

THE EFFECTS OF TEMPERATURE AND MOISTURE ON DARK RESPIRATION IN THE FOLIOSE LICHEN *UMBILICARIA ANTARCTICA*

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SUMMARY

The dark respiration of field-fresh thalli of *Umbilicaria antarctica* Frey et Lamb is reported for temperatures from -5.5 to 19°C , and water contents from saturation to dryness. Detailed analysis of the respiratory response with changing water content has suggested that Michaelis–Menten kinetics appear to provide a useful model. Q_{10} values are used to indicate possible ice formation in the thallus and water loss characteristics are explained in terms of thallus anatomy. The ecological implications of this approach are discussed.

Key words: Antarctic, ecophysiology, lichen, Michaelis–Menten models, *Umbilicaria antarctica*, water-content.

INTRODUCTION

Terrestrial habitats in Antarctica encompass some of the most extreme climatic conditions on earth. Fluctuations in both water availability and temperatures are frequent and often large. Lichens are a major constituent of the Antarctic flora (Smith, 1984), and must therefore be able to withstand these physical stresses. The ecophysiological significance of respiration in lichens is poorly understood, and has largely been viewed as a negative process in net-photosynthesis studies (Kershaw, 1985). Yet for all lichens, and more especially those occupying marginal or exceptionally stressful habitats, the control of respiration will be a principal determinant of growth.

Previous gaseous exchange studies on the physiology of Antarctic lichens have been summarized by Kappen (1983) and Ino (1985). *Umbilicaria antarctica* Frey et Lamb, a widely distributed species, was chosen as representative of Antarctic foliose lichens for the purpose of examining in detail the dependence of dark respiration on moisture and temperature. The ecophysiology of several northern species of *Umbilicaria* has also been studied by Larson (1979a, b, 1980, 1982, 1984a, b) at sites in south-central Ontario.

The form of physiological response curves can be modelled algebraically. Kirchner, Heasley & Lauenroth (1981) suggested that modified Michaelis–Menten equations might provide a model for the sigmoidal response curves that have been published for several lichen species. Gates (1980), Link, Moser & Nash (1984) and Nash *et al.* (1983) have all used them in photosynthetic studies. This approach was used in an analysis of dark respiration data from *U. antarctica* and novel explanations were developed to explain the form of the response curve and its relationship to features of thallus anatomy.

MATERIALS AND METHODS

Lichen material

Experiments were conducted between 5 February and 31 March 1982 at Signy Island ($60^{\circ} 43' S$, $45^{\circ} 38' W$) with the foliose lichen *Umbilicaria antarctica* Frey et Lamb. A single size class of thallus of mean dry weight 0.88 g (SE = 0.06, $n = 16$) was used (Larson, 1984b). Field-fresh material was used to avoid any storage effects (Brown, Snelgar & Green, 1981; Larson, 1982). All thalli were collected from one side of a quartz mica-schist boulder. Prior to experiment, each fresh thallus was fully hydrated in double-distilled water for 15 min and then kept at a high level of hydration for 24 h under natural light conditions to eliminate any resaturation respiration effects (Farrar & Smith, 1976). At the start of each experiment, the thallus was again resaturated, together with a filter-paper wad control (three Whatman, 44 ashless, 7.0 cm diam. discs) by immersion in double-distilled water for 15 min followed by light shaking to remove excess surface water. The thallus respiration was then measured as it dried out within the chamber at a fixed temperature.

The thallus and filter-paper control were placed on silver-wire frames in identical 340 ± 5 ml analysis and reference perspex chambers. An open-flow measuring system inside a controlled temperature room was used to measure simultaneously the rate of thallus dark respiration and water loss at -5.5 , 0 , 7 , 13 and $19^{\circ}C$. Four replicates were used at $19^{\circ}C$ and three at all other experimental temperatures.

