Cryptogamic Botany

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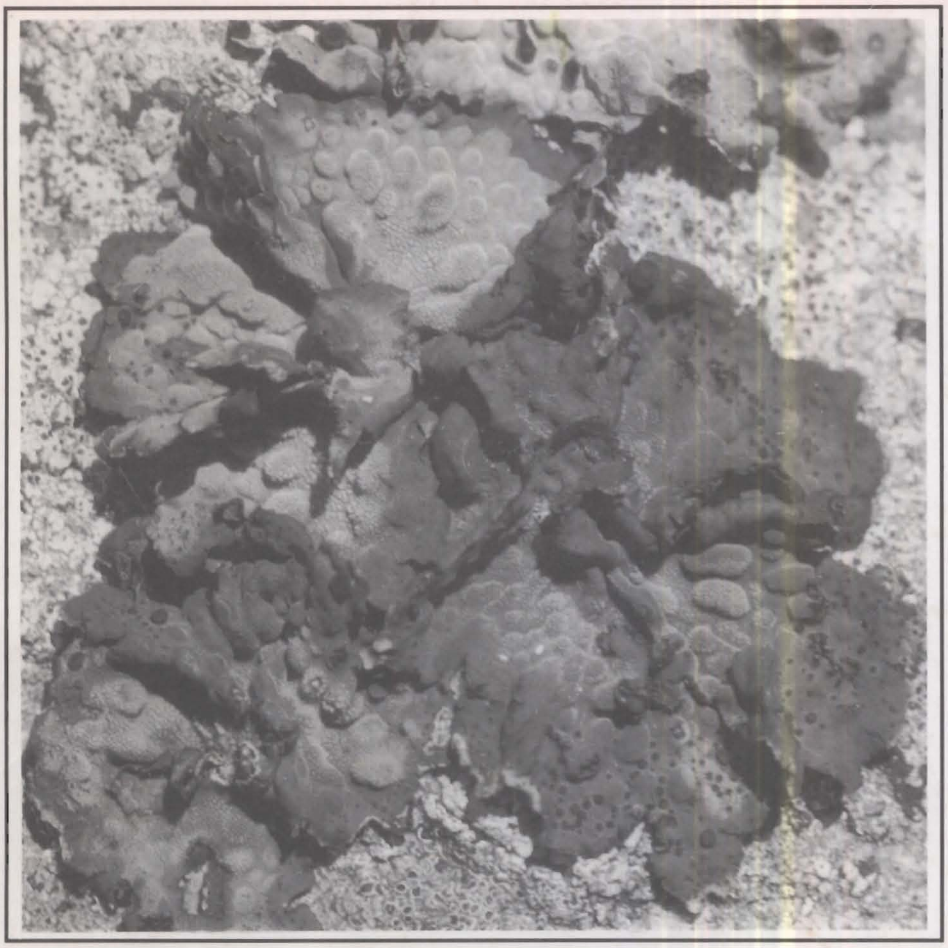

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Front cover, large figure: Half wet and half dry state of thalli from previous figures (Sancho, Valladares and Ascaso).

Inset figure: Mature fruit bodies of *Lentinius boryanus* growing on blocks of *Carpinus caroliniana* wood shavings. (Mata and Guzmán)

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Effect of hydration on colour and temperature in thalli of *Umbilicariaceae*

L. G. Sancho, F. Valladares[1] and C. Ascaso[2]

[1] *Departmento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense de Madrid, 28040 Madrid, Spain*

[2] *Centro de Ciencias Medioambientales, C. S. I. C., Serrano 115 dpdo., 28006 Madrid, Spain*

