Lichenologist 23(3): 267–282 (1991)

ECOPHYSIOLOGICAL ADAPTATIONS OF THE LICHEN GENERA *PSEUDOCYPHELLARIA* AND *STICTA* TO SOUTH TEMPERATE RAINFORESTS

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Abstract: Temperate rainforests are a poorly researched habitat with respect to lichen ecophysiology in comparison to desert and polar regions. The evergreen, broadleaf forests provide a dim, moist environment that is relatively stable throughout the year. Lichens are abundant in both quantity and species diversity with the large foliose genera *Sticta* and *Pseudocyphellaria* normally being dominant, visually and in terms of biomass. These lichens exhibit a great diversity of both form and habitat range. Physiological and morphological adaptation has also been demonstrated. *Pseudocyphellaria dissimilis* shows changes in thallus water storage capacity with evaporative demand and is also highly shade-adapted. The species has the lowest light saturation and compensation values for photosynthesis yet known for lichens (20 and 1 μmol m^{-2} s^{-1}, PAR, respectively). Unexpectedly it is also highly desiccation-sensitive with some thalli being killed after only 20 h exposure to 15% relative humidity. Photobiont versatility is also a feature of these genera. Photosymbiodemes occur, i.e. a single thallus containing both green algal and cyanobacterial sectors. Because the different sectors have the same fungal partner and grow in the same habitat, it is possible to investigate whether particular physiological traits are photobiont determined. The ability to recover photosynthetic activity in humid air is confined to thalli with green algal photobionts whilst the inability of thalli containing cyanobacterial photobionts to tolerate high light stress may be related to their lack of a protective xanthophyll cycle.

Introduction

Research into the ecophysiology of lichens has made exceptional progress during the past two decades to the point where whole books are available on the topic (Kershaw 1985). It is clear, however, that this research has focused on the perceived resistance of lichens to environmental extremes (Kappen 1988). The literature is dominated with studies of the lichens from cold deserts, including both the Arctic and Antarctic, tundra systems, and hot deserts. The ability of lichens to tolerate desiccation is widely studied through investigations into the relationships between thallus water content and CO_2 gas exchange. The process of photosynthesis is a useful indicator of plant productivity and susceptibility to stress. Fortunately, gas exchange equipment has become much more user-friendly, enabling both field and laboratory studies. The rainforests, both tropical and temperate, still remain to be researched. They are important, because of their size and the high lichen biomass and species diversity. This contribution will seek to demonstrate that rainforests are under-researched and have the potential to extend greatly our understanding of lichen ecophysiology.

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0024–2829/91/030267+16 $03.00/0

Rainforest environment

In New Zealand, large foliose lichens of the genera *Pseudocyphellaria* and *Sticta* are visually most obvious in the wetter areas of the lowland (0–700/900 m altitude) mixed podocarp-hardwood forests and throughout the upland (about 600–1200 m) beech forests. Lowland forests, 0–700 m, South Island; 0–900 m, North Island, are dominated by emergent *Dacrydium cupressinum*, *Podocarpus spicatus* and *P. totara* and have a canopy/subcanopy of various hardwoods, particularly *Beilschmiedia tawa* and *Weinmannia racemosa*. In these forests the large lichens are often conspicuous in the moister river valleys where the branches of *Fuchsia excorticata* are a particularly good habitat. However this apparent distribution is misleading because large lichens are common, though unseen, in the canopies of trees. The upland (montane) forests, from 600–900 m to 1200 m, North Island, and 900 m, South Island, are predominantly composed of southern beech species, *Nothofagus menziesii*, *N. fusca* and *N. solandri*. The lichen vegetation of these forests can be abundant, especially foliose species, probably because the forests tend to be more open with better penetration of light to the forest floor. Once again, a large lichen biomass exists out of sight in the canopies. Recent information has been published on the environment of a lowland beech forest (*N. truncata*) (Hollinger 1987) and stream valley of lowland podocarp-hardwood (Green *et al.* 1991).

The dominating feature of the New Zealand temperate rainforests is the evergreen canopy. Only one tree species, *F. excorticata*, is deciduous; all other trees and shrubs retain a full canopy throughout the year. Leaf fall is relatively continuous through the year, a feature which probably explains the lack of a significant ground lichen flora. Robust vertical upward growth forms of bryophytes and filmy ferns, which are not overwhelmed by leaf deposition, tend to confine lichens to rocks, branches of shrubs, and the trunks, buttresses and canopy of trees. The evergreen canopy produces low light levels at and close to the forest floor, in the range of 1–5% of incident light at the canopy (Fig. 1). These values are relatively constant throughout the year so that lichens rarely, if ever, receive high light intensities, minimizing the risk of photoinhibition and requiring extreme adaptations of the photosynthetic apparatus to low light intensities in order to ensure sufficient productivity. Canopy lichens receive much higher photosynthetically active radiation (PAR) values. Temperatures are quite variable through the year and can range from sub-zero to the mid-twenties (°C). The forest interior is, to some extent, buffered from the extremes of the strong radiation fluxes produced by clear skies during the day and night. Green & Clayton-Greene (1981) found greater temperature ranges in the canopy than at the forest floor, and that changes in regional air masses could determine the temperature during any period.

