# PHYSIOLOGICAL ECOLOGY OF *CLADONIA RANGIFERINA*

# PHYSIOLOGICAL ECOLOGY
# OF
# CLADONIA RANGIFERINA

BY

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# ABSTRACT

The net photosynthetic and dark respiration response to moisture, light level and temperature is discussed with reference to the unique Cladonia rangiferina (L.) Wigg.-Shrub association in Cladonia stellaris (Opiz.) Pouz. Spruce Woodland at Hawley Lake, Ontario. Field measurements provide a description of the summer and winter environmental complex. Winter data shows an exceptional thermal insulation afforded by snow cover, protecting lichen thalli from extreme air temperatures. Summer environmental data highlights the need to dissociate periods of thallus hydration (metabolic activity), and thallus dehydration in order that meaningful comparisons may be made with experimentally derived levels of metabolic activity. Experimentally derived physiology of the hydrated thallus showed a broad amplitude of tolerance to light level and temperature correlating with the wide range of temperature and light level experienced during a single thallus drying cycle in the field. Heat stress experiments illustrate this is indeed, a sensitive species restricted to the more ameliorated temperature regime of mature Spruce-Lichen Woodland. Heat sensitivity may also act to restrict C. rangiferina to the cooler micro-site afforded by the elevated shrub-hummocks.

A spring to summer series of collections of a Muskoka population of C. rangiferina were coursed through heat stress experiments. Significant heat tolerance acclimation emerged as an essential response to withstand the high summer temperature regime.

# ACKNOWLEDGEMENTS

I wish to express my good fortune in finding a real friend and excellent supervisor, Dr. Kenneth Kershaw, whom provided for me the opportunity to become a man of knowledge. I also wish to express my appreciation for the spontaneous moral support, and superb technical and scientific expertise from Ms. Maggie Webber and Dr. John D. MacFarlane. Ms. Judy Grenville must also be thanked for her dedication to transforming my scrawl into a professional typescript.

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# 1. INTRODUCTION

Ecology the science of all sciences in relation to living organisms remains an infant in its discoveries, and for many major ecosystems the very basic descriptive index of species and their associations still does not exist. Recent work by ecologists in the specialized areas of microclimatology and physiology have served to increase our understanding of some of the complex intricacies of biotic-abiotic interactions. Microclimatology for example, provides a closer approximation of some key environmental parameters as experienced at an organismal level, and previously undetectable features of a species niche now appear as a pattern of influence to which the occupant responds. This response may be interpreted in the way of a dependent feature of the species requirements or a tolerated stress variable which precludes the habitation by other species. As niche definition becomes more precise, it follows that measurement of the physiological response of a species to the niche confines, must also be more exacting in order that an ecological level of significance may be applied to each micro-environmental character. This then is the current pursuit of ecophysiology; to provide a species-environment interaction picture of maximal resolution.

Plant Physiology has supplied much univariate information of a plant's response to the environmental influences of light, temperature and moisture over the past twenty years (see <u>Environmental and Biological Control of Photosynthesis</u>, Marcelle, 1975). Thus we have a species response to single variables without any understanding of second, tertiary or possibly higher order interactions. Few physiological studies fulfill the ecological objectives of determining how an individual species or group of associated species, simultaneously copes with the milieu of biotic and abiotic influences from hour to hour, day to day, and season to season. The financial and time commitments required in operating a full scale field programme, coupled to laboratory-based physiological work, has resulted in ecophysiological data which is largely univariate. A comprehensive understanding of how even the three key parameters of light, temperature and moisture interact to evolve a species niche is still largely lacking.

Larson and Kershaw (1975a) outlined an experimental $CO_2$ gas exchange measurement system which permitted a more practical multivariate experimental design. The technique used is currently restricted to lower plants which respond quite naturally to experimental manipulation in glass cuvettes, no complications arise from a soil environment, roots or stomata. With lichens as experimental material, and a sensitive gas analysis system considerable progress was made in our understanding of the ecological significance of respiration and photosynthesis.

These methods have been applied to a distinctive sub-arctic ecosystem Spruce-Lichen Woodland (Kershaw, 1977c). Lichen woodlands represent a successional stage in the post-fire recovery sequence leading eventually to closed canopy woodland. Due to the extremely fire susceptable nature of the lichen surface only relatively rarely will tree density reach a level which suppress lichen growth, a reburn and subsequent recovery cycle usually occurs first. During the first stage of recovery following fire the following environmental changes have been identified: Early snow melt and the absence of thick lichen cover leads to low soil moisture. As a result mid-summer latent heat fluxes are reduced and there is a corresponding increase in the sensible heat flux producing microclimate conditions analogous to a semi-desert. Notable, are very high surface temperatures, extremely large diurnal fluctuations of soil and surface temperatures, with summer ground frost, and pronounced ground cooling prior to snow fall. Initial re-colinization, characterized by a dominance of *Polytrichum piliferum*, results in a slow accumulation of humus which gradually modifies the long wave radiation and thus moderates the harsh surface microclimate. In addition, pH of the surface layer will change facilitating the establishment of characteristic *Cladonia* spp. which dominate the second recovery phase. Very open lichen woodland with high surface albedo modulates the temperature regime, as seen in lower surface temperatures, and a less severe diurnal fluctuation. The final full development of a lichen surface acts as an effective mulch and elevates the soil mositure status to field capacity throughout the summer period. This in turn may allow the full development of lichen woodland with an average inter-tree distance approaching ten metres.

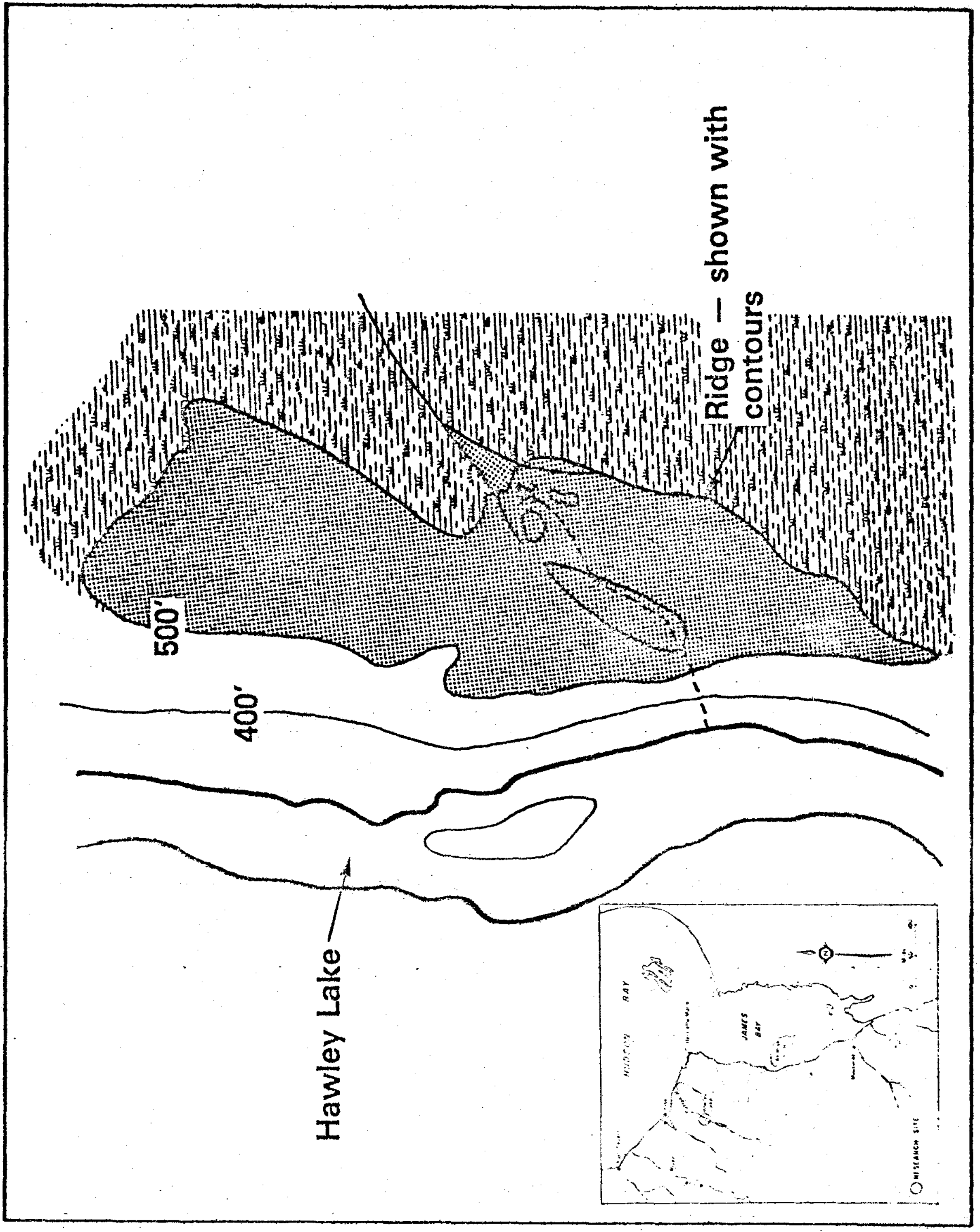
To date work has proceeded largely in *Stereocaulon*-Spruce Woodland in the Abitau-Dunvegan Lakes region of the Northwest Territories. The response of net photosynthetic, respiratory, and nitrogenase activity, to light, temperature, and moisture has been fully documented on a seasonal basis for the dominant member of the mature woodland phase, *Stereocaulon paschale* (L.) Hoffm. (Crittenden and Kershaw, 1978 and 1979; Kershaw and Rouse, 1976; Kershaw and Smith, 1978). However, no comparable data is available for Cladonia-Woodland and this thesis presents the first ecophysiological inventory of Cladonia-Spruce Woodland. C. rangiferina's ecophysiology has been analyzed on a seasonal basis together with field microclimate studies to characterize the adaptive regime of the lichen thallus. The net photosynthetic and respiratory response of C. rangiferina were measured in summer and fall under a full range of interacting levels of light, moisture and temperature. Thallus temperature was measured in winter and summer to aid in the interpretation of the physiological response matrix.

Since thermal stress has been implicated in the recovery sequence of Stereocaulon Woodland (Kershaw and Rouse, 1976) the heat tolerance limits of C. rangiferina were also examined and contrasted with a southern population from the Muskoka region of southern Ontario.

## 1.1 The Hudson Bay Lowlands Research Site

Field studies and the collection site of lichen material for this research project was at Hawley Lake, Ontario, between September 1977 and June 1979. Hawley Lake, located within the Hudson Bay lowlands of Northern Ontario (latitude 54° 10' longitude 84° 90') is characterized by a local topography of 200 to 400 foot higher elevation than the surrounding lowlands (see Fig. 1). Intrusive rock, with a topping of glacial till, provides improved drainage, in contrast to the more prevalent, stagnant water and meandering rivers (Hustich, 1957) of the lowlands. The tremendous ecological importance of drainage is readily seen when flying over the Hudson Bay lowlands, as well developed, full grown Spruce (largely

Figure 1. Map of Hudson Bay region showing the location of Hawley Lake. Enlargement illustrating precise location of research site (marked x) within largely burnt uplands (shaded). Note the extension of esker into the wet lowlands.


Hawley Lake
400'
500'
Ridge — shown with contours
HUDSON BAY
JAMES BAY
N
RESEARCH SITE

_Picea_ _mariana_ (Mill.) BSP.) occur only where drainage is facilitated, as along the margins of rivers and lakes, or on the tops of eskers and raised beach ridges (Kershaw and Rouse, 1971a). Extensive eskers and moraines at Hawley Lake provide such a well drained and continuous area for colonization by _P_. _mariana_.

Climatological data shows that the area experiences a long winter of eight months, with air temperatures reaching -42.0 Celsius. Summer air temperatures fluctuate between 28°C to 0°C, depending both on the position of the arctic front, and thus whether the winds are from the north off of Hudson Bay, or from the warm south. Rainfall during the favourable season is moderate, but the poorly developed sandy till soils offer little water holding capacity.

Consistent with this type of environment both to the north-east in Quebec/Labrador (Fraser, 1956) and the north-west in Northwest Territories (Kershaw, 1977b) is a plant association termed, Spruce-lichen Woodland. Structurally, the association consists of widely spaced (two to three meters) Spruce trees reaching heights of 10 to 15 meters, with an almost monospecific lichen ground cover, 5 to 15 centimeters thick (see Fig. 2).

Spruce-lichen woodland surrounding Hawley Lake is largely burnt and is now in the characteristic stages of the succession sequence (see page 3) following major burns in 1965 and 1945 (Chokomolon, personal communication). These two recovery stages are characteristically phase 1 and phase 2 (Figs. 3, 4) prior to the establishment of mature lichen woodland (Ahti, 1967; Kershaw and Rouse, 1976; Maikawa and Kershaw, 1976; Strang, 1973). The reburn cycle is approximately 80 years (Rouse, 1976). One unburnt section of mature Spruce-lichen woodland which was utilized in this study, persists due to its protected position on an esker extending out into the surrounding low, wet, scrub spruce vegetation so typical of the Hudson Bay lowlands (see

Figure 2. *Cladonia stellaris* woodland at Hawley Lake, Ontario.

Figure 3. *Cladonia stellaris* woodland at Hawley Lake twelve years after a major fire. Dead standing *Picea mariana* with heavy recolinization by *Ledum groenlandicum*.

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Figure 4. Cladonia stellaris woodland at Hawley Lake twenty-one years after a major fire. Re-establishment of Picea mariana evident.

Fig. 2). The mature woodland is composed of P. mariana, reproducing largely by layering (Hustich, 1951) giving the trees a very full appearance (see Fig. 5). Infrequently observed trees within the lichen woodland are Larix laricina (DuRoi) K. Koch. and Populus tremuloides Michx. Ground cover is a continuous light yellow mat of Cladonia stellaris (Opiz) Pouz. and Vezda (formerly Cladonia alpestris (L.) Rabenh.). Scattered throughout the lichen mat are the shrubs, Ledum groenlandicum Oeder. and Shepherdia canadensis (L.) Nutt., each clump forming a small mound due to the persistence of these species, via the root mass, through the fire cycle.

Cladonia rangiferina, the species under investigation in this study, occurs as a sub-dominant lichen in the ground cover. It may occur diffusely in the C. stellaris mat, adjacent to shrub hummocks, but more often it forms a dense mono-specific clone beneath the shrubs, covering the entire dome (see Figs. 6, 7, 8). During an examination of pattern in lichen woodland at Hawley Lake this marked association was described as a primary interaction worthy of further investigation (Kershaw and Rouse, 1971b). This same pattern has been observed in lichen woodlands of Pen Island, Hudson Bay (K.A. Kershaw, personal communication) and Churchill, Manitoba. C. rangiferina may also occur beneath the layering spruce boughs and indeed in small clones in open areas of the C. stellaris mat, these individuals were not utilized in this study. Herberium specimens of the material used in this study are located in the lichen herberium of Dr. K. A. Kershaw, McMaster University.

## 1.2 The Muskoka Collection Site

A population of C. rangiferina, from the Muskoka region in Central Ontario was also utilized in this study. The environment at Muskoka is

Figure 5. Abundant vegetative reproduction of Picea mariana by layering giving the trees a very robust appearance.

Figure 6. *Cladonia stellaris* woodland at Hawley Lake, Illustrating the distinct association of *Cladonia rangiferina* (grey fruticose lichen) with the shrub, *Ledum groenlandicum*. Light yellow coloured fruticose lichen is *C. stellaris*.

Figure 7. Close-up, illustrating the *Cladonia rangiferina* - *Shepherdia canadensis* association.

Figure 8. *Cladonia rangiferina* - *Ledum groenlandicum* association illustrating the hummock resulting from the shrubs persistent root mass.

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comparable to the Lichen Woodland environment where the exposed granitic outcrops provide a sufficiently harsh environment to preclude the development of a closed canopy forest and allow a good lichen ground cover to develop. Lack of soil development, extreme dryness, and renewal by fire, all environmental parameters corresponding to those of Spruce-Lichen Woodland at Hawley Lake, are also instrumental in the maintence of this system. Between the widely spaced _Quercus_ _velutina_ Lam., rounded granitic shield substrate provides an environment well suited to colonization by lichens. _C_. _rangiferina_ occuring in dense clones amongst numerous other ground lichens provides a comparison with the Hawley Lake population of this species.

