Growth and Vitality of Epiphytic Lichens. II. Modelling of Carbon Gain Using Field and Laboratory Data

Author(s): Bodil Sundberg, Kristin Palmqvist, Per-Anders Esseen and Karl-Erik Renhorn

Source: *Oecologia*, Vol. 109, No. 1 (1997), pp. 10-18
Published by: Springer in cooperation with International Association for Ecology
Stable URL: http://www.jstor.org/stable/4221486
Accessed: 17-07-2016 18:44 UTC

Oecologia (1997) 109:10–18

Bodil Sundberg · Kristin Palmqvist
Per-Anders Esseen · Karl-Erik Renhorn

Growth and vitality of epiphytic lichens

II. Modelling of carbon gain using field and laboratory data

Received: 15 April 1996 / Accepted: 20 June 1996

Abstract Photosynthetic and respiratory CO_2 gas exchange was measured under controlled climate conditions in the laboratory in two epiphytic lichens, *Lobaria pulmonaria* and *Platismatia glauca*, with the aim of modelling their net productivity using field microclimate data. For both, the thallus water content (WC) and the light intensity had the greatest impact on photosynthesis. *L. pulmonaria* had optimum net photosynthesis (NP) at WCs between 75–175% of the thallus dry weight (DW), while *P. glauca* required a WC of c. 85% for maximal NP without depression at higher WCs. Both species reached light compensation of NP at 5–10 μmol photons m^{-2} s^{-1} and were saturated at 100–150 μmol photons m^{-2} s^{-1}. Respiratory CO_2 loss corresponded to 35–40% of gross photosynthesis at 85–100% WC and 15° C, in both species. Growth of the two species were followed in transplanted thalli during a 16-month period at two contrasting sites, a forest edge adjacent to a 15 year old clear-cut and within the interior of a mature *Picea abies* forest. At these sites, the microclimate parameters; light, temperature, relative humidity (RH) and thallus WC were also monitored. Judged from the microclimate data, the lichens were active for 13–19% of the time with thallus WC monitoring, where >60% of the active time occurred in darkness. When photosynthetically active, the edge transplants received a 2–3 times higher light dose and were active for a longer accumulated time compared to the interior transplants. The field microclimate data in conjunction with the laboratory data predicted a 4 times higher DW yield of the edge transplants compared to the interior transplants. However, the DW yield of *L. pulmonaria* was overestimated at the edge and underestimated for *P. glauca* in the interior by our model. Possible reasons for these discrepancies and the validity of using laboratory data and microclimate monitoring to predict growth rates of lichens under varying field conditions are discussed.

Key words CO_2 gain · Lichen growth · Microclimate · Photosynthesis · Respiration

B. Sundberg · K. Palmqvist (✉)
Department of Plant Physiology, Umeå University,
S-901 87 Umeå, Sweden
fax: +46 90 166676; e-mail: Kristin.Palmqvist@plantphys.umu.se

P.-A. Esseen · K.-E. Renhorn
Department of Ecological Botany, Umeå University,
S-901 87 Umeå, Sweden

Introduction

Lichens, which are symbiotic associations between a green algal or cyanobacterial autotrophic host (photobiont) and a heterotrophic fungus, are generally regarded as slow-growing organisms. This feature can be attributed to at least three major characteristics of these organisms. First, lichens are poikilohydric and are only active when the water content in their immediate environment is high enough to restore and maintain their metabolism (e.g. Lange et al. 1986; Green and Lange 1995). Subsequently, as lichens are often found in rather dry habitats such as deserts, arctic tundras, heaths and tree canopies, they remain metabolically inactive most of the time, which in itself predicts a slow growth. Second, the fungal hyphae constitute up to 90% of the lichen biomass (Ahmadjian 1993) and respiratory CO_2 losses associated with growth and maintenance respiration of the fungal partner is therefore relatively larger than in higher plants when compared on a dry weight (DW) or thallus (leaf) area basis (Green and Lange 1995). Third, maximum net photosynthetic rates (NP) in lichens are lower than in other terrestrial plants due to their relatively low amount of photosynthetic cells, both per unit DW and per unit area, compared to the amount of mesophyll cells in leaves of higher plants. However, the photosynthetic capacity *per se* is not lower in lichens as their NP_{max} is more similar to that of higher plant leaves when related to the chlorophyll (Chl) content (see Green and Lange 1995 for a more detailed discussion).

Numerous field studies have documented photosynthetic and respiratory patterns of lichens in their natural

environment (e.g. Schulze and Lange 1968; Moser and Nash 1978; Moser et al. 1983; Lange et al. 1993; Hovenden et al. 1994). Such data have also been used in conjunction with microclimate data to estimate annual CO_2 budgets (Kappen et al. 1979; Nash et al. 1982; Paterson et al. 1983; Matthes-Sears and Nash 1985; Bruns-Strenge and Lange 1991; Lange and Bruns-Strenge 1991; Kappen et al. 1995). However, even though there are some reports on annual DW yields of lichens (e.g. Denison 1988; Boucher and Nash 1990; Silett 1994; Renhorn and Esseen 1995) only one of these compared actual growth rates with rates predicted from physiological and meteorological measurements (Boucher and Nash 1990).

This study tests the validity of using laboratory data of CO_2 exchange in conjunction with field data on microclimate and thallus water contents to predict net CO_2 gain in two epiphytic lichens. The lichens, *Lobaria pulmonaria* and *Platismatia glauca*, were transplanted to two contrasting sites, a forest edge adjacent to a 15 year old clear-cut and the interior of a mature *Picea abies* forest. The transplants were harvested and weighed after 16 months with the aim of comparing predicted with actual growth. The two lichens have different green algal hosts which differ in their modes of acquiring CO_2 for photosynthesis (Palmqvist et al. 1994). It was thus of interest to see whether this difference in photosynthetic strategy in the photobiont has any impact on growth under natural conditions.