The constancy of the radiation environment, coupled with the high, well-spread rainfall (2000–3000 mm p.a.), leads to high relative humidities (r.h.) within the forest (Fig. 1). Water vapour saturation will be reached on most nights and minimum r.h. values may be high (around 70% r.h.). The high r.h. and low radiation combine to produce very low evaporative stress even during warmer periods. Green & Clayton-Greene (1981) found that the giant polytrichaceous moss, *Dawsonia superba*, which has limited water conduction potential, was never water limited but had a growth rate entirely determined by

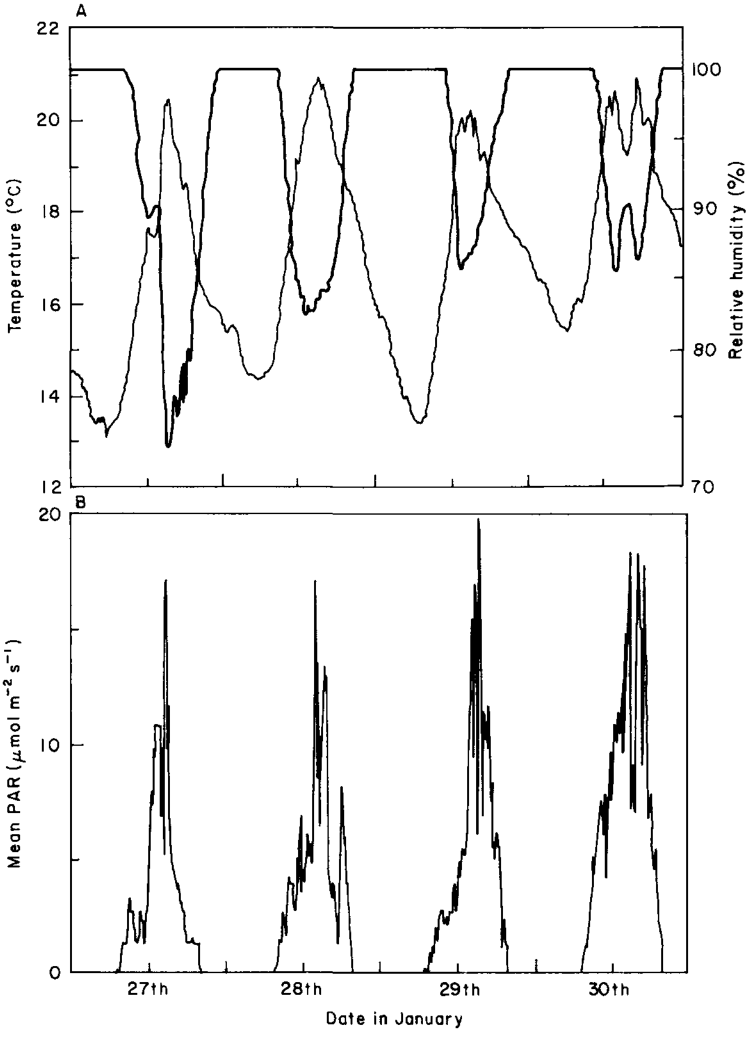

FIG. 1. Microclimate measurements from the habitat of the deep-shade form of *Pseudocyphellaria dissimilis*. Measurements were made directly adjacent to undisturbed lichen thalli. Full details of location and methodology are given in Green *et al.* (1991). A: relative humidity and mean temperature; B: mean PAR, µmol m^{-2} s^{-1}.

temperature. Extensive periods of many weeks in duration occurred in the winter when the r.h. never fell below 100% at the research site (alt. 700 m in forest). Jane & Green (1984) found that cloud caps, which form commonly in some upland areas, markedly reduce evaporation so that soil water content was continuously in excess of field capacity. Lichens are abundant in these areas. Snelgar & Green (1981) measured evaporation from a Piché evaporimeter at a mean rate of 0·14 mg cm^{-2} s^{-1} adjacent to the lichen *Pseudocyphellaria dissimilis*

TABLE 1. *New Zealand* Sticta *and* Pseudocyphellaria *species**

Genus	Number of species	Photobiont	
		Green algal	Cyanobacterial
Pseudocyphellaria	42	25	17
Sticta	13	8	5

*Source: D. J. Galloway (1985).

in a lowland rainforest. This rate is well below the 1·0 mg $cm^{-2} s^{-1}$ used by Proctor (1979) when discussing the water relations of bryophytes.

The general picture of these rainforests is of a dim, moist environment with ample rainfall and low evaporation within the forest. A marked contrast with the environments of the Northern Hemisphere broadleaf forests reflects the annual constancy of the environment, imposed by the evergreen canopy. Similar environments do occur in some northern conifer forests, for example the coastal forests of Washington State, USA, where abundant lichens are also found.

