Carbon Dioxide Exchange in Cladina Lichens from Subarctic and Temperate Habitats

Martin J. Lechowicz *
Department of Botany, The University of Wisconsin, Madison, WI 53706, USA

Summary. The survival potential of lichens in a given habitat is determined by the response of CO₂ exchange to photosynthetically active radiation (PhAR), thallus temperature, and thallus relative water content (RWC). Therefore morphologically similar lichens from contrasting climatic environments 1) should differ in their CO₂ exchange responses, and 2) these differences should reflect adaptations to their climatic regimes. The CO₂ exchange responses of a subarctic (55°N, 67°W) Cladina stellaris (Opiz) Brodo population and a temperate (29°N, 82°W) Cladina evansii (Abb.) Hale and W. Culb, population were used to test these two related hypotheses.

Infrared gas analysis with lichens collected in September-October 1975 established that the two populations differed in their responses to incident PhAR, thallus temperature, and thallus RWC. Net photosynthesis in C. stellaris had an optimum at a lower temperature and a greater relative photosynthetic capacity at low temperatures than did C. evansii. Cladina evansii maintained net photosynthesis above 35°C thallus temperature; C. stellaris did not. In both species the optimum temperature for net photosynthesis increased with increasing irradiance. The C. stellaris light saturation point was consistently lower than that of C. evansii. Both species had maximal rates of net photosynthesis at 70–80% relative water content. In C. evansii the CO₂ exchange rates, expressed as percentages of the maximum rate, declined more rapidly under suboptimal conditions. The absolute CO₂ exchange rates of C. evansii were greater than those of C. stellaris. At 20°C and 90–95% RWC, resaturation respiration occurred in both species and continued until 6–7 h after wetting.

Contrasts in the temporal patterns of thallus condition at each collection site suggest that not all differences in the two response surfaces reflect climatic adaptation. The two populations appear well adapted to incident PhAR and thallus temperature regimes but the 70–80% RWC optimum for net

* Present address: Biology Department, McGill University, 1205 McGregor Street, Montreal, Quebec H3A 1B1, Canada

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photosynthesis common to both species is puzzling since their water regimes differ markedly. The overall adaptedness of the CO₂ exchange responses in the two species cannot be judged without a comprehensive quantitative analysis of carbon balance under differing climatic regimes.

Introduction

Carbon balance provides a good indication of material and energy availability for plant survival and reproduction (Mooney, 1972a, b). The responses of CO₂ exchange to environmental conditions over a plant's lifetime determine its carbon balance. If a more positive carbon balance indicates a greater Darwinian fitness, selection should lead to plant responses that maximize carbon gains in a given environmental regime. There should be an adaptive correspondence between a plant's CO₂ exchange responses to environmental variables and the temporal pattern of environment in the plant's habitat.

Physiological plant ecologists have accumulated evidence of this adaptive correspondence in an extensive series of comparative studies (Strain and Billings, 1974; Cooper, 1975; Larcher, 1975). Since the difficulties of determining a complete response surface for all environmental variables affecting CO₂ exchange are substantial, comparisons of responses to single environmental variables predominate. Observations of more completely defined response surfaces provide refined tests for the adaptive coupling between response and environmental pattern.

Lichens are advantageous experimental organisms for these more complete comparative studies of adaptation in CO₂ exchange response (Lechowicz et al., 1974; Larson and Kershaw, 1975a). In a series of papers Larson and Kershaw show adaptive differentiation in the response surfaces of subarctic lichen populations (Larson and Kershaw, 1975a, b, c; Kershaw, 1975). They document seasonal acclimation in CO₂ exchange responses and demonstrate some correspondence between responses and habitat microclimate. Lechowicz and Adams (1974) show comparable patterns of acclimation and microdistributional variation in response surfaces for temperate lichen species. Geographical contrasts in response surfaces have also been documented (Lechowicz et al., 1974; Larson and Kershaw, 1975a) but only over a limited latitudinal range.

