

Diel Patterns of CO₂-Exchange for Six Lichens from a Temperate Rain Forest in New Zealand

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Received January 25, 1995; Accepted March 16, 1995

Abstract

The gas exchange of six temperate rain forest lichens was measured in the field in the Urewera National Park, New Zealand. Two shade species, *Collema laeve* and *Sticta filix*, were measured only in the forest; two open ground species, *Cladia retipora* and *Cl. aggregata*, only outside the forest and two marginal species, *Pseudocyphellaria colensoi* and *P. faveolata*, at both locations. The diel measurements for each species were analysed so that a net photosynthesis (P_n) response to both thallus water content (WC) and light (PFD) could be obtained. It proved possible to delineate limits and to determine WC/PFD combinations that would allow maximal P_n at the given habitat conditions. It was found that the lichens were rarely, between 3–13% of measurements, at maximal P_n. Lichens were limited mainly by low PFD and high WC in the forest, and by low WC and low PFD outside the forest. At WC which allowed positive P_n, the two open ground *Cladia* species were unaffected by full sunlight whereas the forest margin lichens were damaged by high PFD within one day. It is suggested that evidence is growing that

Presented at the Fifth Intl. Mycological Congress IMC5, Aug. 14–21, 1994, Vancouver, BC, Canada.

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lichens are rarely able to experience situations where Pn would be maximal. In these forests high production is possible because of the long periods during which the lichens are wet so that Pn continues for long periods although often at much lower than maximal potential.

Keywords: cyanobacterial lichens, green algal lichens, gas-exchange, photosynthesis, *Cladia*, *Pseudocyphellaria*, *Sticta*, *Collema*.

1. Introduction

New Zealand is known for its abundant lichens with the temperate *Nothofagus*-dominated rain forest being particularly rich in foliose species (Galloway 1985). The latter lichens, especially the genera *Pseudocyphellaria* and *Sticta*, have been the subject of many ecophysiological studies (Green and Lange 1991). Initial investigations on the response of photosynthesis to thallus water content (WC) led to suggestions as to how the thallus structure could maintain effective CO₂-exchange in the presence of stored water (Green et al., 1985). Adaptation of thallus structure to different environmental water status was also shown (Snelgar and Green 1981) and the cyanobacterial species, *Pseudocyphellaria dissimilis*, found to be desiccation-sensitive and to be killed by low humidity (below 50% rh) even if exposed for periods less than 24 hours (Green et al., 1991). The unusual joined thalli of photosymbiodemes in *Pseudocyphellaria* allowed the differences between cyanobacterial and green algal lichens to be investigated using plants of identical growth history. The disparity in their ability to utilise water from air humidity alone was shown to be maintained within single joint thalli (Lange et al., 1988). The balance of environmental conditions that appears to allow the mixed thalli to develop was also clarified (Demmig-Adams et al., 1990 b; Green et al., 1993).

However, the above work was mostly on small numbers of thalli in the laboratory. Research on lichens in other ecosystems has often included extensive studies on the day-to-day performance of the plants most often with the responses of individual thalli also being determined for comparison. The performance of lichens has been investigated in this manner in several ecosystems (see Kappen 1988). Early studies were on the desert lichen *Ramalina maciformis* (Lange et al., 1970) and later ones on fog communities of the Namib Desert (Lange et al., 1991). Temperate lichens were studied in Germany (Schulze and Lange 1968; Hahn et al., 1989; Bruns-Streng and Lange 1991) and tundra species, in an extensive programme, in Alaska (Hahn et al., 1993). Kappen and coworkers have achieved considerable success with studies on antarctic lichens, especially *Usnea* and *Umbilicaria* species, again being able to link laboratory performance with field studies (Kappen 1993). Zotz

and Winter (1994) and Lange et al. (1994a) have extended the work to cover species in tropical rain forests.

In all these studies an important objective has been the clarification of the environmental and thalline factors that limited production of the lichens, the overall aim being to achieve the ability to predict annual production from climate data. Schroeter et al. (1995) have found that the antarctic lichen, *Usnea antarctica*, may not often function in the so-called optimal sections of photosynthetic response curves. Also, Lange et al. (1993) have shown that supraoptimal thallus water contents previously thought to be rare, are apparently both common and detrimental to CO₂-exchange in the field. It is now clear that knowledge of the behaviour of New Zealand forest lichens in the field would be useful to complement the existing laboratory results. An introductory study was therefore carried out in the lichen-rich Urewera National Park, New Zealand with the main objective being the obtaining of field performance data for a variety of lichen species. We now report diel patterns for six lichens and, also, that the lichens do indeed seem to operate only rarely at maximal photosynthetic rates.

2. Materials and Methods

Research site and methods

The research site was located in the Aniwhaniwa River valley in the neighbourhood of the Urewera National Park headquarters at Lake Waikaremoana, North Island, New Zealand (latitude 38° 45' S, longitude 177° 9' E). Both the site and the methods used have been fully described in Lange et al. (1993) and Green et al. (1993). The following points are, however, of importance to this study. Two research sites were used. The first site was inside the forest (evergreen and dominated by *Nothofagus menziesii*, *Ixerba brexioides* and *Dacrydium cupressinum*). The canopy was fully closed at 20–25 m. Subsequently the measuring equipment was moved to the second site which was about 30 m distant and just outside the forest margin in a clearing. Lichens studied at each site were those found in the immediate vicinity, only a small number of species (all forest margin species) were studied at both sites.

For ease of measurement of photosynthetic and respiratory CO₂-exchange the lichen thalli were fixed in wire-mesh baskets (3.8 cm diameter, 1–1.5 cm high, mesh width 1.6 mm). CO₂-exchange rates were measured as described in Lange et al. (1993) by brief, 1–2 minute, enclosure of each sample in a small cuvette under natural ambient conditions. Several samples were measured in sequence with the result that each sample would be remeasured at 40–90 minute intervals, depending on sample numbers and time of day. In general, the need to

survey a wide range of species necessitated that only one or two samples could be measured for each species. In order to minimise problems from inter-thalli variability we used as large a sample as possible, made up of thallus portions from several larger lichen thalli. Preliminary tests, in which we compared several samples (3 to 5) of selected species, demonstrated that this methodology gave excellent replication of lichen response. Between measurements the samples were returned to a moss-covered log (inside forest) or ground (outside forest) where they were exposed to natural conditions of PFD, humidity and temperature. At each determination the lichen plus basket was also weighed so that thallus water content could be determined later. In this manner the diel pattern of CO₂-exchange could be constructed for several samples. The entire measuring period was from 30 October to 13 November 1991.

