Rhizine-Strands in *Cladonia sulphurina* (Michaux) Fr.

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Abstract

Cladonia sulphurina has exceptionally well-developed rhizine-strands. The growth and development of these rhizine-strands have been studied in detail with some experiments on their function. There is no evidence that the rhizine-strands serve for regeneration and colonization of the habitat. A positive influence of the rhizinal system on the water relations in the thallus could be observed, especially by strongly delaying the process of desiccation of wet lichens.

1. Introduction

Many lichens bear appendage organs on their lower surface or, less commonly on their margin, which, depending on their position on the thallus as well as on their assumed function, can be described by different names. In this connection we can distinguish between rhizines, rhizinomorphs, rhizine-strands and adhesive discs amongst others (Hannemann, 1973). These structures were seen to be important in the anchoring of the thallus to the substrate (Galloe, 1913; Poelt and Baumgartner, 1964) but in addition, advantages for the water relations of the lichen and for the supply with minerals were also suggested

(Sandstede, 1931; Vogel, 1955). The second kind of function was however frequently questioned (Stocker, 1956; Poelt and Baumgartner, 1964; Hannemann, 1973). Other studies have shown that the development of rhizines can be important in water relations, although a direct water uptake and transport by the rhizines, comparable to that in the roots of higher plants, occurs only to a small degree. However, as the rhizines tend to lift the thallus slightly above the substrate, a capillary space develops between the thallus and substrate which can serve for water storage (Ott, 1987).

The large network of hyphal strands which grow from the thallus into the substrate in lichens from several genera is particularly striking. Vogel (1955) compared the habit and supposed function of these structures to the root system of "Fensterpflanzen" from general of the phanerogames growing in desert regions. This comparison implies that the hyphal strands of the lichens can be seen as adaptations to dry habitats. Contrary to this idea, Poelt and Baumgartner (1964) suggest that the rhizine-strands only attach the lichens to an unstable substrate and have no function in water relations. A totally different function was observed for the rhizine-strands of *Endocarpon pusillum* and *Siphula*. In these lichens adventive lobuli develop from the hyphal strands and therefore the outgrowing lateral rhizines seem to serve for regeneration and colonization of the area around the original thallus (Malone, 1977; Wagner and Letrouit-Galinou, 1988; Mathey, 1971). Similar observations were made by Sanders and Rico (1992).

A final explanation of the function of rhizines and rhizine-strands suggests a connection with nutrition. Sandstede (1931) postulates for the genus *Cladonia* a general importance of the rhizinal structures to the nutrition of the thallus, probably meaning the uptake of minerals dissolved in water. Crittenden (1991) believes that the upward transport of organic substances should also be taken into consideration, although in this context he relates to the substances released from old parts of the thallus and not to the absorption of organic substances from the ground. For such a supply of the apical growing parts of the thallus, it is necessary however, to presume a vertical transport from the base to the top of fruticose lichens. If such a vertical transport does exist, organic material from the substrate could be transported, as well as substances from the basal parts of the thallus. In this connection, it should be investigated whether certain mycobionts of lichens are capable of saprobic nutrition.

The research so far has mainly concentrated on the description of the morphology of fully developed apendage organs from mature thalli and on classifying the structures. Statements concerning the function are mostly based on assumptions or on preliminary experiments. This is especially true for the

question of water supply. The function of rhizines as runners and their importance to growth and distribution has been studied in detail in *Endocarpon pusillum*. However, the question of how far this mechanism plays a role in other lichen species, has still to be answered. It seemed desirable therefore, to study in detail the growth and development of rhizine-strands in another species together with some experiments on their function. For these observations *Cladonia sulphurina* was chosen because the rhizine-strands in this species are exceptionally well developed (Galloe, 1954).

2. Materials and Methods

Habitat

The material was collected in South Sweden near Mullsjö/Somneryd. The lichen grows in loose, humus woodland soil in an open pine forest. It is mainly associated with *Cladonia cornuta*. The specimens were collected with the substrate and freed from the adhering soil in the laboratory.