# 2. METHODS

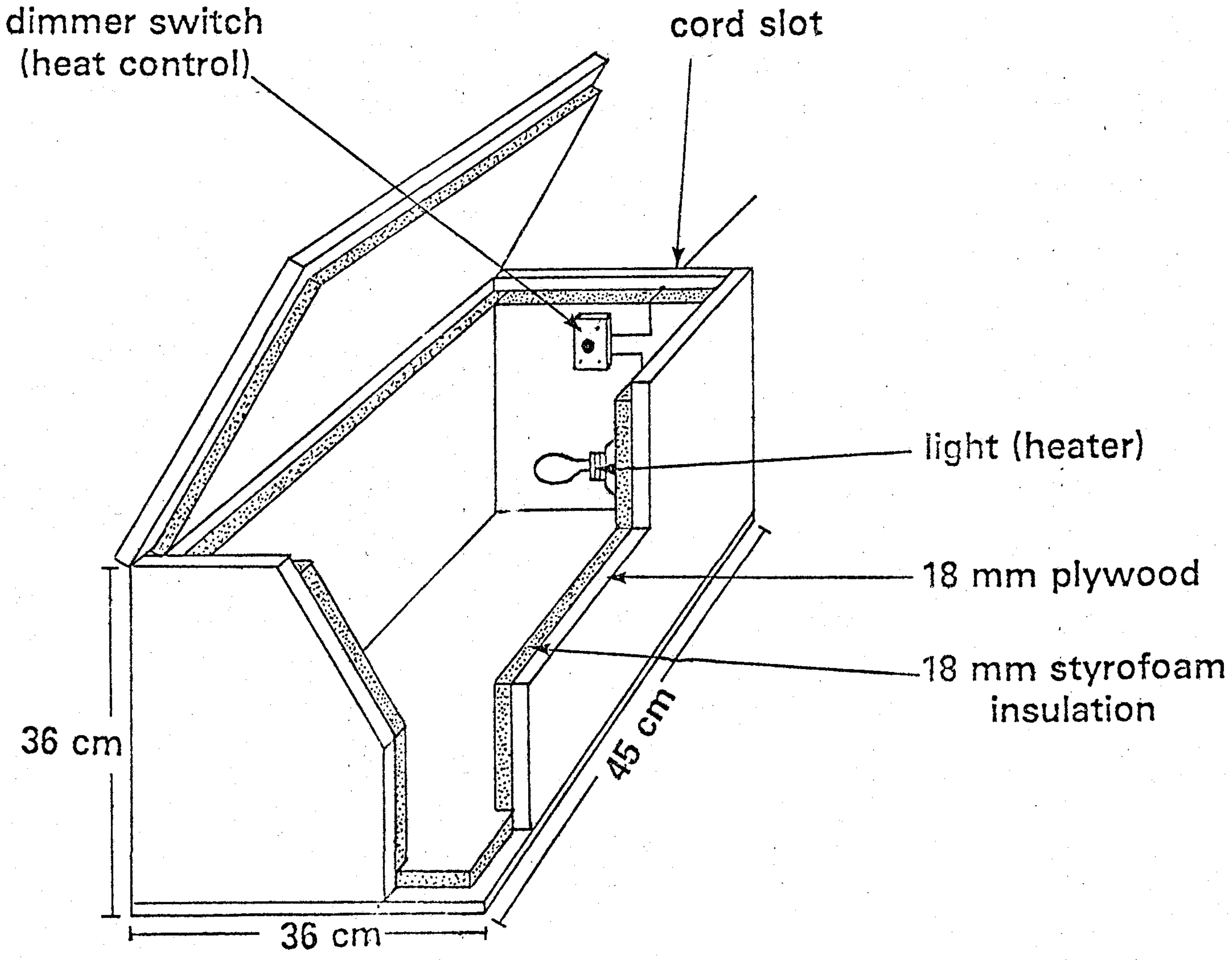
## 2.1 Field Methods

### 2.1.1 Temperature Measurement

Temperatures were recorded during the winter (December, 1977) and summer (June, 1978) only. Surface readings were made using thermocouples inserted into the hollow podetia (Fig. 9) of *C. stellaris* and *C. rangiferina*. The air temperature profile was measured to a height of 100 centimeters above the lichen mat. In all cases micro-thermopiles were constructed utilizing 5, 42 gauge (0.064 millimeter), copper-constantan, thermocouples connected in series. Micro-thermocouples provide a rapid response time (Tanner, 1963), incure small radiation error (Pieters and Schurer, 1973) and when connected in series produce a stable, averaged signal compensating for low electromotive force, high noise, and small local fluctuations (Field, Larson and Kershaw, 1974). All micro-thermopiles, once constructed, were calibrated at 0°C. The thermopiles have a linear response within 1°C from -40°C to +40°C (Schimmelpfennig, 1975). Ice reference for the sensors was supplied by an electrically powered Omega, model TRC, Ice Point Cell. As this unit was not designed for use in ambient temperatures below 0°C, it was necessary to construct a housing unit which could be heated for winter use. Figure 10 illustrates a simple solution, consisting of an insulated plywood box with a light bulb heater. Temperature is easily controlled by varying light bulb size, and, more precisely, with a dimmer switch. Multiple readings of thallus and air temperature were integrated with a stepping switch (Field *et al.*, 1974) which scanned 18 signals every 3 minutes, and incoming signals were recorded on a Rikadenki strip-chart recorder. The sampling pattern at the research site is given

Figure 9. _Cladonia rangiferina_ - _Ledum groenlandicum_ association, showing thermocouples insitu.

Figure 10. Sketch of insulated plywood box with simple light bulb heater. Used to permit winter, field operation of Omega, Ice Point Cell ($0^{o}C$ temperature reference for thermopiles).


dimmer switch
(heat control)
cord slot
light (heater)
18 mm plywood
18 mm styrofoam insulation
36 cm
45 cm
36 cm

in Figure 11 and shows all recording points and the associated shading patterns which enables a full interpretation of the results to be made (see also Figs. 23, 24).

### 2.1.2 Light Measurement

Photosynthetically active incoming solar radiation was measured at the ground, or snow surface, every 30 minutes. A Lambda Instruments, model L1 185A, sensor was placed horizontally at the surface to measure photon flux density in microeinsteins per square meter per second ($\mu E\ m^{-2}s^{-1}$) within the 400 to 700 nanometer waveband. Full sunlight and shade readings were made during the winter and summer trip whenever full scale temperature measurement was in progress.

### 2.1.3 Lichen Thallus Moisture Content Measurement

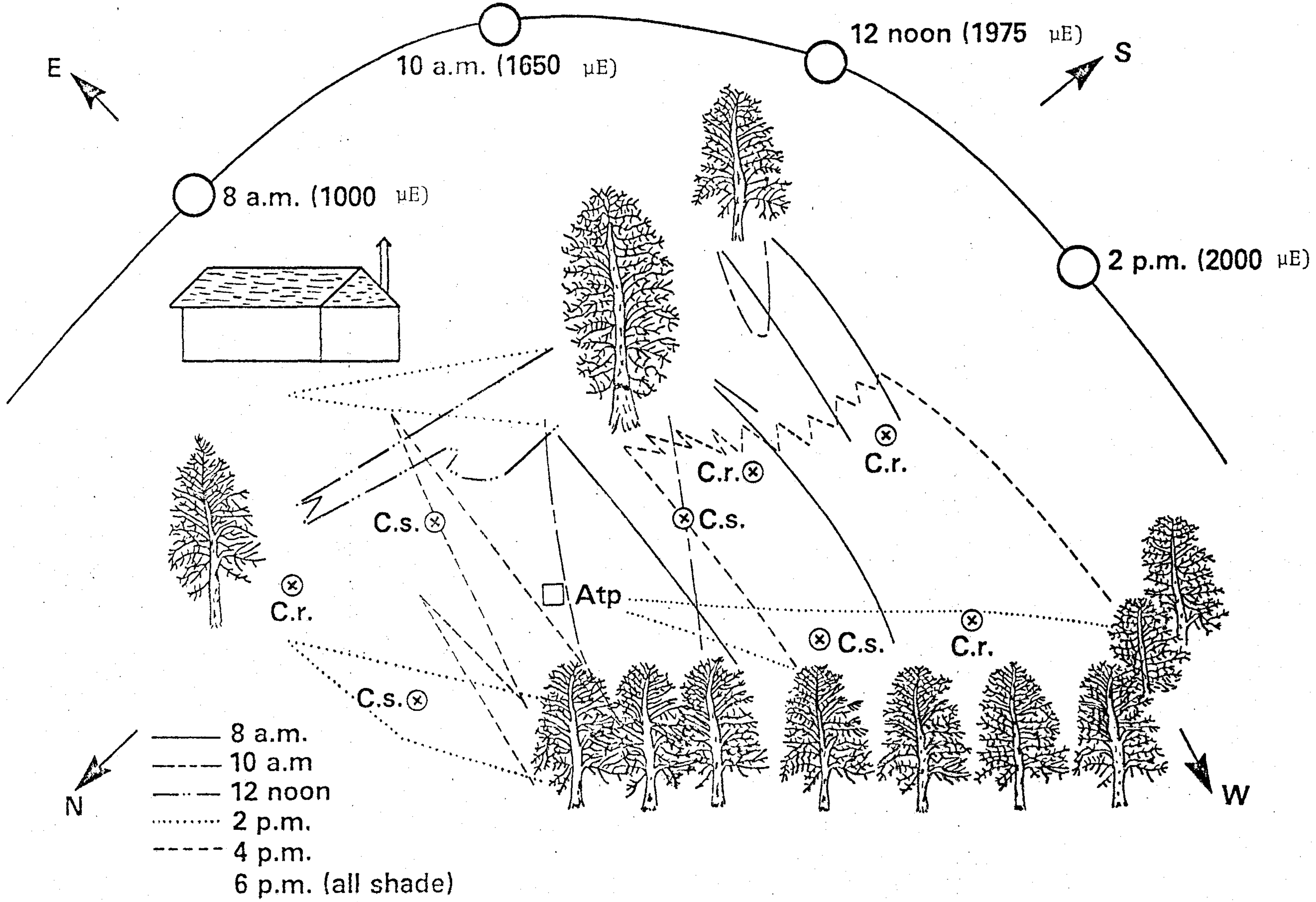
During the summer field season thallus hydration levels following rain or heavy dew were determined. Subsequent water loss over time, was monitored, again, in parallel with other environmental measurements, to provide a drying curve. Determination of thallus water content was by destructive sampling of _C. rangiferina_, weighing on a Cahn Electro Balance, model RTL, and then storing in small plastic tubes, half filled with dryerite. Upon return to the laboratory, the individual samples were oven dried, reweighed and the field fresh weight expressed as a percentage of the oven dried weight.

## 2.2 Experimental Methods

### 2.2.1 Selection of Lichen Material

Intraspecific physiological variation correlated with changes in thallus morphology has previously been shown in lichens. Harris (1971)

Figure 11. Sketch of Hawley Lake research site illustrating the pattern of temperature measurement with the associated shading patterns. (C.s., *Cladonia stellaris*; C.R., *Cladonia rangiferina*; Atp, Air temperature profile). Sun's position over day, also shown, with associated light intensity in $\mu E\ m^{-2}s^{-1}$ ($\mu E$).


E
10 a.m. (1650 μE)
12 noon (1975 μE)
S
8 a.m. (1000 μE)
2 p.m. (2000 μE)
C.r.
C.r.
C.s.
C.s.
C.r.
Atp
C.s.
C.r.
C.s.
N
W
8 a.m.
10 a.m
12 noon
2 p.m.
4 p.m.
6 p.m. (all shade)

describes variations in the net photosynthetic rate of Parmelia caperata Ach. which are correlated with changes in algal cell density of lichen thalli from tree top or tree base habitats. Topographical variation and its effect on local moisture status of the environment has been shown to be a causal factor in the intraspecific, physiological variation of Alectoria ochroleuca (Hoffm.) Mass., and Cetraria nivalis (L.) Ach. (Larson and Kershaw, 1975b, c). Lechowicz and Adams (1973) have shown differences in morphology and net photosynthetic rates for sun and shade populations of Cladonia mitis (Sand.). Similarly intraspecific variation of C. rangiferina is potentially large. Some evidence of variation can be derived from the distinctive branching pattern and colouration of sun and shade populations of this species (Thomson, 1967), and such variation was conspicuous at Muskoka.

Accordingly only non-fruiting clones were used for net photosynthetic studies, collected from uniform woodland and only sampled from open areas with uniform solar radiation. Lichen material was collected, when possible, in an air-dry state, transit times from the field to the laboratory, were between 24 and 36 hours. Upon arrival at McMaster University lichens were immediately stored in Conviron, E7 growth chambers under similar temperature and daylength conditions to those encountered in the field. Collections of C. rangiferina were made at Hawley Lake in: October, 1977; January, 1978; April, 1978; July, 1978; and October, 1978.

In addition to the Hawley Lake material, a comparative population of C. rangiferina, from Muskoka was collected in January, 1979; April, 1979; May, 1979; and June, 1979. Again only vegetative clones from uniform open areas were used.

### 2.2.2 Experimental Pretreatment

Air-dry C. rangiferina stored at low ambient humidity, was shown experimentally to remain physiologically healthy for a period of over six weeks and all subsequent experimentation was restricted to within four weeks from the collection date. Storage conditions for summer collections of material was; 16/8 hours day/night cycle at 300 micro Einsteins (μE) $m^{-2}s^{-1}$ with a day/night temperature of 20/15°C. Fall collections received a 12 hour day/night cycle with temperatures of 15°C/7°C respectively. Winter material received an 8 hour day at 2 to 4°C with a 16 hour night at 0°C. The daytime temperatures above 0°C were necessary to facilitate proper functioning of the growth chamber.

Prior to an experimental period the replicates were soaked over night in distilled water at the night storage temperature. This pretreatment eliminates any wetting burst of respiration (Farrar, 1973).

The highly stratified nature of the lichen podetia has been well documented by Andreev (1954), Karenlampi (1970), and Kershaw and Harris (1971), and in corticolous lichens such as C. rangiferina only the top 2 to 3 cm of the podetium contain phycobiont. Furthermore, Karenlampi (1970) has demonstrated a linear relationship between net photosynthesis and chlorophyll content in C. stellaris. Since the lower portions of the podetia are purely fungal and hence a large source of respiration, any measurement of the rate of net photosynthesis is thus entirely dependent on what proportion of photosynthetic material in the podetium is used. In C. rangiferina the abrupt transition of podetia from the upper ashy-grey-green, healthy portion to the lower blackened decaying portion serves as a reference for choice of material, only portions of the thallus 1 cm above the dead zone were used.

Five or six podetia, weighing approximately 0.3 gms, were removed from the distilled water, given a gentle bounce on a wad of paper towels and used as a "fully" saturated experimental replicate.

### 2.2.3 Measurement of Gas Exchange

The measurement of gas exchange in C. rangiferina followed the method of Larson and Kershaw (1975a). Replicate podetia were sealed within a 200 ml cuvette, and the ambient concentration of $CO_2$ measured before and after an incubation period. Thus a 3 ml sample of air was mixed in with ambient air sealed within the cuvette and a 3 ml sample of air withdrawn and the $CO_2$ concentration measured with a Beckman 865 IRGA. Following the incubation period a 3 ml gas sample is removed and analyzed, the difference in $CO_2$ concentration between the beginning and end of the incubation period giving the activity due to respiration, if in the dark, or net photosynthesis if in the light. This change in $CO_2$ concentration is expressed, mg $CO_2$ $gm^{-1}hr^{-1}$; mg Carbon as the IRGA is calibrated with known concentrations of $CO_2$, per gm dry wet of tissue as lichen samples are oven dried at 80°C, per hour as the length of the incubation period is known.

Due to the closed cuvette design of the experiment, $CO_2$ limitation during incubation is an important consideration, Larson and Kershaw (1975a) state "...certainly this ($CO_2$ limitation) must be tested on each species for which a physiological data matrix is to be generated." A $CO_2$ limitation point, similar to Larson (1975) at 150 ppm ambient $CO_2$ was found for C. rangiferina. Subsequent experimentation was conducted to preclude the occurrence of $CO_2$ limitation during an incubation period.

This experimental design permits the simultaneous use of several cuvettes each containing a lichen replicate at: (1) a single experimental temperature controlled by the walk-in growth chamber, (2) a range of light intensities controlled by an adjustable bank of Westinghouse Cool White SHO flourescent tubes, $0 \mu E\ m^{-2} s^{-1}$ was obtained by placing experimental replicates in a dark box, (3) known levels of thallus hydration determined by weighing the lichen material at the termination of an incubation period.

By the use of embedded microthermocouples temperature of the replicate lichen thalli at all light levels, were monitored during each experiment. Extremely tight temperature control, often $\pm$ 0.5°C, 0 to 600 $\mu E\ m^2 s^{-1}$, and never more than $\pm$ 1.0°C, was achieved in the walk-in growth chamber. Experimental temperatures chosen for a physiological data matrix were; 5°C, 15°C, 25°C and 35°C. A photosynthetically active light spectrum, 400 to 700 nanometers, was measured with a Lambda, model L1 185A, the sensor was placed within a glass cuvette and positioned horizontally beneath the light bank just as the lichen replicates would be during incubation. Light levels chosen to form a second axis in the physiological data matrix were; 0, 200, 400 and 600 $\mu E\ m^{-2} s^{-1}$.

A typical experiment lasts four hours, during which time each replicate (16 replicates in all, four at each light level) undergoes six, approximately 20 minute, incubation periods. This takes the lichen samples from an initial saturated state, to final dryness. Accurate weight determinations made at the end of each of the six incubations provided an estimate of the level of thallus hydration for the proceeding incubation period. Thallus hydration is expressed as a percentage of the oven dry weight of the lichen. The data of the four replicates for a single light level is classed into 50% moisture segments and then averaged to yield a single moisture response curve. Moisture, therefore being the third axis of the data matrix.

Variability of experimental gas exchange rates are expressed as Standard Error. Standard Error (S.E.) was calculated for the mean of each 50% moisture segment by the formula S.E. = $\sqrt{S^2/n}$ where S equals the standard deviation (S = $\sqrt{\frac{\Sigma(x-\bar{x})^2}{n}}$ for a single moisture segment. The Standard Error bars in Figs. 17 and 18 are the maximum S.E. obtained for all moisture segments, at all light levels, at the corresponding temperature.

### 2.2.4 Heat Sensitivity

A portion of the *C. rangiferina* collected in the fall of 1978 was subjected to a series of heat stress experiments. These involved storage of lichen material at potentially stressful temperatures and subsequent examination of the net photosynthetic and respiratory efficiency.

Portions of air-dry lichen mat were stored at day/night temperatures of: $15^{o}C/15^{o}C$, $25^{o}C/15^{o}C$, $35^{o}C/15^{o}C$, $45^{o}C/15^{o}C$. Day/night cycle length in all treatments was 12/12 hours at 300 $\mu E\ m^{-2}s^{-1}$.

