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Water status related photosynthesis and carbon isotope discrimination in species of the lichen genus *Pseudocyphellaria* with green or blue-green photobionts and in photosymbiodemes

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Summary. Green lichens have been shown to attain positive net photosynthesis in the presence of water vapour while blue-green lichens require liquid water (Lange et al. 1986). This behaviour is confirmed not only for species with differing photobionts in the genus *Pseudocyphellaria* but for green and blue-green photobionts in a single joined thallus (photosymbiodeme), with a single mycobiont, and also when adjacent as co-primary photobionts. The different response is therefore a property of the photobiont. The results are consistent with published photosynthesis/water content response curves. The minimum thallus water content for positive net photosynthesis appears to be much lower in green lichens (15% to 30%, related to dry weight) compared to blue-greens (85% to 100%). Since both types of lichen rehydrate to about 50% water content by water vapour uptake only green lichens will show positive net photosynthesis. It is proposed that the presence of sugar alcohols in green algae allow them to retain a liquid pool (concentrated solution) in their chloroplasts at low water potentials and even to reform it by water vapour uptake after being dried. The previously shown difference in $\delta^{13}C$ values between blue-green and green lichens is also retained in a photosymbiodeme and must be photobiont determined. The wide range of $\delta^{13}C$ values in lichens can be explained by a C_3 carboxylation system and the various effects of different limiting processes for photosynthetic CO_2 fixation. If carboxylation is rate limiting, there will be a strong discrimination of $^{13}CO_2$, at high internal CO_2 partial pressure. The resulting very low $\delta^{13}C$ values (−31 to −35‰) have been found only in green lichens which are able to photosynthesize at low thallus water content by equilibraiton with water vapour. When the liquid phase diffusion of CO_2 becomes more and more rate limiting and the internal CO_2 pressure decreases, the ^{13}C content of the photosynthates increases and less negative $\delta^{13}C$ values results, as are found for blue-green lichens.

Key words: Photosymbiodeme – Phycosymbiodeme – Delta^{13}C – Lichen – Photosynthesis

Early observations on the water relations of lichen thalli (e.g. Zukal 1895) revealed that differences could be found depending on thallus form (homoiomerous or heteromerous) or thallus structure (presence of cyphellae). Differences also occurred during wetting of the thallus (with water or humidity) or in drying conditions. It was also noted that some lichens may survive and grow without any significant source of liquid water relying instead on water vapour uptake. Recent quantitative studies carried out by Larson and Kershaw (1976) recognized that changes in form, particularly in the ratio of edge length to area, could significantly alter thallus water loss. Essentially lichens could still be regarded as behaving like a gel but the form of the gel could be altered in an adaptive manner. These concepts were further advanced when changes in thallus thickness and rhizinae development could be found to produce alterations in thallus water storage that reflected habitat evaporative demand (Larson 1979; Snelgar and Green 1981). Green et al. (1985) were able to provide an explanation for thallus form in *Sticta* spp. and *Pseudocyphellaria* spp. in terms of a compromise between water storage and interference of the stored water with photosynthetic gas exchange.

Until recently no comparison had been made between the photosynthesis of thalli with differing photobionts with respect to the origin of thallus water. Lange and Kilian (1985) noted that, whereas thalli with green photobionts were able to attain positive net CO_2 assimilation by water vapour uptake alone, the three lichens studied with blue-green photobionts could not do so. A broader survey found this to be a constant difference between blue-green and green lichens, even within the same genus (Lange et al. 1986). A difference was also found between the carbon isotope discrimination values of the thallus material of blue-green and green lichens (Lange and Ziegler 1986). Green lichens had discrimination values between −17‰ to −35‰, while blue-green lichens showed a much smaller range that was restricted to higher values from −14‰ to −23‰ (homoiomerous thalli) and −17‰ to −23‰ (heteromerous thalli). It was proposed that the requirement for liquid water by the blue-green lichens for positive net photosynthesis resulted in higher diffusion resistances in the thalli for CO_2 which then caused the less negative discrimination values (cf. Vogel 1980).