Rainforest lichens

The New Zealand rainforests possess a wide diversity of lichen species. The most visually obvious are the large, foliose members of the genera *Sticta* and *Pseudocyphellaria*. A summary of species number and photobiont type of these two genera is given in Table 1. These genera are so rare in northern hemisphere countries that, in the United Kingdom for example, both are listed for photography only, and not for collection (Richardson 1975, Table 30). In New Zealand by contrast *Sticta* species have even been collected from street trees in Hamilton (population 100 000, North Island).

Lichen biomass, from the forest floor to 2 m in height in a beech (*N. menziesii*, *N. fusca*) forest, has been estimated at 100 kg dw ha^{-1}, with 80% being the single species *P. homoeophylla* (Green *et al.* 1980). The high biomass, coupled with the known nitrogen fixation rates, suggest that these lichens may play a role in the nitrogen budget of these forests (Green *et al.* 1980).

The genera *Pseudocyphellaria* and *Sticta* are ecologically diverse and individual species distributions can be related to the major environmental factors such as light intensity (Table 2). The *Pseudocyphellaria* and *Sticta* species appear to be fast growing. Rates up to 27 mm radial growth per year have been found and most are around 10 mm radial growth per year (Table 3). Two species, *P. homoeophylla* and *S. subcaperata*, measured in detail, were found to grow continuously throughout the year (Fig. 2). The radial growth rates of the same lichens were also found to increase with increase in thallus size (Snelgar & Green 1982). This is interesting as growth would normally be expected to be constant or declining in larger thalli but this phenomenon has also been reported previously for *Lobaria* species in North American evergreen forests (Rhoades 1977). A simple energy balance analysis suggests that better water

TABLE 2. *Distribution of selected species with respect to light environment*

Light environment*	Species	Photosynthetic light saturation (μmol m^{-2} s^{-1}, PAR)‡	Photobiont§
High intensity; canopy	*Pseudocyphellaria coronata*	—	G
	P. colensoi	110	G
	P. delisea	160	G
	P. crocata	—	C
Medium intensity; branches	*P. rufovirescens*	100	G
Low intensity; above forest floor (shrub branches, tree trunks)	*P. faveolata*	—	G
	P. lividofusca	100	G
	Sticta latifrons	90	G
Low intensity; forest floor (trunks, buttresses)	*P. homoeophylla*	100	G
	S. subcaperata	—	G
	S. filix	—	G
Deep shade	*P. dissimilis*	20	C

*Distributions based on personal observations in lowland podocarp/hardwood forests near Hamilton and montane beech forests at Waikaremoana, Urewera National Park.

‡From Snelgar (1981) except *P. dissimilis* (Green *et al.* 1991). Light saturation was measured at 350 μbar CO_2 and optimal values of thallus water content and temperature.

§Photobiont: G = green; C = cyanobacterial. All green algal photobiont lichens have cephalodia.

TABLE 3. *Growth rates of* Pseudocyphellaria *and* Sticta *species*

Species	Maximum mean annual radial growth rate (mm)
Pseudocyphellaria lividofusca	6·4 (3)*
P. colensoi	8·6 (1)
P. faveolata	12·5 (2)
P. homoeophylla	13·2 (22)
Sticta subcaperata	7·0 (40)
S. filix	11·6 (3)

*Number of replicates.
All lichens measured over 20 months at Lake Waikareiti, Urewera National Park (Snelgar 1981).

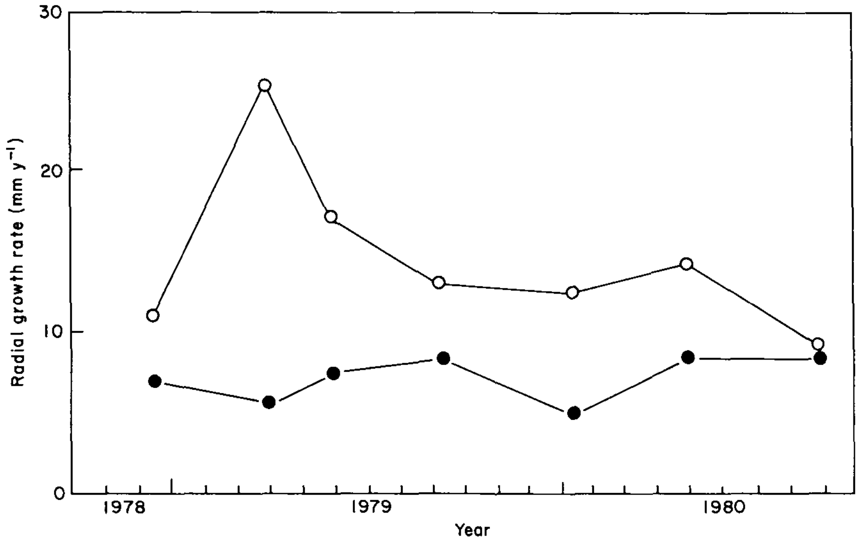

FIG. 2. Annual pattern of radial growth of *Pseudocyphellaria homoeophylla* (○) and *Sticta subcaperata* (●) in the montane *Nothofagus* forests of the Urewera National Park. Photographs were taken at intervals over 21 months and growth of individual lobes was measured on 12 thalli of each species. Corrections were made for parallax errors (Snelgar & Green 1982).

