Ecology of Cladonia lichens. II. Comparative physiological ecology of C. mitis, C. rangiferina, and C. uncialis¹

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The net CO₂ exchange responses of Cladonia mitis, C. rangiferina, and C. uncialis from the Wisconsin Pine Barrens to irradiance, thallus temperature, and thallus relative water content were statistically compared for fall, spring, and summer. The absolute net photosynthetic rate of C. rangiferina exceeded that of C. uncialis under essentially all conditions and in all seasons; C. mitis's absolute net photosynthesis fluctuated with the seasons between these two contrasting species. Cladonia mitis showed significant intraspecific seasonal variation in net photosynthetic responses to temperature and irradiance. Cladonia rangiferina showed significant seasonal variation in dark respiratory response to temperature. Cladonia uncialis showed no significant intraspecific seasonal variation in net CO₂ exchange responses. Significant interspecific differences in net CO₂ exchange responses centered on the net photosynthetic responses to thallus temperature and relative water content.

Despite its low net photosynthetic rates, C. uncialis is the most prevalent lichen in the Wisconsin Pine Barren ground-layer community. We attribute this not to broad physiological tolerance, but to its significantly slower drying rate. Lichens photosynthesize only when wetted. Cladonia uncialis photosynthesizes at generally lower rates than C. mitis or C. rangiferina, but it photosynthesizes longer under comparable environmental drying regimes. This and other aspects of the physiological ecology of the three species are discussed in relation to microdistribution and microhabitats within the Wisconsin Pine Barrens.


L'échange net de CO₂ a été déterminé chez Cladonia mitis, C. rangiferina et C. uncialis provenant des "Pine Barrens" du Wisconsin, en réponse aux variations de l'irradiance, de la température du thalle et de la teneur relative en eau du thalle; ces données ont été comparées statistiquement pour l'automne, le printemps et l'été. Le taux photosynthétique net absolument de C. rangiferina était plus élevé que celui de C. uncialis dans toutes les conditions et à toutes les saisons; chez C. mitis, ce taux fluctuait selon les saisons entre celui des deux autres espèces. Cladonia mitis a présenté une variation saisonnière significative dans sa réponse photosynthétique nette à la température et à l'irradiance. Cladonia rangiferina a présenté une variation saisonnière significative, selon la température, dans sa respiration à l'obscurité. Cladonia uncialis n'a présenté aucune variation saisonnière significative dans ses échanges nets de CO₂. Les différences interspécifiques significatives dans les échanges nets de CO₂ ont été retrouvées au niveau des réponses à la température du thalle et à la teneur relative en eau du thalle.

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Introduction

Previous multivariate analyses of cryptogamic ground-layer communities in Ontario and Wisconsin (Lechowicz and Adams 1974) have indicated some interesting ecological relations between the frequently sympatric lichens Cladonia mitis, C. rangiferina, and C. uncialis. In a species ordination based on data from stands across northern Ontario, the three species appeared tightly grouped, indicating their essentially similar responses to macroenvironmental and succes-

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be principally for the photosynthetic system which produces the greatest yield of carbon over time, under the stresses imposed by the habitat." Ahmadijan (1967) and Hale (1967) recognized thallus water content, incident radiation, and thallus temperature as key factors determining lichen net CO₂ exchange; Smith (1962) reviewed these and other aspects of the organismal biology of lichens. We report here primarily the seasonal CO₂ exchange response patterns of C. mitis, C. rangiferina, and C. uncialis to these three factors and consider the adaptive coupling of species physiology and microhabitat environment.

Methods

Collections

Lichen material in this study was collected from three sites, each about 2 ha in size and all near Mauston, Juneau County, Wisconsin, U.S.A. One site already described (Lechowicz and Adams 1974) closely resembles the second, only 0.2 km distant; the remaining site occupies an abandoned field now dominated by a Pinus banksiana stand about 25 years old. The geology, climate, vegetation, and floristic affinities of the Wisconsin Pine Barrens in which all three collection sites occur have been described (Curtis 1959).