Gas exchange was examined after 1, 2, 4, 7, 14 and 21 days of heat stress. The $15^{o}C$ storage replicates served as a control and were examined on days 1 and 21 only. A 12 hour soaking in distilled water at $15^{o}C$ served as experimental pretreatment for all replicates. Potential effects of heat stress on net photosynthesis and respiration were examined at 15°C under 400 $\mu E\ m^{-2}s^{-1}$ and 0 $\mu E\ m^{-2}s^{-1}$.

In addition to the _C_. _rangiferina_ from Hawley Lake a more southerly population was examined as a latitudinal comparison. The experimental procedure followed that described above. Material collections were made sequentially in April, end of May, and early July, 1979 to examine any possible seasonal changes in heat tolerance.

# 3. RESULTS

## 3.1 Winter Field Data

### 3.1.1 Light Intensity Measurements

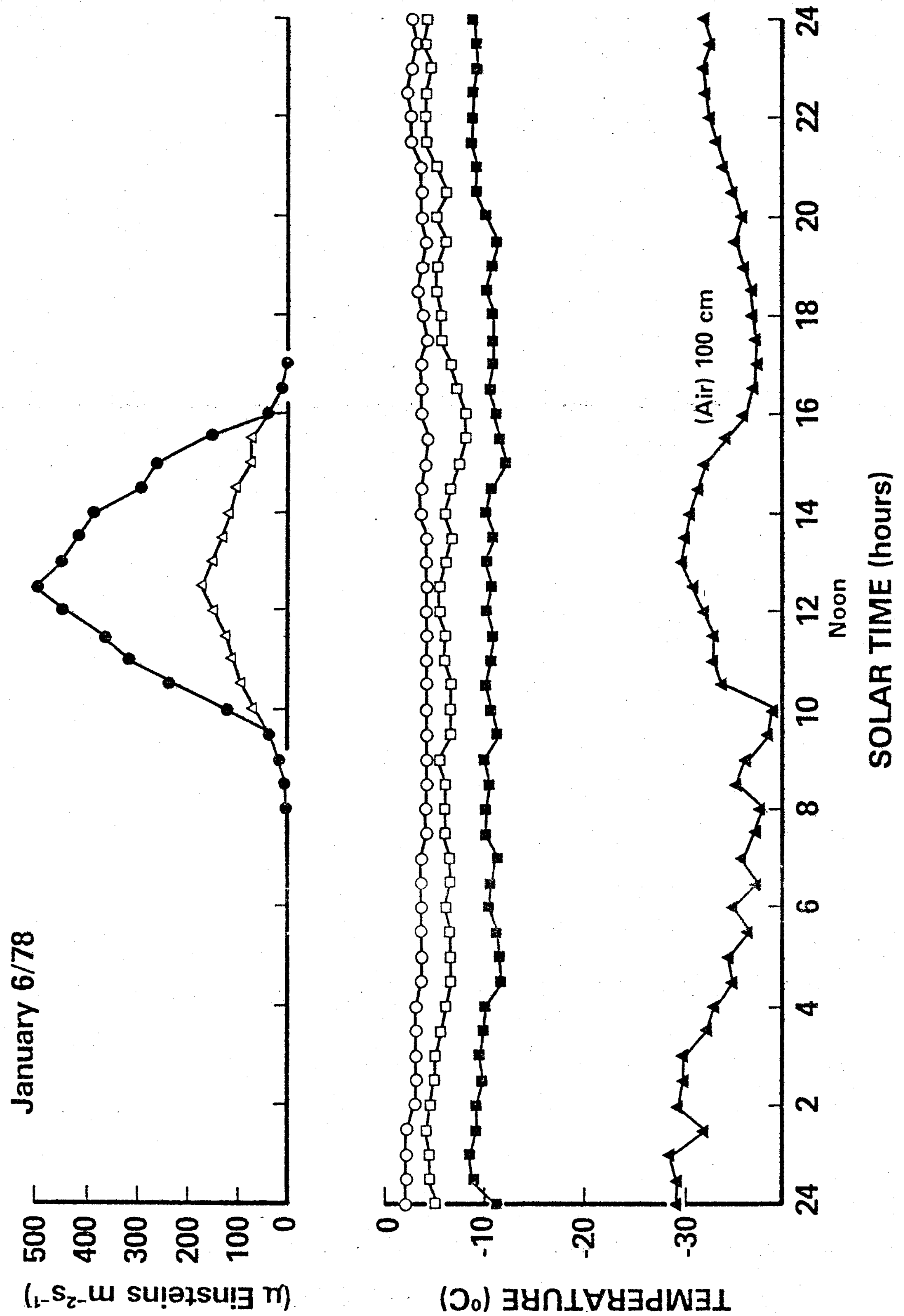
Light measurements of January 6, 1978 (Fig. 12), two weeks after winter solstice, show only an 8 hour day with a maximum light intensity of 500 $\mu$E $m^{-2}s^{-1}$. Low solar angle, responsible for the short solar day, also results in a high degree of shading of the snow surface within Spruce Lichen Woodland, consequently a more realistic maximum light intensity, representing greater than 60% of the surface at 1200 hours, is 175 $\mu$E $m^{-2}s^{-1}$. Successively greater percentages of shading occur on either side of 12 o'clock noon, as the sun occupies more oblique angles; for example, during the first and last two hours of each day, greater than 90% of the snow surface is shaded, with substantially lower light intensities (Fig. 12).

### 3.1.2 Snow Depth Measurements

During the two weeks at Hawley Lake in the winter of 1977/78, light, fluffy, snow fell at irregular intervals, with a total accumulation of 5 cm. Measurements of the snow pack within Spruce Lichen Woodland, gave uniform depths of 70 to 85 cm. In contrast, measurements on the ten year old burn (see Fig. 3) showed snow depths of 35 to 40 cm. This suggests the ability of the widely spaced spruce trees in mature Lichen Woodland to act as a snow fence, resulting in greater accumulation throughout the winter season.

Joe Chokomolon, leader of the local Indian population, related that most of the snowfall at Hawley Lake occurs in late January and through

Figure 12. Winter field data, January 6, 1978. Photosynthetically Active Radiation (PAR) graphed, readings taken horizontally at snow surface in full sunlight (●——●) and shade (△——△). Temperature profile through the snowpack ( 85 cm total depth snow) at; 0 cm or lichen thallus (○——○), 15 cm (□——□), 25 cm (■——■), 100 cm or air (▲——▲), above ground level.


January 6/78
PAR
(μ Einsteins m-2s-1)
500
400
300
200
100
0
TEMPERATURE (°C)
0
-10
-20
-30
(Air) 100 cm
24
2
4
6
8
10
12
Noon
14
16
18
20
22
24
SOLAR TIME (hours)

February. This comment was confirmed during a one day collection trip on April 4th, 1978, when snow depth had doubled, despite a degree of compaction.

### 3.1.3 Temperature Data

The data of Fig. 12 was recorded under conditions of clear skies, with high atmospheric pressure, and resultant extreme cold temperatures. Air temperatures remained more or less constant around -35°C throughout the 24 hr cycle, and the fluctuations were the result of major weather changes rather than a diurnal cycle. Within the snowpack, 25 cm and 15 cm from the ground surface temperature recordings were considerably warmer, this shows the insulating capacity of snow cover. Thallus temperatures over the same 24 hr cycle (Fig. 12) are between -2°C and -4°C accordingly the lichen mat is not exposed to cold winter temperatures.

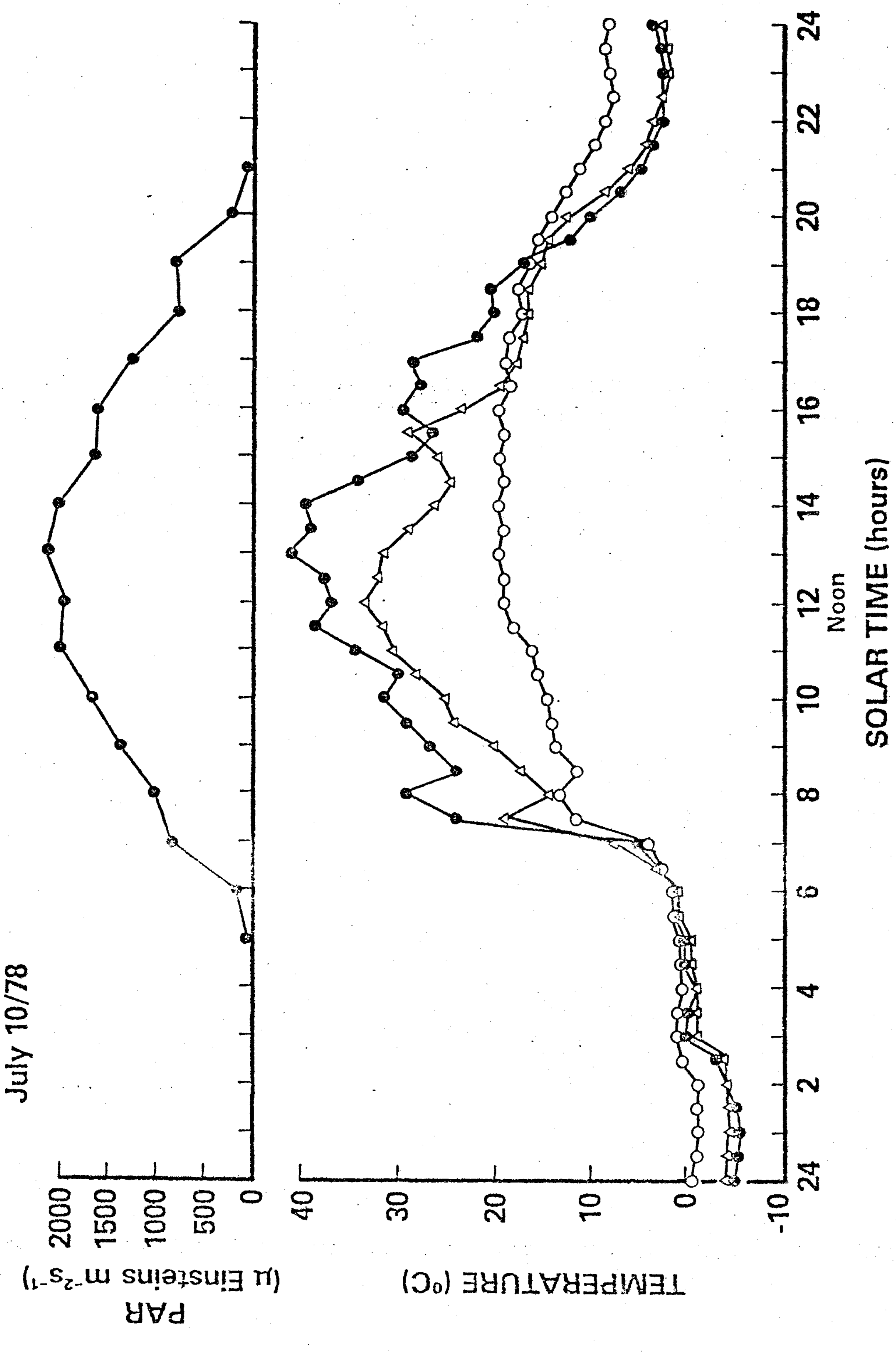
## 3.2 Summer Field Data

### 3.2.1 Light Measurements

Summer light measurements under clear skies show a long 16 hour day with a maximum light intensity of 2100 $\mu E\ m^{-2} s^{-1}$ (Fig. 13). The high solar angle results in light intensity of greater than 500 $\mu E\ m^{-2} s^{-1}$ reaching over 80% of the ground surface for 12 hours, this suggests a large daily input of solar energy. Due to the very open branching of shrubs associated with *C. rangiferina* no significant differences in light intensity were seen when a comparison was made with light readings over the *C. stellaris* mat.

Figure 14 presents the light regime which prevails under heavy overcast skies. The light curve is broad but considerably flattened with

Figure 13. Summer field data, July 10, 1978. Photosynthetically active radiation (PAR), full sunlight only plotted, over course of typical hot, high pressure summer day. Temperature traces are averaged values for; air, taken at 100 cm above ground (○—○), *Cladonia rangiferina* thallus (△—△), and *Cladonia stellaris* thallus (●—●).


July 10/78
PAR
(µ Einsteins m-2s-1)
2000
1500
1000
500
0
TEMPERATURE (°C)
40
30
20
10
0
-10
24
2
4
6
8
10
12
Noon
14
16
18
20
22
24
SOLAR TIME (hours)

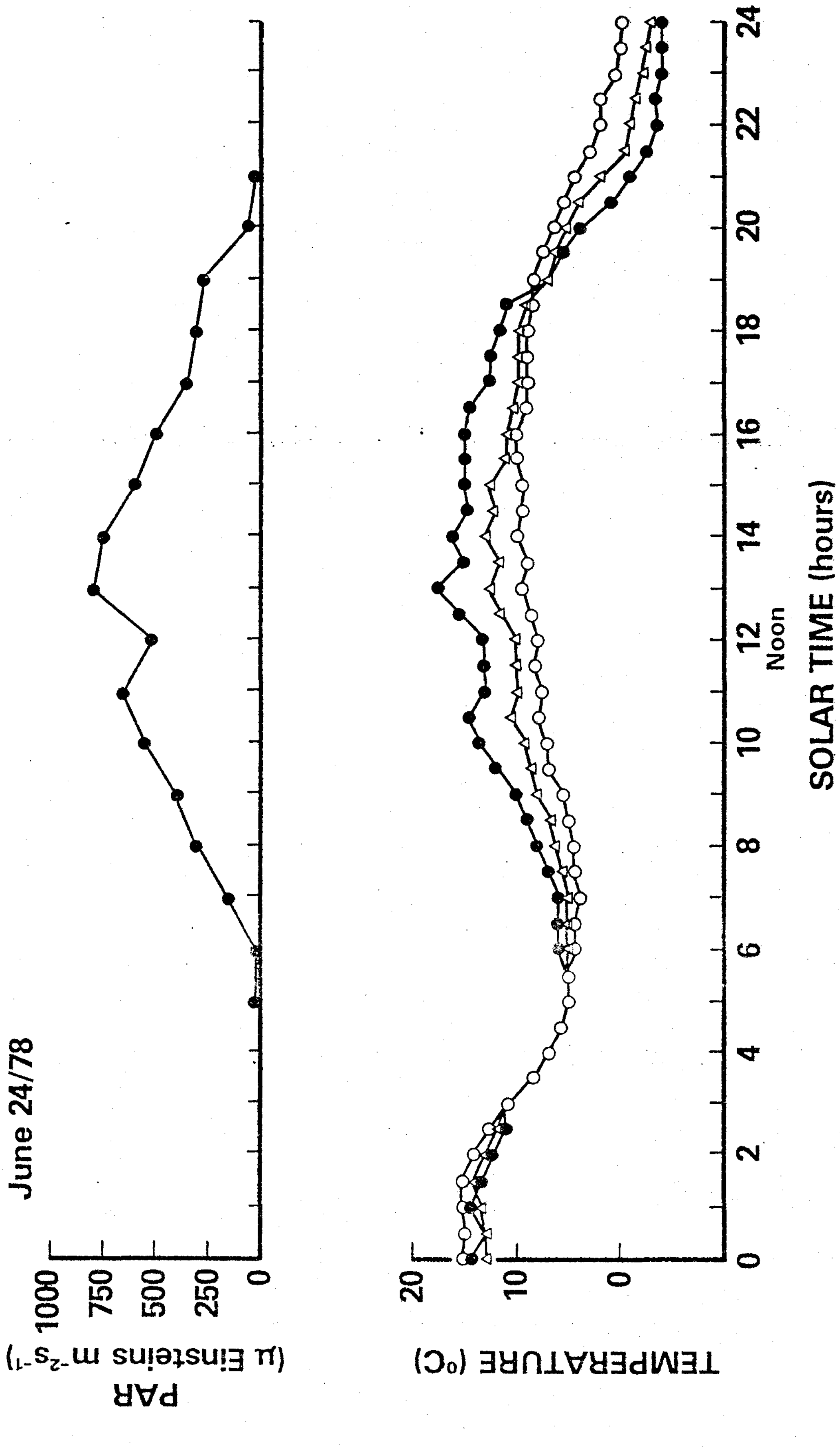
a maximum intensity of 800 μE $m^{-2}s^{-1}$, intensities greater than 500 μE $m^{-2}s^{-1}$ occur for only seven hours. The occurrence of cloudy days, often with intermittent rain, are associated with a southerly movement of cool air off Hudson Bay, and are of some ecological significance as it is often at this time the lichen flora is rehydrated, see section 3.2.3.

### 3.2.2 Temperature Data

The regional climatic data from Winisk and Trout Lake (Table I) shows favourable air temperatures for lichen growth occur from June to October. Diurnal air temperature fluctuations from $-3^{o}C$ at night to above $20^{o}C$ at mid-day (Fig. 13) occur as cold air masses move inland off Hudson Bay. Less severe diurnal fluctuations as in Fig. 14 occur when heavy night-time cloud cover maintained night air temperatures of $15^{o}C$, followed by cool day-time temperatures, of $15^{o}C$. When the weather eventually shifted to the north, air temperatures quickly dropped to $0^{o}C$. Several times throughout June and July 1978 this same pattern was repeated.

The high albedo of the light coloured lichen mat reduces temperature differences between the surface and air at 100 cm. On a warm day with clear skies the C. stellaris mat temperature reached $41^{o}C$, while air temperature was $21^{o}C$ (Fig. 13), a substantial $20^{o}C$ difference. During periods of heavy cloud cover temperature differences of $10^{o}C$ were recorded (Fig. 14). At night surface temperatures may drop to $-2^{o}C$ or $-3^{o}C$ while air temperature remains at $0^{o}C$. Overall the lichens inhabiting the surface experience a much more extreme temperature regime than air temperature readings alone would suggest.