Materials and methods

Lichen material

Lobaria pulmonaria (L.) Hoffm. is a tripartite lichen with two photobionts, the green alga *Dictyochloropsis reticulata*, which constitutes its primary photobiont and the nitrogen-fixing cyanobacterium, *Nostoc* sp. *Platismatia glauca* (L.) W. Culb. & C. Culb. is a bipartite lichen with green algal *Trebouxia* sp. photobionts. Both species have foliose thalli not, *L. pulmonaria* grows mainly on trunks of deciduous trees in sheltered woods while *P. glauca* is found on slightly acid bark, decaying wood and shaded cliffs (Moberg and Holmåsen 1987). Both species were collected from two Norway spruce (*Picea abies*) forests in Northern Sweden in April and September 1993, as specified in Renhorn et al. (1996). Thalli used for laboratory measurements were air dried at 10° C and stored dark at 4° C for up to 2 months. Prior to experimental use the thalli were sprayed with water and allowed to reactivate for at least 3 days at 15° C, 90–95% relative humidity (RH) and a light intensity of 30–35 µmol photons m^{-2} s^{-1} (14 h photoperiod) provided by a bank of fluorescent tubes (Luxline-ES; Sylvania, Danvers, Mass., USA; cool-white F36 W/184).

Gas exchange measurements

CO_2 gas exchange was measured on full-sized and intact lichen thalli with a flow-through gas-exchange system (Compact Minicuvette System 400, gas mixing unit GMA1 and cuvette GK-022; H. Walz, Effeltrich, Germany). The CO_2 concentration in the cuvette was kept at ≈35 Pa throughout, measured by an absolute CO_2 analyser (LCA-2; ADC Hoddesdon, Herts., UK). Light was provided by a slide projector (250 W, 24 V) and reflected by a mirror mounted so that the whole upper surface of the lichen was exposed to a uniform light. Different light intensities were obtained with neutral density filters. The light intensity was measured at the surface of the thallus with the in-built cuvette light sensor, which had been calibrated against a quantum sensor (Li-189; Li-Cor Inc., Lincoln, Neb., USA). The lichen thalli were soaked in water for 10–15 min prior to measurements and thereafter mounted on wire trays. Excess water was removed by gentle blotting with tissue paper before placing the tray in the cuvette. The water content (WC) of the thalli was determined gravimetrically outside of the cuvette when steady-state rates of photosynthesis and/or respiration had been reached for a specific combination of microclimate conditions. Steady-state rates were usually reached within 10–20 min. Light response curves were obtained by exposing the thalli to consecutive increases in light intensity (0–500 µmol photons m^{-2} s^{-1}) at different temperatures and at optimal WC. To maintain an optimal WC the samples were occasionally re-wetted by spraying with water. A low rate of desiccation of samples was also achieved by keeping the dew-point temperature (T_{DP}) of the incoming air at 0.5° C below the cuvette temperature. Measurements of WC response curves started with fully hydrated lichen thalli and proceeded until CO_2 uptake ceased due to water deficit. WC response curves were made at different temperatures and the WC of the samples was determined every 15–20 min as specified above. Temperature response curves were made at optimal WC, obtained as specified above, at saturating light or in darkness and by increasing the temperature stepwise. After all measurements the thalli were dried over night in a calcium chloride desiccator to determine the dry weight (DW). The chlorophyll content was determined by dissolving 4–5 randomly punched 0.87-cm^2 discs of each thallus in $MgCO_3$ saturated dimethyl sulphoxide at 60° C for 40 min according to the procedure of Ronen and Galun (1984).

Modelling of field and gas exchange data

Lichen thalli of the same origin as the samples characterised in the laboratory were used in a parallel field study where growth of transplanted samples of the two lichens was followed over 16 months (8 July 1993 to 27 October 1994), detailed in Renhorn et al. (1996). Two climate stations, one situated at a forest edge and one in a forest interior, were mounted on 16 August 1993 where the microclimate in terms of light, relative humidity and temperature was monitored continuously until harvest in 27 October 1994: Thallus WCs were measured according to the impedance method (Coxson 1991), detailed in Renhorn et al. (1996), on four separate thalli of each species at each climate station during the periods when the temperatures generally exceeded 0° C, i.e. from 16 August 1993 to 29 October 1993 and from 9 May 1994 to 27 October 1994. The empirical growth model presented here was tested against the actual DW yield of the 16 thalli of each species that were mounted adjacent to each climate station (see Renhorn et al. 1996).

The microclimate data were used to characterise the environmental conditions that occurred during the transplant period. A total of 72 microclimate and thallus WC combinations were used consisting of six light intervals (0–5; 5–10; 10–25; 25–50; 50–100; >100 µmol photons m^{-2} s^{-1}), four WC intervals (0–40; 40–85; 85–175; >175%) and three temperature intervals (0–5; 5–15; >15° C). Expected CO_2 exchange rates for each environmental combination was then extrapolated from the gas exchange curves where the WC and the incident light were used as major determinants of metabolic activity. The lichens were assumed to be metabolically inactive when the WC was below 40% of the DW rather than below 25% as indicated by the response curves shown in Results. This assumption was in part due to the impedance-WC regression equations where a few thalli obtained an equation yielding 40% WC even though the impedance value indicated a dry thallus. This assumption was also related to the difficulties in distinguishing whether a WC record between 25–85% was obtained before or after the thallus had been fully hydrated. Such low WCs before full hydration result in no, or very low, metabolic activity of these lichens. The assumption of no activity for all records below 40% WC may thus be regarded as a good compromise. The accumulated time of each of the 54 environmental combinations

resulting in potential metabolic activity was multiplied by the extrapolated CO_2 exchange rates and finally totalled to predict the net CO_2 gain of the transplanted lichens. In this estimation, it was assumed that the majority of the DW was made up of sugar equivalents and that 6 mole assimilated CO_2 was required for each 1 mole of reduced sugar. There were two major sources of error in the model. The first was caused by variation in the thallus WC content of the four thalli used for these measurements. This variation corresponded to 13% at the edge and 8% in the forest interior, based on calculations of standard deviation. The other major source of variation was related to the variation in photosynthetic capacity between individual samples, discussed and presented in the results part. This variation, based on standard error was less than 5%.

The accumulated incident light dose received by the transplants was summed for the active periods and an apparent energy conversion efficiency of the actual growth of the transplants was calculated assuming that the energy content of dry lichen thalli is equal to the energy content of sugar, i.e. 2.66 kJ g^{-1}. It was also assumed that the light absorbed per unit area of the transplants was equal to the light received by the light sensors (cf. Renhorn et al. 1996) during the periods with potential metabolic activity. The energy content of this light was set equal to the energy content of a green photon (550 nm), i.e. 216.8 kJ mol^{-1}, representing the average energy content of all photons recorded by the sensors.

