

# PHOTOSYNTHESIS AND RESPIRATION OF *COLOBANTHUS QUITENSIS* AND *DESCHAMPSIA ANTARCTICA* FROM THE MARITIME ANTARCTIC

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**ABSTRACT.** The effects of irradiance level, temperature and cultivation conditions on net photosynthesis and respiration are described for the two maritime Antarctic flowering plant species *Colobanthus quitensis* and *Deschampsia antarctica* under controlled laboratory conditions. The optimum temperature for net photosynthesis occurred at about 13°C for the grass and 19°C for the pearlwort. However, both species achieved around 30% of their maximum rate at 0°C, possibly their most important feature for survival in the Antarctic. The highest photosynthetic rates recorded were 8.8 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup> for *D. antarctica* and 14.5 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup> for *C. quitensis*. The diurnal course of assimilation in mid-summer at 60° S latitude is predicted from a combination of field microclimate data and the laboratory metabolic measurements, and net daily uptake of 55–105 and 35–73 mg CO<sub>2</sub> dm<sup>-2</sup> is projected for the grass and pearlwort, respectively. Neither the pearlwort nor the grass appear to have developed specialized metabolic adaptations for survival under Antarctic conditions. Their existence in maritime Antarctic regions is dependent upon a combination of genetical, morphological and ecological strategies and occupation of relatively favourable habitats. *Colobanthus* and *Deschampsia* are most vulnerable during the few weeks following the spring melt.

## INTRODUCTION

Despite the uniqueness of *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv. in being the only angiosperms to have colonized Antarctic regions, little has been published on their physiology under field or laboratory conditions besides Gannutz's observation (in Ahmadjian, 1970) that *D. antarctica* ceases to photosynthesize below 0°C and respire down to -10°C. Holtom and Greene (1967) had earlier demonstrated that alternating temperature conditions were most favourable for the growth of both species and that continuous temperatures of 18°C or above eventually proved fatal. The development of a carbon dioxide analysis system and controlled temperature growth cabinets by the British Antarctic Survey enabled the effects of irradiance level and temperature on the metabolism of the two species to be investigated, using material brought from the Antarctic and maintained in Birmingham. The provenance of the plants spanned 13° of latitude.

## METHODS

An open flow gas-exchange system, based on an infra-red CO<sub>2</sub> analyser, was operated differentially. The plant chamber, a rectangular double-walled box of transparent acrylic was contained within a growth cabinet which provided a background temperature around freezing. Fine temperature control was achieved by circulating coolant around the jacket of the chamber. Chamber and plant surface

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temperatures were monitored with copper/constan thermocouples and a Comark electronic thermometer. Illumination was provided by 180 W low pressure sodium lamps and photosynthetically active radiation (PAR) was measured with a Lambda quantum sensor. The air stream was humidified before being directed to the plant chamber but the relative humidity was not monitored during the experiments.

Calibration gases (Rank Precision Instruments) were independently checked at Rothamsted Experimental Station and found to be 263.3 and 326.3 ppm CO<sub>2</sub>. Output from the Grubb Parson IRGA model S.B.2 was to a potentiometric recorder. To minimize leakage and diffusion of carbon dioxide the permanent airlines were of nylon tubing. Flow rates were controlled at 0.4 dm<sup>3</sup> min<sup>-1</sup> with rotameters. The formula of Janac and others (1971, equation 3.21) was used to calculate fixation rates.

For each trial between 10 and 20 healthy shoots of either *D. antarctica* or *C. quitensis* were used. To minimize decomposer respiration as much dead material as possible was removed. Also, to minimize variability caused by differences in root biomass all roots were excised and the intact shoots inserted immediately into a small piece of saturated sponge. These were then sealed in the plant chamber with a thermocouple arranged to record the temperature of the underside of one of the 30–60 leaves. The chamber and living material were left to equilibrate for 15–20 minutes at *c.* 10°C with the cabinet lights giving irradiance of *c.* 300  $\mu\text{E m}^{-2} \text{s}^{-1}$ .

To investigate temperature effects the chamber was held under constant bright illumination during each trial as the plant temperature was reduced from 10°C to below freezing and then warmed again to above 30°C. Irradiance levels varied between trials from 225–400  $\mu\text{E m}^{-2} \text{s}^{-1}$  and dark respiration was measured periodically by completely covering the chamber with aluminium foil.

To study the effects of variation in light intensity the chamber was shaded with increasing layers of tissues, whilst maintaining a constant temperature. After each series of photosynthetic measurements at decreasing light intensities, the plant material was allowed to re-adjust to maximum light intensity while the temperature was stabilizing at a new level. None of the plant material tested showed signs of water stress when removed for dry-weight determination. Mean leaf breadth was determined by measuring a sub-sample of ten leaves and leaf area estimated by multiplying this by the total leaf length of all shoots.

Material from a number of different populations and localities was tested. Plants from Cumberland East Bay on South Georgia (54° 17' S, 36° 30' W), Lynch Island\* and Signy Island in the South Orkney Islands (60° 43' S, 45° 36' W), and Blaiklock Island in Marguerite Bay (67° 33' S, 67° 04' W) were transported in a frozen condition. Some were kept in growth cabinets under either a 8°C/0°C or 15°C/–2°C day/night regime. Other plants were grown outside under English summer conditions, which ranged from 9° to 27°C.

Microclimate data were obtained during January 1970 at a typical mixed vascular plant community on the west coast of Signy Island using a Grant type D microclimate recorder similar to that described by Walton (1982). Readings were taken automatically at hourly intervals on pressure sensitive paper and visits to check batteries, probe position and calibration were made every three days. Temperatures were recorded by thermistor beads encased in 3.5 mm stainless steel tubes and nine such probes were placed as follows:

- 1 Shaded air temperature, 12 cm above the vegetation.

\* This material was sampled before Lynch Island was designated a Specially Protected Area (SPA No. 14 in the Antarctic Treaty Area).

- 2,3 Wet and dry 'bulb' temperatures in a ventilated psychrometer, 5 cm above the vegetation.
- 4 Soil temperature, 3 cm deep beneath intermixed *D. antarctica*/*C. quitensis* shoots.
- 5,6 Temperatures just below the main leaves of *C. quitensis*.
- 7-9 Temperatures between the leaves of *D. antarctica*.

Probes were inserted 1 cm into cushions of *C. quitensis* and 1.5 cm into tufts of *D. antarctica*. One plant of each species growing in a shallow, moist east-facing gully was monitored as well as plants on a drier, more exposed north-facing slope. In addition, temperatures were recorded in a grass plant growing in a permanently wet north-facing depression. The accuracy of such data has been reviewed by Wright (1975) and Walton (1977) and is normally  $\pm 1.2^\circ\text{C}$  or better for most of the data (Walton, 1982).