Figure 14. Summer field data, June 24, 1978. Photosynthetically active radiation (PAR) plotted over course of a typical heavy overcast day with cool air moving in from the north. Temperature traces are averaged values for; air, taken at 100 cm above ground (○—○), *Cladonia rangiferina* thallus (△—△), and *Cladonia stellaris* thallus (●—●).

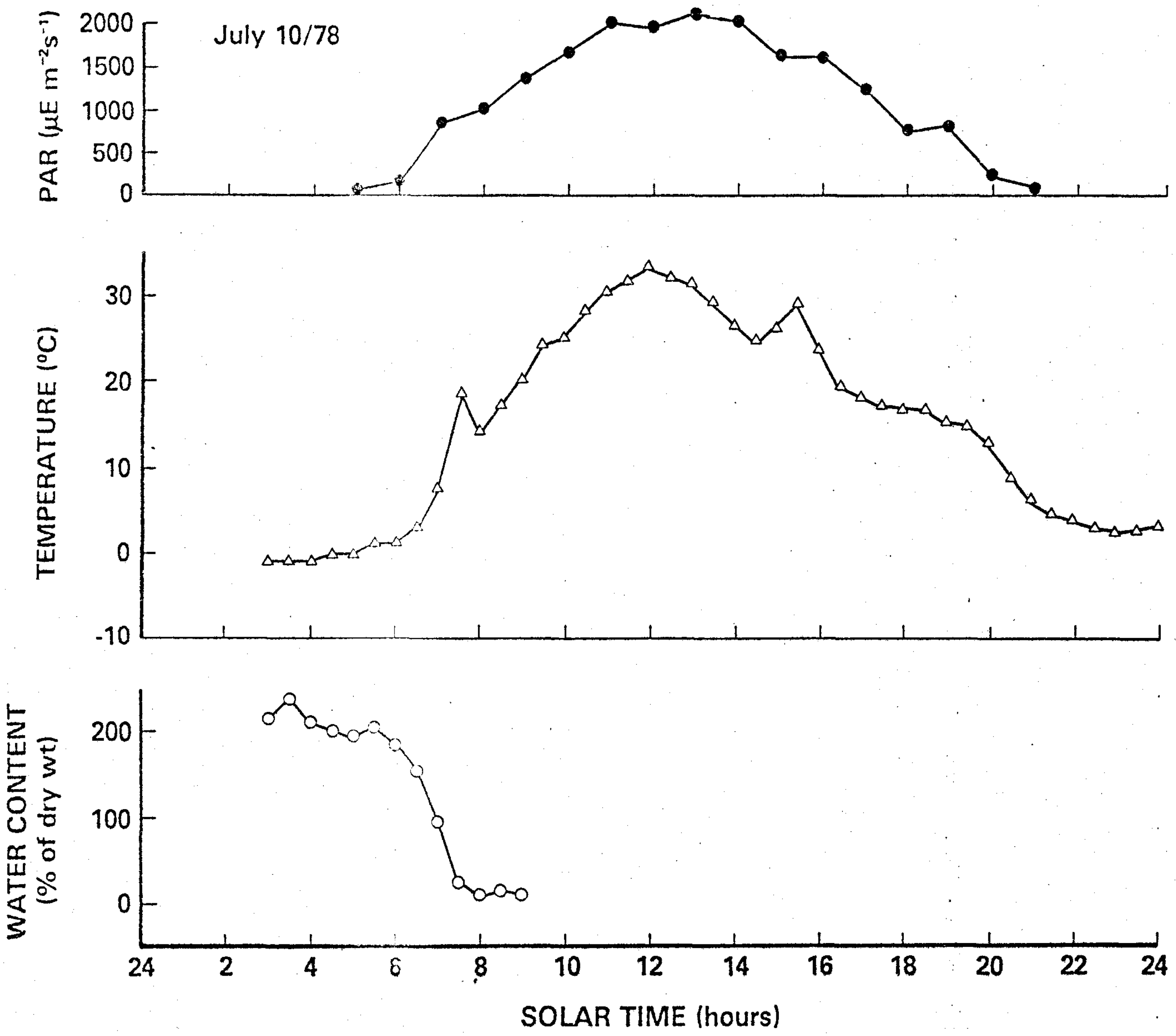

June 24/78
PAR
(μ Einsteins m-2s-1)
1000
750
500
250
0
TEMPERATURE (°C)
20
10
0
0
2
4
6
8
10
12
Noon
14
16
18
20
22
24
SOLAR TIME (hours)

Temperature differences occur between the microsites of C. stellaris and C. rangiferina. C. rangiferina never reaches the high temperatures experienced by C. stellaris, Fig. 13 shows C. stellaris reaches a maximum of 41°C while the C. rangiferina mat remains 5° to 10° cooler. From early morning when increased solar radiation begins to warm the environment C. rangiferina's thallus temperature remains intermediate to air at 100 cm, and the C. stellaris thallus, even on an overcast day, with the associated diffuse radiation, C. rangiferina's microhabitat remains cooler (Fig. 14). Night thallus temperatures are equivalent for both C. rangiferina and C. stellaris.

### 3.2.3 Thallus Drying Curves

Thallus moisture level is an important ecological parameter since the ability of lichens to carry on photosynthesis and respiration is entirely dependent on the level of moisture within the thallus (Hale, 1974). Photosynthetic and respiratory rates for a hydrated lichen thallus far exceed those of a dry thallus. Following overnight rainfall thallus hydration level reaches 225% moisture by weight (Fig. 15). With increasing light intensities at 600 hours surface temperatures rise rapidly from 0°C to 20°C by 800 hours, light intensity is now at 1000 $\mu E\ m^{-2}s^{-1}$, during this same two hour period there is a rapid loss of water from the lichen thalli resulting in air-dryness (10 to 20% moisture by weight). Consequently, only two hours existed when the lichen mat was hydrated and receiving sufficient solar energy to photosynthesize. For the remainder of the day, and indeed until the next wetting, metabolic activity would be restricted.

Figure 15. Summer field data, July 10, 1978, illustrating the thallus water content for *Cladonia rangiferina* and the coincidental light regime of photosynthetically active radiation (PAR), plus thallus temperature for *C. rangiferina*.


July 10/78
PAR (μE m$^{-2}$s$^{-1}$)
2000
1500
1000
500
0
TEMPERATURE (°C)
30
20
10
0
-10
WATER CONTENT
(% of dry wt)
200
100
0
24
2
4
6
8
10
12
14
16
18
20
22
24
SOLAR TIME (hours)

The period of saturation preceeding day light would presumably allow for respiration to proceed, however, as will be shown later, rates are very slow at these low temperatures.

Figure 16 shows a day of overcast skies with moderate light intensity, 750 $\mu$E $m^{-2}s^{-1}$ and air temperature around $10^{o}$C. Rehydration of C. rangiferina occurred with a brief rainfall at 500 hours, and during the course of the day a slow drying process proceeded until air dryness was achieved at 1500 hours. This day provided ten hours of suitable moisture, temperature, and light conditions for photosynthesis and respiration to proceed.

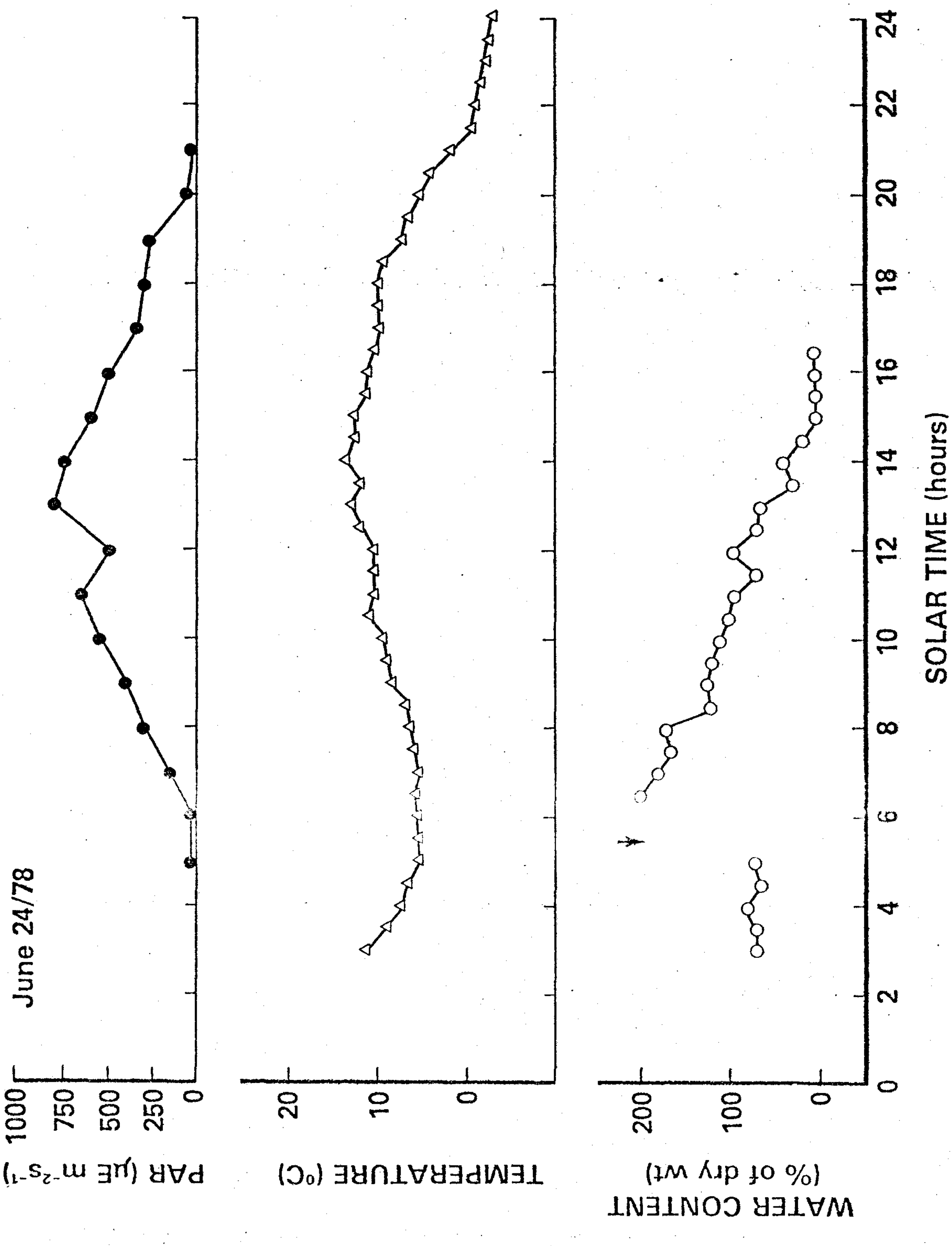
Periods of thallus hydration paired with favourable light and temperature for metabolic activity were an infrequent occurrence during the summer of 1978 at Hawley Lake. It is known lichens are capable of receiving moisture through dew formation and from high ambient humidity (Lange, Schulze, Kappen, Buschbom and Evenari, 1975), these sources did not provide significant rehydration of lichen thalli at Hawley Lake (see also Kershaw and Rouse, 1971a).

## 3.3 Experimental Data Matrix

### 3.3.1 Influence of light level on $CO_2$ gas exchange

Dark respiration rates are presented under the headings of moisture, temperature, seasonality and pretreatment. The net photosynthetic measurements are a function of approximately 5% algal biomass and are consequently dominated by fungal respiration even in the light, and it is assumed here that normal dark respiration rates prevail in the light.

Figure 16. Summer field data, June 24, 1978, illustrating the thallus water content for _Cladonia_ _rangiferina_ and the coincidental light regime of photosynthetically active radiation (PAR), plus thallus temperature for _C_. _rangiferina_. Arrow corresponds to the occurrence of rainfall.


June 24/78
PAR (μE m⁻²s⁻¹)
1000
750
500
250
0
TEMPERATURE (°C)
20
10
0
WATER CONTENT (% of dry wt)
200
100
0
0
2
4
6
8
10
12
14
16
18
20
22
24
SOLAR TIME (hours)

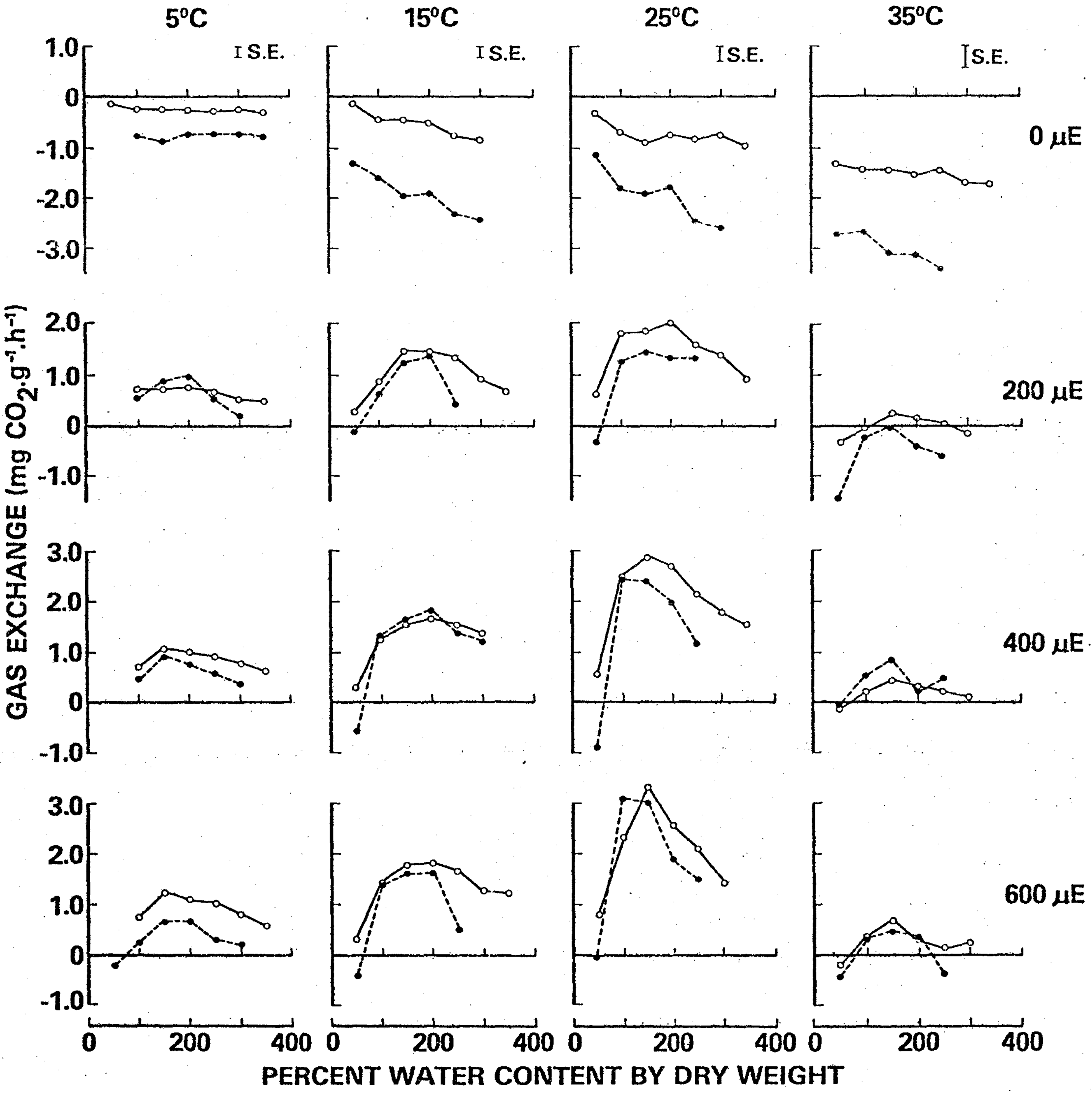
Net photosynthesis exhibits increasing levels of activity with increasing light intensity. At 200 μE $m^{-2}s^{-1}$, sufficient light energy is present to allow a positive net photosynthetic gain (Figs. 17, 18). An increase of the light intensity to 400 μE $m^{-2}s^{-1}$ results in a 25% to 50% greater $CO_2$ uptake at all experimental temperature and moisture levels (Figs. 17, 18). As experimental light intensity is further increased to 600 μE $m^{-2}s^{-1}$ there is only a slight additional increase in the rate of net photosynthesis, and since these rates lie within the standard error bars, the increases are not significant. A light saturation plateau therefore exists between 400 and 600 μE $m^{-2}s^{-1}$.

### 3.3.2 Influence of Thallus Moisture level on $CO_2$ gas exchange

Each of the 16 graphs in a data matrix is made up of a y-axis relating $CO_2$ fluxes and an x-axis, the percent water content of the lichen thallus by weight. At the onset of an experiment each lichen podetia is in a fully saturated state, containing a maximum of 300% to 400% water by weight. During the course of an experiment water is slowly lost from the thallus concluding with the lichen in an air dry state, the final moisture segment is from 0% to 50% water content by weight.