To further test the correspondence between CO₂ exchange responses and climatic environment, this paper compares a subarctic Cladina stellaris (Opiz) Brodo population with a temperate Cladina evansii (Abb.) Hale and W. Culb population from Florida. These two lichens are closely related, allopatric (Fig. 1), and similar in growth form and thallus structure (Ahti, 1961). Physiological adaptations to their strongly contrasting climatic environments should be relatively unconfounded by possible interactions between morphological and physiological adaptations (Mooney, 1974). Therefore the CO₂ exchange responses of C. stellaris and C. evansii should differ considerably and these differences should reflect physiological adaptation to their contrasting climatic environments.
Fig. 1. North American ranges of *C. stellaris* and *C. evansi* showing collection sites and climatic data sites. *Cladina stellaris* collections used in all gas analysis experiments came from Schefferville, Quebec (1) as did the climatic data applicable to *C. stellaris*. *Cladina evansi* collections came from the Ocala National Forest, Florida (2) but climatic data applicable to *C. evansi* came from nearby Orlando, Florida (3). The ranges are adapted from Ahti (1961) and from an unpublished *C. stellaris* range map supplied by Professor John W. Thomson.
Materials and Methods

Collection Sites and Storage Procedures. Figure 1 locates the collection sites within the North American ranges of the two species. Personnel at the McGill Sub-Arctic Research Laboratory in Schefferville, Quebec (55°N, 67°W) collected a nearby C. stellaris population in October, 1975. A C. evansi population from the Ocala National Forest, Florida (29°N, 82°W), was collected in September, 1975. All lichen samples were airmailed in dormant condition to Madison, Wisconsin and stored at 0° C until used in the experiments.

Vowinckel et al. (1975) describe the vegetation around Schefferville, and Kershaw (1977) presents a broader view of lichen woodland vegetation. At Schefferville, treeless ridges are covered by lichen and moss mats interspersed with Betula nana shrubs. In the valleys continuous mats of C. stellaris occur in an open parkland of Picea and Larix trees as photographed in Vowinckel et al. (1975). Vegetation at the Florida collection site is a sand-pine scrub community (Laessle, 1942, 1958, 1967) with an almost continuous lichen groundlayer dominated by C. evansi. The open Pinus clausa canopy with Serenoa repens and Lyonia ferruginea dominant in the shrub layer shades the lichen groundlayer more than the sparser tree and shrub layers at the Quebec site.

Infrared Gas Analysis Procedures. The CO₂ exchange responses of C. stellaris and C. evansi were monitored with an open system of infrared gas analysis similar to that used in earlier work on fruticose lichens (Lechowicz et al., 1974). Larson and Kershaw (1975a) argue for an alternate gas analysis system for lichens. However, their proposed system, which can only be used at low PhAR levels, presents difficulties in monitoring tissue temperature, and may lead to CO₂-limited rates under many conditions. For these reasons and because interest centers here on the ecological response of the intact mat, a traditional IRGA system, described in detail by Lechowicz (1976), was used in these experiments.

Pretreatment and Experimental Procedures. To study resaturation respiration (Farrar, 1973, 1976; Smith and Molesworth, 1973) in C. stellaris and C. evansi, I determined the time course of CO₂ exchange rate in the dark at 20° C and 91–95% RWC. A steady RWC was maintained by removing the lichen sample from the gas analysis chamber and rewetting it. All lichen samples were cleaned of debris and dead, discolored podetial tissue to avoid spurious respiratory exchange. The results from five replicates of this experiment (Fig. 2) indicate that elevated respiration rates prevail until 6–7 h after wetting in both species.

To avoid the confusing effects of resaturation respiration in determining CO₂ exchange responses, I presoaked each cleaned lichen sample 1–2 h in distilled water, stored the wetted lichen 12–16 h in a dark incubator at 20–25°C, resoaked the sample 0.5–1 h, vigorously shook water from the sample, and then introduced it into the gas analysis system. A new lichen sample was used in each experiment. Randomizing the order in which experiments were run minimized potential storage-related effects on the subsequent regression analysis.

