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CRITICAL RESEARCH PROBLEMS ON THE ECOLOGY OF
LICHENS IN SUBARCTIC QUEBEC

by

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Abstract: The Schefferville region of northern Québec has a rich lichen flora which offers many opportunities to study the comparative ecology of lichens differing in morphology, physiology, and distribution. Until recently most research has been on the caribou lichen, Cladina stellaris, which is very abundant in the spruce-lichen woodlands of this subarctic region. This past research is summarized and some interesting directions for future studies are suggested. These center on the general problem of the temporal dynamics of lichen productivity which are very dependent on cycles of thallus wetting and drying.

Résumé: La région de Schefferville dans le Québec septentrional abrite une riche flore lichénique, et offre de nombreuses possibilités de comparer l'écologie d'espèces différant par leur morphologie, leur physiologie, et leur distribution. Jusqu'à récemment, la plupart des recherches effectuées ont essentiellement touché le lichen à caribou, Cladina stellaris, espèce très abondante dans la taïga de cette région subarctique. Ces études sont ici résumées et des avenues intéressantes pour d'autres recherches sont suggérées. Celles-ci sont centrées autour du problème général de la dynamique temporelle de la productivité des lichens, laquelle dépend fortement des cycles d'hydratation et de dessiccation que subissent les thalles dans leur environnement.

As in many other northern ecosystems (Ahti, 1977; Oksanen and Ahti, 1982; Thomson, 1982), lichens are a significant component of the plant communities around Schefferville in the north central portion of the Labrador-Ungava Peninsula. Lichens occur in all terrestrial habitats but are most conspicuous in the spruce-lichen woodlands and the alpine tundra. In the late-successional woodlands the groundcover of the caribou lichen Cladina stellaris alone commonly reaches 70% or more; C. mitis, C. rangiferina, and Stereocaulon paschale are also frequent but

less important components of the vegetation (Lechowicz, 1984; Rencz and Auclair, 1978). In tundra communities, lichens also often dominate the groundcover, but quantitative studies of such habitats have not been done in Nouveau-Québec. Our observations indicate that the most abundant species in local alpine environments include Alectoria ochroleuca, Cetraria cucullata, Cladonia stellaris, and C. rangiferina. On the higher and more exposed peaks Bryoria nitidula and Coelocaulon divergens are most abundant. Both this relative abundance of lichens in northern compared to more temperate ecosystems and their diverse ecological roles in northern ecosystems (Lechowicz, 1982a) make an understanding of lichen production ecology essential to our ability to effectively manage northern ecosystems.

The net annual production of lichens in this subarctic region is low even compared to the generally slow growth of lichens from more temperate regions. The mean annual height increment of individual thalli of C. stellaris in late-successional lichen woodlands near Schefferville was 2.1 mm/yr, or 22.5 mg/yr on a mass basis, based on the growth of the youngest six years of growing tissues (Lechowicz, unpublished). This is in accord with values of 5.8 mm/yr for C. stellaris growing along the eastern shore of Hudson Bay where growth was calculated over all the living tissues (Ouzilleau and Payette, 1975). In alpine sites near the altitudinal limit of C. stellaris at Schefferville, annual height increment averaged only 1.6 mm/yr, or 17.0 mg/yr on a mass basis (Lechowicz, unpublished). Growth rates reported for other northern species and regions (Andreev, 1954; Ouzilleau and Payette, 1975) confirm the generalization that the net primary productivity of lichens in northern ecosystems is very low.

Despite the considerable literature on lichen ecophysiology that has accumulated in recent years (Matthes and Feige, 1982), we have surprisingly little quantitative understanding of the dynamics of lichen production in nature. The principal factors controlling photosynthesis and respiration, the physiological underpinnings of production, are well documented; in natural environments these include irradiance, thallus temperature and thallus water content (Lechowicz, 1980). Lichens are dormant when dry, and it is only in relatively brief intervals after precipitation that conditions are favorable for lichen growth. It is the alteration of episodes of dormancy and activity under natural precipitation regimes that especially complicates the analyses of lichen productivity. Only a few published papers have attempted to study lichen production ecology from this dynamic point of view (Lange and Tenhunen, 1982; Lechowicz, 1981b).