SUMMARY

Many foliose lichen with a pale coloured thallus in the dry state show remarkable darkening when they become wet. This phenomenon has been studied here in certain species belonging to the family *Umbilicariaceae*. The evaluation of colour changes of thallus upper surface in relation to different water content was made by means of automatic image analysis. Changes in the inner temperature of the thallus due to changes of hydration under a constant infrared-rich radiation were measured with a microsensor inserted between the algal layer and the lower cortex. *Lasallia hispanica*, a species which became very dark when fully hydrated, returned to its original whitish grey colour while its water content was still above 130% dry weight. At this point, a sharp decrease of the inner thallus temperature was observed. This thermal fall was maintained during a relatively long period of time before the final increase in thallus temperature associated with the progressive dehydration of the lichen. These results are compared with those of species which showed slight or no appreciable darkening with hydration (*Umbilicaria crustulosa* and *U. polyrrhiza* respectively). The possible ecophysiological implications of the relationship between upper surface albedo and inner thallus temperature found here are discussed.

Introduction

It is a well-known fact that some foliose lichens with a pale coloured thallus experience a marked darkening when they are fully hydrated (3). This is a result of the light absorption by the water content in the upper cortex, an effect that can also be observed in many textiles and cellulosic fabrics. In all cases, they return to the original light colour as they dry. However, in contrast to the fabrics, these foliose lichens posses a heteromerous structure with layers of very different textures. This internal arrangement allows the thallus to retain water in different amounts across its section, and, subsequently, the water-loss kinetics can also be considerably different across the anatomical layers (2, 6). Hence the fact that the upper cortex of some species may be more or less dry and light in colour whilst the rest of the thallus still remains wet. Given that most lichens show a photosynthetic optimum at moderate hydration (10), the change of colour is likely to coincide with an optimal hydration level of the thallus. If this is the case, it will have a remarkable ecophysiological implication. On the one hand, it seems logical that an increase in the upper surface albedo (i. e. reflection of the incident radiation) could diminish the inner thallus temperature, an important phenomenon in order to obtain an increase in the net photosynthesis by attenuation of the respiration (10). The influence of the colour of the thallus on its temperature induced by light radiation has been reported by a number of authors (3, 8, 10, 11, 18). On the other hand, during the upper cortex drying, a decrease in the diffusion resistance of CO_2 can be expected (2). Both processes could have a positive synergic effect on net photosynthesis.

For this study we have selected some species of the family *Umbilicariaceae* with very different responses in colour

