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Pseudocyphellaria dissimilis: a desiccation-sensitive, highly shade-adapted lichen from New Zealand

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Summary. *Pseudocyphellaria dissimilis,* a foliose, cyanobacterial lichen, is shown not to fit into the normal ecological concept of lichens. This species is both extremely shade-tolerant and also more intolerant to drying than aquatic lichens previously thought to be the most desiccation-sensitive of lichens. Samples of *P. dissimilis* from a humid rain-forest site in New Zealand were transported in a moist state to Germany. Photosynthesis response curves were generated. The effect of desiccation was measured by comparing CO_2 exchange before and after a standard 20-h drying routine. Lichen thalli could be equilibrated at 15° C to relative humidities (RH) from 5% to almost 100%. Photosynthesis was saturated at a photosynthetically active radiation (PAR) level of 20 μmol m^{-2} s^{-1} (350 μbar CO_2) and PAR compensation was a very low 1 μmol m^{-2} s^{-1}. Photosynthesis did not saturate until 1500 μbar CO_2. Net photosynthesis was relatively unaffected by temperature between 10° C and 30° C with upper compensation at over 40° C. Temporary depression of photosynthesis occurred after a drying period of 20 h with equilibration at 45–65% relative humidity (RH). Sustained damage occurred at 15–25% RH and many samples died after equilibration at 5–16% RH. Microclimate studies of the lichen habitat below the evergreen, broadleaf forest canopy revealed consistently low PAR (normally below 10–20 μmol m^{-2} s^{-1}) and high humidities (over 80% RH even during the day time). The species shows many features of an extremely deep shade-adapted plant including low PAR saturation and compensation, low photosynthetic and respiratory rates and low dry weight per unit area.

Key words: Desiccation – Drought – Lichen – Light – Photosynthesis

Tropical and sub-tropical humid forests provide an environment in which lichens may form an obvious component of the vegetation both on the forest floor and in the canopy. While much work has been done recently on the growing conditions, water relations and primary production of lichens in arid habitats, both hot and cold (see review by Kappen 1988), much less is known about the ecophysiology of humid rain forest species. Research on the lichens of the humid subtropical/temperate forests has concentrated on some properties of gas exchange, morphology and water relations of the large *Pseudocyphellaria* and *Sticta* species (Green et al. 1985). However, there has been little work on the response of photosynthesis to light or on desiccation effects. This paper reports a detailed investigation into the gas exchange characteristics and desiccation sensitivity of *Pseudocyphellaria dissimilis,* a deep shade, forest floor, blue-green lichen. The study not only shows the lichen to be extremely shade-adapted, possessing most of the classic features of a shade plant, but also to be highly desiccation-sensitive. The latter property does not fit into the normal ecological concept of lichens because the species is much more desiccation-sensitive than even aquatic lichens.

Materials and methods

Plant material

Pseudocyphellaria dissimilis (Nyl.) D. Galloway et P. James (Lobariaceae) is an Australasian, foliose lichen with a cyanobacterial photobiont *(Nostoc)* that forms thalli 5–20 cm wide composed of linear-elongate lobes. According to Galloway (1985) the species is widely distributed throughout New Zealand in low-light habitats of lowland, evergreen, native forests. It is often the only lichen to be found on the forest floor or other deeply shaded habitats. Collections were made in a native forest in the Hakarimata Ranges near Ngaruawahia from the steep side of a stream gully with a northerly aspect but deeply shaded and covered with mosses. Samples were returned to the laboratory in darkened plastic bags and couriered, without drying, to Würzburg for experimentation. On arrival the thalli were first carefully cleaned of any attached material, damaged portions removed and then stored moist in a growth chamber at 15° C, high humidity and a 12:12 hour dark/light (9.5 μmol m^{-2} s^{-1} photosynthetically active radiation, PAR) regime. The lichen was maintained moist at all times from collection to the growth chamber. Thalli in the growth chamber were sprayed once a day with deionized water and remained alive and fully photosynthetically active for several months. However, samples were used as soon as possible for experimentation.