Morphological studies

The preparation of the underground strands from the soil was carried out mainly mechanically with a fine jet of water. Some specimens were treated with an enzyme solution (Biozym S, Fa. Ökolab/Mira Mey Neuss) in order to remove sticky gelatinous substances consisting of acidic polysaccharides. Particles of substrate still remaining after water and enzyme treatment were removed with tweezers and needles under the stereomicroscope. Sections were made with the freezing microtome and stained in Lactophenol-Cottonblue. For SCAN examination (Cambridge Stereoscan 200), the air dried samples were sputter-coated with gold.

Experiments on the water relations

Measurements of the water transport were carried out on living material. The air dried lichens were brought into a culture chamber and preserved for a maximum of two months. They were kept under the following conditions: Day–14 hr light (12 klux), 13° C, 60% rel. hum; Night–10 hr, 10° C, 60% relative humidity. Every other day the lichens were sprayed with water. Their vitality was checked immediately after collecting and rechecked six weeks later by IR-spectroscopy following the method of Schroeter (1991).

The water content of different parts of the thallus was measured by the conductivity of the tissue (Schuster et al., 1982; Schuster, 1985). The experiments

were carried out in a closed aquarium with a defined air humidity. For the control of the relative humidity, salt solutions were used. A small ventilator in the aquarium guaranteed the necessary air circulation.

3. Results

The thallus of *Cladonia sulphurina* consists of podetia several cm in height which grow from a leaf-shaped horizontal thallus. The upper part of the thallus verticalis is densely covered by farinosa soredia which, further down, become somewhat coarse-grained and are finally replaced near the base of the podetium by phyllocladia. Apothecia develop on the upper margin of the irregularly shaped podetia. Usually ascocarps are not numerous and propagation seems mainly to depend on vegetative reproduction by soredia. The development cycle from soredium to the adult lichen will be described here.

Development of the thallus horizontalis

The soredia are shed from the old podetium, individually, or in groups. The separate soredia are produced mainly in the farinose upper part of the thallus while groups of soredia are released from the more basal parts. At any rate, the production of soredia is so great that the substrate near the adult thalli is closely covered with the vegetative diaspores. The soredia consist of several algal cells enclosed by short-celled hyphae. After dispersal, some hyphae quickly grow from the soredia (Fig. 1) and penetrate into the substrate. Usually many soredia lie close together on the ground. In these groups many hyphae grow from the diaspores connecting them by a net-like system of interwoven hyphae (Fig. 2). This growth process results in an undifferentiated lump of tissue which almost totally conceals the original shape of the soredia (Fig. 3) and which may establish contact to other soredia by additional outgrowing hyphae (Fig. 4). Up to this point, the development therefore follows the basic pattern which has already been observed in other lichens (Schuster, 1985; Ott, 1987). At this stage of development, it can be observed that the volume of fungal tissue, in comparison to the quantity of algae, is largest at the point of contact of the lump of tissue with the substrate. Here, numerous hyphae in an unorganized net-like structure penetrate the soil surface, a process significant to the future development of the rhizine-strands. With this differentiation into dorsiventrally arranged tissues, the base of the hyphal lump becomes the starting point of the rhizines.