Fluorescence measurements

After harvest, the photosynthetic activity of the transplanted thalli were analysed from measurements of modulated chlorophyll *a* fluorescence at different irradiances. Prior to this analysis the transplants were dried, stored and reactivated as specified above. All experiments were carried out within 2 weeks after harvest. A 1.14-cm^2 sample was punched from each thallus and placed on top of moist foam and a grid in a thermostated (10° C) cuvette housing (LD2, Hansatech Ltd., King's Lynn, UK). Light to and from the cuvette was guided through a fluorescence fibre fitted to the cuvette house lid. Humid air (100% RH, 10° C, 35–40 Pa CO_2) was circulated through the cuvette during the 50–60 min measuring period. Pulse-amplitude modulated fluorescence was measured with a PAM 100 (H. Walz, Effeltrich, Germany) and calculated as in Genty et al. (1989). Each measurement was started by a 5-min dark period whereafter the sample was exposed to the weak measuring beam (0.05 and 0.08 µmol photons m^{-2} s^{-1}, modulated at 1.6 kHz, for *L. pulmonaria* and *P. glauca* respectively) and the F_0 (base fluorescence yield) was taken as the average of this signal during the first 5 s. A saturation pulse of high-intensity white light (1300 µmol photons m^{-2} s^{-1}; PAM flash light source FL 103) was then applied to produce full closure of photosystem II (PSII) reaction centres, i.e. the F_M level. Each sample was then exposed to five consecutive and increasing actinic light intensities, ranging from 10 to 390 µmol photons m^{-2} s^{-1} to obtain the steady-state fluorescence yield (F_S). The actinic light was regulated by the light source settings (PAM, FL 101) and by different combinations of Schott neutral density filters (Schott AG, Mainz, Germany). Saturating flashes of white light (1300 µmol photons m^{-2} s^{-1}) were given at regular time intervals (every 90 s) to produce full closure of PSII reaction centres ($=F_M'$). Far-red light (10 W m^{-2}), provided by a fibre branch connected to the actinic light source (85 µmol photons m^{-2} s^{-1}) and a cut-off filter (Schott, RG 715) was used to produce maximal oxidation of PSII electron acceptors ($=F_0'$). All parameters were determined when steady-state photosynthesis had been reached, generally within 15–20 min. The apparent quantum yield of PSII electron transport (ϕ_{PSII}) was determined during steady-state photosynthesis from the following relation; $\phi_{PSII}=[(F_M'-F_S)/F_M']$ (Genty et al. 1989).

Results

Laboratory measurements

Both species showed a similar response to light with light compensation of net CO_2 assimilation at 5–10 µmol photons m^{-2} s^{-1} and light saturation at 100–150 µmol photons m^{-2} s^{-1} (Fig. 1). For both species, the photosynthetic light response curve was also characterised by a rather high convexity (rate of bending) as the transition from light limited to light saturated rates occurred within a rather narrow light interval. However, two of the eight *L. pulmonaria* thalli differed in this respect as photosynthesis continued to increase even when the light exceeded 200 µmol m^{-2} s^{-1} (Fig. 1A). Maximum rates of net CO_2 assimilation (NP_{max}) varied considerably between individual samples and particularly so in *L. pulmonaria*. Some of this variation may be coupled to the assay temperature. However, it cannot solely be attributed to this parameter as e.g. two *L. pulmonaria* thalli assayed at 15° C displayed the largest difference in NP_{max} (Fig. 1A). Differences in the rates of fungal respiration between

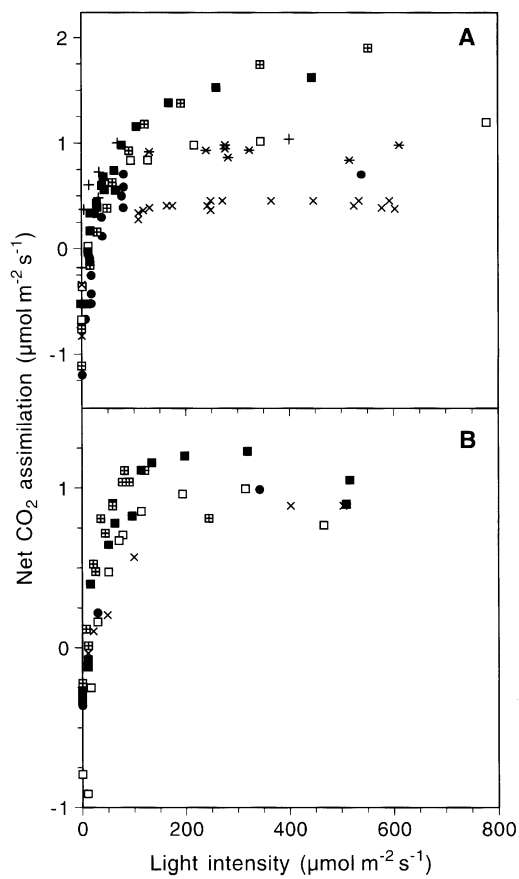

Fig. 1 Net rate of CO_2 assimilation as a function of incident light (PPFD) measured at thallus water contents (WC) of 85–175% and above 85% of the dry weight (DW) for **A** *Lobaria pulmonaria* and **B** *Platismatia glauca*, respectively. *Symbols* represent individual thalli measured at 5° C (+), 8° C (×, ⁎), 15° C (□, ■, ⊞) and 20° C (●)

Table 1 Some physiological characteristics of *Lobaria pulmonaria* (n=18) and *Platismatia glauca* (n=15). The data (mean±SE) is based on the samples that were used for the response curve measurements presented in Figs. 1–3. All rates reflect maximal activity of each full-sized and intact lichen thallus under optimal light, water and temperature conditions and in ambient air (35 Pa CO_2) (*DW* dry weight, *Chl* chlorophyll)