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Gas-exchange measurement

For all gas-exchange measurements and drying treatments, thallus lobes (about 100 mg dry weight or 36 cm^2 projected area) were attached to small wire trays. Photosynthesis measurements were carried out according to exchange procedures fully described in Lange and Redon (1983) and Lange *et al.* (1986). The trays, with attached lichen, were exposed in cuvettes submerged in a water bath and illuminated by mercury vapour lamps (Osram HQL) with different PAR intensities achieved by grey filters. CO$_2$ exchange was measured in the differential mode by means of an infrared analyser (Binos, Leybold, Hanau, FRG). Humidity and CO$_2$ partial pressure could be controlled in the air stream which passed through the cuvettes. Thallus temperature was recorded by a touching thermocouple and incident light by a quantum sensor (LiCor, Lincoln, Nebraska, USA). Stepwise changes in the conditions allowed generation of light, temperature and CO$_2$ response curves for CO$_2$ exchange. Prior to these experiments the lichen thalli to be used were moistened by first spraying and subsequent blotting, with paper tissue, of the underside. The thallus water content achieved produced optimal photosynthetic rates (Snelgar 1981).

All CO$_2$ exchange measurements for determination of desiccation resistance were made at 15° C, saturating light intensity of 120 µmol m^{-2} s^{-1} PAR, optimal hydration (see above) and a saturating CO$_2$ concentration of 1670 µbar (to eliminate the possible influence of thallus diffusion resistances on photosynthesis, Lange and Tenhunen 1981). Measurements were made on all samples for 2 h before the drying treatment, 1 and 3 h after rewetting, and after 2 or 3 days recovery in the growth chamber. Selected samples were maintained in the growth chamber for up to 68 days after the drying treatment, with weekly gas exchange measurements, in order to observe long-term recovery from drying. Water content was expressed as a percentage of dry weight (48 h at 105° C). Gas exchange rates were calculated on a similar dry weight basis (mg CO$_2$ g^{-1} h^{-1}); however, to standardize responses, in the desiccation treatments all results are then given as a proportion of the initial, pre-drying values. A similar standardization procedure (proportion of maximum photosynthetic rate) was used to facilitate comparisons of many samples with different absolute rates of net photosynthesis in other studies, such as response to CO$_2$ concentration. When calculating light responses and quantum efficiencies it was necessary to relate photosynthesis to a thallus area basis (µmol CO$_2$ m^{-2} s^{-1}). However, determination of thallus area is only possible with relatively large errors for the highly dissected and uneven lobes of this lichen. Where required, gross photosynthesis was calculated as the sum of net photosynthesis and dark respiration.

Drying treatment protocol

A standard, short-term drying treatment was applied using a second gas-exchange system in which the dew point of the air stream could be controlled. Fully hydrated and subsequently blotted thalli were attached to trays and exposed in cuvettes similar to those used for photosynthesis measurement. Cuvette temperature was 15.0°±0.1° C (in darkness), maintained by a water bath. Dew point of the air stream was controlled by Peltier-operated water vapour traps (Heinz Walz Meß- und Regeltechnik, Effeltrich, FRG) to ±0.1° C giving cuvette relative humidities (RH) from about 5% to nearly 100%. The initially moist thalli lost water until equilibrium was achieved between thallus water potential and air stream water vapour pressure. As an example, the investigation of the time course of equilibration by repeated weighing showed that thalli exposed to air streams of 35.8% RH or 9.6% RH reached equilibrium thallus water content of 12.5% and 8.9%, respectively, after 10–15 h. A routine drying time of 20 h was used for all of the experiments.

