

2.7 Net CO₂ Exchange in Relation to Thallus Moisture and Temperature in two Fruticose Lichens *Usnea antarctica* and *Usnea aurantiaco-atra* from the Maritime Antarctic

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Summary: Species of *Usnea* (*Neuropogon*) are a major component of considerable areas of the fellfield vegetation of Signy Island, South Orkneys Islands. Although morphologically similar the respiratory and photosynthetic responses of the two species to the same experimental conditions were totally different. Despite similar growth forms the two species required different thallus water contents for maximum photosynthesis. It is suggested that this may be attributable to changes in the number of diffusion pathways with changing water content, possible differences in their light responses, and the possession of different reproductive structures commensurate with their differing life cycles.

Zusammenfassung: *Usnea*-Arten bilden die Hauptkomponente in der Rohbodenvegetation von Signy Island, South Orkney Islands. Trotz morphologischer Ähnlichkeit sind Atmung und Photosynthese beider Arten sehr unterschiedlich. Für maximale Nettophotosyntheseraten benötigen sie unterschiedliche Wassermengen. Diese Unterschiede mögen darin begründet sein, daß die Diffusionswege im Thallus bei wechselndem Wassergehalt verschieden sind, daß die Flechten unterschiedlich auf Licht reagieren und daß die unterschiedliche Art sich zu reproduzieren einen Einfluß auf die Lebensweise der Arten haben.

1. INTRODUCTION

Of the wide variety of terrestrial ecosystems those in Antarctic regions are amongst the most extreme. They are restricted to a series of isolated snow-free areas which comprise approximately 1% of the Antarctic, and temperature and water availability in these ecosystems are subject to large and not infrequent change.

Due to their poikilohydrous nature lichen metabolic processes, particularly gaseous exchange, can vary greatly with changes in thallus moisture content (LANGE 1980). PERKINS (1945) drew attention to the possible effect of water availability on the local distribution of lichens in Antarctic ecosystems. Globally the importance of thallus moisture content to the survival and growth of lichens has since been extensively studied in a range of environments and summarised by KERHSAW (1985). Gaseous exchange studies using Antarctic lichens have been summarised by KAPPEN (1983, 1985) and INO (1985).

Neuropogon is the only subgenus of fruticose lichens to be prominent in both the continental and peri-Antarctic flora (KAPPEN 1985 and LAMB 1964). *Usnea* is the dominant fruticose genus in the flora of Signy Island (60°43'S, 45°38'W), South Orkney Islands (SMITH 1972, 1984). HOOKER (1980) has recently studied the growth rates of *Usnea fasciata* (= *U. aurantiaco-atra* Walker 1985) and *Usnea antarctica* on Signy Island — maritime Antarctic — and KAPPEN (1983, 1985) has recently investigated aspects of the gaseous-exchange and water-relations of *Usnea fasciata* (= *U. aurantiaco-atra* Walker 1985) and *Usnea sulphurea* (= *U. sphaelata* Walker 1985) in the maritime and continental Antarctic.

The habitat and distribution of *U. antarctica* and *U. aurantiaco-atra* on Signy Island in the peri-Antarctic has been described by HOOKER (1980), HUNECK et al. (1984), LONGTON (1985), SMITH (1972, 1984) and WALTON (1984). The environmental factors, temperature and water availability exert a significant influence on the survival of terrestrial organisms in Antarctica, along with substrate availability — possibly the dominant factor — and wind. They are inextricably linked in their action on biological systems, and may largely determine the survival not only of individuals, but also of their populations, communities, and species polar ecosystems (BLOCK 1985). The aim of this paper is to compare the role of these two variables on the net CO₂ exchange of *Usnea aurantiaco-atra* and *Usnea antarctica*.