Experimental Design. A factorial design using incident PhAR, thallus temperature, and thallus RWC provided data on the C. stellaris and C. evansi CO₂ exchange responses to the three factors. Five levels of incident PhAR (0, 100, 300, 600, and 1000 μEinsteins·m⁻²·s⁻¹) and eight levels of thallus temperature (0, 5, 10, 15, 20, 25, 30, and 35°C) were selected. I weighed the lichen in the chamber as it dried to monitor thallus RWC which could not be effectively held at fixed levels; data from 2–100% RWC for C. stellaris and 9–98% for C. evansi were obtained. Because of an unexpected shortage of C. stellaris samples, only the following PhAR/temperature combinations were run for both species: 0/5, 0/15, 0/25, 0/35, 100/10, 100/20, 100/30, 300/5, 300/10, 300/15, 300/20, 300/30, 300/35, 600/0, 600/10, 600/15, 600/20, 600/25, 600/30, 1000/5, 1000/10, 1000/15, 1000/20, 1000/25, 1000/30 and 1000/35. These factor levels were chosen to provide good definition of response surfaces expected from preliminary experiments on C. stellaris and C. evansi and from previous work with related species (Lechowicz and Adams, 1974; Lechowicz et al., 1974; Lechowicz, unpublished data). I did not replicate any factor combinations, but 867 C. stellaris and 872 C. evansii data points were recorded. These data may be found in Lechowicz (1976).

Analysis of Response Data. To effectively present the multi-dimensional response surfaces, the C. stellaris and C. evansi data were fitted by least square, multiple linear regression (Draper and Smith, 1966). This analytic strategy summarized the large data set for easier graphical compari-
Fig. 2. Time course of dark respiration in *C. stellaris* and *C. evansii* at 20°C thallus temperature and 91–95% thallus RWC. Bars indicate one standard deviation about the mean.

Fig. 3A–D. Plots of residuals, $R$, against the CO$_2$ exchange rates predicted by the polynomial functions, $\tilde{Y}$, fitted to the data for *C. stellaris* in the light (A) and dark (B) and for *C. evansii* in the light (C) and dark (D). In the light $\tilde{Y} = \ln(P_N + 1.0)$ where $P_N$ is the estimated net photosynthetic rate in mg CO$_2$·g$^{-1}$·h$^{-1}$. In the dark $\tilde{Y} = \ln(R_0 + 2.0)$ where $R_0$ is the estimated rate of dark respiration in mg CO$_2$·g$^{-1}$·h$^{-1}$. The residual, $R$, is the difference between the transformed measured and estimated CO$_2$ exchange rates. A few outlying points are omitted from the graphs; many symbols near the $R=0$ axes represent multiple rather than single data points.
sons and has been satisfactorily used in other recent analyses of lichen CO₂ exchange (Kallio and Kärenlampi, 1975; Lange et al., 1977).

High order polynomials including interaction terms provided functional models of response. Mead and Pike (1975) noted the impossibility of extrapolation beyond the available data range associated with polynomial models. Subsequent graphical analyses stayed within the data range except for temperature responses between 35–40°C where extrapolation appeared biologically consistent. Separate regressions for CO₂ exchange responses in the light and dark gave the most reasonable biological results.

Scatter plots of the residuals in early analyses with the dependent variable, CO₂ exchange rate, untransformed showed consistent increases in residuals with increases in the dependent variable. The dependent variable was subsequently taken as the natural logarithm of CO₂ exchange rate. Scatter plots of residuals versus the estimated CO₂ exchange rate (Fig. 3) and against the three original independent variables showed that the function fits the data well. I did not correct for bias in retransforming regression predictions to CO₂ exchange rates (Beauchamp and Olson, 1973).

The final regression model in the light predicted the natural logarithm of CO₂ exchange rate using a 3rd order polynomial including interaction terms and based on the original three independent factors: incident PhAR, thallus temperature, and thallus RWC. The function accounted for 77% of the variance in the C. stellaris data and 92% in C. evansii. In the dark a comparable 3rd order polynomial based on thallus temperature and thallus RWC accounted for 92% of the variance in the C. stellaris data and 91% in C. evansii. The full regression equations appear in Lechowicz (1976).