Environment of collection site

A Campbell CR21 micrologger (Campbell Scientific, Inc.; Logan, Utah, U.S.A.) was used to obtain environmental information at the collection site. Standard Campbell probes were used to measure relative humidity (201 humidity sensor), air temperature (101 thermistor) and PAR (LiCor, LI 190SB quantum sensor). Subsequent calibrations of the humidity sensors showed that the readings were inaccurate above 90% RH. Humidity measurements therefore had to be recalculated using air temperature and by extracting the absolute humidities below 90%. Measurements were made every minute and mean, maxima and minima were stored at 10-min intervals. Data were collected for 6 weeks in January and February 1988, an unusually dry period with no rain in the 3 weeks prior to the monitoring.

Results

Carbon dioxide exchange

Rates of photosynthesis. The maximum net photosynthetic rate at 350 µbar CO$_2$ was about 1 mg CO$_2$ g^{-1} d.wt. h^{-1} which is at the lower end of the range (1.1 to 3.0 mg g^{-1} h^{-1}) found for other *Pseudocyphellaria* species (Snelgar 1981; Snelgar et al. 1980). When expressed on an area basis the rates were much lower, 0.2 µmol m^{-2} s^{-1} compared to 1.0–1.5 µmol m^{-2} s^{-1} (Snelgar et al. 1981). This can be explained by a lower weight per unit area for thalli growing in deep shade (Snelgar and Green 1981).

Rates of respiration. Dry-weight related rates of dark respiration at 15° C are about 70% ot those reported for other *Pseudocyphellaria* species (Snelgar 1981). However, when expressed on an area basis, respiration rates are only 20% of previously reported values, as might be expected for a shade-adapted plant (Boardman 1977).

Carbon dioxide concentration. Light-saturated net photosynthesis increased almost linearly with increase in external CO$_2$ concentration to 70 µbar and saturation was not reached until about 1500 µbar (Fig. 1). Net photosynthesis at 350 µbar was less than 40% of rates at CO$_2$ saturation and large increases in photosynthetic rates would be possible if ambient CO$_2$ levels at the forest floor were higher than normal global values. There appears to have been no systematic investigation of CO$_2$ levels so far in these forests.

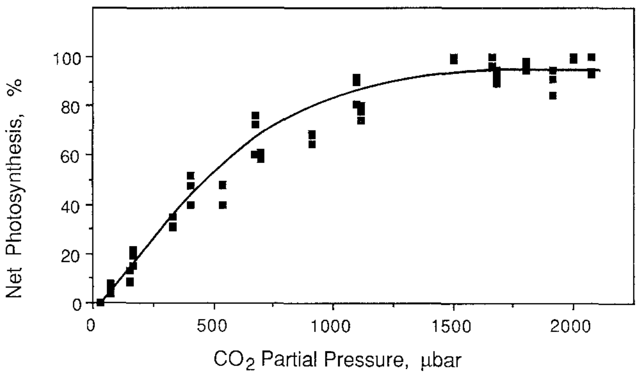

Fig. 1. Response of net photosynthesis (*ordinate*, percentage of maximum rate) to external carbon dioxide partial pressure (*abscissa*) at 15° C, saturating PAR and optimal thallus water content. Six different samples were used. Their maximal net photosynthesis varied between 2.99 and 1.48 mg CO$_2$ g^{-1} h^{-1} (dry weight related) and amounted to an average 2.19 mg CO$_2$ g^{-1} h^{-1}. The standardization procedure was used to enable comparison

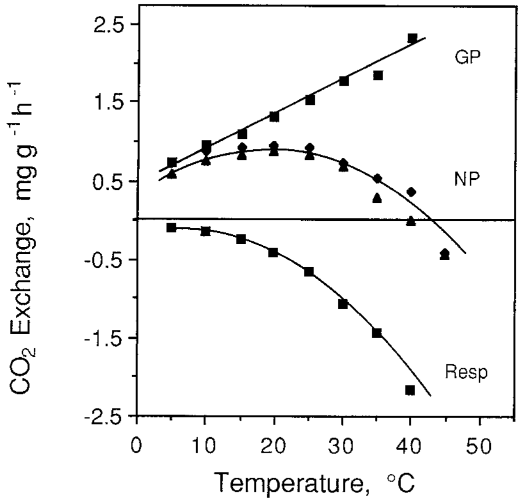

Fig. 2. Temperature dependence of lichen CO_2 exchange: *NP*, net photosynthesis (saturating light, 350 µbar CO_2 partial pressure, optimal thallus water content); *Resp*, dark respiration; *GP*, gross photosynthesis (net photosynthesis plus respiration). The responses of 3 samples were averaged; 1 g dry weight amounted to ca. 155.8 cm^2 thallus area