	L. pulmonaria	*P. glauca*
DW per unit area		
g m^{-2}	132±8	94.7±3.6
Chl per unit area		
mg Chl m^{-2}	224±9	47.6±4.3
Chl per unit DW		
mg Chl (g DW)$^{-1}$	1.74±0.10	0.48±0.06
Gross CO_2 uptake		
μmol CO_2 m^{-2} s^{-1}	2.18±0.05	1.21±0.05
μmol CO_2 (mg Chl)$^{-1}$ h^{-1}	35±8	87±17
mg CO_2 (g DW)$^{-1}$ h^{-1}	2.74±0.05	1.83±0.08
Net CO_2 uptake		
μmol CO_2 m^{-2} s^{-1}	1.30±0.03	0.81±0.03
μmol CO_2 (mg Chl)$^{-1}$ h^{-1}	21±4	58±9
mg CO_2 (g DW)$^{-1}$ h^{-1}	1.62±0.03	1.21±0.04

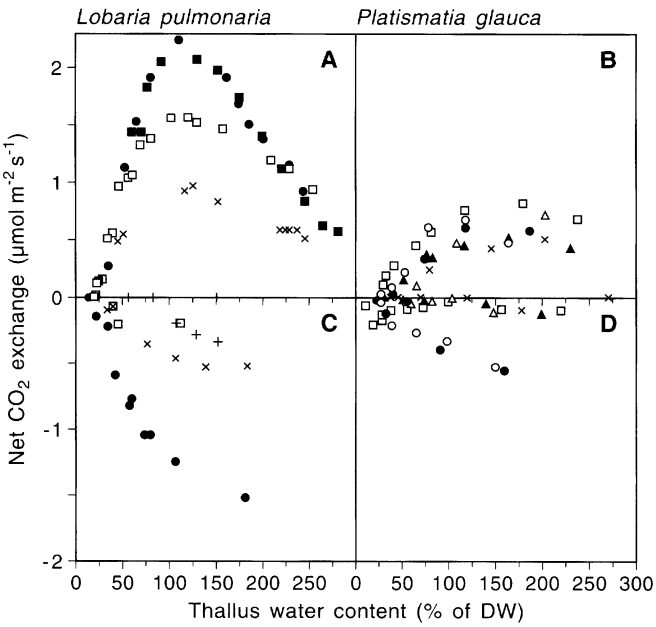

Fig. 2 Net rate of **A**, **B** CO_2 assimilation and **C**, **D** respiratory CO_2 release as a function of thallus WC for *L. pulmonaria* and *P. glauca*. Measurements started with fully hydrated thalli, proceeded until CO_2 uptake or release ceased due to water deficit and were made either at light saturation (photosynthetic photon flux density, PPFD=300 μmol photons m^{-2} s^{-1}) or in darkness. *Symbols* represent individual thalli measured at 5° C (+), 8° C (×), 10° C (△), 12° C (▲), 15° C (□, ■), 17° C (○) and 20° C (●)

thalli can neither explain the variation in net photosynthesis between samples, as gross photosynthesis also varied to the same extent (Table 1). The variation in maximum photosynthetic capacity between individual thalli is therefore most probably related to varying amounts of photobiont cells and hence photosynthetic units as reflected by a similar variation in Chl both per unit DW and area (Table 1). When the average rates of net and gross photosynthesis at light saturation and optimal WC were calculated for the two species, *L. pulmonaria* had the highest capacity both per unit area and weight (Table 1). Interestingly though, when photosynthesis was expressed per unit Chl, *P. glauca* was the most efficient. Moreover, even though *P. glauca* had almost a five times lower Chl content per unit area this species had only a 40% lower rate of net photosynthesis per unit area (0.81±0.03 μmol CO_2 m^{-2} s^{-1}) compared to *L. pulmonaria* (1.30±0.03 μmol CO_2 m^{-2} s^{-1}; Table 1).

The two lichens differed significantly in their responses to varying water contents. In *L. pulmonaria* there was a clear optimum in NP at WCs between 85 to 175% of the DW followed by a significant depression at higher WCs (Fig. 2A). This was in clear contrast to *P. glauca* which reached maximum rates of NP when the WC had exceeded 85% without any depression with further increases (Fig. 2B). Similar to the light response, the WC response of NP appeared to be relatively temperature independent (Figs. 2A–B) with a larger variation in NP_{max} between individual thalli than between different assay temperatures. CO_2 release in darkness, which may mainly be attributed to fungal respiration, was also sensitive to changes in the WC with an increasing rate of CO_2 loss with increasing WC in both species. However, in contrast to the WC response of NP, the increase in respiration with increasing WC was enhanced by temperatures above 15° C (Figs. 2C–D).

Although there appeared to be larger variations in photosynthetic capacity between individual thalli than between different assay temperatures, both species displayed a clear temperature dependence when the same thallus was exposed to different temperatures. Both species showed at least a two-fold increase in NP when the temperature was increased from 5 to 15° C (Fig. 3), with an optimum in *L. pulmonaria* between 15–25° C (Fig. 3). Unfortunately, however, no reliable data could be obtained for *P. glauca* at temperatures exceeding 20° C as thalli of this species dried out within a few minutes at these temperatures. Respiratory CO_2 loss also increased significantly with increasing temperature (Fig. 3) with a Q_{10} of about 2 for both species. However, the overall lower absolute rate of respiration in *P. glauca*, as already indicated in the WC response curves (Figs. 2C–D), was evident also in these measurements.

Fluorescence yield of transplants after harvest

The photosynthetic activity of the transplants positioned adjacent to the two climate sections (cf. Renhorn et al. 1996) was analysed immediately after harvest in October 1994 by means of a fluorescence quenching analysis and calculations of the fluorescence yield parameter ϕ_{PSII}. This analysis would show if the light response characteristics of the lichens had been changed during the transplant period (cf. Genty et al. 1989). However, the fluo-