In this paper results are presented that show that these differences are maintained not only within a single genus but also within a single thallus where different photobionts

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Table 1. Lichens (*Pseudocyphellaria* ssp.) used for gas exchange or carbon isotope discrimination and their collection sites

Lichen species	Collection site[a]
Ps. allani D. Galloway	1
Ps. anomala Magn.	5
Ps. anthraspis (Ach.) Magn.	5
Ps. carpoloma (Delise) Vainio	1
Ps. colensoi (Church. Bab.) Vainio	1, 2
Ps. coriacea (J.D. Hook. et Taylor) D. Galloway et P. James	1
Ps. coronata (Müll. Arg.) Malme	3
Ps. delisea (Fee ex Delise) D. Galloway et P. James	2
Ps. dissimilis (Nyl.) D. Galloway et P. James	1, 3
Ps. episticta (Nyl.) Vainio	1
Ps. hookeri (Church. Bab.) D. Galloway et P. James	3, 4
Ps. lividofusca (Krempelh.) D. Galloway et P. James	3
Ps. psilophylla (Müll. Arg.) D. Galloway et P. James	3
Ps. unknown	6
Photosymbiodeme (*Ps. murrayi* and *Ps. rufovirescens*)	1
Free-living photosymbiodeme species	
Ps. murrayi D. Galloway	1, 2
Ps. rufovirescens (Church. Bab.) D. Galloway	1, 3

[a] Collection sites:
1 Hakarimata Reserve, Ngaruawahia, New Zealand
2 Stubb's Farm, Waitomo, New Zealand
3 Te Kauri Reserve, Kawhia, New Zealand
4 Mangaotaki Reserve, Pio Pio, New Zealand
5 Hastings Natural History Reservation, Monterey County, California, USA
6 Ottertrail, Tsitsikama, S.-Africa

Table 2. Carbon isotope discrimination values for free-growing *Pseudocyphellaria* species (*BG* = blue-green photobiont; *G* = green photobiont)

Species	(origin)	Photobiont type	Carbon isotope discrimination (‰)
Ps. anthraspis	(California)	BG	−20.62
Ps. anomala	(California)	BG	−21.28
Ps. hookeri	(NZ)	BG	−23.22
Ps. hookeri	(NZ)	BG	−24.44
Ps. lividofusca	(NZ)	G	−25.13
Ps. carpoloma	(NZ)	G	−25.13
Ps. allani	(NZ)	BG	−25.31
Ps. episticta	(NZ)	G	−25.45
Ps. dissimilis	(NZ)	BG	−25.45
Ps. dissimilis	(NZ)	BG	−25.61
Ps. coriacea	(NZ) (n = 3)	G	−25.87 (−25.79 to −25.92)
Ps. psilophylla	(NZ)	G	−28.48
Ps. unknown	(South Africa)	G	−31.19
Ps. colensoi	(NZ)	G	−33.17
Ps. delisei	(NZ)	G	−33.29
Ps. colensoi	(NZ)	G	−34.24
Ps. coronata	(NZ)	G	−35.35

are present. Such compound thalli have been defined as 'photosymbiodemes' and have distinct sectors present with green or blue-green photobionts but sharing the same mycobiont (Renner and Galloway 1982). The carbon isotope discrimination values are also discussed taking into account published information on the importance of internal carbon dioxide concentration and quantitative estimates of diffusion resistance values.

Materials and methods

Lichens were collected in several locations as detailed in Table 1. Thalli were chosen to be as free of extraneous material as possible and were airmailed to Würzburg after air-drying in the laboratory. Gas exchange measurements were then carried out according to the procedures fully described in Lange et al. (1986). These involved rewetting and cleaning the thalli then holding them at 10° C in a 12:12 h dark/light (17 μmol m^{-2} s^{-1} photosynthetically active radiation – PAR) regime for four days. The thalli were subsequently dried to 1% to 4% of their dry weight in a desiccator over silica gel for 3.5 days. The dry thalli were then allowed to carry out water vapour uptake in a moist (96%–97% RH) air stream at 15° C predominantly in the dark with great care being taken to prevent any water condensation. Gas exchange readings in the dark and in short light breaks (30 min, 150 μmol m^{-2} s^{-1} PAR) were made over a period of about 70 h. By that time water potential equilibrium had been reached between the lichen thalli and ambient air. Thalli were then sprayed with water to allow measurements at high thallus water contents, and these were continued as the lichens were allowed to dry in a 80% RH, 15° C, air stream. Only a selection of thalli could be used for gas exchange studies but samples of all species were analysed for carbon isotope discrimination at the Institut für Hydrologie, GSF München, according to standard procedures (Osmond et al. 1975). Considerable care was taken in the isotope discrimination analyses since the differences being investigated were not expected to be large. Measurements made on multiple samples from single lichen thalli were very consistent, with the largest range of $\delta^{13}C$ values being only 1.5‰ and the lowest 0.17‰ (Tables 2, 3).