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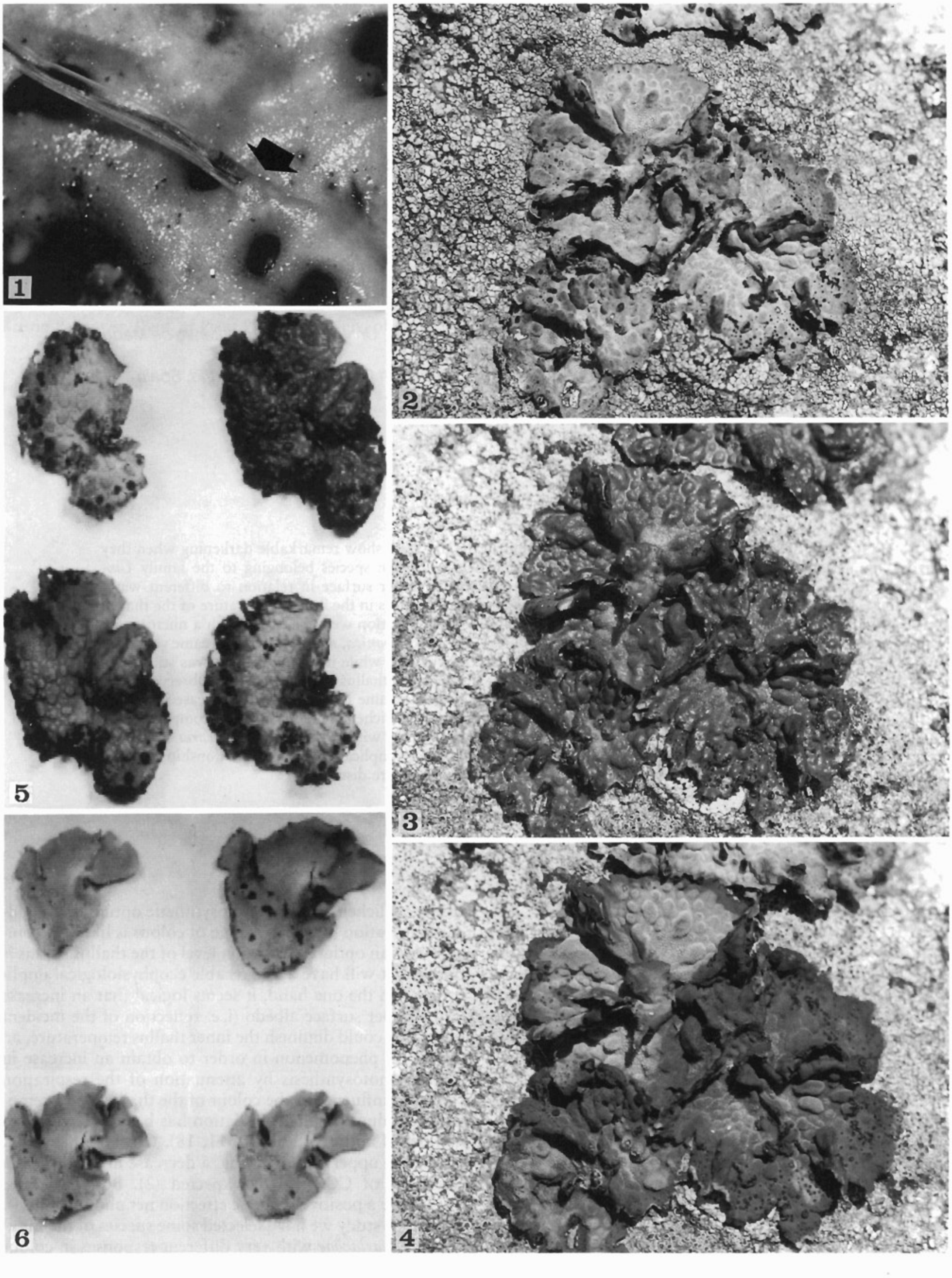
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change due to hydration. This family is relatively well known through many ecophysiological studies (4, 5, 13, 14, 15, 16, 24) which have made clear the significant influence of the thallus anatomy and morphology on its water relations. The aim here was to contribute to this topic new information about some possible ecophysiological effects of the upper cortex anatomy. We focussed the study on the change of colour of the upper surface by hydration and the associated thallus internal temperature changes.

Materials and Methods

Several medium size thalli of *Lasallia hispanica* (Frey) Sancho & Crespo, *Umbilicaria crustulosa* (Ach.) Harm., *U. grisea* Hoffm. and *U. polyrrhiza* (L.) Frey were collected on Spanish Sistema Central (Garganta de Chilla, Sierra de Gredos, Avila, and El Ventorrillo, Sierra de Guadarrama, Madrid). The laboratory experiments were carried out a few days after the collection of material.

The evaluation of colour changes on the upper surface in relation to thallus hydration was made with an automatic image analyzer INCO 10 (MICROM S. A.), capable of distinguishing 255 levels of grey between black (0) and white (255). Thallus weight and an image of its upper surface were recorded every three minutes until drying of the specimen was complete. Prior to the first weighing, thalli were fully saturated and shaken to remove adherent water. Each image was recorded with a resolution of 256 × 256 points, and binarised and screened. The thallus surface was about 85% of the total image surface. For each image the average value of grey and the standard deviation was obtained. The experiment was carried out at 30 °C, 60 µmol $m^{-2}s^{-1}$. PAR, and 45% rel. humidity. Two thalli of each species were measured.