The response of dark respiration (0 μE $m^{-2}s^{-1}$) to thallus moisture shows a maximum $CO_2$ efflux at the initiation of an experiment when the lichen podetia are fully saturated, followed by a linear response of slightly lower $CO_2$ efflux, from 250% to 100% saturation. Below 100% saturation there is a rapid decline in activity concluding with a very slow respiration rate below 50% saturation. The response pattern of respiration rate to the level of thallus hydration is consistent for all

Figure 17. Physiological data matrix for fall (○—○) and spring (●--●) collections of *Cladonia rangiferina*. The response of dark respiration to varying temperature and thallus moisture content is illustrated in the first horizontal row of four graphs. The net photosynthetic response, illustrated in the remaining twelve graphs, expresses gas exchange rates under varying temperature, light level (microEinsteins metre$^{-2}$ second$^{-1}$, µE), and thallus moisture content. Rates of gas exchange are expressed as milligrams of Carbon dioxide gram$^{-1}$ hour$^{-1}$ (mg$CO_2$ gm$^{-1}$ h$^{-1}$) assimilated by the lichen thallus (positive rate) or lost from the thallus (negative rate). Standard Error bars depict the maximum value obtained at all light levels and thallus moisture levels for a single experimental temperature.


5°C
15°C
25°C
35°C
I S.E.
0 μE
200 μE
400 μE
600 μE
1.0
0
-1.0
-2.0
-3.0
2.0
3.0
GAS EXCHANGE (mg $CO_2$·g⁻¹.h⁻¹)
0
200
400
PERCENT WATER CONTENT BY DRY WEIGHT

experimental temperatures, light levels, seasonal collections, and pretreatment (see 0 μE $m^{-2}s^{-1}$, Figs. 17, 18).

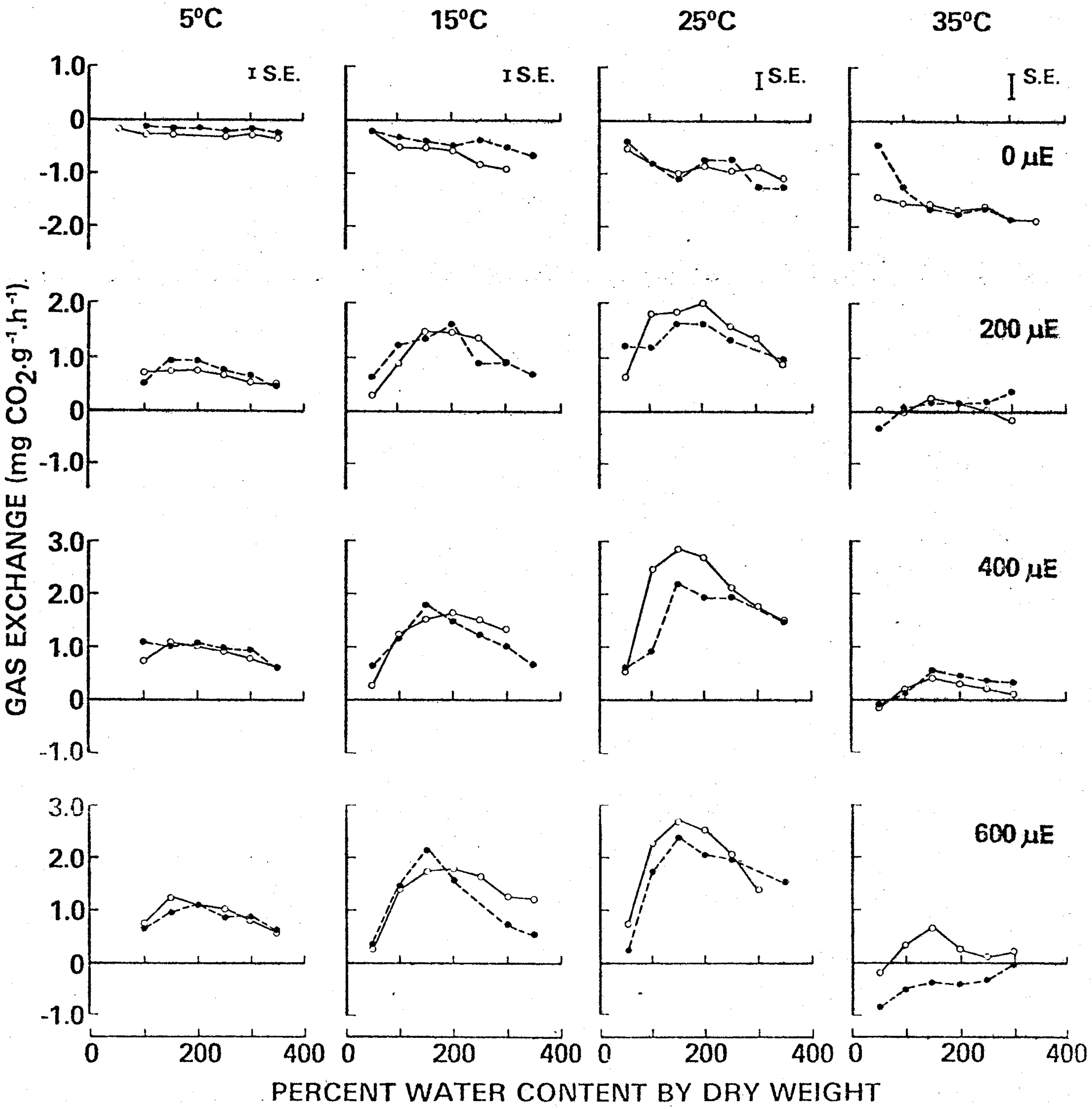
Maximum net photosynthetic activity is achieved at intermediate levels of thallus hydration of 100% to 200% saturation (Figs. 17, 18). At the wet end of the moisture axis, 300% to 400% saturation, gas exchange rate is only 40% to 50% of the maximum rate attained, at an experimental temperature of 35°C, this results in a negative $CO_2$ gas exchange rate. At the dry end of the moisture axis the lichen thallus enters into a metabolically inactive state, consequently gas exchange rates drop off from the maximum activity above 100% saturation to an often negative $CO_2$ gas exchange when completely air-dry, below 50% saturation (Figs. 17, 18).

Although the general net photosynthetic moisture response curve is consistent for all other experimental treatments the peaking of maximum rates between 100% to 200% saturation is most distinct under optimum conditions of temperature and light. Low temperature (5°C) or low light level (200 μE $m^{-2}s^{-1}$) causes a much more flattened moisture response curve.

### 3.3.3 Influence of temperature on $CO_2$ gas exchange

As temperature is increased from 5°C to 15°C dark respiration rates double (Fig. 17). A smaller 15% increase in respiration rates occurs as experimental temperature is increased from 15°C to 25°C or 25°C to 35°C. This suggests rate limiting influences are operating. The response of respiration to temperature was consistent regardless of experimental pretreatment, moisture level, or time of year when the lichen material was collected.

Figure 18. Physiological data matrix for the fall collection of *Cladonia rangiferina*. The two curves illustrate the gas exchange response for normal, cool stored fall material (○——○) and warmer than normal stored fall material (●---●). The response of dark respiration to varying temperature and thallus moisture content is illustrated in the first horizontal row of four graphs. The net photosynthetic response, illustrated in the remaining twelve graphs, expresses gas exchange rates under varying temperature, light intensity, and thallus moisture content. Standard Error bars depict the maximum value obtained at all light levels and thallus moisture levels for a single experimental temperature.


5°C
15°C
25°C
35°C
S.E.
0 µE
200 µE
400 µE
600 µE
1.0
0
-1.0
-2.0
2.0
3.0
GAS EXCHANGE (mg $CO_2 \cdot g^{-1} \cdot h^{-1}$)
0
200
400
PERCENT WATER CONTENT BY DRY WEIGHT

For net photosynthesis an increase of experimental temperature from 5°C to 15°C results in a 100% increase of gas exchange rates under optimum thallus moisture and high light intensity (Figs. 17, 18). At the dry or wet ends of the thallus moisture regime the effects of increased temperature are much less evident, this gives the moisture response curve a bell shape as rates at the intermediate moisture levels show proportionately greater rate increases. A closer examination of the 0% to 50% moisture segment reveals that as temperature is increased from 5°C to 15°C there is no change in gas exchange rates, the lichen is in a metabolically inactive state. At 25°C a 40% to 60% increase of maximum net photosynthetic rate occurs, also there is a further accentuation of the bell shaped curve as the extreme moisture levels, especially the dry end, again remain unaffected by temperature. A maximum net photosynthetic rate of 3.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ is recorded at 25°C under high light, 600 $\mu E$ $m^{-2} s^{-1}$, and intermediate moisture, 150% saturation (Fig. 17). At an experimental temperature of 35°C, net photosynthesis is drastically impaired, minimum gas exchange rates occur. A positive balance of $CO_2$ exchange is maintained at optimum levels of thallus hydration, however, excessive moisture or dryness leads to a net efflux of $CO_2$. Due to the apparent stressful nature of a 35°C experimental temperature, standard errors are large, and indeed the data exhibits such irregularities as maximum net photosynthetic rates when the thallus is fully saturated (see Fig. 18).

### 3.3.4 Influence of Seasonality on $CO_2$ Gas Exchange

Summer and fall data matricies for C. rangiferina are overlayed in Fig. 17. Dark respiration rates in the summer material are consistently higher at all experimental temperatures and all thallus moisture levels. The response pattern of respiration rate to thallus saturation, and to temperature, is identical in the two collections, but, in the summer material the rate of $CO_2$ efflux is doubled. Net photosynthetic rates of summer and fall material remain unchanged under all experimental light levels, moisture levels and temperatures when the standard error bars are applied to each point. This result was substantiated by a second full response matrix both for summer and fall material (see Fig. 18 and Table II).

### 3.3.5 Influence of storage temperature on $CO_2$ gas exchange

A portion of the lichen material returned in October, 1978 from Hawley Lake was stored at higher than normal fall temperatures. This was of some interest due to the disparity of summer and fall dark respiration rates, and would therefore expose any tendancy of C. rangiferina to revert back to a "summer state" in response to a temperature cue. The results show there is no significant change of dark respiration or net photosynthesis when fall lichen material is stored under summer-like temperatures (Fig. 18). This reverse storage format was repeated on the summer material by storage at colder than normal temperatures, again, no changes in the net photosynthetic or respiratory rates occurs (see Appendix Table II).

## 3.4 Heat Sensitivity Experiments

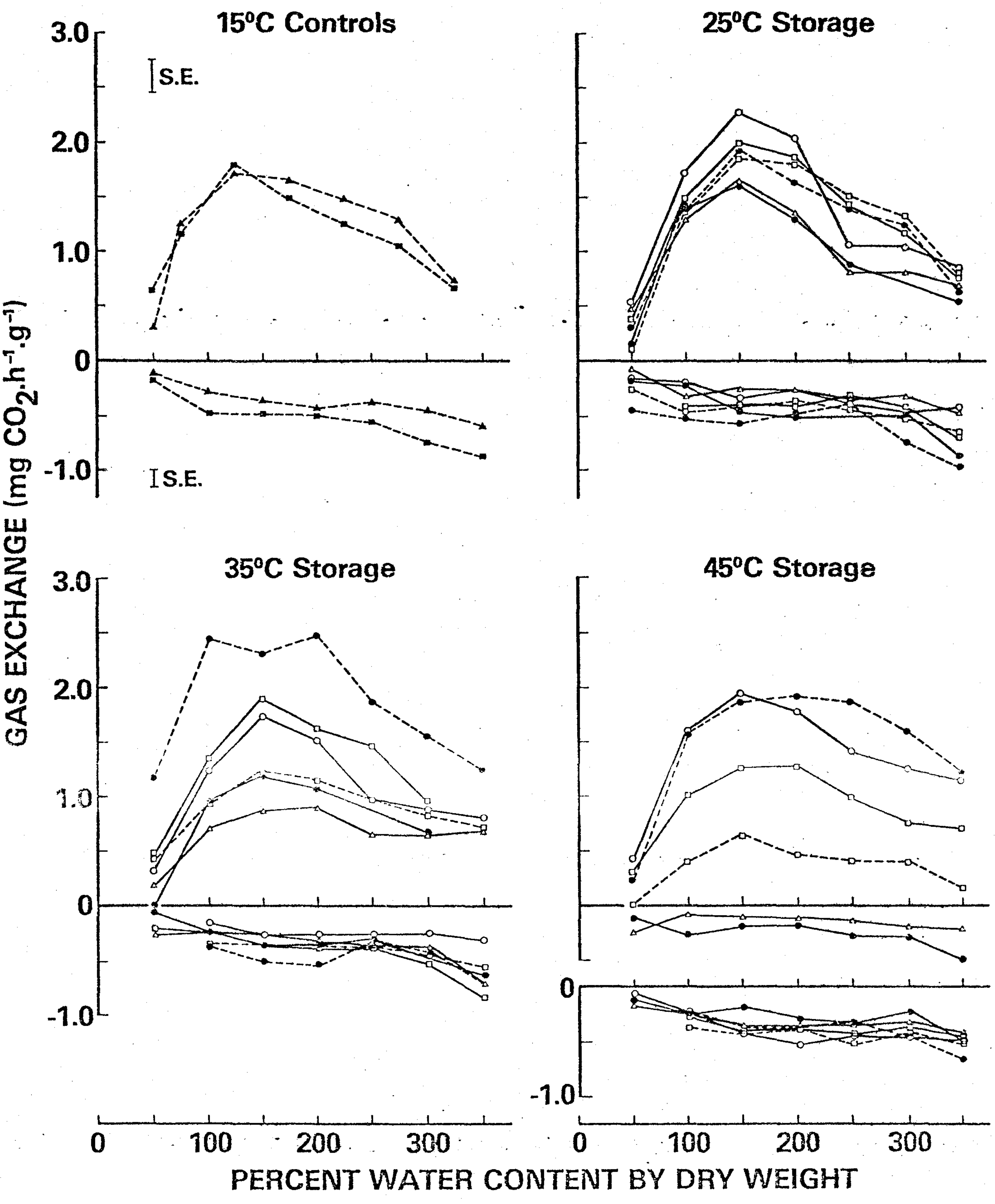
High environmental temperatures, similar to those recorded in the field for C. rangiferina, have been shown to inflict damage on photosynthesis, respiration, and nitrogen fixation in lichens (MacFarlane and Kershaw, 1978). Significantly, damage will occur in lichen thalli which are in an air-dry state, previously believed to be a resistent condition, and allowing survival through periods of drought and high temperature (Farrar, 1973; Lange, Schulze, Kappen, Buschloom and Evenair, 1975; Larcher, 1975; Raven, Evert and Curtis, 1975). Differences in the maximum temperatures recorded at the adjacent microsites of C. stellaris and C. rangiferina, and the marked disruption of net photosynthesis during experiments run at 35°C, indicated heat tolerance should be investigated.

The experimental heat treatment, as described in the Methods section, 2.2.4, follows a heat stress application schedule similar to previous experiments performed in the area of heat sensitivity (MacFarlane and Kershaw, 1978; MacFarlane and Kershaw, 1980a). The square wave application of potentially stressful temperatures, twelve hours of high heat stress, 25°C or 35°C or 45°C, followed by a twelve hour recovery period, corresponds to the natural environment of C. rangiferina in that these stressful temperatures may be realized at some point in the day.

### 3.4.1 Hawley Lake Heat Stress Experiments

The results of C. rangiferina collected at Hawley Lake in the fall of 1978 are presented in Fig. 19. Standard error bars represent the maximum value computed for either net photosynthesis or respiration over the entire experimental series. The material stored at 15°C, and referred to as controls, shows a maintenance of respiratory and net photosynthetic activity over the twenty-one day experimental period. This confirms that there is no effect resulting from simple deterioration during experimental

Figure 19. Heat Sensitivity in a fall collection of *Cladonia rangiferina* from Hawley Lake, Ontario. Net Photosynthesis and respiration rates are measures of the severity of thermal stress. Thallus replicates were stored air-dry at; 15°C (control), 25°C, 35°C and 45°C. The response to stress was monitored after; Day 1 (●- - -●), Day 2 (○——○), Day 4 (□——□), Day 7 (□- - -□), Day 14 (△——△), and Day 21 (●——●). Control replicates were monitored on Day 1 (■- - -■) and Day 21 (▲- - -▲).


15°C Controls
25°C Storage
35°C Storage
45°C Storage
S.E.
S.E.
3.0
2.0
1.0
0
-1.0
GAS EXCHANGE (mg $CO_2$.h$^{-1}$.g$^{-1}$)
0
100
200
300
PERCENT WATER CONTENT BY DRY WEIGHT

storage. Variations in net photosynthesis or respiration of heat stored material may then be taken as a function of stress temperature and duration of application.

The results of 45°C stored material (Fig. 19) show a progressive decline in net photosynthetic activity over the twenty-one day treatment period, while dark respiration rates remain unchanged. Initially, net photosynthetic rates are maintained at control levels, maximum rate following day 2 is 2.0 mg $CO_2$ $gm^{-1}$ $hr^{-1}$, following day 4 of 45°C heat application, a 35% reduction in maximum net photosynthetic rate occurs, at day 7 there is a 50% reduction and at day 14 no net gain of carbon is achieved by the lichen when in the light. A further week of 45°C heat application has no further effect. Net photosynthetic rates remain around -0.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Furthermore, the 45°C treatment results in a flattening of the net photosynthetic moisture response curve, and the distinct peaking as maximum net photosynthetic rates are reached over the intermediate hydration levels of 100 to 200 percent mositure is absent.

