CARBON DIOXIDE EXCHANGE IN LICHENS: RELATIONSHIP BETWEEN THE DIFFUSIVE RESISTANCE OF CARBON DIOXIDE AND WATER VAPOUR

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Abstract: Gaseous diffusion resistances for carbon dioxide and water vapour, thallus water content and thallus water potential were experimentally determined on species of the Stictaceae. The diffusion resistance to water loss was high only at low water contents and correlated closely with thallus water potential. Carbon dioxide diffusion resistances, however, were high at both low and high water contents and, even at medium water contents, were still an order of magnitude greater than the water resistance. These results indicate that carbon dioxide and water vapour exchange occur by different pathways in these lichens. Consequently it is suggested that the lichens have structural adaptations which separate the functions of water uptake, water storage and carbon dioxide exchange.

Introduction

In vascular plants, particularly angiosperm leaves, diffusive resistances have proved to be of considerable significance in the study of photosynthesis and water relations (Jarvis 1971). It is unfortunate that the study of carbon dioxide and water vapour diffusive resistances has been given little emphasis in lichen physiology. Published estimates of carbon dioxide diffusion resistances have only recently appeared for lichens, the first being that of Collins & Farrar (1978) who obtained a value of 138 s cm^{-1} for *Xanthoria parietina*. Studies on large foliose members of the New Zealand Stictaceae have shown that minimum carbon dioxide resistances varied from 30 to 70 s cm^{-1} and that increases may occur at both high and low water contents (Snelgar *et al.* 1981*b*). Diffusive resistances to water loss have rarely been calculated but very low values in the range of 0·035 to 0·40 s cm^{-1} at medium thallus saturation found by Larson (1979) would be typical (Harris 1976, Larson & Kershaw 1976).

There have been no published comparisons of the magnitudes of the carbon dioxide and water diffusive resistances at different thallus water contents. Collins & Farrar (1978) make the point that ' one consequence of a high r_c (cortex resistance) for carbon dioxide is a similarly high resistance to water loss and hence, during desiccation, the rate of loss of water from algal cells will be reduced '. This is a view that originates from studies of higher plant stomatal diffusion resistances where there is a simple linear relationship between the two resistances. Such a relation holds only where both the carbon dioxide and water are diffusing in air and would not be expected where carbon dioxide is moving in solution. The latter situation is found in the cuticular layers of leaves where the water and carbon

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dioxide resistances differ considerably. The water moves by mass flow and evaporates directly from the surface whilst the carbon dioxide has to diffuse slowly through the water to the chloroplasts (Jarvis 1971). A similar situation might be expected to occur in the cortical layers of lichens where few gaseous pathways appear to exist (Collins & Farrar 1978, Lange 1980). In this study a comparison of the water and carbon dioxide diffusion resistances was made at various water contents in an attempt to clarify the relationship between the two.

Materials and Methods

Abbreviations: Σr_{CO_2}, total CO_2 diffusion resistance, s cm^{-1}; Σr_{H_2O}, total diffusion resistance for water loss, s cm^{-1}; r_c, part of Σr_{CO_2} attributed to cortex of lichen, s cm^{-1}; RH, relative humidity, %; ψ; water potential, bar; NP, net photosynthesis; mg CO_2 per gram dry weight per h.

Material: Specimens of *Sticta latifrons* Rich., *Pseudocyphellaria colensoi* (Bab., Vainio, *P. billardierii* (Del.) Räsanen and *P. homoeophylla* (Nyl.) Dodge were collected from the Waikareiti area of the Urewera National Park (NZMS 1 N96 619437), North Island, New Zealand. Lichens were stored air dry in the dark over silica gel for a maximum of 3 weeks.

Carbon dioxide resistance determinations: these were carried out as described in Snelgar *et al.* (1981*b*) and involved the determination of the slope of net photosynthesis rate against CO_2 concentration at several water contents. All measurements were made at a saturating light intensity of 150 µE m^{-2} s^{-1} and under microaerobic conditions (1% oxygen), in order to minimize photorespiratory activity.

Diffusion resistance to water loss: This was determined with a ΔT series 2 automatic porometer, using the standard methods of measurement and calibration as described by the manufacturer. Lichen thalli were allowed to dry down under normal laboratory conditions or were equilibrated at fixed relative humidities (RH) generated by saturated salt solutions in a desiccator at 20°C. Measurements were limited to low and medium water contents since the porometer is not designed for use where surface water is present. Water potentials were obtained from standard tables (Slavik, 1974), and water contents are expressed as mg water per mg thallus dry weight.