Incoming solar radiation was monitored by a Kipp and Zonen type CM5 solarimeter mounted at ground level, with the instrument disc parallel to the general  $40^\circ$  north-facing slope of the sward. The spot radiation measurements were totalled multiplied by 60 to give daily integrated values. It is not possible to exactly equate these radiation measurements with the intensity measurements taken in the laboratory studies for, although PAR is approximately 48% of the total incoming radiation, the precise value varies according to the degree to which the sky is overcast. Based on the solar constant and details supplied by the manufacturers of the quantum sensor, a radiation receipt of  $1 \text{ J m}^{-2} \text{ s}^{-1}$  was taken to be approximately equivalent to a photon flux of  $1.48 \mu\text{E m}^{-2} \text{ s}^{-1}$ .

## RESULTS

### *Photosynthetic response to temperature*

Nine series of measurements were made of net photosynthetic rate and its fluctuation with temperature with *D. antarctica*, and seven trials were carried out using *C. quitensis*. Because the maximum net photosynthetic rate recorded in each trial showed considerable variation, possibly reflecting the different age, vigour and environmental history of the plants, comparison was most suitably effected by a simple transformation of the raw data, expressing the net photosynthesis values from each trial as percentages of the maximum rate observed during that trial. This procedure also has the advantage of making the temperature response curves at least partly independent of any calibration errors inherent in the gas analysis system and the small differences in light levels between trials, and, in addition, accentuates the optimum temperature range and the positions of the upper and lower compensation points. Fig. 1 shows the scatter of values for the photosynthetic rate of *D. antarctica* from three localities at non-limiting irradiance levels. The maximum rates of  $\text{CO}_2$  uptake ranged from 2.3 to  $8.8 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ , the latter with material from Lynch Island at  $10^\circ\text{C}$  and  $268 \mu\text{E m}^{-2} \text{ s}^{-1}$ , and the mean maximum rate was  $4.3 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ . The results suggest that the grass shows a broadly similar response to temperature throughout the southern part of its range. Any slight difference in optimum temperature for photosynthesis between Antarctic and sub-Antarctic material does not appear to be significant and there was no evidence that the compensation points of the grass from different localities varied greatly.

Since there appeared to be no major difference in photosynthetic behaviour of plants from different localities, data from the nine trials were amalgamated to produce an average temperature response curve for *D. antarctica* (Fig. 2). The lower

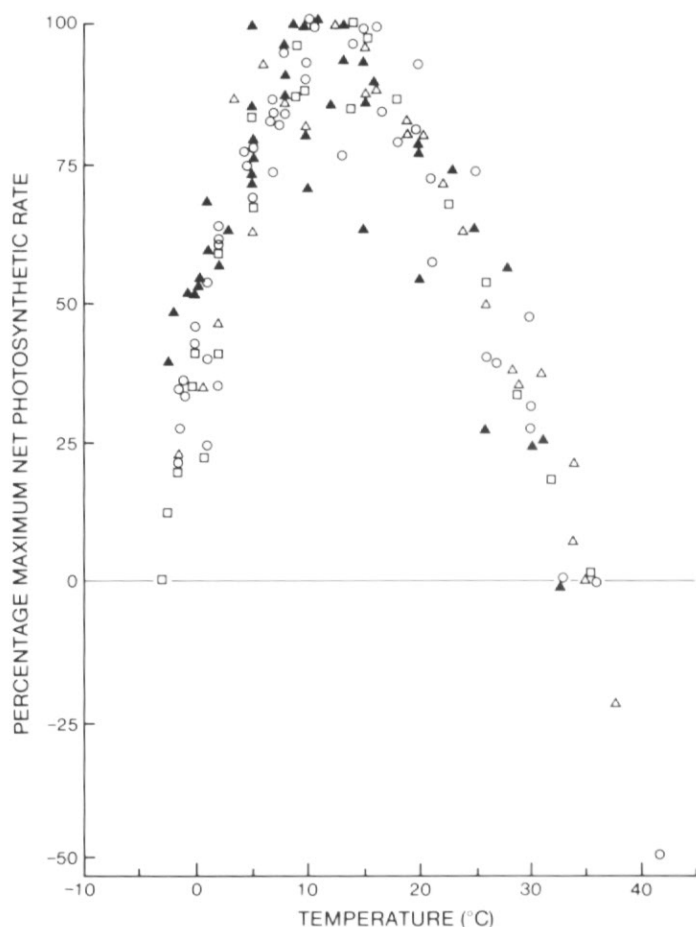


Fig. 1. Effect of temperature on net photosynthesis of *Deschampsia antarctica* from South Georgia (○), South Orkney Islands (△), and Marguerite Bay (□). Closed symbols are values for plants which had never been exposed to UK environmental conditions. Irradiance levels 250–460  $\mu\text{E m}^{-2} \text{s}^{-1}$ .

compensation point was not reached, but extrapolation from this graph suggests that it would be in the region of  $-2$  to  $-4^\circ\text{C}$ , and net photosynthesis at  $0^\circ\text{C}$  was found to be *c.* 40% of the maximum. Fig. 2 suggests that the upper compensation point for the grass is at  $35^\circ\text{C}$  and that the optimum temperature for photosynthesis is around  $13^\circ\text{C}$ .

Figs 3 and 4 shows the corresponding temperature response for *C. quitensis*. There was greater variability in this species and the maximum rates of net photosynthesis recorded ranged from 2.5 to 14.5  $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ , the latter with South Georgia material at  $10^\circ\text{C}$  and 321  $\mu\text{E m}^{-2} \text{ s}^{-1}$ . The mean maximum rate was 6.4  $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$  and the average curve appears slightly broader in overall form than that of the grass, with the temperature optimum between 14 and  $22^\circ\text{C}$ . Again the lower compensation point was not reached but extrapolation indicates this to be in the region of  $-5^\circ\text{C}$ . The upper compensation point appeared to be around  $+40^\circ\text{C}$ , and at  $0^\circ\text{C}$  the pearlwort was able to photosynthesize at approximately 30% of its maximum rate.

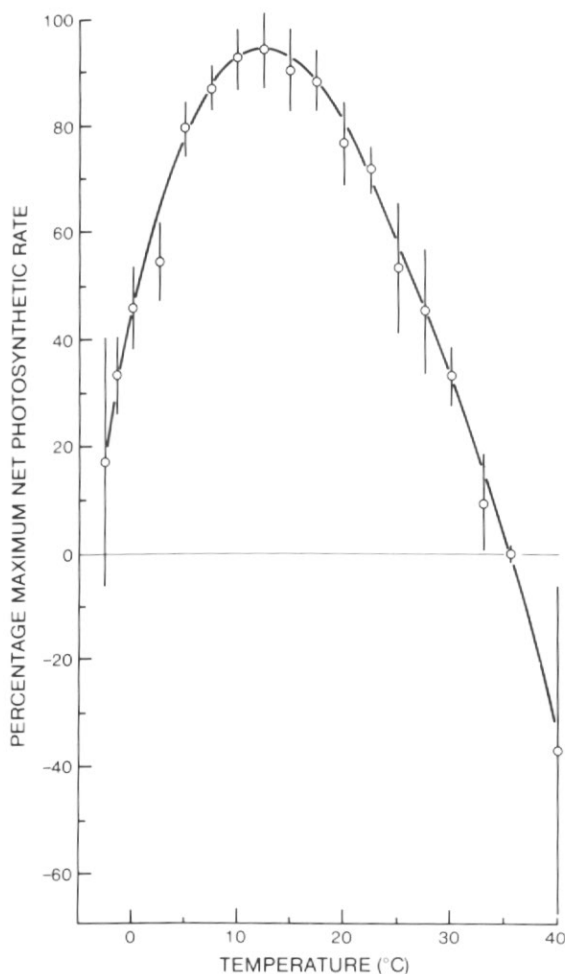


Fig. 2. Mean temperature response curve for *Deschampsia antarctica* at non-limiting irradiance levels ( $250\text{--}460\ \mu\text{E m}^{-2}\ \text{s}^{-1}$ ). Vertical lines represent one standard deviation either side of the mean (derived from data in Fig. 1).