Microclimate

Microclimate parameters were recorded routinely during the CO₂-exchange measurements and air temperature and PFD (photosynthetic photon flux densities, $\mu\text{mol m}^{-2} \text{s}^{-1}$) are presented with each diel graph of CO₂-exchange (Figs. 3–5). Temperature and rainfall data were also available from a nearby meteorological station (Lake Waikaremoana) and a summary is given in Table 1 for the experimental period and for the whole year in Fig. 1. The CO₂ environment has been reported by Tarnawski et al. (1994) and, for the lichens, is not significantly different from the surrounding air. However, CO₂ levels within the forest are consistently higher than for outside air.

Lichen species

Species reported are listed in Table 2 together with brief habitat details and research site(s) at which they were studied. The species represent only six of the 23 studied (for complete list see Lange et al. 1993) but have been selected because they were measured over several days and come from a range of habitats. *Collema laeve* (cyanobacterial) and *Sticta filix* are typical of the deep shade areas of the forest. *Pseudocyphellaria faveolata* and *P. colensoi* are found in forest margin habitats with *P. colensoi* being in the brighter areas. Both species grow within the forest canopy and would receive direct sunlight only in the form of sunflecks. *Cladia retipora* and *Cl. aggregata* are ground species of open grassy or scrub habitats where exposure to full sunlight is possible. Of the two, *Cl. aggregata* prefers slightly more protected sites. *Collema laeve* and *S. filix* were studied only within the forest and *Cl. retipora* and *Cl. aggregata* only outside the forest. The other two forest margin species were measured through the entire experimental period.

Table 1. Summary of climate parameters for the experimental period 30th October to 13th November. All data, except for the PFD, are from the Lake Waikaremoana weather recording station about 250m from the measuring site. The PFD data are from the actual measurement site, it should be noted that the maximal PFD reported in the forest normally represents a single high value and should be interpreted with the PFD distribution given in Fig. 2. Measurements were made inside the forest from 30th October to 8th November and outside the forest from 10th to 13th November (inclusive).

Date	PFD max. $\mu\text{mol m}^{-2} \text{s}^{-1}$	Temperature ($^{\circ}\text{C}$)			Rainfall (mm)
		min	max	range	
Oct 30	31	6.3	7.9	1.6	21
Oct 31	72	6.7	11.5	4.8	3
Nov 1	580	1.7	19.9	18.2	1
Nov 2	65	5.6	16.5	10.9	0
Nov 3	14	6.1	8.7	2.6	34
Nov 4					176
Nov 5					174
Nov 6	73	9	15.6	6.6	11
Nov 7	29	8	11.6	3.6	3
Nov 8	420	8.9	16.1	8.9	12
Nov 9					6
Nov 10	1,906	1.9	24	22.1	5
Nov 11	1,900	4.1	19.8	15.7	3
Nov 12	2,000	7.3	19.9	12.6	3
Nov 13	1,612	7.7	19.9	12.2	1

3. Results

Microclimate

The Waikaremoana district has a wet temperate climate with cool wet winters and summers that are warmer and drier (Fig. 1) but still with considerable day-to-day variability. The weather during the 15 day experimental period was very typical for early summer with considerable differences between days (Table 1). There was only one completely dry day although nine had rainfalls of 6 mm or lower. On two days, 7th and 11th November, showers during the day rewetted previously dry lichens: There were two exceptionally wet days, with 176 and 174 mm of rain, during which

Table 2. Lichen species studied with brief habitat information and the duration of their respective measurement periods. Only *P. faveolata* and *P. colensoi* were measured both inside and outside the forest. Lichen names are according to Galloway (1985).

Lichen species	Thallus morphology*	Normal habitat	PFD status	Measuring site	Days measured
<i>Collema laeve</i> J.D. Hook. et Taylor	BG foliose, gelatinous, homoiomerous	forest floor	deep shade	forest	7
<i>Sticta filix</i> (Sw.) Nyl.	G (c) foliose heteromerous	forest tree trunks	deep shade	forest	6
<i>Pseudocyphellaria faveolata</i> (Delise) Malme	G (c) foliose heteromerous	forest twigs	moderate shade	forest and clearing	12
<i>Pseudocyphellaria colensoi</i> (Church. Bab.) Vainio	G (c) foliose heteromerous	forest margins	moderate shade	forest and clearing	9
<i>Cladia retipora</i> (Labill.) Nyl.	G fruticose heteromerous	open ground	sunny	clearing	4
<i>Cladia aggregata</i> (Sw.) Nyl.	G fruticose heteromerous	open ground	sunny	clearing	4

*Thallus morphology: G = green algal photobiont, (c) with cephalodia;
BG = cyanobacterial photobiont.

experimentation proved impossible. Wetter days (eg.: 30th October, 3rd November) had smaller temperature ranges, under 5°C, than drier days (1st, 2nd and 10–13th November) with ranges reaching 20°C. Extreme temperature minima were lower than 2°C and extreme maxima 24°C, both occurring on clear days. Temperatures within the forest were very similar to those at the weather station (compare Figs. 2–4 with Table 1). The PFD environment was very different between the inside and the outside of the forest (Fig. 2). Daytime PFD exceeded 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the forest for only 6% of the measurements whilst, in contrast, outside the forest only 8% of measurements were below 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

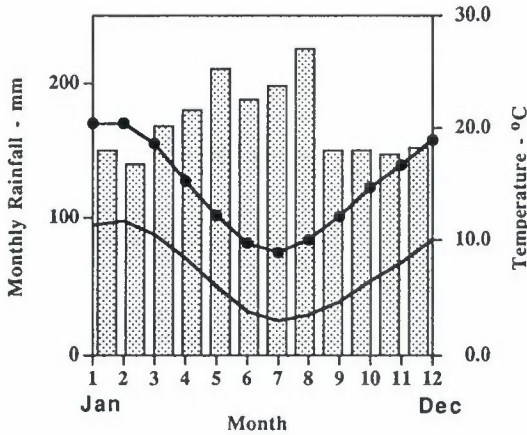


Figure 1. Climatic data from the Waikaremoana weather station: monthly means are given for rainfall (bars), maximum (upper line with dots) and minimum (lower line) temperatures. The research period was exceptional in that twice the mean monthly rainfall for November fell in only two days, however other days were typical for the area. Periods of brief, intensive rainfall are possible at any time of the year.

Table 3. Maximal photosynthetic rates found during experimental period. Measurement techniques are given in the methods and all data were obtained under natural ambient conditions in the field. Full lichen authorities are given in Table 2.