The algae in the basal parts of the primordium die and those near its surface multiply by intensive dividing activity, initiating the differentiation of the
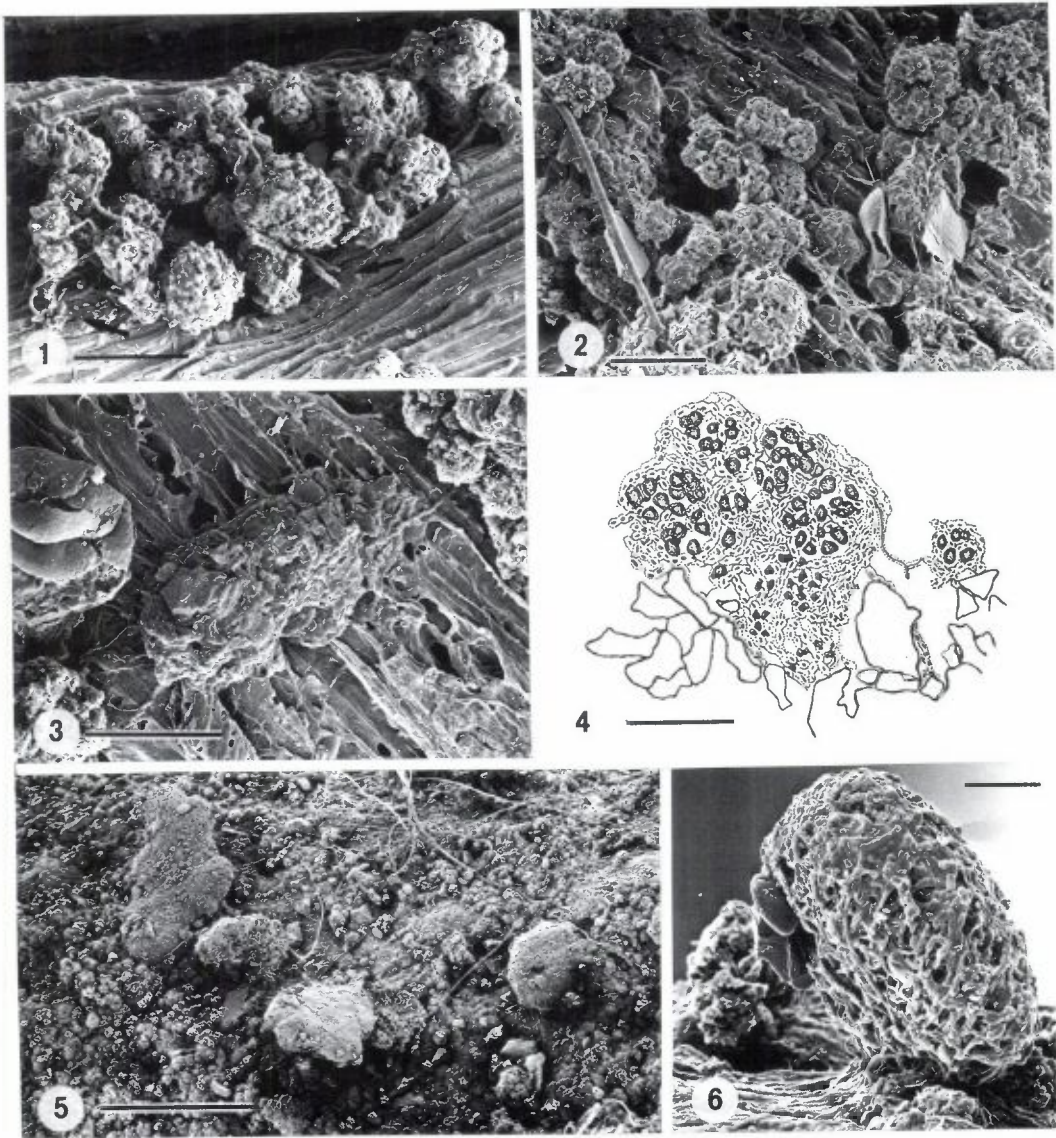
Figures 1-6. (1) Dispersed soredia with outgrowing hyphae penetrating the substrate (arrow) (bar = 50 μm); (2) Soredia connected by interwoven hyphae (bar = 50 μm); (3) Undifferentiated lump of tissue grown from fused soredia (bar = 50 μm); (4) Outgrowing hyphae of a primordium contacting other soredia (bar = 50 μm); (5) Young lobes and soredia on the substrate (bar = 500 μm); (6) Marginal upward growth of a small lobe (bar = 25 μm).

medulla and algal layer. At this point, the emerging lobe starts its marginal growth, its rim is separated from the substrate and grows upwards at an angle of 70–80° (Fig. 5). On the lobes growing separately upwards the ecorticated lower surface and the incomplete, and still not closed cortex on the upper side, can be distinguished (Fig. 6). At this stage, a compact bundle of hyphae emerges from the former base of the primordium which, as a young rhizine-strand, grows into the substrate (Fig. 7). The hyphae of the cord are mostly arranged parallel to each other.