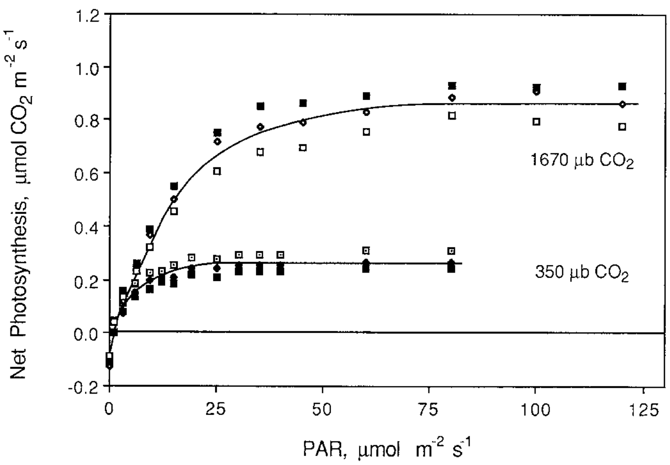

Fig. 3. Response of net photosynthesis to PAR at 15° C, natural (350 µbar) or saturating (1670 µbar) external CO_2 partial pressure; *ordinate*, area-related CO_2 exchange, uptake is positive; *abscissa*, incident photosynthetic active radiation (PAR). *Lines* represent a mean fit to three lichen samples

Temperature. Light and CO_2 saturated gross photosynthesis increased linearly with temperature to a maximum rate of 2.4 mg g^{-1} h^{-1} over the surveyed temperature range of 5° C to 40° C (Fig. 2). Respiration showed an expected exponential increase with temperature, with a Q_{10} of approximately 2 at all temperatures. Consequently net photosynthesis showed a broad maximum, at 0.7–0.8 mg g^{-1} h^{-1}, from 10° C to 30° C, but fell to compensation at about 42° C.

PAR. Net photosynthesis showed a curvilinear response to increasing PAR reaching saturation at 60 µmol photons m^{-2} s^{-1} in saturating, 1670 µbar CO_2 but at only 20 µmol m^{-2} s^{-1} in 350 µbar CO_2 (Fig. 3). Light compensation values were also very low at, or even below, 1 µmol m^{-2} s^{-1}. No photoinhibition or any decrease in photosynthesis at PAR as high as 120 µmol m^{-2} s^{-1} was detected during the time period of the experiments. Apparent photon yield (quantum efficiency *F*, related to incident radiation) was difficult to estimate because of the low values of PAR and non-linear response, even at the lower light levels. An estimate of 0.09 mol CO_2 fixed per mol quanta is obtained using the first two data points which, although high, is almost identical to low-light *F*, related to incident radiation, for Antarctic mosses (Green 1982). Estimates of 0.077 and 0.060 (first three data points, including dark respiration, at saturating and natural CO_2, respectively) are similar to values reported by Björkman and Demmig (1987) for a diversity of vascular plants but are still higher than many other reported values (Ehleringer and Pearcy 1983).

