-occurring lichens. *Sticta tomentosa* is the earliest described tropical species in the genus *Sticta*, collected by Olof Swartz from Jamaica between 1784 and 1786 and published as *Lichen tomentosa* Swartz in 1788 (Galloway, 1995). It is widespread throughout the tropics, and occurs corticolously and on mossy banks in forests of higher altitude. In East Africa, it grows at altitudes of 1200–2100 m above sea level (Swinscow & Krog, 1988), whereas Kappelle & Sipman (1992) found it as high as 2700 m above sea level in Costa Rica. It is also reported as a 'typical' lichen species from cloud forests in Hawaii (Smith, 1991) or from lower montane forest in Ecuador (Arvidsson, 1991).

We documented the *in situ* CO_2 gas exchange and the water relations of this species and also investigated the response of net photosynthesis to changes in temperature, thallus water content, and incident light.

MATERIALS AND METHODS

Study site and organism

Our study was performed in the lower montane rain forest of the Fortuna watershed (Cordillera Central, Republic of Panama, approx. 8° 43′ N, 82° 14′ W) in September and October of 1993 at the Centro de Investigaciones Tropicales Jorge L. Arauz of the Instituto de Recursos Hidraulicos y Electrificacion (IRHE). The study site was at *c.* 1100 m above sea level on an eastern slope at a forest edge. Rainfall data for the research station are available for the period August 1990–September 1993 (IRHE, unpublished). Annual precipitation in 1991 and 1992 was 3509 mm and 3113 mm, respectively. Monthly rainfall was never < 100 mm in the 3 yr before our study; our study month (Sept. 1993) was one of the wettest during that period with *c.* 500 mm of rain.

The forest at Fortuna has an open canopy. Trees are generally 20–30 m tall, but emergents reach up to 40 m. A list of the phanerogamic species (Adames, 1977) and a description of the vegetation (Cavelier, 1992) are provided elsewhere. The physiognomic characteristics suggest that the forest is a lower montane rain forest *sensu strictu* (Grubb, 1977). Bryophytes are abundant both in the understorey and in the canopy, whilst macrolichens are most common at open sites, characteristic genera being *Coccocarpia*, *Leptogium*, *Usnea*, or *Sticta*. One of the

locally common species of the last genus is *Sticta tomentosa* (Swartz) Ach. The lichen is of the foliose lobate type; the photobiont is a species of *Nostoc*. Voucher specimens are deposited in the herbarium of the University of Panama, Republic of Panama. At the University of Würzburg, specific thallus parameters were determined on all experimental samples. Plant C content was analysed with a CHNO-Rapid analyser (Foss Heraeus, Hanau, Germany). Chlorophyll content was determined following Ronen & Galun (1984). The specific thallus mass was $134 \cdot 1 \pm 34 \cdot 5$ g m^{-2} ($n = 20$), chlorophyll content was $0 \cdot 61 \pm 0 \cdot 22$ mg g^{-1} d. wt ($n = 20$), C content was $46 \cdot 9 \pm 0 \cdot 4$ % of d. wt ($n = 20$), and mean nitrogen concentration was $4 \cdot 4 \pm 0 \cdot 2$ % of d. wt ($n = 20$). All values are means $\pm$ SD.

Carbon dioxide gas-exchange measurements

The samples of *S. tomentosa*, collected close to the research station, were carefully cleaned and placed in wire-mesh baskets (3·8-cm diameter, 1–1·5-cm height, mesh width 1·6 mm) similar to the standard method used in field measurements of lichen CO_2 gas exchange (Lange *et al.*, 1984, 1994*a*). Gas exchange studies with intact lichen thalli measure net fluxes of CO_2, i.e. the sum of all respiratory and CO_2-consuming processes of all components of the symbiotic system.

Carbon dioxide exchange was studied using three different instruments. Diel courses of CO_2 exchange under quasi-natural conditions were monitored using a CO_2/H_2O porometer (Walz, Effeltrich, Germany). Response curves of net CO_2 exchange under experimentally controlled conditions to changing photosynthetic photon flux density (PFD), temperature, and thallus water content (WC, % d. wt) were studied with a 'click-cuvette system' and a 'mini-cuvette system' (Walz), which were both set up in the research station. Artificial illumination was provided by lamps with fibre optics (KL 1500 electronics, Schott Glaswerke, Wiesbaden, Germany). Only the 'mini-cuvette system' allowed CO_2 exchange measurements under fully controlled temperature, light and humidity conditions. Because of its limited temperature control, the 'click-cuvette system' was only used when ambient temperature was close to the desired value of 20 °C. All CO_2 measurements were made using BINOS infra-red gas analysers (Rosemount, Hanau, Germany) operating in differential mode. All systems were open systems and differences in the CO_2 concentration could be measured to $\pm 0 \cdot 1$ ppm, or to within 0·1 ppm for the mini-cuvette. The absolute CO_2 concentration of the air which was flowing through the systems was determined with an additional BINOS operating in absolute mode. After the measurements, samples were dried for 4 d at 70 °C to determine d. wt.
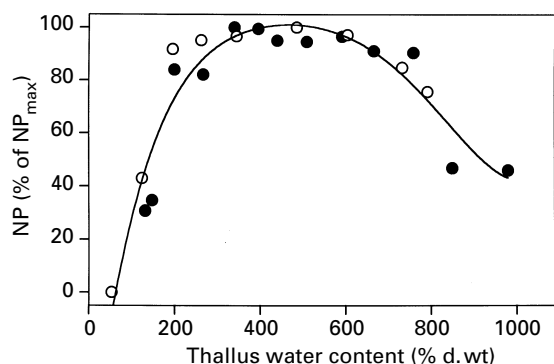
Figure 1. Effect of changes in the thallus water content on the net CO_2 exchange (NP, in $\%$ NP_{max}) of *Sticta tomentosa*. Different symbols represent different thalli. Cuvette temperature was 20 °C and PFD was 160 μmol m^{-2} s^{-1}. The r.h. inside the cuvette ranged from 90 to 96 $\%$. The solid line is a 5th degree polynomial regression ($r^2 = 0.90$).

