

The Fungal Community

**Its Organization and Role
in the Ecosystem**

Second Edition

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3

The Niche at the Organismal Level: Lichen Photosynthetic Responses

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The dominant and traditional view of the niche in ecology is rooted in questions about the organization of communities. The niche in its various guises (Giller, 1984; Wallace, 1987; Shugart et al., 1988; Futuyma and Moreno, 1988) is most often tied to concepts about how species are packed into an environmental space to form communities, to questions of the location of species along spatio-temporal gradients in the environment. The classic modern example of this community-based view is Robert MacArthur's (1958) study of the way that warbler species feed in different parts of coniferous trees and the mathematical models inspired by this field study that attempt to predict aspects of community organization (Cody and Diamond, 1975). This classical perspective has always been closely allied with the idea that interspecific competition structures communities. In Hutchinson's (1958) terms, investigators have more often focused on the realized niche, that is on the niche as an environmental space to which a species is restricted by competitors despite its potential to occur more widely. It now seems increasingly unlikely that these community-based concepts of the niche can find wide application outside vertebrate ecology (Strong, this volume). Nonetheless, this broad stream in the ecological literature continues to run strong and has led to a wide variety of field studies including some in lichen ecology (review in Lawrey, 1984; Larson, 1984a; Armstrong, 1986; Ryan, 1988; McCune, 1988; John and Dale, 1989). It is not this community-based concept emphasizing the realized niche that I will consider here, but another, related view that has been subordinate the past few decades.

This alternative view is closer in spirit to Hutchinson's concept of the fundamental niche, the full potential range of environmental space that a species could occupy. It focuses not on the location of species along shared environmental or resource gradients, but rather on the autecology of species' responses to such gradients. In the literature of vertebrate ecology, there is a reflection of this view in inferences about diet breadth drawn from data on bill size or mouth gape (Futuyma and Moreno, 1988): it is a property of the organism itself that informs our analysis of the niche rather than the location

of the organism along environmental resource gradients. From this perspective, Maguire (1973) spoke of niche response structure, the ecophysiological responses of an organism to such gradients. In this more organismal view of the niche the focus is on variation in the functional responses of organisms, on how environmental factors influence metabolic activities like photosynthesis or rates of growth. These studies have their roots in comparative physiology and questions about the functional basis of an organism's tolerance range along environmental gradients. In a larger view, questions about the evolution of niche response structures are a subset of contemporary interests in evolutionary ecology. The nature of evolved adaptations at the level of the whole organism and the evolution of specialization (Futuyma and Moreno, 1988) now subsume earlier interests in the fundamental niche. The net photosynthetic response surfaces of lichens, viewed as niche response structures (Lechowicz, 1981), can be considered from this point of view.

The questions that traditionally have organized research on niche response structure are primarily two. First, what are the environmental variables that regulate a response of interest and what is the shape of the response surface in this environmental space? Second, what is the nature of variation in the shape of this response surface across species and environmental regimes?

The general approach to answering these questions has been ecophysiological and has emphasized phenotypic responses without consideration of the genetics underlying the observed response. We can distinguish two major variants: the development and testing of theory to predict a response and the comparison of the natural diversity in a response. The first begins by creation of a model based on known principles of organismal function underlying a particular response and proceeds by deductive inference to predict variation in the response across environmental gradients. The most interesting botanical work using this approach focuses on problems of design in vascular plants: canopy architecture (Niklas, 1986), leaf form (Givnish, 1987), stomatal function (Givnish, 1986), and the like. Although models that bear on the evolution of structural or physiological variation in lichens are conceivable, they do not exist at this time. This leaves the second, comparative approach as the method of choice to begin an analysis of the evolutionary options for variation in the structural and physiological design of lichens. This approach uses a broad interspecific database to induce the general relationships among responses and environment. In this review, I will use this comparative approach to summarize variation in lichen photosynthetic responses across environmental gradients.