Collections made on October 2, 1971; April 13, 1972; and July 26, 1972, from the same lichen mats in each season are subsequently referred to as fall, spring, and summer, respectively. Care was taken to distribute the sampled lichen mats over the full range of species' habitats and collection sites. Collections, taken with a sampler giving a 20-cm-diameter plug from the lichen mat, were placed in labeled kraft-paper bags, returned to Madison, Wisconsin, air-dried for a day, and stored at 0° to 3° until used within, at most, 6 weeks. Thomson's (1967) key with microchemical tests was used in identification, and voucher specimens were placed in the Lichen Herbarium, University of Wisconsin, Madison.

Gas Analyses

The open system of infrared gas analysis used to assess net CO₂ exchange responses to thallus water content, light, and temperature has been described (Eickmeier and Adams 1973; Lechowicz and Adams 1973). Light response of net photosynthesis was determined following the methods of Lechowicz and Adams (1973) with the additional measurement of photosynthetically active radiation (400-700 nm) using a photon sensor (Lambda Instruments, Inc.). Temperature responses of net photosynthesis and dark respiration were measured at discrete intervals allowing a stable rate to be achieved at each temperature. Thallus dehydraion was partially checked by hydrating the inflowing chamber air; each experiment ran about 2 to 3 h, including the time for stabilization of the initial dark respiratory rate, and thallus dehydration was not excessive. Thallus temperature was considered to be the average of values from two microthermocouples inserted in the thallus and a foil shielded macrotomocouple in the mat center. Thallus moisture responses of net photosynthesis and dark respiration were followed as by Eickmeier and Adams (1973). Thallus moisture, expressed as relative water content or RWC (Barrs 1968), was monitored at 15-min intervals; chamber air temperature was held at 25° ± 1° and inflowing air was at 6% relative humidity (RH). Light levels in the determination of both temperature and thallus moisture responses of net photosynthesis were 3.9 ± 0.2 x 10⁻⁴ ergs·cm⁻²·s⁻¹ or 1135 ± 52 µeinstein·m⁻²·s⁻¹. This represents about 55% of the active photosynthetic radiation of full sunlight. In all experiments, chamber air speed was 2.6 km·h⁻¹ as measured by a Hastings-Raydist (Hampton, Va.) RM-1 Air Meter.

For each season, collections were randomly assigned to experimental runs to provide a sound statistical basis for response comparisons. With few exceptions three replicates were available for each statistical population. We routinely calibrate new standard CO₂ tanks against the previous standard thus assuring comparable absolute CO₂ exchange rates in all our studies. Net CO₂ exchange rates are expressed as milligrams CO₂ per gram (ovendry weight) per hour. Ovendry weights were in the range 3 to 9 g.

Average Annual Production

As an integrated measure of the adaptive coupling of physiological response and habitat microenvironment of species, average annual height and weight increments over the past 4 years were determined. Kärenlampi's (1971) provided a recent summary of the length growth and weight distribution method that we used, which is based on the annual podetial branching pattern of the reindeer lichens. Measurements were made on a stratified random sampling of the lichen material used in the summer 1972 physiological response studies. Average annual height and weight increments were treated as variates in statistical comparison of species average annual production. Kärenlampi's (1970) discussion of thallus age, weight, diameter, and height relationships in C. alpestris suggests that this simple assessment of average annual production is adequate here.

Field Studies

Frequent visits to the three collection sites were undertaken from fall 1971 to fall 1972. Measurements comparing microenvironmental regimes at the various sampling sites were recorded. Light regimes were compared using up to 5 Belfort Pyrheliographs. Also, on August 2, 1972, comparison of incident radiation on 133 quadrats used in a previous study (Lechowicz and Adams 1974) was undertaken with a chemical light meter (Marquis and Yelenosky 1962); this day was characterized by scattered clouds and 1.35 x 10⁶ ergs·cm⁻²·total diurnal radiation measured in the open with a Belfort Pyrheliograph. Moisture regimes were traced by previously described methods (Lechowicz and Adams 1973) with five replicates. Air, soil, and lichen-mat temperatures were measured with a thermistor Telethermometer (Yellow Springs Instruments, Inc.). Limited on-site rainfall and relative humidity records were also kept. The National Weather Service at Mauston, 3 km from the collection sites, provides a good general climatic record (Fig. 1).
Specific results of microenvironmental comparisons are not tabulated in this report; these measurements and commonly accepted micrometric principles have led to the microhabitat comparisons discussed subsequently.