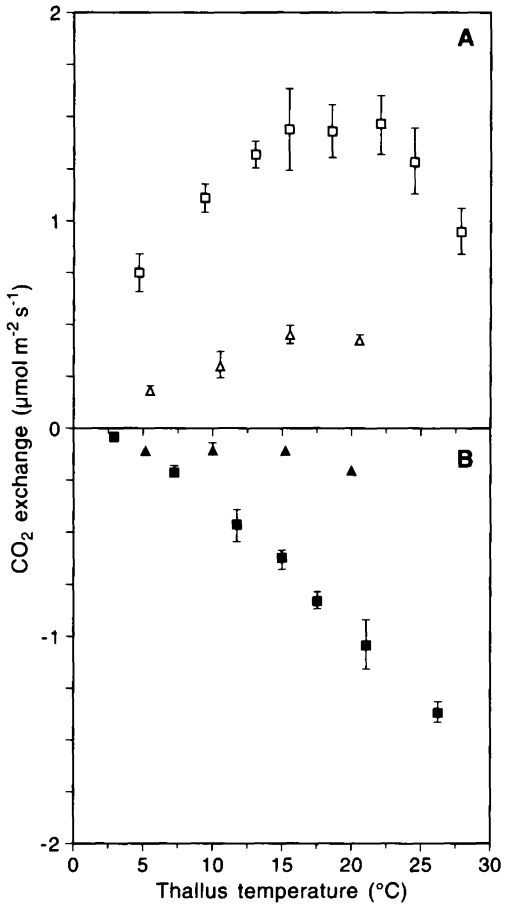

Fig. 3 Net rate of **A** CO_2 assimilation (□, △), and **B** respiratory CO_2 release (■, ▲) as a function of thallus temperature. Measurements were made either at light saturation (PPFD=300 μmol photons m^{-2} s^{-2}) or in complete darkness at WCs of 85–175% for *L. pulmonaria* (□, ■) and above 85% for *P. glauca* (△, ▲). *Error bars* (±SE) are indicated when they exceed the symbol size; $n \geq 4$ for each combination

rescence yield (ϕ_{PSII}) value approached its minimum at around 150 μmol photons m^{-2} s^{-1} in all four sets of transplants (data not shown), indicating light saturation of photosynthesis at about the same light intensity as before transplantation (Fig. 1). Also, there were no clear differences in ϕ_{PSII} between edge and interior transplants in neither of the species, even though *L. pulmonaria* at the edge showed a somewhat higher yield in the intermediate light range (data not shown). It may hence be concluded that the lichens had apparently not acclimated to the higher light environment at the forest edge (see below and Renhorn et al. 1996), which would have shown up as a higher light saturation value also of ϕ_{PSII}.

Modelling of field and laboratory data

The data obtained from the field was used to calculate the number of hours each of the 72 different environmental combinations occurred for the four sets of transplants during the whole transplant period. However, the impedance method that was used to measure the WC of the thalli is only applicable when the thallus temperature exceeds 0° C (Coxson 1991) and the carbon gain model thus had to be based on the 5164 h with valid WC measurements at the forest edge and the 5097 h of valid measurements in the forest interior. As shown in Table 2, the lichens remained metabolically inactive during most of this time (>80% of the time), irrespective of species and transplant site. The edge transplants were, however, active for a longer accumulated time compared to the interior transplants with the former sets of transplants being active for about 17–19% of the period while the interior transplants were active for 14–16% of the time. At least half of the active time occurred when the light intensity was below light compensation of NP, i.e. at light intensities below 5 μmol photons m^{-2} s^{-1}. The potentially deleterious effects that this may have had on the carbon budget of the lichens, due to respiratory CO_2 losses, was though in part compensated by the lower temperatures during periods of metabolic activity in the dark (Fig. 4).

Table 2 Total time with potential metabolic activity of the transplants during periods with microclimate and thallus water content (WC) monitoring. The lichens were assumed to be active at all WCs exceeding 40% of the DW. Positive net photosynthesis (NP) was assumed at light intensities above 5 μmol photons m^{-2} s^{-1}. Values represent mean±SD of the thalli used for the WC measurements. Values in brackets reflect percent of total monitored time, corresponding to 5164 h at the edge and 5097 h in the interior forest. The incident light dose is the mean light received by two light sensors mounted at each climate station (cf. Renhorn et al. 1996) summed for all periods with WCs above 40%

Species	Active in darkness hours (%)	Active in light hours (%)	Incident light dose mol·m^{-2}
L. pulmonaria			
Edge	542±269 (10%)	370±187 (7%)	77.5
Interior	534±185 (10%)	298±126 (6%)	32.1
P. glauca			
Edge	601±234 (12%)	385±201 (7%)	72.2
Interior	447±198 (9%)	234±103 (5%)	25.2

Although the total accumulated time of metabolic activity was rather similar in the two species transplanted at the same site (Table 2), the WC differed between them. *L. pulmonaria* spent a proportionally longer period with WCs above 175% of the DW, while *P. glauca* spent a longer period with WCs between 40–85% (Fig. 4). The edge transplants of *P. glauca* moreover spent a markedly longer period in an active state at air temperatures above 15° C compared to the other three sets of transplants (Fig. 4). The light intensity was consistently higher at the edge than in the forest interior (Renhorn et al. 1996) and thus, the edge transplants received a 2–3 times higher accumulated light dose during their metabolically active periods compared to the interior transplants (Table 2). Moreover, the interior transplants seldom experienced light intensities above 50 μmol photons m^{-2} s^{-1} (Fig. 4), an intensity well below the light required to saturate photosynthesis in both species (Fig. 1).