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2. MATERIALS AND METHODS

2.1 General

CO₂ exchange and thallus water content measurements were made in the light and dark using the methodology described in HARRISSON et al. (1986). Experiments were conducted between 22 May and 3 December 1982. Single thallus size classes of mean dry weights 0.81 g (SE = 0.05, n = 26) and 2.26 g (SE = 0.13, n = 26) for *Usnea antarctica* and *U. aurantiaco-atra* respectively were collected from quartz mica schist cliff faces. At the start of each experiment the saturated thallus water content (SAT, gg⁻¹) was estimated by fully hydrating the thallus in double-distilled water for 15 min followed by light shaking to remove excess surface water. Four replicates were used in the light experiment and three replicates for dark experiments for each species. Thallus temperatures of -5, 0, 5, 10, 15, 20 and 25° C were used in the light and dark with two exceptions. 25° C was unattainable for both species in the dark and only 19° C was used instead of 20° C for *Usnea aurantiaco-atra*. An irradiance level in the 400—700 nm waveband — which was thought to be typical of field conditions on Signy Island — of 200 μmol m⁻²s⁻¹ was used in all the net photosynthesis measurements. Unfortunately, no experiments could be performed to investigate the pattern of response of net photosynthesis to increasing irradiance levels — at individual thallus water contents.

2.2 Parameter Identification

The following photosynthetic and respiratory parameters were identified and analysed:

DRMAX and NPMAX (mg CO₂ g⁻¹h⁻¹) are the maximum rates of dark respiration and net photosynthesis respectively. At each temperature — for both species — for each individual thallus, maximum rates of dark respiration (DRMAX) occurred at the highest recordable thallus water contents. Whereas NPMAX occurs at sub-saturated thallus water contents. These sub-saturated water contents form the third parameter to be analysed — WCNPMAX (gg⁻¹). The thallus water content at which the maximum rate of net photosynthesis (NPMAX) occurs is both easy to measure and clearly shows the inextricable link between the two important environmental variables temperature and water in the lichen thallus. The fourth parameter SAT (gg⁻¹) is the saturated thallus water content. This parameter may give information of the relative water storage capacity of the two lichen thalli. However, this parameter does not give any information on the location or nature of the water storage sites. The final parameter %DEP (%) is the percentage depression in net photosynthesis occurring at full thallus hydration (SAT). It is given by the equation:

$$\% \text{ DEP} = ((\text{NPMAX} - \text{NPSAT})/\text{NPMAX}) \times 100$$

where NPSAT is the rate of net photosynthesis at full thallus hydration. Once more this is an easy parameter to measure. As the thallus water content increases the rate of net photosynthesis (NP) increases and reaches a maximum value (NPMAX) at a sub-saturated water content (WCNPMAX) a further increase in thallus water content results in a decline or depression in NP. By studying the dependence of this depression in NP on temperature it may be possible to elucidate the mechanism(s) causing the depression.

2.3 Analysis of Parameter Dependence on Temperature

The responses of the two species were compared using a two-way analysis of variance. Differences in mean pattern response were examined by testing for a statistically significant interaction. Where no interaction was detected, i.e. indicating parallel responses with temperature, we tested for a consistent species difference across the range of temperatures used. In some cases, the variables were first transformed by calculating the log_e of the variable before analysis to allow for increased variation amongst replicates as the response increased. In these analyses species differences are measured as proportionate temperature effects, and species differences are proportionate change differences as opposed to absolute differences. Also Q₁₀ values (SCHMIDT-NIELSEN 1975) were calculated to study the dependence of the rates of change of the maximum rates of dark respiration and net photosynthesis on temperature.

3. RESULTS

Figures 1a and 1b show the temperature and moisture dependencies of net photosynthesis (NP) very clearly. Under the light regime used maximum rates of net photosynthesis (NP_{MAX}) occur at 0° C for *Usnea aurantiaco-atra* and at 5° C for *U. antarctica*. This would be an expected result if *aurantiaco-atra* is not light saturated. Unfortunately, no experiments could be performed to ascertain light saturation levels for either species. The responses of individual replicates at these temperatures are shown in more detail in Figures 1c and 1d. A degree of variability in the pattern and absolute rates of response is apparent. The variability in the absolute rates of net photosynthesis of the individual replicates could be due to between replicate differences in the total thallus chlorophyll content and or algal cell number. The differences in the patterns of response could be caused by between replicate differences in the water storage capacity of the thalli. There is also a difference between species in the depression in net photosynthesis at full thallus hydration. The depression in net photosynthesis is greater in *U. aurantiaco-atra* as is also clearly shown in Table 1. It should be noted that at -5° C Figure 1a shows virtually no depression in net photosynthesis (NP) for *U. aurantiaco-atra*, and Figure 1b shows no depression in NP for *U. antarctica*. However, Table 1 shows small depressions in NP for the two species. This is because the saturated thallus water content (SAT) is difficult to measure, which results in a wide variation of values for this parameter. This is visible in Figures 1c and 1d where the individual replicate data is plotted. Figures 1a and 1b show the mean rates of NP, where n=4 for each temperature. This restricts the water content range of the plotted data because, as water content increases, some thalli are recorded as being saturated before others, and as soon as n=3 or less no more data can be plotted. Therefore the effective lack of a depression in NP at -5° C in Figures 1a and 1b is an unavoidable artefact of data presentation. At a glance Figure 1 shows the rates of net photosynthesis for *U. antarctica* are greater than for *U. aurantiaco-atra*.