**Statistical Analysis**

With the single exception of dark respiratory response to thallus RWC, all net CO₂ exchange responses were compared for significant intraspecific and interspecific differences by multivariate analysis of variance using program GMANOV, written by Robert R. Kowal. Values of net photosynthesis at 11 light intensities provided variables for tests of the light responses. Dark respiration rates at nine temperatures were treated as variates in the tests of respiratory temperature response. Data on net photosynthesis response to temperature and thallus RWC were condensed by parabolic regression of net photosynthetic rates on temperature and RWC respectively; the three coefficients of the parabolic equation were then treated as variates in the multivariate analyses of variance. With only minor exceptions the correlation coefficient of the regressions was good ($r > 0.90$).

Because of our methods of measuring RWC and unsatisfactory results in fitting all respiratory RWC response curves with available regression routines, statistical tests of respiratory RWC response were not undertaken. Discussion of our results here is conservative and emphasizes apparent qualitative and marked quantitative differences.

Drying rates and average annual production data were also tested by multivariate analysis of variance. The slope and y intercept of linear regressions of thallus RWC on elapsed time taken from the net photosynthetic and dark respiratory drying response experiments were treated as variates ($r > 0.95$) in the tests of drying rates. Other tests mentioned were by analysis of variance.

**Results**

(1) Net CO₂ Exchange Responses

**Overall Comparison**

Figures 2 and 3 display the overall patterns of seasonal intraspecific and interspecific variation. The seasonal variability of *C. mitis* net photosynthetic responses and of *C. rangiferina* respiratory responses contrast the seasonal stability of *C. uncialis*. The interspecific differences over the year show a continuing physiological differentiation between *C. rangiferina* and *C. uncialis* with *C. mitis* having seasonally fluctuating relations to these two contrasting species. The strongest differentiation between species centers on the net photosynthetic responses to temperature and thallus RWC while spring is the season of greatest overall interspecific differentiation.

**Light Responses**

No significant interspecific differences ($P = .42$) in net photosynthetic light response at near optimal temperature and thallus RWC were demonstrated. Overall seasonal variation in light response was significant ($P = .02$) only between *C. mitis* in the summer and fall; this significant difference may be attributed to the higher fall light saturation intensity (Fig. 4, Table 1) and greater net photosynthesis at irradiance above about $1.1 \times 10^5$ ergs cm⁻² s⁻¹. Replicate variability was high in the light response studies and

![Figure 1](https://example.com/figure1.png)

**Fig. 1.** The seasonal temperature and precipitation regimes drawn from U.S. Weather Bureau records for Mauston, Wisconsin, about 3 km from our study area. Mean monthly temperatures with mean maxima and minima are shown as points with range lines. Monthly precipitation totals appear as bar graphs with a partitioning of days of precipitation by diurnal accumulation classes at the base of each month's record. Winter snows are reported as water equivalents; periods of snow on the ground are indicated with broken lines showing discontinuous cover.
Fig. 2. Significance levels for intraspecific seasonal variation in *C. mitis*, *C. rangiferina*, and *C. uncilis*. Comparisons between fall 1971, spring 1972, and summer 1972 were tested by multivariate analyses of variance as described in the text. Dark respiratory drying response was not amenable to statistical testing. Significant contrasts were recognized at $P \leq .05$.

Fig. 3. Significance levels of interspecific contrasts between *C. mitis*, *C. rangiferina*, and *C. uncilis* in fall 1971, spring 1972, and summer 1972. Comparisons are by multivariate analyses of variance as described in the text. Dark respiratory drying response was not amenable to statistical testing. Significant contrasts were recognized at $P \leq .05$. 
has perhaps masked what, with higher replication levels impossible in this study, may well be further significant differences in both seasonal and interspecific light responses.