relations, lower water loss per unit area, in these constant low radiation forest environments may extend the photosynthetic period for these large thalli (Green *et al.* 1985). The two genera also show a great diversity of thallus form. Species of *Sticta* can be stipitate (*S. latifrons* and *S. filix*), a form that allows excellent light interception for species growing on tree trunks, or foliose, in which case they may be broadly lobate to highly dissected, with all gradations occurring in the single species *S. subcaperata. Pseudocyphellaria* species are all

TABLE 4. *Water holding capacity and calculated period of photosynthetic activity for different* Pseudocyphellaria *species*

Species	Water storage (mg cm^{-2})		Photosynthetic period (h)*	
	Internal	External	0·14‡	0·88‡
Pseudocyphellaria dissimilis				
sun	10	5	12	2·1
shade	6	15	50	7·9
P. rufovirescens	20	5	23	3·9
(top full)§	20	50	64	11·0
P. colensoi	15	13	26	4·4
P. homoeophylla	21	23	87	14

*Photosynthetic period is calculated as the time taken for a saturated lichen thallus to dry, at the specified evaporation rate, to the thallus water content at which there is zero net photosynthesis.
‡Evaporation rate (μg cm^{-2} s^{-1}), calculated from Piché evaporimeters over a 12-day period. Although not likely to be identical this rate is expected to be similar for wet lichen thalli, which have often been referred to as having the water relations of filter paper (Snelgar & Green 1981*a*).
§The faveolate depressions on the upper thallus surface are full of water.

foliose but can be strongly or weakly faveolate, occasionally pubescent and with variable, nude to dense, lower tomentum. Pseudocyphellae may be found on upper as well as lower surfaces (*P. lividofusca*). Thus, these rainforests possess large lichens that grow rapidly and show diversity between and within species in form and ecology.

Environment: structure interactions

CO_2 gas exchange/structure relationship

The CO_2 gas exchange parameters of several *Pseudocyphellaria* and *Sticta* species have been investigated with an emphasis on obtaining information about diffusion pathways and diffusion resistances (Green *et al.* 1985). The major features of this work can be summarized as follows. First, the pseudocyphellae and cyphellae, which characterize these lichens, are the major CO_2 exchange pathways (Green *et al.* 1981) whereas water loss occurs over the whole thallus surface (Green & Snelgar 1982). Second, the pseudocyphellae or cyphellae represent a diffusion resistance that is higher than the remainder of the CO_2 diffusion pathway. This feature may enhance internal recycling of respiratory CO_2 (Snelgar & Green 1981*b*) and produce a moist, internal atmosphere inside the lichen that protects the photobiont from excessive drying. Third, there is some circumstantial evidence for protected (waterproofed by lichen substances) CO_2 diffusion pathways inside the medulla (Green *et al.* 1985). Fourth, by confining CO_2 diffusion to a limited area, other parts of the lichen surface and internal medulla are available for water storage. The faveolate upper surface of *P. rufovirescens* can act as an important water store (Table 4, adapted from Green *et al.* 1985). Thus the thallus of those lichens forms a complex structure adapted to combine CO_2 exchange through gas

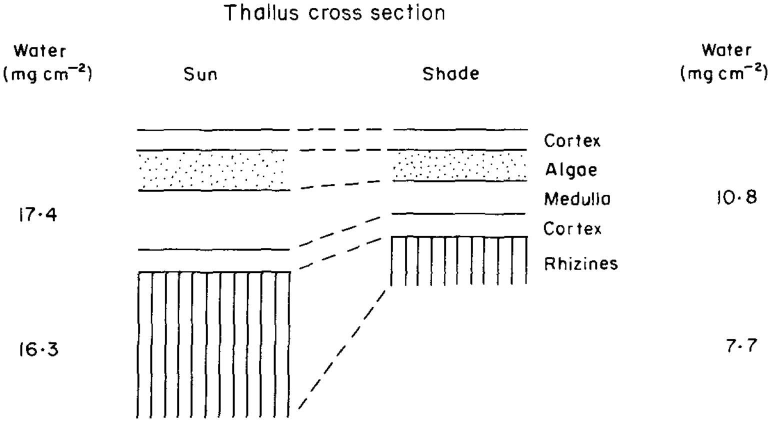

FIG. 3. Thallus dimension and water storage capacity in two populations of *Pseudocyphellaria dissimilis*. Definitions of ' sun ' and ' shade ' populations and full measurement details are in Snelgar & Green (1981*a*). Thallus dimensions are in μm.

exchange pores, which are kept clear of blockage by water that is stored elsewhere on and in the thallus. Water storage is a feasible adaptation in these lichens because of the constant, low radiation environment. This reduces the risk of photoinhibition or high light damage that would exist if the thalli experienced light stress before the thallus had dried.