Figures 2a and 2b show the temperature and moisture dependencies of dark respiration (DR) very clearly. In both species DR increases with temperature and is greatest at the highest experimental temperatures. At a glance Figures 2a, 2b, 2c and 2d show that the dark respiration rates of *U. antarctica* are greater than that of *U. aurantiaco-atra* at similar thallus temperatures and water content. The dark respiration (DR) rates show different moisture dependent responses in both species. These responses are approximately linear for *U. antarctica* and curvilinear for *U. aurantiaco-atra*. Rates of DR increase with increasing thallus water content. At each temperature — for both species — for each individual thallus maximum rates of DR (DR_{MAX}) occurred at the highest recordable thallus water contents (SAT). Figures 2c and 2d indicate the degree of variability in the DR rates. This saturation water content is species dependent — *U. antarctica* (U.a.) mean SAT = 2.13 gg⁻¹ (SE = 0.04, n = 46) and *U. aurantiaco-atra* (U.a-a.) mean SAT = 1.78 gg⁻¹ (SE = 0.03, n = 46) where the SAT ratio, U.a./U.a-a. = 1.20 — indicating that *U. antarctica* has the higher water storage capacity. However, this data sheds no light on the nature or location of the water storage sites in the two species.

The statistical analysis of the selected photosynthetic and respiratory parameters can be summarised as follows:

%DEP: (%) for both species a curvilinear increase with temperature is apparent (Tab. 2). However, it is possible that the formula used to calculate %DEP could give extreme values when NP_{MAX} is very low at high temperatures. Whether this should be treated as an artefact or a real effect can be debated. The curvilinearity of the response may in reality be less marked than the analysis suggests. Differences between species varied with temperature ($F_{6,42} = 3.28$; $p < 0.01$). The species effect is, however, probably best measured as a ratio of *U. antarctica* to *U. aurantiaco-atra*. These ratios are given in Table 1. Thus, apart from the high value — around unity — at 25° C, when the observed responses are very similar, the ratios are relatively stable. The above findings and the observation that between replicate variation increases with the response suggested repeating the two-way analysis of variance using log_e transformed data. Even after log_e transformation there is a statistically significant interaction ($F_{6,42} = 4.16$; $p < 0.01$) indicating some temperature dependence of the ratios, presumably most of the effect is due to the observation at 25° C.

One last point concerning the dependence of %DEP on temperature is that some curvilinearity is still present in the relationship between log_e (%DEP) and temperature (Tab. 2).

WCNP_{MAX} (gg⁻¹): for both species there is some decline with temperature. For *U. antarctica*, some curvilinearity in the relationship is apparent (Table 2). Two-way analysis of variance shows a statistically significant interaction