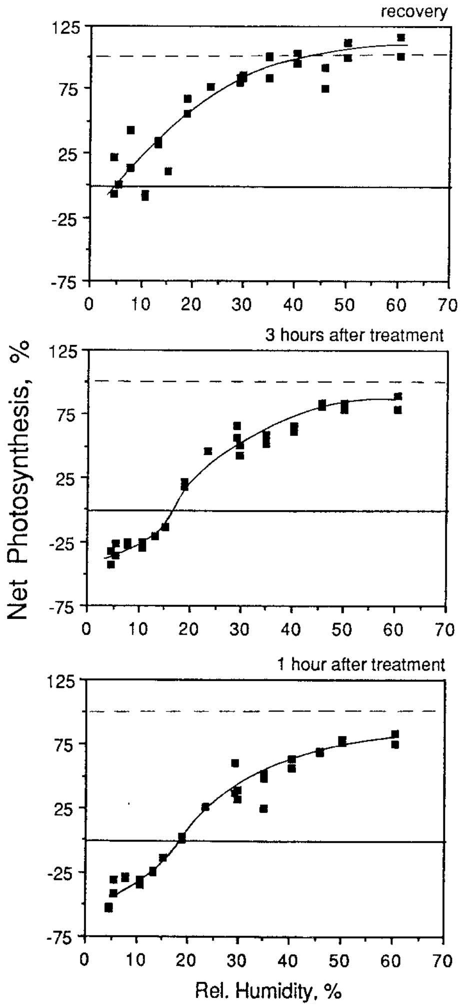

Fig. 4. Lichen net photosynthesis (saturating light and CO_2, 15° C, optimal water content) after a drying treatment at different air humidities. *Ordinate*, net CO_2 exchange, uptake positive, as a percentage of the rate before the drying treatment; *abscissa*, relative air humidity during the 20-h drying period. Photosynthesis was measured 1 h *(bottom)* and 3 h *(centre)* after rehydration, and after a recovery period of 2–3 days *(top)*

Desiccation tolerance

The effect of the standard 20-h drying routine on both net and gross photosynthesis depended on both the RH to which the thalli equilibrated and the length of the recovery period after treatment (Figs. 4 and 5). The

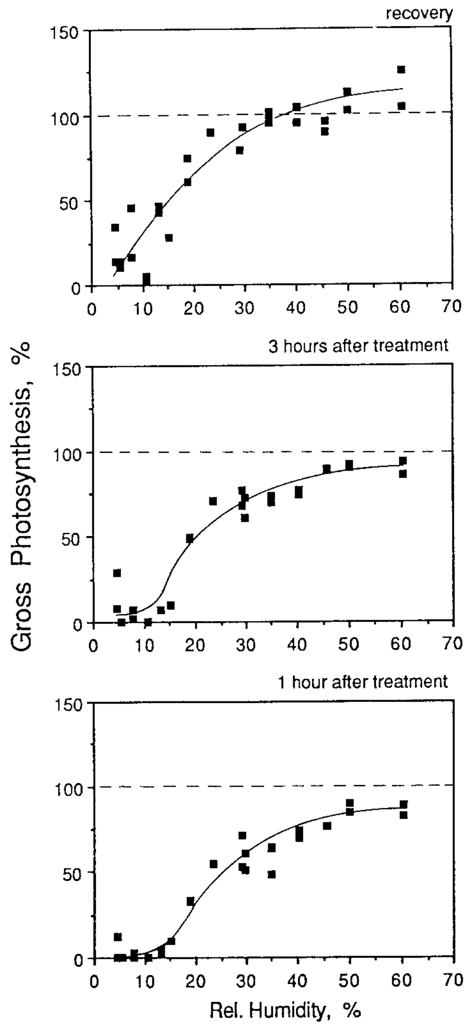

Fig. 5. Same as Fig. 4 but for gross photosynthesis (sum of net photosynthesis and respiration)

lichen response can be roughly divided into four phases related to relative humidity.