#### Photosynthetic response to irradiance level

*Deschampsia antarctica* from Blaiklock Island, which had been grown under a  $15^\circ\text{--}2^\circ\text{C}$  regime in Birmingham, was tested under varying light intensities at five different constant temperatures. The results (Fig. 5a) confirm that the optimum temperature for this species is between  $10$  and  $20^\circ\text{C}$  and suggest that temperature, and possibly carbon dioxide concentration, is more likely to be limiting to photosynthesis than light intensity. Net photosynthetic rates were largely independent of irradiance levels above  $150\ \mu\text{E m}^{-2}\ \text{s}^{-1}$  and, since quantum flux measurements under full midday sun can reach around  $2000\ \mu\text{E m}^{-2}\ \text{s}^{-1}$  it would appear that *D. antarctica* is able to utilize even heavily overcast daylight as low as 7.5% of the maximum intensity. It would therefore appear that light intensity would be saturating for the major part of each day during the growing season.

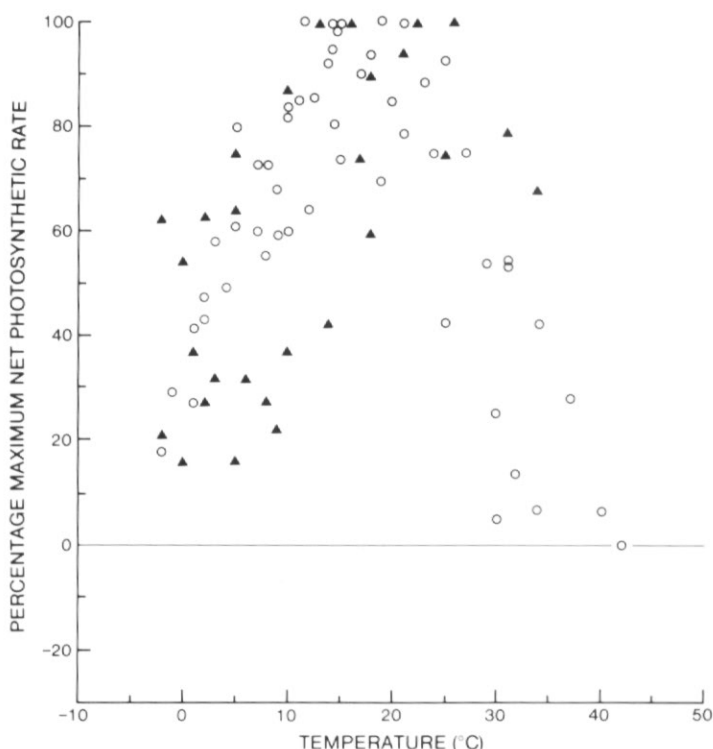


Fig. 3. Effect of temperature on net photosynthesis of *Colobanthus quitensis* from South Georgia (○), and the South Orkney Islands (△). Closed symbols are values from plants which had never been exposed to UK environmental conditions. Irradiance levels 225–480  $\mu\text{E m}^{-2} \text{s}^{-1}$ .

The curves for *Colobanthus quitensis* from South Georgia (Fig. 5b) show a broadly similar response to light intensity, with highest rates of photosynthesis being recorded under bright illumination at 10°C. As with *D. antarctica*, they indicate that below 20°C the compensation point is very low, a light intensity of around 10  $\mu\text{E m}^{-2} \text{s}^{-1}$  being sufficient for photosynthesis to balance respiration, but that at 30°C higher light intensities were required to reach compensation. However, light saturation proved more difficult to obtain with *C. quitensis*, especially at the higher temperatures. The pearlwort showed light saturation at 50  $\mu\text{E m}^{-2} \text{s}^{-1}$  at 0°C and at 100  $\mu\text{E m}^{-2} \text{s}^{-1}$  at 5°C but at 10°C and above, even the highest intensities obtained experimentally appeared still to be limiting photosynthesis.

#### *Photosynthetic response to cultivation conditions*

Fig. 6 shows the results of trials using plants of *D. antarctica* which had been returned to the UK, divided and then cultivated in different environments for the next 3 months. The limited data available suggest that when material from South Georgia and the South Orkney Islands, which had previously been regularly subjected to sub-freezing temperatures in a growth cabinet, was cooled to below freezing and then raised to higher temperatures, net photosynthesis at each temperature resumed at a

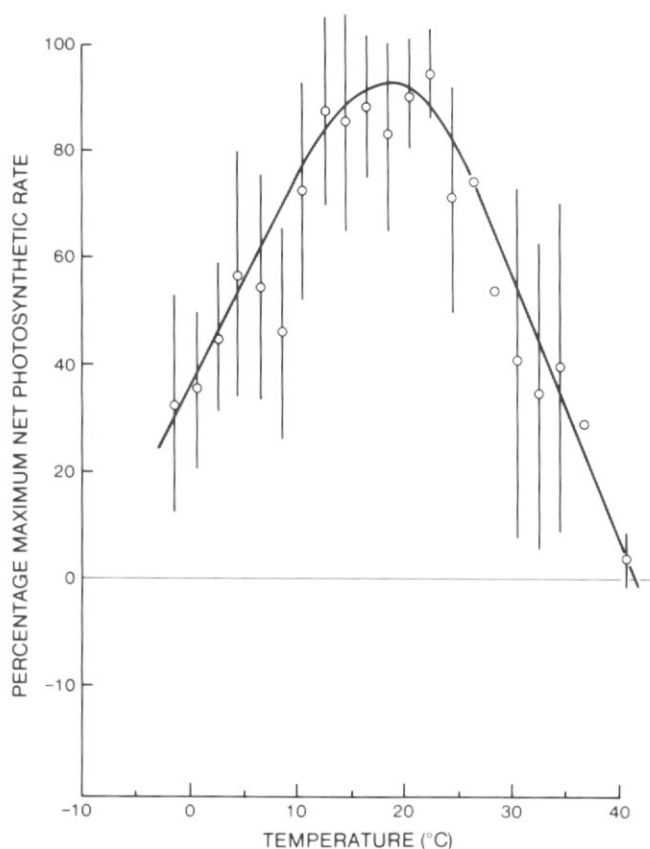


Fig. 4. Mean temperature response curve for *Colobanthus quitensis* at non-limiting irradiance levels ( $225\text{--}480\ \mu\text{E m}^{-2}\ \text{s}^{-1}$ ). Vertical lines represent one standard deviation either side of the mean (derived from data in Fig. 3).