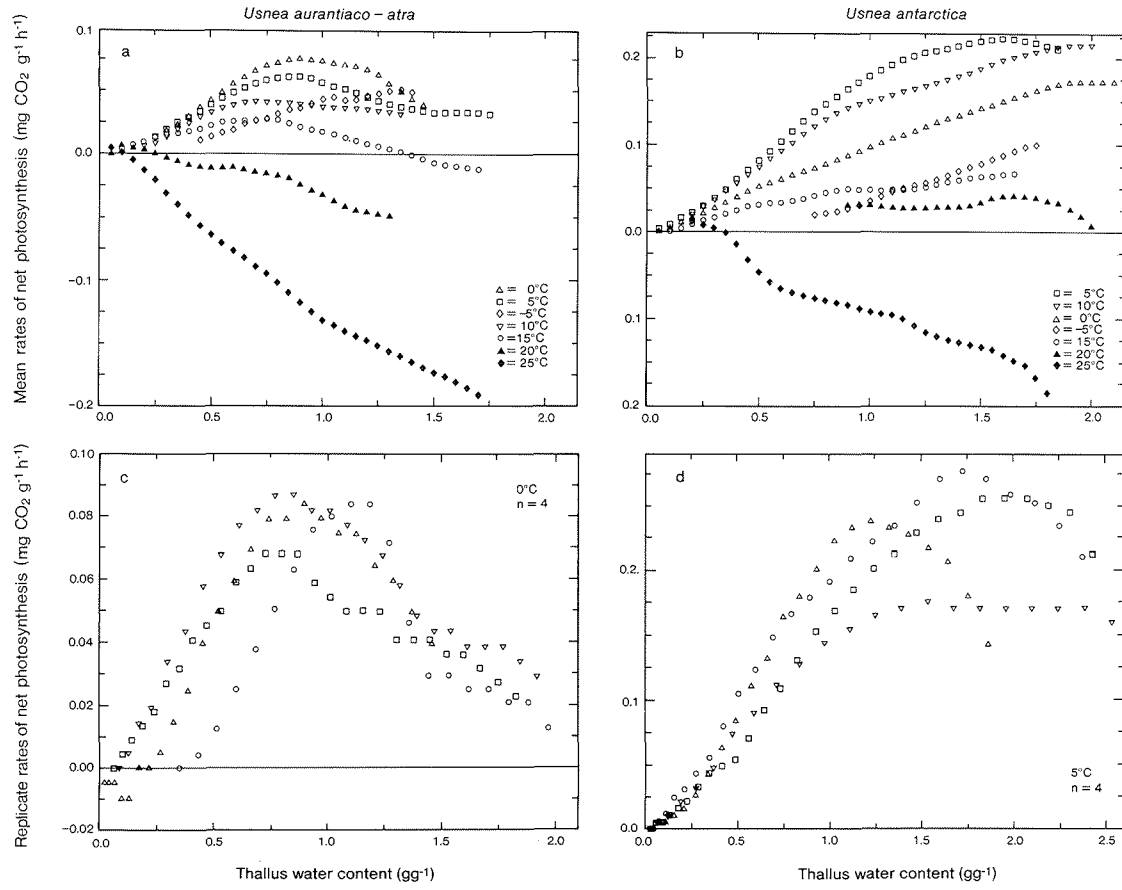


Fig. 1: Rates of net photosynthesis plotted against water content at different temperatures under 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ irradiance in the 400–700 nm waveband.

($F_{6,42} = 4.19$; $p < 0.01$). Differences between *U. antarctica* and *U. aurantiaco-atra* (from Tab. 1) over the range

| Temperature(°C) | %DEP(%). | | Parameters | | WCNPMAX (gg ⁻¹) | |
|-----------------|--------------|--------------|--------------|-----------|-----------------------------|--|
| | Species | | %DEP ratio | | Species | |
| | U.a. | U.a.-a. | U.a./U.a.-a. | U.a. | U.a.-a. | |
| -5 | 5.0± 5.0 | 31.7± 4.1 | 0.16 | 1.84±0.09 | 1.34±0.16 | |
| 0 | 8.3± 1.8 | 67.8± 6.4 | 0.12 | 2.14±0.20 | 0.92±0.08 | |
| 5 | 22.7± 6.6 | 55.4± 17.2 | 0.41 | 1.61±0.16 | 0.89±0.03 | |
| 10 | 9.2± 2.4 | 51.3± 4.8 | 0.18 | 2.08±0.22 | 0.69±0.08 | |
| 15 | 35.0± 10.7 | 171.2± 46.1 | 0.20 | 1.50±0.27 | 0.66±0.15 | |
| 20 | 187.9±106.2 | 1177.5±205.4 | 0.16 | 1.62±0.25 | 0.16±0.03 | |
| 25 | 1737.7±537.6 | 1560.0±502.1 | 1.11 | 0.20±0.02 | 0.11±0.04 | |