Morphology and environmental drying potential

Pseudocyphellaria dissimilis shows changes in thallus morphology that can be related to the evaporative conditions of the environment. Modifications of the thallus, especially the rhizinae, allow greatly increased water storage under more drying conditions (Snelgar & Green 1981*a*). The differences in morphology and water storage are shown diagrammatically in Fig. 3, and clearly correlate with the extended drying period due to the extra water storage (Table 4).

Physiological adaptations to the rainforest environment

Adaptation to deep shade

Pseudocyphellaria dissimilis, which occurs in environments with lower PAR than any other species in the genus, is highly adapted to deep shade (Table 5) (Green *et al.* 1991). Thus, photosynthesis saturates at very low PAR (20 μmol m^{-2} s^{-1}) with PAR compensation at 1 μmol m^{-2} s^{-1} (0·05% full sunlight). These are the lowest values yet known for lichens and, indeed, analysis of the distribution of PAR at the lichen growth sites shows very low values, even in summer. For example, over a 5-day period the most frequent PAR category (excluding zero PAR) was 2 μmol m^{-2} s^{-1}, and over 80% of the total light quanta occurred below 10 μmol m^{-2} s^{-1} (Fig. 4). Simple CO_2 exchange modelling by combining the PAR response curve of photosynthesis (Green *et al.* 1991) with the PAR distribution data shows 60% of positive net CO_2

TABLE 5. *Shade adaptations of* Pseudocyphellaria dissimilis

Photosynthesis*		
PAR-saturation	20 μmol m^{-2} s^{-1}	[lowest known]
-compensation	1 μmol m^{-2} s^{-1}	[lowest known]
Rate (dw basis)	1 mg g^{-1} h^{-1}	[80% normal]‡
(area basis)	0·2 μmol m^{-2} s^{-1}	[20% normal]‡
Respiration*		
Rate (dw basis)	0·3 mg g^{-1} h^{-1}	[60% normal]‡
(area basis)	0·1 μmol m^{-2} s^{-1}	[20% normal]‡
Thallus Features		
	Light Environment§	
	Shade	Sun
Thickness (μm)§	190	396
Weight per unit area (g m^{-2})§	59	90
	—	260 (*Ramalina maciformis*)♯
	—	100 (*Peltigera aphthosa*)§
Chlorophyll (mg g^{-1})§	0·24	0·18
		0·4–2·0 (other lichens)♯

*Data from Green *et al.* (1991).
‡Normal is the mean value for other *Pseudocyphellaria* and *Sticta* lichens (Snelgar 1981).
§Terminology and dimensions from Snelgar & Green (1981*a*).
♯Data from Demmig-Adams *et al.* (1990*a*).

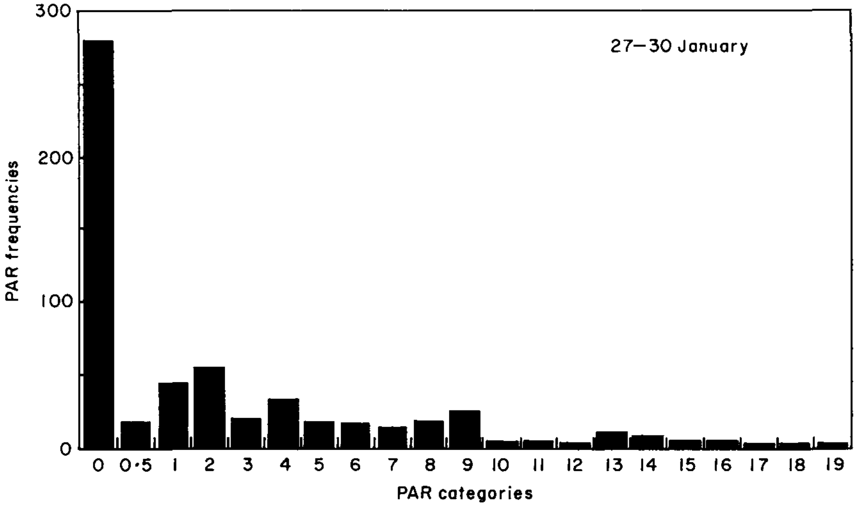

FIG. 4. Analysis of the distribution of PAR in the deep-shade habitat of *Pseudocyphellaria dissimilis*. Measurements of mean PAR were determined for 10 min intervals for 27 to 30 January 1988 (inclusive) as described in Green *et al.* (1991). Frequency distribution of PAR: columns are the number of occurrences of particular PAR categories (eg: category O contains all measurement periods showing zero PAR, 0·5 = values between 0 and 0·99 μmol m^{-2} s^{-1}, 1 = values between 1·0 and 1·99, and so on).