similar or slightly enhanced rate to that prior to the sub-zero exposure. When material of the same age and genotype had been grown in a relatively warm temperature regime, net photosynthetic rates were slightly depressed by a period of cooling to below zero. It was not possible to detect any shift in optima or compensation points with cultivation conditions, as was shown in *Oxyria digyna* by Billings and Mooney (1968). The higher rates of photosynthesis obtained with material grown in a cool growth cabinet are only apparent when the results are expressed on a leaf area basis and are not reproduced when the results are calculated per gram dry weight of plant. The reason for this appears to be a change in the density of leaf tissue in plants grown under the different conditions; material from Lynch Island grown under cool conditions maintained its field appearance and had a dry weight of  $0.07\ \text{g dm}^{-2}$  leaf area, but there was an increase in the leafiness of the shoots of plants grown out of doors in UK summer conditions ( $0.05\ \text{g dm}^{-2}$ ). The South Georgian plants were slightly more robust but also showed a difference in the density of leaf tissue, the respective dry weights being  $0.12\ \text{g dm}^{-2}$  and  $0.07\ \text{g dm}^{-2}$ . The apparently lower rates of photosynthesis recorded when material was cultivated in

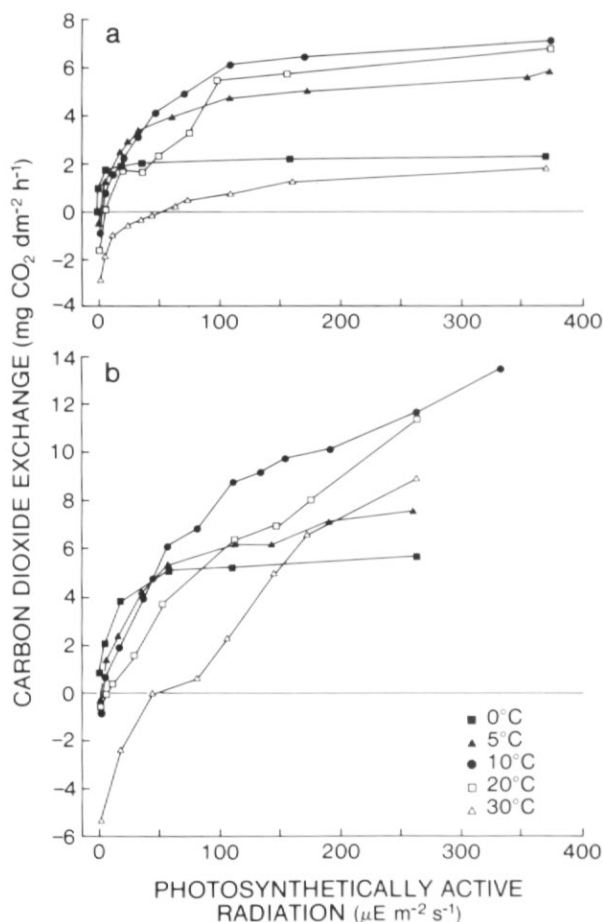


Fig. 5. Effect of light intensity on carbon dioxide flux at various temperatures for *Deschampsia antarctica* (a) and *Colobanthus quitensis* (b).

abnormally warm conditions are correlated with an increase in leafiness of the shoots, caused partly by a greater expansion of leaf tissue. Unfortunately, no comparable data are available for *C. quitensis*.

#### Dark respiration rates

There was no significant difference in the respiration rates of either *D. antarctica* or *C. quitensis* when temperatures were below 10°C but there was a noticeable increase when the plants were exposed to higher temperatures and complete darkness. Sub-Antarctic populations from South Georgia had a slightly lower rate of respiratory increase (Fig. 7). Exposure to sub-zero temperatures and a subsequent warming led to an increase in the respiration rate over that initially recorded in most of the trials. In some cases a lowering of temperatures to zero led to a reduction in the respiration rate but further cooling to  $-1$  or  $-2^\circ\text{C}$  caused a slight increase in respiration. As it was difficult to reach lower temperatures than this, it was not possible to verify