Light-saturated net photosynthesis at near optimal temperature and thallus RWC varies with season and species in the range of 1.27 to 2.21 mg CO$_2$ g$^{-1}$ h$^{-1}$ (Fig. 4). *Cladonia uncialis* and *C. rangiferina* have low and high saturated rates, respectively, with *C. mitis* fluctuating seasonally between them. Light saturation and compensation points at optimal temperature and thallus RWC for the three Wisconsin Pine Barrens *Cladonia* species vary somewhat with season in the ranges of 2.0 to 3.5 $\times$ 10$^4$ and 0.16 to 0.21 $\times$ 10$^5$ ergs cm$^{-2}$ s$^{-1}$ respectively (Table 1). *Cladonia rangiferina* is light-saturated at lower irradiance than either *C. mitis* or *C. uncialis*. The *C. mitis* light compensation point, during spring 1972, of 0.21 $\times$ 10$^5$ ergs cm$^{-2}$ s$^{-1}$ may be compared with the 0.36 $\times$ 10$^5$ ergs cm$^{-2}$ s$^{-1}$ value found for Wisconsin Pine Barrens *C. mitis* in spring 1971 (Lechowicz and Adams 1973).

**Temperature Responses**

Significant seasonal variation in the temperature response of net photosynthesis (Fig. 5a) occurs ($P = .01$, Fig. 2); significant individual contrasts are between *C. mitis* in fall compared with both spring ($P = .001$) and summer ($P = .001$). Overall seasonal variation in tem-

### TABLE 1

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**Fig. 4.** Mean light dependence of net photosynthesis for *C. mitis* (△), *C. rangiferina* (○), and *C. uncialis* (□) in fall 1971, spring 1972, and summer 1972 at 25° ± 1° thallus temperature and near optimal thallus relative water content. Net CO$_2$ exchange is expressed as mg CO$_2$ g$^{-1}$ h$^{-1}$. Light levels are as both photosynthetically active radiation (PhAR = 400–700 μm) and total short-wave irradiance (280–2600 μm). Dark respiration is a mean of rates measured before and after exposure to the light levels. Figures 2 and 3 show the significance levels of intraspecific and interspecific contrasts.
temperature response of dark respiration (Fig. 5b) falls below significance ($P = .17$), but the individual contrast of $C. \text{rangiferina}$ spring vs. summer response is just significant ($P = .05$). Similarly, overall interspecific variation over the seasons is significant for net photosynthetic temperature response ($P = .004$) but not for dark respiratory temperature response ($P = .36$). $Cladonia \text{rangiferina}$ and $C. \text{uncialis}$ differ significantly in all seasons (Fig. 3) but $C. \text{mitis}$ in the fall differs significantly from $C. \text{rangiferina}$, in the spring from $C. \text{uncialis}$, and in the summer from neither. Only the spring contrast between $C. \text{rangiferina}$ and $C. \text{uncialis}$ shows significant differences in dark respiratory temperature response. Figures 2 and 3 summarize the statistically significant differences in temperature response; in consideration of Figs. 5a and 5b, points of ecological importance become apparent.

Temperature optima for photosynthesis at light saturation and favorable thallus RWC fall between 15 and 25° for the three Wisconsin Pine Barren species. $Cladonia \text{mitis}$ has an estimated mean annual net photosynthetic optimum at 24.5°, $C. \text{rangiferina}$ at 22.6°, and $C. \text{uncialis}$ at 21.3° (Table 2); in spring all species show high net photosynthetic efficiencies in a 5° range about the optima and $C. \text{uncialis}$ maintains this broad optimal efficiency range in all seasons (Fig. 5a). Net photosynthetic rates at optimal temperature, light saturation, and near optimal thallus RWC fall between 0.72 and 2.55 mg CO$_2$·g$^{-1}$·h$^{-1}$ with $C. \text{rangiferina}$ and $C. \text{uncialis}$ consistently different over the seasons and $C. \text{mitis}$ seasonally fluctuating between them.