The airstream piping was made of polypropylene. Temperature control for the thallus was generally better than $\pm 1^{\circ}C$. Outside air was drawn through a buffering volume, and switched into two equal streams by pumping through an ADC Gas-Diluter (type GD600) operating in the non-absorbing mode. The average CO_2 content of the reference airstream was $331.3 \mu l l^{-1}$. Air flow rates of $24 l h^{-1}$ (absolute accuracy $\pm 3.6 l h^{-1}$) at 7.13 and $19^{\circ}C$ and $12 l h^{-1}$ (absolute accuracy $\pm 3.6 l h^{-1}$) at -5.5 and $0^{\circ}C$ were controlled by Rotameters. The ADC series 225 IRGA was operated in the differential mode (absolute accuracy $\pm 0.5 \mu l l^{-1} CO_2$) after calibration by the alternative path length method (Parkinson & Legg, 1971), using a substandard determined against a triple checked $317 \mu l l^{-1}$ (absolute accuracy $\pm 1 \mu l l^{-1}$) CO_2 standard. A Vaisala (HMP14) humidity-temperature probe in the analysis airstream very close to the IRGA measured relative humidity (absolute accuracy of $\pm 2\%$ r.h. in the range 0 to 80 % and $\pm 3\%$ r.h. at 100 % r.h.) and temperature (absolute accuracy $\pm 0.1^{\circ}C$) of the gas stream just before entering the IRGA. This minimized the lag period between the measurements of water content and CO_2 , which is considered to be less than 2 min. A potentiometric dotting chart-recorder (Jaquet, series KSQ 500) recorded IRGA output, temperature, and % r.h. to $\pm 0.25 \mu l l^{-1}$, $\pm 0.5^{\circ}C$, and $\pm 1\%$ r.h. respectively.

Data analysis

CO_2 flux density ($mg CO_2 g^{-1} h^{-1}$) was calculated from the formula of Sestak, Catsky & Jarvis (1971) applicable to rotameters. Thallus water loss was calculated using the formula of Luxmore, Stolzy & Holdeman (1981). Thallus water-content was expressed as $g g^{-1}$ d. wt. Weighings (absolute accuracy, ± 1 mg) were made at the beginning (thallus-saturation) and the end (thallus-dehydration) of an experiment.

The graphical form of dark respiration plotted as a function of water content

can be broken down into one or two linear sections, and a Michaelis–Menten section which spans approximately 75 % of the metabolically active water content range. These are shown schematically in Figure 1; they proved to be common to all experiments except those at -5.5°C . The points of intersection between linear and Michaelis–Menten sections were estimated by eye. All variables used in this paper are defined in Figure 1.