Analysis of the climatic control of lichen productivity poses one of the more interesting challenges for further research

on lichens in the varied communities around Schefferville. In the following pages, we briefly review the published work on lichen ecology in the Schefferville region, report the results of recently completed studies, and suggest some fruitful avenues for continued research in this area.

Essentially all the published studies of lichen ecology at Schefferville focus on the abundant caribou lichen, *C. stellaris*, which was formerly called *Cladonia alpestris*. Lechowicz (1978) compared the ecophysiological characteristics of this species to its close relative, *C. evansii*, which occurs only in south temperate regions. He found that *C. stellaris* achieved maximal photosynthesis at lower irradiance and temperature than its southern relative -- attributes consistent with the cool, overcast summers in the Schefferville region (Lechowicz and Adams, 1978). Maximal photosynthesis in both species, however, was achieved at the same thallus water content. Lechowicz (1982b) showed that the photosynthetic responses of lichens to water content did not generally correspond to their geographic distributions or simple climatic parameters like annual precipitation.

These studies were done with entire living thalli of *C. stellaris*, but Carstairs and Oechel (1978), also working at Schefferville, found essentially similar responses for different layers in the lichen mat. The living portions of mature mats of *C. stellaris* in the vicinity of Schefferville are between 6 and 9 cm deep; living tissues can be up to about 20 years old with the average mat having tissues no more than 15 years old (Lechowicz, unpublished). Carstairs and Oechel (1978) reported that the uppermost, younger tissues were most active. Lechowicz (1983) confirmed this age-dependence for photosynthesis and related it to gradients in thallus color; the dark, discolored tissues older than about 15 years which are found at the base of the mat are no longer metabolically active. Kershaw and Field (1975) analyzed the microclimatic gradients within mats of *C. stellaris* and also found substantial changes in temperature, irradiance, and humidity from the top of the lichen mat down to the underlying soil surface. The upper portions of the mat tended to be better lit, warmer, and drier. These gradients have implications not only for mat metabolism, but also for the local hydrology. On a warm, dry summer day the mat surface is often dry and brittle while the older, senescent bases are quite wet. The mat thus acts as a mulch impeding evaporation from the underlying soil (Wright, 1981). The dry mats carry ground fires that are probably the single most important source of mortality for *C. stellaris* in the lichen woodlands; especially around Schefferville, fire frequencies have increased since the mining activities began and mature, undisturbed lichen woodlands have become less common.

Acid precipitation, another anthropogenic stress which is becoming important in the Schefferville region (Drake, 1980; Lewis and Hrebenyk, 1979), may also pose a long-term threat to lichen productivity. After two summers of weekly waterings with

simulated acid rain as low as pH 2.5, C. stellaris in a lichen woodland near Schefferville showed no measurable decline in growth (Lechowicz, 1984). The lichen thalli were, however, discolored by simulated rains below pH 3.5. When the treatments were continued a third summer, growth was significantly depressed by rains below pH 4.5 which were acidified by solutions richer in sulfuric than nitric acid (Lechowicz, unpublished). It appears that the effects of chronic acidification on the growth of C. stellaris are only gradually expressed and may lead to declines in productivity rather than immediate mortality.

We have recently investigated some of the more subtle aspects of lichen production ecology in an attempt to better assess the potential impact of environmental stresses on lichen growth. Our efforts have focussed on factors affecting metabolic activity after wetting, especially the possible role of sugar alcohols (polyols) as "physiological buffers" against stress. Michel Groulx has made a detailed comparison of the production ecology of Cladonia stellaris and Alectoria ochroleuca, the two most abundant lichens near Schefferville. Susan Dudley made a comparison of polyol levels in 23 lichen species from different microclimatic regimes.