LICHEN PHOTOSYNTHETIC RESPONSES

In many respects, lichens are especially useful organisms with which to explore questions of the range of possible designs that might evolve in photosynthetic responses (Lechowicz, 1981). Compared to vascular plants, they have less complicated patterns of growth and differentiation and far simpler mechanisms of reproduction (Lawrey, 1984). A lack of roots and ease of storage after collection from the field make lichens amenable to a statistically sound characterization of gas exchange responses; many replicates can be assayed under many conditions using a number of different infrared gas analysis systems (Lawrey, 1984; Link et al., 1984). As a consequence, investigators have studied the gas exchange responses of very many lichens and this literature offers an excellent basis for comparative analysis of variation in the lichen photosynthetic response.

Since I first reviewed this literature circa 1980 (Lechowicz, 1981, 1982), it has essentially doubled. Not only the magnitude but also the qualitative scope of the data base has increased dramatically. Studies of a tropical basidiolichen (Coxson, 1987a, 1987b), several crustose species (Coxson and Kershaw, 1983, 1984), a gelatinous lichen (Kershaw and MacFarlane, 1982), and several South American lichens (Lange and Redon, 1983) have been carried out, which strengthen the generality of comparisons. Species have been sampled from latitudes between 16 and 72 degrees for detailed studies of gas exchange, although half of these samples originate between 44 and 54 degrees. The numerically dominant studies of temperate species have been extended into more diverse habitats such as coastal areas with Mediterranean climatic regimes (Matthes-Sears et al., 1987). The important desert habitat has been sampled more widely (Nash et al., 1982; Lange and Redon, 1983) as have the Antarctic lichens (Kappen, 1983; Kappen and Redon, 1987; Harrison et al., 1989). Alpine species in both North America (Coxson and Kershaw, 1983, 1984) and Europe (Türk, 1981, 1983) are now better known. Many important genera of macrolichens like *Alectoria* (Türk, 1981, 1983), *Cladonia* and *Cladina* (Türk, 1981, 1983; Kershaw et al., 1983; MacFarlane et al., 1983), *Cetraria* (Türk, 1981, 1983), *Parmelia* (Nash et al., 1982; Kershaw and Watson, 1983), *Peltigera* (Brown and Kershaw, 1984), *Ramalina* (Lange and Redon, 1983; Kappen and Redon, 1987; Matthes-Sears et al., 1987), and *Umbilicaria* (Harrison et al., 1989) are better represented. In addition 10 genera (*Acarospora*, *Caloplaca*, *Collema*, *Cora*, *Everniopsis*, *Heterodermia*, *Himantormia*, *Rhizocarpon*, *Thamnolia*, and *Usnea*) have been newly added to the earlier data base (Lechowicz, 1982). A relatively small pool of investigators have created this data base, almost certainly the most extensive available for the comprehensive comparison of photosynthetic responses measured by consistent protocols in any plant group.

In this review, I will draw on this data base to illustrate certain basic patterns of variation in lichen photosynthetic responses to three factors: incident photon flux density (PFD), thallus temperature, and thallus water content. All three are well established as important factors regulating lichen gas exchange (Lechowicz, 1981; Lawrey, 1984; Kershaw, 1985). Both thallus temperature and thallus water content are determined by the interaction between lichen morphology and thallus microclimate, which in turn is governed by well understood biophysical laws (Kershaw, 1985). If we were to try to study lichen photosynthetic responses to all the environmental variables that determine these summary variables, we would be overwhelmed. The niche would be defined on far too many axes and hopelessly confounded by lags in the response to rapid temporal variation in these abiotic environmental factors. This reference of the niche axes to parameters measured at the organism, the use of "internal environment" as a summary for diverse aspects of the "external environment", is characteristic of the study of niche response structure. In contrast to the community-based niche concept, the analysis is rooted at the level of the organism and focuses on an ecophysiological response to the ambient, internal factors that directly regulate that response. In taking data from the literature for this review, I have held to the same restrictions and limitations as in my earlier analysis (Lechowicz, 1982). I will provide a copy of all the data used in the current analysis on request.