Diel courses of CO_2 exchange, thallus water content, incident radiation, and cuvette air-temperature were studied in the period of 17–26 Sept. 1993. A sample was enclosed in the cuvette of the porometer system in intervals of *c.* 50–60 min and an individual measurement typically lasted only 2 min. The conditions inside the cuvette approximated ambient temperatures. Immediately after a measurement the f. wt of the samples was determined by weighing wire-mesh baskets plus sample (PM 460, Mettler, Giessen, Germany). Between measurements samples were horizontally exposed to the natural conditions on a tray made of wire mesh in *c.* 50-cm height at the forest edge. In addition, we studied the influence of different exposures on the diel patterns of CO_2 gas exchange. Lichen thalli from the north, south, west and east side of a tree trunk were collected and exposed vertically, similar to their natural exposure, on a square wooden pole (height 0·5 m, width 0·1 m). As controls we included two horizontally exposed samples in the experiment. For the porometer measurements, the samples were enclosed in the same cuvette as described above, but the cuvette was inclined in the different cardinal directions. The experiment lasted for 3 d.

The response of CO_2 exchange to different water contents was studied as follows: samples were submerged in distilled water for several minutes, taken out and surface water was removed by vigorous shaking. Samples were then placed into the cuvette of the 'click-cuvette system' at *c.* 20 °C and 160 μmol m^{-2} s^{-1} PFD. Ambient CO_2 concentrations ranged from 330 to 360 μl l^{-1}. Carbon dioxide exchange was measured as soon as equilibrium was reached. Then samples were removed, weighed immediately and allowed to dry for a few minutes. Samples were then placed into the cuvette again. This procedure resulted in a stepwise water loss and was continued until there was no more change in the relative water content.

For the study of net CO_2 exchange in relation to changes in PFD, samples were moistened by spraying to reach an optimal WC (400–600 $\%$ of d. wt), inserted in the cuvette of the 'mini-cuvette system', and illuminated with PFD of *c.* 150 μmol m^{-2} s^{-1}. PFD was then lowered in small steps until 0 μmol m^{-2} s^{-1} and subsequently increased in larger steps to a maximum PFD of *c.* 300 μmol m^{-2} s^{-1}. Each light level was maintained until a steady-state net CO_2 uptake was reached (usually 5–10 min) and then changed to the next level. The samples were weighed before and after the experiment. The PFD response curves were analysed by fitting a 'Smith-function' to the 9–10 data points of each sample, using STATISTICA® software (Statsoft Inc., Tulsa, OK, USA):

$$NP = \alpha \frac{PFD}{1 + \dfrac{\alpha^2\,PFD^2}{(NP_{max} + R_D)^2}} - R_D.$$

This function (modified after Smith, 1937, 1938) allows the determination of α, the initial slope of the curve, NP_{max}, the maximum rate of NP, and R_D, the rate of dark respiration. When NP is expressed on an area basis, the initial slope equals the apparent quantum yield for incident light ($\alpha = \Phi$, Green *et al.*, 1997).

Recovery of metabolic activity after desiccation was studied with six different thalli. Samples were allowed to dry naturally and were kept dry for 60–120 min. Subsequently, they were thoroughly moistened by submerging and spraying for *c.* 2 min. After removal of surface water the samples were immediately enclosed in the cuvette of the 'mini-cuvette system'. Carbon dioxide gas exchange was measured in the light (three thalli, PFD = 100 μmol m^{-2} s^{-1}) or in the dark (three thalli) over a period of 50–80 min. Cuvette temperature was 20 °C. At the end of the experiment the samples were weighed. The WC was 700–900 $\%$ of d. wt.