The further growth of the young lobe takes place at the upturned margin. Irregular growth phases result in an undulated and slightly lacerated rim (Fig. 8). The hyphae of the medulla below the algal layer form a net-like pattern, but on the lower surface they merge into strands which are easily recognized near the basal part of the scale (Fig. 8). The figure shows quite clearly, that close to the point of attachment, the cords become thicker and merge with each other until finally, the lobe is sitting on a short stalk (Fig. 9). Even at this stage, additional soredia are still incorporated into the thallus (Fig. 9).

In spite of the continued growth of the young thallus horizontalis, the arrangement of the tissues remains unaltered. The subterranean rhizine-strand continues to grow and forms marginal branches which can again anastomose and grow around particles of the substrate, sometimes incorporating them into the tissue. In this way a three-dimensional, underground net of rhizine-strands is developed. The differentiation of the strands occurs parallel to the development of the scale of the horizontal thallus and the future point of attachment between lobe and subterranean rhizines can be observed, even before the differentiation of tissues in the scale is completed.

The mature lobes of the thallus horizontalis are up to one cm in length and above ground are situated on a short stalk which can be several mm long. This stalk is an extension of the rhizine-strands forming the big subterranean net (Figs. 10,11). Underground, the strands are up to 2.5 cm long and in their upper part, 3–4 mm thick. After the substrate has been removed, their ridged irregular surface absorbs water immediately. The branches anastomose with cords of the same lobe just as well as with those originating from other scales. In this way, beneath a group of thalli, an interconnected system of strands is developed. The anatomy of the strands is uniform. A cross section (Fig. 12) shows that the hyphae are arranged parallel to each other. The strand is not completely homogeneous but compact cords alternate with fissures and small cavities. This segmentation of the strands into subunits facilitates the formation of ramifications and anastomoses.
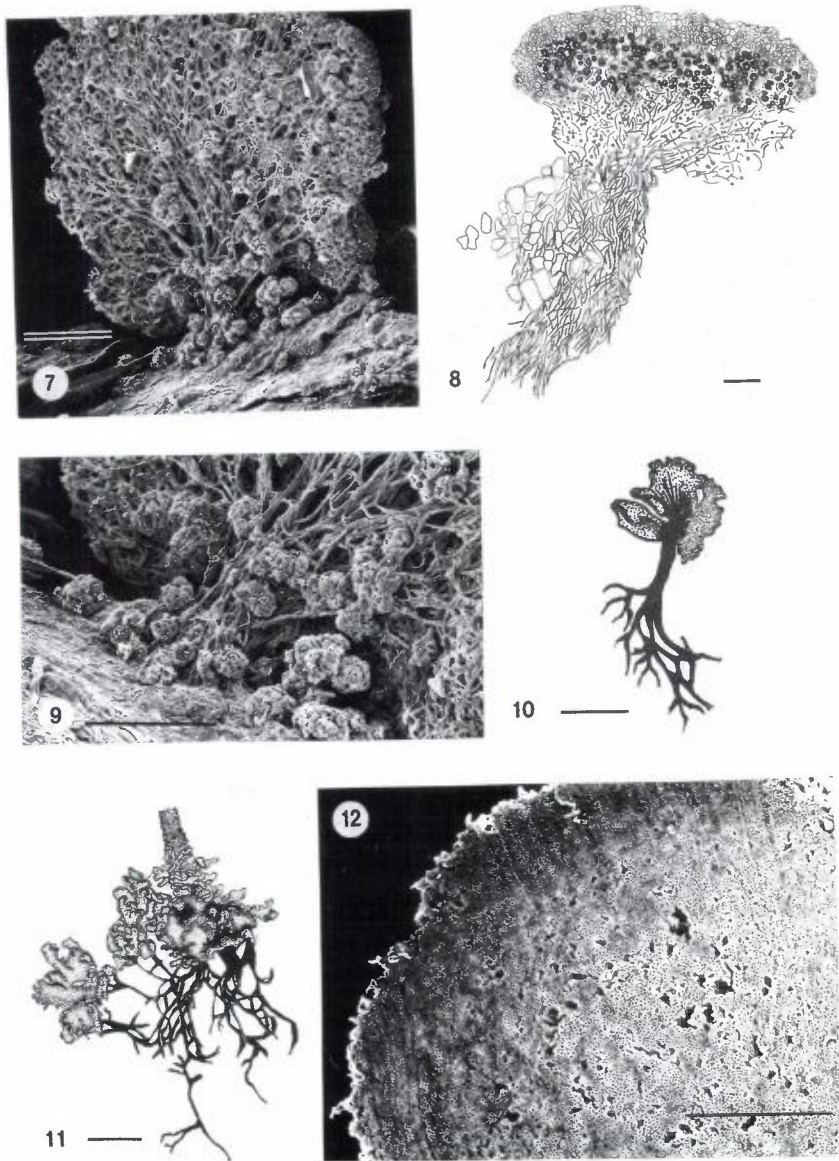
Figures 7–12. (7) Upward growing lobe with ecorticated lower surface and bundle of hyphæ at the base (bar = 100 μm); (8) Anatomy of a young lobe (bar = 50 μm); (9) Rhizine-strand at the base of a lobe. Incorporation of additional soredia (bar = 100 μm); (10) Relatively young lobe with typical rhizine-strands (bar = 5 mm); (11) Mature specimen with lower part of the thallus verticalis, the lobes of the thallus horizontalis and the rhizine-strands (bar = 5 mm); (12) Cross section of rhizine-strand (bar = 100 μm).