Species	Maximal photosynthetic rate		
	nmol g ⁻¹ s ⁻¹	μmol m ⁻² s ⁻¹	nmol (mg chl) ⁻¹ s ⁻¹
<i>Collema laeve</i>	17.41	na	7.72
<i>Sticta filix</i>	14.97	2.12	3.89
<i>P. colensoi</i>	9.33	2.09	7.54
<i>P. faveolata</i>	12.41	1.59	7.1
<i>Cladia retipora</i>	6.08	na	31.69
<i>Cladia aggregata</i>	6.84	na	7.01

Maximal photosynthetic rates

Maximal Pn, dry weight basis, found in the diel studies was highest for the shade lichens, intermediate for the forest margin species and least for the open ground species (Table 3). Rates on an area or chlorophyll basis were relatively

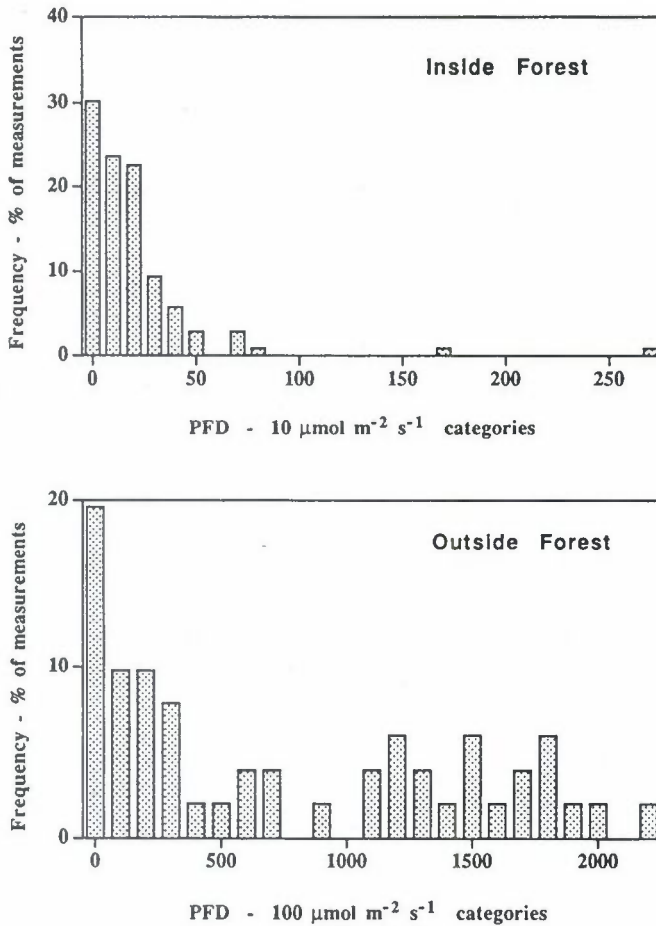


Figure 2. Distribution of PFD categories inside (upper panel) and outside (lower panel) the forest. PFD categories are $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ wide for inside the forest and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ wide outside the forest. Labels on the horizontal axis indicate the lower boundary for each category i.e.: 10 on the upper panel indicates 10 to $19 \mu\text{mol m}^{-2} \text{s}^{-1}$ etc. Note that in the lowest categories (labelled 0) for both panels the frequencies given do not include values of $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ since these would represent overnight readings. Frequency of measurement (vertical axis) indicates the number of times a particular PFD value was measured, measurements were made at the conclusion of each gas exchange determination.

constant and it seems that mass per unit area declined with prevailing PFD, a typical shade response known from higher plant leaves. *Sticta filix* had a low and *Cl. retipora* a very high Pn on a chlorophyll basis. In the case of *Cl. retipora* other samples had higher chlorophyll contents and, therefore, lower