RESULTS

Dependency of carbon dioxide exchange on hydration, light, and temperature

Measurements of the net CO_2 exchange (NP) of *S. tomentosa* with different water contents yielded a relationship (Fig. 1) with a rather broad optimal range of NP from 350 to 600 $\%$ WC, whilst higher thallus WC lead to an increasing depression of CO_2 uptake. At maximum hydration (*c.* 900 $\%$ of d. wt), NP was less than half of the optimum value.

The dependency of NP on light is shown in Figure 2 for five replicate samples. Variation in the light-saturated rates of CO_2 uptake was not very pronounced when expressed on the basis of chlorophyll content ($23\cdot8 \pm 2\cdot7$ nmol CO_2 (mg Chl)$^{-1}$ s^{-1},
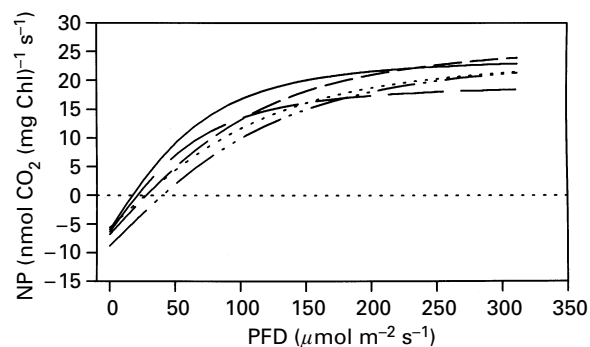
Figure 2. Light response curves of the net CO_2 exchange (NP, in nmol CO_2 (mg Chl)$^{-1}$ s^{-1}) in *Sticta tomentosa*. All lines were computed by fitting a 'Smith-function' to the original data ($r^2 > 0.99$ for all curves, 9–10 data points per curve). The same thalli as in Figure 5 were used. Cuvette temperature was 20 °C. Thallus water content (WC, % d. wt) was in the optimal range of 350 – 600 % (compare Fig. 1); ······, zero gas exchange.
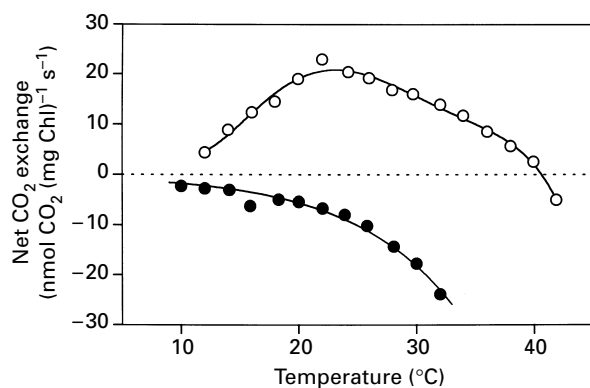
Figure 3. Relationship of gas exchange parameters (○, net photosynthesis, NP; ●, dark respiration, R_D) and temperature for *Sticta tomentosa*. Thallus water content was 800–1000 %, PFD was *c.* 150 μmol m^{-2} s^{-1}. Both NP and R_D were determined with the same individual thallus on 2 successive days. A 5th degree polynomial regression was fitted to the NP data ($r^2 = 0.98$) and an exponential function to the R_D data ($R_D = 0.53$ e$^{0.117\,T}$; $r^2 = 0.98$). ······, zero gas exchange.

means ± SD, $n = 5$), whilst the values varied much more on a d. wt basis or an area basis (14·5 ± 4·6 nmol CO_2 g^{-1} d. wt s^{-1}, 1·9 ± 0·4 μmol CO_2 m^{-2} s^{-1}, means ± SD, $n = 5$). Dark respiration rates ranged from 5·6 to 8·8 nmol CO_2 (mg Chl)$^{-1}$ s^{-1}, corresponding to about a third of the maximum rate of net CO_2 uptake (NP$_{max}$) at 300 μmol m^{-2} s^{-1}. The light compensation point was 17–36 μmol m^{-2} s^{-1}. The mean apparent quantum yield for incident light was 0·021 ± 0·004 mol CO_2 mol^{-1} photons ($n = 5$).

The temperature response of the CO_2 exchange is shown in Figure 3. Net photosynthesis is clearly adapted to high temperatures, with an optimum at *c.* 22 °C. The upper temperature compensation point was reached at *c.* 40 °C. After a short exposure to 42 °C, the sample was allowed to recover at ambient temperatures (20–25 °C) for 1 h before NP was remeasured at 20 °C. No hysteresis was detectable

(data not shown). Dark respiration increased exponentially with temperature from 2·2 nmol CO_2 (mg Chl)$^{-1}$ s^{-1} at 10 °C to almost 24 nmol CO_2 (mg Chl)$^{-1}$ s^{-1} at 32 °C.

Diel courses of in situ *carbon dioxide exchange and water content*

Figure 4 shows the diel patterns of CO_2 exchange and water content for 9 d of continuous measurements, together with temperature and light records. Integrated C budgets and daily PFD are given in Table 1. The maximum rates of net CO_2 uptake reached or exceeded 30 nmol CO_2 (mg Chl)$^{-1}$ s^{-1} on all days; the absolute maximum observed during the measuring period was 48·8 nmol (mg Chl)$^{-1}$ s^{-1} (equalling 61·5 nmol CO_2 g^{-1} d. wt s^{-1} or 5·8 μmol m^{-2} s^{-1}).

