

**ECOPHYSIOLOGY OF OROMEDITERRANEAN LICHENS.
FUNCTIONAL AND MORPHOLOGICAL ADAPTATIONS OF
LICHENS FROM THE SPANISH MEDITERRANEAN MOUNTAINS**

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Lichen flora and climatic conditions in the Spanish Mediterranean mountains

The Mediterranean region is a very well established biogeographic concept, and there are some species of lichen that can be considered Mediterranean, especially those with a thermal or xerophytic ecology. In high mountains, however, Arctic-alpine, bipolar or cosmopolitan lichen species predominate, to the extent that it is difficult to find typically Mediterranean *taxa*, even when the population includes submediterranean *taxa*.

The question is then can oromediterranean lichen flora be defined the same way vascular plants are defined, if the former includes lichens of wide distribution that have adapted to the peculiarities of the Mediterranean climate?

Indeed, only 16% of the lichen flora of the Spanish Central System, including the so-called submediterranean *taxa*, can be termed Mediterranean (Fig. 1) [Sancho, 2000].

The majority of the high-mountain lichens in the central Iberian Peninsula belong to a widely distributed Arctic-alpine (38%) and cosmopolitan flora (27%) that is found mostly outside the Mediterranean basin.

The marked decrease in precipitation during the Mediterranean summer is the main climatic difference between the high-mountain region of the Mediterranean and the Alpine region, and causes significant hydric stress to poikilohydric organisms. The lack of water during the summer, and the descent in metabolism in winter due to the drop in temperature and snow accumulation, greatly reduces the potential productivity of oromediterranean lichens.

The high-mountain regions of the Mediterranean can receive more than 2000 mm of precipitation yearly, but when the unfavorable periods for plant growth converge, the scarcity of water becomes a limiting factor in many cases.

For instance, at the bottom of Gredos Cirque, where the snow accumulates in a thick layer during the winter, lichen vegetation in localities affected by thick snow cover in winter is determined by the low water the distribution patterns of lichen communities are clearly determined by aridity. Although the amount of precipitation in these mountains is one of the highest in Europe, there are many

habitats in which lichens use water only during the short period of time between snow-melt at the end of spring and the beginning of the dry summer.

For this reason, lichen growth is often limited to the north side of boulders or along cracks. These observations suggest that the lichen vegetation in localities affected by thick snow cover in winter, is determined by the low water availability during the summer (Sancho, 2000; Sancho *et al.* 2001).

The situation is radically different, however, for lichen communities growing on walls and ridges that have practically no snow cover. Here the lichen vegetation is as rich in biomass as it is in biodiversity, and thrives even throughout the long winter, thanks to frequent intervals during which photosynthesis takes place under favorable conditions.

Some examples of physiological adaptations and phenotypic plasticity of oromediterranean lichens

One approach to study lichen adaptation in high-mountain areas is to examine their ecophysiological behavior along altitudinal gradients. To do this it is possible to select a single species with a wide ecological amplitude, but it is easier to use species within a single genus or family that cover the whole altitudinal range. For example, the species of the family *Umbilicariaceae* are widespread, appearing in basal areas and on the highest summits. Their wide distribution makes it possible to observe fundamental patterns in their photosynthetic behavior. In fact, there are studies that show that the species in basal areas have higher photosynthesis rates and higher temperature optima than those at high altitudes (Sancho & Kappen, 1989), which is well correlated with a higher chlorophyll content of the species in the basal areas.

Phenotypic plasticity is also an important feature that allows a single species to survive under varying environmental conditions within a single locality. The data available for *Ramalina capitata* var. *protecta* found on surfaces with northern and southern exposures display clear differences in morphology, water relations (absorption and storage), chlorophyll contents and net photosynthesis (Pintado *et al.*, 1997). The research also shows that the populations on the southern exposures are adapted to shorter periods of metabolic activity by increasing the water retention capacity of the thalli, the chlorophyll content and the net photosynthetic rates.

Bipolar species offer a striking opportunity to study adaptive strategies along latitudinal gradients. *Umbilicaria nylanderiana*, for example, is found in both hemispheres, including the Arctic and the Antarctic. The Antarctic populations, in contrast to the Mediterranean ones, display much greater physiological differences within a single species than within the different species along the altitudinal gradient. In the extreme Antarctic environment the species showed a net photosynthetic rate that was ten times lower than that of the Mediterranean populations and a notably lower temperature optima (Fig. 2). The extraordinary

ecological plasticity of *Umbilicaria nylanderiana* is probably feature of many other bipolar or cosmopolitan lichens (Sancho *et al.*, 2000a).

To understand this behavior it is useful to study the anatomy of the thallus. The population of algae in the thalli of the Antarctic *U. nylanderiana* is much lower than the population in thalli from the Mediterranean region, showing also a much lower chlorophyll content. Also, the upper cortex is more compact and thicker in the Antarctic population, which substantially reduces the light at the level of the algal layer.

Probably one of the most stressful oromediterranean environments is associated with the cold, continental steppes of the eastern Mediterranean basin and the high Iberian plateaus. Here the climate is characterized by extensive periods of drought throughout the year combined with subfreezing temperatures during the long winter. Lichens in these regions show spectacular adaptations. This is specially true in the so-called vagrant lichens, such as *Aspicilia fruticulosa*. This species displays a typically spherical and compact thallus that contains a very small algae population, and like the Antarctic lichens, it produces a very low net photosynthesis (Sancho *et al.*, 2000b).

