

Review article

The Effects of Wetting and Drying on Symbiont Interactions in Lichens

D.H.S. RICHARDSON

School of Botany, Trinity College, University of Dublin, Ireland

Tel. 353-1-772941, ext 1274, Fax 353-1-772694

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Abstract

Water uptake and loss in lichens is briefly reviewed with particular reference to symbiont interactions. Remarkable progress has been made in recent years, especially in understanding the difference between the water relations of lichens containing green algae and those containing cyanobacteria as photobionts. However several aspects require further elucidation or experimental clarification. It is hoped that this review which formed the basis of a paper presented at the International Congress on Symbiosis held in Jerusalem, Israel, will encourage researchers to undertake studies that will address the outstanding problems and so lead to a more complete understanding of the lichen symbiosis.

1. Introduction

The lichen symbiosis involves over 20,000 species of fungi (mostly Ascomycotina) and some 20 different genera of green algae or cyanobacteria. So successful is this symbiosis that lichens have colonized habitats that vary from the most inhospitable deserts to the rainforest with their bountiful water supply (Galun, 1988). The growth form varies from crustose, through leafy to shrubby but they share the ability to take up water rapidly often reaching in excess of 150% of their dry weight within 10 to 30 min. The time taken to reach saturation depends on the surface area to weight ratio (Larson, 1981).

Lichens have a number of adaptations which enhance the rate and amount of water taken up or the rate of subsequent water loss via evaporation. In the genus *Umbilicaria* these include rhizinae (hair-like anchoring structures), and plates on the lower surface as well as the presence of specialised hyphae in the medulla (central region of the lichen thallus) (Sancho and Kappen, 1989). Such strategies have penalties when a lichen is subject to insulation since these plants are easily harmed as a result of exposure to high temperatures when moist. Even the very tolerant desert lichen *Chondropsis semiviridis* is damaged by a half hour exposure to 45°C under these conditions but can withstand 65°C when dry (Rogers, 1971). The various strategies evolved by lichens from particular habitats in relation to the dilemma as to whether greater advantage accrues from drying rapidly or slowly are discussed by Kershaw (1985) and Kappen (1988).

2. Uptake of Liquid Water

Water is generally considered to accumulate in lichens in the gelatinous upper and lower cortex and in the medulla (Stocker, 1927; Jahns, 1984). However recent ultrastructural studies have suggested that the hyphae, at least within the algal layer, are covered by a non-wettable layer which maintains, under normal circumstances, an internal gaseous environment (Honegger, 1991). This would seem to make the idea that the interior of the lichen can act as a water reservoir by capillary uptake unlikely. However studies on *Teloschistes lacunosus* which has no coherent lower cortex indicate a depression of photosynthesis at high water levels (Palmer and Friedman, 1990). This would suggest a diffusion barrier in the form of a water saturated medulla. Further experimental work is clearly necessary to define the path of water uptake in various lichens and the areas of the thallus which act as water reservoirs.

One consequence of the rapid uptake of liquid water was shown first by Smith and Molesworth (1973). In *Peltigera polydactyla*, there was an initial burst of carbon dioxide release; followed by a period of enhanced respiration. In the 'resaturation respiration', the initial release reflects carbon dioxide-rich air displaced from the cells and the cell walls. The period of enhanced respiration occurs as the cells re-establish fully intact membranes and as the systems related to photosynthesis and other aspects of metabolism regain their full activity. These authors also found that in lichens from more xeric habitats, e.g. *Xanthoria aureola*, resaturation respiration was less pronounced. Further studies were carried out by Link and Nash (1984) on *Parmelia praesignis*, a lichen from southwestern USA which is naturally subject, in July, to wetting by

thunderstorms after a prolonged dry period. They found that on initial rewetting, the lichen respired excessively for more than 5 min and that it took more than an hour to achieve full net photosynthetic activity. However if dried, and then rewetted after twenty-four hours, the recovery time was reduced by about half. After a third cycle of wetting, the lichen was fully active within 11 min. Kershaw (1985) has added further complexity to interpreting the impact of this resaturation respiration by suggesting that both the length of drought prior to rewetting and the season can affect the occurrence and intensity of this metabolic response. Clearly more research is needed to understand the phenomenon fully.