**Fig. 5.** (A) Mean temperature dependence of net photosynthesis for $C. \text{mitis}$ ($\triangle$), $C. \text{rangiferina}$ ($\circ$), and $C. \text{uncialis}$ ($\square$) in fall 1971, spring 1972, and summer 1972 at light saturation and near optimal thallus relative water contents. Net CO$_2$ exchange rates are mg CO$_2$·g$^{-1}$·h$^{-1}$; temperatures are the mean of values from two microthermocouples in the thallus and a macrothermocouple in mat center. Figures 2 and 3 show the significance levels of intraspecific and interspecific contrasts. (B) Mean temperature response of dark respiration for $C. \text{mitis}$ ($\triangle$), $C. \text{rangiferina}$ ($\circ$), and $C. \text{uncialis}$ ($\square$) in fall 1971, spring 1972, and summer 1972 at near optimal thallus relative water contents. Net CO$_2$ exchange rates are mg CO$_2$·g$^{-1}$·h$^{-1}$; temperatures are the mean of values from two microthermocouples in the thallus and a macrothermocouple in mat center. Figures 2 and 3 show the significance levels of intraspecific and interspecific contrasts.
The temperature range in which a positive net carbon balance may be maintained under optimal light and thallus RWC also relates to species microhabitat selection. The three species seem generally similar in this respect with an annual net CO₂ fixation range of 1.9 to 48.9° but a slight tendency to rank as *C. mitis*, *C. rangiferina*, and *C. uncialis* from warmer to cooler tolerances (Table 2). The actual temperature response curves (Fig. 5a) of the Wisconsin Pine Barrens *Cladonia* suggest a slight overestimation here of the low temperature compensation points.

Within these comparable ranges of net CO₂ fixation for the Wisconsin *Cladonia* species, relative efficiencies at different temperatures must be considered. Close examination of Fig. 5a suggests that *C. mitis* at optimal light and moisture conditions has a photosynthetic apparatus better adapted to temperatures above about 25° than either *C. rangiferina* or *C. uncialis*. For example, in summer the percentage maximum net photosynthetic rates at 30° are 96% maximal for *C. mitis* but only 83% for *C. rangiferina* and *C. uncialis*; at 35° the values are 73% versus 49% and 38% respectively. Conversely, summer midtemperature responses such as 60%, 57%, and 75% for *C. mitis*, *C. rangiferina*, and *C. uncialis* respectively, at 15° perhaps somewhat favor *C. uncialis*. The low temperature net photosynthetic efficiencies during autumn indicate greater efficiencies in the sequence *C. uncialis*, *C. rangiferina*, and *C. mitis*. For example, at 4° in the fall net photosynthetic efficiencies of 20%, 7%, and -2% prevail for *C. uncialis*, *C. rangiferina*, and *C. mitis* respectively. In general, *C. mitis* shows best high temperature photosynthetic efficiencies and *C. uncialis* best low temperature efficiencies, with *C. rangiferina* essentially intermediate; these relative efficiencies must, however, be assessed also in terms of the strong contrast between *C. rangiferina* with high, *C. uncialis* with low, and *C. mitis* with fluctuating intermediate net photosynthetic rates (Fig. 5a).

*Cladonia mitis*, *C. rangiferina*, and *C. uncialis* temperature responses of dark respiration all showed an increasing respiratory rate with increasing temperature (Fig. 5b). The only exceptions to this trend are in the spring when *C. uncialis* and *C. rangiferina* respiratory rates are lowest at 10° and in the summer when the *C. mitis* 10° rate is lowest. The only significant contrasts in dark respiratory response are between *C. uncialis* and *C. rangiferina* in spring and between the spring and summer rates of *C. rangiferina* (Figs. 2 and 3). These data support the frequently accepted observation (Ahmadjian 1967) that lichen dark respiratory rates show less seasonal variation than net photosynthetic rates.

The absolute rates of dark respiration in *C. mitis*, *C. rangiferina*, and *C. uncialis* from the Wisconsin Pine Barrens generally range up to 0.92 mg CO₂·g⁻¹·h⁻¹ at 35° and in the case of *C. rangiferina* in the spring average 1.31 mg CO₂·g⁻¹·h⁻¹ at 35°. At 25° respiratory rates in the range of 0.34 to 0.74 mg CO₂·g⁻¹·h⁻¹ prevail; mean dark respiration rates immediately after a light response assessment at 25° fall between 0.32 and 0.45 mg CO₂·g⁻¹·h⁻¹ (Fig. 4).

**Thallus Relative Water Content Responses**

No significant seasonal variation (P = .81) was found in *C. mitis*, *C. rangiferina*, or *C. uncialis* net photosynthetic response to thallus RWC at light saturation and near optimal temperature (Figs. 2, 6a). Seasonal variation in dark respiration is not marked but spring respiratory rates appear to exceed summer rates.