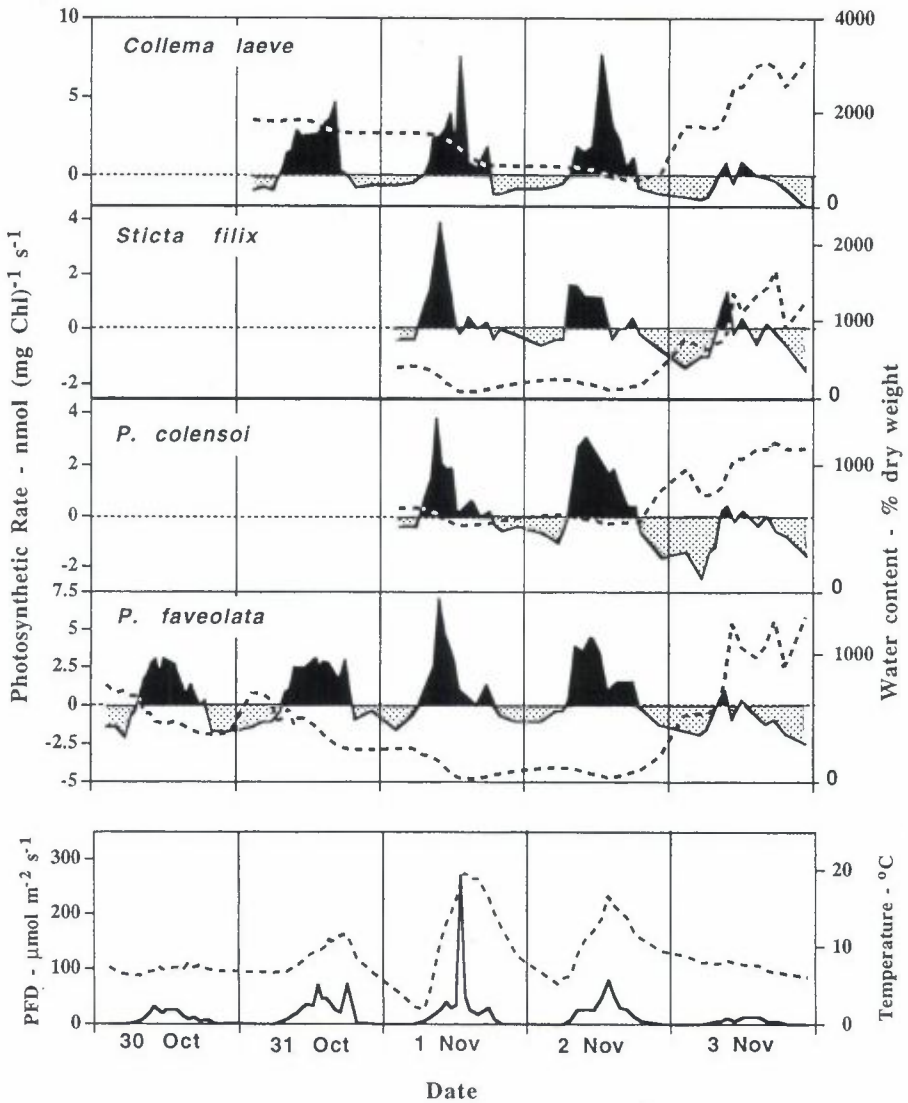


Figure 3. Diel pattern of gas-exchange for the first measuring period from 30th October to 3rd November inside the forest. Lower panel shows PAR (solid line) and Temperature (dashed line). Upper panels are for the indicated lichen species and show Photosynthetic Rate (Pn) on a chlorophyll basis (solid line) and Thallus Water Content (WC), on a dry weight basis (dashed line). Periods of positive net photosynthesis have a black filling, periods of respiratory CO₂ release a dotted filling. Note that the vertical axes for photosynthesis and thallus water content have different scales for the different species. Results for a single thallus that was representative of the replicates used. Different thalli are used for Figs 3-5.

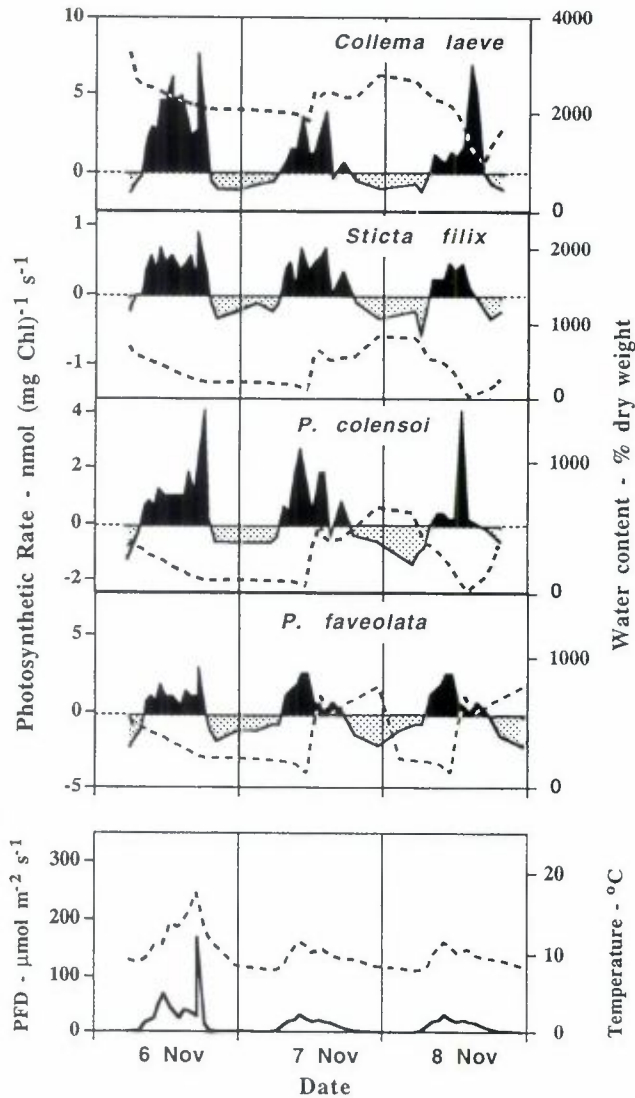


Figure 4. Diel pattern of gas-exchange for the second measuring period from 6th November to 8th November inside the forest. Other details are as for Fig. 3.

P_n on a chlorophyll basis; the reason for the low chlorophyll value for the particular sample used is not known. The P_n maximal rates fall within the range of those measured by eg. Snelgar et al. (1980) and in Alaska, Hahn et al. (1993), and do not appear to be exceptional.

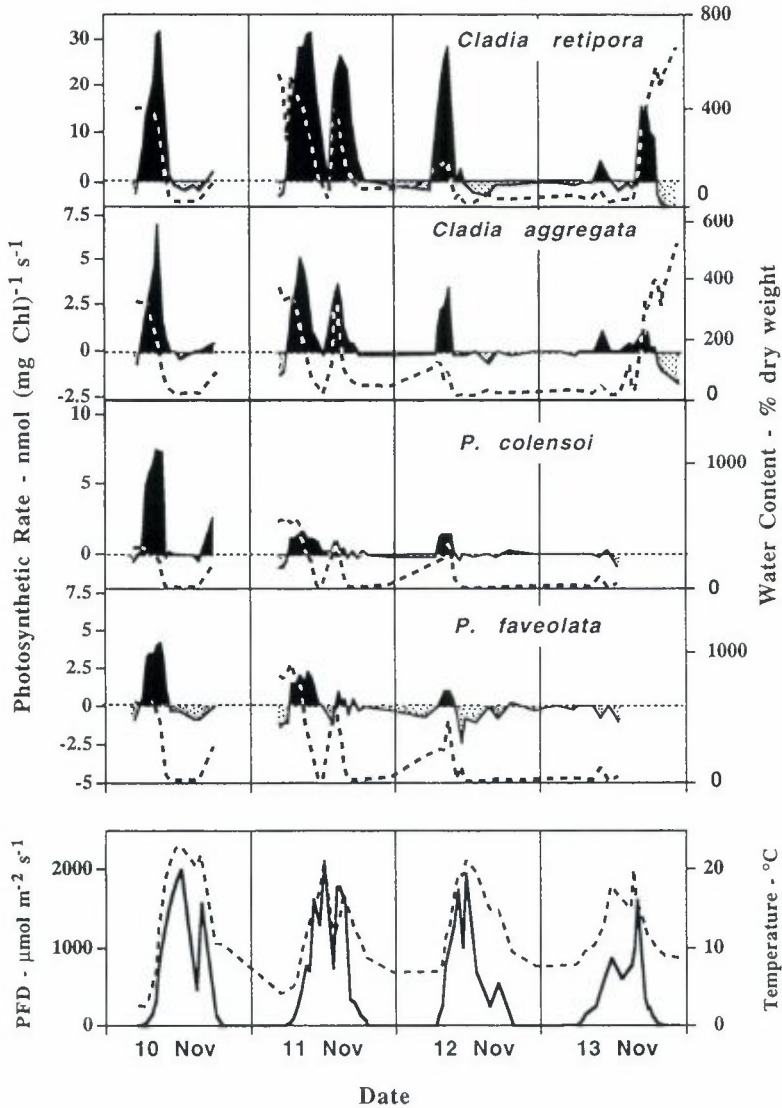


Figure 5. Diel pattern of gas-exchange for the third measuring period from 10th November to 13th November outside the forest. Other details are as for Fig. 3. Note that the two of the species studied have changed.