3. Uptake of Water Vapour

Being wetted by liquid water from the fully dried state appears to be rather uncommon for lichens growing in many habitats. Usually a period of high humidity precedes rainfall and lichens, unlike nearly all flowering plants and mosses, can absorb about 60% of their dry weight of water from humid air (>75% RH) within 24–48 hr (Lange, 1988). Under these conditions resaturation respiration is absent or undetectable when the lichen is subsequently wetted with liquid water. While lichens with both green and cyanobacterial photobionts accumulate moisture from humid air, only the former are able to begin photosynthesis in the absence of added liquid water. If lichens containing green algae are saturated by rainfall, the net photosynthetic rate is actually depressed as a result of the water-swollen cortex and water films interfering with gaseous diffusion into the thallus. This is particularly marked in the case of lichens like *Roccella fucoides* which have a dense thallus (Lange, Killian and Ziegler, 1986). A very interesting insight into the difference between lichens containing green and cyanobacterial photobionts has been gained by the study of photosymbiodemes. These are lichens in which a single species of fungus can associate with either a green algal photobiont or a cyanobacterial photobiont to form a characteristically shaped and coloured lichen thallus. Often the two forms are connected. In New Zealand, *Pseudocyphellaria rufovirens* is the thallus with the green alga and *Pseudocyphellaria murrayi* is the thallus containing the cyanobacterium. Experiments on the two lichens confirm that it is the photobiont which dictates whether, following water uptake from humid air, photosynthesis can begin (Lange, Green and Ziegler, 1988). It is interesting that observations of free living cyanobacteria in the Negev desert and other situations suggest that cyanobacteria thrive only where there is periodic liquid water in the form of dew or run-off (J. Garty, pers. commun.). This may be related to the inability of blue green algae to couple photosystem II

with the phycobilisomes when only partly hydrated (Bilger et al., 1989). In contrast, epiphytic green algae can absorb water from humid air and begin to photosynthesize (Lange et al., 1990). There is indeed no evidence from this very recent study to confirm the earlier view that lichen fungi might protect lichen algae from the effects of drought.

4. Role of Sugar Alcohols

The importance of sugar alcohols (polyols) in the physiology of lichens is well known (Richardson, 1985; Kershaw, 1985; Smith and Douglas, 1987). In lichens containing green photobionts (c. 90% of all species), the alga synthesizes a sugar alcohol (ribitol in lichens containing *Trebouzia* and erythritol in lichens containing *Trentepohlia*) which is released to the fungus that converts it into other sugar alcohols, especially mannitol. It has been postulated that one role of sugar alcohols within the green photobionts is to enhance the osmotic potential of the cells and thereby maintain a pool of liquid water during dry periods (Lange et al., 1988). The other value of sugar alcohols is as a respiratory substrate to support resaturation respiration but it may be, for reasons given above, that this is of less significance in the natural habitat of lichens that was hitherto thought. Indeed the idea that these compounds are of key importance in providing physiological buffering in plants subject to cycles of wetting and drying now needs re-investigation (Farrar, 1988). When lichens are re-wetted, it has been shown that sugar alcohols are released from the thallus and that the magnitude of the loss is related to the sugar alcohol content of the thallus (Dudley and Lechowicz, 1987). Release is greatest within the first 15 min and is negligible within an hour. However, in pollution-stressed lichens, release may continue and damage may result from the lichen being unable to retain its carbohydrate reserves for the various important roles, as yet to be fully clarified, that they play in the physiology of these plants (Roser et al., 1992).

5. Conclusions

In conclusion, I hope that it is clear that a lichen is more than the sum of its two symbiotic parts. There are still many aspects of the water relations of lichens that require further study (Table 1). In trying to investigate the water relations of lichens from widely divergent habitats, I am sure that we will inadvertently find out more about the interactions between the two symbionts of lichens which make them such a fascinating subject for study.

Table 1.

Some questions with respect to lichen water relations which require clarification or further experimental study.

Where does water accumulate in lichen thalli and by what pathway does it reach the photobiont?

- Is the main water reserve in the gelatinous cortex?
- Can and how does water accumulate in the medulla?
- Does water reach the photobiont solely via the apoplast?

Why are cyanobacteria-containing lichens unable to begin photosynthesis following uptake of water from humid air. Is it due to:

- lack of continuity of a hydrophobic layer covering both symbionts?
- a barrier to water diffusion posed by the gelatinous sheath of the photobiont?
- inability to couple photosystem II with phycobilisomes when only part hydrated?
- lack of intracellular polyols to retain internal liquid water pools?

Why do lichen algae and fungi produce high levels of sugar alcohols? Is their principal role:

- as respiratory reserves for resaturation respiration?
- to maintain osmotic potential within the cells during drought stress?
- to ensure sufficient levels that loss, due to periodic leaching after rain, will not seriously deplete carbohydrate reserves?

Do lichen photobionts gain any benefit in terms of water relations from being in a symbiotic association? Do lichen fungi:

- protect photobionts from exposure to low water potentials?
- buffer photobionts against very rapid loss or uptake of water?

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