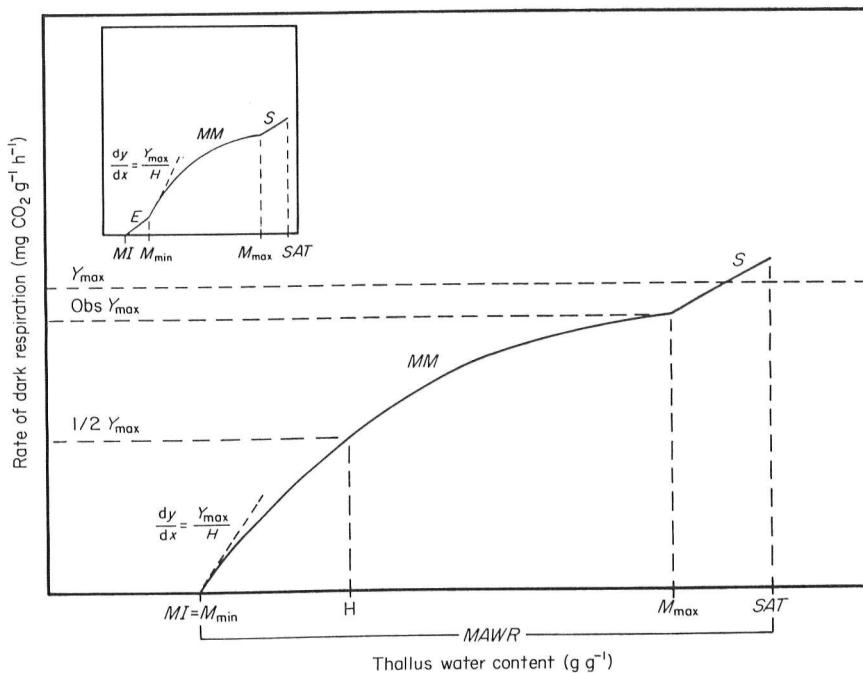


Fig. 1. Schematic diagram showing the graphical form of dark respiration plotted as a function of water content with the end-slope (E) absent. Inset: shows the end-slope (E) present. Abbreviations: S, linear start-slope for dehydration; SAT, saturated water content; M_{\max} , observed water content at point of intersection between rectangular hyperbola curve and linear phase response; MM, modified diphasic Michaelis–Menten rectangular hyperbola; M_{\min} , observed water content at point of intersection between Michaelis–Menten curve and end-slope (E); E, linear end-slope for dehydration; MI, observed water content at metabolic inactivity; MAWR, metabolically active water content range; $S\% = ((SAT - M_{\max})/MAWR) \times 100$; $MM\% = ((M_{\max} - M_{\min})/MAWR) \times 100$; $E\% = ((M_{\min} - MI)/MAWR) \times 100$; Y_{\max} , estimated Michaelis–Menten asymptote; Obs Y_{\max} , maximum rate in water content range ($M_{\max} - M_{\min}$); H, water content yielding $\frac{1}{2} Y_{\max}$; Obs % $Y_{\max} = (\text{Obs } Y_{\max}/Y_{\max}) \times 100$; X_0 , estimated water content at point of intersection between Michaelis–Menten curve and end-slope (E); AS, average start-slope.

Starting from saturation hydration levels, dehydration initially produced a linear rate of decline S (start-slope) in dark respiration, delimited by SAT (saturated water content) and M_{\max} water contents. This was followed by a non-linear rate of change, which can be described by a modified diphasic Michaelis–Menten rectangular hyperbolic curve (MM), delimited by M_{\max} and M_{\min} water contents. In some cases, this was followed at low hydration levels by another linear rate change E (end-slope), delimited by M_{\min} and MI (water content at metabolic inactivity). If this was absent then $MI = M_{\min}$. The initial slope of the Michaelis–Menten curve is given by $dy/dx = Y_{\max}/H$. M_{\min} is the lower limit of the water

content the range described by Michaelis–Menten kinetics. X_0 and M_{\min} can be equal, X_0 being the estimated parameter and M_{\min} the observed value.

Michaelis–Menten kinetics were assumed to be appropriate in this instance since the changing water content was taken as an analogue of substrate concentration. The equation is

$$y = \frac{Y_{\max}}{1 + (H/(X - X_0))}$$

where X is the water content, y is the dark respiration rate, Y_{\max} is the asymptotic dark respiration rate, H is the water content yielding half Y_{\max} and X_0 is the minimum water content for metabolic activity. Least squares estimates of Y_{\max} , H and X_0 were obtained by fitting the Michaelis–Menten model using the statistical package GENSTAT (Alvey *et al.*, 1983). Variations in parameter values with temperature were analyzed by one-way analysis of variance, using individual replicate values, and linear regression to test for trends.

Errors

Estimates for the total errors for dark respiration and water content measurements: with a flow-rate of 12 l h^{-1} absolute accuracies are $\pm 0.078\text{ mg CO}_2\text{ g}^{-1}\text{ h}^{-1}$ and $\pm 0.05\text{ g g}^{-1}$ respectively, and with a flow-rate of 24 l h^{-1} absolute accuracies are $\pm 0.097\text{ mg CO}_2\text{ g}^{-1}\text{ h}^{-1}$ and $\pm 0.06\text{ g g}^{-1}$ respectively. Flow-rate inaccuracies were the major component of the error term. Errors for SAT , MI , $MAWR$, M_{\max} , M_{\min} and $MM\%$ are given in Table 1.

RESULTS

Physiology

The mean dark respiration rates for four temperatures are plotted as a function of water content in Figure 2. At each temperature the mean plot terminates at the minimum saturated water content for an individual replicate, in order to keep the value of n constant in the calculations of the means at 0.05 g g^{-1} intervals. The absolute mean saturated water contents measured at the various temperatures are given in Table 1. At -5.5°C there was no detectable metabolic activity for one replicate. The other two replicates, plotted individually, showed a linear decline in respiration rate and reached metabolic inactivity at high thallus water contents (1.77 and 1.95 g g^{-1}). It seems probable that, for these replicates, only the start slope was detectable.

Within each temperature group the replicates showed a considerable degree of variability in absolute values but very similar patterns in their response curves. Data for 19°C are shown in Figure 3 as an example. The degree of absolute respiratory variation was unexpected given the experimental standardization on a single size class from what was assumed to be one population.

Mean values for the estimated Michaelis–Menten and other parameters are given in Tables 1, 2 and 3 and in linear regressions of these parameters on temperature Table 4. Respiratory loss rate at low water contents (E) (Table 3) was not tested because of the paucity of replicates. It is inferred that the parameters Y_{\max} , Y_{\max}/H and S are highly temperature dependent, whereas MI and $MAWR$ are less temperature dependent, and H and $\text{Obs \% } Y_{\max}$ are only slightly temperature dependent. The appearance of an end slope at higher temperatures causes M_{\min} to diverge from MI with increasing temperature.