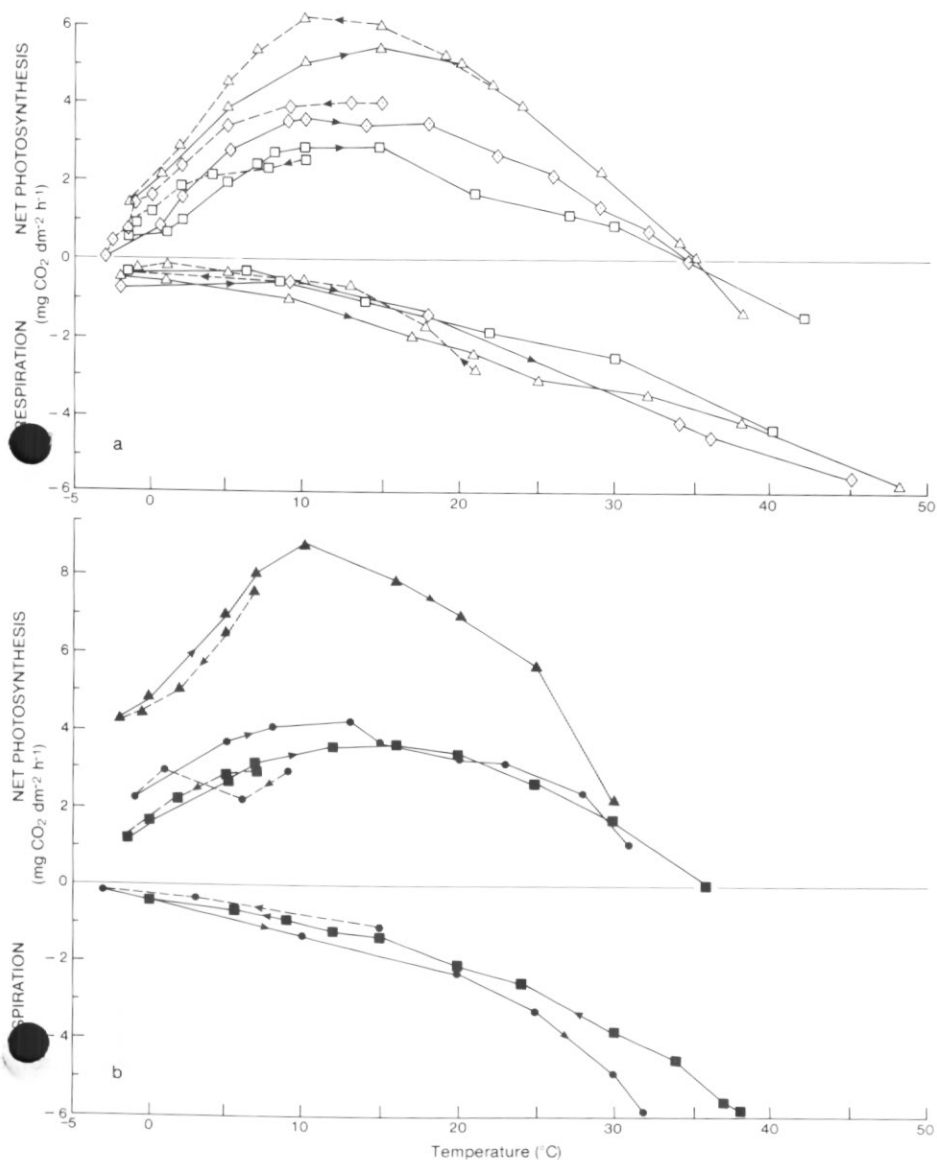


Fig. 6. Net photosynthesis (at  $c. 300 \mu\text{E m}^{-2} \text{s}^{-1}$  and dark respiration of *Deschampsia antarctica* before (broken lines) and after (continuous lines) exposure to freezing temperatures. (a) Material grown outdoors in UK. (b) Material maintained in a cool growth cabinet. ■, South Georgia material (268); □, South Georgia material (293); ▲, Lynch Island material (268); △, Lynch Island material (268); ●, Signy Island material (385); ◇, Blaiklock Island material (254). Values in brackets are actual irradiance levels ( $\mu\text{E m}^{-2} \text{s}^{-1}$ ) used for each photosynthesis trial.

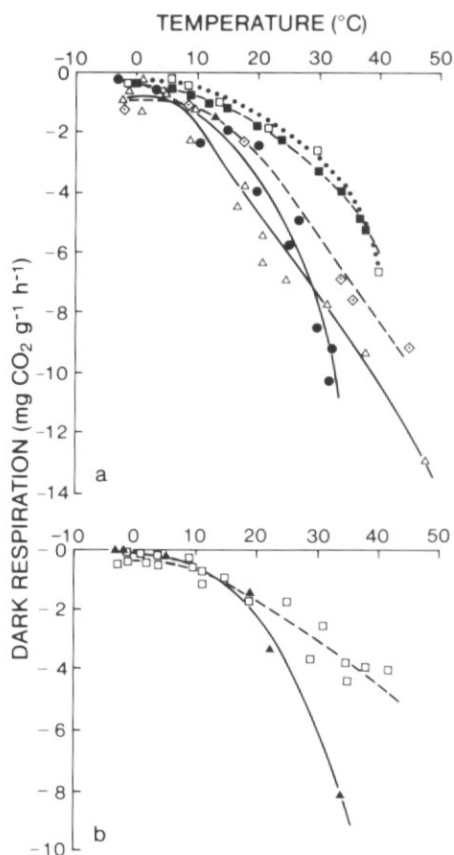


Fig. 7. Effect of temperature on dark respiration rates of *Deschampsia antarctica* (a) and *Colobanthus quitensis* (b) from South Georgia ( $\square$ ), Lynch Island ( $\triangle$ ), Signy Island ( $\bullet$ ), and Blaiklock Island ( $\diamond$ ). Closed symbols are values from plants which had never been exposed to UK environmental conditions. Curves fitted by eye.

Gannutz's observation (in Ahmadjian, 1970) that *D. antarctica* continues to respire at high rates down to  $-10^{\circ}\text{C}$ . The practice of periodically covering the chamber in aluminium foil was found to have no effect on the subsequent photosynthetic rate, which invariably returned to its former level within 15 minutes of the removal of the foil.

#### Field microclimate conditions

Some details of the variation of temperatures within the flowering plant communities on the South Orkney Islands during summer and winter have been provided by Edwards (1972). However, the daily duration within specific temperature ranges is of much greater significance than isolated measurements in determining their metabolic rates and periods of growth or development.

Thermal conditions were recorded within a *D. antarctica/C. quitensis* community over a period of 20 days during January 1970, the weather during this period being fairly typical of summer on Signy Island. Fig. 8 summarizes the microclimate

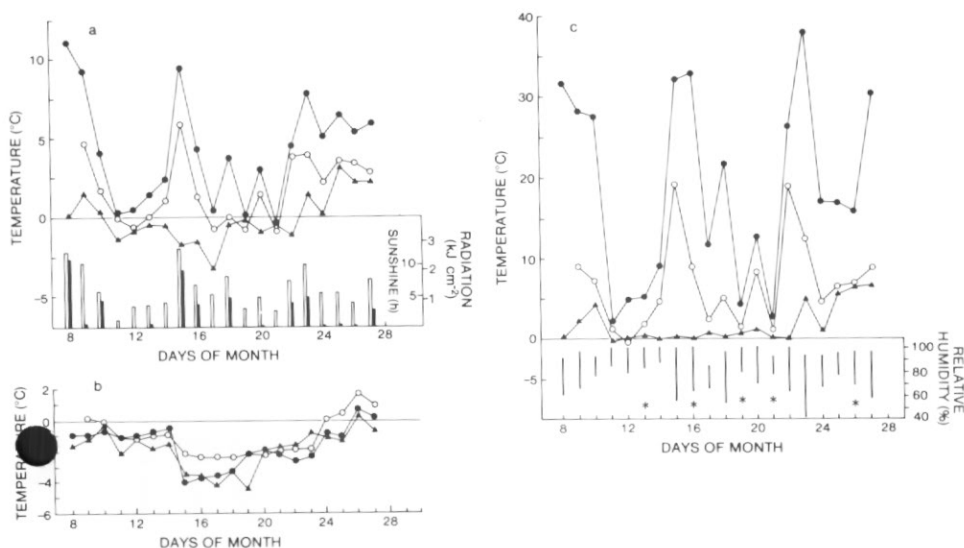


Fig. 8. Comparison of daily mean (a), daily minimum (b) and daily maximum (c) temperatures, recorded with daily radiation receipt and humidity at vegetation level, in a *Deschampsia antarctica* stand near Sprindrift Rocks, Signy Island. Microclimate data collected during January 1970. ●, Temperature of *D. antarctica* in a dry position; ○, temperature of *D. antarctica* in a moist position; ▲, air temperature 12 cm above vegetation; I, total sunshine received by a Campbell-Stokes recorder; |, total radiation estimated by integration of hourly Kipp and Zonen solarimeter measurements; |, daily range of humidity 5 cm above vegetation; \* days with precipitation.

variation within *D. antarctica* tufts during this period. The temperatures recorded 12 cm above the vegetation differed little from air temperature at the meteorological station on the other side of the island 3.7 km to the south-east. It can be seen that the maximum, mean and minimum grass temperatures were all generally higher than the meteorological data would suggest, the degree of difference being dependent on the total incoming radiation. The graphs also indicate the effect of local soil moisture conditions, the grass in a wet area never becoming as warm as that on well drained soil, but not being exposed to such low temperatures during cold spells.