Results

Gas exchange: lichens with green photobionts

The four green species investigated all showed a similar pattern of gas exchange (Fig. 1, upper panel). Both respiration and positive net photosynthesis reached maximum values after around 20 h exposure of the dry thallus at 96%–97% RH, 15° C. Thallus water contents stabilized between 40% and 50% (dry weight basis). On addition of liquid water after 70 h there was an immediate change in gas exchange. Dark respiration rates increased markedly, then fell slightly to a stable value before a further decline as the thallus dried out. Net photosynthesis initially fell, then recovered to a maximum value that exceeded the rate before the addition of water in all species except *Pseudocyphellaria episticta*. Net photosynthesis then declined as the thallus dried. The dramatic change in respiration rates is typical of the resaturation respiration that follows the addition of water to dry thalli (Smith and Molesworth 1973; Farrar and Smith 1976). The changes in net photosynthesis are those expected when there is a sudden increase in respi-

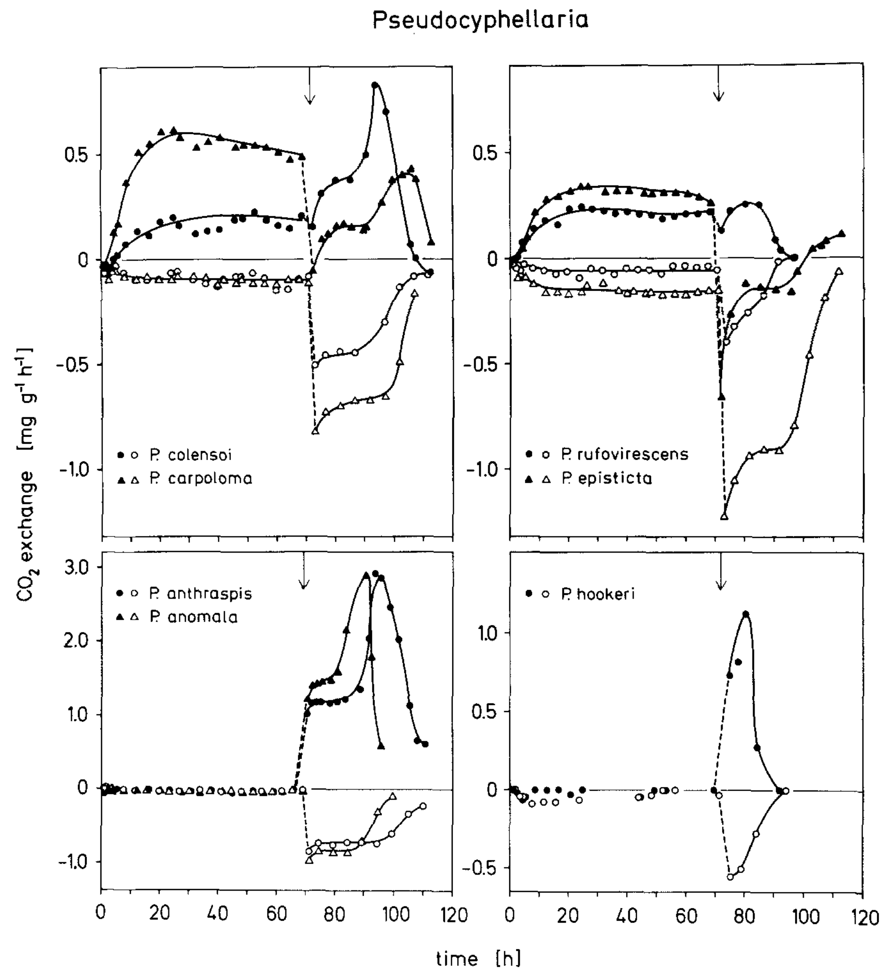

Fig. 1. Net photosynthesis and respiration rates of green and blue-green species of *Pseudocyphellaria* during water vapour uptake and subsequent rewetting with water. Upper panels: green species; lower panels: blue-green species. Net photosynthesis: *closed symbols;* Respiration: *open symbols.* All measurements were made at 96%–97% RH, 15° C during water vapour uptake and 80% RH, 15° C after addition of water (addition time indicated by arrow at top of each panel). Net photosynthesis measurements were made at 150 µmol m^{-2} s^{-1} PAR in short light periods not exceeding 30 min

ration rate and also increased diffusion resistances at high thallus water contents (Snelgar et al. 1981; Lange and Tenhunen 1981). These response patterns correspond exactly to those previously reported (Lange and Kilian 1985; Lange et al. 1986; Lange and Ziegler 1986).