Tab. 1: Mean estimates (±SE) for %DEP and WCNPMAX with appropriate ratios at seven temperatures. U.a. = *Usnea antarctica* and U.a.-a. *Usnea aurantiaco-atra*

| Parameters | Species | | | | | |
|-------------|------------------------------|----|----|-------------------------|----|----|
| | <i>Usnea aurantiaco-atra</i> | | | <i>Usnea antarctica</i> | | |
| | b | QE | LF | b | QE | LF |
| %DEP | 47.2*** | ** | NS | 36.4** | ** | ** |
| Log (%DEP) | 0.128*** | ** | ** | 0.176*** | * | * |
| WCNPMAX | -0.04*** | NS | * | -0.05*** | ** | NS |
| DRMAX | 0.009*** | ** | NS | 0.018*** | * | ** |
| Log (DRMAX) | 0.128*** | * | NS | 0.133*** | ** | * |
| NPMAX | -0.002** | NS | ** | -0.005** | ** | ** |

Tab. 2: Levels of significance and estimated regressions of the parameters on temperature. Levels of significance are indicated: *p 0.05; **p 0.01; ***p 0.001; NS = not significant; b = estimated regression coefficient; QE = quadratic effect; LF = lack-of-fit test. Refer to tables 1 and 3 for units.

-5 to 25° C are as follows: 0.41, 1.22, 0.72, 1.39, 0.84, 1.46, and 0.09 gg⁻¹ (SE (dif) = 0.21). Thus, *U. antarctica* emerges as higher over the range -5 to 20° C with the difference being most pronounced in the range 0 to 20° C.

DRMAX (mg CO₂ g⁻¹ h⁻¹): both species show a significant curvilinear increase with temperature (Tab. 2). Over the range -5 to 20° C *U. aurantiaco-atra* changes 24-fold and *U. antarctica* 32-fold. As judged by the analysis of variance on the raw data, there is a highly statistically significant species by temperature interaction ($F_{5,24} = 31.1$; $p < 0.001$). However, similar considerations to those for %DEP show that the analysis of ratios is more relevant to the species comparison. The *U. antarctica*: *U. aurantiaco-atra* ratios over -5 to 20° C are given in Table 3. Again, these appear to be relatively stable over the temperature range used. This is supported by the observed lack of statistically significant interaction ($F_{5,24} = 2.49$; $p < 0.05$). Thus, values of DRMAX for *U. antarctica* are approximately twice those for *U. aurantiaco-atra* over the observed temperature range. Using log_e transformed data still shows some curvilinearity in the relationship with temperature for both species (Tab. 2).

NPMAX (mg CO₂ g⁻¹ h⁻¹): *U. aurantiaco-atra* shows a statistically significant decrease with temperature, where as for *U. antarctica* there is a pronounced quadratic effect with NPMAX increasing to a peak between 5 to 10° C and then falling off again (Tab. 2). Two-way analysis of variance shows a highly statistically significant

| Temperature (°C) | DRMAX(mgCO ₂ g ⁻¹ h ⁻¹) | | Parameters | | NPMAX(mgCO ₂ g ⁻¹ h ⁻¹) | | NPMAX ratio | |
|------------------|---|-------------|--------------|-------------|---|--------------|--------------|--|
| | Species | | DRMAX ratio | | Species | | U.a./U.a.-a. | |
| | U.a. | U.a.-a. | U.a./U.a.-a. | U.a. | U.a.-a. | U.a./U.a.-a. | | |
| -5 | 0.015±0.003 | 0.009±0.002 | 1.7 | 0.107±0.013 | 0.060±0.004 | 1.8 | | |
| 0 | 0.055±0.004 | 0.029±0.003 | 1.9 | 0.186±0.020 | 0.081±0.004 | 2.3 | | |
| 5 | 0.118±0.014 | 0.051±0.004 | 2.3 | 0.224±0.021 | 0.063±0.003 | 3.6 | | |
| 10 | 0.285±0.027 | 0.085±0.015 | 3.4 | 0.216±0.023 | 0.045±0.005 | 4.8 | | |
| 15 | 0.276±0.009 | 0.167±0.013 | 1.7 | 0.086±0.008 | 0.032±0.009 | 2.7 | | |
| approx | | | | | | | | |
| 20 | 0.487±0.008 | 0.220±0.023 | 2.2 | 0.050±0.025 | 0.008±0.002 | 6.3 | | |
| 25 | - | - | - | 0.013±0.006 | 0.004±0.001 | 3.3 | | |