Another outcome of the increased investigations of lichen ecophysiology in the past decade has been the recognition of additional factors that can be important in determining lichen photosynthetic responses. These include factors such as atmospheric CO₂ level (Nash et al., 1983), which although deemed of little ecological importance 10 years ago (Lechowicz, 1981), now appears more important as atmospheric CO₂ levels

continue to rise rapidly. Other factors such as tolerance of temperature extremes (Nash et al., 1987; Larson, D.W., 1989), tolerance of desiccation and high insolation in lichens from moist, shaded habitats (Coxson, 1987a, 1987b; Fritz-Sheridan and Coxson, 1988), and salt resistance (Nash and Lange, 1988) cannot be ignored in certain habitats; they certainly influence gas exchange and species distribution. Thallus age and size effects (Larson, 1984b) exist, but are unlikely to compromise a broad, interspecific analysis. The fundamental distinctions in water relations of photosynthesis between lichens with blue-green versus green algal symbionts (Lange et al., 1986) influence the interpretation, but not the conduct, of lichen gas exchange comparisons. Whatever the influence of additional environmental factors in certain habitats, PFD, thallus temperature, and thallus water content are of universal and undoubted importance as regulators of lichen gas exchange. The patterns of variation in lichen photosynthetic responses reviewed below may require an addendum in particular situations, but their overall generality is well-grounded.

THE MAGNITUDE OF LICHEN PHOTOSYNTHESIS

The maximum rates reported for lichen photosynthesis range from as low as 0.1 mg $\text{CO}_2/(\text{g} \cdot \text{hr})$ in polar species (Kappen, 1983; Kappen and Redon, 1987) to 25.0 mg $\text{CO}_2/(\text{g} \cdot \text{hr})$ in the tropical Basidiomycete, *Cora pavonia* (Coxson, 1987a, 1987b). Half the reported maxima lie between 0.6 and 2.7 mg $\text{CO}_2/(\text{g} \cdot \text{hr})$ with a median rate of 1.4 mg $\text{CO}_2/(\text{g} \cdot \text{hr})$. In general, the higher a species' maximum photosynthetic rate, the higher also is its respiratory rate (Fig. 1) although there is a wide range of variability in this relationship. Since by far the greatest part of lichen biomass is fungal tissue (Lawrey, 1984), this illustrates an interesting aspect of the relationship between the fungal and algal partners in the lichen symbiosis. A larger or more photosynthetically active algal population generally supports a greater rate of fungal respiration. It would be interesting to know if the higher rates of fungal respiration correlate to faster rates of growth as well but these data are not available.

Only one significant correlation exists between the maximum rate of photosynthesis and the climatic regime in which the lichen was growing: lichens from colder regions tend to have lower maxima (Fig. 2). For a given summer temperature regime, there can be a wide range of possible maxima and the effect is clearly weaker in warmer regions. The same climatic variables considered in my earlier review (Lechowicz, 1982) of this literature were reconsidered: mean January and July air temperatures, mean annual global solar radiation, mean January and July global solar radiation, mean annual evaporation, mean annual precipitation, and mean annual frost free period. In addition, the mean annual, January, and July hours of bright sunshine were included in the analyses and data on latitude were used with the temperature data to calculate an index of continentality (Conrad, 1946). None of these other macroclimatic variables were significant predictors of maximal photosynthesis.

ENVIRONMENTAL OPTIMA FOR PHOTOSYNTHESIS

There appears to be some constraints on the combinations of PFD, thallus temperature, and thallus water content at which maximal photosynthesis can be attained (Fig. 3). The ability of a species to exploit high irradiance is greater the higher the species' photosynthetic temperature optimum, but is unrelated to the optimal level of thallus relative water content. There is no indication that growth form limits optimal conditions