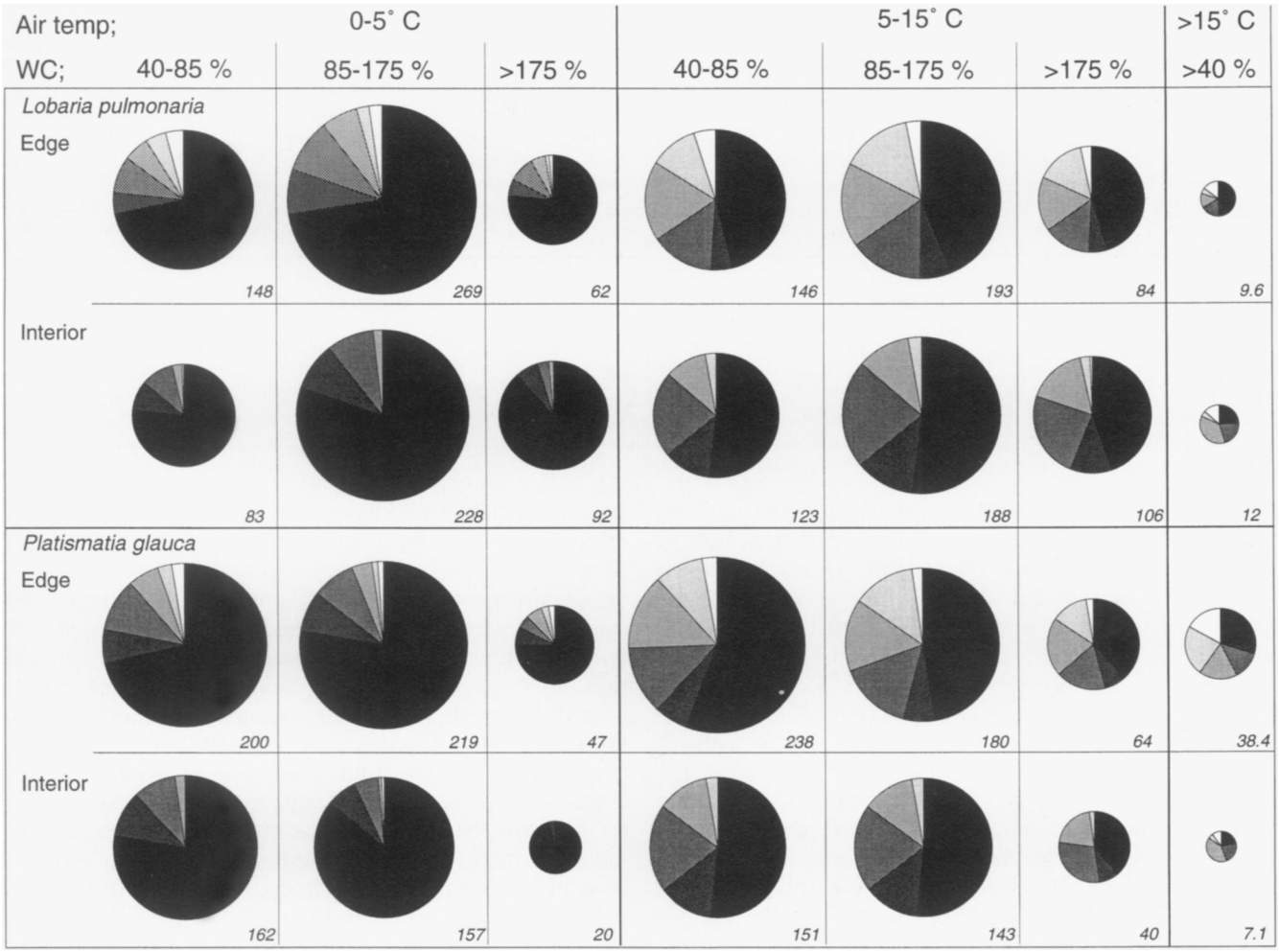

Fig. 4 Frequency (% of time) of the 54 combinations of microclimate and thallus WC conditions at the edge and in the forest interior assumed to result in metabolic activity. Each circle represents a combination of an air temperature and a thallus WC interval divided into 6 different light intervals: PPFD=0–5 (■); 5–10 (■); 10–25 (■); 25–50 (■); 50–100 (■) and >100 (□) µmol photons m^{-2} s^{-1}. *Circle area* is proportional to the number of hours (given in italics) each condition occurred. Data were pooled for temperatures above 15° C for all WCs above 40% as such conditions were relatively infrequent

The response curves presented in Figs. 1–3 were used to extrapolate CO_2 gas exchange rates for the 54 environmental combinations that were assumed to result in metabolic activity. These rates in conjunction with the data presented in Fig. 4 and Table 2 were then used to estimate the net carbon gain (DW yield) of the transplants. Evidently, the model predicted the carbon gain rather well as the estimated DW yield was clearly within the same order of magnitude as the actual (Table 3). The carbon gain was best predicted for *L. pulmonaria* in the interior and for *P. glauca* at the edge, while there was 4- to 5-fold overestimation of the actual gain in *L. pulmonaria* at the edge. The model underestimated the carbon gain of *P. glauca* in the forest interior, by a factor of about 5.

Discussion

This study aimed at testing the validity of using controlled laboratory measurements of CO_2 gas exchange in conjunction with field microclimate data to predict net carbon gain in epiphytic lichens. We also wanted to test whether the model would also accurately predict the carbon gain of lichens under conditions known to induce environmental stress. If so, it would then be possible to use field microclimate and laboratory gas-exchange data to predict the effects of stress on different species of lichens. From the data presented here it was possible to extract the environmental conditions required for optimal CO_2 gain in the two species and to compare this with the field data. *L. pulmonaria* showed maximum rates of NP when the WC was between 85–175% of the DW, the light intensity was above 100 µmol m^{-2} s^{-1} and the temperature between 15–20° C (Figs. 1–3). However, even though the WC of the transplants of *L. pulmonaria* was 85–175% during at least half of their metabolically active periods, both the temperature and particularly the light intensity were lower than optimal during most of this time (Fig. 4). Interestingly, the relatively high increase in respiratory rate with increased temperature in *L. pulmonaria* (Fig. 3) may not have been a significant

Table 3 Actual and estimated DW yields of the transplants. Actual growth of the transplants at the two climate stations was extracted from Renhorn et al. (1996) using only the 16 transplants of each species positioned adjacent to each climate station. Values represent mean±SE for [*n*] number of thalli. Estimation of the DW yield during the transplant period was made from the CO_2 gas exchange rates presented in Figs. 1–3, recalculated on a DW basis, and the number of hours each criterion occurred in the field (Fig. 4). It was assumed that the majority of the DW was made up of sugar equivalents and that 6 moles of assimilated CO_2 was required for each mole of reduced sugar. The estimation represent mean±SD, where the error is based on the SD in the WC measurements