### Table 2

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<td>21.8</td>
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<td><em>C. uncialis</em>: range</td>
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<td></td>
<td>optimum</td>
<td>19.9</td>
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at most RWC's in all three species (Fig. 6b). Significant interspecific differences \((P = .03)\) in thallus RWC net photosynthetic response at light saturation and near optimal temperatures do occur. The primary importance of thallus RWC in lichen net CO2 exchange is well established (Smith 1962; Hale 1967; Ahmadjian 1967), and variation in thallus RWC responses could weigh heavily in habitat differentiation (Kershaw 1972). Cladonia rangiferina and C. uncials show significant differences in thallus RWC response at light saturation and near optimal temperature in all seasons (Fig. 3); C. mitis and C. rangiferina differ in spring \((P = .05)\). A qualitative separation of C. mitis and C. rangiferina from C. uncials may be made on the basis of a previously reported dark respiratory plateau at mid-RWC (Adams 1971; Lechowicz and Adams 1973); here this differentiating pattern appears most markedly in spring (Fig. 6b).

At light saturation and 25°, C. uncials evidences optimal net photosynthesis at between 75 and 85% RWC; C. rangiferina at about 55% RWC; and C. mitis at between 55 and 75% RWC.

In interpretation of microdistributional relations on our Wisconsin Pine Barren site, patterns of net photosynthetic efficiency at optimal temperature and irradiance but non-optimal RWC are also important (Fig. 6a). Net photosynthesis at RWC greater than about 90% is inhibited in all three species. Similarly, at RWC less than about 20% all three species have less than about 10% maximal net photosynthetic rates. Since our field measurements indicate that air-

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**Fig. 6.** (A) Mean thallus relative water content (RWC) dependence of net photosynthesis for C. mitis (△), C. rangiferina (○), and C. uncials (□) during fall 1971, spring 1972, and summer 1972 at an air temperature of 25° ± 1° and light saturation. Net CO2 exchange rates are as mg CO2·g⁻¹·h⁻¹; relative water content follows Barrs (1968). Thallus relative water content could not be continuously followed with available equipment. Thus, points are means of net CO2 exchange from all replicates in 10% RWC segments plotted at the segment mean RWC. Figures 2 and 3 show the significance levels of intraspecific and interspecific contrasts, tested as described in the text. (B) Mean thallus relative water content (RWC) response of dark respiration for C. mitis (△), C. rangiferina (○), and C. uncials (□) in fall 1971, spring 1972, and summer 1972 at an air temperature of 25° ± 1°. Net CO2 exchange rates are as mg CO2·g⁻¹·h⁻¹; relative water content follows Barrs (1968). Thallus relative water content could not be continuously followed with available equipment. Thus, points are means of net CO2 exchange from all replicates in 10% RWC segments plotted at the segment mean RWC.
dry lichens (about 5% RWC) are wetted only to 15–20% RWC by dew, and dry by 10:00 a.m., we agree with Kershaw and Rouse (1971) that dew plays a minor role in Cladonia ecology. At RWC in the range of 90 to 20%, C. uncialis relative rates of net photosynthesis fall below both C. mitis and C. rangiferina as RWC falls below about 65%. In the range of about 50 to 20%, C. rangiferina relative rates exceed those of C. mitis. For example, consider the summer relative rates at about 45% RWC which are 97%, 75%, and 30% of maximal photosynthesis for C. rangiferina, C. mitis, C. uncialis respectively. At between about 65 and 80% RWC, C. rangiferina has somewhat lower net photosynthetic efficiency than the near equal C. mitis and C. uncialis; consider, again, summer relative rates at about 74% RWC of 94%, 93%, and 82% for C. uncialis, C. mitis, and C. rangiferina respectively.

The dark respiratory response to RWC is important in discussion of net CO2 losses when the lichen thallus is wetted but in unfavorable photosynthetic conditions. In all seasons C. uncialis shows a generally steady dark respiratory decline at 25° with decreasing RWC. Cladonia mitis and C. rangiferina, to varying degrees depending on season, show a “plateau” effect (Lechowicz and Adams 1973) in which respiration rate levels or even increases after a steady decline from 100% RWC to some RWC between 60 and 85%. Absolute values of respiration range between 0.57 and 0.73 mg CO2·g-1·h-1 at RWC greater than 90% at 25°; at RWC about 65% these rates fall to between 0.25 and 0.56 mg CO2·g-1·h-1. Generally good agreement with rates from the experiments on the temperature dependence of respiration was found.