On a typical day, there was some fog in the early morning, followed by a period of full sunlight (PFD: 1000–2000 μmol m^{-2} s^{-1}). The afternoon was characterized by much lower PFD, due to either increasing cloud cover or heavy rainstorms of varying duration. This pattern repeated itself on almost all days from 17–25 Sept. (Fig. 4), exceptions being 18 Sept. with nearly continuous drizzling and rain, and 21 and 22 Sept. with an additional short rain event in the morning. Despite the consistently high r.h. and the frequent and heavy rainstorms, there was a distinct period around noon when thalli dried out to near the moisture compensation point, on all days except 18 Sept. The highest C gains were registered on this and two other days with only very brief interruptions of photosynthetic activity (19 and 23 Sept., Table 1).

At night, thalli invariably were well hydrated with WC of 600–1100 % of d. wt (Fig. 4). Nocturnal temperatures were also uniform, decreasing from 20 °C at dusk to 16 or 17 °C at the end of the night. Consequently, night-time losses of CO_2 were high, but relatively constant (Table 1). On average, 56·4 ± 13·6 % (means ± SD, $n = 9$) of the diurnal C gain was lost during the night.

Although epiphytic lichens can grow on top of substrates such as branches or twigs and thus might be exposed horizontally similar to our initial set-up, others grow on the sides of branches or tree trunks. We studied the influence of different exposures on the diel patterns of CO_2 gas exchange with additional measurements (Fig. 5, Table 2). The samples used in the experiment were differently exposed at their natural growing site (compare 'Materials and Methods'), but this did not result in significant differences in their photosynthetic characteristics (Fig. 2).

On all 3 d, we observed very pronounced differences in incident radiation in spite of the tropical latitude, and a consistent pattern in the water relations and in the diurnal gas exchange. The east-
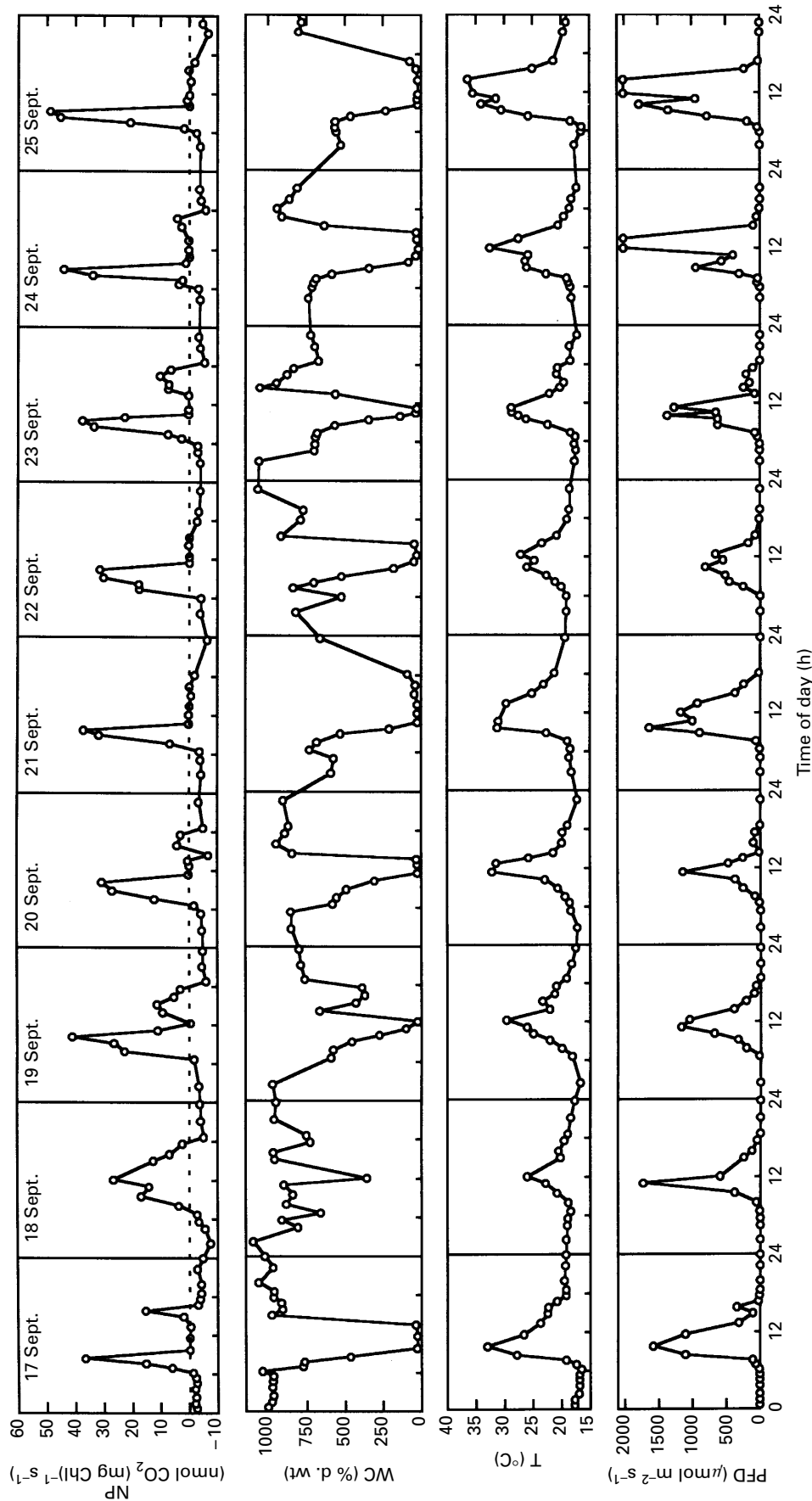
Figure 4. Diel courses of net photosynthesis (NP, nmol CO₂ (mg Chl)⁻¹ s⁻¹, upper panel), cuvette air-temperature (T, °C, third panel), and incident photon flux density (PFD, μmol m⁻² s⁻¹, bottom panel) for *Sticta tomentosa* from 17 Sept. to 25 Sept. 1993. Sudden increases of WC indicate rain events. 1 nmol CO₂ (mg Chl)⁻¹ s⁻¹) equals 1·26 nmol CO₂ g⁻¹ d. wt s⁻¹ or 0·12 μmol CO₂ m⁻² s⁻¹. Integrals of NP and PFD are given in Table 1.