Tab. 3: Mean estimated (±SE) for DRMAX and NPMAX with appropriate ratios at eight temperatures. U.a. = *Usnea antarctica* and U.a.-a. = *Usnea aurantiaco-atra*. DRMAX:NPMAX ratios between -5 to approximately 20° C for U.a. and U.a.-a. respectively are: U.a.: 0.14, 0.30, 0.53, 1.32, 3.21, 9.74; U.a.-a.: 0.15, 0.36, 0.81, 1.89, 5.22, 27.50

interaction effect ($F_{6,42} = 14.1$; $p < 0.001$) confirming the obvious that the difference between *U. antarctica* and *U. aurantiaco-atra* varies with temperature. Over the range -5 to 25°C the differences between *U. antarctica* and *U. aurantiaco-atra* (from Tab. 3) are as follows: 0.047, 0.105, 0.161, 0.171, 0.054, 0.042, and 0.009 $\text{mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ (SE (dif) = 0.019). Thus, *U. antarctica* has a rate which is consistently higher than for *U. aurantiaco-atra* and most marked in the range 0 to 10°C .

The variation in Q_{10} values for DRMAX and NPMAX across the experimental temperature range is presented in Table 4. The DRMAX:NPMAX Q_{10} value ratio remains relatively stable between -5 and 10°C in *U. aurantiaco-atra* and then increases between 10 and 20°C . The equivalent ratios are more variable in *U. antarctica* but show an overall increasing trend across the same temperatures range.

| Q_{10} values for parameters | Species | Temperature interval ($^\circ\text{C}$) | | | | | |
|-----------------------------------|---------|---|-----------|-----------|-----------|-----------|-----------|
| | | -5-0 | 0-5 | 5-10 | 10-15 | 15-20or20 | 20-25 |
| DRMAX | U.a.-a. | 10.38±5.84 | 3.09±1.69 | 2.78±2.38 | 3.86±2.80 | 1.99±2.09 | - |
| NPMAX | U.a.-a. | 1.82±0.83 | 0.60±0.39 | 0.51±0.64 | 0.51±1.59 | 0.06±0.70 | 2.25±5.39 |
| Q_{10} DRMAX/ Q_{10} NPMAX | U.a.-a. | 5.7 | 5.2 | 5.5 | 7.6 | 33.2 | - |
| DRMAX | U.a. | 13.44±5.77 | 4.60±2.21 | 5.83±2.71 | 0.94±0.72 | 3.11±0.48 | - |
| NPMAX | U.a. | 3.02±2.08 | 1.61±1.33 | 0.97±1.01 | 0.14±0.38 | 0.34±2.18 | 0.05±1.10 |
| Q_{10} DRMAX/ Q_{10} NPMAX | U.a. | 4.5 | 2.9 | 6.0 | 6.7 | 9.1 | - |

Tab. 4: Q_{10} values, and ratios, for the mean values of DRMAX (from Table 2) and NPMAX (from Table 2) with approximate \pm SE. U.a. = *Usnea antarctica* and U.a.-a. = *Usnea aurantiaco-atra*.

4. DISCUSSION

The depression in net photosynthesis at full thallus hydration is greater in *U. aurantiaco-atra* than *U. antarctica* at all temperatures studied except 25°C (Tab. 1). This could possibly be interpreted by LANGE (1980) as being due, in part, to an increase in the resistance of CO_2 diffusion through water in the liquid phase, as opposed to through the air. However, diffusion need not be through water to increase the resistance, there could be fewer air diffusion pathways. However, the *U. antarctica* thallus contains more water at full hydration than *U. aurantiaco-atra*. If the higher water content of *U. antarctica* results in a reduction of air diffusion pathways as compared to *U. aurantiaco-atra*, this may result in a greater resistance to CO_2 diffusion in the *U. antarctica* thallus at full hydration, and thus lead to a greater depression in net photosynthesis in this species when compared with *U. aurantiaco-atra*. With the exception at 25°C the reverse is observed. Higher rates of CO_2 fixation in *U. antarctica* could offset some of the effects a higher fully hydrated water content would have in decreasing the rate of CO_2 diffusion from the air to the algal cells. However, we would expect that this gain would be offset by the much greater rates of dark respiration in *U. antarctica*, therefore, another reason must be sought.

The increased depression in net photosynthesis values in *U. aurantiaco-atra* compared with *U. antarctica* could be due to a greater ratio of net respiration to net photosynthesis in the former species. This possibility is suggested by a comparison of the DRMAX:NPMAX ratios in Table 3 which are always greater in *U. aurantiaco-atra*. This is also paralleled in the ratio of the DRMAX:NPMAX Q_{10} values in Table 4, where overall they are greater in *U. aurantiaco-atra*.