A more detailed analysis of temperatures in different parts of the vegetation is recorded on a percentage frequency basis in Table I. Although the air temperature 12 cm above the grass was above 0°C for 35% of the time, temperatures amongst the vegetation were above freezing for between 49% (dry *Colobanthus*) and 62% (dry *Deschampsia*) for this period. Soil temperatures were below freezing for only a quarter of the time. There was little difference between the higher temperatures in plants of *D. antarctica* and *C. quitensis* in dry open positions; each experienced temperatures of 30°C or more for a similar amount of time (c. 1.6% of the 20-day period), with maxima of c. 38° and 36°C being attained in the grass and pearlwort, respectively. For plants in more shaded and slightly moister habitats temperatures rarely rose above 20°C and were above 10°C for only 10% of the time. An even more equable microclimate was recorded in an area of permanently moist grass nearby where the temperature never rose above 20°C nor fell below -2.5°C; in fact, 73% of all temperatures recorded within this grass during the 3-week period were within the -2.5° to 2.5°C threshold.

The correlation between diurnal vegetation temperature and solar radiation is

Table I. Distribution of hourly microclimate temperatures recorded at a grass site north of Spindrift Rocks, Signy Island

Position of thermistor	Percentage frequency of recordings within each temperature increment							
	Below -5.0°C	-5.0 to -0.1	0 to 4.9	5.0 to 9.9	10.0 to 14.9	15.0 to 19.9	20.0 to 24.9	Above 25.0°C
In air and soil								
12 cm above ground level	1.3	63.7	27.4	7.2	0.4	—	—	—
3 cm below ground level	—	24.0	49.7	14.3	6.3	3.7	2.0	—
In <i>Deschampsia antarctica</i>								
Waterlogged tuft	—	40.4	45.8	9.9	1.8	2.1	—	—
Moist shaded tuft	—	47.6	34.3	9.2	5.0	2.8	1.1	—
Dry exposed tuft	—	38.3	33.5	10.8	8.0	4.2	2.0	3.7
In <i>Colobanthus quitensis</i>								
Moist shaded cushion	—	44.1	33.4	11.0	6.4	1.8	2.7	0.6
Dry exposed cushion	—	51.2	22.7	10.2	6.8	3.5	2.0	3.6

Data collected between 8–27 January 1970 inclusive and subsequently grouped into 5°C increments.

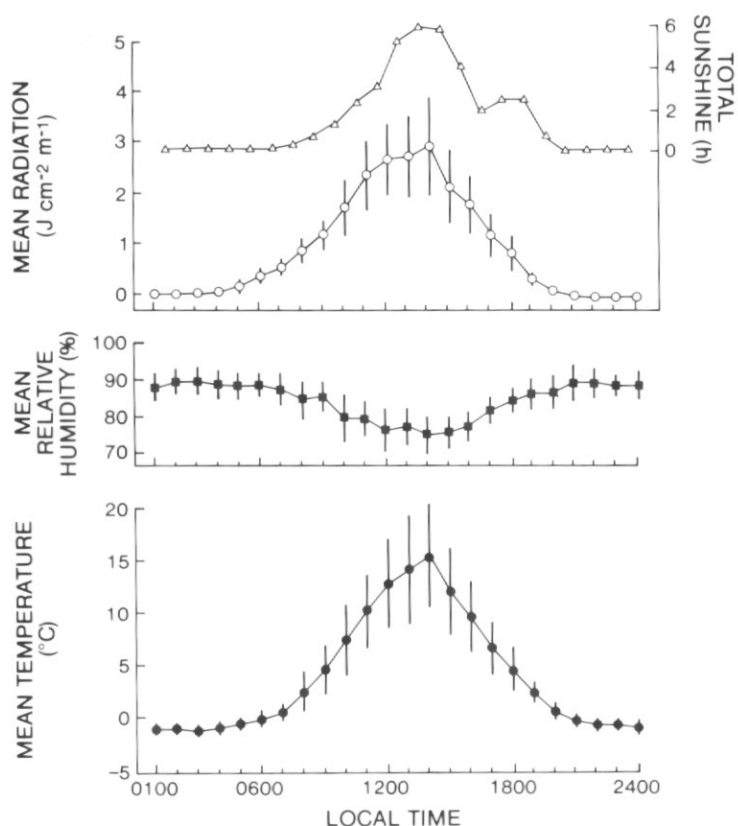


Fig. 9. Diurnal variation in summer microclimate at a mixed vascular plant community on the west coast of Signy Island, recorded between 8 and 27 January 1970. Vertical lines indicate 95% confidence limits either side of the mean. ●, Temperature amongst *Deschampsia antarctica* in a dry situation (measured by thermistor); □, relative humidity (measured by ventilated psychrometer); ○, radiation (measured by Kipp and Zonen solarimeter); △, hourly integrated total sunshine (measured by Campbell-Stokes recorder).

shown in Fig. 9. The greatest radiation receipt occurred between 1100 and 1500 h local time, which coincided with the period of highest temperatures in the sward. Fig. 9 suggests that the average January day for the Signy Island vascular communities has around 17 hours of usable daylight, vegetation temperatures of around  $-1^{\circ}\text{C}$  from 2100 to 0600 hours with air temperatures amongst the leaves rising to  $10\text{--}15^{\circ}\text{C}$  between 1100 and 1600 h. Naturally, there was much variation: the highest radiation intensity recorded was  $7.1\text{ J cm}^{-2}\text{ min}^{-1}$ , at 1100 hours on 15 January whilst on a very overcast day the maximum intensity recorded was only one-tenth of this ( $0.67\text{ J cm}^{-2}\text{ min}^{-1}$  at 1700 h on 11 January). Fig. 8c illustrates that the temperatures in the grass on the latter day failed to rise above  $3^{\circ}\text{C}$  whilst on the former day they reached  $33^{\circ}\text{C}$ . During the monitoring period the incoming radiation was measured hourly and averaged  $1369\text{ J cm}^{-2}\text{ day}^{-1}$ . Thus the total radiation received over the 20-day period amounted to around  $27390\text{ J cm}^{-2}$  or approximately  $42500\text{ J cm}^{-2}$  for the whole month of January. This is approximately 44% of the maximum possible radiation for latitude  $60^{\circ}\text{S}$  and similar to the radiation receipt recorded at the Signy Island Reference Sites for this time of year (Walton, 1982).

In contrast to the incident radiation and vegetation temperature values, the relative humidity of the air layer just above the vegetation showed little diurnal change. The mean daily maximum RH was 89%, recorded at 0300 and 0600 h, whilst the mean daily minimum values of 75% occurred from 1200 to 1500 h. The air surrounding the plants was above 70% RH for 88% of the time and on only one occasion was a RH lower than 50% recorded. The values obtained with a ventilated psychrometer 5 cm above the vegetation surface differed only slightly from those recorded in a Stephenson screen 3.7 km away on the other side of the island, reflecting the uniformly moist oceanic climate. These data demonstrate that the atmosphere at plant level was generally moister and more often totally saturated than air at a greater distance above the ground but on days with appreciable sunshine, the minimum humidity close to the ground was lower.