Species	Actual growth % Increase in DW	Estimated growth % Increase in DW	Energy conversion efficiency % Biomass yield incident light^{-1}
L. pulmonaria			
Edge	1.7±1.4 [15]	7.7±3.0	0.04
Interior	2.9±1.0 [16]	1.7±1.2	0.15
P. glauca			
Edge	4.5±1.7 [14]	4.8±2.5	0.07
Interior	6.5±1.5 [14]	1.3±0.6	0.30

problem in the field. This is because, for this species, more than 75% of the active periods in darkness, both at the forest edge and in the forest interior, occurred when the temperature was below 5° C (Fig. 4). *P. glauca* required a WC above 85%, a light intensity above 100 μmol m^{-2} s^{-1} and a temperature between 15–20° C to attain optimal net photosynthesis (Figs. 1–3). This species thus spent a proportionally large fraction of its metabolically active time at sub-optimal conditions also with respect to WC (Fig. 4). Despite this and even though the overall active time was not longer for this species (Table 2), the actual carbon gain was higher in *P. glauca* than in *L. pulmonaria* both at the forest edge and in the forest interior (Table 3). This was even more surprising as the maximum NP rates were lower in the former species both per unit area and weight (Table 1). However, the Chl content, both per unit area and per unit weight, was much lower in *P. glauca* than in *L. pulmonaria* (Table 1). This indicates that the relative investment and maintenance of photosynthetic units (i.e. photobiont cells and chloroplast proteins) is lower in *P. glauca* than in *L. pulmonaria*, which might enhance growth indirectly in the former due to a lower maintenance respiration (see also discussion in Green and Lange 1995). The two lichens spent the majority of their metabolically active periods in darkness both at the edge and in the forest interior (Table 2, Fig. 4). It is therefore possible that factors related to respiration might in fact have had a larger impact on the final carbon gain of the two species than their photosynthetic capacity. The lower respiratory activity (Figs. 2–3) of *P. glauca* compared to that of *L. pulmonaria* would thus predict a higher growth rate in the former species during equal environmental conditions. Moreover, the relatively lower WC of *P. glauca* during the active periods (Fig. 4) would yield an even lower respiratory CO_2 loss in this species.

The modelled carbon gain for both lichen species was within the same order of magnitude as the actual growth (Table 3). However, the model overestimated the growth of *L. pulmonaria* transplanted to the forest edge and underestimated the growth of *P. glauca* in the forest interior. This suggests that the model was too simple and that additional factors will have to be included in future modelling. There may be several explanations for the overestimation of *L. pulmonaria* growth at the forest edge, such as a reduction in photosynthetic capacity during the transplant period, an increased leakage of reduced carbon from the apoplast and/or an increased rate of respiration in the mycobiont. As >90% of the photosynthetically active periods in the edge transplants occurred when the light intensity was below 100 μmol photons m^{-2} s^{-1} (Fig. 4), i.e. below light saturation of photosynthesis (Fig. 1), it appears that the edge transplants were unable to maintain the rate of NP at sub-saturating intensities obtained in the laboratory in the field. When the Chl content was measured before, during and after the transplant period it was found that the edge transplants of *L. pulmonaria* had a 30–40% reduction in Chl throughout the transplant period (data presented in Renhorn et al. 1996). However, even if this reduction was accompanied by an equally high reduction in photosynthetic capacity, the loss of Chl may only partially explain the overestimation, as there was 4– to 5-fold overestimation in growth (Table 3). There is also the possibility, though, that the edge transplants may have suffered from photoinhibitory stress (Demmig-Adams et al. 1990; Manrique et al. 1992) during the occasional periods with supraoptimal light. If this was the case, photoinhibition may transiently have caused a reduced capacity of photosynthesis even under lower light following the high light periods. This hypothesis is supported by the data of Demmig-Adams et al. (1990) showing that it may take several hours to fully restore photosynthesis even in moderately photoinhibited *L. pulmonaria* thalli. Clearly though, even if such damage occasionally occurred during the transplant period, the photosynthetic apparatus of the edge thalli seemed to have been repaired and restored before the late autumn harvest in October 1994 when the fluorescence yield did not reveal any significant differences between edge and interior thalli (data not shown). The overestimated growth of this species at the edge may also be related to other factors, such as the faster re-wetting and drying of the edge transplants compared to interior (Renhorn et al. 1996). It has previously been suggested that

an increased rate of re-wetting and drying of lichen thalli may both increase the leakage of reduced carbon from the apoplast and influence the physiological status of the lichen when entering the dormant, desiccated state (Lechowicz and Adams 1973).

The underestimated growth of *P. glauca* in the forest is also interesting (Table 3). These transplants spent 65% of their metabolically active time in darkness (Table 2, Fig. 4) and it can therefore be hypothesised that this underestimation might be related to an overestimation of respiration. In these thalli, several dark periods occurred without any preceding active period in the light (data not shown), whereas the modelled respiratory activity was based on thalli that were fully re-activated in the light. Thus, it is possible that the field-grown thalli may have had a lower rate of respiration due to a lower access to easily respirable metabolites. Evidently though, these hypothetical differences in respiration between the field transplants and the thalli assayed in the laboratory were not as profound in *L. pulmonaria*, as the model accurately predicted the growth of the forest interior transplants of this species, which spent 64% of their metabolically active periods in darkness.

Finally, even though the energy conversion efficiencies calculated for the four sets of transplants should mainly be regarded as a rough estimate, there are some interesting conclusions that may be made from these data (Table 3). The efficiency of photosynthetic DW yield for temperate crop plants, such as barley, sugar-beet and maize is generally in the range of 2–4% of the total incident radiation (Hall et al. 1985), a value close to the theoretical maximum. Natural ecosystems, however, have lower photosynthetic energy conversion efficiencies with e.g. evergreen temperate forests converting 0.8% of the total radiation into dry matter (Hall et al. 1985). Thus, the 0.3% efficiency of photosynthesis in *P. glauca* transplanted in the forest interior was not dramatically lower than the overall efficiency of a boreal forest. The efficiency of *L. pulmonaria* was though lower, which probably reflects the higher respiratory activity of this species. The somewhat lower efficiency of this species may also be related to the nitrogen fixation activity of its cephalodial *Nostoc* cells as the energy cost of nitrogen fixation is generally higher than more direct ammonium and/or nitrate assimilation (Chapin et al. 1987). At the edge, however, both species had a significantly lower photosynthetic efficiency. This is most probably related to the low light saturation value of the two species (Fig. 1) and their apparent lack of ability to acclimate and make use of the higher irradiance at the forest edge. Our data thus support a view that the slow growth of lichens should mainly be attributed to the scarcity of occasions with metabolic activity (Table 2) rather than a low photosynthetic energy conversion efficiency during their active periods (Table 3).