1. Exposure to RH between 60% and 45% produced only a very small initial depression of net (Fig. 4) and gross (Fig. 5) photosynthesis at 1 and 3 h after rewetting. After 2–3 days rates had returned to levels found before the drying treatment and there was even a slight indication of stimulation.
2. Substantial falls in net and gross photosynthesis occurred after exposure to between 45% and 25% RH but an almost full recovery was found 2–3 days after rewetting.
3. Exposure to between 25% and 15% RH caused sustained damage to photosynthesis with recovery being incomplete at 75% of original rates at 2–3 days after rewetting.
4. Drying under 15% to 5% RH produced initially no gross photosynthesis with net photosynthesis being negative through continued respiration. Lichens, after the recovery period, showed either partial recovery or total death at least of the phycobient (no gross photosynthesis). Dead lichens were easily identified because leakage of a brown stain occurred on remoistening indicating severe cellular damage. Considerable inter- and intra-lichen variability occurred in the response to severe drying. Some thalli were totally killed whilst in others only individual lobes died with the remainder of the thallus showing recovery. No explanation for this variability is available at present.

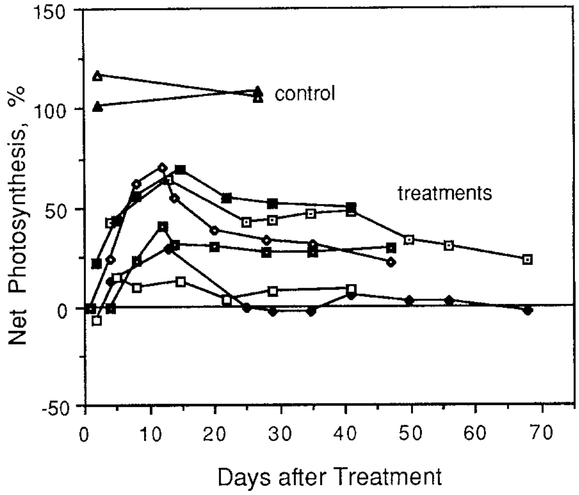

Fig. 6. Long-term performance of thalli without (control) and after a drying treatment. *Ordinate*, net photosynthesis uptake positive, as the percentage of rate before drying treatment or at the start (controls); measurements under saturating light, 15° C, optimal water content and saturating CO_2 partial pressure. *Abscissa*, time in days after drying treatment. Thalli were held in the growth chamber. In most cases low photosynthetic rates indicated death of part of the thallus with a few healthy lobes remaining

Long-term consequences of the drying treatment were assessed by repeated gas exchange measurements on experimental thalli held in the growth chamber. In Fig. 6 time courses are plotted for various samples which had initially shown greater than 50% depression in their net photosynthesis immediately after the drying treatment. Considerable differences were found between thalli but there appeared to be a period of maximal recovery after the first 10–15 days. This was possibly due to continued recovery after the drying treatment and/or new growth of algae. After longer time periods net photosynthesis generally declined and this agreed with progressing disintegration of the thalli. In some cases a few lobes remained healthy in appearance for longer than 68 days within an otherwise dead thallus; such thalli showed continued low levels of photosynthesis.

Lichen environment

Measurements over 6 weeks confirmed that the lichen collection site had a very dim and moist environment. Humidity was consistently high and minimum values, reached in mid-afternoon, were rarely below 80% RH although 72% RH was recorded on one day (Fig. 7A). No rain fell in the period covered by the measurements. Water vapor saturation (100% RH) occurred regularly from about midnight to mid-morning. Temperatures were between 13° C and 23° C for the measure-