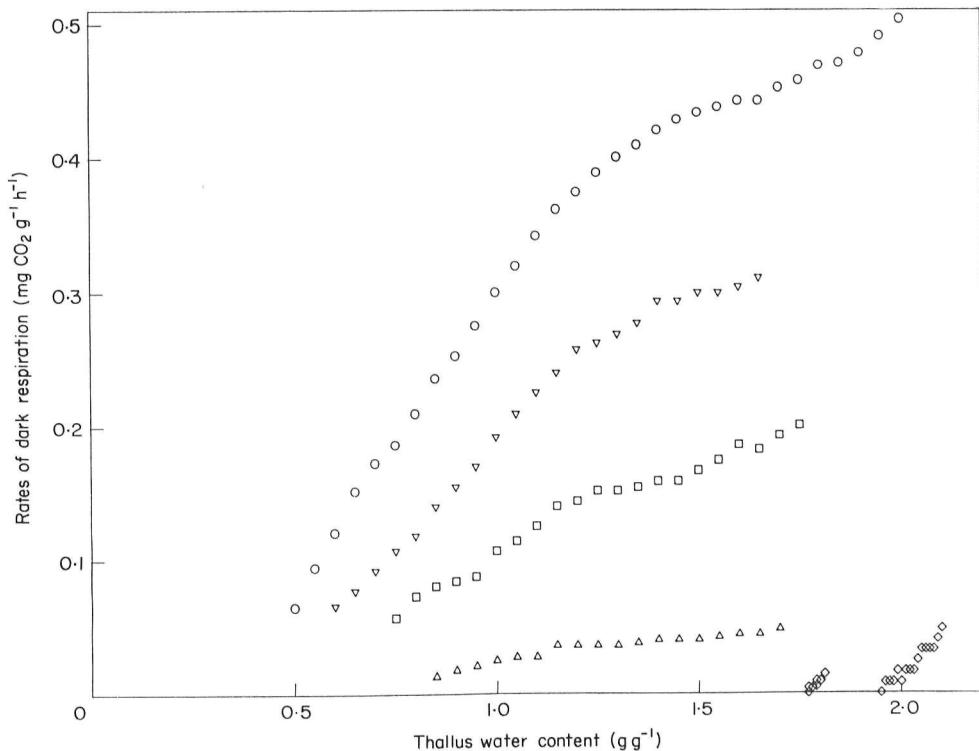


Fig. 2. Mean dark respiration rates plotted as a function of thallus water content for *Umbilicaria antarctica*. Key: $\circ = 19^\circ\text{C}$; $\nabla = 13^\circ\text{C}$; $\square = 7^\circ\text{C}$; $\triangle = 0^\circ\text{C}$; and $\diamond = -5.5^\circ\text{C}$.

Table 1. Mean estimates ($\pm \text{SE}$) for moisture dependent respiration parameters and the estimated difference between M_{\min} and MI at four temperatures

Parameters	Temperature ($^\circ\text{C}$)			
	0 $n = 3$	7 $n = 3$	13 $n = 3$	19 $n = 4$
$SAT (\text{g g}^{-1})$	1.84 ± 0.11	1.98 ± 0.20	2.45 ± 0.40	2.22 ± 0.14
$MI (\text{g g}^{-1})$	0.64 ± 0.12	0.50 ± 0.11	0.41 ± 0.10	0.36 ± 0.04
$MAWR (\text{g g}^{-1})$	1.20 ± 0.22	1.48 ± 0.10	2.04 ± 0.32	1.86 ± 0.11
$M_{\max} (\text{g g}^{-1})$	1.60 ± 0.05	1.72 ± 0.24	2.23 ± 0.29	1.98 ± 0.17
$M_{\min} (\text{g g}^{-1})$	0.64 ± 0.12	0.58 ± 0.18	0.52 ± 0.20	0.63 ± 0.13
$MM\% (\%)$	80.0 ± 3.8	77.0 ± 2.6	83.8 ± 8.4	72.6 ± 4.9
$M_{\min} - MI$	0.00	0.08 ± 0.22	0.11 ± 0.22	0.27 ± 0.14