In all young scales a thin rhizine-strand emerges from the base of the primordium and penetrates into the substrate where it mostly fuses with thick cords from older thalli. There is no evidence whatsoever that new scales are developed from the old strands by the trapping of free living algae and relichenization. The entire structure and development of the thin strands beneath the young lobes contradicts such a theory. Although it cannot be excluded altogether, that in rare cases, such a relichenization may occur, it can be stated that in general and, contrary to the conditions in *Siphula* and *Endocarpon*, the rhizine-strands of *Cladonia sulphurina* do not serve for regeneration and colonization of the habitat.

Development of the thallus verticalis

The thallus verticalis grows on the scales of the thallus horizontalis. The starting point of development is a generative tissue which is differentiated in the algal layer and the upper medulla. Ontogenetically, the primordium is part of the ascocarp, but the sexual organs are only formed at the tip of the mature podetium. The generative tissue and the primordium of the podetium are formed in *C. sulphurina* close to the base of the leaf but not directly above the rhizine-strand. It is therefore obvious that the rhizine-strand is part of the leaf and not of the podetium, as Hannemann (1973) already stated.

Very young podetia are nearly free of algae. Possibly, the primordia grow so fast during the first phase of their development, that the few algae carried upwards by the growing fungal tissue do not have enough time to propagate. It is also possible that more free-living algae reach the surface of the podetium from the outside. While the upper part of the podetia forms powdery soredia, in the lower part, algae containing lumps of tissue differentiate into phyllocladia (Fig. 11). These secondary lobes on the podetia are anatomically divided into the same tissue layers as the leaves of the horizontal thallus, however, they do not form rhizines of rhizine-strands. There is no evidence either that new podetia emerge from the secondary lobes. The phyllocladia on the podetia therefore seem to function primarily as an enlargement of the photosynthetic area.