Table 1. *Gas exchange balances of horizontally exposed thalli of* Sticta tomentosa *during the measurement period from 17 Sept. to 25 Sept., 1993.*

Date	NP_{day} (μmol CO_2 (mg Chl)$^{-1}$ 12 h^{-1})	R_D (μmol CO_2 (mg Chl)$^{-1}$ 12 h^{-1})	NP_{24h} (μmol CO_2 (mg Chl)$^{-1}$ d^{-1})	(mg C g C^{-1} d^{-1})	PFD_{24h} (mol m^{-2} d^{-1})
17 Sept.	243·7	−154·6	89·1	2·9	24·4
18 Sept.	482·3	−228·5	253·8	8·1	16·9
19 Sept.	515·5	−178·9	336·7	10·8	18·1
20 Sept.	334·2	−213·7	120·6	3·9	12·1
21 Sept.	258·3	−206·1	52·1	1·7	27·3
22 Sept.	366·6	−204·0	162·6	5·2	14·4
23 Sept.	401·7	−165·8	235·9	7·6	17·7
24 Sept.	296·4	−182·6	113·8	3·7	30·4
25 Sept.	365·1	−218·3	146·8	4·7	41·8

Shown are diurnal integrals of CO_2 uptake (NP_{day}), nocturnal CO_2 losses (R_d), and 24-h CO_2 and carbon budgets (NP_{24h}). The average 24-h carbon gain was 167·9 μmol CO_2 (mg Chl)$^{-1}$ d^{-1} or 5·4 mg C g$_C^{-1}$ d^{-1}, respectively. Also shown are the diel integrals of the photon flux densities (PFD_{24h}). Figures based on g d. wt or m² area can be obtained by multiplying the CO_2 budgets by 1·26 and 0·12, respectively.

exposed thallus was the first to receive direct sunlight in the early morning associated with high rates of net CO_2 uptake (Fig. 5), but also dried out first and thus showed the longest periods of desiccation. Overall, the west-exposed sample was photosynthetically active longer than any other, exceeding the east-exposed by *c*. 2 h d^{-1} (Table 2). The integrated diurnal CO_2 uptake (NP_{day}) of the west-exposed sample was on average *c*. 50 % higher than that of the east-exposed sample. The north-exposed and south-exposed thalli were intermediate in terms of periods of activity, but showed mostly lower NP_{day}. Diurnal C gain was positively correlated with duration of activity ($r^2 = 0·44$, $P < 0·01$), but not with the integrated PFD during that period (PFD_{act}, $r^2 = 0·02$, $P = 0·61$). The latter finding is not surprising since net CO_2 uptake saturates at rather low light intensities (Fig. 2). The two horizontal controls showed similar 24-h patterns in PFD, WC, and net CO_2 exchange as depicted in Figure 4 (data not shown). As summarized in Table 2, they received far more PFD than any thallus with vertical exposure, but were between extremes as far as periods of activity and diurnal C gain were concerned (Table 2).