Lichens with blue-green photobionts

The performance of the blue-green lichens during water vapour uptake and subsequent spraying with water contrasted strongly with that of the green lichens (Fig. 1, lower panel). In the three species studied, no positive net photosynthesis could be detected during the 70 h of water vapour uptake although thalli reached water contents similar to the green lichens. On addition of water, positive net photosynthesis occurred together with increased respiratory rates. Gas exchange then declined as the lichens dried. This pattern is again typical of that found in other blue-green lichens.

Photosymbiodemes

Renner and Galloway (1982) proposed the term 'phycosymbiodeme' to describe a joined lichen thallus composed of two closely similar 'species' apparently differing in the presence of a green or blue-green phycobiont. The modified term 'photosymbiodeme' is used here to cover the non-algal status of the cyanobacteria (Ahmadjian 1982). The two members of a photosymbiodeme are capable of independent existence and may sometimes be found as separate individuals in close proximity to each other. Photosymbiodemes appear to be a feature of the Peltigerinae and have now been reported for the genera *Peltigera, Sticta, Lobaria, Nephroma,* and *Pseudocyphellaria* (James and Henssen 1976; Renner and Galloway 1982; Tonberg and Holtan-Hartwig 1983). The photosymbiodemes possess obvious potential as research material in lichen physiology.

The gas exchange patterns for the separated green and blue-green sectors of a photosymbiodeme are shown in Fig. 2. The two members of the photosymbiodeme are called *Ps. rufovirescens* (green photobiont) and *Ps. murrayi* (blue-green photobiont) when growing separately. The different responses to water vapour uptake and water addition shown by separate green and blue-green lichens are retained by the photobionts even when growing within a single thallus. Since the different sectors of the photosymbiodeme have grown under the same conditions and share the same mycobiont the different gas exchange patterns must be specific to the photobiont.

Lichens with differing co-primary photobionts

There have been recent reports that there is considerably more versatility with respect to the photobiont in the Pelti-

Table 3. Carbon isotope discrimination values for Photosymbiodemes and their separate free-growing members (New Zealand) (*BG* = blue-green photobiont; *G* = green photobiont)

Lichen species	Photobiont type	Number of samples	Carbon isotope discrimination (average)	Range
Photosymbiodeme: Specimen 1				
Ps. rufovirescens	G	(n = 10)	−26.95	(−26.12 to −27.60)
Ps. murrayi	BG	(n = 10)	−23.36	(−22.61 to −23.77)
Photosymbiodeme: Specimen 2				
Ps. rufovirescens	G	(n = 3)	−26.78	(−26.70 to −26.87)
Ps. murrayi	BG	(n = 2)	−23.14	(−23.07 to −23.21)
Free growing members				
Ps. rufovirescens specimen 1	G	(n = 10)	−26.77	(−26.25 to −27.08)
Ps. rufovirescens specimen 2	G	(n = 10)	−34.73	(−34.32 to −35.22)
Ps. rufovirescens specimen 2	G	(n = 1)	−26.56	
Ps. rufovirescens specimen 4	G	(n = 1)	−35.29	
Ps. rufovirescens specimen 5	G	(n = 1)	−35.32	
Ps. murrayi specimen 1	BG	(n = 10)	−23.31	(−23.06 to −23.61)
Ps. murrayi specimen 2	BG	(n = 1)	−23.35	