*Predicted photosynthesis, respiration and production under field conditions*

Using the temperature and radiation data in conjunction with the experimentally determined light and temperature response curves, an attempt can be made to predict the diurnal course of photosynthesis and respiration of the vascular plants in the field. Light was not limiting for the grass above  $10 \mu\text{E m}^{-2} \text{s}^{-1}$  at  $0^\circ\text{C}$  and  $150 \mu\text{E m}^{-2} \text{s}^{-1}$  at higher temperatures, which approximate to radiation values of  $0.04$  and  $0.6 \text{ J cm}^{-2} \text{ min}^{-1}$ , respectively. Both the pearlwort and grass reached compensation at similar intensities under all temperature conditions and were light saturated at similar intensities, providing the temperature was  $5^\circ\text{C}$  or below. Fig. 9 indicates that, during January on Signy Island, both species would therefore be light saturated for photosynthesis between 0500 and 2000 hours so long as temperatures were below  $5^\circ\text{C}$ . Such temperatures do generally occur at dawn and dusk but, as Fig. 9 shows, they are frequently exceeded amongst the leaves between 0900 and 1800 hours. During this period the net photosynthetic rate of *D. antarctica* would still be determined primarily by leaf temperature and it is possible that this also applies to *C. quitensis*, although there would appear to be more likelihood of light limitation in this species. In view of this,  $\text{CO}_2$  uptake for most of the day was estimated from the temperature response curves (Figs 2 and 4), with 100% taken as the maximum net photosynthetic rates measured in the laboratory with South Orkney Islands material. For *D. antarctica* this was  $8.78 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$  (at  $10^\circ\text{C}$  with  $268 \mu\text{E m}^{-2} \text{s}^{-1}$ ) and for *C. quitensis* was  $7.18 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$  (at  $22^\circ\text{C}$  with  $370 \mu\text{E m}^{-2} \text{s}^{-1}$ ). These data were recorded with plants originating from Lynch Island which had been subsequently maintained in cool growth cabinets. Production of  $\text{CO}_2$  at night was estimated from Fig. 7.

The resulting predicted patterns of metabolism for the grass and pearlwort (Fig. 10) are broadly similar. The histograms for the 'average' Signy Island summer day were constructed using the hourly mean temperature and radiation values from Fig. 9 and indicate that, for *D. antarctica*, photosynthetic rate would reach a plateau between 1100 and 1600 hours, while in *C. quitensis* it would peak between 1300 and 1400 hours. However, calculation of field rates from an 'average' day masks differences in photosynthetic production on warm sunny and cold overcast days, so histograms were also produced using the upper and lower confidence limits for radiation and temperature shown in Fig. 9 and hourly data from an extremely sunny day (15 January 1970) and from a very overcast day (21 January 1970). From these results it is postulated that on days with prolonged sunshine (Fig. 10d, e) there will be a midday depression in net photosynthesis due to the stimulation of respiration by the elevated vegetation temperatures at this time. This feature is not as pronounced in *C. quitensis* as in *D. antarctica* because of the slightly higher temperature optimum of the former species. Such a depression has also been shown to occur in Arctic species

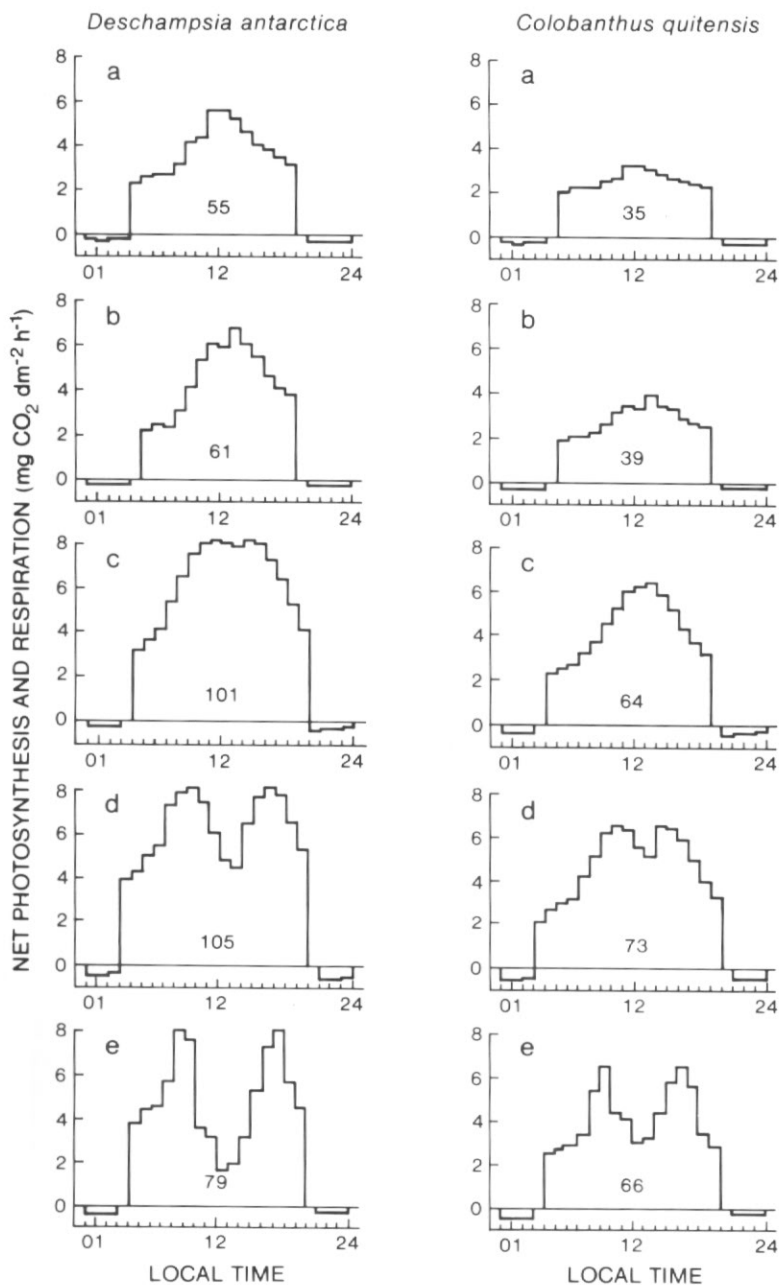


Fig. 10. Predicted mid-summer diurnal course of photosynthesis and respiration for *Deschampsia antarctica* and *Colobanthus quitensis* on Signy Island. The value inside each histogram is the projected net daily absorption of  $\text{CO}_2$  expressed on a leaf area basis ( $\text{mg CO}_2 \text{ dm}^{-2} \text{ day}^{-1}$ ). (a) 21 January 1970 – an extremely overcast day. (b) Hypothetical overcast day – derived from the lower confidence limits on Fig. 9. (c) Hypothetical 'average' day – derived from the mean values on Fig. 9. (d) Hypothetical sunny day – derived from the upper confidence limits on Fig. 9. (e) 15 January 1970 – a very sunny day.