The A. ochroleuca population studied by Michel Groulx grew in the alpine tundra atop a ridge and the C. stellaris population in a lichen woodland in the adjacent valley. Mean temperature and total rainfall were lower on the ridge than in the valley, but irradiance and windspeed were higher. Under identical conditions in the laboratory, A. ochroleuca dried twice as fast as C. stellaris. These differences in microclimate and intrinsic drying dynamics both contribute to marked differences in the wetting and drying cycles of the two contrasting species. During July through September, 1982, A. ochroleuca had 46 periods of metabolic activity with an average duration of 129 hours compared to only 28 activity periods in C. stellaris with an average duration of 41 hours. Overall, C. stellaris was active 41% more hours than A. ochroleuca.

Given these contrasting cycles of wetting and drying, we initially hypothesized that A. ochroleuca would have a "fast recovery" capacity characterized by both a more rapid photosynthetic recovery and a lower intensity and duration of the resaturation respiration associated with the period after wetting of the dry, dormant thallus. This would minimize carbon losses at the beginning of activity periods and maximize net carbon gains during short periods of activity. Photosynthetic recovery was complete in A. ochroleuca 90 min after wetting, while recovery in C. stellaris proceeded gradually over 24 hr. There were, however, no differences in the resaturation respiration of the two species.

We had also hypothesized that A. ochroleuca, which is typically exposed to short cycles of activity interrupted by longer periods of dormancy than C. stellaris, would be more resistant to unusual stress events. In C. stellaris respiration

is indeed severely impaired after eight weeks of continuous desiccation and photosynthesis, altered after five weeks and actually ceases after eight weeks' desiccation. In contrast, respiration in A. ochroleuca continues at high rates after eight weeks' desiccation and photosynthesis is only impaired after 12 weeks. Similarly, experimental reduction of polyol levels through dark starvation has no effect on the CO₂ exchange of A. ochroleuca, but reduces both respiration and photosynthesis of C. stellaris. Conversely, increasing thallus polyol concentrations by immersion in polyol solutions, increases both respiration and photosynthesis in C. stellaris but has no effect on A. ochroleuca. These data confirm our hypothesis that A. ochroleuca would be better buffered against unusual cycles of wetting and drying than C. stellaris.

Susan Dudley had initially hypothesized more generally that high polyol contents in lichens - 1 to 10% percent dry weight - acted as a physiological buffer against the effects of stress. We expected that lichens from habitats where cycles of wetting and drying made conditions less favorable for achieving net gains of carbon during episodes of activity would maintain high polyol reserves. She showed, however, that lower, not higher, polyol contents were found in lichens from more stressful environments. Moreover, polyol content was also correlated with the water holding capacity of the lichen. Species that held more water per unit dry weight had significantly higher polyol concentrations. Polyols are also lost upon rewetting: about 10% of the polyols present are leached in each rewetting event.

All these results taken together call into question the postulated role of polyols as reserve compounds that contribute directly to the rates of metabolic recovery after a dormant lichen is wetted by precipitation. In C. stellaris and A. ochroleuca there is no general relationship between tissue polyol concentrations and rates of recovery. Similarly, diverse species from strongly contrasting microenvironmental regimes show no association of polyol levels with differences in their cycles of wetting and drying. High rates of respiration that are observed in lichens shortly after wetting (Groulx, unpublished; Lechowicz, 1978), probably arise from leakage through poorly reconstituted membranes rather than from any direct involvement of polyol oxidation in metabolic recovery. The implications of such leakage for thallus carbon balance may prove to be the critical control on lichen distribution and abundance, especially considering the high loss of polyols by leaching during wetting (Dudley, unpublished).

The best way to test this supposition would be to model the net carbon balances of many different lichen species that differ in their cycles of wetting and drying. These labor-intensive comparisons could be better planned if we had a firm quantitative understanding of lichen community ecology in the Schefferville region. Studies like that of Clayden and Bouchard (1983) that use modern ordination techniques to investigate species interrelationships across environmental gradients would allow a

more judicious choice of species for detailed physiological investigation. Finally, it would also be of interest to collaborate with others in an investigation of mean annual growth rates of Cladina species throughout the Labrador-Ungava Peninsula; these data would provide a geographically comprehensive baseline against which any future effects due to acid deposition can be compared.

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