Calculated parameters for the linear start- and end-slopes of individual replicates are in Table 3, and demonstrate the variability inherent in even one size class of thalli. The range of the Michaelis–Menten curve was defined by eye and linear regressions were used to estimate the slope of the linear start- and end-slopes. Mean R^2 values for the fitted start- and end-slope lines were 96.4% ($\text{SE} = 1.5$, $n = 12$) and 98.7% ($\text{SE} = 0.4$, $n = 6$) respectively. Mean standard deviations about the line for the fitted start- and end-slope lines were 0.0038 ($\text{SE} = 0.0006$, $n = 12$) and

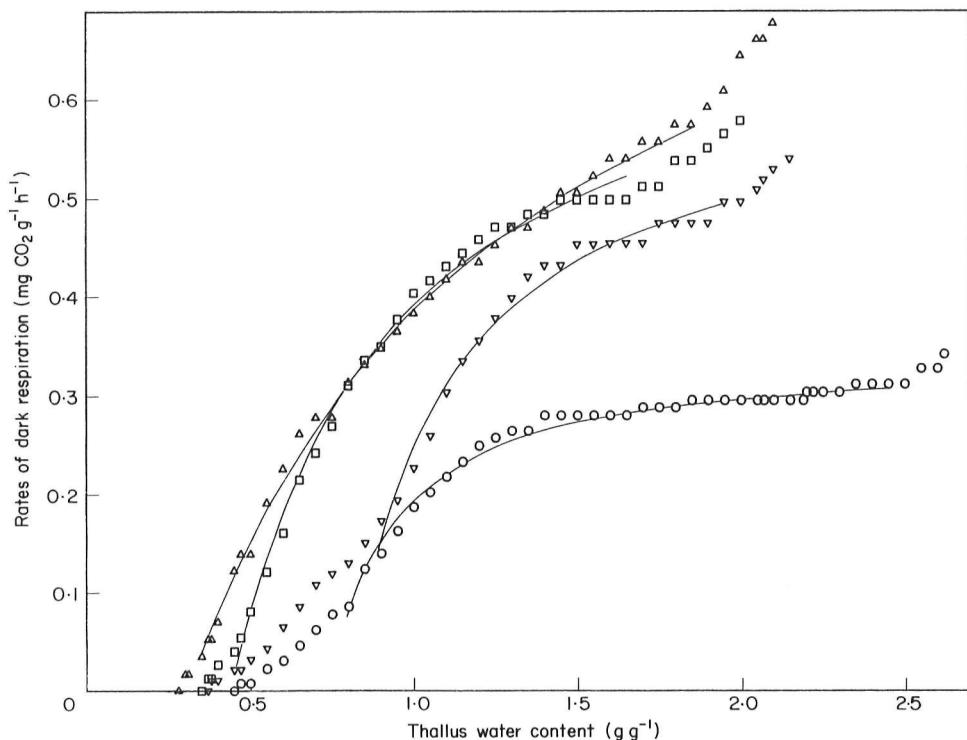


Fig. 3. Dark respiration rates of individual replicates of *Umbilicaria antarctica* at 19 °C plotted as a function of thallus water content. Data points are plotted together with a Michaelis-Menten generated model curve.

Table 2. Mean estimates (\pm SE) for respiration parameters from the Michaelis-Menten equation (H , Y_{\max} and X_0) and derived values (Y_{\max}/H and Obs % Y_{\max}) at four temperatures

Parameters	Temperature (°C)			
	0 $n = 3$	7 $n = 3$	13 $n = 3$	19 $n = 4$
H (g g ⁻¹)	1.35 ± 0.20	1.27 ± 0.10	1.09 ± 0.11	1.07 ± 0.08
Y_{\max} (mg CO ₂ g ⁻¹ h ⁻¹)	0.07 ± 0.002	0.28 ± 0.03	0.45 ± 0.11	0.66 ± 0.12
X_0 (g g ⁻¹)	0.63 ± 0.12	0.56 ± 0.17	0.53 ± 0.18	0.57 ± 0.12
Y_{\max}/H (mg CO ₂ g ⁻¹ h ⁻¹)	0.05 ± 0.01	0.22 ± 0.01	0.41 ± 0.06	0.62 ± 0.09
Obs % Y_{\max} (%)	55.3 ± 6.6	63.9 ± 13.6	74.3 ± 7.7	74.4 ± 6.4
R^2 (%)	95.7 ± 0.7	98.0 ± 0.7	97.1 ± 1.7	99.1 ± 0.3
$SDL (\times 10^{-3})$	2.7 ± 0.3	6 ± 1	13 ± 5	10 ± 2

Values for R^2 and the SD about the line (SDL) for least squares best fits are given (\pm SE).