The phyllocladia are largest near the base of the podetium and they are arranged like tiles on a roof. As a result of this growth from the lobe of the thallus horizontalis, from which the podetium has grown, is often totally shaded and dies. In this case, the subterranean net of rhizine-strands remains intact and does now seem to originate directly from the base of the podetium. As a result of the strong lateral growth of the podetium, it is hardly perceptible

anymore that originally the podetium developed not above, but next to the base of the rhizines.

Absorption and release of water

Lichens with the adhering natural substrate and specimens with cleaned rhizine-strands were used in parallel experiments on water relations. These alternative measurements did not show any significant differences above the usual deviations between individual specimens. The presence or absence of the substrate therefore, seems to be of little importance for the aspects measured in our experiments. The water storage capacity of the soil, its influence on relative humidity of the air and other aspects were not studied, but in this area, properties of the substrate will naturally be of importance.

Desiccation of the podetium

The rhizoidal system, with or without the attached soil, was put into a small beaker with water. Around the base of the podetium, the surface of the soil and the glass were closed with parafilm, so that the transport of water from the soil to the top of the podetium was possible only by the rhizine-strands. Any noticeable evaporation of water from the soil and its reabsorption from the air by the upper parts of the lichen was excluded.

The water content was measured at the tip, in the middle and at the base of the podetia. The podetia were saturated with water by spraying (water content 80–100% dry weight) and then the beakers were placed in a closed aquarium with a defined relative air humidity. The relative humidity in the aquarium could be controlled and changed from the outside. These arrangements only give individual curves for each experiment. As it is not possible to reproduce exactly the water content at the starting point of the desiccation experiment, a statistical analysis of repeated experiments is not possible and standard deviations cannot be given. However, it could be clearly seen that in principle the curves were identical in the control observations.

Figure 13 shows the desiccation at the top, in the middle, and at the base of a podetium. At the start of the experiment, the relative humidity was kept at 80%, under which conditions, thalli without additional water supply dry out very quickly (Jahns, 1987). In the experiment, after an adaptation time of 30 min, this resulted in a water content at the tip of the podetium of only 40% (Fig. 13). This value hardly decreases during the next four hours under a humidity of 80%. Since a podetium of *Cladonia* in equilibrium with this relative humidity would only show a water content of about 20% dry weight, water must obviously be absorbed through the rhizoidal system and
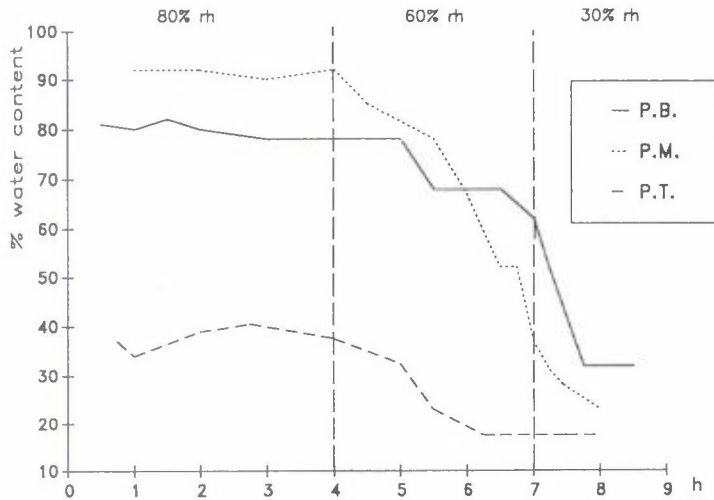
Figure 13. Desiccation of the podetium – (see text) (PT – top of the podetium, PM – middle part of the podetium, PB – basal part of the podetium, water content in % dry weight of the thallus).

be transported to the top of the podetium. The water flow is not strong enough to raise the water content above this level.

At the base and in the middle of the podetium, the water transport is strong enough that a level of 80–90% can be held throughout several hours. After 3.5 hr the water content in the middle drops but remains unchanged at the base. After 4 hr the humidity in the chamber was lowered to 60% and then to 30% after another 2.5 hr. At all three points of measurement in air with 60% relative humidity, the water content decreased, a process which did however, start with a noticeable delay at the base of the podetium (Fig. 13). A water content of 15%, the lowest value that can be measured by the apparatus, is reached by the top of the podetium already at a relative humidity of 60% while the middle only dries out to this point at 30%. The base of the podetium, even at 30%, retains a water content of 30% dry weight.

The measurements show clearly that as a result of the evaporation of water from the upper parts of the lichen, humidity from the soil is absorbed and transported passively into the podetium. This can only be affected by the rhizoidal system. The transport is not strong enough to achieve an equal distribution of the water, but a humidity gradient develops. As can be expected, the water content of the thallus depends on air humidity, but even at a relative humidity of 60–80% the water content is high enough for photosynthesis. This is in contrast to other lichens without easy access to water in the substrate.

Water absorption by the dry podetium

In a second experiment lichens with dry podetia and rhizoidal system and ad-
hering substrate were brought into beakers, isolated with parafilm and placed
into chambers with 80% relative humidity. The beakers were then filled with
water from the outside, with a small tube, and the water content of the thalli
was again measured at the top, the middle, and the base of the podetium. All
points of measurement showed a very slow increase of water content, up to
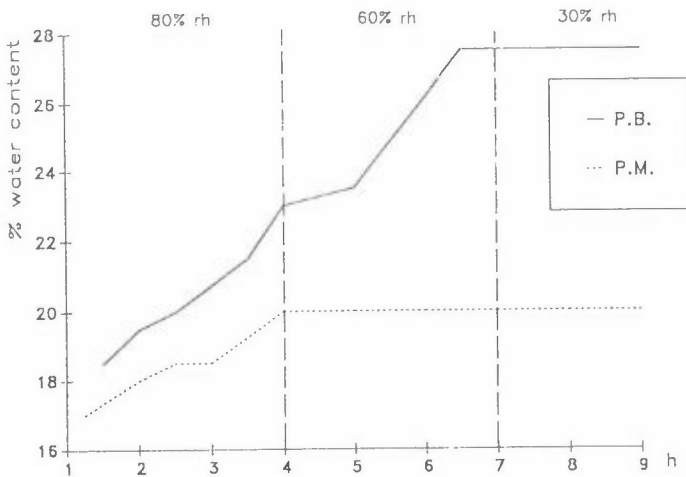about 20–25% dry weight (Fig. 14). This water content corresponds with the

Figure 14. Water absorption of the podetium – (see text) (PM – middle part of the podetium,
PB – basal part of the podetium, water content in % dry weight of the thallus).

value which can be expected in equilibrium with air of 80% relative humid-
ity. As the water uptake was very slow in all places with the establishment
of only a small gradient from base to top, it can be concluded that the water
was mainly absorbed from the surrounding air. Obviously, the completely dry
lichen does not absorb significant quantities of water from the substrate with
help of the rhizine-strands. This result is in keeping with the observations
made by Hannemann (1973) who did not notice any moistening of the totally
dry thallus of *Cladonia coccifera* through the rhizine-strands. It is generally
known that completely dry lichens are often somewhat water repellent and
absorb water more slowly than slightly moistened specimens.

As a general conclusion, it can be stated that dry lichens can hardly be

moistened with the help of the rhizoidal system, but that the process of desiccation of wet lichens can be strongly delayed. The latter is particularly true in connection with a high air relative humidity in the lichen habitat.