The measurements of the inner thallus temperature during its dehydration under a constant radiation were done by means of microsensors 0.4 mm wide (thermistor, Grant). They were inserted into the medullary layer through the lower surface (Fig. 1). It was not possible to introduce the microsensor inside the very thin and delicate thalli of *U. grisea*. Beneath each thallus, just in contact with its lower surface, another temperature sensor 1.5 mm wide (thermistor, Grant) was installed. The two sensors were connected to a datalogger (Squirrel, Grant). The recording interval was 30 seconds and every three minutes an average of the values obtained for each sensor was stored. Two thalli of each species were measured simultaneously in a temperature-humidity-controlled chamber (Heraus-Vötsch, HPS500) at 10 °C and ca. 80% relative humidity, with an air stream of 0.5 m. sec^{-1}. The standard chamber source of light of 250 µmol.sec^{-1} and 60 Watts.m^{-2} was enriched by infrared radiation with an Osram lamp IR 250. The total amount of radiation was 350 µmol $m^{-2}s^{-1}$ and 260 Watts.m^{-2}. Once the sensors were installed the thalli were fully saturated with water at the chamber's temperature.

Results

While the darkening of the upper surface colour with hydration was imperceptible in the dark brown thalli of *Umbilicaria polyrrhiza*, it was remarkable in the whitish grey ones of *Lasallia hispanica*, both at the field (Figs. 2–4) and at the image analyzer screen (Fig. 5). However, whitish grey thalli of other species, such as *U. crustulosa* and *U. grisea* (Fig. 6), showed intermediate behaviours with only slight darkenings of the thallus surface when fully hydrated.

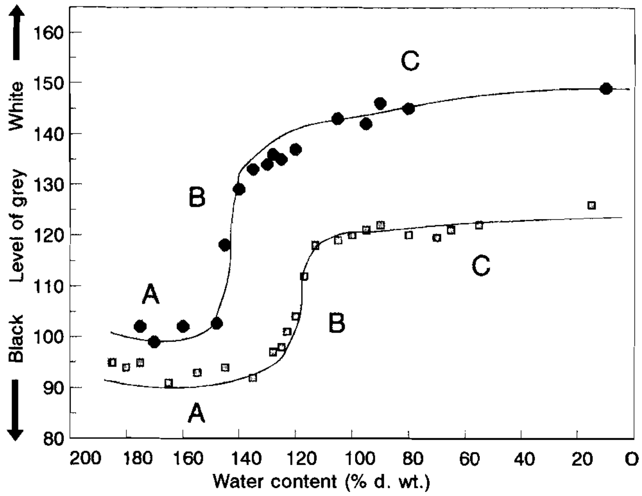

Fig. 7. Evolution of the average grey level of the upper surface of two thalli of *Lasallia hispanica* with decreasing thallus water content. Three main phases (A, B and C) are distinguished in the process.

The analysis of the average grey level evolution of the upper surface with thallus dehydration reflected previous field observations. The sharp change between dark green (wet state) and whitish grey (dry state) of *L. hispanica* was associated with a change in more than 30 units of grey (Fig. 7). The slight change of colour between the wet and the dry state of the thalli of *Umbilicaria crustulosa* (Fig. 8) and *U. grisea* (Fig. 9) was congruent with a difference lesser than 20 units of average grey between the two states. Moreover, the strong brightening of *L. hispanica* took place with a decrease in thallus water content of only 10% (between 150–140% d. wt. in the smallest thallus and

◀ Figs. 1–6. 1. Temperature microsensor inserted in the medulla of *Lasallia hispanica* through the lower surface. The arrow points to the insertion point. 2. Dry state (whitish grey) of a group of undisturbed thalli of *L. hispanica* at the natural habitat. 3. Fully hydrated state (dark green) of thalli from previous figure. 4. Half wet and half dry state of thalli from previous figures. 5. Photograph of four images of one thallus of *L. hispanica* recorded with the image analyzer; from top-left to bottom-right, the dry thallus just before the beginning of the measurements, the completely hydrated thallus at the beginning of the measurements, the thallus at an intermediate state of hydration and colour, and the dry thallus at the end of the measurements. 6. The same as in the previous figure but with a thallus of *U. grisea*.