(Hodges, 1966; Shvetsova and Vosnesenskii, 1971) and some desert plants (Lange and others, 1970) where it might be increased through water stress, although limitation of photosynthesis through lack of moisture on Signy Island is unlikely. Because of these lower rates of assimilation around midday, it is predicted that the total  $\text{CO}_2$  fixation of *D. antarctica* on sunny days would differ only slightly from the  $101 \text{ mg CO}_2 \text{ dm}^{-2}$  fixed on an 'average' day, in spite of the longer time spent above compensation point. On very sunny days a substantial decrease in total net fixation is postulated for this species. The data suggest that assimilation by *C. quitensis* will increase on warm sunny days but that the total  $\text{CO}_2$  fixed may not be very different from that on the 'average' day if vegetation temperatures are raised to above  $20^\circ\text{C}$  for a lengthy period. On cold overcast days (Fig. 10a, b) it is suggested that the photosynthetic rate would be slower to increase in both species, reaching a peak at around 1200–1400 h, and the amount of  $\text{CO}_2$  fixation would be significantly reduced to around half of the totals for the hypothetical 'average' day. It is not at all certain that the total fixation for *C. quitensis* would be less than for *D. antarctica* since the mean maximum photosynthetic rate recorded for the pearlwort was approximately 50% greater and the highest recorded rate was 65% above that of the grass, but this was with sub-Antarctic material and only data relating to the South Orkney Islands were used to prepare Fig. 10.

On Signy Island most of the larger grass swards are generally clear of snow from early December to late March, giving a short potential growing season of approximately 110 days. By applying the predicted photosynthesis data for a typical Signy day (Fig. 10c) it is possible to estimate annual production and photosynthetic efficiency for *D. antarctica*. A mean daily assimilation of  $c. 100 \text{ mg CO}_2 \text{ dm}^{-2}$  would indicate a production of  $c. 69 \text{ mg dry weight dm}^{-2} \text{ day}^{-1}$ , taking  $1 \text{ g CO}_2$  as equivalent to  $0.6 \text{ g dry weight}$  (Lewis and Callaghan, 1976). Smith and Walton (1973) recorded a mean energy content of  $19.85 \text{ kJ g}^{-1}$  for this species on South Georgia, so this production is equivalent to an energy fixation of  $c. 1.37 \text{ kJ dm}^{-2} \text{ day}^{-1}$ , representing a photosynthetic efficiency of 1.0%, since average incoming radiation recorded at the microclimate site was  $1369 \text{ J cm}^{-2} \text{ day}^{-1}$ . A sward near the research station on Signy Island had an average leaf area index of  $2.225 \text{ m}^2 \text{ leaf area m}^{-2}$  of ground and, if applied to this site, the daily dry weight increase would equate to an annual production of  $c. 1700 \text{ g m}^{-2}$  for *D. antarctica*. This is very likely to be an overestimate since the net photosynthesis measurements did not take root respiration into account, and the predicted diurnal assimilation curve represented average mid-season conditions; production earlier and later in the season would be expected to be less. It is also unrealistic to give a single production value for *D. antarctica* swards since cover is rarely continuous and shoot density may vary according to plant age and habitat conditions; this is reflected in the leaf area index measurements which ranged between  $150\text{--}550 \text{ dm}^2 \text{ m}^{-2}$  in different parts of the sward referred to earlier.

#### DISCUSSION

It might be expected that there would be some degree of genotype control over net photosynthesis, with more southerly populations having lower temperature optima than those farther north, since differences between arctic and alpine populations have been described by Mooney and Billings (1961) and Mooney and others (1964). The evidence from the present study, however, does not support the view that Antarctic and sub-Antarctic populations of *D. antarctica* and *C. quitensis* are very different in their photosynthetic responses to temperature, although data on the response of different populations to light intensity are lacking. The fact that maximum rates of



photosynthesis were reached at around 13 and 19°C by *D. antarctica* and *C. quitensis*, respectively, and that light compensation was achieved at low irradiance levels by both species suggests some adaptation to the relatively harsh climate, and parallels similar adaptations reported for grasses from Marion Island (Bate and Smith, 1983; Pammenter and others, 1986) and for many arctic and alpine species (Bliss, 1971; Tieszen, 1973). However, the low irradiance needed for saturation, particularly in *D. antarctica*, is at variance with observations on Marion Island where Pammenter and others (1986) suggest that photosynthesis in *Agrostis* spp. is limited by light, rather than temperature. However, the two genera have quite different canopy structures and the Marion Island measurements were made on single attached leaves, whereas the Signy data come from whole plants (excluding roots) where there must have been some mutual leaf shading. The *D. antarctica* and *C. quitensis* material also included older leaves and Bate and Smith (1983) have shown a substantial reduction in photosynthetic rate with leaf age, and these facts may account for the minimal photosynthetic response observed with Antarctic material to irradiances raised above  $150 \mu\text{E m}^{-2} \text{s}^{-1}$ .

Possibly the most important specialization of both grass and pearlwort is their ability to photosynthesize at around 30% of their maximum rate at 0°C. However, Pharis and Hellmers (1964) demonstrated a similar phenomenon in some species of *Abies* and *Pinus* and since then this has been noted in a range of tundra plants (Mayo and others, 1977; Tieszen, 1978; Tieszen and others, 1980). Certainly such an ability would enable the grass and pearlwort to remain metabolically active for a longer period during summer. It is the 'physiological growing season' which is critical to the survival of many species (Callaghan, 1974; Tallwin, 1977) and which is probably the principal determinant in controlling the distribution of *D. antarctica* and *C. quitensis* in the Antarctic. Tieszen and others (1980) observed destruction of enlarging cells in *Dupontia fisheri* at -4°C, even though photosynthesis continued below this temperature, and it may be that the length of the growing season in the Antarctic is determined by such tissue damage in meristematic regions rather than by a cessation of assimilatory metabolism.

Both Billings and Mooney (1968) and Woledge and Jewiss (1969) have demonstrated shifts in physiological activity of plants cultivated under different regimes, and Billings and others (1971) showed that optimum temperatures for photosynthesis and the upper and lower compensation points were shifted to higher temperatures when alpine populations of *Oxyria digyna* were grown under warm conditions, while the photosynthetic optima of arctic ecotypes grown in warm and cold regimes did not differ greatly. Similarly, Tieszen and Helgager (1968) reported that an alpine population of *Deschampsia caespitosa* showed greater flexibility in its photosynthetic response to temperature than a population from the Arctic. The present study indicated that rates of photosynthesis and respiration of *D. antarctica* which had been allowed to acclimate to UK summer conditions did not differ greatly from plants which had not been exposed to such warmth and, in this respect, showed similarities with arctic ecotypes of other species. This may imply that the nature and properties of their enzymes and metabolism are under fairly strict genetical control. *C. quitensis* exhibits greater morphological variation than the grass (Holtom and Greene, 1967) and, in contrast to *D. antarctica*, considerably higher rates of photosynthesis were observed with the pearlwort from South Georgia than with plants from the Antarctic. The present study suggests that *C. quitensis* can photosynthesize over a wider temperature range than the grass, possibly indicating a greater metabolic flexibility.

However, although the pearlwort has the same geographical distribution as the

grass in the Antarctic (Greene and Holtom, 1971; