The FUNGAL COMMUNITY

ITS ORGANIZATION AND ROLE IN THE ECOSYSTEM

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Chapter 6

ADAPTATION AND THE FUNDAMENTAL NICHE: EVIDENCE FROM LICHENS

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I. INTRODUCTION

When Hutchinson (1958) formalized the concept of the niche, he emphasized the species' limits of tolerance to environmental conditions. On an environmental gradient there is a range of tolerance over which a species can survive and reproduce. All the environmental variables affecting a species' survival and reproduction can be taken together as the axes of a multidimensional space. The hypervolume bounded by the species' tolerance limits on each environmental axis Hutchinson called the *fundamental niche*. This fundamental niche describes the breadth of environmental conditions over which species can exist when removed from competition. In natural communities of competing species an organism is often excluded by competitors from some part of the environment it could potentially utilize. Hutchinson called this truncated fundamental niche which arose under competition with other species the *realized niche*. These concepts of the niche, by explicitly relating the survival and reproduction of a species to environmental variables, are particularly appropriate in the analysis of possibly adaptive relationships between organisms and their environment.

The empirical and theoretical work on the niche that followed Hutchinson's seminal paper has primarily drawn on the concept of the realized niche to analyze competition and community structure (Colwell and Fuentes, 1975), while the evolution and the adaptive significance of a species' fundamental niche has received less attention. The observation that no organisms seem able to survive and reproduce equally well under all environmental conditions suggests two interesting questions about the fundamental niche of a species. First, can we predict the niche breadth that will be favored by natural selection in a given environmental regime? Some theoretical analyses of optimal niche breadths have been made (Roughgarden, 1972; Slatkin and Lande, 1976) but remain largely untested by empirical studies. Second, can we predict how a species' survival and reproductive capacities will vary within the boundaries of its fundamental niche? This second question involves an extension of Hutchinson's concept of the fundamental niche and has not yet been analyzed theoretically. The net photosynthetic responses of lichens discussed in this chapter bear on both questions. It is hoped that this review will encourage additional mycological work toward a general theory predicting the optimal shape of the fundamental niche for a population in a given environment. As McNaughton (Chap. 5) points out, an analysis of the properties of fundamental niches will contribute to our understanding of the mechanisms organizing community composition and dynamics.

II. FITNESS AND THE FUNDAMENTAL NICHE

A. Definitions

The concept of fitness, rigorously defined by Sewall Wright in early work on population genetics, describes "the average contribution which the carriers of a genotype, or a class of genotypes, makes to the gene pool of the following generation relative to the contribution of other genotypes" (Dobzhansky, 1968a). Another only slightly different view, stemming from the work of Fisher (1930), places less emphasis on the relative contribution of genotypes to subsequent generations and instead measures fitness as the intrinsic rate of increase for individuals of a particular genotype in the population. Both measures of fitness depend on the survival characteristics and lifetime reproduction of individuals in the population. Hutchinson's concept of the fundamental niche, based on the environmental limits of survival and reproduction, provides an appropriate conceptual framework for an examination of the interrelationships between an organism's characteristics and its environment that together ultimately determine fitness.

Since environmental conditions are variable and not wholly predictable, to successfully colonize a habitat an organism must survive both the normal environmental conditions and occasional extreme variations from these norms. If there is a genetic basis for rates of growth and reproduction, natural selection will lead to the evolution of responses maximizing successful reproduction in the particular environmental regime of the habitat. Elements of the growth and reproductive responses to environmental variables will then reflect adaptations to environmental pattern. In deciding how well-adapted an organism is to its environment, not only the boundaries of the fundamental niche but also organismal responses within those boundaries are of evolutionary significance (Maguire, 1973; Emlen, 1973, pp. 210-214). Figure 1 gives an example of variation in a lichen net photosynthetic response within the boundaries of a fundamental niche defined for simplicity by only two environmental axes. To the degree that net photosynthesis determines survival and reproduction in this lichen, its fitness will clearly depend on the pattern of tissue temperatures and water contents prevailing in its habitat.

B. Describing the Lichen Niche

In describing the response of an organism within its fundamental niche, two questions have to be resolved: (1) What response best measures an organism's adaptation to an environmental condition? (2) What environmental axes affect this response and determine fitness?

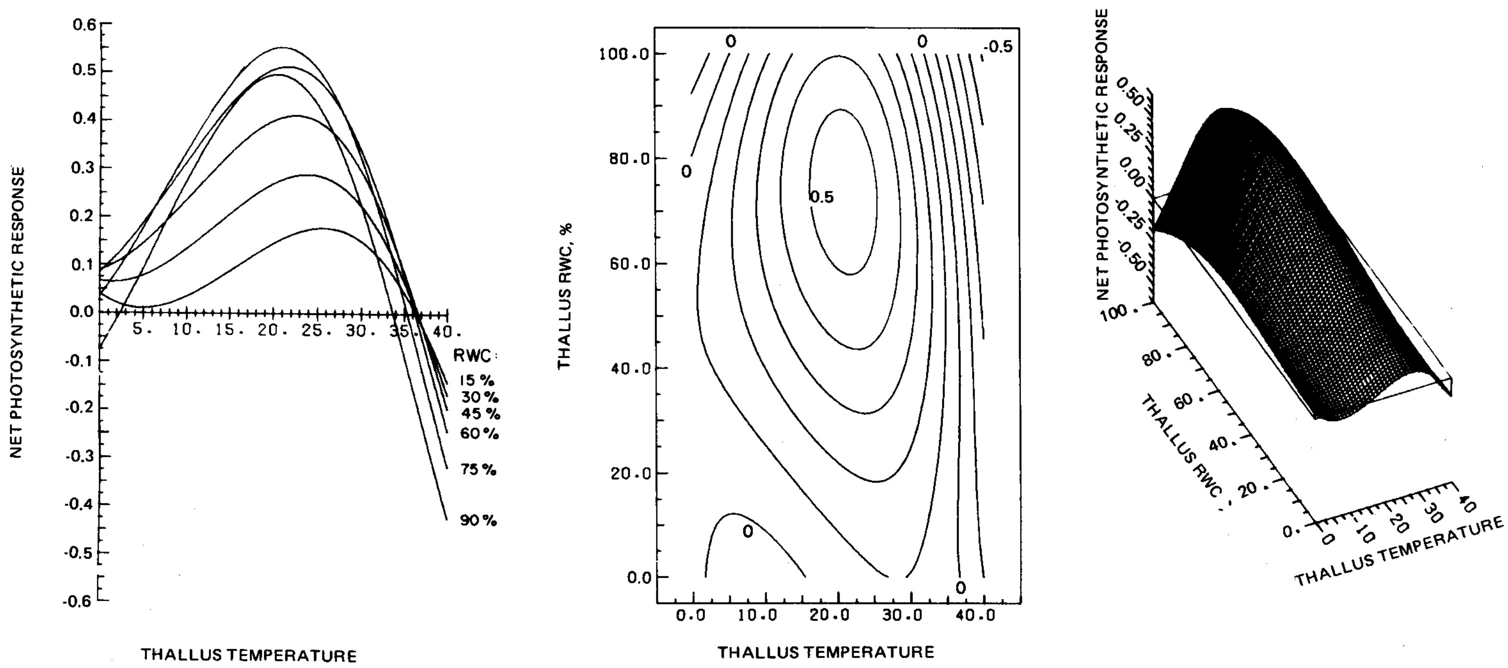

Fig. 1 The net photosynthetic response of the lichen *Cladina stellaris* on two axes of its fundamental niche, tissue temperature and relative water content. The same data are presented in the three graphs, each illustrating a common method of depicting multidimensional response surfaces. Net photosynthesis is measured as milligrams of CO_2 g^{-1} h^{-1} at an irradiance of 600 μEinsteins m^{-2} s^{-1}.

The response chosen should both be practical to measure and contribute significantly to fitness. Rates of growth and reproduction are perhaps most meaningful but not always easily determined over an extensive range of environmental conditions. Related variables such as rates of assimilation or net photosynthesis are feasible alternatives.

Most modern studies of the adaptation of higher plants have assumed that net photosynthetic responses to environmental variables are a critical determinant of fitness. For example, Björkman and Holmgren (1963) showed that, under high irradiance, populations of *Solidago virgaurea* from sunny habitats took up CO_2 at greater rates than did populations from shaded habitats. Conversely, in low light the shaded populations had the higher rates of net photosynthesis. These responses were shown to be in part genetically determined and were taken as evidence that natural selection favored genotypes leading to greater carbon gains in each population's habitat. Similar inferential evidence from numerous studies in physiological plant ecology has been recently reviewed (Strain and Billings, 1974; Cooper, 1975). In addition, Mooney (1972, 1975, 1976) has emphasized the central role of carbon metabolism in plant growth and reproduction and argued that, generally, the greater a plant's net carbon gain over time, the greater its fitness.

Comparable arguments apply in lichens, perhaps more strongly since complications from differing strategies of carbon allocation to specialized organs such as roots, leaves, and flowers do not arise. Compared to higher plants, lichen thalli are relatively undifferentiated (Jahns, 1973) and vegetative propagules are, in many taxa, the primary or only reproductive mode (Bowler and Rundel, 1975; Bailey, 1976). The greater an individual lichen's net carbon balance, the greater its available resources for growth and reproduction. In taxa reproducing largely by vegetative propagules, including simply the dispersal of thallus fragments, increased growth in itself represents an increased reproductive potential. Although information on the competitive ability of lichens is scanty (see Topham, 1977), it appears likely that faster-growing individuals have a competitive advantage. With both the survival and reproduction of lichens enhanced by increasing photosynthetic carbon gains, natural selection will favor individuals with net photosynthetic responses that maximize carbon gain in the lichen's habitat. Thus net photosynthetic rates provide a good response variable to define the fundamental niche of lichens.

The axes of the fundamental niche should ideally include all the environmental variables that alter the chosen response and thereby affect fitness. For simplicity it is useful to combine the interacting effects of many environmental factors by considering only the operational environment (Spomer, 1973), the environmental variables that directly affect the observed response. For example, tissue temperature is determined by the complex interaction of organismal characteristics and such environmental factors as air temperature, humidity, windspeed, solar radiation, and infrared radiation from the surroundings (Monteith, 1973). All these environmental variables can be subsumed on a single niche axis, tissue temperature, which directly controls most biological processes. It may often be very demanding to determine which environmental variables adequately describe the fundamental niche, but any analysis of the adaptive significance of a niche rests on it complete description.

Without undue sacrifice of analytic precision, the environmental axes defining the fundamental niche of many lichens can be reduced to three: tissue temperature, tissue water status, and the incident radiation in the 400-700 µm waveband used in photosynthesis (Farrar, 1973; Richardson, 1973; Kallio and Kärenlampi, 1975). Farrar (1973) suggested that tissue nutrient status did not limit lichen growth, and recent experimental evidence supports this view (Farrar, 1976a; Carstairs and Oechel, 1978). The normal wind regimes of most lichen habitats allow for sufficient convective exchange to maintain fairly uniform ambient CO_2 concentrations; limited evidence (Larson and Kershaw, 1975a) also indicates that CO_2 concentration may not limit net photosynthesis in lichens as it does in higher plants. The generally minor effects of vertebrate (Richardson and Young, 1977) and invertebrate (Gerson and Seaward, 1977) herbivores can be avoided by judicious choice of the species or populations studied. Pollutants like SO_2 which have a marked effect on lichen photosynthesis (Nieboer et al., 1976) are unlikely to represent an equilibrium adaptation open to evolutionary interpretation. Populations from polluted areas can best be neglected unless the actual process of natural selection is to be studied in a population under pollution stress. It is unlikely that all lichen species have so advantageously few niche dimensions; further research is required to determine additional significant environmental variables and their effects on the measured responses. For clarity the discussion in this chapter emphasizes the adaptive significance of net photosynthetic responses to only light, temperature, and water in lichens from diverse habitats.

III. ADAPTEDNESS OF LICHEN NICHES

A. Assessing Adaptedness

A well-chosen response and full definition of its environmental control are the foundations for an analysis of what Dobzhansky (1968a,b) has called *adaptedness*, a measure of how a trait like the response characteristics of the fundamental niche contributes to the probability of successful survival and reproduction in a given environmental regime. Assuming that lichen fitness does increase with increasing carbon gains, we can reason that the greater the net photosynthetic response to a particular combination of light, temperature, and water content, the better adapted the lichen is to that environmental condition. As the environment varies over time in the habitat, the adaptedness of the lichen's fundamental niche then increases as the integral of net photosynthetic response to the sequence of environmental conditions. We lack the necessary long-term data on environmental regimes to quantitatively integrate a lichen's net photosynthetic response over time and must remain limited to a qualitative analysis for the present.

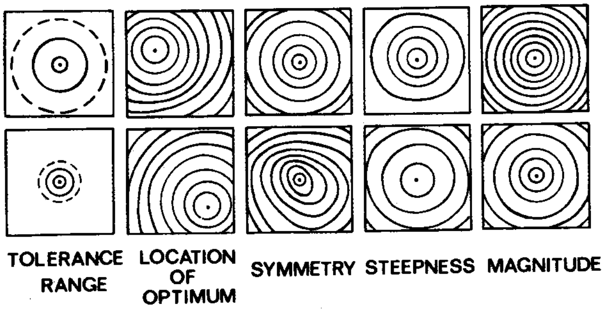

Fig. 2 Qualitative characteristics used to assess the adaptedness of the net photosynthetic responses to environmental variables. A response surface on only two environmental axes is drawn for simplicity. The upper and lower graphs above each heading illustrate a qualitative contrast in that characteristic of the net photosynthetic response. For further discussion, see the text.

Five qualitative characteristics of a net photosynthetic response are useful in assessing its adaptedness (Fig. 2); (1) the range of environmental conditions which can be tolerated; (2) the environmental conditions giving maximal rates of carbon gain; (3) the symmetry of the response surface away from this set of environmental conditions; (4) the steepness of the response surface, that is, the rate of change in CO_2 flux with change in environmental conditions; and (5) the actual magnitude of the maximal CO_2 flux. These five traits qualitatively characterize the net photosynthetic response surface at a single point in time. Any temporal changes in the response surface may also have adaptive significance, particularly regular seasonal changes in response that contribute toward maximizing carbon gain in the lichen's habitat.

Various authors have reviewed aspects of the environmental control of net photosynthesis in lichens, but most have not focused primarily on the adaptive significance of observed responses. Smith (1962) provides a good summary of early work in this area; this is supplemented in recent reviews by Farrar (1973) and by Kallio and Kärenlampi (1975). Kappen (1973) thoroughly considers the effects of extreme environmental conditions on net photosynthetic capacity. Unfortunately, much of the published work in the physiological ecology of lichens is difficult to interpret from an evolutionary perspective. Usually either the net photosynthetic response to all significant environmental variables has not been reported or insufficient information is available on the natural environmental regime in the lichen's habitat to permit judgment as to the adaptedness of the observed responses. The relatively complete studies that will be reviewed here illustrate the use of the niche concept to assess physiological adaptations in lichens.

B. Tolerance Range

The range of tolerance to environmental extremes determines the boundaries of a lichen's fundamental niche and should generally exceed the range of environmental variation in the lichen's habitat. Most species studied seem well able to withstand the periods of environmental stress likely to occur in their habitats. *Ramalina maciformis* from the Negev Desert in southern Israel, for example, can withstand a year at a water content as low as 1% of dry weight without reduction of net photosynthesis under subsequently more favorably conditions (Lange, 1969a). Dry *R. maciformis* can withstand brief exposures to 65°C without subsequent reduction of its net photosynthetic capacity (Lange, 1969a), but when the lichen is wetted temperatures above 35°C are detrimental (Lange, 1965). Temperatures as low as -196°C do not, however, reduce the subsequent photosynthetic performance of wetted *R. maciformis* (Kappen and Lange, 1972). The intense irradiance regime of the desert, with values from darkness up to 886 $W\ m^{-2}$ (Lange et al., 1970a,b), does not appear to impair net photosynthesis. Even the net photosynthesis of wetted *R. maciformis* is not inhibited by irradiance equal to about 50% of the maximal solar radiation measured in the Negev Desert (Lange, 1969a). Comparable data, very thoroughly reviewed by Kappen (1973), indicate a remarkably large tolerance range for most lichens, sometimes in excess of any environmental conditions likely to occur in most natural habitats. While the range limits of some lichens may be set by their intolerance of environmental extremes (Rogers, 1971; Kappen and Lange, 1972), the net photosynthetic responses within the niche boundaries probably more often control distribution and certainly control abundance.

C. Maximal Response

What is the optimal relationship between the environmental conditions giving maximum net photosynthesis and the environmental regime that will be favored by natural selection? Early studies, usually based on response to a single environmental variable, lead to a number of generalizations founded on the premise that the most frequent environmental conditions should determine the optimal response. Thus lichens from cold regions should have maximum net photosynthesis at lower temperatures than lichens from warmer regions (Larcher, 1975; Rogers, 1977). Lichens from dry habitats should have maximum net photosynthesis at lower water contents than lichens from more moist habitats (Kershaw, 1971). By analogy to higher plants, lichens from shaded habitats would be expected to reach maximum net photosynthesis at lower irradiance than those from exposed habitats (Lechowicz and Adams, 1973). There are, unfortunately, a number of problems with these intuitively appealing predictions relating the maximal net photosynthetic response to environmental conditions of high frequency.

Kershaw (1977a) has discussed the danger of drawing conclusions from net photosynthetic responses that are not defined in relation to all significant environmental axes. The optimum response to a single environmental variable invariably depends on the levels of other variables controlling net photosynthesis. In *Cladina stellaris*, for example, the optimum temperature for net photosynthesis at 60% relative water content is 22°C at 600 μEinsteins m^{-2} s^{-1}, 20°C at 300 μEinsteins m^{-2} s^{-1}, and only 15°C at 50 μEinsteins m^{-2} s^{-1} (Lechowicz, 1978). A fully defined response surface has a net photosynthetic maximum at a single combination of light, temperature, and water content levels. It is this global maximum that characterizes the lichen's net photosynthetic response surface, not the innumerable local maxima recognized when response to only a single variable at a time is considered.

Recent, relatively complete studies of lichen net photosynthetic responses (Kallio and Kärenlampi, 1975; Kershaw, 1977a; Lange, 1969a; Lange et al., 1975, 1977; Larson and Kershaw, 1975b,c; Lechowicz, 1976, 1978) only partially support the early generalizations that the net photosynthetic optimum is determined by the most frequent environmental conditions. Lechowicz (1978) compared a *Cladina stellaris* population from northern Quebec with *Cladina evansii* from northern Florida. An analysis of hourly weather data for the collection sites (Lechowicz, 1976; Lechowicz and Adams, 1978) reveals that the two lichens had distinctly different environmental regimes. In the early fall when the response surfaces were measured, the active periods of *C. stellaris* were characterized by lower irradiance, lower tissue temperatures, and higher tissue water content than those of *C. evansii*. The maximum net photosynthesis of *C. stellaris* occurred at about 600 μEinsteins m^{-2} s^{-1}, 20°C, and 70% relative water content; the *C. evansii* maximum occurred at about 1000 μEinsteins m^{-2} s^{-1}, 28°C, and 75% relative water content. These responses to irradiance and temperature follow the early generalizations, but their nearly equal relative water contents at maximum net photosynthesis do not since *C. evansii* grows under considerably more arid conditions than *C. stellaris*. Similarly unexpected net photosynthetic responses to water content are reported for *Cetraria nivalis* and *Alectoria ochroleuca* growing on raised-beach ridges in northern Ontario (Larson and Kershaw, 1975b, c). The ridge tops are a more arid microhabitat than the ridge troughs (Kershaw and Larson, 1974), yet *C. nivalis* from either microhabitat had maximal net photosynthesis at water contents of about 150% dry weight, as did *A. ochroceuca* at about 100% dry weight. The apparent failure of either intra- or interspecific correspondence of the maximal net photosynthetic response and habitat moisture regime suggests that the frequency of environmental conditions alone cannot be the selection pressure explaining observed net photosynthetic responses.

Lechowicz and Adams (1979) have proposed an alternative explanation of the effects of environmental patterns on the evolution of net photosynthetic response. Suppose that irradiance dominates the evolution of the net photosynthetic response surface and that responses to water content and temperature are controlled in part by the light regime. Water contents or temperatures that tend to occur at low light levels offer less potential for carbon gain simply because fewer photons are available for capture. Natural selection may lead to maximal net photosynthesis at an infrequent temperature or water content associated with high irradiance. The frequency of temperatures and water contents in an environmental regime weighted by co-occurring photon flux densities perhaps determines the maximal net photosynthetic response favored by natural selection. The higher the photon flux densities occurring with a particular temperature or water content, the more its impact on natural selection for the maximal net photosynthetic response. This hypothesis assumes that natural selection operates to maximize carbon gain under all irradiances and applies only within the environmental limits of active photosynthesis. For most lichens high irradiance, high temperatures, and very low water contents are a frequent condition in their natural habitats, but photosynthetic activity is then limited by water content. Within these limits, however, the maximal net photosynthetic response of photosynthetically active lichens is hypothesized to be controlled by patterns of temperature and water content weighted by irradiance.

This hypothesis might explain the similar optimal water contents for net photosynthesis observed in *C. stellaris* and *C. evansii* (Lechowicz, 1978). During summer and fall, rains in Florida are usually intense late-afternoon thunderstorms, whereas in northern Quebec rains can come at any hour and are more frequent (Byers and Rodebush, 1948; Lechowicz, 1976; Lechowicz and Adams, 1978). Since neither lichen photosynthesizes when dry, the active periods of the two species are qualitatively distinct as a result of these different rainfall and drying regimes: *C. stellaris* will maintain high water contents for extended periods, whereas *C. evansii* will actively photosynthesize most often in the morning hours following a thunderstorm the previous day. The 70% optimal relative water content of *C. stellaris* corresponds to its water content during extended periods of overcast with low light and temperature levels; the 75% optimal water content of *C. evansii* corresponds to its water content during the high-light and moderate-temperature conditions that often prevail the morning after a storm. The relatively low optimal temperature for net photosynthesis in the desert lichen *Ramalina maciformis* gives additional support to this hypothesis, since active photosynthesis is limited to early mornings after dewfall (Lange, 1969a; Lange et al., 1970a). More work is necessary to establish whether or not the evolution of the optimal environmental conditions for lichen net photosynthesis depends on patterns of temperature and water content weighted by irradiance.

D. Symmetry of Response

The environmental conditions affecting net photosynthesis are strongly interrelated in most natural habitats, and net photosynthetic responses are likely to reflect adaptation to these interrelationshps. For example, air temperature generally increases with increasing irradiance, which suggests that even allowing for the role of evaporative cooling in the lichen energy balance (Hoffman and Gates, 1970; Lechowicz, 1976), tissue temperature will also increase with increasing irradiance. Figure 3 shows an example of this expected relation taken from hourly readings of tissue temperatures and irradiance in *Cetraria cucullata* from the Alaskan Arctic tundra. The *C. cucullata* was often dry during the monitoring period, but when the lichen is wet the relationship shown is maintained. Because of such correlations among environmental variables, the net photosynthetic response of lichens is unlikely to be symmetrical around its optimum.

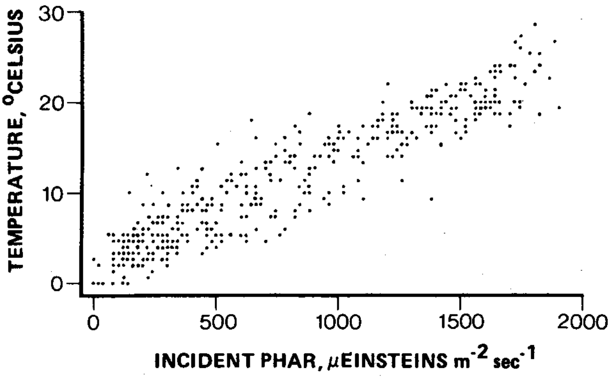

Fig. 3 The relationship between tissue temperature and irradiance for *Cetraria cucullata* growing in dry ridge tundra at Atkasook, Alaska (70°N, 157°W). Readings were taken hourly from June 28 through July 17, 1977.

Considering the relationship between tissue temperature and irradiance, we might predict that maximal net photosynthesis at a particular water content will occur at greater temperatures as the light level increases. This prediction is borne out by *Neuropogon acromelanus*, *Buellia frigida*, and *Xanthoria mawsoni* from Antarctica (Lange and Kappen, 1972), by *Ramalina maciformis* from the Negev Desert (Lange, 1969a), by *Cetraria nivalis* from subarctic Finland (Kallio and Kärenlampi, 1975), by *Cladina stellaris* from subarctic Quebec, and by *Cladina evansii* from temperate Florida (Lechowicz, 1978). Comparable increases in the optimal temperature for net photosynthesis with decreasing water content have also been described (Lechowicz, 1978). Since carbon gains will be increased by responses coordinated with combinations of environmental conditions that occur at disproportionately high frequency, such asymmetries in the response surface of lichen net photosynthesis are of adaptive significance.

E. Steepness of Response

If a narrow range of environmental conditions occurs predictably in a habitat, it may be advantageous for a lichen to specialize in fixing carbon rapidly under these conditions. This strategy could result in a low photosynthetic rate over a broad range of tolerated, relatively infrequent environmental conditions and a steep increase in net photosynthesis as the predictable and frequent environmental conditions are approached. In habitats of either low predictability or a predictably broad range of environmental conditions, more generalist responses may be favored. This aspect of net photosynthetic response to environmental variables requires investigation but is beset by technical difficulties. The data needed to rigorously test ecological theories predicting the occurrence of generalist versus specialist responses (Levins, 1968a,b) are not easily obtained with lichens. Monitoring or estimating the environmental regime is difficult over a long enough period to establish the predictability of environmental patterns, and the predictability of a multidimensional environmental condition cannot be quantitatively described by presently available methods (Colwell, 1974). Despite its possible adaptive significance, variation in the steepness of net photosynthetic responses is unlikely to be carefully analyzed with present limitations in environmental monitoring.

F. Magnitude of Response

If the magnitude of net photosynthesis could be increased without limit, discussion of the response to particular environmental conditions would become largely irrelevant. Although this evolutionary option is impossible, the absolute rates of net photosynthesis in lichens from different habitats can be of adaptive significance. Data available from completely defined net photosynthetic responses (Fig. 4) show that maximal rates of net photosynthesis decrease with increasing latitude. This trend, also supported by earlier data tabulated in Kallio and Kärenlampi (1975), may represent a trade-off of photosynthetic capacity against some other physiological trait necessary for surviving stress associated with environments in the more north-

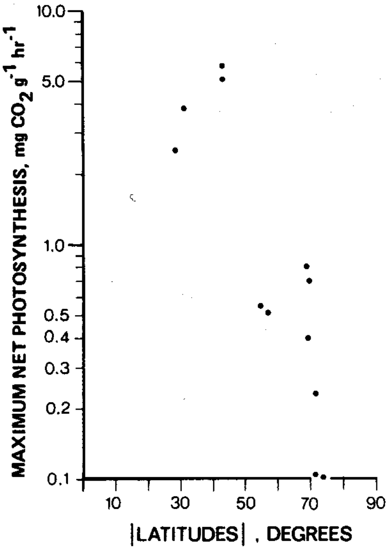

Fig. 4 Latitudinal trend in maximum rates of lichen net photosynthesis. [Data are from Kallio and Kärenlampi (1975), Kershaw (1977a,b), Lange (1969a), Lange and Kappen (1972), Larson and Kershaw (1975a,b,c), and Lechowicz (1978; also unpublished data).]