Photosynthesis rates: NP determinations were made using an ADC series 225 infra-red gas analyser in a closed loop system described in Snelgar, *et al.* (1981*b*). All determinations were at 350 µl CO_2 l^{-1}, 16°C and were carried out at several thallus water contents starting with a saturated lichen thallus which was dried slightly between each determination. All results are expressed as mg CO_2 fixed per gram dry weight per hour (mg CO_2 g^{-1} h^{-1}).

Results

The relationships between water potential (ψ) and water content for *Sticta latifrons*, *Pseudocyphellaria colensoi*, *P. billardierii* and *P. homoeophylla* all show a similar pattern in which there is at first a slow decrease in ψ with decrease in thallus water content changing to a more rapid decrease below a water content of about 0·5 (Fig. 1). *P. colensoi* is distinguished from the other species by a lower water content for any particular ψ; this is clearly seen at $\psi = -50$ bar where it has a water content of about 60% of the other species (Fig. 1B). A similar relationship is found between Σr_{H_2O} and thallus water content for *S. latifrons* and *P. homoeophylla* (Fig. 2). Figure 2A was constructed from Σr_{H_2O} values obtained separately from the top and bottom surfaces of thalli of *S. latifrons* that were allowed to dry in air and measured at various water contents, and also from the top surface of thalli equilibrated to constant water content at several values of RH. A single line is a good fit for all data points and no detectable differences in Σr_{H_2O} exist between top and bottom thallus surfaces or between thalli of similar

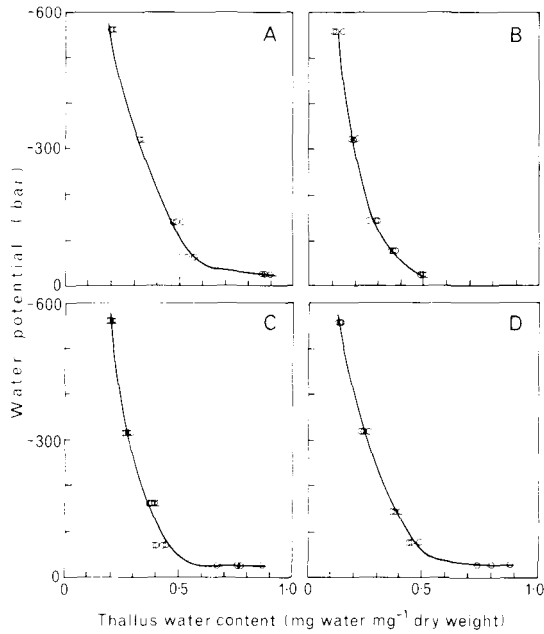FIG. 1. Relationship between water potential (ψ, bar) and thallus water content (mg water mg^{-1} dry weight) for: A, *Sticta latifrons*; B, *Pseudocyphellaria colensoi*; C, *P. billardierii*; D, *P. homoeophylla*. Thalli were allowed to equilibrate to constant thallus water content at a known RH generated by a standard salts solution at 20°C.
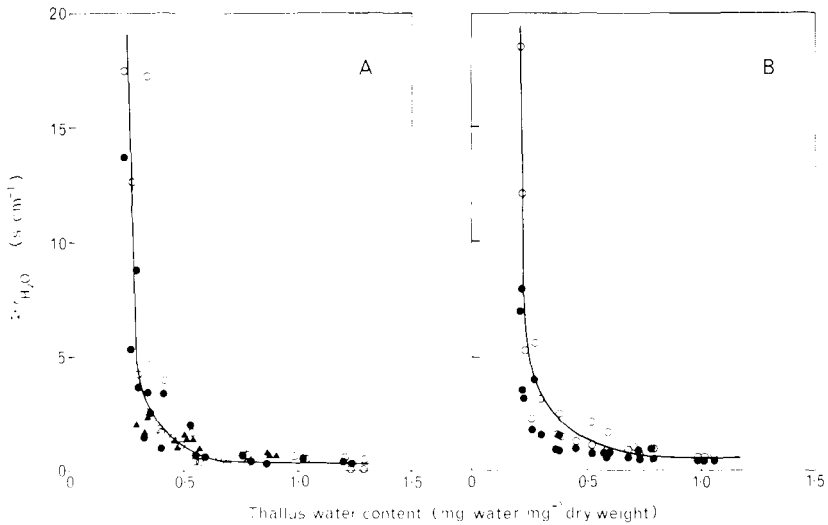