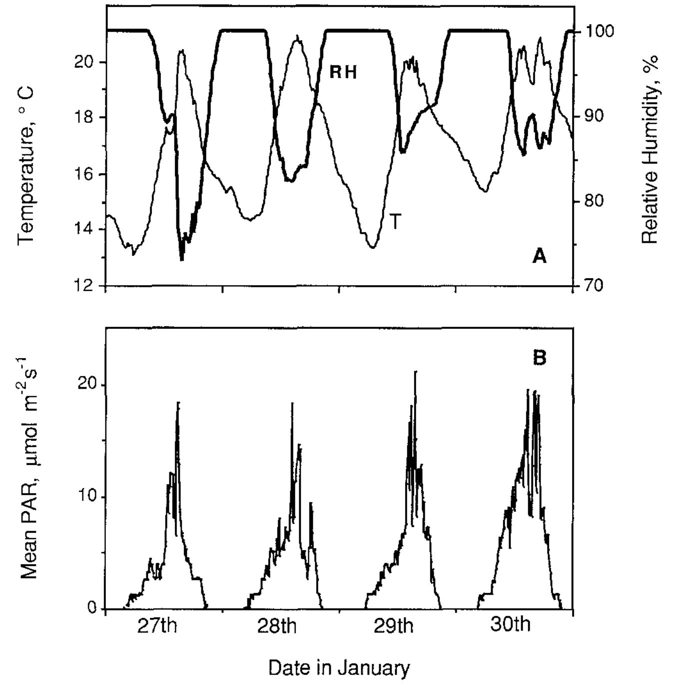

Fig. 7A, B. Microclimate data for the period 27 to 30 January: a measurement was taken every minute for each parameter and a mean value calculated at 10-min intervals. All measurements were made with sensors adjacent to lichens used for the experiments. **A** temperature (T, °C) and relative humidity (RH, %); **B** Light (PAR, µmol m^{-2} s^{-1})

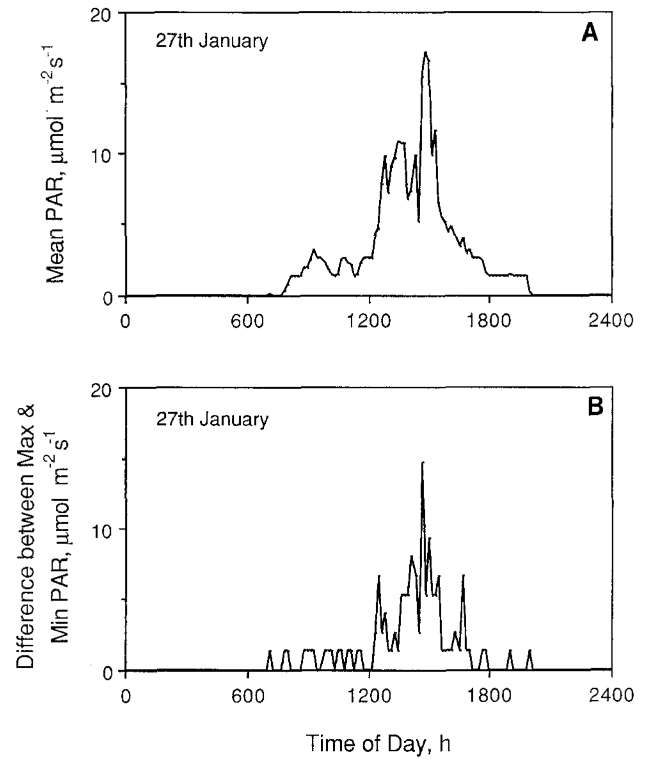

Fig. 8A, B. Light climate data for a single day. Measurements were made as in Fig. 7. **A** PAR (µmol m^{-2} s^{-1}) calculated as a 10-min mean. **B** Difference between the maximum and minimum PAR in each 10-min period. Note how the difference normally approaches the same magnitude as the mean indicating that sun-flecking is an important feature of the light microclimate

ment period and probably represent normal values for the season. The time of maximum PAR, minimum humidity, and maximum temperature coincide between 1400 hours and 1600 hours. PAR levels were always very low with means rarely exceeding 20 µmol m^{-2} s^{-1} (1% of full sunlight) and below 10 µmol m^{-2} s^{-1} for the majority of the day (Fig. 7B). Values of maximum PAR around 40 µmol m^{-2} s^{-1} occurred on rare occasions in early afternoon. A large difference between maximum and minimum PAR values (within each 10-min recording period) was found throughout the day (Figs. 8A and B). This range indicates the dominant contribution of subdued sunflecking under the evergreen, broadleaf canopy. A distribution analysis of the PAR (10-min mean values during sunlight hours) showed the majority of the light to be in the range 0–9 µmol m^{-2} s^{-1} which further emphasizes the deep shade of the environment.