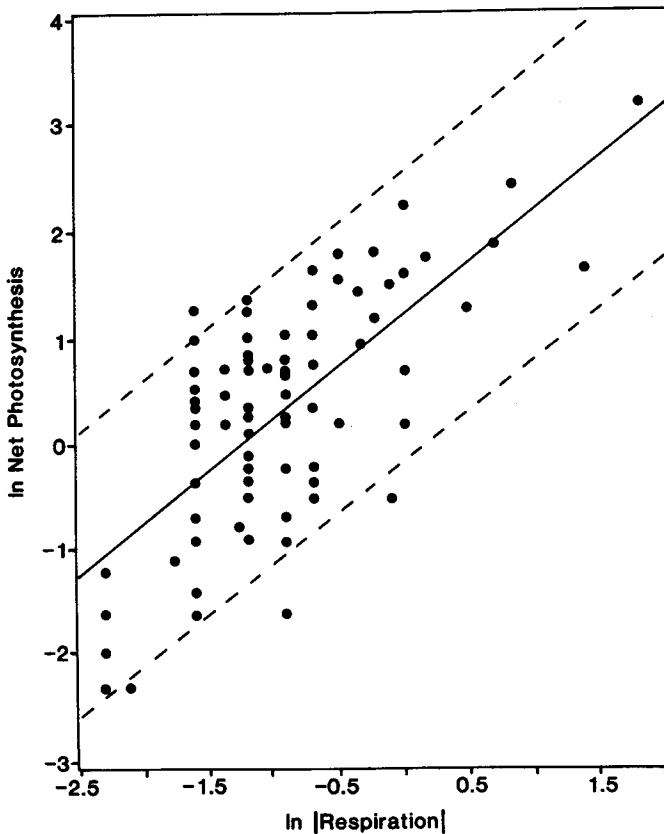


Figure 1 Natural logarithm of the maximum photosynthetic rate plotted against the natural logarithm of the respiratory rate in the dark under the same assay conditions. The graph shows the least square regression line with its 90% confidence interval fitted to the data; each point represents the data from a different lichen assay gleaned from the published literature (see text).

for lichen photosynthesis. Optimal relative water contents vary among species from 26% in a *Parmelia* species to 100% in a *Peltigera*; the optima of half the species fall between 41 and 71% with a median of 55%. The photosynthetic temperature optimum varies between 1°C in an antarctic *Lecanora* and 35°C in a temperate zone *Peltigera* respectively. The temperature optima of half the species fall between 12° and 24°C with a median of 15°. Photosynthesis is saturated anywhere from 200 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in an *Umbilicaria*, a foliose species, to 1200 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in a *Cetraria*, a mat-forming species. The photosynthesis of half the species was light saturated somewhere between 450 and 820 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ with a median of 600 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$.

CLIMATIC PREDICTORS OF OPTIMAL PHOTOSYNTHETIC CONDITIONS

The photosynthetic rate of lichen species that occur in sunnier and more continental climates tends to be saturated at higher PFD levels (Fig. 4). This relationship, based on data for 44 lichens, accounts for 42% of the variance in the saturation level and is

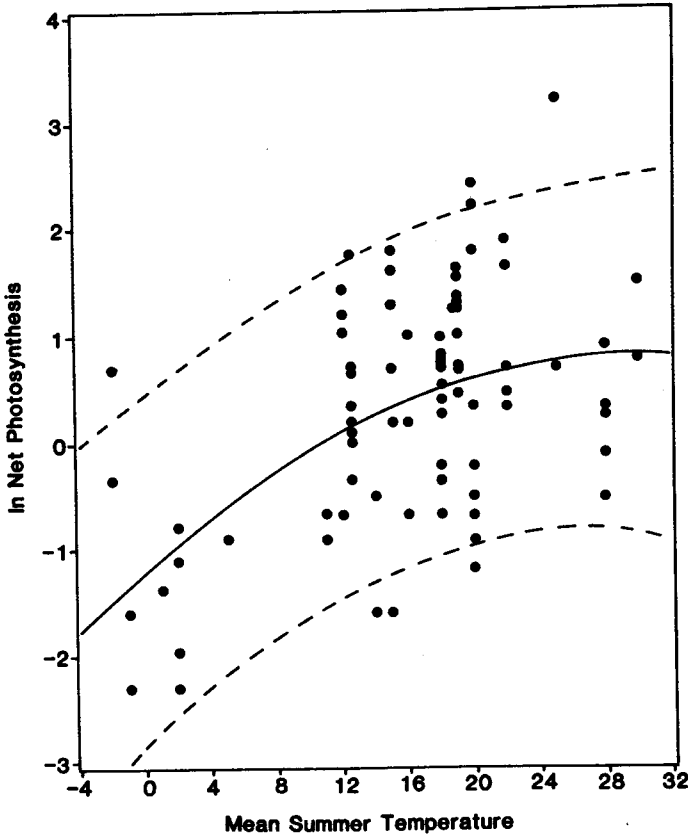


Figure 2 Natural logarithm of the maximum photosynthetic rate plotted against the mean summer temperature in the locality where the assayed lichens were collected. The graph shows the least square regression line with its 90% confidence interval fitted to the data as a quadratic polynomial; each point represents the data from a different lichen assay gleaned from the published literature.

highly significant ($p < .0001$). None of the other climatic variables available improves the prediction of saturating PFD level.