125–115% d. wt. in the biggest). The process of brightening in *L. hispanica* could be divided into three phases (Fig. 7): A, relatively long, the thalli lost between 30 and 50% d. wt. of the water they held when fully hydrated and kept their dark green colour; B, very short, the thalli changed quickly to whitish grey but lost only 10% d. wt. of their water content; C, very long, the thalli remained whitish grey and dried (100–140% d. wt. of water loss).

Thallus thermal behaviour was also very different among different species. *L. hispanica* exhibited three phases (Fig. 10), in clear correspondance with the already mentioned phases occurred during dessication and brightening. Initially, phase A, the thalli of *L. hispanica* maintained a stable internal temperature (above 18 °C, at climatic chamber conditions). Afterwards, phase B, thalli inner temperature showed a sharp decrease of 2–3 °C. Finally, phase C, the thalli became dry and increased its temperature 4–5 °C above the temperature of phase A. The thermal evolution during dessication of *Umbilicaria crustulosa* coincided with its hardly noticeable change of colour. The drop in the inner temperature of *U. crustulosa* during the phase B was much smaller than that of *L. hispanica* (only 0.5–0.8 °C below the temperature of the initial phase). The inner thallus temperature of *U. polyrrhiza*, whose black-brown thallus did not show change of colour, increased continuously from the beginning, until reaching 9–10 °C above the initial temperature.

The external sensors situated under the lower surface of the thalli showed aproximately the same oscillations than those of the microsensors but considerably attenuated. The external temperature at the lower surface was always slightly cooler than the inner one.

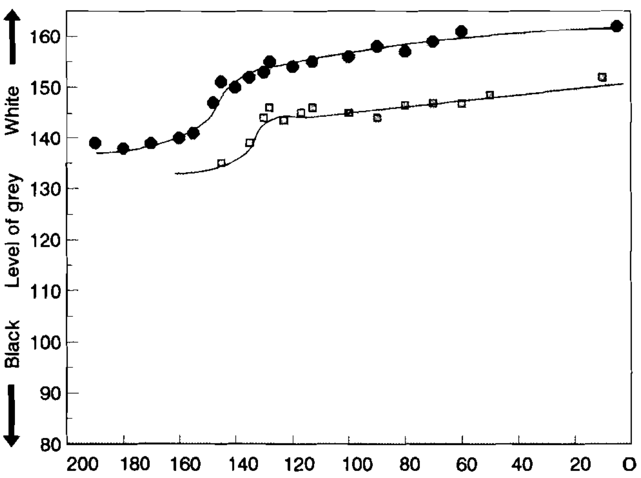

Fig. 8. Evolution of the average grey level of the upper surface of two thalli of *Umbilicaria crustulosa* with decreasing thallus water content.

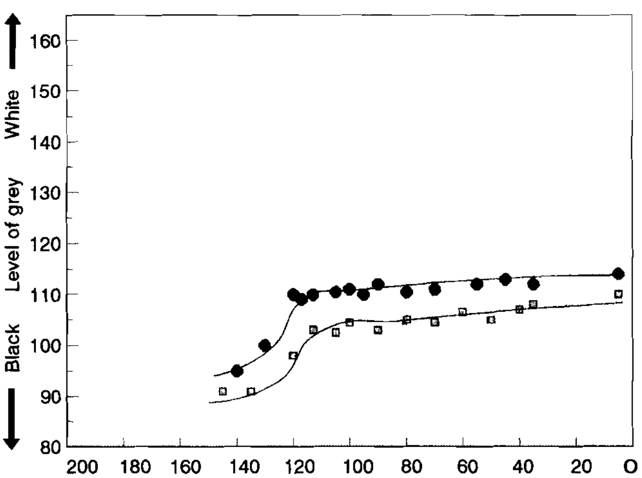

Fig. 9. Evolution of the average grey level of the upper surface of two thalli of *Umbilicaria grisea* with decreasing thallus water content.