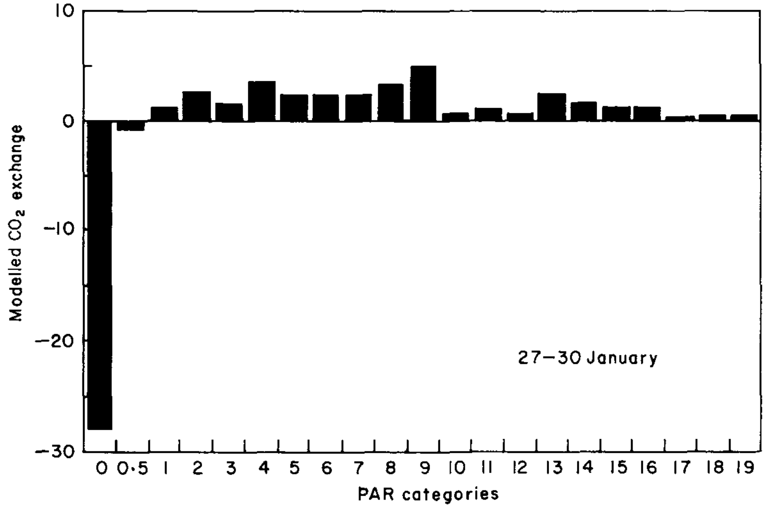

FIG. 5. Distribution of CO_2 exchange with respect to PAR categories. CO_2 exchange was calculated by combining the response of CO_2 exchange to PAR (Green *et al.* 1991) with the number of occurrences of the particular PAR category. The calculation does not take temperature into account but this may not be a major error since CO_2 exchange is relatively stable between 15°C and 30°C, and night temperatures average about 15°C. Optimal thallus water content is assumed and this is discussed in the text.

exchange to occur below 10 μmol m^{-2} s^{-1} and only 9% above 14 μmol m^{-2} s^{-1} (Fig. 5). The model also shows 95% of production to be lost by respiration when PAR was below light compensation (Fig. 5). The model is crude and relies on the thalli being at optimum water content all day, an unlikely situation. It is more likely that the pattern is broadly similar, although more extended in time, to that shown by *Ramalina maciformis* (Lange *et al.* 1970). In that case the thallus becomes wetted by dew or moist air during the night and then dries slowly during the morning, which is also possible in rainforests through drip from canopy leaves. The balance between respiration and photosynthesis is determined, in part, by the relative periods during the night and day when the thallus was wet. Unfortunately no data exist for thallus water contents in the field for New Zealand lichens.

Pseudocyphellaria dissimilis also shows major changes in thallus thickness and weight per unit area with environmental PAR (Table 5). The result of these changes is a strong depression (to 20% of other species) in the photosynthetic rate and respiration when expressed on an area basis (Table 5). Thallus weight per unit area and chlorophyll content are also lower than for other, high-light-requiring lichens. These changes are typical of those expected for the shade response by higher plants and it is interesting that the modifications are similar across such taxonomically different plants (Boardman 1977).

Desiccation sensitivity

The dominant feature of the rainforest environment is its constancy. The constant low light levels have led to shade-adapted thalli. It is now known that

TABLE 6. *Effect of drying for 20 h at various relative humidities on the gross photosynthesis of* P. dissimilis

	Gross photosynthesis* at different time periods (h) after rewetting		
Humidity (%)	0 h	3 h	24–48 h
45–60	80	90	105
25–44	70	75	90
15–24	25	50	60
5–14	5→0	20→0	40→0

*Gross photosynthesis is rate of gross CO_2 uptake after the desiccation treatment as % original rate. For details see Green *et al.* (1991).

under the constant high humidity *P. dissimilis* has evolved to be desiccation sensitive. Green *et al.* (1991) challenged *P. dissimilis* with a standard drying routine in which wet thalli were allowed to equilibrate with air streams of known r.h. for 20 h. CO_2 exchange of the thalli was measured under optimum light, temperature and thallus water content before and after the drying treatment, and after 24–48 h recovery (thalli rewetted and maintained at 100% r.h. in low light). Depressions in gross photosynthesis were found immediately after all treatments below 60% r.h. (Table 6). After 24–48 h recovery, continued depression was found in treatments below 25% r.h. and some thalli were killed (no detectable gross photosynthesis, loss of cyanobacterial pigments and bad smell) below 15% r.h. This is exceptional sensitivity to desiccation for a lichen, especially a terrestrial lichen, and exceeds the sensitivity reported for aquatic lichens (Ried 1960).

Humidity sensitivity

A complicated situation has been revealed by an investigation into the effect of various r.h. percent on lichen CO_2 exchange. Three species (*P. crocata, P. rufovirescens* and *S. latifrons*) were kept for 11 days in desiccators at a range of r.h. at 20°C, 12 h light (20 μmol m^{-2} s^{-1}, PAR), 12 h dark. The CO_2 exchange of each lichen replicate was measured both before and after the desiccation treatment at optimal thallus water content, 15°C, 350 μbar CO_2 and 150 μmol m^{-2} s^{-1} PAR (saturating for photosynthesis) or 0 μmol m^{-2} s^{-1} (for respiration). Gross photosynthesis (as % original rate) was unaffected at any r.h. for *P. crocata*, a high-light species; depressed at r.h. less than 50% for *S. latifrons*, a low-light species; but depressed above 60% r.h. for *P. rufovirescens*, a medium-light species (Fig. 6). These results are not easy to comprehend. Extreme sensitivity to low humidities has previously been found for *P. dissimilis* (see previous section) but sensitivity to high humidities is unexpected. One possible explanation has been suggested by Lange (1969) who found *R. maciformis* to die when held at 65% r.h. for 28 weeks. Under the treatment conditions the lichens may be moist enough to become metabolically activated but not to show positive net photosynthesis so that the plants, in effect, respire themselves to death.