HARRISSON et al. (1986) analysed the shape of the moisture dependent dark respiration curves for the foliose lichen *Umbilicaria antarctica*. They concluded that the diphasic moisture dependent relationship indicated that water was being stored in the intercellular air spaces in the medulla of the thallus. If this proposition is true then the moisture dependent forms of the dark respiration responses in Figure 2 would indicate that *U. aurantiaco-atra* — with its moderately diphasic moisture dependent response — has a moderately high intercellular water storage capacity — assumed to be primarily located in the medulla — similar to that of *Umbilicaria antarctica*. However, *Usnea antarctica* with its virtually linear moisture dependent response would appear to have a very low intercellular water storage capacity, which is also assumed to be primarily located in the medulla.

HARRISSON et al. (1986) used Q_{10} values to suggest the presence of ice within the thallus of *Umbilicaria*

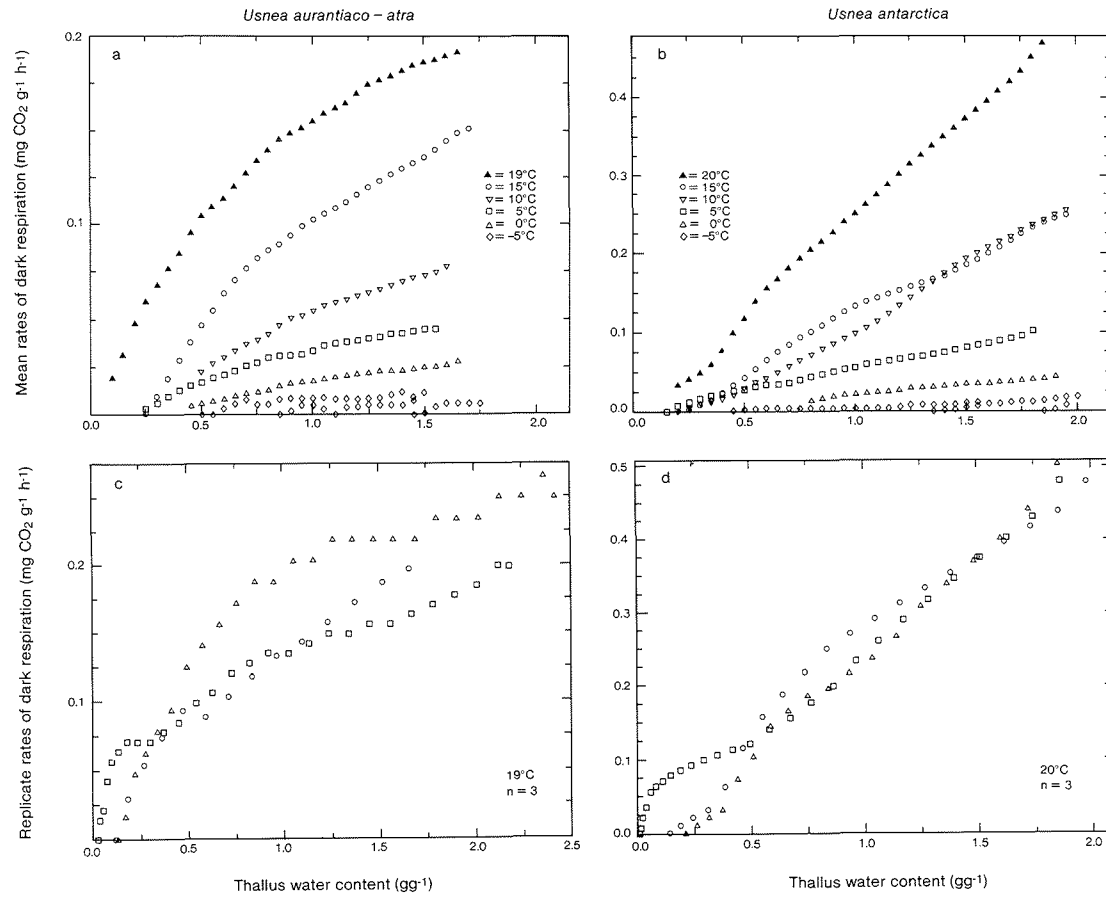


Fig. 2: Rates of dark respiration plotted against water content at different temperatures.