Discussion

The interaction of lichen colour with thallus temperature has been examined by various authors (e.g. 8, 10, 11). Kershaw (9) documented the significant influence of the albedo of a lichen thallus in regulating its temperature. Lange (11) and Kershaw (8) reported strong temperature differences under high radiation between normal dry thallus branches and black painted branches. Our data, obtained from undisturbed thalli, showed also a consistent difference of 6–7 °C in inner thallus temperature between the dry whitish thalli of *Umbilicaria crustulosa* and *Lasallia hispanica* and the dry blackish-brown thallus of *U. polyrrhiza*. However, when the thalli were fully hydrated, the difference in thallus temperature between species of a dark colour when hydrated (*L. hispanica* and *U. polyrrhiza*) and those with a light colour in the saturated state (*U. crustulosa*) was only about 2 °C, in agreement also with other studies (8). This fact could be explained by the evaporation rate controlling the heating of the thallus (21).

It has been proved that photosynthetic CO_2 exchange is not at its maximum at water saturation of the lichen thallus (10, 12, 19). Optimum water content for photosynthesis between 100–150% d. wt. (40–60% of the total water retention capacity) has been reported for lichens belonging to the family *Umbilicariaceae* (4, 7, 15, 17, 19). The percentages of thallus water content obtained by us during the colour change of the thalli fell within this range. Therefore, it seems clear that the lightening of thallus upper surface and an optimum thallus water content occur at the same time in this family. In addition, Sancho & Kappen (24) observed that changes of thallus colour in several *Umbilicariaceae* were useful indicators of the photosynthetically relevant water status.

In *Lasallia hispanica* the colour change was associated with a sharp inner temperature decrease of 2–3 °C. From this combination of optimum thallus water content, lightening of the upper thallus surface, and cooling, some relevant ecophysiological implications can be deduced. The optimum temperature of *L. hispanica* at high light intensity is around 15 °C (24). We can see, then, that above this temperature (a very common situation in the sunny days of Mediterranean mountains) a cooling of the thallus could mean an increase of its net photosynthetic rates. Another important fact is that a small drop in thallus temperature may be very significant in diminishing the rates of water loss (20). Moreover, during thallus drying, water loss from the upper cortex occurs first, reducing resistance to CO_2 exchange at the time when the algal layer is still relatively saturated (2, 20, 21).

Considering all these questions together with the natural habitats where the lichens studied are found, some adaptative implications of thallus colour change capacity arise. *L. hispanica* is principally found in fairly exposed sites in the western Mediterranean mountains. Short periods of rain or snow are usually followed by sunny weather, in this area. During rain or snow the irradiance level is low and the air temperature can be relatively cold. In this situation, the saturated thallus becomes more transparent and its dark colour will be advantageous as the decreased albedo may produce a temperature rise. When the sun shines after these events, the upper cortex dries quickly and a change of colour occurs, resulting in cooling. This protects the thallus against excessive heating, just when the water content and conditions for CO_2 exchange are optimal for photosynthesis. *U. crustulosa* and *U. polyrrhiza* grow in more sheltered localities than *L. hispanica*. *U. crustulosa* grows principally in water channels in high mountains. Within this microhabitat, it is reasonable to expect long periods of saturation of the thalli under high irradiance levels. Here, thalli ability for keeping their whitish colour even when they are completely wet, seems to be very advantageous. This is the case with *U. crustulosa* (and also with other *Umbilicaria* growing in similar localities, like *U. hirsuta* and *U. vellea*). *U. polyrrhiza*, however, grows typically in forest regions on the less-illuminated slopes of rocks, where the humidity is highest. The low irradiance levels of this habitat could be linked to the dark colour of this species, capable of a significant increase in thallus temperature with light absorption. This is also applicable to other sympatric *Umbilicaria*, like *U. spodochroa* subsp. *carpetana* and *U. polyphylla*.