Net carbon dioxide exchange after rehydration

Immediately after rewetting in the afternoon, we repeatedly observed a burst of CO_2 release, e.g. on 20 Sept., 1400 hours or on 22 Sept., 1430 hours (Fig. 5). Respiration was particularly high in the south-exposed sample on 20 Sept. This release of CO_2, which lasted for only *c*. 20 min, cannot be explained by low irradiation in the course of a rainstorm. Although PFD was indeed quite low, 20–60 μmol m^{-2} s^{-1} would still allow NP to be close to zero or even positive under steady state conditions (Figs 1, 2).

For a further analysis of the phenomenon known as 'resaturation respiration' (Smith & Molesworth, 1973) we studied the recovery of CO_2-exchange after experimental rehydration (Fig. 6). Approx. 3 min after rewetting (the earliest moment for measurement for technical reasons), R_D was up to four times higher than the steady-state value (Fig. 6, closed symbols). The six thalli showed much quantitative variation in their response, but the pattern of recovery was quite similar in the light and in the dark. After *c*. 15–20 min, both NP and R_D had reached steady-state values.

DISCUSSION

Sticta tomentosa has the potential for high photosynthetic C gain. Irrespective of whether chlorophyll content, d. wt, or thallus area were used as reference, the maximum rates of net CO_2 uptake observed in the field exceeded those of most other lichens (Green
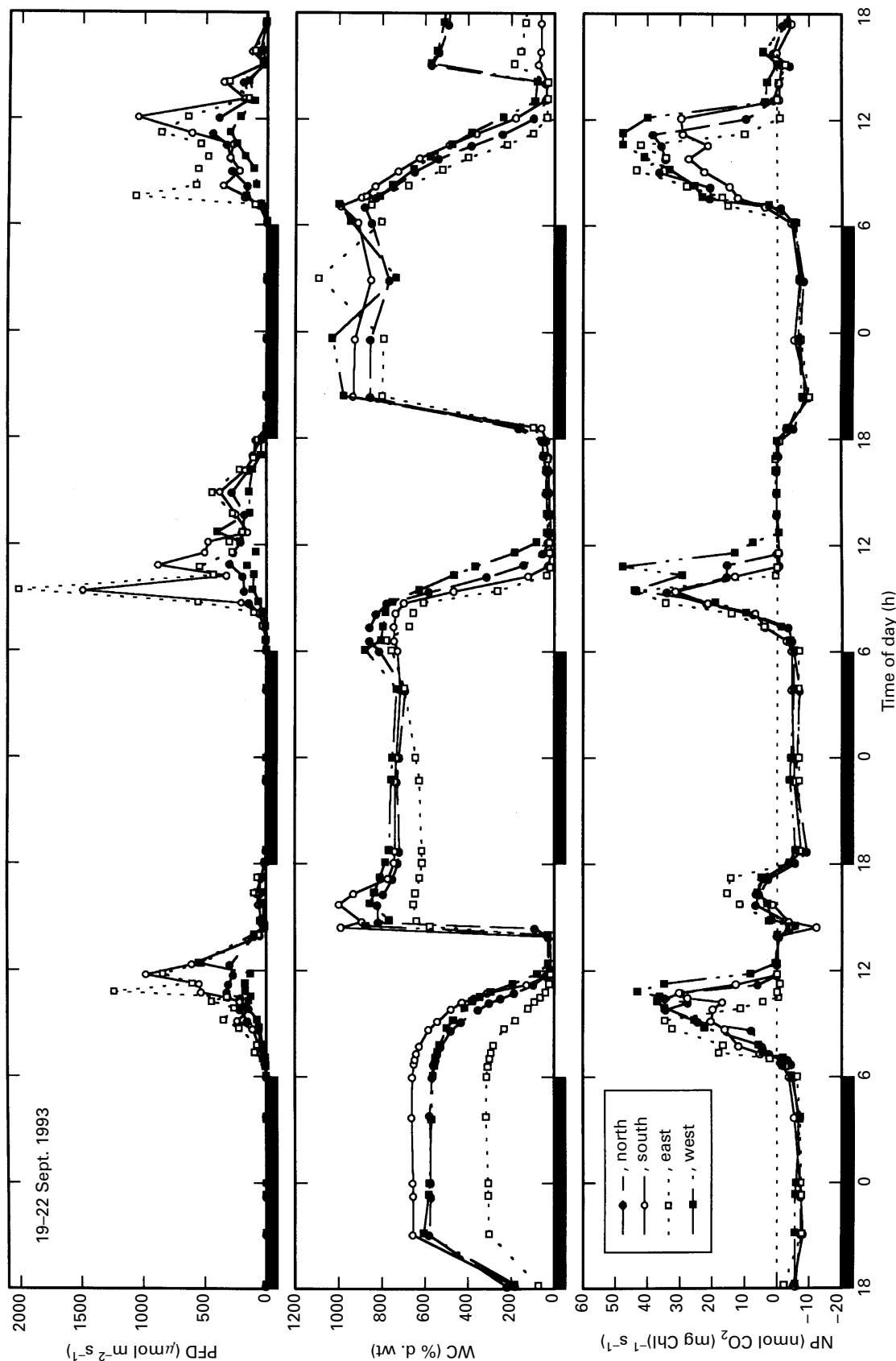
Figure 5. *In situ* gas exchange of differently exposed thalli of *Sticta tomentosa*. Shown are net photosynthesis (NP, nmol CO_2 (mg Chl)$^{-1}$ s^{-1}, upper panel), thallus water content (WC, % d. wt, centre panel), and incident photon flux density (PFD, μmol m^{-2} s^{-1}, bottom panel) from 19 Sept. (1800 hours) until 22 Sept. 1993 (1800 hours). Cuvette temperatures were similar to those shown in Figure 4. Integrals of NP and PFD are given in Table 2.