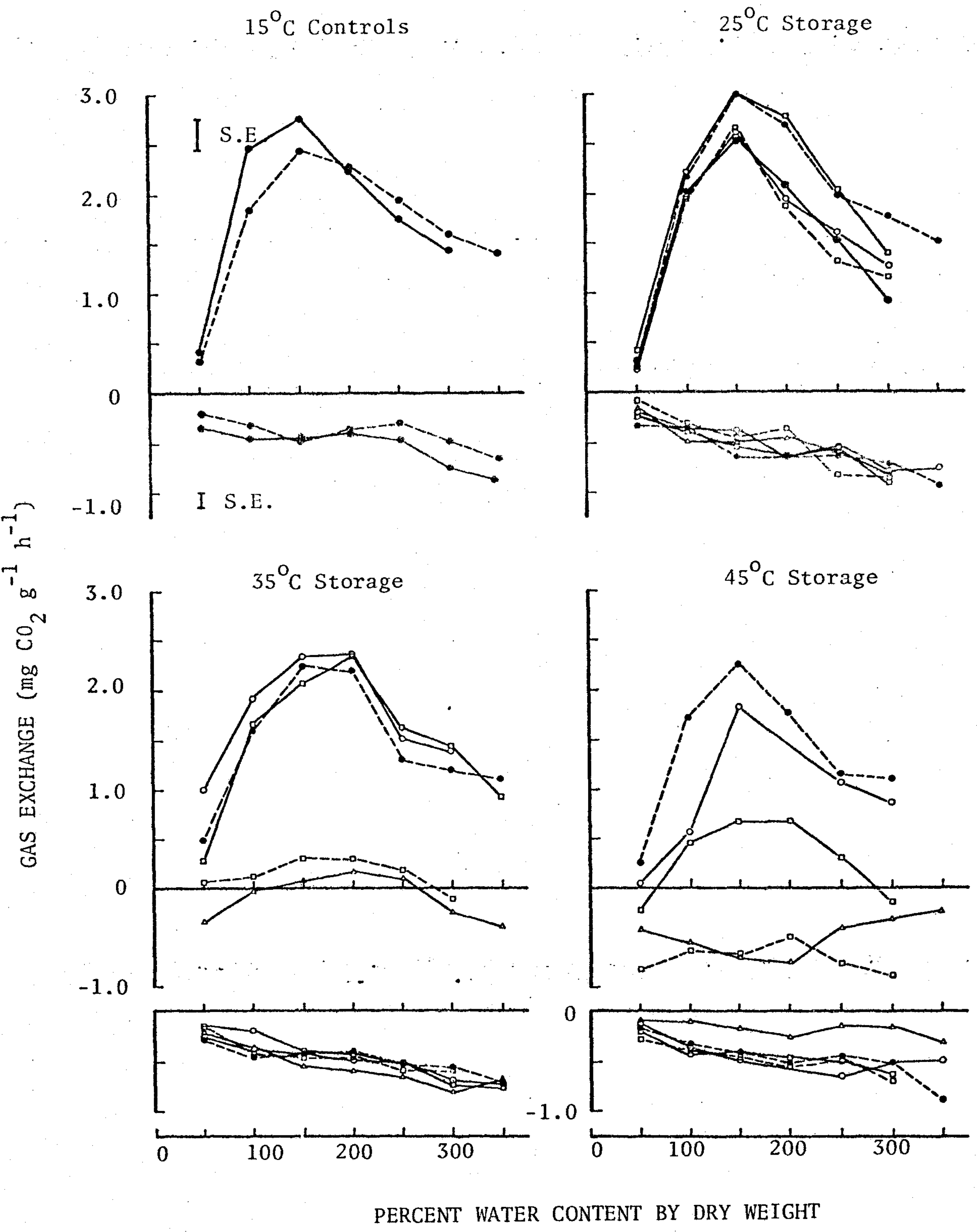
Material stored 1, 2, 4 and 7 days with a 25°C heat stress show a response consistent with control experiments, net photosynthetic rate is circa 2.0 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ and respiration rate is circa -0.4 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Slightly lower maximum rates of carbon uptake, 1.6 mg $CO_2$ $gm^{-1}$ $hr^{-1}$, follow 14 and 21 days of 25°C storage, within experimental error no change in net photosynthetic rates can be assumed. Heat stress of 35°C results in a decline of net photosynthetic rates intermediate to the 25°C and 45°C storage data, while dark respiration rates remain unaffected. Days 2 and 4 of 35°C heat treatment show net photosynthetic rates closely within the limits of the control rates. Day 1 exhibits an unusually high rate of carbon uptake, 2.5 mg $CO_2$ $gm^{-1}$ $hr^{-1}$, but similar to the maximum rate attained in day 2 of 25°C stored material, 2.3 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Following days 7 and 14 a reduction in the net photosynthetic capacity is visible, maximum rate is circa 1.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$, a 40% reduction from control rates. Day 21 shows a further reduction in activity as maximum rate is only 0.9 mg $CO_2$ $gm^{-1}$ $hr^{-1}$, a 55% reduction from controls.

Thus C. rangiferina collected in the early fall from Hawley Lake exhibits a marked reduction in net photosynthetic capacity after 21 days of 35°C and 45°C temperature storage, at the extreme temperature of 45°C this results in a negative balance of carbon exchange. Dark respiration rates are not influenced by 21 days of 45°C heat stress application. Controls at 15°C storage and 25°C heat treatment maintain net photosynthetic and respiratory rates over the 21 day experimental period.

### 3.4.2 Muskoka Region Heat Stress Experiments

Figure 20 represents the early spring response of a Muskoka population of C. rangiferina to heat stress. Over the 14 day experimental period, controls stored at 15°C show a maintenance of net photosynthesis, maximum rate is 2.7 mg $CO_2$ $gm^{-1}$ $hr^{-1}$, and respiration, at circa -0.5 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. After 1 and 2 days storage at 45°C, net photosynthesis maintains substantial activity, maximum rate is 2.0 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Following day 4 net photosynthetic rates at the wet and dry ends of the moisture axis do not compensate respiration, maximum rate achieved is

Figure 20. Heat Sensitivity in an early spring collection of *Cladonia rangiferina* from Muskoka region, Ontario. Net Photosynthesis and respiration rates are measures of the severity of thermal stress. Thallus replicates were stored air-dry at; 15°C (control), 25°C, 35°C, and 45°C. The response to stress was monitored after; Day 1 (●---●), Day 2 (○——○), Day 4 (□——□), Day 7 (□---□), and Day 14 (△——△). Control replicates were monitored on Day 1 (●---●) and Day 14 (●——●).

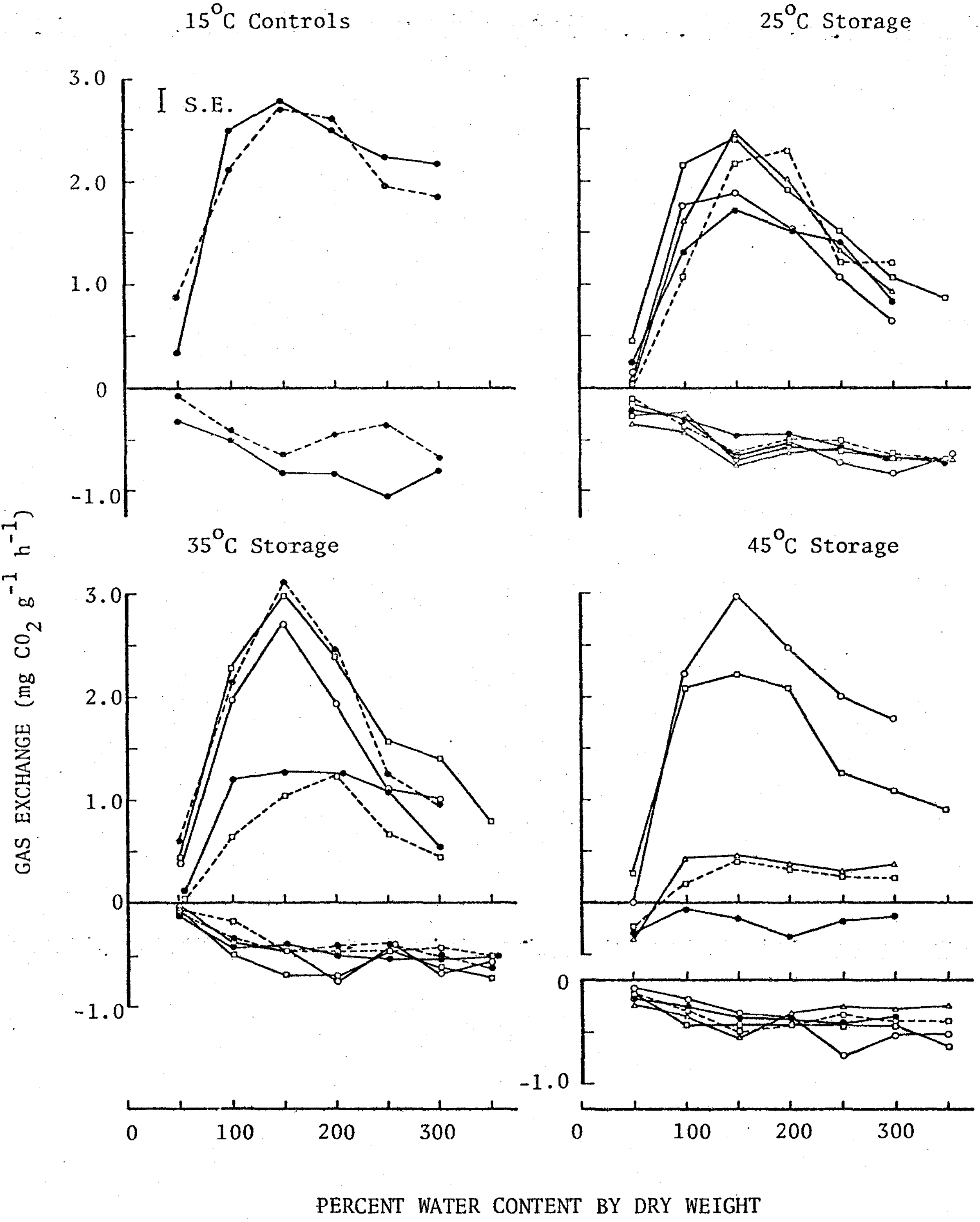

15°C Controls
25°C Storage
35°C Storage
45°C Storage
S.E
S.E.
3.0
2.0
1.0
0
-1.0
GAS EXCHANGE (mg CO$_2$ g$^{-1}$ h$^{-1}$)
0
100
200
300
PERCENT WATER CONTENT BY DRY WEIGHT

0.7 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Lichen material stored 7 and 14 days at 45°C shows only a carbon efflux when exposed to 400 μE $m^{-2}s^{-1}$, this shows photosynthesis has been completely eliminated with residual metabolic activity of largely fungal origin (MacFarlane and Kershaw, 1980a). Further evidence of the sensitivity of this collection of C. rangiferina to high temperature stress is the occurence of a reduction in dark respiration rates. Days 1 through 7 show rates of respiration consistent with controls, however, day 14 rates are only 50% of normal, maximum efflux being 0.25 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. It might also be added that following the normal twelve hour soak-up of material stored 14 days at 45°C the distilled water had taken on a marked colouration and distinctive odour evincive of the severe damage which had occurred.

No alteration of net photosynthetic rates occurs in 35°C heat treatment following days 1, 2 or 4, on day 7 maximum uptake falls to 0.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$, and a further week of 35°C heat application has little further effect. Respiration rates of 35°C stored material remain unaltered over the 14 day experimental period, circa 0.5 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ efflux. A 25°C heat stress causes no change in net photosynthesis or dark respiration over the 14 day experimental period.

Lichen material used in the second set of heat sensitivity experiments (Fig. 21) has experienced spring's warmer ambient temperatures in the month of May. Through the 21 day experimental period controls, and 25°C heat treated material, show consistent rates of net photosynthesis, maximum uptake is 2.8 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. The respiration rates of the controls and all treated material are maintained over the 21 day experimental period at circa 0.5 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ efflux. The effects

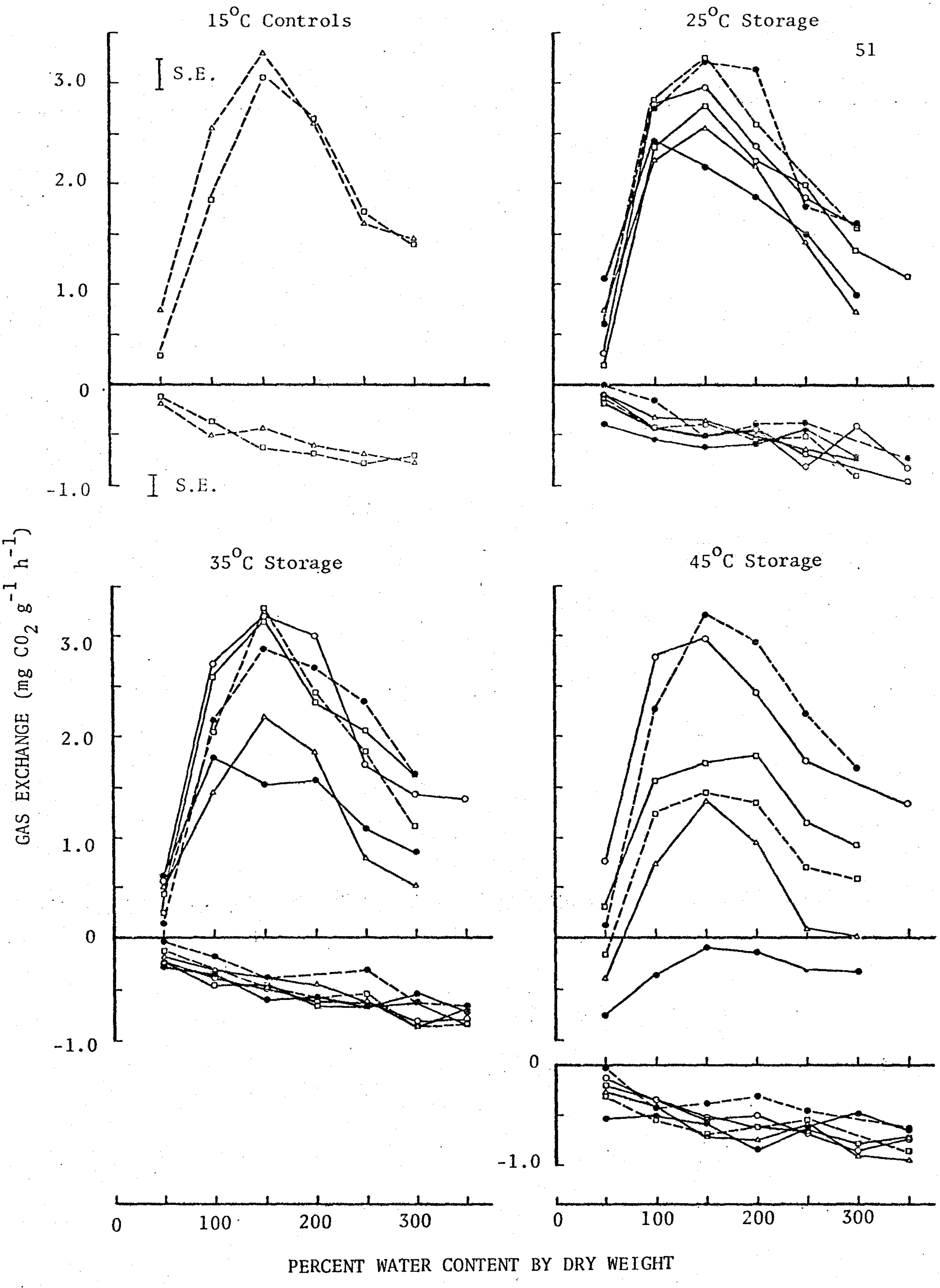
Figure 21. Heat Sensitivity in a late spring collection of *Cladonia rangiferina* from Muskoka region, Ontario. Net Photosynthesis and respiration rates are measures of the severity of thermal stress. Thallus replicates were stored air-dry at; 15°C (control), 25°C, 35°C and 45°C. The response to stress was monitored after; Day 1 (●- - -●), Day 2 (○——○), Day 4 (□——□), Day 7 (□- - -□), Day 14 (△——△), and Day 21 (●——●). Control replicates were monitored on Day 1 (●- - -●) and Day 21 (●——●).


15°C Controls
25°C Storage
35°C Storage
45°C Storage
S.E.
3.0
2.0
1.0
0
-1.0
GAS EXCHANGE (mg $CO_2$ $g^{-1}$ $h^{-1}$)
0
100
200
300
PERCENT WATER CONTENT BY DRY WEIGHT

of 45°C and 35°C heat storage are seen in reduced net photosynthesis. Following four days of 45°C stress net photosynthetic rates are little affected, maximum rate is 2.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$, three additional days of heat stress, day 7, shows a rapid decline in activity, maximum rate is 0.4 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Similar rates to day 7 occur on day 14, and material of day 21 shows further stress as net photosynthesis remains in a negative state of carbon exchange. The net photosynthetic response of material stressed at 35°C shows a degree of tolerance over the first four days, following day 7 however, maximum rates declined to 1.3 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. This level of activity remains through to 21 days of 35°C storage, and representes a stress response intermediate to a 45°C or 25°C heat stress.

In the final set of heat sensitivity experiments C. rangiferina which had been exposed to the Muskoka's summer regime was utilized (Fig. 22). The control material maintained metabolic rates after 21 days of storage, maximum net photosynthetic carbon uptake is 3.3 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ and dark respiration rate is circa -0.6 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. The progressive decline in net photosynthetic activity characteristic of 45°C treated material results in a 50% reduction of rates in days 4, 7 and 14 treatments, circa 1.5 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Day 21 has a further effect, with maximum rate now -0.1 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Lichen thalli stored at 35°C show reduced rates of net photosynthesis after 14 days of stress application, maximum rate is 2.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Day 21 shows further disruption of photosynthetic activity, maximum rate now at 1.8 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. Results of 25°C storage are variable maximum rates of net photosynthesis are between 2.5 to 3.3 mg $CO_2$ $gm^{-1}$ $hr^{-1}$, however, no severe reduction in rates occurs. Dark respiration in all treated material remains unaffected,

Figure 22. Heat Sensitivity in a summer collection of *Cladonia rangiferina* from Muskoka region, Ontario. Net Photosynthesis and respiration rates are measures of the severity of thermal stress. Thallus replicates were stored air-dry at: 15$^{\circ}$C (control), 25$^{\circ}$C, 35$^{\circ}$C and 45$^{\circ}$C. The response to stress was monitored after; Day 1 (●- - -●), Day 2 (○——○), Day 4 (□——□), Day 7 (□- - -□), Day 14 (△——△) and Day 21 (●——●). Control replicates were monitored on Day 3 (△- - -△) and Day 22 (□- - -□).