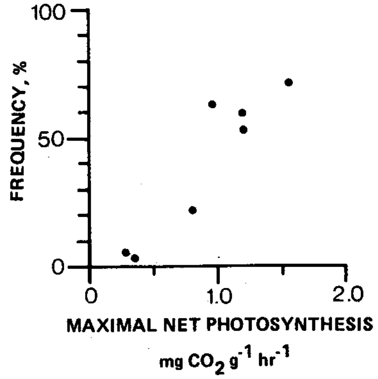

Fig. 5 Relationship between the maximum rates of net photosynthesis and the frequency of species occurrence in an arboreal lichen community. [Data are from Nowak (1973).]

erly or southerly latitudes (Berry, 1975). Data from a single site in Germany (Nowak, 1973) provide evidence that greater net photosynthetic rates enhance survival and reproduction in an arboreal lichen community (Fig. 5). Nowak examined both the dominance relations and CO_2 exchange responses of species in a lichen community growing on oak and beech in a forest unaffected by air pollution. If the frequency of the species is plotted against the maximal net photosynthetic rates observed for each species, it is apparent that dominance in the community increases with photosynthetic capacity. For lichens in general, increasing absolute rates of net photosynthesis probably increases fitness.

G. Seasonal Changes in Response

The extensive studies of Kershaw and Larson (see Larson and Kershaw, 1975b,c,d; Kershaw, 1975, 1977a,b) have confirmed seasonal changes in lichen net photosynthetic responses first noted as early as 1939 by Stålfelt. A central question is to what degree these observed seasonal changes in net photosynthetic responses are adaptive in either lichens or other plants (Oechel, 1976). Kershaw (1977a) has shown that the seasonal changes in the temperature responses of net photosynthesis in both *Peltigera polydactyla* and *Peltigera canina* var. *rufescens* are an acclimation to the thermal regime of their temperate forest habitat. Maximal net photosynthesis is attained throughout the year at about 500 μEinsteins m^{-2} s^{-1} and at water contents about 250% of dry weight, but the temperature optimum in both species increases from spring through summer and then decreases to winter. Unfortunately, sufficient data on seasonal patterns of tissue water contents, temperatures, and irradiance in the habitat are unavailable and the adaptedness of these seasonal patterns in the net photosynthetic responses cannot be ascertained. Similarly, more environmental data are necessary to decide whether changes in net photosynthetic responses observed over a few days (Kershaw, 1977b) represent rapid acclimation of adaptive significance in the natural habitat or only transient responses to stress (Lange, 1969a; Kallio and Heinonen, 1971). Although it seems likely that the adaptedness of lichens can be enhanced by seasonal changes in net photosynthetic response, a comparison of changes observed in lichens from habitats with well-defined seasonal patterns of environmental conditions will be necessary to elucidate the full import of such acclimation.

IV. THE CARBON BALANCE OF LICHENS

Net photosynthetic responses contribute to increasing carbon gain, but the impact of these gains on fitness must be weighed against associated losses of carbon. It is growth, not rates of net photosynthesis, that is more closely tied to fitness. Growth may be defined as the change in lichen biomass over time and described by a simple mass balance equation:

$$B_{t+1} = B_t + kF_{CO_2} \qquad (1)$$

The biomass B_{t+1} depends on the biomass, B_t, in the previous time interval and the carbon dioxide flux during the interval, F_{CO_2}. The constant, k, is a conversion of milligrams of CO_2 to milligrams of biomass derived by consideration of the chemical composition of lichen tissue. The flux of CO_2 has two components:

$$F_{CO_2} = {}_aF_{CO_2} + {}_{rs}F_{CO_2} \tag{2}$$

The term ${}_aF_{CO_2}$ represents this flux of CO_2 from the fully active lichen. During periods of activity CO_2 may be gained or lost at a rate determined by irradiance, temperature, and water content; this is the net photosynthetic response emphasized in the previous discussion. This response at zero irradiance is often distinguished as dark respiration. The term ${}_{rs}F_{CO_2}$ represents a negative flux of CO_2 that occurs for some time after a dry and dormant lichen is rewetted; this loss of carbon associated with rewetting has been called *resaturation respiration* (Smith and Molesworth, 1973) and may represent the carbon cost of reactivating the dormant lichen's metabolism (Farrar, 1976b; Farrar and Smith, 1976). These carbon fluxes integrated over time determine the lichen's net carbon balance and its consequent growth. The greater the coordination of flux responses to the environmental regime of a lichen's habitat, the greater the potential growth.

The contribution of these components of the lichen carbon balance to survival and reproduction has been most thoroughly studied in *Ramalina maciformis* (Lange and Bertsch, 1965; Lange, 1965, 1969a,b; Lange et al., 1969, 1970a,b, 1977; Kappen and Lange, 1972). These results are summarized in Lange et al. (1975). *Ramalina maciformis* growing in the Negev Desert was shown to be tolerant of the extremes of temperature and water content in this habitat. Water contents sufficient for photosynthetic activity could be attained by vapor uptake or dewfall as well as rainfall. At water contents as low as 20% of dry weight, *R. maciformis* could maintain positive net photosynthesis under favorable light and temperature conditions; maximal net photosynthetic responses were achieved at a water content of only 60% of dry weight, 20°C, and 48,500 lux (about 900 μEinsteins m^{-2} s^{-1}). Estimation of the lichen's annual carbon balance was simplified because, like another desert lichen, *Chondropsis semiviridis* (Rogers, 1971), *R. maciformis* did not have significant resaturation respiration. Field studies in the Negev Desert showed that net photosynthetic responses give sufficient carbon gain under the natural environmental regime to counter losses during darkness and allow an annual growth rate of some 5-10% dry weight.

In *Cetraria cucullata* from the Alaskan Arctic tundra, resaturation respiration is a significant component of the carbon balance (Fig. 6) and complicates assessment of the lichen's adaptedness. Fully active *C. cucullata* has maximal net photosynthesis at over 1200 μEinsteins m^{-2} s^{-1}, 10°C, and about 90% relative water content (Fig. 7). Although few environmental data are available (Conover, 1960; Haugen et al., 1976; Clebsch and Shanks, 1968), the net photosynthetic response of *C. cucullata* seems reasonably well adapted to the arctic summer. Yet, during the period July 1

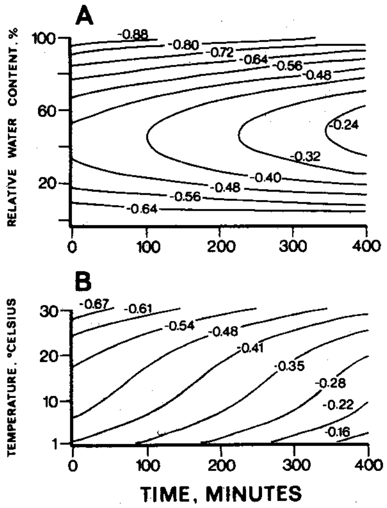

Fig. 6 The time course after wetting of CO_2 flux in the dark for *Cetraria cucullata* as a function of relative water content (A) and tissue temperature (B). The *C. cucullata* was collected in June-July from a dry ridge tundra community near Atkasook, Alaska (70°28'N, 157°23'W). The CO_2 flux is given as milligrams of CO_2 g^{-1} h^{-1}. In part A the tissue temperature is 10°C; in part B the relative water content is 60%.