Another observation is that the water storage capacity of the *Aspicilia fruticulosa* thallus is much lower (around 120% d.wt.) than that of any other species, which leads us to believe that the apparent depression in net photosynthesis at maximum thallus water content is due to dark respiration at maximum hydration rather than to barriers in the diffusion of CO₂. Nevertheless, the pseudocyphells may also play an important role in maintaining a good rate of gas exchange at full hydration. In fact, the curve of gross photosynthesis reveals that the exchange remains practically constant until the thallus dehydrates. This could indicate that the depression of net photosynthesis under conditions of maximum hydration is simply the consequence of the high, dark respiration rate of the enormous mass of fungi that drops little by little: while the algae maintain constant photosynthetic activity until the thallus dehydrates.

The spherical shape of the most compact thalli makes it physically difficult for symbiosis to be maintained. As the thallus grows, the mass of fungi increases in proportion to its volume, i.e. geometrically, while the population of algae on the surface increases linearly. A clear inverse correlation is established between the weight of the thallus and net photosynthesis, in that the heaviest thallus barely reach the compensation point for photosynthesis (Fig. 3). This creates a physiological limitation that impedes growth, which is exceptional not only for lichens, but for all photosynthetic organisms.

This correlation is much less evident in the less compact thalli which can, theoretically, grow indefinitely, *Aspicilia fruticulosa* is an extreme case of adaptation to aridity. As a response to the low availability of water, this lichen develops an extraordinarily compact thallus, with very limited water storage capacity, a small algae population and low rates of net photosynthesis.

Is it possible to establish generalities from these results?

One method for doing this is to compare these lichens to those that grow in environments that are completely dissimilar such as temperate or tropical rain forests.

There are some species of *Collema*, *Coccocarpia* or *Peltigera* that can absorb so much water that the thallus weight increases to 1000 - 2000% of the dry weight (Green *et al.*, 1994; Lange *et al.*, 1996). This means that these lichens have 10-20 times higher water storage capacity than *Aspicilia fruticulosa*. Likewise, net photosynthesis is as much as 18 times higher for lichens from humid forests. The results of this comparison suggest that a close correlation can be established between the water storage capacity of lichen thalli and their net photosynthetic rates.

Axes of variations in lichen physiology. Making the connections

Theoretical plant ecology seeks to understand the adaptive strategies that allow lichens and other photosynthetic organisms to evolve. Plant ecologists recognize, however, that they are unlikely to achieve this objective without some form of simplification. The growing consensus among experts is that they should establish some major axes of variation, such as response to disturbance or capacity for competitive dominance.

Presently, the most widely used axis is the capacity to exploit resources from the environment. In the search for a single trait that expresses the ecophysiological information of this axis in vascular plants, SLA or specific leaf areas (leaf area per unit dry mass) is the most powerful parameter, since it indicates the direct correlation with A_{max} , nitrogen content and photosynthetic efficiency (Weiher *et al.*, 1999; Wilson *et al.*, 1999).

Despite its acceptance, however, SLA can be difficult to use when working with cacti or leafless stems, and most lichens, since the leaf area in these plants can hardly be measured. Recently, another leaf trait has been proposed that focuses on leaf water content (LWC), sometimes referred to as tissue density or leaf dry-matter content (Weiher *et al.*, 1999; Wilson *et al.*, 1999). This trait compares the dry and fresh weights of the leaves at maximum turgor. Some authors have clearly shown that LWC is much less variable than SLA and can better predict the location of plants on an axis of resource capture, usage and availability.

This method could also be applied to lichens if maximum water content (MWC) is used instead of leaf water content at maximum turgor. For example, for the species of the family *Umbilicariaceae* there is a clear correlation between their MWC and the availability of water in their natural environment. The species of the genus *Umbilicaria* that grows on walls and ridges and are considered aerohygrophytic (without rhizinomorphs) showed the lowest MWC, while the substratohygrophytic species (with rhizinomorphs), found in water

channels and on protected surfaces, exhibited the highest MCW. The same was true in comparing the MWC of the species of *Ramalina* and *Pseudephebe* from different habitats (Fig. 4).

With the maximum water content (MWC) on the Y axis, it should be possible to locate different species of lichens on the axis for water availability, net photosynthesis, chlorophyll content and nitrogen content. This axis correlates very well with the primary habitats colonized by lichens that include arid regions, alpine and polar regions, mesic zones, temperate forests, and rain forests (Fig. 5). As for vascular plants, it is an axis of resource capture (light and nutrients) usage and availability.

Within this framework, oromediterranean lichen vegetation could be identified as consisting mainly of species from alpine and arid regions that have adapted to the Mediterranean climate (Fig. 5). More in-depth research should be conducted to determine whether the relationships between the maximum water content (MWC) of the thallus and its anatomical plasticity and resource capture capacity (net photosynthesis, nitrogen content, chlorophyll content) reveals a trait that is robust enough to explain and predict which strategies lichens will develop in order to adapt to changes in the availability of water. The Mediterranean region, including the high mountains, with its highly variable rates of annual rainfall, would be an excellent study site to test this hypothesis.

The proposal that I would like to advance is that in order to find common traits for functional ecology, lichens should be considered as leaves. By doing so, the Maximum Water Content of the thallus may become as good an indicator for lichens as Leaf Water Content is for vascular plants.

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