15°C Controls
25°C Storage
35°C Storage
45°C Storage
S.E.
S.E.
3.0
2.0
1.0
0
-1.0
GAS EXCHANGE (mg $CO_2$ $g^{-1}$ $h^{-1}$)
0
100
200
300
PERCENT WATER CONTENT BY DRY WEIGHT

rates are similar to the controls, carbon efflux circa 0.5 mg $CO_2$ $gm^{-1}$ $hr^{-1}$.

Considering the three preceeding sets of high heat sensitivity experiments some observations may be made regarding the differential response to heat stress as the season passes from spring into summer. Briefly, 45°C stored lichen material from an early spring collection exhibits a complete ellimination of positive net photosynthetic carbon uptake, after only seven days of treatment, in order to illicit a similar reduction of rates in the summer material twenty-one days of treatment are required. Also, it is only the spring material which shows a marked disruption of dark respiration after fourteen days of 45°C storage. Further examples of increased tolerance to heat stress may be seen by close examination of all net photosynthetic rates from 35°C and 45°C storage, April through May to July.

# 4. DISCUSSION

## Environmental Measures and the Gas Exchange Response of *Cladonia rangiferina*.

Temperature data of the winter environment at Hawley Lake shows the lack of low temperature stress which the lichen mat experiences. Snow accumulation of 80 cm, similar to Spruce Lichen Woodland at Thor Lake, North West Territories (Kershaw and Rouse, 1976), acts as an effective insulator against the very cold ambient air temperatures, circa -35°C. Similar capacity for snow insulation against cold air temperatures has been reported in studies on hibernating arctic mammals where winter survival is correlated with snow depth (Pruitt, 1970). Reduced snow depth recorded over the phase 1 and phase 2 recovery sites at Hawley Lake and also at Thor Lake suggest surface temperatures closer to the low winter air temperature due to the decreased insulating layer. Furthermore, as snow in the spring contributes to the water content of the soil the large accummulation within Spruce Lichen Woodland results in a higher soil water status with subsequent amelioration of high surface temperatures by an increased latent heat flux (Kershaw and Rouse, 1976).

Summer temperature recordings from Hawley Lake show that *C. rangiferina* experiences consistently cooler temperatures than the adjacent carpet of *C. stellaris*. Potentially, it is the avoidance of stressful temperatures which restricts *C. rangiferina* to its shrub-hummock association. This may be further substantiated by the additional habitat of C. rangiferina which is often found growing in the shade beneath the lower boughs of Spruce. MacFarlane and Kershaw (1980a) give the ecological definition of heat stress and show how slightly cooler temperatures may influence C. rangiferina's distribution. "Even if death does not result directly from the stress and even if recovery is possible the resultant reduction of competitive ability sequentially integrated over a field season, will lead to the potential elimination of such non-adapted species from such a stressful environment."

The data for thallus drying curves for the summer field environment are given in Figs. 15, 16. These show when C. rangiferina is hydrated there are a number of additional features in the prevailing regime of temperature and light which significantly affect rates of photosynthesis and respiration. As seen during mid-day rain shower activity, once hydrated C. rangiferina's capacity to retain water is quite poor (Table IV). Rapid dehydration may be attributed to the very open branching of the thallus (Figs. 7, 9), the elevated position of clones on shrub hummocks providing greater air circulation (Fig. 8), and the lack of a fully developed outer cortex which might inhibit water diffusion (Thomson, 1967). Hydration of C. rangiferina occurs over longer periods with rainfall at night, and Figure 15 shows dark respiration occurring during the night with a very low thallus temperature of $0^{o}C$, followed by photosynthesis in the early morning at temperatures ranging from $3^{o}C$ to $20^{o}C$ and a light regime of up to 1000 $\mu E\ m^{-2}s^{-1}$. In this instance only two hours were available for positive assimilation before it was eliminated by the rapid drying of the lichen thallus. Net assimilation in fact, ceased prior to full light intensities and elevated surface temperatures. Occasionally extended periods of hydration, and thus metabolic activity, occur when the sun is shaded by clouds, field data of June 24, 1978 (Fig. 16) shows that as the thallus slowly dried temperature and light intensity respectively changed from 6°C to 13°C and 200 µE $m^{-2}s^{-1}$ to 750 µE $m^{-2}s^{-1}$, consequently net positive assimilation of carbon could occur for eight hours. These observations show that for _C_. _rangiferina_ periods of thallus hydration are an irregular occurrence largely dependent on rainfall and, furthermore during any _single metabolically active period_ temperature may vary from below 0°C up to 20°C and light level from 0 µE $m^{-2}s^{-1}$ up to 1000 µE $m^{-2}s^{-1}$. Consequently the metabolic adjustment of _C_. _rangiferina_ must include the utilization of a wide range of _interacting_ temperatures, light levels, and levels of thallus hydration.

Previous experimental work on _C_. _rangiferina_ show very low rates of net photosynthetic activity, Bliss and Hadley (1964) give maximum rates of 0.38 mg $CO_2$ $gm^{-1}$ $hr^{1}$ and Adams (1971 a, b) gives maximum rates of 0.6 mg $CO_2$ $gm^{-1}$ $hr^{1}$. Alternate experimental techniques including extremely high light intensities and no control over what portion of the podetia is used might account for these unusually low rates. More recent work by Lechowicz and Adams (1974b) show similar net photosynthetic rates to this study, with maximum rates of 3.0 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ even with the use of intact lichen mat and a flow-through infra-red gas analysis experimental system. Prior to the introduction of the closed cuvette system developed by Larson and Kershaw (1975a) most net photosynthetic analysis used the flow system with infra-red gas analysis. Several problems arise when using the flow system, such as; substantial error, as it is extremely difficult to accurately control the gas flow which subsequently will directly affect the gas exchange rates which are computed; also there is not the same degree of control over experimental material, as one replicate must constitute around 30 gms of lichen; and long tedious experiments mean it is impossible to achieve complete multivariate analysis on a seasonal basis which has lead some workers to look at net photosynthetic rates in saturated lichen thalli only, an unsatisfactory approach given the moisture response curve of C. rangiferina. By using the closed cuvette system our multivariate data is replicated and shows tight experimental control, and it may be generated on a monthly basis to make definitive statements regarding seasonal changes in the gas exchange response. Furthermore, when environmental conditions are maximal net photosynthetic rates of 9.0 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ have been shown in Peltigera canina var. praetextata (MacFarlane and Kershaw, 1980a) and so the very low reported net photosynthetic rates previously considered characteristic of lichens is not true.

Thallus hydration is essential to the expression of metabolic activity as shown in Figures 18 and 19, and each data matrix consists of several graphs which plot gas exchange rate against thallus hydration level. A three to four fold weight increase at maximum experimental saturation is consistent with previous experimental work (Adams, 1971a), but, inconsistent with the field results where maximum hydration reaches 225% water content by weight (Figs. 15, 16). The complete immersion of experimental replicates in distilled water does not correspond to normal rehydration by rainfall in the field, however, during the period of snowmelt higher saturation levels may occur as the lichen mat is fully inundated. Net photosynthetic rates at full experimental saturation (300% to 400% water by weight) are somewhat depressed, but, even at less than optimum temperature and light level a positive assimilation rate is maintained. The stability of net photosynthetic rates irrespective of temperature and light levels is remarkable, for example, as light level within a single temperature segment is increased from 200 μE $m^{-2}s^{-1}$ to 600 μE $m^{-2}s^{-1}$ there is no increase in the rate of $CO_2$ uptake and this is true for a wide range of temperatures. This is interpreted as a result of excess water which impedes gas exchange (Hale, 1974) and also screens incoming radiation (Rundel, 1972). However, as the field data show these high levels of thallus saturation never occur and accordingly are outside the necessary range of adaptation.

Optimum rates of net photosynthesis occur around 100% to 200% water content by weight (Figs. 18, 19) giving the moisture response curve a distinctive peak as rates lag behind in the saturated or dry thallus. Adams (1971 a, b) gives an identical moisture response curve. To describe *C. rangiferina*'s moisture response as an adaptation to a dry environment as has frequently been done previously for other lichen species with a similar response curve (Kershaw, 1972; Harris, 1976) is not necessarily correct. For example, Larson and Kershaw (1975 b, c) working with *Alectoria ochroleuca* and *Cetraria nivalis*, both from xeric environments, have reported a flat moisture response curve. Similarly, *Stereocaulon paschale* (L.) Hoffm. from open Spruce Lichen Woodland in the Northwest Territories has a linear moisture response from thallus saturation to very near air-dryness (Kershaw and Smith, 1978). Conversely, looking at two lichen species from the wet-mesic habitat of dense, closed-canopy Spruce Moss Woodland in northern Ontario: *Peltigera scabrosa* Th.Fr. shows a distinctly peaked moisture response curve with optimum net photosynthetic rates at intermediate thallus hydration levels while *Peltigera aphthosa* (L.) Willd. shows a flat moisture response curve (MacFarlane and

Kershaw, 1980b). Furthermore, Peltigera canina var. praetextata Hue. and Peltigera canina var. rufescens (Weis.) Mudd. both found growing in central and southern Ontario each possess distinctly peaked net photosynthetic moisture response curves with severely reduced rates at full thallus saturation, and yet P. canina var. praetextata is only found inhabiting mesic deciduous woodland while P. canina var. rufescens grows in the xeric habitat of open roadsides (MacFarlane, 1979). Clearly optimum net photosynthetic rates at low or high moisture levels does not necessarily correspond with the moisture regime of the lichen's habitat. Rather, C. rangiferina shows optimum net photosynthetic rates at levels of hydration which were most frequently recorded in the field. This hypothesis of maximal activity at normal field level of hydration was also suggested by Larson (1975).

At low moisture levels (i.e. 0% to 50% moisture segment) there is a rapid transition from maximum net photosynthetic rates to metabolic inactivity. The passive loss of moisture and subsequent low gas exchange rates in C. rangiferina is a trait of poikiohydric organisms including lichens (Ahmadjian and Hale, 1973) and mosses (Busby and Whitfield, 1978; Oechel and Collins, 1976). This may be related to waters essential role in plant metabolism including; respiration, photosynthesis, protein synthesis, nucleic acid synthesis and macroergic combinations (Blum, 1973). Further, the shut down of metabolic activity can be seen as important to survival through periods of stress (Levitt, 1972).

The net photosynthetic response to temperature is a step-like increase in assimilation rate passing from 5°C to 15°C and then to 25°C. At 35°C net photosynthetic rates drop to below the 5°C response and compare with the high temperature compensation point of 32.5°C to 35°C shown by Adams (1971a). This obviously stressful temperature may result in a marked decline of net photosynthetic rate during a single experiment (see for example Fig. 19, 200 $\mu$E $m^{-2}s^{-1}$ and 600 $\mu$E $m^{-2}s^{-1}$). At this experimental temperature the normal net photosynthetic response pattern to moisture and light disappear and the resultant response curve suggests that damage is occuring.

This net photosynthetic response to 35°C, as well as the field data which shows the hydrated thallus never experiences temperatures greater than 20°C to 25°C, emphasises the tremendous importance of temperature to lichen ecology (MacFarlane and Kershaw, 1980a; Levitt, 1972). The experimental data shows Cladonia rangiferina has an optimum temperature for net photosynthesis of 25°C with rates increasing from circa 1 mg $CO_2$ $gm^{-1}hr^{-1}$ at 5°C up to 3.2 mg $CO_2$ $gm^{-1}hr^{-1}$ at 25°C. Field data in contrast, however, shows most net photosynthetic activity occurs at 5°C to 15°C and rarely if ever is 25°C experienced. Consequently, the temperature optima which has previously been correlated with field environment temperatures (Adams, 1971a) does not appear to apply to C. rangiferina, nor does an extremely broad temperature optima exist even though the field drying curves have shown that a range of temperatures are experienced during each period of rehydration. The environmental data base is, however, restricted to a single field season which may have been abnormally cool (Kershaw, personal communication). Despite this potential data limitation here, it is often difficult to fully equate experimental temperature optima with realistic field optimal temperatures. The data here is no exception.

Cladonia rangiferina is light saturated at between 400 μE $m^{-2}s^{-1}$ and 600 μE $m^{-2}s^{-1}$ with substantial activity being maintained at 200 μE $m^{-2}s^{-1}$, this finding is closely similar to that of Lechowicz and Adams (1974b). Lichens are generally saturated at quite low light intensities and are often able to maintain near optimal rates even at 150 μE $m^{-2}s^{-1}$. This seems a normal adaptive strategy of a lichen which is dependent on moisture for its metabolic activity, but, equally rapidly dries under high levels of illumination. This is exemplified, for example, in the drying curves for C. rangiferina where light intensities above 750 μE $m^{-2}s^{-1}$ were rarely experienced and under these conditions the thallus was completely air-dry.

Hale (1974) has suggested a linear relation between increasing respiration rate and thallus water content. C. rangiferina, however, shows that the maximum rates at full saturation fall off slightly, to a stable carbon efflux between 250% to 100% water content by weight and then near air-dryness the rates fall off still further into metabolic inactivity. This three stage response of dark respiration suggests the internal environment of the lichen thallus may be stabilized over the intermediate moisture levels or that respiration has a broad response to ambient moisture recalling that field saturation does not exceed 225% water by weight. Absolute rates of dark respiration from C. rangiferina fall within the range reported for other lichens (Ahmadjian and Hale, 1973).

Photosynthetic acclimation shown in many lichens (Carstairs and Oechel, 1978; Kershaw, 1977 a,b; Kershaw and Smith, 1978; Larson, 1980) was not evident in the net photosynthetic response matrix of C. rangiferina from Hawley Lake (Fig. 18). Nor could changes which might be considered as acclimation be induced by colder than normal storage of summer material

(Table II) or by warmer than normal storage of fall material (Fig. 19). Consequently, photosynthetic acclimation can not be considered a strategy possessed by all lichens as suggested by Larson and Kershaw (1975d). Although the ability to acclimate photosynthetic temperature optima may be advantagous in some environmental situations C. rangiferina is a case where temperature and light, the two parameters most often involved in acclimation (Troughton, 1975) are highly variable during periods of metabolic activity. Consequently, no environmental pattern exists to which metabolic activity can adjust and a broad amplitude of response on a continuous basis offers a more attractive alternative strategy. It is possible that photosynthetic acclimation is a quite restricted strategy in lichens, perhaps to those species where environmental conditions are not fluctuating on an hour to hour basis. In C. rangiferina it would seem the gains from continually shifting the net photosynthetic optima are outweighed by a broad response which achieves substantial activity at 5°C in the low light of the early morning followed in two hours by continued activity at 20°C under moderately high light.

Winter hardening, brought on by colder ambient temperatures and changes of insolation density, duration and quality (Salisbury and Ross, 1969) has been shown in numerous higher plants and recently in some lichens (Levitt, 1972; Kershaw, 1977a, b; Larson, 1980). Hardening marks the onset of an extended cold period where growth and development cease, tolerance of this stressful period is best afforded by dormancy and indeed an inverse relationship between cold temperature tolerance and respiration rate has been shown (Levitt, 1972). Winter hardening in C. rangiferina can be seen as a reduction of the dark respiration rates in late September when temperature and light have changed from the summer regime (Fig. 18). In lichens this is the first time respiration changes have been shown as a winter hardening response (Tegler and Kershaw, 1980b) though it is a typical situation of higher plants (Levitt, 1972). Larson (personal communication) has examined a winter hardening response in the lichen genus Umbilicaria and reduced respiration rate were characteristic. The significance of this winter hardening response is difficult to interpret: However, decreased respiration rate may occur due to protoplasmic stiffening which reduces gas and water diffusion and further may be due to a complete redistribtion of photosynthetic products away from respiration which might slowly depleat non-replenishable reserves over the winter period (Levitt, 1972). In summary, despite the snow cover which affords some protection for C. rangiferina, winter hardening occurs. This points to the potential frost stress which may occur during September and October or April and May when no snow is present and temperatures can be below 0°C.

## 4.2 High Heat Tolerance

Within Spruce Lichen Woodland at Hawley Lake summer is dominated by warm dry weather and the cold season persists for a greater part of the year. As a result, C. rangiferina is most frequently in a dehydrated state. This accounts for the slow growth rates reported in Cladonia rangiferina of similar habitats, Scotter (1963) recorded a 4 mm linear growth rate per year in a Canadian sub-arctic population, Pegau (1968) 5 mm to 6 mm per year in Alaska and in what Lindsay (1975) referred to as a "favourable antarctic environment because of abundant available moisture" annual length increase was 5 mm or a 5% to 6% weight increase.