0.0038 (SE = 0.0007 , $n = 6$) respectively. End-slopes were not found at 0 °C nor for some replicates at 7 and 13 °C. Except for one replicate at 13 °C, all replicates had start-slopes.

To compare the temperature dependence of dark respiration in *Umbilicaria* with physiological activities in other organisms, Q_{10} values (Schmidt-Nielsen, 1975)

Table 3. Individual replicate and mean estimates ($\pm \text{SE}$) for calculated moisture dependent parameters of respiration

Parameters	Temperature (°C)												
	0				19								
	Replicate number	1	2	3	Replicate number	1	2	3	Replicate number	1	2	3	4
S (mg CO ₂ g ⁻¹ h ⁻¹)	0.11	0.04	0.08	0.23	0.18	0.27	—	0.12	0.23	0.43	0.23	0.31	0.22
Y _{max} /H (mg CO ₂ g ⁻¹ h ⁻¹)	0.06	0.07	0.04	0.23	0.22	0.21	0.38	0.31	0.51	0.72	0.78	0.57	0.37
E (mg CO ₂ g ⁻¹ h ⁻¹)	—	—	—	—	—	0.27	—	0.26	—	0.47	0.52	0.32	0.25
E% (%)	—	—	—	—	—	14.37	—	17.07	—	3.85	6.06	29.78	16.13
AS (mg CO ₂ g ⁻¹ h ⁻¹)	0.08 ± 0.02	—	0.23 ± 0.03	—	0.18 ± 0.06	—	0.18 ± 0.06	—	0.30 ± 0.05	—	—	—	—
S% (%)	20.0 ± 3.78	—	17.6 ± 4.4	—	13.8 ± 1.6	—	13.8 ± 1.6	—	12.90 ± 2.9	—	—	—	—

Table 4. *Estimated linear regressions of the anatomically and metabolically determined respiration parameters on temperature*

Parameters	Slope	SE
H (g g^{-1})	-0.015	0.008*
Obs % Y_{\max} (%)	1.05	0.55*
MT (g g^{-1})	-0.015	0.006**
$MAWR$ (g g^{-1})	0.039	0.014**
Y_{\max} ($\text{mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$)	0.30	0.003***
Y_{\max}/H ($\text{mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$)	0.027	0.003***
S ($\text{mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$)	0.010	0.003***

Levels of significance are indicated: * $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$

were calculated. Each rise of 10 °C would be expected to produce an increase in respiration rate of two or three times, unless thermally induced enzyme inactivation was occurring. Q_{10} values for Y_{\max} and Y_{\max}/H (Table 5) are not unusual except for those between 0 and 7 °C, which are higher than expected. Increasing internal CO_2 diffusion resistances may be caused by ice formation within the thallus at around 0 °C (temperature in the present experiments was only accurate to ± 1 °C) and could probably produce these elevated Q_{10} values. The small decrease in average start-slope (AS) between 7 and 13 °C (Table 3) produces a large decrease in Q_{10} (Table 5) and indicates that, although the start-slope is highly temperature dependent (Table 4), there may be real variations in cortical metabolic activities within a population. The same phenomenon can be observed for the 7 to 13 °C range end-slope Q_{10} of 0.94. If the physiological basis of the end-slope is the same as that of the start-slope and is observed after the masking effect of the Michaelis-Menten rate change has been removed by water loss, then this result would not be surprising. A lower cortical metabolic activity will produce a lower start-slope. Small changes in the average start-and end-slope values, between 7 and 13 °C, may then be directly correlated resulting in Q_{10} values of less than unity in both cases.

At the higher temperatures of 13 and 19 °C, where rates of CO_2 release are higher (Fig. 2), the start slope is always less than that of Y_{\max}/H (Table 3). This may be a purely physical phenomenon related to the decreasing solubility of both oxygen and CO_2 in water with increasing temperature. At the lower temperatures of 0 and 7 °C the start-slope is less than, equal to, or greater than the Y_{\max}/H slope, indicating that neither the diffusion of CO_2 through water, which is over a thousand times slower than through air, nor the solubility of CO_2 in water is limiting CO_2 release at lower temperatures. It is suggested that, at these temperatures, there may be small variations in the potential rates of CO_2 release per unit

Table 5. Q_{10} values for the average values of the respiration parameters Y_{\max} , Y_{\max}/H and S ($\pm SE$)

Q_{10} values for parameters	Temperature interval (°C)		
	0-7	7-13	13-19
Y_{\max} (from Table 2)	7.25 ± 1.15	2.21 ± 0.98	1.89 ± 0.96
Y_{\max}/H (from Table 2)	8.30 ± 2.43	2.82 ± 0.72	1.99 ± 0.68
S (from Table 3)	4.52 ± 1.82	0.66 ± 0.39	2.34 ± 1.45

volume between the medulla and cortical regions. This is not observable at the higher temperatures because of either the reduction in the solubility of CO_2 or a limitation in the availability of oxygen.