4. Discussion

The morphological investigations have shown that the rhizine-strands are part of the thallus horizontalis. Secondly, the thallus verticalis takes over the rhizoidal system from the scale from which the primordium of the podetium emerged. It is interesting that the first developmental stage of the rhizines is differentiated very early during ontogeny. The soredia develop into an undifferentiated lump of tissue which simultaneously differentiates into thalline layers and into rhizine-strands. The emerging young thallus lobe is already fastened with a cord of rhizinal hyphae to the substrate, and the hyphae at this stage have grown far into the soil. A comparable early differentiation of appendix organs was also observed in other lichens (Jahns and Ott, 1990; Ott, 1987). The functions for attachment of the thallus and for water relations which the rhizines in many cases fulfil, seem to make an early differentiation of these structures in the life cycle of the lichen desirable.

In comparison to the thallus horizontalis and verticalis growing above ground, the subterranean system of rhizine-strands in *Cladonia sulphurina* is very extensive. The relation of overground thallus to rhizinal net is 3.4 : 1. The photosynthetic gain of lichens may be reasonably large under favourable conditions, but due to long times with unfavourable conditions, the average yield over longer periods is not high. Hence the underground system of rhizines means an enormous expenditure of energy which should normally be justified by some substantial gain. It is, however, not easy to find a satisfactory explanation. On the other hand, speculations on utility should keep in mind that not all structures can be interpreted in relation to function.

For an attachment to the substrate, the existing system of rhizine-strands is certainly excessive. The lichen is not exposed to a special or unusual mechanical strain in its habitat and the associated *Cladonia cornuta* can exist without a similar system. Contrary to the observations on *Siphula* (Mathey, 1971) and *Endocarpon* (Malone, 1977; Wagner and Letrouit-Galinou, 1988) the system of rhizine-strands in *C. sulphurina* does not play a significant role in the propagation of the lichen. The cords do not function as runners which develop new thalli by the trapping of algae and relichenization. Young thalli may often be connected with the underground net of rhizines, but the contact is the result of secondary fusions. The lobes are derived from soredia and differentiate their own rhizine-strands which later on, are integrated into the common net.

The water uptake and water transport is a further possible function of the rhizine-strands. Reports on this function are often contradictory. Stocker (1956) and Vogel (1955) assume the absorption of water by appendage organs but Poelt and Baumgartner (1964) and Hannemann (1973) are of an opposite opinion. The experiments described here demonstrate that in *C. sulphurina* the situation is more complicated. The dry lichen does not absorb much water from the ground by way of the rhizines, a fact which corresponds with the opinion of Poelt and Baumgartner (1964) and Hannemann (1973). On the other hand, the desiccation of a wet lichen in humid air is noticeably delayed by the absorption of water from the ground. A relative humidity of 60–80%, which in combination with the absorbed water, is sufficient for keeping the basal parts of the podetium wet, is common in the montane and nordic woodland habitats of the lichen. But even in a habitat where the humidity sinks to a relatively low percentage during the day, the desiccation after dewfall or rain will certainly be delayed by hours. Such a short delay can be important to the metabolic balance, as the times of photosynthetic activity are sometimes very short, and alternate with periods of physiological inactivity (Lange et al., 1970). Of special importance in this context is the water gradient in the podetium, which results in a long period of high water content in the basal parts. It is remarkable that this part of the thallus verticalis is closely covered with scales, which significantly enlarge the photosynthetically active area. The main part of the photosynthetic area is therefore situated where the best water supply is provided. It is also possible that this higher water content induces, or at least supports, the differentiation of the scales.

The positive influence of the rhizinal system on the water relations indirectly improves the photosynthetic yield. The subsequent growth also requires a good mineral transport to the algae. As we have seen, the rhizine-strands absorb water from the ground and naturally with the water, minerals can be carried upwards. This passive transportation system could also carry organic substances upward, which are derived either from dead basal parts of the lichen (Crittenden, 1991) or from saprophytic activity of the mycobiont. Saprophytic nutrition has not been proven for these lichen mycobionts, but the water transport in the podetium at least demonstrates that basically, such a passive transport would be feasible.

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