During these extensive periods of dehydration *Cladonia rangiferina* has to survive periods of thermal stress which are unrelieved by evaporative cooling (MacFarlane and Kershaw, 1980a). Heat sensitivity experiments show that *C. rangiferina* is stressed after four days of exposure to 35°C and that a 45°C stress completely eliminates positive net photosynthesis after fourteen days (Fig. 19). This degree of sensitivity certainly restricts *C. rangiferina* to the ammeliorated thermal regime of *mature* Spruce Lichen Woodland as surface temperatures of recently burnt woodland have been shown to exceed 50°C (Kershaw, Rouse, Bunting, 1973). Heat sensitivity may also be a determining factor in the distinctive *C. rangiferina* - shrub association as this niche has consistently cooler temperatures than the adjacent *C. stellaris* mat, much like the thermally determined distribution reported for *Peltigera canina* var. *praetextatata* and *P. canina* var. *rufescens* (MacFarlane, 1979). Unfortunately the experimental method, which applies stressful temperatures in 12 hour doses, limits the extent to which data may be compared with field temperatures which do not follow the same square wave function.

Temperature acclimation of higher, and lower plants has been shown as increased heat tolerance (Alexandrov, Lomaquin, and Feldman, 1970; Lange, 1955). A Muskoka population of *Cladonia rangiferina* was examined from early spring into summer for changes in heat tolerance, mean monthly air temperatures during this period increased from 3.3°C to 17.9°C with a maximum recorded value of 24.8°C in July (Table III) and temperatures of *C. rangiferina* inhabiting granitic outcrops would be considerably higher (Geiger, 1971). The experimental results (Figs. 20, 21, 22) show that in early spring the lichen is easily stressed. After seven days of 35°C storage photosynthesis barely compensates respiration, whereas material collected in May and exposed to the same stress has a net photosynthetic rate of 1.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. The July collection with a further increase of net photosynthetic rate to 2.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ after 7 days of 35°C stress points to a 10°C increase of tolerance to temperature stress during the summer months (Tegler and Kershaw, 1980a). It seems probable that the Hawley Lake population of Cladonia rangiferina will also have seasonal changes in heat stress tolerance as indeed was demonstrated with the winter hardening response (Fig. 17).

In summary the response matrix of Cladonia rangiferina at Hawley Lake agrees well with the concept of the ameliorated environment of Spruce Lichen Woodland as proposed by Kershaw (1977c). It remains to contrast the response matrix of Cladonia stellaris with these current findings.

## 5. SUMMARY

1) The Winter Environmental complex of C. rangiferina at Hawley Lake, Ontario was defined in terms of temperature, light and snow depth. A short solar day, eight hours, and low light intensities, 500 μE $m^{-2}s^{-1}$ maximum, accounted for low ambient air temperatures, circa -35°C. However, a thick snow blanket, 85 cm, acted to insulate the lichen mat, thallus temperatures remained at only 2°C to 3°C below zero.

2) The Summer Environmental complex of C. rangiferina at Hawley Lake, Ontario was best defined by dividing data into periods of thallus hydration (metabolically active) and thallus dehydration. During periods of rainfall thalli reached 200% moisture content by weight, and experienced temperatures ranging from -5°C to 25°C and light level between 0 μE $m^{-2}s^{-1}$ and 1000 μE $m^{-2}s^{-1}$. The dehydrated thallus experienced more intense values of temperature up to 35°C, and light levels of up to 2100 μE $m^{-2}s^{-1}$. Additional data from the open C. stellaris mat showed consistently higher temperatures, the difference ranging from 5°C to 10°C under intense insolation (above 1000 μE $m^{-2}s^{-1}$) and 2°C to 3°C under moderate insolation (500 μE $m^{-2}s^{-1}$ to 1000 μE $m^{-2}s^{-1}$).

3) An experimentally derived gas exchange response matrix was generated for C. rangiferina collected in summer from Hawley Lake, Ontario. A broad amplitude of tolerance to thallus hydration, light level, and temperature was discerned. Maximum net photosynthetic activity of 3.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ occurred at intermediate thallus

moisture, 25$^{o}$C temperature and 600 μE m$^{-2}$s$^{-1}$. Light saturation was determined to be between 400 μE m$^{-2}$s$^{-1}$ and 600 μE m$^{-2}$s$^{-1}$ though substantial net photosynthetic activity was maintained at 200 μE m$^{-2}$s$^{-1}$. Lower temperatures of 15$^{o}$C and 5$^{o}$C ellicited a step-like decline in net photosynthetic activity, though a positive rate of 1.0 mg $CO_2$ gm$^{-1}$ hr$^{-1}$ was maintained at 5$^{o}$C and 200 μE m$^{-2}$s$^{-1}$. A 35$^{o}$C experimental temperature evoked an erratic net photosynthetic response and because of the field environment data was deemed outside the necessary range of adaptation for the hydrated thallus. Dark respiration rates show a three stage response to thallus hydration level. Maximum rates are achieved at saturation, while a stable $CO_2$ efflux occurs over intermediate moisture levels, and thallus drying causes metabolic inactivity.

4) The gas exchange response matrix for C. rangiferina collected in the fall from Hawley Lake, Ontario was idential with the summer matrix, with the exception of the respiration response. In the fall response matrix dark respiration rates were reduced by 50%, though the response to thallus moisture content, and temperature remained consistent with summer material. This latter metabolic shift was interpreted as a winter hardening response to assist survival through the extended cold period. Alternate storage of fall material at summer-like conditions evoke no alternate response.

5) Heat Sensitivity experiments on a fall collection of C. rangiferina from Hawley Lake, showed that after one week of 35$^{o}$C heat stress net photosynthetic rates were reduced to 1.2 mg $CO_2$ gm$^{-1}$ hr$^{-1}$. A 45$^{o}$C heat

stress resulted in the elimination of positive $CO_2$ assimilation after 14 days. These results suggest the restriction of this species to mature Spruce Lichen Woodland as a result of its poor heat tolerance. Further speculation suggest the temperature differences recorded at the adjacent microsites of C. rangiferina and C. stellaris restrict C. rangiferina from the open lichen mat with its more severe temperatures.

6) A series of Heat Sensitivity Experiments on a Muskoka population of C. rangiferina collected in April, May and July show a significant improvement in heat tolerance from spring to summer. Net photosynthetic results following seven days of 35°C stress left April material barely compensating respiration whilst in summer rates were 2.2 mg $CO_2$ $gm^{-1}$ $hr^{-1}$. A 45°C heat stress completely eliminated photosynthetic activity of spring material in seven days and even disrupted the more heat tolerant dark respiration as seen by reduced rates after fourteen days of treatment. Summer rates with a 45°C stress were 1.4 mg $CO_2$ $gm^{-1}$ $hr^{-1}$ net photosynthetic uptake after seven days of treatment and dark respiration was not affected even following twenty-one days of heat stress.

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## 7. APPENDIX

### TABLE I

[1]Monthly Temperature and Precipitation Data for 1974, from two Meteorlogical Stations close to Hawley Lake

| | | [2]Temperature (°C) | | | Precipitation (cm) | |
|---|---|---|---|---|---|---|
| | | Monthly Maximum | Monthly Minimum | Daily Average | Total | Accumulated Snow |
| Jan. | Trout Lake | -23.4 | -33.6 | -28.5 | 1.3 | 60.0 |
| | Winisk | -26.1 | -36.3 | -31.2 | | |
| Feb. | T.L. | -15.5 | -30.2 | -22.9 | 1.7 | 70.0 |
| | W. | -20.6 | -30.8 | -25.7 | | |
| Mar. | T.L. | -11.1 | -26.9 | -19.0 | 3.1 | 77.5 |
| | W. | -16.8 | -28.7 | -22.7 | | |
| Apr. | T.L. | 2.2 | -11.9 | -4.8 | 0.6 | Trace |
| | W. | -3.9 | -17.2 | -10.6 | | |
| May | T.L. | 7.4 | -2.7 | 2.4 | 0.3 | |
| | W. | 2.4 | -3.9 | -1.2 | | |
| June | T.L. | 15.3 | 6.2 | 10.7 | 5.2 | |
| | W. | 10.0 | 2.9 | 6.4 | | |
| July | T.L. | 22.2 | 12.3 | 17.3 | 6.0 | |
| | W. | 17.5 | 7.3 | 12.4 | | |
| Aug. | T.L. | 17.9 | 9.1 | 13.5 | 13.6 | |
| | W. | 15.0 | 6.1 | 10.6 | | |
| Sept. | T.L. | 7.8 | 0.9 | 4.4 | 6.1 | |
| | W. | 6.8 | -0.4 | 3.2 | | |
| Oct. | T.L. | 2.7 | -5.6 | -1.4 | 1.2 | |
| | W. | 1.4 | -4.2 | -1.4 | | |
| Nov. | T.L. | -3.1 | -8.9 | -6.0 | 5.4 | 15.0 |
| | W. | -2.1 | -8.0 | -5.1 | | |
| Dec. | T.L. | -9.8 | -19.5 | -14.6 | 2.7 | 32.5 |
| | W. | -12.2 | -18.6 | -15.4 | | |

[1] See reference, Canada 1974.

[2] Readings taken four feet above ground in a Stevenson Screen.

## TABLE II

Gas Exchange Rates from a summer collection of *Cladonia rangiferina* from Hawley Lake, Ontario.
Storage temperature 10°C day/7°C night.

| | Experimental Temperature | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5°C | | | 15°C | | | 25°C | | | 35°C | | |
| Experimental Light | [1]50% | 150% | 250% | 50% | 150% | 250% | 50% | 150% | 250% | 50% | 150% | 250% |
| 0 µE | [2]-0.9 | -1.1 | -1.0 | -1.5 | -2.3 | -2.8 | -1.5 | -2.1 | -2.5 | -3.0 | -3.1 | -3.4 |
| 200 µE | - | +1.1 | +0.5 | -0.2 | +0.8 | +0.6 | -0.7 | +1.3 | +1.3 | +1.5 | -0.1 | -0.8 |
| 400 µE | +0.2 | +0.6 | +0.3 | -0.6 | +1.3 | +1.3 | -0.9 | +2.2 | +2.2 | -0.1 | +0.4 | +0.1 |
| 600 µE | - | +0.5 | +0.4 | -0.2 | +1.7 | +1.7 | -0.7 | +3.3 | - | -0.5 | +0.9 | +0.3 |

Note 1- % corresponds to thallus hydration, % water content by weight.

2 - body of the table contains values in units mg $CO_2$ $gm^{-1}$ $hr^{-1}$.

## TABLE III

[1]Monthly Temperature and Precipitation Data for 1978, from Muskoka A Meteorological Station

| | Temperature (°C) | | | Precipitation | |
|---|---|---|---|---|---|
| | Max | Min | Mean | Rainfall (mm) | Snowfall (cm) |
| April | [2]8.3 | -1.8 | 3.3 | 47.1 | 10.3 |
| May | 19.6 | 6.2 | 12.9 | 89.9 | T |
| June | 21.4 | 11.8 | 17.2 | 67.6 | 0 |
| July | 24.8 | 11.8 | 17.9 | 56.2 | 0 |

[1] See reference, Canada 1978

[2] Readings taken four feet above ground in a Stevenson Screen.

## TABLE IV

_Cladonia_ _rangiferina_ carbon exchange rates at low levels of thallus hydration.

Experimental temperature 25°C

A - % moisture by dry weight

B - carbon exchange rate, mg $CO_2$ $gm^{-1}$ $hr^{-1}$

| 0 µE | | 200 µE | | 400 µE | | 600 µE | |
|---|---|---|---|---|---|---|---|
| A | B | A | B | A | B | A | B |
| * 69.6 | -1.694 | 51.9 | +1.155 | 80.3 | +2.097 | 48.5 | +1.781 |
| 37.3 | -0.701 | 37.5 | -0.221 | 50.6 | +2.143 | 24.0 | +0.212 |
| 3.3 | -0.731 | 16.0 | -0.669 | 16.7 | -0.336 | 7.0 | -1.140 |
| 82.1 | -2.095 | 50.5 | +0.672 | 58.9 | +2.273 | 71.4 | +2.632 |
| 23.4 | -1.159 | 28.4 | -0.169 | 27.0 | +0.635 | 40.3 | +1.080 |
| 12.2 | -0.901 | 5.0 | -0.587 | 3.8 | -0.948 | 4.5 | -0.949 |
| 68.3 | -1.789 | 62.9 | +1.085 | 62.0 | +2.492 | 38.1 | +1.751 |
| 46.1 | -1.319 | 34.4 | -0.340 | 20.9 | +0.321 | 15.6 | -0.658 |
| 18.3 | -0.947 | 13.9 | -0.538 | 4.7 | -1.542 | 5.4 | -1.190 |
| 77.6 | -1.911 | 95.9 | +1.272 | 73.0 | +1.737 | 81.4 | +2.525 |
| 59.4 | -1.084 | 47.1 | -0.578 | 27.7 | +0.576 | 43.6 | +1.780 |
| 35.6 | -0.854 | 5.0 | -0.917 | 16.2 | -0.887 | 13.6 | -0.780 |

* Note each data set is from single experimental replicates over three incubation periods

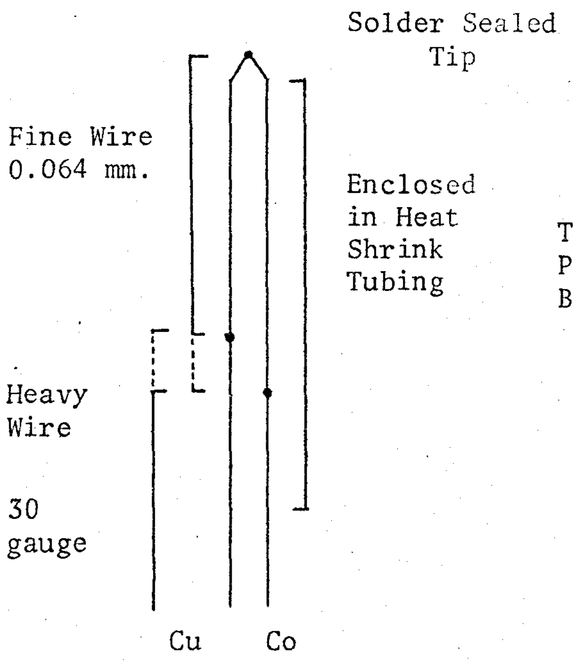
## TABLE V

*Cladonia rangiferina* thallus hydration levels at Hawley Lake, Ontario, Summer 1978.

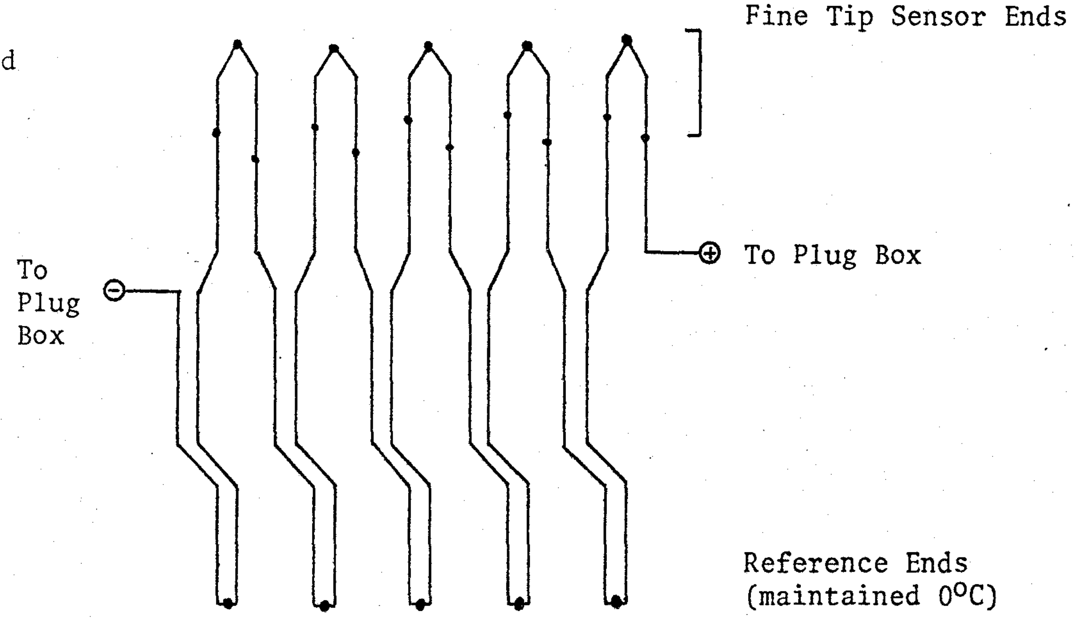
| | Time | Light ($\mu E\ m^{-2} s^{-1}$) | Temperature ($^{o}$ Celsius) | Thallus Hydration (% Moisture by Weight) |
|---|---|---|---|---|
| June 27 | 4:45 am | 150 | 2.5 | 97 |
| | 5:15 | 230 | 3.5 | 83 |
| | 5:45 | 400 | 5.5 | 51 |
| | 6:15 | 550 | 8.0 | 34 |
| | 6:45 | 800 | 11.0 | 19 |
| July 2 | 11:05 am | 450 | 7.5 | 150 |
| | 11:20 | 900 | 11.0 | 105 |
| | 11:37 | 700 | 12.0 | 86 |
| | 11:50 | 1400 | 17.0 | 35 |
| | 12:05 | 2150 | 22.0 | 17 |
| July 6 | 2:30 pm | 800 | 11 | 109 |
| | 2:45 | 1450 | 12 | 100 |
| | 3:04 | 1450 | 17 | 62 |
| | 3:20 | 1600 | 24 | 14 |

Figure 23. Detail of Temperature Sensor

SINGLE THERMOCOUPLE



FIVE POINT AVERAGING THERMOPILE



Total length, sensor to reference, is dependent on distance from point of measurement to 0°C reference.

Figure 24. Typical Set-Up for Field Temperature Measurement.

## TYPICAL FULL SCALE FIELD TEMPERATURE MEASUREMENT