Results

For both C. stellaris and C. evansii, CO₂ exchange response to PhAR and temperature varied primarily in absolute magnitude as RWC changed. Figure 4 illustrates the response pattern using RWC at 60%. The qualitative features shown here were maintained at higher and lower RWC values (Lechowicz, 1976); the net photosynthesis rates of C. evansii remained substantially higher than those of C. stellaris.

Three qualitative features of these responses are important in considering the adaptation of the two species to their climatic regimes. First, net photosynthetic rates in both species declined rapidly above optimal temperatures. Even at a high incident PhAR, C. stellaris did not maintain positive net exchange above 35°C, while C. evansii showed reduced but positive CO₂ exchange at least up to 40°C. Second, in both species, as incident PhAR increased, the temperature optimum of net photosynthesis also increased. Third, at optimal temperature C. stellaris became light saturated at about 600 µEinsteins m⁻² s⁻¹; C. evansii did not show light saturation at optimal temperature even at 1000 µEinsteins m⁻² s⁻¹.

Four features of the CO₂ exchange response to thallus RWC and thallus temperature (Fig. 5) should be emphasized. The overall net photosynthetic rates of C. evansii exceeded those of C. stellaris. At 1000 µEinsteins m⁻² s⁻¹ the optimal relative water contents of both species were between 70 and 80%, but the temperature optimum of C. evansii at 28°C was much higher than the 20°C optimum of C. stellaris. In C. stellaris the temperature optimum for net photosynthesis increases as relative water content decreases but C. evansii has a steady temperature optimum at all relative water contents. In contrast to C. evansii, C. stellaris does not maintain positive net photosynthesis above 35°C. These features are maintained at lower levels of incident PhAR (Lechowicz, 1976).
Fig. 4A and B. The CO₂ exchange response to incident PhAR and thallus temperature for *C. stellaris* (A) and *C. evansi* (B) at RWC = 60%. Incident PhAR is in μEinsts·m⁻²·s⁻¹ and thallus temperature is in degrees Celsius. Response isopleths are at 0.1 mg CO₂·g (dry weight)⁻¹·h⁻¹ intervals. The wetted lichens were preincubated at 20 to 25°C in the dark for at least 12 h to avoid the confounding effects of resaturation respiration.

Fig. 5A and B. The CO₂ exchange response to thallus RWC and thallus temperature for *C. stellaris* (A) and *C. evansi* (B) at 1000 μEinsts·m⁻²·s⁻¹. Relative water content is in percent and thallus temperature in degrees Celsius. Response isopleths are at 0.1 mg CO₂·g (dry weight)⁻¹·h⁻¹ intervals. The wetted lichens were preincubated at 20 to 25°C in the dark for at least 12 h to avoid the confounding effects of resaturation respiration.
In the dark *C. evansii* had more negative CO₂ exchange rates than *C. stellaris* in response to thallus RWC and thallus temperature (Fig. 6). Relative water content little affected *C. stellaris* dark exchange rates until below 60% RWC. The positive rates were a striking feature of CO₂ exchange response in the dark. *Cladina evansii* showed substantial positive exchange that increased steadily with decreasing RWC below about 20% RWC. *Cladina stellaris* showed lower positive dark exchange rates but included CO₂ uptake at high RWC when thallus temperatures were low. Examination of the raw data showed that this anomalous non-photosynthetic fixation was not an artifact of the regression analysis.

**Discussion**

Bryson and Hare (1974) document the contrast in the climatic environments of these subarctic *C. stellaris* and temperate *C. evansii* populations. The diurnal and seasonal patterns of incident PhAR, thallus temperature, and thallus RWC that control lichen CO₂ exchange rates are set largely by these climatic environments. Biophysical models explicitly coupling thallus condition to climatic vari-
ables have been presented (Hoffman and Gates, 1970; Kershaw and Harris, 1971; Harris, 1972; Lechowicz, 1976). To better compare the temporal patterns of *C. stellaris* and *C. evansii* thallus condition, Lechowicz (1976) analyzed hourly climatic records for 1953–1970 from Schefferville, Quebec and Orlando, Florida. These data, considered with a biophysical model coupling thallus condition to climatic variables, lead to the following generalizations. In the period June 25 through November 1, the natural summer and fall of Bryson and Lahey (1958), *C. evansii* was dry and dormant more often than *C. stellaris*. Rains in Florida were less frequent although more often intense; post-rain periods of lichen activity were shorter for *C. evansii*. During active periods *C. stellaris* generally had higher thallus RWC, lower thallus temperatures, and lower incident PhAR than *C. evansii*. Some adaptations in CO₂ exchange responses that lead to increased carbon gains can be predicted for *C. stellaris* and *C. evansii* by considering their contrasting environmental regimes.