(2) Drying Rates

Under identical laboratory conditions, essentially equal mat-area samples of C. mitis, C. rangiferina, and C. uncialis showed significant differences (P = .03) in overall drying rates (see Fig. 7a, b). In the dark, C. mitis and C. rangiferina drying rates do not differ (P = .90), but both dry significantly faster than C. uncialis (P = .009 and P = .01 respectively). In the light C. rangiferina dries significantly faster (P = .05) than C. uncialis, but C. mitis dries at an intermediate rate differing significantly from neither. All three species dry significantly slower (P = .01) in the dark than in the light.

These laboratory drying rates have followed trends evident in our field work although microsite differences somewhat affect the comparisons. A comparison of water content over 26 h for five Cladonia species growing together on a microsite in open oak–pine–aspen forest in Michigan (Heatwole 1966) indicates a greater moisture content in C. uncialis compared with C. rangiferina and C. mitis in the important 2–3 h after sunrise. The ecological effects of different drying rates depend heavily on the pattern of precipitation (Fig. 1), which needs to be considered in relation to Jack’s (1935) observation of 0.30-cm rainfall uptake by C. rangiferina mats. In 1971, 42% of the days when snow was off the ground had measurable precipitation; the photosynthetic time gained by the slower drying C. uncialis after these frequent rainfalls could significantly affect its comparative ecological relations to C. mitis and C. rangiferina.

(3) Mean Annual Production

Mean annual production of C. rangiferina and C. mitis does not differ significantly (P = .92) on the Wisconsin Pine Barrens; both species, however, differ significantly (P = .001) from C. uncialis in mean annual production (Table 3). The same patterns of significance occur in univariate analyses of mean height and weight increments. Cladonia mitis and C. rangiferina exceed C. uncialis in average annual production.

### TABLE 3


<table>
<thead>
<tr>
<th>Species</th>
<th>Δ height, mm</th>
<th>Range, mm</th>
<th>Δ weight, mg</th>
<th>Range, mg</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. mitis</td>
<td>5.5</td>
<td>3.6–7.2</td>
<td>5.3</td>
<td>2.1–8.0</td>
</tr>
<tr>
<td>C. rangiferina</td>
<td>5.5</td>
<td>3.9–7.0</td>
<td>5.5</td>
<td>3.4–9.0</td>
</tr>
<tr>
<td>C. uncialis</td>
<td>4.2</td>
<td>3.0–5.3</td>
<td>3.7</td>
<td>1.2–6.8</td>
</tr>
</tbody>
</table>
Discussion
Lichens must be wetted to photosynthesize and grow; when they are dry, only very low respiration prevails, and the essentially dormant plant is highly resistant to environmental stress (Ahmadjian 1967; Hale 1967). Thus, habitat water regime has long been recognized as an important determinant of lichen survival (Smith

Fig. 7. (A) Thallus relative water content (RWC) decline over time in the light for *C. mitis* (△), *C. rangiferina* (○), and *C. uncialis* (□). Curves are taken from 10 replicates from all seasons averaged in 5% RWC segments and plotted at the segment midpoint. (B) Thallus relative water content (RWC) decline over time in the dark for *C. mitis* (△), *C. rangiferina* (○), and *C. uncialis* (□). Curves are taken from nine replicates from all seasons averaged in 5% RWC segments and plotted at the segment midpoint.
1962). In an explanation of the comparative, ecophysiological basis of *C. mitis*, *C. rangiferina*, and *C. uncials* microdistribution on the Wisconsin Pine Barrens, water relations appear to play a primary role.

Based on 166 quadrats (0.5 m²) at our principal study site on the Wisconsin Pine Barrens (Lechowicz and Adams 1974), *C. uncials* has 64% presence in the lichen-moss ground-layer community while *C. mitis* and *C. rangiferina* have only 14% and 22% presence respectively. The degree of species microsite co-occurrence assessed from this quadrat data by a percentage similarity measure (Bray and Curtis 1957) suggests that the three species have different microdistributional patterns. *Cladonia mitis* and *C. rangiferina* have only a 24% microdistributional similarity; *C. uncials* tends to occur in different microsites from either *C. mitis* (31% similarity) or *C. rangiferina* (35% similarity). Moreover, our field studies suggest that these low microdistributional similarities reflect selection for somewhat different microhabitats. *Cladonia uncials* appears tolerant of a broad microenvironmental range; it forms large mats from hot, dry, open areas through cooler, damp, shaded microsites. Only a decrease in stature distinguishes exposed from shaded mats; morphologic intergradation with *C. caroliniana* did not present a field identification problem. *Cladonia mitis* occurs in moderately open, warm microsites protected somewhat from xeric moisture regimes by surrounding vegetation. *Cladonia rangiferina* occurs in relatively shaded, cool microsites with mesic moisture regimes often amid vascular ground-layer vegetation. The ecophysiological basis of these occurrence patterns lies in the consideration of not only net CO₂ exchange capacities but also drying rates.