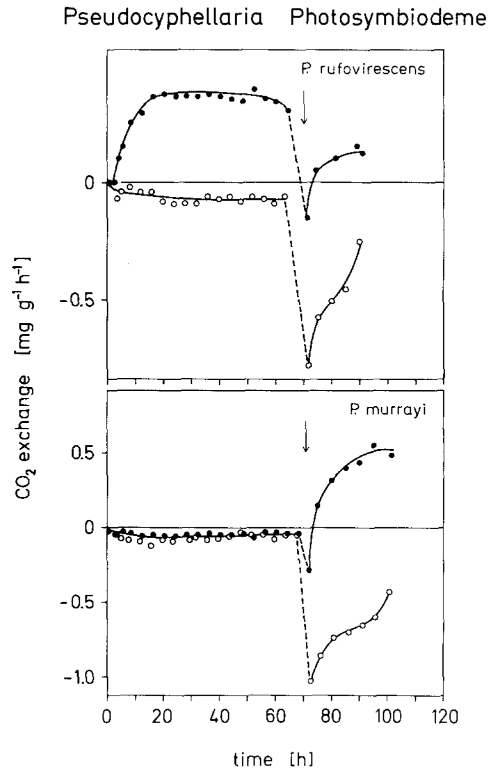

Fig. 2. Net photosynthesis and respiration rates of the separated green (*Pseudocyphellaria rufovirescens*) and blue-green (*Ps. murrayi*) sectors of a single photosymbiodeme during water vapour uptake and subseqeunt wetting with water. Net photosynthesis: *closed symbols*; Respiration: *open symbols*. Other conditions as for Fig. 1

gerinae than previously expected. Green et al. (1987) have shown that apparently blue-green members of *Pseudocyphellaria* (e.g. *Ps. hookeri*) can also contain populations of green algae acting as a co-primary photobiont and physically adjacent to the blue-green photobiont. Since significant (up to 40%) of the thallus simple carbohydrates can be those of the green photobiont a mixed gas exchange response would also be expected during water vapour uptake and water addition. Such a response is shown in Fig. 2 (lower panel, right) for a specimen of *Ps. hookeri* which tends to exhibit rates of low photosynthesis (compensation point reached in the light in comparison to only dark respiration present) during water vapour uptake (minor green photobiont) and a large increase in net photosynthesis on addition of water (major blue-green photobiont). The different response of the two photobionts seems to be retained even when adjacent in the same thallus.

Carbon isotope discrimination

Carbon isotope discrimination has previously been found to differ between blue-green and green lichens within the same genera (*Lobaria, Peltigera* and *Nephroma*, Lange and Ziegler 1986). An almost identical pattern was found for species within the genus *Pseudocyphellaria* (Table 2). Blue-green species varied from −20.62‰ to −25.61‰ and green species from −25.13‰ to −35.35‰. The same differences between photobiont type were retained when members of a photosymbiodeme were sampled both when growing separately or when part of a joined thallus (Table 3). Analysis of multiple samples taken from lobes with different photobionts in a single photosymbiodeme showed no overlap of carbon isotope discrimination values. The retention of the different discriminations even when linked by a common mycobiont is a further indication of the photobiont as the determinator of the discrimination value. It also suggests that carbon exchange between sectors with different photobionts in a photosymbiodeme must be very low.

Discussion

It has proved possible in this investigation to further extend comparisons between the water vapour uptake and response to liquid water addition of blue-green and green

Table 4. A comparison of photosynthetic rates and thallus water contents obtained by water vapour uptake or drying a wet thallus. This table has been constructed from the data of Snelgar et al. (1980). Photosynthesis at 55% water content has been interpolated from the photosynthesis versus water content curves with 55% being chosen since it was the mean water content reached by lichens at 96.5% RH, 15° C, in Lange and Kilian (1985). Values marked * for *Ps. rufovirescens* and *Ps. colensoi* were taken at thallus water contents of 47% and 40% respectively, these being the actual values obtained for these species. It should be noted that the blue-green species do not achieve positive carbon dioxide exchange at thallus water contents that can be reached in humid air

Species	Water content (% of dry weight)		Photosynthesis (mg CO_2 g^{-1} h^{-1})		
	at photosynthetic compensation	at maximum photosynthesis	at 55% water content	maximum	at 55% water content as % maximum photosynthesis
Blue-green photobionts					
Peltigera dolichorrhiza	180	400	−0.2	6.5	–
Ps. dissimilis	85	200+	−0.1	1.5	–
Green photobionts					
Ps. rufovirescens	15	110	1.75*	3.0	63
Ps. colensoi	15	90	0.55*	1.2	45
Ps. homoeophylla	20	120	1.1	1.6	69
Sticta subcaperata	20	150	0.8	2.0	40
S. latifrons	30	130	0.3	0.8	38

lichens. Members of a further genus are compared (*Pseudocyphellaria*) and also different photobionts forming sectors in a combined thallus with single mycobiont (photosymbiodeme), and adjacent to each other as co-primary photobionts in an apparently blue-green thallus. The results obtained, both for gas exchange and carbon isotope discrimination, reinforce and completely support the earlier conclusions. The photosymbiodeme results are particularly compelling since the two photobionts share an identical mycobiont and growing conditions yet still retain their separate responses to water vapour and carbon discrimination.