The optimal temperature for photosynthesis is also well predicted by sunniness and continentality (Fig. 5). The photosynthetic temperature optimum tends to be higher in more continental climates and when days are sunnier. A number of *Cladonia* and *Cladonia* species are unusual for their high optimal temperatures despite their origins in weakly continental climates that are sunny. This overall relationship, based on data for 62 lichens, is weaker than that for saturating PFD; it accounts for only 27% of the variance in temperature optima, but is highly significant ($p < .0001$). None of the other climatic variables available have a significant influence on optimal temperature.

Unlike the saturating level of PFD and the optimal temperature, the relative water content at which maximum photosynthesis occurs is not predicted by continentality and sunniness. Instead there is a relationship between precipitation amounts and solar radiation levels (Fig. 6). With the singular exception of *Ramalina maciformis* in the Negev Desert, lichens from wetter regions with greater mean levels of solar radiation during the summer tend to have higher relative water contents at their photosynthetic max-

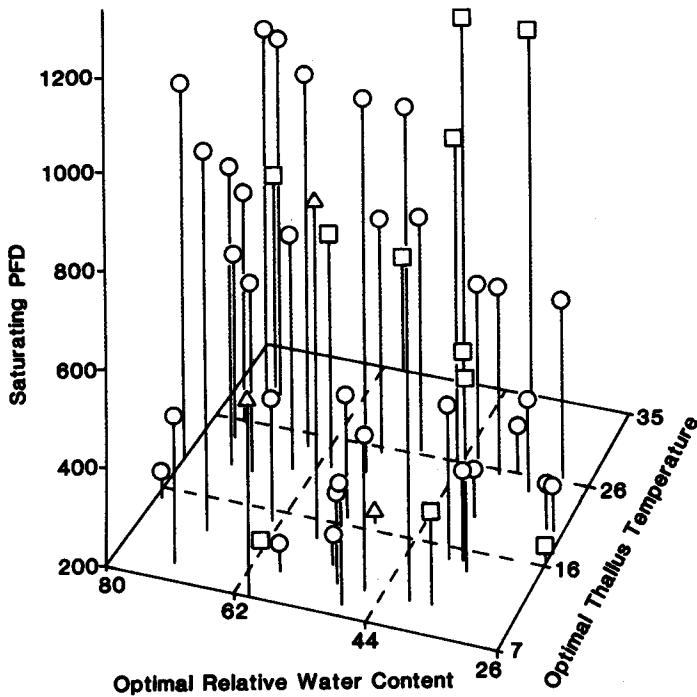


Figure 3 Three dimensional scatter plot of the conditions under which the assayed lichens achieve their maximum photosynthetic rates; only data from studies that reported responses to a very broad range of all three factors was used in preparing this graph. Circles represent fruticose species, squares foliose species, and diamonds crustose species in this and all subsequent figures.

imum. *Ramalina* is known to be unusually dependent on dew rather than rain as a water source (Lechowicz, 1981). The significance of this relationship, based on 53 lichens, is weakened by the *Ramalina* outlier, but is still highly significant ($p < .0023$). Although the relation accounts for only 21% of the variance in optimal relative water content, no other climatic variable among those available improves the prediction of the optimum.

Lichen ecophysiologicalists frequently express water content in absolute rather than relative terms, that is as a percentage increase over dry mass of the thallus. Based on studies where both measures are reported or can be estimated, it is clear that the optima expressed in either frame of reference are similar (Fig. 7). Attempts to predict the absolute rather than relative optimum from climatic variables were no more successful (not shown here).

SUMMARY

There are two aspects of these results that require emphasis: evidence of internal, functional constraints on the lichen photosynthetic response and evidence of an adaptive relationship between response and environment.