Table 2. *Important parameters of the* in situ CO_2 *exchange of differently exposed thalli.*

Date exposure	NP_{24h} (μmol (mg Chl)$^{-1}$ d^{-1})	R_D (μmol (mg Chl)$^{-1}$ 12 h^{-1})	NP_{day} (μmol (mg Chl)$^{-1}$ 12 h^{-1})	PFD_{24h} (mol m^{-2} d^{-1})	PFD_{act} (mol m^{-2} d^{-1})	T_{act} (h)
20 Sept.						
North	−17·6	−300·3	282·7 (49)	5·2 (41)	2·8	9·5 (106)
South	−8·7	−270·8	262·0 (39)	8·7 (69)	3·7	9·6 (107)
East	59·5	−295·0	354·4 (72)	10·6 (84)	3·5	8·5 (94)
West	179·2	−259·0	438·2 (84)	4·7 (37)	2·0	10 (111)
21 Sept.						
North	−81·1	−300·9	219·7 (58)	6·8 (27)	2·8	5·5 (122)
South	−52·6	−230·6	178·0 (40)	14·0 (55)	5·6	5 (111)
East	−63·3	−301·7	238·4 (74)	15·6 (62)	7·8	4 (89)
West	192·3	−203·9	396·2 (115)	4·8 (19)	1·8	6·7 (149)
22 Sept.						
North	171·7	−314·7	486·4 (85)	7·6 (50)	7·0	10·5 (105)
South	130·0	−275·1	405·1 (61)	11·7 (77)	10·1	10·5 (105)
East	159·1	−308·6	467·7 (96)	15·1 (99)	12·8	9·5 (95)
West	427·6	−280·5	708·0 (136)	4·9 (32)	4·9	12 (120)

All gas exchange rates are expressed on the basis of the chlorophyll content. Shown are the 24-h CO_2 budgets (NP_{24h}), nocturnal respiration (R_d), the diurnal integrals of CO_2 uptake (NP_{day}) and as a percentage of the two horizontal controls (in parentheses). Also given are the diel integrals of the photon flux densities (PFD_{24h}, mol m^{-2} d^{-1} and in % of the two controls), and the duration (T_{act} in h and in % of the two controls) and integrated PFD (PFD_{act}) of the physiologically active period during daytime (thallus WC > 30%).
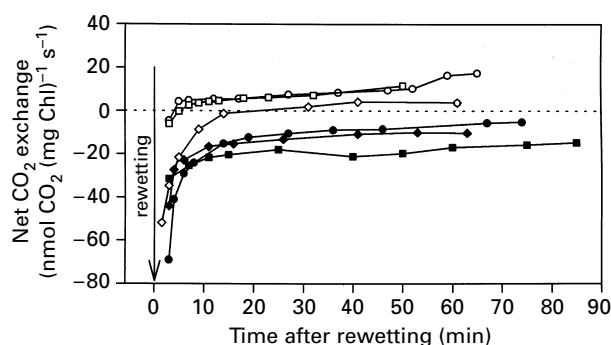
Figure 6. Recovery of metabolic activity of *Sticta tomentosa* after desiccation. CO_2-gas exchange was measured in the light (PFD = 100 μmol m^{-2} s^{-1}, open symbols) or in the dark (closed symbols), respectively. Cuvette temperature was 20 °C. Data collection began immediately after rehydration of the thalli, which had been naturally desiccated for 60–120 min. Thallus WC at the end of the experiment was *c*. 700–900 % d. wt. Each symbol stands for a different sample; ······, zero gas exchange.

& Lange, 1994, but see: Lange *et al.*, 1994*a*, *b*). The absolute maximum of 5·8 μmol m^{-2} s^{-1} (Fig. 4) might even rival light-saturated rates of net photosynthesis of some rain forest trees (Zotz & Winter, 1996). As a major difference to these plants, however, lichens are poikilohydric and can therefore maintain such high rates only for brief periods, when an optimal combination of PFD (Fig. 2), thallus temperature (Fig. 3), and hydration (Fig. 1) is given. The last parameter, in particular, is of principal importance. In water-saturated lichens, NP was depressed by > 50 % (Fig. 1), whilst *S. tomentosa* was inactive due to low WC on an almost daily basis (Figs 4, 5). Rewetting in the early afternoon led again to high thallus WC. Since this period was associated with much lower PFD, the patterns of activity in the light can basically be described by one single, steep peak of net CO_2 uptake in the hours between dawn and noon. Even when a second peak occurred in the afternoon, it was always considerably lower.