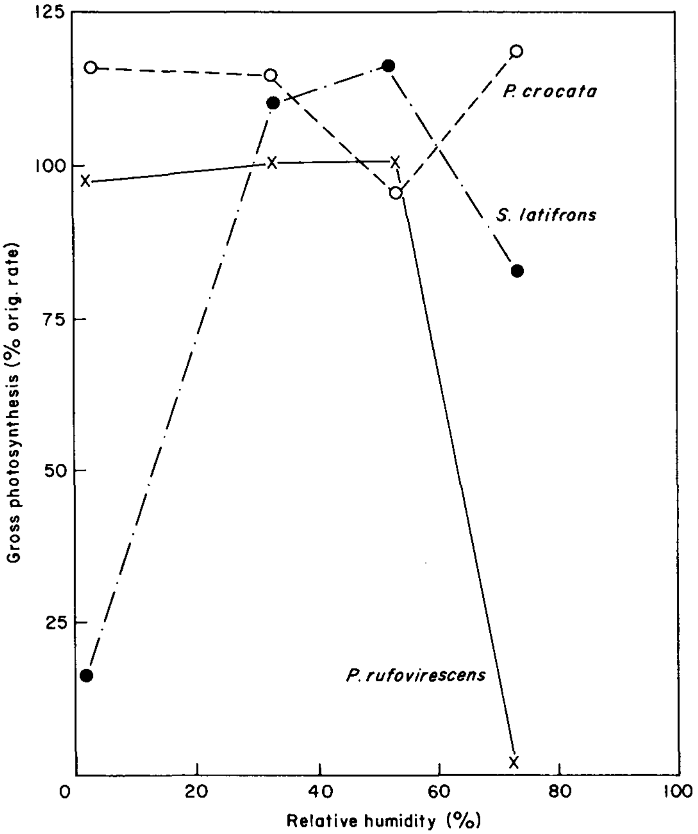

FIG. 6. Effect of storage at various humidities on the gross photosynthesis of *Sticta latifrons* (G), *Pseudocyphellaria crocata* (C) and *P. rufovirescens* (G). Gas exchange measurements were made at 15°C, 150 µmol $m^{-2} s^{-1}$ (saturating), 350 µbar CO_2 and optimal thallus water content. Replicates were held moist at 22 µmol $m^{-2} s^{-1}$, 13°C for 24 h before gas exchange measurements prior and after humidity treatments. Humidity treatments were over saturated salt solutions at 1%, 32·3%, 52% and 72·6% r.h. at 20°C for 11 days; PAR was 0 or 20 µmol $m^{-2} s^{-1}$ on a 12/12 h diel cycle. Each point is the mean of five replicates. Lichens were collected from adjoining *Dacrycarpus dacrydioides* trees near the Mangaotaki Scenic Reserve, Pio Pio.

Photobiont versatility

Photobiont versatility in *Sticta* and *Pseudocyphellaria* was first discussed in detail by James & Henssen (1976). The article concentrated on possible morphological changes produced by a change in photobiont. One example was the coralloid *Dendriscocaulon* (cyanobacterial photobiont) bearing flat, foliose lobes of *Sticta filix* green algal photobiont, both sharing the same mycobiont. It is now apparent that photobiont versatility is much more widespread but leads to little morphological change in *Pseudocyphellaria*. Green *et al.* (1987) demonstrated that several apparently cyanobacterial photobiont *Pseudocyphellaria* species actually contain a significant (contributing up to 30% of net photosynthesis) green algal co-primary photobiont. However, the most impressive demonstration of this versatility is the occurrence of photosymbiodemes. Photosymbiodemes (Renner & Galloway 1982) are combined thalli containing both green algal and cyanobacterial sectors (see Brodo & Richardson 1978; Demmig-Adams *et al.* 1990*b* for pictures). When growing separately the green algal and cyanobacterial forms are regarded as distinct species.

Photosymbiodemes provide unique physiological material since sectors with different photobionts have grown under identical environmental, particularly PAR, conditions. It is possible to use these plants to discover whether certain physiological traits are photobiont-determined since they are regarded as possessing the identical mycobiont. Two examples have been published of their use.