Bachmann (1) reported that water accumulation in *Umbilicaria* is concentrated in the medulla. Sancho & Kappen (24) have also documented for this group of lichens the importance of thallus anatomy and, above all, the structure of the medulla for the water retention capacity and for the water loss kinetics. These findings point to differential rates of water uptake and water loss between different thallus layers. In this way, a combination of a prosoplectenchymatic medulla, with the highest water retention capacity (24), and a fine and deeply areolate, hygroscopic, upper cortex may be considered as very advantageous for an optimal hydric performance of the thallus. And such is the characteristic anatomy of *Lasallia hispanica* (22, 23). But, in fact, this combination of anatomical features is rather uncommon in the genus *Umbilicaria*. Hygroscopic whitish upper cortex that allows a change of colour by hydration occurs typically in aerohygrophitic *Umbilicaria* species, which show in general loosely-woven arachnoidal medulla. Within the Mediterranean species, only in *U. decussata* is possible to recognize a partially prosoplectenchimatic medulla together with a hygroscopic upper cortex. Prosoplectenchymatic medullae can be used by the thallus as a water reservoir of great importance not only for keeping the thallus wet and metabolically active but also in order to prolong the process of cooling due to evaporation.

In the family *Umbilicariaceae* the capacity for colour change seems to be linked to the sudden changes of environmental conditions. Our findings also emphasize the strong interaction between the anatomy of the thallus and its ecophysiological behaviour. In the future, it may be necessary to test the extent of these current findings under natural conditions, and also to investigate more carefully the water retention capacity within the lichen thallus.

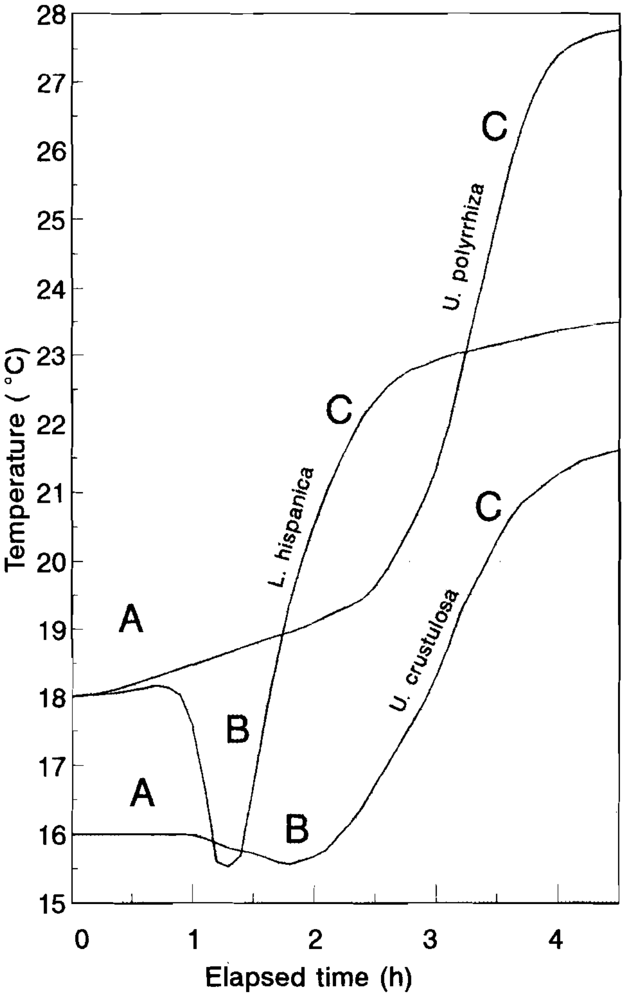

Fig. 10. Time evolution of the inner temperature of a thallus of *Lasallia hispancia, Umbilicaria polyrrhiza,* and *U. crustulosa.* The thalli were fully saturated in water at the begining of the measurements and left in the climatic chamber under an infrared rich radiation (350 mol m^{-2} s^{-1} and 260 Watts. m^{-2}) at 10 C and 80% relative humidity until were dry. Three phases (A, B, and C) could be appreciated in the process, although phase B is missing in *U. polyrrhiza.*

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Key words: thallus colour, albedo, hydration, temperature, image analysis, *Umbilicariaceae*

L. G. Sancho, Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense de Madrid, 28040 Madrid, Spain