In addition, desiccation did not only limit C gain by cessation of CO_2 uptake, but the rewetting of the thalli was associated with additional losses of CO_2. This resaturation respiration (Smith & Molesworth, 1973) could be observed on several occasions *in situ* (Figs 4, 5) and was also consistently found under controlled conditions (Fig. 6). We suppose, that it actually occurred during all rehydration events in the 9 d, but simply was not captured, because our measurement intervals were mostly longer than the short duration of these resaturation bursts. The importance of the resaturation respiration under natural conditions is under debate. For example, Lechowicz (1981) studied the post-desiccation recovery of the CO_2 gas exchange of the arctic lichen, *Cetraria cucullata*, in the laboratory. His predictions on the *in situ* gas exchange, however, could not be verified by observations in the field (Hahn *et al.*,

1993). Our results show that the resaturation respiration does occur under natural tropical conditions. Although the limited data base does not allow a statistical treatment of the impact of the resaturation respiration on the integrated C gain, we can provide a rough estimate based on the data from Figure 6: the additional losses due to resaturation respiration equal an integrated R_D of a duration of 0·25–1 h under steady-state conditions. Thus, we conclude that the resaturation respiration in *S. tomentosa* is not important ecologically.

Overall, an average 24-h net C gain for a horizontally exposed thallus of 5·4 mg C (g C)$^{-1}$ d^{-1} (= 0·54 % d^{-1}, Table 1) is considerably higher than most known estimates for other lichens (e.g. desert lichens, *Ramalina maciformis*: 0·01–0·04 % d^{-1}, Kappen *et al.* (1980); Antarctic lichens: 0·01 % d^{-1}, Kappen (1985); temperate coastal lichens: 0·22 % d^{-1}, Bruns-Strenge & Lange (1992)). Interestingly, even higher estimates, i.e. 0·62 % d^{-1}, were reported for another tropical lichen, *Dictyonema glabratum*, growing in the same premontane area, by Lange *et al.* (1994*a*).

The results of our experiment with differently exposed thalli (Fig. 5, Table 2) can be discussed in both ecological and methodological terms. Carbon gain is a function of many parameters, among them incident radiation and hydration (Green & Lange, 1994). Increased PFD might allow higher rates of net CO_2 uptake, but at the same time increase evaporative water loss and, consequently, decrease the period of metabolic activity. Since net photosynthesis in *S. tomentosa* is light-saturated at rather low PFD (Fig. 2), incident radiation above *c*. 200 μmol m^{-2} s^{-1} will only yield marginal increases in C gain, whilst considerably accelerating desiccation. It is therefore not surprising that the highest values of NP_{day} were observed in the sample with westerly exposure. This sample received only moderate rates of PFD (averaging 60, 75 and 120 μmol m^{-2} s^{-1} during its active periods on 20–22 September, Table 2), but was active for much more time than any other thallus (Table 2). The predominant importance of the period of metabolic activity for photosynthetic productivity rather than incident light has also been stressed by Kappen and co-authors in a study with the desert lichen *Ramalina maciformis* (Kappen *et al.*, 1975, 1980). Both the amount of dew and the duration of dew imbibition varied strongly with exposure. A detailed analysis of the diurnal patterns of net CO_2 exchange of north-exposed and east-exposed thalli yielded results similar to ours: lower rates of NP for longer periods in north-exposed samples resulted in daily integrals *c*. 25 % higher than those of the eastern exposure, with higher rates of NP for short periods. These differences in physiological activity could then be correlated with the conspicuous differences in lichen abundance on the different slopes of desert

mesas (Kappen *et al.*, 1980). It is interesting to speculate that exposure might be similarly important in humid tropical environments, in particular in lowland forests, where climatic conditions are generally not very conducive to growth of lichens and mosses (Sipman, 1989; Frahm, 1990). Slight differences in diurnal C gain might determine whether thalli grow and survive, or die, in these marginal habitats.

Furthermore, our results also have methodological implications. In field studies on lichen photosynthesis, samples are frequently exposed horizontally (Lange *et al.*, 1990; Hahn *et al.*, 1993; Lange *et al.*, 1994*a*; Green *et al.*, 1995), which allows easy comparison of the *in situ* gas exchange of a number of co-occurring species. Clearly, the photosynthetic performance varies with exposure, but our results show that C budgets and periods of activity of horizontally exposed thalli are well in the range of vertically exposed specimens, in spite of the much higher irradiation (Table 2). Moreover, important observations, such as the almost daily desiccation around noon, can be made independent of exposure (Figs 4, 5).

In conclusion, our study shows that *Sticta tomentosa* has the potential for very high carbon gain. Under natural tropical conditions, this potential is limited by a number of factors, but most surprisingly, and consistent with the results of earlier studies with tropical rain forest lichens, by frequent desiccation.

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