Diel patterns of CO₂-exchange

Results are reported over three time periods which totalled twelve days: in the first two periods (30th October to 3rd November and 6th to 8th November)

measurements were within the forest, and outside the forest for the third period (10th to 13th November). During the first period lichens gradually dried initially (Fig. 3). Both *P. faveolata* and *Co. laeve* showed photosynthetic rates (P_n) that tracked PFD on 30th and 31st October. This situation more or less continued for the next two days for *Co. laeve*, however, the other three lichens all showed limitation from low thallus water content (WC) late in the days with some remoistening overnight. PFD levels were always low and rarely above $50 \mu\text{mol m}^{-2} \text{s}^{-1}$. On the final day, 3rd November, there was heavy rainfall with lichens attaining very high WC, all above 1000% dry weight. PFD was also very low, never exceeding $14 \mu\text{mol m}^{-2} \text{s}^{-1}$, so that P_n was only occasionally above compensation. During the next two days rainfall was even higher and prevented experimental work. On these days the lichen P_n would have probably been depressed to an even larger extent by the low PFD and very high WC.

During the second measurement period (Fig. 4) low PFD again seemed to prevail. PFD was higher on 6th November but was still predominantly below $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ and all lichens showed a response in P_n to a PFD transient that reached $170 \mu\text{mol m}^{-2} \text{s}^{-1}$, although high WC prevented maximal rates. The situation continued on 7th November until the middle of the day when a shower of rain sharply increased the previously declining WC. Thallus water contents did not reach the high values of the first measuring period but were still sufficient to produce depressed P_n , this being especially obvious for *P. faveolata*. P_n was restored to more normal levels on the next day as WC declined. Over both measurement periods the cyanobacterial lichen, *Co. laeve*, had the higher WC and was least affected by drying out. Although a more severe effect of low PFD might have been expected for the marginal habitat lichens, *P. faveolata* and *P. colensoi*, this was not apparent in the results. This is possibly because of the continuously very low PFD which was probably below P_n saturation for all the species so that their full photosynthetic potential could not be appreciated.

During the third period (Fig. 5) the measurements were made outside the forest and the two shade lichens were replaced by *Cl. retipora* and *Cl. aggregata*, both open habitat lichens. The environmental conditions were more variable with both PFD and temperature showing large diel ranges. Desiccation stress was greater, all the lichens showed larger changes in WC and dried down to below moisture compensation for P_n on every day. Rain showers returned WC to higher values on both the 10th and, especially, the 11th November. The consequent P_n response was particularly well shown by both *Cladia* species with a pronounced double peak that exactly followed the changes in WC. Whereas both *Cl. retipora* and *Cl. aggregata* resumed photosynthesis on rewetting it was apparent that the marginal habitat

lichens, *P. faveolata* and *P. colensoi*, did not do so. Under what would be expected to be favourable conditions both species showed depressed Pn on the 11th November and almost no photosynthesis on 13th November.

Throughout the entire measuring period the overall diel patterns were similar but there were also clear differences between individual species. Of significance was the suspected high light damage in *P. faveolata* and *P. colensoi* after these marginal species had been moved outside the forest into the full sunlight. *Collema laeve*, the sole cyanobacterial lichen reported here, had a substantially higher maximal WC which certainly appeared to buffer it from the desiccation that affected some of the other, green algal lichens. Within the forest it seemed that the lichens carried a double burden of low PFD and supraoptimal WC whilst outside it appeared that low WC was limiting. These possible limitations are investigated in the next section.

PFD, WC and maximal Pn

Diel Pn patterns are determined by various combinations of PFD and WC. Interpretation of diel performance can be problematic since it is often difficult to decide exactly which, if any, factor is predominantly controlling Pn. However, with many diel data points, as in this investigation, it is possible to determine satisfactory envelope curves for Pn response to PFD and WC. The process requires a series of steps and is normally started by plotting all data points to see if the envelope curve is obvious. The next step is to construct a Pn response to PFD at moderate WC. Often this can be done from the envelope curve or by using the early morning measurements on a selected day, a good example was the morning of 10th November for the four species measured outside (see Fig. 8). The process is not so easy where high PFD data points are rare, as for the within forest measurements, and for those cases use was made of published curves of Pn response to WC, obtained under controlled experimental conditions, in order to set some starting values. The measurements made on the first day outside the forest on the marginal lichens, *P. colensoi* and *P. faveolata*, were particularly useful in fixing the PFD responses although these data were not used in the final analyses below. The curves for *Cl. retipora* are shown in Fig. 6.

Once the response construction has been completed it is possible to set levels for PFD and WC which would produce maximal Pn under the prevailing conditions. For PFD this will be the level below which Pn becomes limited. For WC there can be two boundaries, always a lower one below which there is a lack of water and, in many cases, an upper boundary above which there is an excess of water causing lower Pn because of increased diffusion resistances (Cowan et al., 1992; Lange et al., 1993). When these levels are drawn onto a

plot of WC against PFD they delineate a zone within which Pn would be maximal. These are shown for all lichens in Fig. 7 where all measurement points of Pn have been plotted in terms of WC and PFD and a 'maximal zone' has then been defined using the relationships extracted from the diel measurements. It is thus possible to see how many of the measurements were made at combinations of WC and PFD that would have produced maximal Pn. Only daytime measuring points with PFD above zero were used in this analysis and data for the marginal lichens were only from measurements within the forest. These boundaries should be treated with a little caution since there will be an interaction between PFD required for saturation and thallus WC.