Lange et al. (1986) and Lange and Ziegler (1986) proposed that blue-green photobionts require liquid water for positive net photosynthesis. The presence of the liquid water would produce increased diffusion resistances to CO_2 exchange and this would lead to lower carbon isotope discrimination (less negative), since $^{12}CO_2$ and $^{13}CO_2$ are not discriminated during diffusion in liquid water. These concepts are further discussed here taking into account further published data on gas exchange resistances and their relative values.

Water vapour uptake and liquid water

An important first question is whether the photobionts at similar thallus water content behave differently after hydration through water vapour or liquid water. Information towards answering this question can be obtained by comparing the gas exchange patterns of thalli that have identical water contents which have been attained by either water vapour uptake or by liquid water addition and subsequently drying the wet thallus. The two situations could be conceived as being distinct since a thallus remoistened by water vapour uptake may not have 'liquid water' present in the cell or cell wall pores. A thallus that has been moistened with liquid water and then dried to an identical water content would certainly have such water present. A cell wall pore of 21 nm radius (5 nm is a reasonable accepted value for cell walls) would be sufficient to hold pure water by surface tension against 95% RH at 20° C (Nobel 1983). Lange et al. (1986) found no hysteresis effect in thallus water relations for both blue-green and green lichens. Thalli with water contents in equilibrium with 96%–97% RH at 15° C achieved by either water vapour uptake or drying from moistened condition had identical gas exchange patterns. This suggests that the origin of the water in the thallus, whether from liquid or vapour, might be unimportant.

Further, published CO_2 exchange/water content relationships obtained, by drying wet thalli, for identical or similar lichens to those used in this study show the same net photosynthetic rates as those achieved by water vapour uptake at the same thallus water content (Table 4). As examples (from Snelgar et al. 1980): *Ps. dissimilis* and *Peltigera dolichorrhiza* (both blue-green) do not achieve positive net photosynthesis until thallus water contents of 85% and 180% respectively, whereas *Ps. colensoi* and *Ps. rufovirescens* (both green) do so at 15%. At 96%–97% RH, 15° C, thallus water contents of 40%–55% would be expected which would allow only respiration by the blue-green species but up to 60% of maximum net photosynthesis in the green species. It would appear that the mode of hydrating the lichens has no effect on their gas exchange abilities. The major difference is that all lichens, whether blue-green or green, can rehydrate to water contents of between 40% and 60% with water vapour, but that this is below the compensation water content for blue-green lichens. Green lichens seem to have consistently lower thallus water contents for photosynthetic compensation and maximum photosynthesis (15%–30% and 80%–150%) than even heteromerous blue-green lichens (100%–200% and 200%–300%) (see Kershaw 1977; MacFarlane and Kershaw 1977; Snelgar et al. 1980; Kershaw and MacFarlane 1982). In general the thallus water content at which blue-green lichens reach compensation is very similar to that at which green lichens reach maximum photosynthesis. No explanation so far exists for this variation. It is important to note that water contents have traditionally been expressed on a dry weight basis and, therefore, differences in dry weight per unit area could lead to different water contents (Snelgar and Green 1981). However the similarity in the water contents achieved by both blue-green and green lichens when taking up water vapour is a possible argument against this explanation.

In all the above examples the differences between the blue-green and green photobionts were retained whatever the origin of the water. However, in all cases, the final thallus water content had been achieved by equilibrating the lichens with atmospheric water starting with either a dry thallus or a wet thallus. Evidence exists that cyanobacteria behave quite differently depending on whether the environmental water potential is achieved by osmotic means or by equilibration with atmospheric water vapour. It has been shown that the cyanobacterium *Microcoleus* has maximal net photosynthesis at water potentials of −1.8 MPa when grown in liquid suspension but no detectable photosynthesis at the same water potential when equilibrated with moist air (Brock 1975). This strongly suggests that cyanobacteria can photosynthesize at low water potentials but only if liquid water is present. They appear to have no capacity to retain water when in contact with unsaturated air. This argument is further reinforced by the fact that blue-green lichens exhibit positive net photosynthesis down to a water potential of −4.7 MPa when stressed in osmotic solutions whereas they perform no CO_2-assimilation when the same water potentials are generated through water vapour uptake (unpublished results).

The presence of sugar alcohols in the green algae may provide a possible explanation for the different behaviour of the photobionts with respect to water vapour uptake (Hawksworth and Hill 1984). Sugar alcohols have often been suggested to be able to replace water molecules during severe desiccation and to promote stability of large molecules (Parker 1968; Mazur 1968; Webb 1965). It is accepted that they may also act as osmoregulators in both algae and fungi (Hellebust 1976). In the photobionts of green lichens sugar alcohols may act as osmoregulators in the sense that they produce concentrated solutions and, therefore, liquid water at low water potentials. Sugar alcohols must reach high concentrations in the green photobiont, e.g.: in *Ps. rufovirescens* ribitol may be 2%–3% of thallus dry weight or approximately 20%–30% of photobiont dry weight assuming the photobiont forms 10% of the total thallus dry weight (Green, unpublished results). It has been calculated for *Hypogymnia physodes* that the respective osmotic potential contributions of sugar alcohols in the photobiont and mycobiont are: −0.6 and −0.45 MPa at 250% water content and −15.8 and −10.1 MPa at 10% water content (Farrar and Smith 1976). This is sufficient osmotic ability to allow equilibration at 96%–97% RH, 15° C, when the water potential is −4.6 MPa.

In clarification: the green algae could be imagined as containing a sugar alcohol solution plus other cell contents, whilst the blue-green algae contain mainly water plus proteins. In equilibrium with air humidity or after drying the green algae would still contain liquid water in the form of a strong solution down to low total water contents. In contrast cyanobacteria would have dried out leaving only matric water on the proteins even in equilibrium with almost vapour saturated air. It seems probably that such a 'liquid pool' is found in the green algal chloroplast which can occupy almost the entire cellular volume in *Trebouxia* ssp. Although it is easy to visualize the loss of water from the algae when a wet lichen is being dried down and the chloroplast shrinks, it is very difficult to understand how a water pool could reform in a dry lichen in a short period of time during water vapour uptake. However, electron microscope studies in which water-free fixation techniques were used have shown that the cellular (chloroplast) volume of *Trebouxia* does indeed substantially increase and becomes 'turgid' during water vapour uptake by a lichen that had been dried over silica-gel (Brown et al. 1987). It might be that the sugar alcohols in the photobiont chloroplast behave sufficiently like hygroscopic substances to allow a solution to reform by water vapour uptake alone. Such an ability would certainly explain the differences between the photobionts during water vapour uptake.

In summary, it is suggested that green photobiont chloroplasts possess an internal aqueous solution that is not only retained during desiccation, but can also be reformed by water vapour uptake. This is in contrast to the cell of the cyanobacteria which contain such pools only after liquid water has been added to the thalli.

Carbon isotope discrimination

Lange and Ziegler (1986) have used the model of Vogel (1980) to explain the differences in carbon isotope discrimination between blue-green and green lichens. Vogel (1980) developed a ratio, $\beta = R_c/R_d$ (R_c = carboxylation resistance, R_d = diffusion resistance) and stated that at high values (β = 10) high discrimination would be expected (−34‰), but at low values ($\beta = {}^1/_{30}$) discrimination would also be low (−11.1%). At $\beta = 1$ ($R_c = R_d$) a discrimination of around −22‰ would be found. Vogel concluded that for C_3 plants the ratio would be around $\beta = 2$ (range 1 to 10), and R_c would be dominant. Lange and Ziegler (1986) proposed that the presence of liquid water in the lichen thallus would lead to high diffusion resistances, low β and low discrimination. This would explain why blue-green lichens, which require liquid water, tend to have lower discrimination values.

The factors which determine and limit carboxylation resistance (or its inverse, carboxylation efficiency) have been the subject of considerable debate in recent times. Recent modelling suggests that it is better understood as the ribulose bisphosphate-saturated kinetics of ribulose bisphosphate carboxylase and that it cannot be regarded as a true resistance (von Caemmerer and Farquhar 1981). In a further restatement of the same model used by Vogel (1980) carbon isotope discrimination can now be related to diffusion fractionation (−4.4‰ for air), no discrimiation for liquid water, carboxylase fractionation (27‰ for C_3 plants) and the internal CO_2 concentration/external CO_2 concentration ratio (C_i/C_a), the latter being affected by any diffusion pathway resistances and carboxylation resistances (Farquhar et al. 1982). Ratio values around 0.5 would produce a discrimination of −24‰. Lower internal CO_2 (i.e.: resulting from a high diffusion resistance or very efficient carboxylation system) gives a lower ratio and a less negative discrimination value, whereas hgiher internal CO_2 (carboxylase activity limiting with consequent smaller effect due to diffusion pathway) produces a more negative discrimination value. In an attempt to establish the relative magnitudes of diffusion and carboxylation resistances it was found that the lichens studied (all green) produced, on average, values very similar to those suggested by Vogel as typical of C_3 higher plants: $R_c/R_d=2$, C_i/C_a ratio of about 0.6 (Green and Snelgar 1981), discrimination of $-26‰$. Lichens have varied thallus structure and, through their different forms of diffusion pathway, could easily be expected to cover the discrimination range of $-22‰$ to $-27‰$. Less negative values ($-16‰$ to $-20‰$) found for the blue-green lichens must indicate higher diffusional resistance in connection with a high efficiency of the carboxylating systems. Additionally PEP-carboxylation (see discussion in Lange and Ziegler 1986, p. 158), or a HCO_3^+-pumping mechanism might be conceivable; this would supply the photosynthetic apparatus with CO_2 enriched in ^{13}C. These different possibilities cannot be distinguished at the moment but higher diffusion resistances are certainly likely because of the very high thallus water contents required to attain positive net photosynthesis and also because the gelatinous homoiomerous thalli show the least fractionation. A very negative discrimination value ($-30‰$ to $-35‰$) indicates a high internal CO_2 concentration. This would be expected where carboxylation is limited by some factor such as low light or low thallus water content. This is exactly the situation expected for green lichens that have been rehydrated with water vapour below saturation attaining thallus water contents that rarely exceed 55% and are well below the optimum for photosynthesis.

Only green lichens can achieve positive net photosynthesis by water vapour uptake and, therefore, only they would show very negative discrimination values ($-31‰$ to $-35‰$) as well as values for more optimal thallus water contents ($-22‰$ to $-27‰$). The relationship between carbon isotope discrimination and internal CO_2 concentration seems to be an adequate explanation of the wide range of discrimination values found in lichens and the particular difference in values between green and blue-green lichens.

The method of water uptake is of great significance in the ecology of lichens. Only green lichens can grow in areas where the major source of water is atmospheric water vapour. Important locations are the Negev Desert and the coastal deserts of Chile and South Africa. In the Antarctic the cryptoendolithic communities in the drier parts of rocks are dominated by green algae while blue-green associations cover the wetter sides near snow-melt (Friedmann, pers. comm.). The results presented here show that even in the relatively temperature environments of New Zealand the different abilities of the photobionts can be important. An interesting, but at present inconclusive, trend is shown by the surveyed species of Table 2. The less negative discrimination values ($-25‰$ to $-28‰$) are from species found inside the forest on tree trunks. Discrimination values of $-31‰$ to $-35‰$, suggesting a vapour dominated water budged, are found in species from the higher light environment of the canopy. One of these latter species (*Ps. colensoi*) has a very narrow range of thallus water content for net photosynthesis (compensation at 15%, maximum photosynthesis at 80% and thallus water saturation at 150% where photosynthesis is severely depressed; Snelgar et al. 1980). The lichen has no apparent adaptations for water storage and may be adapted for photosynthesis almost entirely through water vapour uptake. *Ps. rufovirescens* (Table 2) shows two discrimination values, one vapour dominated ($-35‰$) and the other in the more optimal water content range ($-27‰$) for thalli collected from two different sites.

The photosymbiodemes represent a particularly interesting case since they must grow in an environment where neither photobiont has a particular advantage. These thalli are characteristically found in marginal environments on the edge of forests in situations where high humidities occur. Small clearings in the forests and stream valleys are suitable areas. However, insufficient information is available at present to be certain which factors control the distributions of the green and blue-green species of *Pseudocyphellaria* in New Zealand. It has been suggested for the *Ps. punctulata* (green) and *Ps. junghuhniana* (blue-green) photosymbiodeme of south-east Asia that the blue-green partner is found in low-light, wet environments, and the green in high-light, canopy branches (James and Henssen 1976). This would be in agreement with the above considerations about the *Pseudocyphellaria* material from New Zealand.

Photosymbiodemes occupy an extremely interesting position in both physiology and ecology. The occurrence together of two different photobionts, which are normally assumed to have different ecologies, has a special relevance to the evolution of lichen species since it indicates the presence of a continuum between two apparently very different lichen types (Wirth 1983).

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