With regard to functional constraints, it appears that there is a necessary correspondence between a lichen's maximum photosynthetic capacity and its rate of dark respiration. The greater its photosynthetic capacity, the greater also is the respiratory rate. Secondly, lichens with low temperature optima for photosynthesis appear unable to also

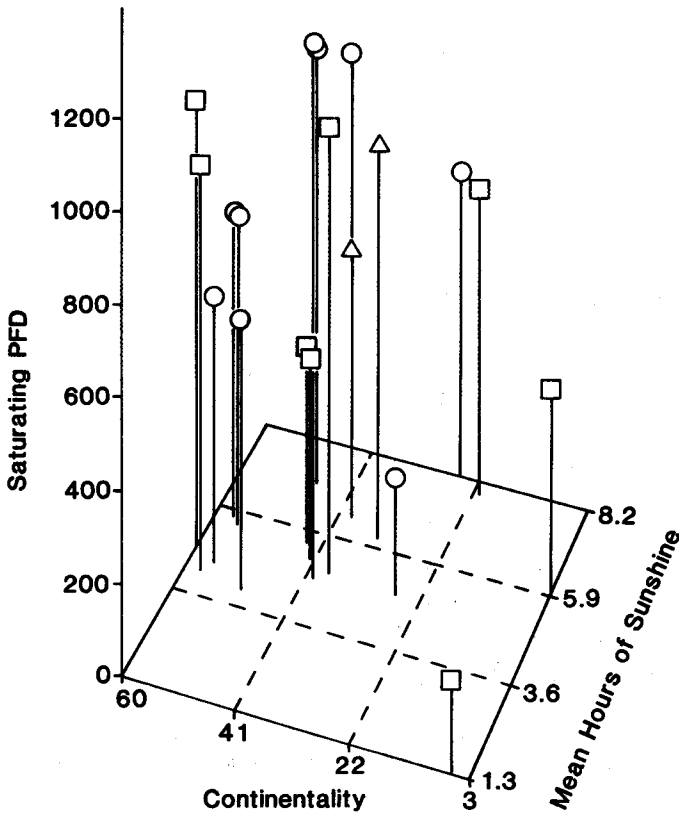


Figure 4 Three dimensional scatter plot of the saturating levels of PFD of lichens in relation to environmental conditions in the localities from which the species were collected. Continuity (Conrad 1946) measures the latitudinally adjusted contrast between temperatures in the warm and cold seasons; the higher the continuity, the greater the annual temperature range in the locality. Mean annual number of sunshine hours are taken from weather records.

utilize high levels of irradiance. Under bright, sunny conditions, even lichens in polar regions can reach fairly high thallus temperatures in sheltered microhabitats, but the capacity to exploit these conditions has not evolved. This cannot be simply because such conditions would also be associated with limitations on photosynthesis by low thallus water content; lichens do exist with photosynthetic optima at high irradiance and low water content. There appears to be some barrier to efficient photosynthesis at both low temperature and high irradiance.

With regard to the environmental correlates of lichen photosynthetic responses, three general points require emphasis. First, as data from a wider geographic and habitat range have become available, it is clear that there is no simple latitudinal dependence in lichen photosynthetic responses. Continuity, which combines latitude and the annual range of temperatures, is important but not latitude alone. Second, both the light and temperature responses of lichen photosynthesis can be predicted from data on the sunniness and continuity of a locality. Lichens from sunnier and more continental climates tend to have higher temperature optima and to become light saturated at higher irradiance levels. In a given locality, species differing in morphology or microhabitat affinities will deviate from these general trends, but those deviations cluster around

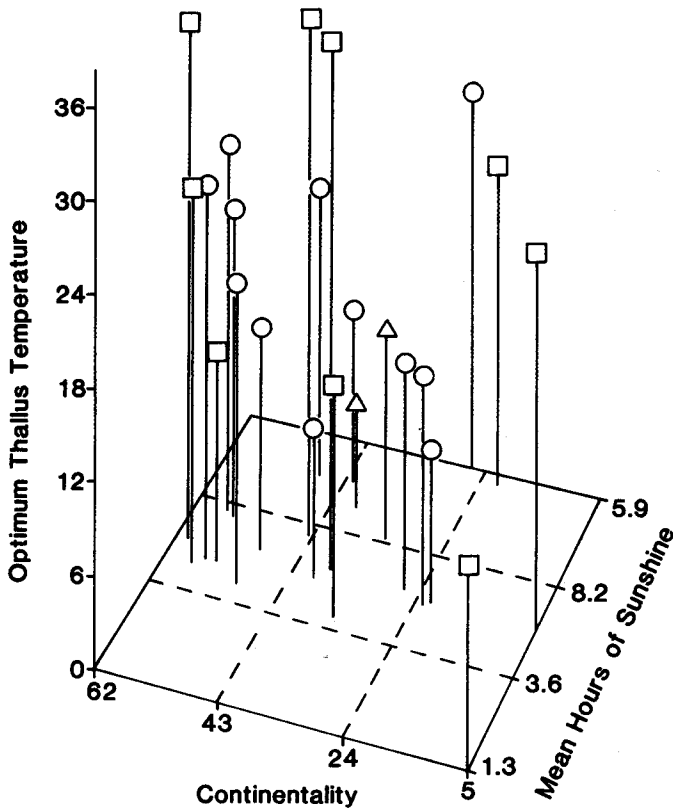


Figure 5 Three dimensional scatter plot of temperature optimum for photosynthesis of lichens in relation to environmental conditions in the localities from which the species were collected.

an average response that is well predicted by sunniness and continentality. Third, the optimal thallus water content for lichen photosynthesis is best predicted by mean annual precipitation levels and measures of mean annual solar radiation. Solar radiation, as opposed to hours of bright sunshine, may give a better estimate of evaporative demand; it is not surprising that the photosynthetic water relations of a poikilohydric group like the lichens would be influenced by climatic variables that affected cycles of wetting and drying (Lechowicz, 1981).

EPILOGUE

This comparative analysis of the literature data on lichen gas exchange responses yields some useful ecophysiological generalizations, but we do not know their evolutionary import. We cannot conclude that these patterns of response are necessarily adaptations to the environmental regimes of the diverse species on which these generalizations are based. To draw firm conclusions about the adaptive value of these photosynthetic responses, we would have to define their contributions to variation in lichen survival and reproduction. Despite the development of sophisticated mechanistic models of lichen gas exchange (Link et al., 1985), it has proven difficult to model the contribution

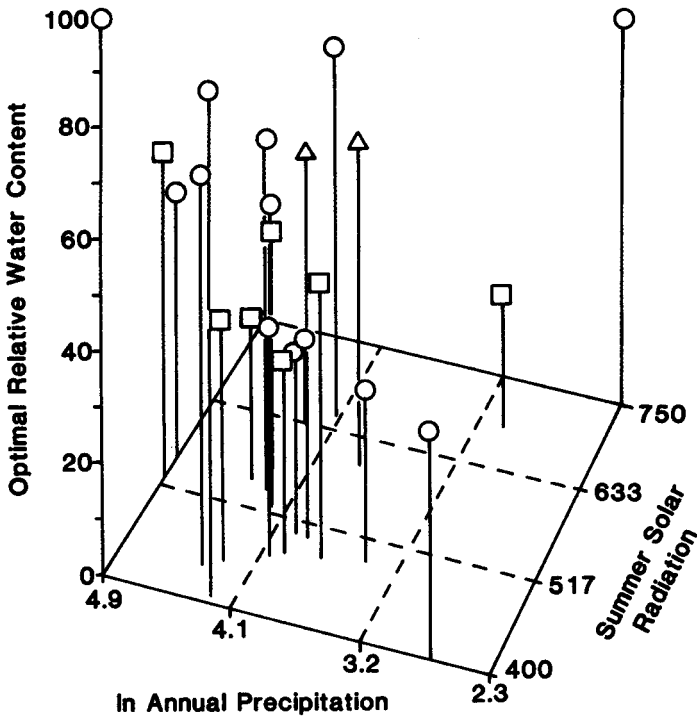


Figure 6 Three dimensional scatter plot of the relative water content optimum for photosynthesis of lichens in relation to environmental conditions in the localities from which the species were collected. The optimum RWC is best related to weather records for solar irradiation in the middle of the warm season (July for northern hemisphere sites) and the natural logarithm of total annual precipitation.