*Cladina evansii* should be relatively better adapted to high thallus temperatures and high incident PhAR than *C. stellaris*. *Cladina evansii* did effectively utilize higher PhAR levels than *C. stellaris* and also maintained net photosynthesis at temperatures above 30° C (Fig. 4). *Cladina stellaris* not only saturated at about 600 μEinsteins·m⁻²·s⁻¹ but was also unable to maintain positive CO₂ exchange above 33–35°C. Field studies near Schefferville show that on a hot clear summer day, wetted *C. stellaris* mats reached maximal thallus temperatures of only 31°C (Kershaw and Field, 1975). At lower temperatures, however, *C. stellaris* had greater CO₂ exchange rates than *C. evansii* relative to their respective optimal rates. Similar correspondences in qualitative features of *Cladonia* and *Cladina* CO₂ exchange responses in contrasting PhAR and temperature regimes have been frequently reported (Adams, 1971; Peet and Adams, 1972; Eickmeier and Adams, 1973; Kershaw and Larson, 1974; Lechowicz and Adams, 1974; Lechowicz et al., 1974; Kershaw, 1975; Carstairs and Oechel, 1978). Two studies (Rundel, 1972; Lechowicz and Adams, 1973) have demonstrated that within single *Cladina* species distinct sun and shade populations did not show significant adaptive differentiation in CO₂ exchange response. With this possible exception, these data suggest that CO₂ exchange in *Cladonia* and *Cladina* lichens is well-adapted to incident PhAR and thallus temperature regimes in diverse habitats.

Considering biophysical arguments (Monteith, 1973), another adaptation of CO₂ exchange response to incident PhAR and thallus temperature can be predicted. Incident PhAR is directly proportional to global solar radiation which in turn often dominates the lichen energy balance during daylight. Higher thallus temperatures will almost always occur at higher irradiance. With convective and latent heat fluxes holding roughly constant, an increased short-wave radiation flux will not only increase incident PhAR but also increase thallus temperature. Because of these correlations, a lichen will be more frequently exposed to certain combinations of incident PhAR and thallus temperature. Particularly at greater incident PhAR a relatively greater frequency of higher thallus temperatures will occur.

Adaptation to this environmental pattern should be reflected in the CO₂ exchange responses of the lichens by an increasing temperature optimum at increasing irradiance. Both *C. stellaris* and *C. evansii* showed this adaptive
response (Fig. 4). Comprehensive studies of lichens from desert, antarctic, and subarctic habitats (Lange, 1969; Lange and Kappen, 1972; Kallio and Kärenlampi, 1975) indicated this adaptive response occurs commonly in lichens. Comparable arguments can explain the increase in the *C. stellaris* temperature optimum with decreasing thallus relative water content (Fig. 5); at lower relative water contents the high resistance of the lichen mat to vapor loss will decrease latent cooling and raise thallus temperature. The asymmetrical shapes of many lichen response surfaces may simply reflect adaptation to patterns of correlation among the variables controlling CO₂ exchange.

During summer-autumn *C. evansii* was more often incompletely wetted by rains and dried more quickly than *C. stellaris*. Considering differing probabilities of high and low RWC in the two species one might predict that *C. evansii* would have high CO₂ exchange rates at lower RWC than *C. stellaris*. Kershaw (1971) presented data for a range of lichen species showing this response. Instead both *C. stellaris* and *C. evansii* had optimal relative water contents around 70–80% at favorable thallus temperatures; at suboptimal RWC *C. stellaris* actually maintained greater CO₂ exchange rates than *C. evansii* relative to their respective optimal exchange rates (Fig. 5). Kershaw (Kershaw, 1975; Larson and Kershaw, 1975a) has questioned his earlier data and recent data from his laboratory (Kershaw, 1975; Larson and Kershaw, 1975b, c) and others (Lange, 1969; Lange et al., 1970; Lechowicz and Adams, 1974; Lechowicz et al., 1974; Carstairs and Oechel, 1978) demonstrate no simple, general relationship between RWC response and water regime.

The consistently greater net photosynthetic response of *C. evansii* (Figs. 4 and 5) may be advantageous in its water regime. The activity periods of *C. evansii* in summer-autumn were shorter than those of *C. stellaris*. The Florida rainfall and evaporative regimes cause *C. evansii* to go in and out of dormancy more frequently than *C. stellaris*. Assuming both that net carbon uptake should be maximized and that carbon losses from resaturation respiration represent a fixed activation cost leads to the hypothesis that net photosynthetic rates should increase with decreasing length of the mean activity period. A thorough quantitative analysis of all aspects of the lichen carbon flux including resaturation respiration will be necessary to test this hypothesis.

The differences in overall shape of the two species' response surfaces in the light may reflect adaptation to the predictability of the Florida and Quebec summer climates. The summer climatic regime in Florida has a very stable diurnal pattern (Byers and Rodebush, 1948; Lechowicz, 1976) but at Schefreville summer days vary irregularly from cool and overcast to clear and warm as different air masses affect the Ungava peninsula (Lechowicz and Adams, 1978). Evolutionary theory (Levins, 1968) suggests that specialists will occur in predictable environments, generalists in less predictable environments. *Cladina evansii* may be considered a specialist, adapted for high net photosynthesis over only a narrow environmental range with rapidly declining rates away from the optimal conditions. *Cladina evansii* CO₂ exchange rates in the light decline more rapidly away from the optimal conditions than do those of *C. stellaris* (Figs. 4 and 5). The differences in the predictability of the summer climatic regimes may explain these contrasting generalist and specialist responses
in *C. stellaris* and *C. evansii*. This explanation could be better tested by a quantitative comparison of the photosynthetic gains and associated respiratory losses for the generalist and specialist responses in each environmental regime.

The unusual uptake of CO$_2$ in the dark by *C. evansii*, and to a lesser degree by *C. stellaris* (Figs. 4 and 6), may be of adaptive advantage. Farrar (1973) makes brief reference to similar non-photosynthetic CO$_2$ uptake at rates 5–10% of light fixation rates. Barashkova (1971) reported the phenomenon in *C. stellaris* and *C. rangiferina* and suggested it might be related to the abundance of acids in lichen thalli. Experiments are planned to test the hypothesis that lichen acids take up CO$_2$ by a physical process during dormancy, release the stored CO$_2$ upon wetting, and thereby increase productivity by enriching ambient CO$_2$ levels in the early hours of each activity period.

Earlier reports (Scholander et al., 1952; Scholander and Kanwisher, 1959) indicated no clear latitudinal trends in lichen respiration. *Cladina evansii* CO$_2$ exchange rates in the dark exceed those of *C. stellaris* and are more dependent on thallus RWC (Fig. 6). Judging the possible adaptedness of these CO$_2$ exchange responses in the dark requires an analysis of the overall carbon balance including resaturation respiration.

In conclusion, the CO$_2$ exchange responses to incident PhAR, thallus temperature, and thallus RWC differ in a subarctic *C. stellaris* population and a temperate *C. evansii* population. Some aspects of the multidimensional response surfaces, such as net photosynthetic temperature optima and light saturation levels, reflect apparent adaptations to the contrasting subarctic and temperate climatic regimes. The adaptedness of the net photosynthetic responses to RWC and of the CO$_2$ exchange responses in the dark are, however, more difficult to assess. Given a particular annual pattern for lichen thallus condition, the optimal shape of the lichen CO$_2$ exchange response surface cannot presently be quantitatively described. Past work in comparative physiological ecology allows only limited predictions of a qualitative nature. An optimization analysis (Rosen, 1967) of annual net carbon balance may lead to better predictions for the shape of CO$_2$ exchange response surfaces in diverse climatic environments.

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