FIG. 2. Relationship between total water diffusion resistance ($\sum r_{H_2O}$, s cm^{-1}) and thallus water content (mg water mg^{-1} dry weight) for: A, *Sticta latifrons*; and B, *Pseudocyphellaria homoeophylla*. $\sum r_{H_2O}$ measured on the upper (●) and lower (○) surfaces of thalli allowed to dry in air; or on the upper surface (▲) of thalli equilibrated to constant thallus water content at a fixed RH.

water content obtained by drying or equilibration. The porometer could be used only at low and medium water contents since at higher water contents liquid water was present. However, for this reason, at high water contents $\sum r_{H_2O}$ would be expected to be identical to, or lower than, the values at the highest water content measured. The results of Harris (1976), Larson & Kershaw (1976) and Larson (1979) tend to substantiate this extrapolation.

Figures 3A–B are a summary for *Sticta latifrons* and *P. homoeophylla* of the relationships between net photosynthesis (NP), $\sum r_{CO_2}$, $\sum r_{H_2O}$, ψ and thallus water content. Both graphs show very similar patterns with $-\psi$ and $\sum r_{H_2O}$ increasing steeply at low water contents, $\sum r_{CO_2}$ increasing at both low and high water contents and NP almost an inverse of $\sum r_{CO_2}$. When comparing $\sum r_{H_2O}$ and $\sum r_{CO_2}$ it is important to note that they differ markedly at high water contents where $\sum r_{H_2O}$ is low but $\sum r_{CO_2}$ rises rapidly, and that $\sum r_{CO_2}$ has considerably higher values than $\sum r_{H_2O}$ at any particular water content. At water contents of $1 \cdot 0$ $\sum r_{CO_2}$ is 180 times greater than $\sum r_{H_2O}$. At no water content is $\sum r_{CO_2}$ less than a factor of ten greater than $\sum r_{H_2O}$.
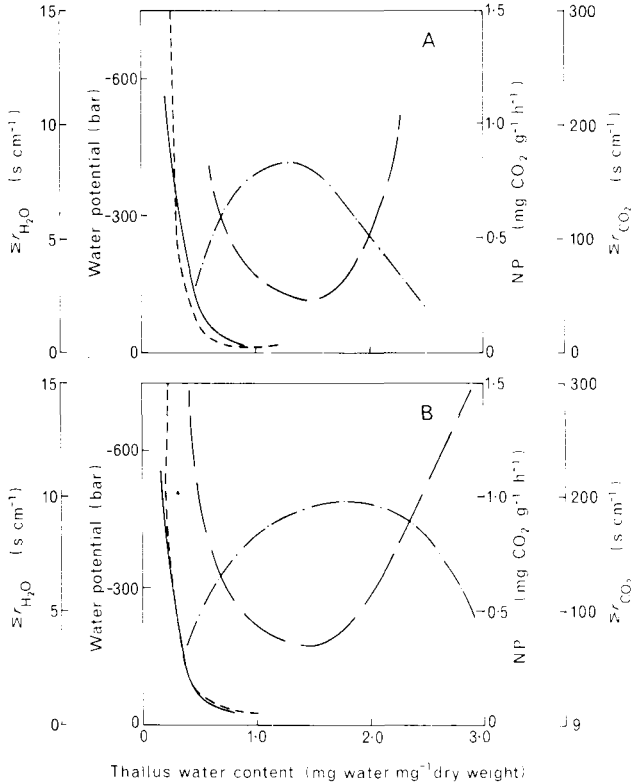

FIG. 3. Summary of the relationship between water potential (ψ, bar), total water diffusion resistance ($\sum r_{H_2O}$, s cm^{-1}), total carbon dioxide diffusion resistance ($\sum r_{CO_2}$, s cm^{-1}), net photosynthesis (NP, mg CO$_2$ g^{-1} h^{-1}) and thallus water content (mg water mg^{-1} thallus dry weight) for: A, *Sticta latifrons*; and B, *Pseudocyphellaria homoeophylla*. ——, ψ; ----, $\sum r_{H_2O}$; —— , $\sum r_{CO_2}$; – · – · –, NP. Values for ψ and $\sum r_{H_2O}$ are from Figs 1 and 2, respectively. The values for $\sum r_{CO_2}$ and NP are from Snelgar (1981).

Discussion

The results summarized in Fig. 3 indicate that the resistance to water loss is determined by the physical properties of the thallus, in particular the thallus water potential. This result is in accord with those of Harris (1976), and Snelgar & Green (1981) which indicate that there are no modifications to limit surface water loss in lichens. A similar direct relationship between thallus water potential and the resistance to water loss has been suggested for intertidal algae (Jones & Norton 1979).

Σr_{CO_2} is a composite resistance made up of the gaseous diffusion resistance plus cellular aqueous diffusion and biochemical resistances. However the presence of cyphellae or pseudocyphellae in these lichens results in the gaseous diffusion resistance forming the major part of Σr_{CO_2} even at optimum thallus water content (Snelgar *et al.* 1981*a*). The data on Σr_{CO_2} show a more complex situation than found for Σr_{H_2O} with high resistances occurring at both low and high thallus water contents. The increased Σr_{CO_2} at low thallus water contents may be attributed to a biochemical inhibition resulting from the low water potentials as indicated by the results of Cowan *et al.* (1979) and Green & Snelgar (1981). Increased Σr_{CO_2} at high thallus water contents appears to be entirely the result of increased resistance to gaseous diffusion of carbon dioxide probably caused by a partial decrease in volume of the gaseous diffusion pathways by water infiltration (Green & Snelgar 1981, Snelgar *et al.* 1981*b*, Lange & Tenhunen 1981). Carbon dioxide diffusion in water is so much slower than diffusion in air that even a short water diffusion path results in a marked resistance increase. The results demonstrate that the relationship between Σr_{CO_2} and Σr_{H_2O} in lichens is complex and cannot be interpreted as a simple linear relationship as found for the stomata of higher plants. Even at low water contents where the responses of both parameters are similar Σr_{CO_2} values are up to 160-fold higher than Σr_{H_2O} values. Further evidence of the lack of correspondence is found at higher water contents where Σr_{CO_2} increases drastically when Σr_{H_2O} must be low. These marked differences between Σr_{CO_2} and Σr_{H_2O} strongly suggest that carbon dioxide and water follow different diffusion pathways in the lichen. Circumstantial evidence obtained by using a split cuvette (Green *et al.* 1981) suggests that carbon dioxide diffuses through the cyphellae or pseudocyphellae of the lower surface of these lichens with the major diffusion resistance lying in the gas exchange structure itself (Snelgar *et al.* 1981*a*).

The porometer evidence presented here indicates that water loss may occur at identical rates by evaporation from both upper and lower surfaces with the water moving by mass flow through the cortex. The situation would be analogous to a higher plant leaf that exchanged carbon dioxide through the stomatal pores of the lower surface but lost water from its entire surface. Normally such a leaf would have a 'waterproof' cuticle that prevented surface water loss and confined it also to the stomatal pores. Such a situation is not feasible for lichens which do not have a continuous internal supply of water from a vascular system. Lichens must also be capable of being moistened by rain or mist and may need to utilize external water reserves (Snelgar & Green 1981*b*). Such a low resistance to water loss also means that there is little advantage, in terms of water loss rate, in internal rather than external water storage.

The stomata of higher plant leaves perform both carbon dioxide and water vapour exchange functions with a consequent close relation between the carbon

dioxide and water vapour gaseous diffusion resistances. The evidence presented here indicates that this could not be so for the lichens studied and that carbon dioxide and water vapour do not follow the same diffusive pathway.

This is an unfortunate situation since the simple linear relationships between the two gaseous resistances for higher plants allows calculation of leaf internal carbon dioxide concentrations from water loss rates. This calculation is therefore not possible for lichens and no simple method appears to exist for obtaining thallus internal carbon dioxide concentrations. At high thallus water contents changes in $\sum r_{CO_2}$ were not reflected by changes in $\sum r_{H_2O}$ so that increased resistance to carbon dioxide exchange did not mean a similar increase in desiccation resistance.

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