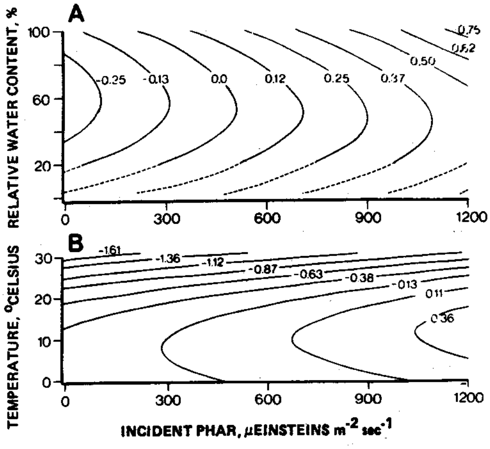

Fig. 7 The net photosynthesis of fully active *Cetraria cucullata* as a function of incident photosynthetically active radiation, relative water content (A), and tissue temperature (B). The *C. cucullata* was collected in June-July from a dry ridge tundra near Atkasook, Alaska (70°28'N, 157°23'W). The lichen was wetted at least 12 hr before the experiments began and was stored at 5°C. The CO_2 flux is given as milligrams of CO_2 g^{-1} h^{-1}. In part A the tissue temperature is 10°C; in part B the relative water content is 60%.

to 17, 1977, *C. cucullata* had a measured relative growth rate of -7.2 mg g^{-1} day^{-1}. During this unusually dry period, the lichen was frequently wetted incompletely by an early morning dew or fog and then rapidly dried by midmorning. The carbon losses sustained in resaturation respiration were thus not completely regained in net photosynthesis before the lichen reentered dormancy. These data support the early hypothesis of Ried (1960) that cycles of wetting and drying can determine a lichen's ability to survive in a habitat. Presumably *C. cucullata*, like the *Cetraria nivalis* studied by Kallio and Kärenlampi (1975), has compensating positive relative growth rates in another season that allow its survival on the dry ridge tundra.

These data also emphasize the importance of considering all components of the carbon balance in judging adaptedness in a particular habitat. The adaptedness of net photosynthetic responses alone can be considered since rates of carbon gain are probably maximized under natural selection, but in actuality lichen fitness is more directly tied to growth rates which are set by the balance of photosynthetic gains and respiratory losses in the habitat. This complicates analysis of the adaptive significance of lichen niches since lichen growth rates are difficult to assess over a broad range of controlled conditions (Armstrong, 1976).

V. NONLICHENIZED FUNGI AND THE NICHE

The growth or reproductive rates of many nonlichenized fungi are easier to measure than those of lichens and provide good fitness-related response variables. There has been considerable research on the environmental control of fungal growth and reproduction (Ainsworth and Sussman, 1968; Griffin, 1972), but studies of responses to single variables have predominated. The concept of the fundamental niche, by emphasizing the multivariate nature of environmental control over organismal response, has a useful heuristic role in the interpretation of fungal response data. Moreover, the qualitative response characteristics illustrated here with lichen net photosynthesis may also be applied to analysis of the adaptive significance of other fungal responses. Such analyses may be easier and more instructive using fungi in soil or aquatic habitats where long-term environmental patterns are more easily estimated than for plants exposed to the atmospheric environment. Fungal ecologists, with thoughtful choice of experimental taxa, should be able to thoroughly describe the relationships between fungal responses to multiple environmental variables and the pattern of those variables in the natural habitats of the taxa. A complete description of these relationships does not exist in the ecological literature and would be an important contribution toward measuring the adaptedness of a fundamental niche.

The limited evidence from lichens reviewed here does not conclusively establish that the fundamental niche has evolved under natural selection as an adaptation to environmental patterns. Adaptive characteristics of the fundamental niche can only evolve if there are heritable differences among the fundamental niches of individuals in a population that lead to differential lifetime reproductive success. Because of the relative ease of isolating and culturing pure strains of many fungi, fungal ecologists can test these critical requirements for evolution of niche characteristics. Clonal isolates from natural populations of fungi can provide valuable data on genetically based variation in the fundamental niche of a species. Competition experiments between strains can establish the adaptedness of responses within the boundaries of the fundamental niche under diverse environmental regimes. By studying relationships between variation in niche characteristics and fitness, fungal ecologists could advance our understanding of the evolution of the niche.

As a final caution, the likely importance of competition in the evolution of fundamental niche characteristics must be noted. The physical environment alone may affect differential survival and reproduction among individuals in populations occurring at low densities like some of the lichens or similar colonizing species. In most communities, however, both intra- and interspecific competition exert selection pressure on growth and reproductive responses. The dynamic interactions of species in a community require that to understand the evolution of the fundamental niche we must consider the effect of biotic as well as physical environmental factors.

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REFERENCES

Ainsworth, G. C., and Sussman, A. S. (Eds.). (1968). *The Fungi*, Vol. III: *The Fungal Population*. Academic Press, New York.

Armstrong, R. A. (1976). Studies on the growth rates of lichens. In *Lichenology: Progress and Problems*, D. H. Brown, D. L. Hawksworth, and R. H. Bailey, (Eds.). Academic Press, New York, pp. 309-322.

Bailey, R. H. (1976). Ecological aspects of dispersal and establishment in lichens. In *Lichenology: Progress and Problems*, D. H. Brown, D. L. Hawksworth, and R. H. Bailey (Eds.). Academic Press, New York, pp. 215-247.

Berry, J. A. (1975). Adaptation of photosynthetic processes to stress. *Science 188*: 644-650.

Björkman, O., and Holmgren, P. (1963). Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. *Physiol. Plant. 16*: 889-914.

Bowler, P. A., and Rundel, P. W. (1975). Reproductive strategies in lichens. *Bot. J. Linn. Soc. 70*: 325-340.

Byers, H. B., and Rodebush, H. R. (1948). Causes of thunderstorms of the Florida peninsula. *J. Meteorol. 5*: 275-280.

Carstairs, A. G., and Oechel, W. C. (1978). Effects of several microclimatic factors and nutrients on net carbon dioxide exchange in *Cladonia alpestris* (L.) Rabh. in the subarctic. *Arctic and Alpine Res. 10*: 81-94.

Clebsch, E. E. C., and Shanks, R. E. (1968). Summer climatic gradients and vegetation near Barrow, Alaska. *Arctic 21*: 162-171.

Colwell, R. K. (1974). Predictability, constancy, and contingency of periodic phenomena. *Ecology 55*: 1148-1153.

Colwell, R. K., and Fuentes, E. R. (1975). Experimental studies of the niche. *Ann. Rev. Ecol. Syst. 6*: 281-310.

Conover, J. H. (1960). Macro- and microclimatology of the Arctic Slope of Alaska. Tech. Rept. EP-139, Quartermaster Research and Engineering Command, U.S. Army.

Cooper, J. P., Ed. (1975). *Photosynthesis and Productivity in Different Environments*. Cambridge Univ. Press, New York.

Dobzhansky, Th. (1968a). On some fundamental concepts of Darwinian biology. *Evol. Biol. 2*: 1-34.

Dobzhansky, Th. (1968b). Adaptedness and fitness. In *Population Biology and Evolution*, R. C. Lewontin (Ed.). Syracuse Univ. Press, Syracuse, pp. 109-121.

Emlen, J. M. (1973). *Ecology: An Evolutionary Approach*. Addison-Wesley, Reading, Mass.

Farrar, J. F. (1973). Lichen physiology: progress and pitfalls. In *Air Pollution and Lichens*, B. W. Ferry, M. S. Baddeley, and D. L. Hawksworth (Eds.). Univ. of Toronto Press, Toronto, pp. 238-282.

Farrar, J. F. (1976a). The uptake and metabolism of phosphate by the lichen *Hypogymnia physodes*. *New Phytol. 77*: 127-134.

Farrar, J. F. (1976b). Ecological physiology of the lichen *Hypogymnia physodes*. II. Effects of wetting and drying cycles and the concept of "physiological buffering." *New Phytol. 77*: 105-113.

Farrar, J. F., and Smith, D. C. (1976). Ecological physiology of the lichen *Hypogymnia physodes*. III. The importance of the rewetting phase. *New Phytol. 77*: 115-125.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford Univ. Press (Clarendon), New York.

Gerson, V., and Seaward, M. R. D. (1977). Lichen-invertebrate associations. In *Lichen Ecology*, M. R. D. Seaward (Ed.). Academic Press, New York, pp. 69-119.

Griffin, D. M. (1972). *Ecology of Soil Fungi*. Chapman & Hall, London.

Haugen, R. K., Brown, J., and May, T. A. (1976). Climatic and soil temperature observations at Atkasook on the Meade River, Alaska, Summer 1975. CRREL Special Report 76-1, CRREL, Hanover, N.H.

Hoffman, G. R., and Gates, D. M. (1970). An energy budget approach in the study of water loss in cryptogams. *Bull. Torrey Bot. Club 97*: 361-366.

Hutchinson, G. E. (1958). Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol. 22*: 415-427.

Jahns, H. M. (1973). Anatomy, morphology, and development. In *The Lichens*, V. Ahmadjian and M. E. Hale (Eds.). Academic Press, New York, pp. 1-58.

Kallio, P., and Heinonen, S. (1971). Influence of short-term low temperature on net photosynthesis in some subarctic lichens. *Rep. Kevo Subarctic Res. Sta. 8*: 63-72.

Kallio, P., and Kärenlampi, L. (1975). Photosynthesis in mosses and lichens. In *Photosynthesis and Productivity in Different Environments*, J. P. Cooper (Ed.). Cambridge Univ. Press, New York, pp. 383-423.

Kappen, L. (1973). Response to extreme environment. In *The Lichens*, V. Ahmadjian and M. E. Hale (Eds.). Academic Press, New York, pp. 311-380.

Kappen, L., and Lange, O. L. (1972). Die Kälteresistenz einiger Makrolichenen. *Flora 161*: 1-29.

Kershaw, K. A. (1971). The relationship between moisture content and net assimilation rate of lichen thalli and its ecological significance. *Can. J. Bot. 50*: 543-555.

Kershaw, K. A. (1975). Studies on lichen-dominated systems. XIV. The comparative ecology of *Alectoria nitidula* and *Cladina alpestris*. *Can. J. Bot. 53*: 2608-2613.

Kershaw, K. A. (1977a). Physiological-environmental interactions in lichens. II. The pattern of net photosynthetic acclimation in *Peltigera canina* (L.) Willd var. *praetextata* (Floerke in Somm.) Hue, and *P. polydactyla* (Neck.) Hoffm. *New Phytol. 79*: 377-390.

Kershaw, K. A. (1977b). Physiological-environmental interactions in lichens. III. The rate of net photosynthetic acclimation in *Peltigera canina* (L.) Willd var. *praetextata* (Floerke in Somm.) Hue, and *P. polydactyla* (Neck.) Hoffm. *New Phytol. 79*: 391-402.

Kershaw, K. A., and Larson, D. W. (1974). Studies on lichen-dominated systems. IX. Topographic influences on microclimate and species distribution. *Can. J. Bot. 52*: 1935-1945.

Lange, O. L. (1965). Der CO_2-Gaswechsel von Flechten nach Erwärmung in feuchten Zustand. *Ber. Deut. Bot. Ges. 78*: 441-454.

Lange, O. L. (1969a). Experimentell-ökologische Untersuchungen an Flechten der Negev-Wüste. I. CO_2-Gaswechsel von *Ramalina maciformis* (Del.) Bory unter kontrollierten Bedingungen im Laboratorium. *Flora Abt. B 158*: 324-359. [Tech. transl. No. 1654, National Research Council of Canada: Ecophysiological investigations on lichens of the Negev Desert. I. CO_2 gas exchange of *Ramalina maciformis* (Del.) Bory under controlled conditions in the laboratory.]

Lange, O. L. (1969b). Die funktionellen Anpassungen der Flechten an die ökologischen Bedingungen arider Gebiete. *Ber. Deut. Bot. Ges. 82*: 3-22.

Lange, O. L., and Bertsch, A. (1965). Photosynthese der Wüstenflechte *Ramalina maciformis* nach Wasserdampfaufnahme aus dem Luftraum. *Naturwissenschaften 9*: 215-216.

Lange, O. L., and Kappen, L. (1972). Photosynthesis of lichens from Antarctica. In *Antarctic Terrestrial Biology*, G. A. Llano (Ed.). American Geophysical Union, Washington, D.C., pp. 83-95.

Lange, O. L., Koch, W., and Schulze, E.-D. (1969). CO_2-Gaswechsel und Wasserhaushalt von Pflanzen in der Negev-Wüste am Ende der Trockenzeit. *Ber. Deut. Bot. Ges. 82*: 39-61.

Lange, O. L., Schulze, E.-D., and Koch, W. (1970a). Experimentell-ökologische Untersuchungen an Flechten der Negev-Wüste. II. CO_2-Gaswechsel und Wasserhaushalt von *Ramalina maciformis* (Del.) Bory am natürlichen Standort während der sommerlichen Trockenperiode. *Flora 159*: 38-62. [Tech. transl. No. 1655, National Research Council of Canada: Ecophysiological investigations on lichens of the Negev Desert. II. CO_2 gas exchange and water relations of *Ramalina maciformis* (Del.) Bory in its natural habitat during the summer dry period.]

Lange, O. L., Schulze, E.-D., and Koch, W. (1970b). Experimentell-ökologische Untersuchungen an Flechten der Negev-Wüste. III. CO_2-Gaswechsel und Wasserhaushalt von Krusten- und Blattflechten am natürlichen Standort während der sommerlichen Trockenperiode. *Flora 159*: 525-538. [Tech. transl. No. 1656, National Research Council of Canada: Ecophysiological investigations on lichens of the Negev Desert. III. CO_2 gas exchange and water relations of crustose and foliose lichens in their natural habitat during the summer dry period.]

Lange, O. L., Schulze, E.-D., Kappen, L., Buschbom, U., and Evenari, M. (1975). Adaptations of desert lichens to drought and extreme temperatures. In *Environmental Physiology of Desert Organisms*, N. F. Hadley (Ed.). Dowden, Hutchinson, and Ross, Stroudsburg, Pa., pp. 20-37.

Lange, O. L., Geiger, I. L., and Schulze, E.-D. (1977) Ecophysiological investigations on lichens of the Negev Desert. V. A model to simulate net photosynthesis and respiration of *Ramalina maciformis*. *Oecologia 28*: 247-259.

Larcher, W. (1975). *Physiological Plant Ecology* (transl. by M. A. Biederman-Thorson). Springer-Verlag, New York.

Larson, D. W., and Kershaw, K. A. (1975a). Measurement of CO_2 exchange in lichens: a new method. *Can. J. Bot. 53*: 1535-1541.

Larson, D. W., and Kershaw, K. A. (1975b). Studies on lichen-dominanted systems. XIII. Seasonal and geographical variation of net CO_2 exchange of *Alectoria ochroleuca*. *Can. J. Bot. 53*: 2598-2607.

Larson, D. W., and Kershaw, K. A. (1975c). Studies on lichen-dominated systems. XVI. Comparative patterns of net CO_2 exchange in *Cetraria nivalis* and *Alectoria ochroleuca* collected from a raised-beach ridge. *Can. J. Bot. 53*: 2884-2892.

Larson, D. W., and Kershaw, K. A. (1975d). Acclimation in arctic lichens. *Nature 254*: 421-423.

Lechowicz, M. J. (1976). Environmental response structure of *Cladonia* lichens from contrasting climates. Ph.D. thesis, University of Wisconsin, Madison.

Lechowicz, M. J. (1978). Carbon dioxide exchange in *Cladina* lichens from subarctic and temperate habitats. *Oecologia 32*: 225-237.

Lechowicz, M. J., and Adams, M. S. (1973). Net photosynthesis of *Cladonia mitis* (Sand.) from sun and shade sites on the Wisconsin Pine Barrens. *Ecology 54*: 413-419.

Lechowicz, M. J., and Adams, M. S. (1978). Diurnal and seasonal structure of the climate at Schefferville, Quebec. *Arctic and Alpine Res. 10*: 95-104.

Lechowicz, M. J., and Adams, M. S. (1979). Net CO_2 exchange in *Cladonia* lichen species endemic to southeastern North America. *Photosynthetica 13*: 155-162.

Levins, R. (1968a). *Evolution in Changing Environments*. Princeton Univ. Press, Princeton, N.J.

Levins, R. (1968b). Toward an evolutionary theory of the niche. In *Evolution and Environment*, E. T. Drake (Ed.). Yale Univ. Press, New Haven, Conn., pp. 325-340.

Maguire, B., Jr. (1973). Niche response structure and the analytical potentials of its relationship to the habitat. *Amer. Natur. 107*: 213-246.

Monteith, J. L. (1973). *Principles of Environmental Physics*. Elsevier, New York.

Mooney, H. A. (1972). The carbon balance of plants. *Ann. Rev. Ecol. Syst. 3*: 315-346.

Mooney, H. A. (1975). Plant physiological ecology: a synthetic view. In *Physiological Adaptation to the Environment*, F. J. Vernberg (Ed.). Educational Publ., New York, pp. 19-36.

Mooney, H. A. (1976). Some contributions of physiological ecology to plant population biology. *Syst. Bot. 1*: 269-283.

Nieboer, E., Richardson, D. H. S., Puckett, K. J., and Tomassini, F. D. (1976). The phytotoxicity of sulphur dioxide in relation to measurable responses in lichens. In *Effects of Air Pollutants on Plants*, T. A. Mansfield (Ed.). Cambridge Univ. Press, New York, pp. 61-85.

Nowak, R. (1973). *Vegetationsanalytische und experimentell-ökologische Untersuchungen über den Einfluss der Luft verunreinigung auf rinden bewohnende Flechten*. Polyfoto--Dr. Vogt KG, Stuttgart, West Germany.

Oechel, W. C. (1976). Seasonal patterns of temperature response of CO_2 flux and acclimation in Arctic mosses growing *in situ*. *Photosynthetica 10*: 447-456.

Richardson, D. H. S. (1973). Photosynthesis and carbohydrate movement. In *The Lichens*, V. Ahmadjian and M. E. Hale (Eds.). Academic Press, New York, pp. 249-288.

Richardson, D. H. S., and Young, C. M. (1977). Lichens and vertebrates. In *Lichen Ecology*, M. R. D. Seaward (Ed.). Academic Press, New York, pp. 121-144.

Ried, A. (1960). Stoffwechsel und Verbreitungsgrenzen von Flechten. II. Wasser- und Assimilationshaushalt, Entquellungs- und Submersionresistenz von Krustenflechten Genachbarter Standorte. *Flora 149*: 345-385. [Tech. transl. No. 1774, National Research Council of Canada: Metabolism and frequency distribution limits of lichens. II. Water utilization and assimilation patterns of crustaceous lichens in adjacent locations and their resistance to drought and submersion.]

Rogers, R. W. (1971). Distribution of the lichen *Chondropsis semiviridis* in relation to its heat and drought tolerance. *New Phytol. 70*: 1069-1077.

Roughgarden, J. (1972). Evolution of niche width. *Amer. Natur. 106*: 683-718.

Slatkin, M., and Lande, R. (1976). Niche width in a fluctuating environment-density independent model. *Amer. Natur. 110*: 31-55.

Smith, D. C. (1962). The biology of lichen thalli. *Biol. Rev. 37*: 537-570.

Smith, D. C., and Molesworth, S. (1973). Lichen physiology. XIII. Effects of rewetting dry lichens. *New Phytol. 72*: 525-533.

Spomer, G. G. (1973). The concepts of "interaction" and "operational environment" in environmental analyses. *Ecology 54*: 200-204.

Stålfelt, M. G. (1939). Der Gasaustauch der Flechten. *Planta 29*: 11-31.

Strain, B. R., and Billings, W. D., Eds. (1974). *Vegetation and Environment*. Junk, The Hague.

Topham, P. B. (1977). Colonization, growth, succession, and competition. In *Lichen Ecology*, M. R. D. Seaward (Ed.). Academic Press, New York, pp. 31-68.