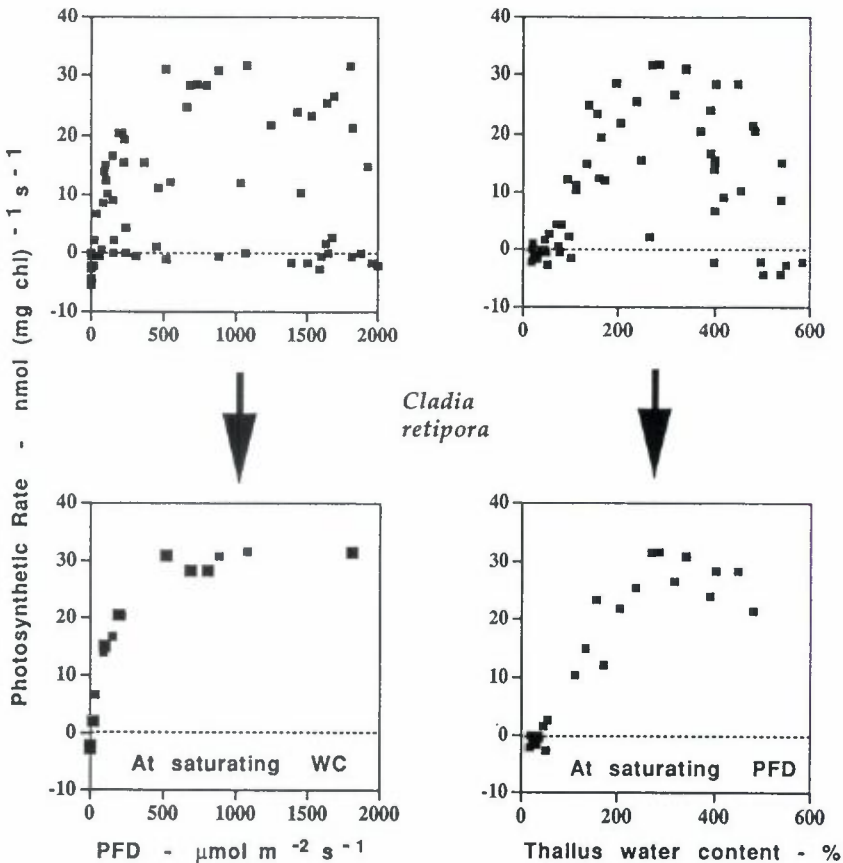


Figure 6. The results of the extraction of the Pn versus WC or PFD dependencies from the total diel data base. The example given is for *Cladia retipora* and is for PFD, left-hand panels and WC, right-hand panels. In each case the total data set is given in the upper panel and the extracted relationship in the lower panel.

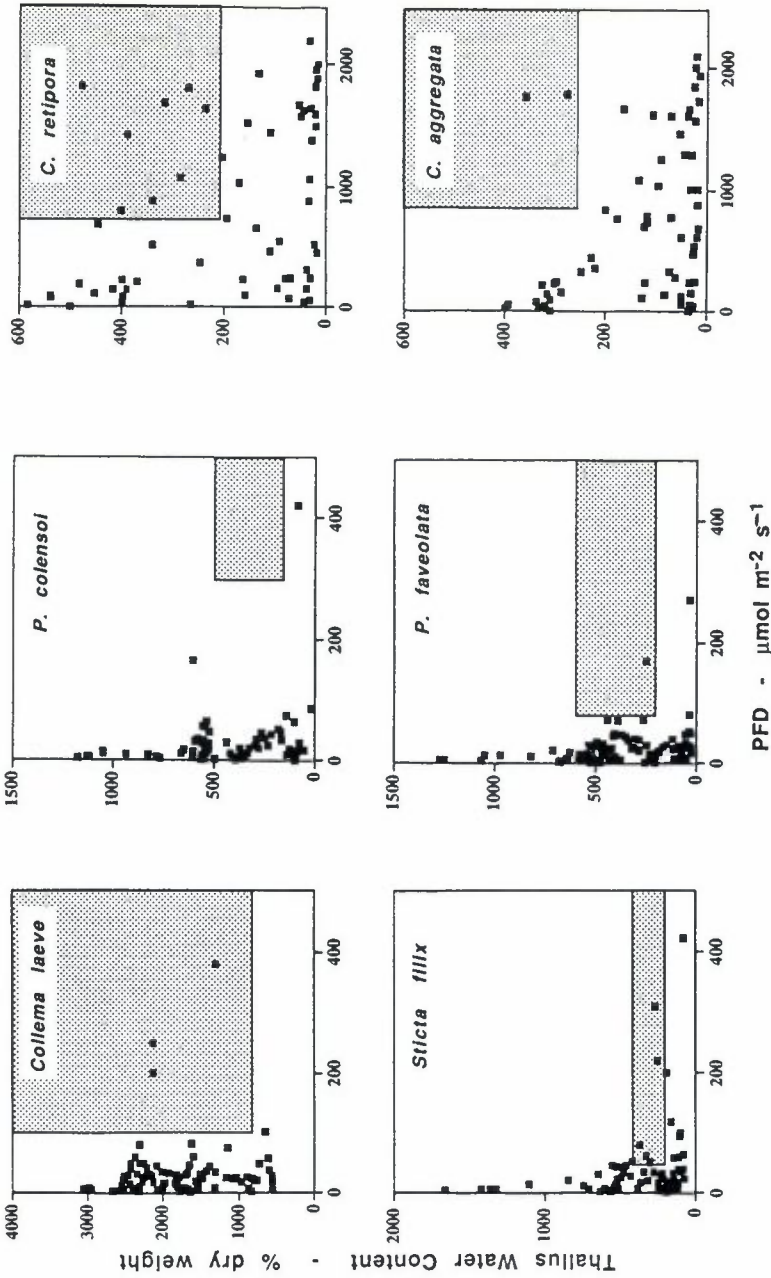


Figure 7. Plots of thallus water content, vertical axes, against PFD, horizontal axes, for all six lichens studied. The 'maximal zones' for each species are proscribed by the shaded panels and have been designated according to the methods described in the text. Each point indicates one measuring point for the particular lichen. Note that the PFD ranges for the horizontal axes are different for the right-hand panels which are for the *Cladia* species measured only outside the forest. All other panels contain data points which were measured during the first two measuring periods, i.e.: only inside the forest. The ranges of the vertical axes are different for the various species but are identical for upper and lower species for the middle and right-hand panels.