Net CO₂ exchange rates alone do not explain the dominance of *C. uncials* on the Wisconsin Pine Barrens. The three *Cladonia* species have generally similar respiration responses and *C. uncials*, the species of highest presence, has the lowest absolute net photosynthetic rates under nearly all conditions tested. Moreover, the percentage maximum net photosynthetic rates indicate that *C. uncials* has optimal net CO₂ exchange under conditions of high moisture, high light, and moderate temperatures. Kershaw (1972) showed that in many lichen species and races a direct correspondence exists between habitat moisture regime and net photosynthetic RWC optimum. The microhabitat relations of *C. uncials*, and to a somewhat lesser degree *C. mitis*, do not show this correspondence; in *C. uncials* a 75–85% RWC net photosynthetic optimum characterizes replicates from mesic through xeric habitats. These apparently anomalous interactions of microdistribution on the Wisconsin Pine Barrens and net CO₂ exchange responses may be resolved by comparing the drying rates of the three *Cladonia* species.

*Cladonia uncials* dries more slowly than *C. mitis* and *C. rangiferina*. Thus, under the same environmental conditions *C. uncials* has the lowest absolute net photosynthetic rates but maintains them the longest; this advantage may be partly countered by more frequent nighttime respiratory losses. The comparative net effects of habitat microenvironment, drying rate, and net CO₂ exchange responses of these three *Cladonia* species may be gauged by their average annual production. *Cladonia uncials* has achieved broad distribution presumably by the advantage of a slower drying rate, but net CO₂ exchange responses limit its annual production. *Cladonia mitis* and *C. rangiferina* have the same annual production, which significantly exceeds that of *C. uncials*; these two species, however, have narrower microhabitat requirements.

The similarly productive *C. mitis* and *C. rangiferina* have low co-occurrence and apparently occupy somewhat differentiated microhabitats congruent with certain differences between them. *Cladonia mitis* has a somewhat slower drying rate in the light than *C. rangiferina*; dependent on the season and environmental conditions, *C. mitis*’s absolute net photosynthetic rates are equal to or below those of *C. rangiferina*. These traits reflect the microhabitat selection by the species on the Wisconsin Pine Barrens and may underlie the observation (Ahti 1964) that in southern Ontario *C. mitis* occurs chiefly on exposed rock outcrops and excessively dry lichen woodlands. Also, *C. rangiferina* seems to be the last lichen which remains in old, fairly dense jack pine–lichen woodlands (Ahti and Hepburn 1967).

Lechowicz (1973) has considered other aspects of the data presented here and compared the lichen responses with those reported in the literature; this paper discusses the physiological adaptations underlying the microdistribution of
C. mitis, C. rangiferina, and C. uncialis on the Wisconsin Pine Barrens. The importance of lichen water relations in affecting microdistribution is evident, but microenvironmental light and temperature regimes also contribute. The physiological adaptations underlying microhabitat selection argue against any single-factor differentiation among the three closely related species. Since it was found that C. uncialis does not grow only where its net CO2 exchange optima suggest, the importance and efficacy of a community perspective in interpretation of autecological work may be emphasized. Further comparative studies on C. mitis, C. rangiferina, and C. uncialis seem best directed to a quantification of the lichen-environment interaction over time. Such a treatment may be possible through simulation studies on an ecophysiological model of lichen environmental response. Kershaw and Harris (1971a, b) have successfully related the macrodistribution of Parmelia caperata in England to precipitation patterns. We are considering this and other approaches to the problem of quantifying the adaptive interactions of organism and environment that moderate questions of competition and distribution.

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