The lack of an end-slope at the lower temperatures may be due to such a low rate of CO_2 release that it was not detectable at water contents below those corresponding to the range where the Michaelis-Menten equation operates.

The general assumption is that photosynthesis is more sensitive than respiration to low water potentials. However, in *Umbilicaria antarctica*, at comparable temperatures the water content at which net photosynthesis ceases is lower than that for dark respiration (unpublished data). This suggests that the algal cells are among the last cells to become metabolically inactive during dehydration, indicating that they may be better protected than fungal hyphae against water loss.

The end slope links the respiration rate directly to final water contents of the thallus (1st-order kinetics) and suggests that the ratio of non-cytoplasmic to cytoplasmic water apparently remains constant during final dehydration at a constant temperature. The ratio of non-cytoplasmic to cytoplasmic water probably increases with increasing temperature, because the gradients in water potential between the cytoplasmic and non-cytoplasmic water storage sites increases with temperature. Thus, the end-slope goes from being just greater than the Y_{\max}/H slope at 7 °C, just less at 13 °C, and much less than at 19 °C, as the final ratio of non-cytoplasmic to cytoplasmic water is increased (Table 3).

It is suggested that ice formation within the thallus, below 0 °C, increases the internal CO_2 diffusion resistance producing anomalously elevated Q_{10} values for the parameter Y_{\max} , Y_{\max}/H and S (Table 5). The start-slope Q_{10} value in the 0 to 7 °C range is much less than the comparable Y_{\max} and Y_{\max}/H Q_{10} values. Ice formation would increase the internal CO_2 diffusion resistance thus depressing CO_2 release.

DISCUSSION

In a review of lichen respiration and growth studies, Kershaw (1985) has suggested that the physiological response curve reflects three interactive parameters: the specific level of thallus moisture at which a restriction on the biochemical events occurs, the interaction of this event with temperature, and the possible interaction of the thallus internal resistance with either oxygen diffusion in or carbon dioxide diffusion out.

In his consideration of the different forms of respiration response curve he noted the need for interpretations of the response patterns. Because respiration has largely been viewed as a negative process in photosynthesis studies, respiration data has rarely been exposed to the rigorous and extensive analysis it deserves.

Lange (1980) suggested that the internal CO_2 concentration was greater at higher water contents due to greater respiratory activity. In the most commonly observed dark respiration response, CO_2 release increases sigmoidally to reach an asymptote with increasing water content. At higher water contents the gradient to the ambient air would be steep enough to ensure that, under steady-state conditions, the outflow of CO_2 equalled internal CO_2 production. Consequently he concluded that respiratory CO_2 release from the thallus would be, to a large extent, independent of diffusion resistances. This has been supported by studies on *Sticta* by Snelgar, Brown & Green (1980), Snelgar, Green & Wilkins (1981b) and Green, Snelgar & Brown (1981). Thus Lange (1980) has provided an

interpretation for the most common response curve, but in all ten general graphical forms of dark respiration as a function of water content have been described (Smyth, 1934; Ried, 1960; Smith, 1962; Kershaw & Smith, 1978; Larson, 1979b; Green *et al.*, 1981; Snelgar & Green, 1981; Snelgar *et al.*, 1981b; Coxson, Brown & Kershaw, 1983; Kappen 1983). Several of these are seen in the data for *Umbilicaria antarctica*.

The following form of the Michaelis–Menten equation (Kirchner *et al.*, 1981) might be a better interpretation of a sigmoidal response curve that is asymptotic towards a maximum respiration rate at high water contents:

$$y/Y_{\max} = (X - X_0^n) / (H^n + (X - X_0^n)),$$

where X is the water content, y is the dark respiration rate, Y_{\max} the asymptotic dark respiration rate, H the water content yielding half Y_{\max} and X_0 the minimum water content for metabolic inactivity. The equation reduces to a Michaelis–Menten response curve for $n = 1$. A higher value of n produces a sigmoidal response curve. Lange (1980) mentions that his interpretation is unable to account for the other graphical forms, whereas the interpretation proposed in this paper does, with the major part of the interpretation involving the application of the Michaelis–Menten equation. Lichens possessing cortices that are thin or contain numerous air spaces may be characterized by a sigmoidal response curve or a rectangular hyperbola. Michaelis–Menten kinetics are applicable because of the water-holding capacity of the thallus. In *Umbilicaria* this is primarily in the medulla (Harrisson & Barber, unpublished). This implies a higher degree of relationship between structure and physiology in lichens than is generally appreciated, although this has already been stressed by Snelgar, Green & Beltz (1981a).