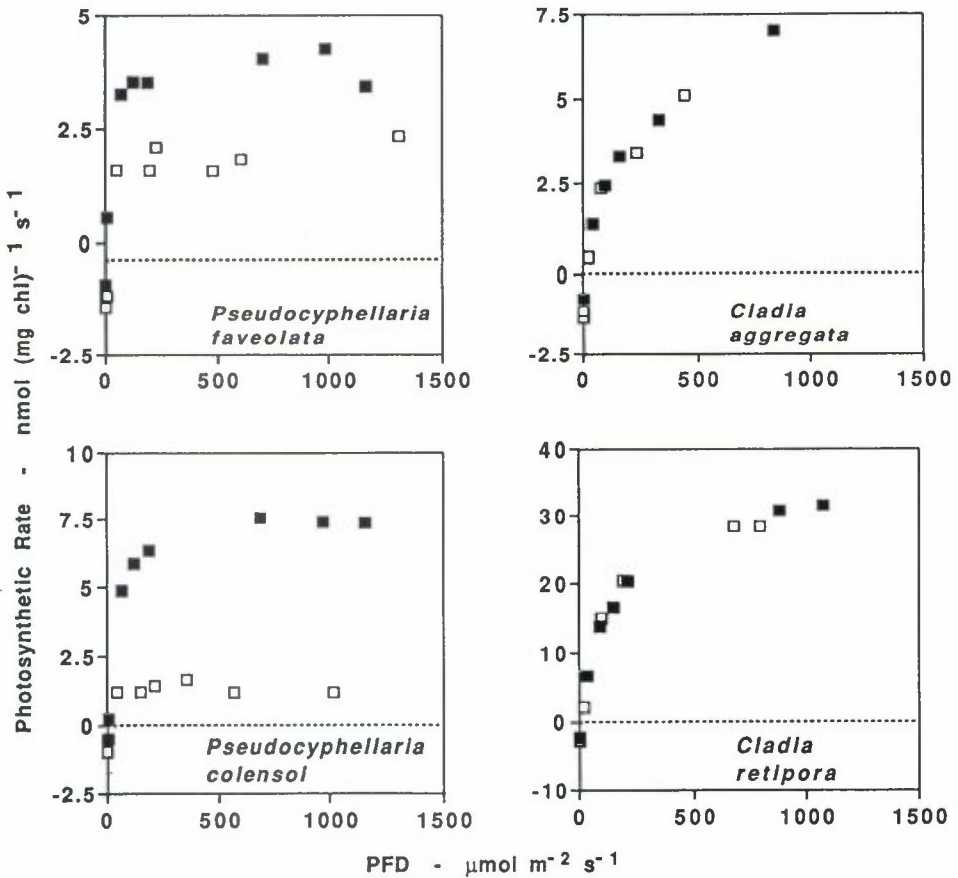


Figure 8. Relationship between photosynthetic rate and incident PFD for the four species on the first two days of the third measuring period which was outside the forest. Solid symbols are for the first day, 10th November, and open symbols for the second day, 11th November. Note how the photosynthetic responses are identical on the two days for the *Cladia* species but are depressed on the second day for the *Pseudocyphellaria* species which are from a forest margin habitat. Data are for thalli that have WC optimal for Pn and, in this figure, results are for single samples extracted from a larger survey programme.

Saturation levels will normally be lower at both high and low WC that inhibit Pn (Lange et al., 1995). However, it must be remembered that the maximal zones set here are for those measurements with combinations of WC and PFD where neither is limiting Pn. Because of experimental variability, it

is difficult to exactly define a saturation value and therefore the levels have been set at about 80–90% of the maximal values achieved in the measurements.

Very few of the daytime measurement points fell into the maximal zones. The proportion that did so are listed in Table 4. The marginal lichens were particularly excluded with *P. colensoi* never being in the optimal zone and *P. faveolata* only for one percent of measurements. There were clear differences between the species within and outside the forest. The forest species were predominantly limited by low PFD in combination with low or high WC. They were only rarely depressed entirely by low WC and never solely by high WC. However, high WC commonly further lowered Pn already depressed by low PFD thus representing a double burden to the lichens (see also Figs. 7B, C and D, Lange et al., 1993). In contrast, the two *Cladia* species were almost equally limited by low light, low WC or a combination of the two. The strong inverse relationship between WC and PFD was clearly shown by *Cl. aggregata*, a species that entered the maximal zone only briefly following a midday rainstorm. When PFD was high then WC was low, and *vice versa*. *Cladia retipora* achieved maximal photosynthesis more than any other lichen studied. This appeared to be a consequence of its higher WC compared to *Cl. aggregata*. This delayed the drying down of the lichen just sufficiently to allow favourable WC, developed overnight or in a rainstorm, to still be present when high PFD occurred. This prolongation, in comparison to *Cl. aggregata*, can best be seen on 11th November (Fig. 5).

Table 4. Proportion of measurements that had a combination of WC and PFD that would be expected to result in maximal Pn. The method of determining the combinations for maximal Pn is given in the text. Overnight measurements with PFD of zero have been excluded. Lichen details in Table 2.

Lichen species	Measurements with WC and PFD combination for maximal Pn (%)	Total number of measurements
<i>Collema laeve</i>	3.4	89
<i>Sticta filix</i>	8.4	71
<i>Pseudocyphellaria faveolata</i>	1	104
<i>Pseudocyphellaria colensoi</i>	0	70
<i>Cladia retipora</i>	13.3	60
<i>Cladia aggregata</i>	3.3	61

Effect of high PFD

Species measured outside the forest received PFD up to $2,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and, in the morning, high PFD could coincide with thallus WC still sufficient to potentially allow photosynthesis. Photoinhibition might be expected in sensitive species under these conditions of above saturation PFD (Demmig-Adams et al., 1990 a, c). Both *Cladia* species showed an identical response of Pn to PFD on the mornings of 10th and 11th November (Fig. 8) indicating that there was no deleterious effect of full sunlight on the wet lichens. In contrast, the marginal habitat lichens, *P. faveolata* and *P. colensoi*, both showed substantial declines in Pn response to PFD on the second day. *P. colensoi*, in particular, exhibited an almost complete collapse with its quantum efficiency, ie. the initial slope of the PFD-response curve, falling from 0.041 to $0.026 \text{ mol CO}_2 (\text{mol PFD})^{-1}$. The diel patterns of these two species both showed little Pn activity, in comparison to the *Cladia* species, after the first day (Fig. 5). Both of the *Pseudocyphellaria* species also showed visible damage from the high light with bleached patches gradually spreading over the thalli.

4. Discussion

The diel patterns and their interpretations reported here present an interesting mixture of adaptation, and apparent lack of adaptation, of the lichens to their environment. The results allow us to perhaps reflect on the strategies of both the lichens and the experimenters. The apparent lack of adaptation of the lichens is suggested because few data points fell in the 'maximal zones' for WC and PFD. The lichens achieved maximal Pn only between 3–13% of the time with one species, *P. colensoi*, never doing so. This result is, perhaps, unexpected since the temperate rain forests have been regarded as one of the better environments for lichens as indicated by both the high biomasses and high growth rates (Snelgar and Green 1982). It is important, therefore, to consider whether these results are flawed in some way or do indicate a true situation. If the latter case, then how do the results compare to studies elsewhere.