antarctica. If their arguments are correct the Q_{10} values in Table 4 would indicate the presence of ice within the thalli of *U. aurantiaco-atra* and *U. antarctica*. The Q_{10} values for the temperature interval -5 to 0° C are exceptionally high for maximum rate of dark respiration — 10.38 and 13.44 for *U. aurantiaco-atra* and *U. antarctica* respectively. HARRISSON et al. (1986) suggested ice formation within the thallus would lead to increased internal CO_2 diffusion resistances, thus elevating the Q_{10} values between -5 and 0° C. The corresponding Q_{10} values for the maximum rate of net photosynthesis are also slightly elevated for the temperature range -5 to 0° C, possibly for the same reasons. However, the effect is negligible because at the maximum rate of net photosynthesis there is less water in the thallus (NASH et al. 1983). This would result in a much reduced volume of ice forming, producing negligible increases in internal CO_2 diffusion resistances. However, it must be admitted that at -5° C the intercellular water may not be frozen, and increases in CO_2 diffusion resistances do not easily explain decreases in respiration rates, since the possibility exists that high local CO_2 concentrations could be expected, which would easily overwhelm the resistance effect. However, it must be noted that a patina of ice always formed on the surface of each thallus at -5° C. Therefore, even if the intercellular water is not frozen there still exists an ice barrier to gaseous diffusion. The possibility of membrane damage occurring at -5° C should be investigated. Such a possibility could provide an alternative explanation for decreased CO_2 exchange rates — in the light and dark — and thus elevated Q_{10} values for the temperature interval -5 to 0° C. If fungal membranes are more susceptible than algal membranes, this could account for the greater elevation in Q_{10} values for dark respiration when compared with net photosynthesis.

LANGE (1980) suggested that interaction between changes in the CO_2 diffusion resistance through water with temperature and the mass of thallus water present might be responsible for the shift in the water content yielding the maximum rate of net photosynthesis (WCNPMAX) to lower water contents at higher temperatures (Tab. 1). NASH et al. (1983) suggested that water contents yielding optimal photosynthetic rates occur when the intercellular spaces are not filled with water, and assumed that CO_2 does not pass through a water layer as it diffuses inward to the algae. Such conditions would be directly analogous to CO_2 travelling through vascular plant stomata and substomatal cavities to the mesophyll cells.

In both species there is some decline in the water content yielding the maximum rate of net photosynthesis with temperature. Values for *U. aurantiaco-atra* are less than for *U. antarctica* which could suggest that the former species has a larger intercellular water mass than the latter. This conclusion was previously reached from an analysis of the shape of the moisture dependent dark respiration curves. For much of the temperature range of *U. antarctica* the low mass of intercellular water — if the suggestion is correct — would result in a relatively high and fairly constant water content yielding the maximum rate of net photosynthesis. Only at higher temperatures would increases in the CO_2 diffusion resistance of water be large enough to require a much reduced thallus water content, in *U. antarctica*, in order to yield the maximum rate of net photosynthesis. Alternatively it must be noted that the greater increase in dark respiration with temperature than photosynthesis would also give this result.

To conclude, although morphologically similar (WALKER 1985) the respiratory and photosynthetic responses of the two species to the same experimental conditions were totally different. The possibility exists that they differ in their light response, but unfortunately no experiments could be performed to ascertain the pattern of response of net photosynthesis to increasing irradiance levels — at each thallus water content and temperature. Also the two species used in the experiments differed with regard to their modes of reproduction. Within the subgenus *Neuropogon* *Usnea aurantiaco-atra* is one of six species which reproduces sexually, by means of abundant ascospore producing apothecia, lacking any vegetative propagules. Whereas, *Usnea antarctica* is one of four asexual species which are occasionally fertile (WALKER 1985). The *U. aurantiaco-atra* thalli used in the experiments bore abundant apothecia. Whereas, the *U. antarctica* thalli possessed abundant soredia. These vegetative propagules are defined as clusters of fungal hyphae and algal cells without cortex, and are classified as secondary in that they are produced on papillae, and unlike species in which soralia develop from the cortex, are not confined to apices or secondary branches (WALKER 1985). The possibility has not been discounted that the presence of these widely different reproductive structures could account for some of the differences in CO_2 exchange between the two species, under the same experimental conditions.

5. ACKNOWLEDGEMENT

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