Analyses of this sort can indicate which of the physiological parameters are anatomically determined and which metabolically. Those parameters showing low temperature dependence could be principally determined anatomically, whereas those with greater temperature dependence may be metabolically determined. However, the viscosity of water changes considerably over this temperature range as do the diffusion coefficients of many water soluble compounds (Johnson & Thornley, 1985). This may account for part of the relationship. MAWR is delimited by the parameters *SAT* and *MI* which are probably anatomically and metabolically determined respectively. It is believed that both H and Obs % Y_{\max} are primarily anatomically determined parameters.

A possible general explanation for the common form of physiological response between replicates could be as follows:

(1) Water is initially lost from cortical hyphal and algal cells in the upper and lower cortex. Thus the initial dark respiration rate is directly proportional to the thallus water-content demonstrating 1st-order kinetics and yielding the start-slope.

(2) However, once water loss from the medulla free-water space begins, two sequential processes occur which mask the start-slope's 1st-order rate kinetics: (i) water loss from the free-water space of the medulla will not dehydrate the medulla hyphal cells, which will remain metabolically active (zero order-rate kinetics); (ii) water loss from the medulla hyphal cells will dehydrate them rendering them metabolically inactive (this is the initial rate Y_{\max}/H demonstrating 1st-order kinetics). These two rate processes, zero and 1st-order kinetics, yield a diphasic rectangular hyperbolic curve for dark respiration plotted as a function of water content. The greater the ratio of free-water space to hyphal volume in the medulla,

the closer the approach to the Y_{\max} asymptote will be as defined by $y = Y_{\max}/(1 + (H/(X - X_0)))$.

(3) An end-slope (if present) is considered to be related to the start-slope. It only appears when the masking effect of the diphasic rate change is removed at the last stages of dehydration. It demonstrates 1st-order kinetics.

However, start- and end-slopes may be based on different processes. For instance, anaerobic respiration may be responsible for the start-slope whilst decarboxylation associated with uncoupled electron flow along damaged mitochondrial membranes might produce the end-slope. Anaerobic respiration may occur when Y_{\max}/H is considerably greater than S . This feature appears to be linked to temperature and occurs at 13 and 19 °C (Table 3) whilst at lower temperatures S is generally similar to or greater than Y_{\max}/H . However, caution in drawing conclusions from all these data is necessary, since there are few replicates.

The use of the Michaelis–Menten model would seem both to simplify comparison of ecotypic or species specific responses as well as allowing more detailed investigation of particular physiological parameters. For instance, Lange (1980) suggested that the initial slope of plots relating photosynthetic CO_2 uptake to water content might be taken to indicate an efficiency of hydration for *Ramalina maciformis*. Gates (1980) has described how the initial slope of Michaelis–Menten derived, light dependent, photosynthesis curves represents the maximum efficiency of incident light-energy conversion, known as the quantum yield. In an analogous manner, the initial slope, Y_{\max}/H (Tables 2 and 3), could be used as a routine, standardized analytical tool to estimate the efficiency of hydration. The slope Y_{\max}/H could be termed the water yield. Differences between population responses and those of individual replicates are not described in the literature. The commonality and temperature independence of the individual replicate responses are masked in the population responses. It is important to examine individual replicates as well as population responses, especially when age or weight class is standardized.

The value of standardizing experimental replicates has been highlighted by Smith (1962), Rundel (1982) and Larson (1984b). Although here the respiratory variation was large given experimental standardization on a single size class, the limited variation of the Michaelis–Menten parameter H was noteworthy. The ecological implications remain to be explored.

The general assumption that the water relations of foliose lichens can be regarded as directly analogous to those of a filter paper disc thus seems untenable. Furthermore, the structure of the thallus appears to be of considerable significance in the interactions between water content and gaseous exchange. Anatomy and morphology are thus important considerations for any study of lichen physiology.

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