We believe that the weather patterns during the experimental period were not atypical for much of the year. Although there were two days of exceptional rain, so heavy that actual mechanical damage was caused to one lichen species (Büdel et al., 1995), the remainder were a normal mix of wetter/cloudy, and clear/drier days. In the forest the main limiting factor was the low PFD often in combination with high WC. On clear days eg.: 2nd November, PFD in the forest remained below $65 \mu\text{mol m}^{-2} \text{s}^{-1}$ and were much lower on cloudy days eg.: 30th October and 3rd November (Fig. 3). Neither

would we expect this situation to change during the year. The forests are completely evergreen and the only gains in PFD would be from the slightly higher elevation of the sun in mid-summer. The very high water contents found were unexpected but certainly contributed to limitation of Pn (Lange et al., 1993). The low PFD would help maintain the high WC so that the lichens never dried out to the same extent as those outside the forest. *Pseudocyphellaria faveolata* and *P. colensoi* never fell below 24.3 and 18.5% WC, respectively, inside the forest but reached 9.2 and 3.4% outside. The difference in drying-down rates on clear days, within and outside the forest, can be easily seen for *P. faveolata* by comparing the mornings of 1st and 10th November (Figs. 3 and 5). However, it must be emphasised that the continuing high WC means that the lichens could be active on most days. Our measurements within the forest had at least one positive net photosynthesis value on every day and the lichens often achieved substantial carbon gain, albeit carbon gained at much less than maximal rate.

Outside the forest there was a clear inverse relationship between WC and incident PFD. Incursions into the maximal Pn zone seem to be transitory and occurred either in the early morning, before the lichens had dried down, or after a daytime rain shower (Fig. 5). However, carbon gain when the lichens were wet was substantial and carbon balance was further improved by the suppression of respiration when the thalli dried to very low WC (Figs. 3–5). Once again, the weather pattern appeared normal and it is difficult to envisage situations that would increase occurrence of maximal rates. The high PFD requirement of the *Cladia* species means that they will be always PFD limited in cloudy conditions, the exact periods when they would be expected to be wet.

It is our opinion that the uncommon occurrence of conditions allowing maximal Pn is a normal feature of these environments. Although initially surprising it is a situation that is in agreement with other lichen ecophysiological studies from a wide range of environments. The phenomenon was noted in studies on the desert lichen, *Ramalina maciformis* (Kappen et al., 1979, 1980; Lange et al., 1970). Later studies on other desert lichens in the Namib (Lange et al., 1991, 1994b), from European, local xerothermic steppe (Hahn et al., 1989), sand dunes of a North Sea island (Bruns-Strenge and Lange 1991, Lange and Bruns-Strenge 1991) and the Alaskan tundra (Hahn et al., 1993) all show similar trends with the lichens being substantially limited by low WC or PFD for much of the daylight hours. Perhaps the largest data set is that on *Usnea antarctica* at Livingstone Island (Schroeter et al., 1995) where, over a two year period, the lichen almost never had a WC/PFD combination that produced maximal Pn. It would seem, therefore, that the New Zealand rainforest lichens fit an emerging pattern that lichens typically do not function

at maximal Pn, however, one unusual feature seems to be that high WC can be an important limiting factor. It is also interesting that although PFD saturation values are very low for these lichens, as low as $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Pseudocyphellaria dissimilis* (Green et al., 1991), they are still not low enough to ensure saturation with the result that Pn is PFD limited for most of the time. The PFD saturation values might provide protection with respect to photoinhibition during the brief periods of higher PFD in sunflecks. Lichens growing in the open avoid sustained high PFD by drying out of the thallus as shown by the data presented here. This option is not possible for sunflecks in the forest since drying rates are so slow. If true then PFD saturation values for forest lichens might well reflect sunfleck frequency and brightness rather than the average habitat PFD.

However, an overall adaptation to the PFD regime is very clear amongst these lichens. The forest species all have lower PFD saturation values than the *Cladia* species, $40\text{--}200 \mu\text{mol m}^{-2} \text{s}^{-1}$ versus $700\text{--}800 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Low to very low PFD saturation values appear typical for lichens from these rainforests and must be a consequence of the generally stable, except for sunflecking, low PFD environment ensured by the evergreen canopy (Green and Lange 1991; Green et al., 1991). Moreover, the ability of the open ground *Cladia* species to tolerate high PFD when wet contrasts with collapse in Pn for the marginal *P. faveolata* and *P. colensoi*. Lichens from the deep shade could well be even more sensitive. The inability of these marginal species to tolerate high light has been previously reported and identified, by fluorescence techniques, as being a consequence of photosystem damage (Demmig-Adams et al., 1990 a-c).

The broad adaptation shown by the lichens to the PFD regimes of habitats inside and outside the forest contrasts to the measured Pn responses. The latter results would suggest a lack of adaptation since maximal Pn was rarely achieved. This apparent lack of adaptation reflects probably more an expectation of the researchers obtained from higher plant studies where maximal Pn often occurs. It seems that lichens do not operate this strategy. The present results form part of the first investigation of lichen photosynthetic performance in the New Zealand rainforests. Measurements were made at only two sites, entirely within or outside the forest. It is perhaps then no surprise that the combinations of PFD and WC in measurements on the marginal lichens, *P. faveolata* and *P. colensoi* were rarely those producing maximal Pn. Their values of one and zero percent time in the maximal zone contrast with the 3.3–13.3% of the other lichens. There can be little doubt that PFD and WC combinations could well be better at a truly marginal site where there would be a higher frequency of sunflecks. Their obvious lack of ability to tolerate full sunlight of more than a few hours duration and their low PFD saturation values

indicates that they were not adapted for a fully open habitat and shows the dangers of studying lichens away from their normal habitat. The fact that this situation is so clearly indicated by the 'maximal analysis' suggests that it could be a useful procedure to interpret ecophysiological data. The question remains as to what extent these lichens can adapt to different PFD environments as is commonly found for higher plant leaves and also, in the form of seasonal acclimation, for lichens (Kershaw 1985).

The limited amount of diel data obtained in this investigation has allowed some insight into the performance of the rainforest lichens. It seems likely that the high, for lichens, productivity of the habitat is a consequence of the long time periods over which the lichens can carry out positive Pn. The fact that most of the time the Pn is not maximal appears to be more general for lichens than previously thought and is a growth strategy deserving of greater physiological investigation. To fully prove its occurrence in these forests it will be necessary to carry out measurements over longer periods, as has been done in other investigations.

Acknowledgements

The work reported here was supported by the Deutsche Forschungsgemeinschaft within the "Sonderforschungsbereich 251 der Universität Würzburg"; the Alexander von Humboldt-Stiftung and Waikato University are thanked for financial support to TGAG. We gratefully acknowledge the collaboration and stimulating discussions of Dr. Ulrich Heber during our field work. The New Zealand Department of Conservation gave its permission for our study in the Urewera National Park; we are especially grateful to the manager of the park, Mr. Malcolm Smith for his lively interest and for his extensive support without which our work would not have been possible.

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