Acknowledgements This investigation was supported by a grant from the Swedish Natural Sciences Research Council to K. Palmqvist and by grants from the World Wide Fund for Nature and the Swedish Environmental Protection Agency to P.-A. Esseen. We also wish to acknowledge Dr. Erling Ögren, Dept. of Plant Physiology, Umeå University, Sweden for lending us vital parts of the data acquisition equipment. Special thanks also to Dr. Darwyn Coxson, UNBC, Prince George, Canada, for all advice and support, particularly with the impedance measurements, to Roland Wass for skilful technical assistance with the microclimate sensors, to Prof. John Raven, Biological Sciences, Dundee, U.K. and Prof. Howard Griffiths, Newcastle upon Tyne, U.K. for valuable comments to earlier versions of this manuscript.

Literatur

Ahmadjian V (1993) The lichen symbiosis. Wiley, New York

Boucher VL, Nash TH (1990) Growth patterns in *Ramalina menziesii* in California: coastal vs inland populations. Bryologist 3:295–302

Bruns-Strenge S, Lange OL (1991) Photosynthetic primary production of the lichen *Cladonia portentosa* in a dune habitat at the island Baltrum in the North Sea. I. Field measurements of microclimate, water relations and CO_2-exchange. Flora 185: 73–97

Chapin III FS, Bloom AJ, Field CB, Waring RH (1987) Plant responses to multiple environmental factors. BioScience 37:49–59

Coxson DS (1991) Impedance measurement of thallus moisture content in lichens. Lichenologist 23:77–84

Demmig-Adams B, Máguas C, Adams WW III, Meyer A, Kilian E, Lange OL (1990) Effect of high light on the efficiency of photochemical energy conversion in a variety of lichen species with green and blue-green phycobionts. Planta 180:400–409

Denison WC (1988) Culturing the lichens *Lobaria oregana* and *L. pulmonaria* on nylon monofilament. Mycologia 80:811–814

Genty B, Briantais J-M, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim Biophys Acta 990:87–92

Green TGA, Lange OL (1995) Photosynthesis in poikilohydric plants – a comparison of lichens and bryophytes. In: Schulze E-D, Caldwell MM (eds) Ecophysiology of photosynthesis. Springer, Berlin Heidelberg New York, pp 319–341

Hall DO, Coombs J, Scurlock JMO (1985) Biomass production and data. In: Coombs J, Hall DO, Long SP, Scurlock JMO (eds) Techniques in bioproductivity and photosynthesis. Pergamon, Oxford, pp 274–287

Hovenden MJ, Jackson AE, Seppelt RD (1994) Field photosynthetic activity of lichens in the Windmill Island Oasis, Wilkes Land, continental Antarctica. Physiol Plant 90:567–576

Kappen L, Lange OL, Schulze E-D, Evenari M, Buschbom U (1979) Ecophysiological investigations on lichens of the Negev desert. VI. Annual course of the photosynthetic production of *Ramalina maciformis*. Flora 168:85–108

Kappen L, Sommerkorn M, Schroeter B (1995) Carbon acquisition and water relations of lichens in polar regions – potentials and limitations. Lichenologist 27:531–545

Lange OL, Bruns-Strenge S (1991) Photosynthetic primary production of the lichen *Cladonia portentosa* in a dune habitat at the island Baltrum in the North Sea. II. A photosynthesis model: development, parametrization based on CO_2 exchange measurements in the laboratory, and validation. Flora 185:214–232

Lange OL, Kilian E, Ziegler H (1986) Water vapour uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. Oecologia 71:104–110

Lange OL, Büdel B, Heber U, Meyer A, Zellner H, Green TGA (1993) Temperate rainforest lichens in New Zealand: high thallus water content can severely limit photosynthetic CO_2 exchange. Oecologia 95:303–313

Lechowicz MJ, Adams M (1973) Net photosynthesis of *Cladonia mitis* (Sandst) from sun and shade sites on the Wisconsin pine barrens. Ecology 54:413–419

Manrique E, Balaguer L, Barnes J, Davidson AW (1993) Photoinhibition studies in lichens using chlorophyll fluorescence analysis. Bryologist 96:443–449

Matthes-Sears U, Nash III TH (1985) The ecology of *Ramalina menziesii*. V. Estimation of gross carbon gain and thallus hydration source from diurnal measurements and climate data. Can J Bot 64:1698–1702

Moberg R, Holmåsen I (1987) Lavar, en fälthandbok. Interpublishing AB, Stockholm

Moser TJ, Nash III TH (1978) Photosynthetic patterns of *Cetraria cucullata* (Bell) Ach at Anuktuvuk Pass, Alaska. Oecologia 34:37–43

Moser TJ, Nash III TH, Link SO (1983) Diurnal gross photosynthetic patterns and potential seasonal CO_2 assimilation in *Cladonia rangiferina*. Can J Bot 61:642–655

Nash III TH, Moser TJ, Bertke CC, Link SO, Sigal LL, White SL, Fox CA (1982) Photosynthetic patterns of Sonoran Desert lichens. I. Environmental considerations and preliminary field measurements. Flora 172:335–345

Palmqvist K, Samuelsson G, Badger MR (1994) Photobiont-related differences in carbon acquisition among green-algal lichens. Planta 195:70–79

Paterson DR, Paterson EW, Kenworthy JB (1983) Physiological studies on temperate lichen species. I. A mathematical model to predict assimilation in the field, based on laboratory responses. New Phytol 94:605–618

Renhorn K-E, Esseen P-A (1995) Biomass growth in five alectorioid lichen epiphytes. Mitt Eidgenöss Forsch Anst Wald Schnee Landsch 70:133–140

Renhorn K-E, Esseen PA, Palmqvist K, Sundberg B (1997) Growth and vitality of epiphytic lichens. I. Responses to microclimate along a forest edge-interior gradient. Oecologia 109:1–9

Ronen R, Galun M (1984) Pigment extraction from lichens with dimethyl sulphoxide (DMSO) and estimation of chlorophyll degradation. Environ Exp Bot 24:239–245

Schulze E-D, Lange OL (1968) CO_2 Gaswechsel der Flechte *Hypogymnia physodes* bei tiefen Temperaturen im Freiland. Flora 158:180–184

Sillett SC (1994) Growth rates of two epiphytic cyanolichen species at the edge and in the interior of a 700-year-old Douglas fir forest in the western Cascades of Oregon. Bryologist 97:321–324