Lange *et al.* (1988) used the photosymbiodeme of *P. rufovirescens* (green algal) and *P. murrayi* (cyanobacterial) to show that the ability to carry out positive net photosynthesis using only water vapour was exclusively a property of green algal photobionts. Different carbon isotope discrimination values were also shown to be photobiont-determined since the differences were maintained in the cyanobacterial and green algal sectors of the photosymbiodeme (−23·14‰ and −26·78‰ respectively).

Demmig-Adams *et al.* (1990*b*) used the same photosymbiodeme to demonstrate the importance of the xanthophyll cycle in protecting against photoinhibitory damage from high light. The value of the photosymbiodeme was that both partners had an identical light environment history. However, the cyanobacterial photobiont did not contain the xanthophyll cycle, whereas the green algal photobiont did. A 2 h high light treatment resulted in large reductions in the efficiency of photosynthetic energy conversion, which were rapidly reversible in the green algal photobiont, but were long lasting, and even irreversible, in the cyanobacterial photobiont (Table 7). Changes in the fluorescence characteristics indicated that the cause of the depression in photosynthetic energy conversion was a reversible increase in radiationless energy dissipation in the green algal photobiont and ‘photoinhibitory damage’ in the cyanobacterial photobiont. This was a clear demonstration of the importance of the xanthophyll cycle as a protection mechanism against high light damage. Demmig-Adams *et al.* (1990*a*,*c*) have extended this work using both photosymbiodemes and individual cyanobacterial and green algal species. This major difference between green algal and cyanobacterial photobionts may well be of importance in the ecology of lichens with different photobionts.

Conclusions

In comparison to lichen ecophysiological studies in other environments research on lichen adaptations to rainforests is still at an early stage. However, the combination of excellent experimental material with modern techniques has produced unexpected and interesting results. The lichens of the genera *Sticta* and *Pseudocyphellaria* are numerous in species number and form. They appear to be fast growing and show considerable adaptation and versatility at several levels. As well as normal specific differences it seems that morphological

TABLE 7. *Effect of high light treatment on the photochemical parameters of the blue-green and green sectors of a photosymbiodeme*

Photochemical parameters*	Before high light	Immediately after high light	After high light (80 h)
Pseudocyphellaria murrayi			
Fv/Fm	0·68	0·00	0·25
Fo (% of control Fm)	33	80	60
Fm (% of control Fm)	100	80	85
Pseudocyphellaria rufovirescens			
Fv/Fm	0·70	0·00	0·58
Fo (% of control Fm)	30	32	30
Fm (% of control Fm)	100	30	78

*The photochemical parameters are: Fm = maximum yield of fluorescence induced by pulses of saturating light; Fo = yield of instantaneous fluorescence; Fv = yield of variable fluorescence (Fm-Fo) induced by pulses of saturating light. Data from Demmig-Adams *et al.* (1990*b*) for the photosymbiodeme of *Pseudocyphellaria rufovirescens* (green algal) and *P. murrayi* (cyanobacterial).

modification by the environmment can occur. At the moment good data are available only for a relationship between water storage and evaporative demand in *P. dissimilis*. Thallus structure itself can be interpreted as an interaction between CO_2 gas exchange and water storage. The ability to store water probably reflects the constant, low PAR found in these evergreen forests, with a low risk of high radiation damage.

The lichens also show a wide range of physiological versatility with some unexpected properties. Unusual desiccation sensitivity is an important extension to our understanding of lichen physiology. Of general interest is the shade response shown by *P. dissimilis*, which appears almost identical to that of higher plants. The complexity of photobiont/mycobiont relationships in these genera has provided some unique experimental material that has allowed some key physiological differences to be confirmed between cyanobacterial and green algal photobionts. The majority of the CO_2 gas exchange research has been carried out at 'normal' atmospheric CO_2 concentration (350 μbar). There is evidence that these lichens may be strongly CO_2-limited (see *P. dissimilis* in Green *et al.* 1991) and higher CO_2 concentrations produce improved photosynthesis and quantum use. High ambient CO_2 concentrations may well be an important, but as yet unreported, feature of these forests as a result of soil respiration.

Overall, the lichens represent a huge ecophysiological resource that has yet to be adequately researched. It is apparent that the complexities of the *Sticta* and *Pseudocyphellaria* genera, combined with the low-light humid constancy of the rainforests, provide considerable scope for future research. Aspects such as response to temperature and changes in performance throughout the year have still to be taken further than initial observations. It is also apparent that many of these complexities will not be solved without measurements being made in the natural lichen habitat. An extensive programme of such experimentation is about to be implemented. It is quite likely that our present conception of the boundaries of lichen ecophysiology will need to change yet again as this work is completed.

The work reported here was supported by the Deutsche Forschungsgemeinschaft (Forschergruppe Ökophysiologie and Sonderforschungsbereich 251 of the University of Würzburg) and the New Zealand University Grants Committee. Dr T. G. Allan Green gratefully acknowledges the support of a fellowship from the Alexander von Humboldt-Stiftung. The Department of Conservation is thanked for permission to collect lichens in reserve areas. Staff of the Urewera National Park are particularly thanked for their continuing support throughout this work.

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Accepted for publication 30 *April* 1991