Discussion

Pseudocyphellaria dissimilis is exceptionally sensitive to desiccation. The results show that equilibration of the thallus water content with 5–15% RH almost invariably kills the lichen. Even exposure to humidities as high as 45–65% produced transient (recovery over 2 or 3 days) depressions in gross and net photosynthesis. The desiccation sensitivity is even more startling when the brevity of the drying treatment is considered, a period shorter than those used by previous workers. Thalli were only exposed to the various humidities for 20 h during which time the plants were at equilibrium with the air humidity for about 8–10 h, which is an ecologically relevant time period. *P. dissimilis,* although a forest lichen, is much more sensitive to desiccation than aquatic lichens (Ried 1960).

The effect of desiccation is almost certainly a result of some form of cellular damage which involves the photobiont as well as the mycobiont. The loss of pigments and the discolouration of the damaged samples found in this work indicates cellular death and increased potassium leakage has been reported for *P. dissimilis* after 24 h at 53% relative humidity (Brown et al. 1981). In contrast there was little effect of exposure to 53% RH up to 7 days on respiration rates and this was taken to indicate a greater sensitivity of the photobiont to desiccation (Brown et al. 1981). The extreme desiccation sensitivity of *P. dissimilis* suggests that even moderate humidities do not occur in its normal habitat. The microclimate data strongly supports this suggestion since the lowest relative humidity recorded was 72% with values normally being much higher. Microclimate recordings were only carried out in the hotter, drier summer months of January and February, so humidities can be expected to be higher in the remainder of the year. Snelgar and Green (1981) used Pichè evaporimeters to measure evaporation at a point about 20 m from the collection site used in this investigation. Evaporation of only 1.6 ml occurred over a 12-day period which was calculated to be equivalent to a steady rate of 0.14 µg cm^{-2} s^{-1}. This was a much lower rate than the 1.0 µg cm^{-2} s^{-1}

used by Proctor (1979) in his study of structure-function relationships in bryophytes. The microrelief at the collection site undoubtedly contributed to the high humidity since it was on the steep face of a small stream valley. However, the dominating feature of the microclimate is the evergreen nature of all the canopy and subcanopy trees which ensures year-round low radiation levels at the forest floor resulting in low evaporation and high humidity.

P. dissimilis also appears to be well adapted to the very low PAR levels (20 μmol m^{-2} s^{-1} or lower) found at the collection site. Photosynthesis was light-saturated at 20 μmol m^{-2} s^{-1} and compensation was 1 μmol m^{-2} s^{-1}. Both these values are exceptionally low for lichens, possibly the lowest yet found, and can be contrasted with the saturating PAR of 700 μmol m^{-2} s^{-1} and compensation of up to 200 μmol m^{-2} s^{-1} for open deciduous forest lichens (Kershaw 1985). Good estimates were not possible for apparent photon yields but values of 0.077 to 0.09 are higher than the 0.056 of *Monoclea forsteri* (Green and Snelgar 1982). Increased photon yield has been suggested as a possible adaptation to deep shade conditions (Björkman et al. 1972). The shade character of *P. dissimilis* is further stressed by the fact that this lichen proved to be extremely sensitive to photoinhibition when it is exposed to high photon flux densities (Demming-Adams et al. 1990). The microclimate data also showed wide variability of PAR within the overall low level indicating sunflecking. In this situation the actual photosynthetic rates could be higher than those measured at continuous light levels because of differences in efficiency of light utilisation (Kirschbaum and Pearcy 1988).

The physiological results obtained in this investigation can be combined with the morphological measurements of Snelgar and Green (1981) to produce a picture of *P. dissimilis* as an extreme shade-adapted plant. The features of low PAR for photosynthesis saturation and compensation, low photosynthetic and respiration rates, low chlorophyll content, low weight per unit area and thin thallus are all features of a shade plant (Boardman 1977). It is interesting that the sun/shade response is so general that it covers plants from trees and shrubs to lichens.

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