of gas exchange to lichen growth. The dynamics of activity and dormancy imposed by climatic cycles of wetting and drying on both fine and coarse time scales complicate the integration of carbon gains and losses over time. Carbon losses in resaturation respiration (Link and Nash, 1984), differences in rates of photosynthetic recovery (Groulx and Lechowicz, 1987), significant resource losses by leaching of carbohydrates and nitrogen (Dudley and Lechowicz, 1987; Millbank and Olsen, 1986), and the ability of lichens with green algal symbionts to photosynthesize after absorbing water vapor (Lange et al., 1986;) all further complicate an already difficult analysis. In short, any analysis of the contribution of variation in photosynthetic responses to variation in some measure of lichen fitness faces difficult, perhaps insurmountable problems.

Furthermore, to really understand the evolutionary ecology of lichens, we would also need to study the selection of their photosynthetic response—this is likely to remain impossible. The complexities of the curious and interesting duality of lichens as organisms and their very slow growth rates (Lawrey, 1984; Hawksworth, 1988) undermine any analysis of lichen response to selection. We know nothing of the genetic interactions between the algal and fungal partners and little of gene flow in lichen populations (Culberson et al., 1988). While growth may be a reasonable approximation to lichen fitness, lichens grow too slowly to allow the use of contemporary methods for the quantification of phenotypic selection on traits like photosynthetic responses (Endler, 1986). Given these impediments to the study of the evolutionary ecology of lichen pho-

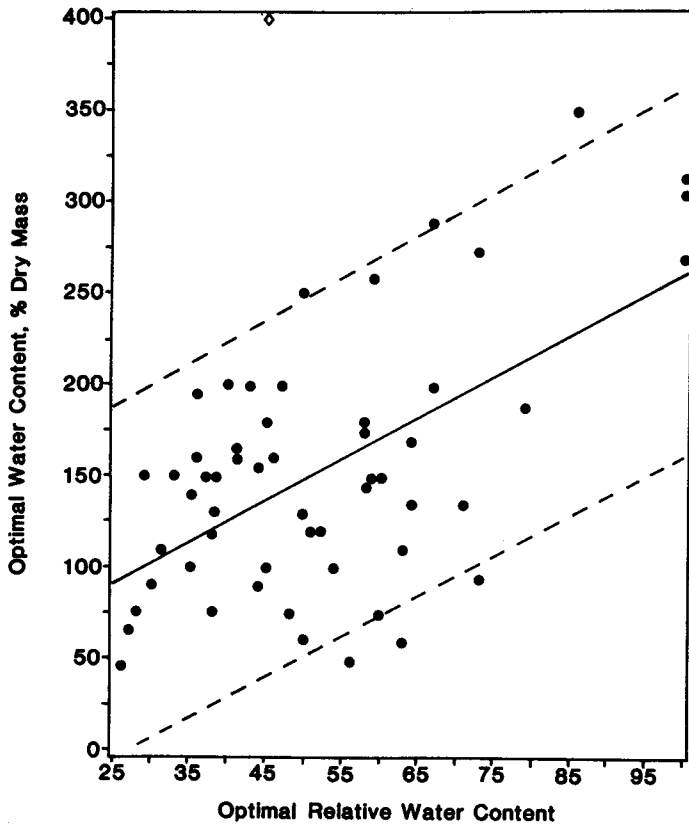


Figure 7 Relationship between thallus water content expressed as a percentage of dry mass versus as a percentage of the maximum water-holding capacity of the thallus. The graph shows the fitted least square regression and 90% confidence interval; the regression is significant at $p = .0001$ with an r^2 of 0.35. The outlier, which was omitted from the regression analysis, is *Collema furfuracea*, the only gelatinous lichen in the data set.

tosynthetic responses, we are unlikely to readily determine the evolutionary basis for variation in lichen photosynthetic responses. The ecological generalizations derived from these comparisons of a large number of lichens, however, stand on their own merit as one of the best examples of general relationships between physiological response and habitat ecology in a group of similar species.

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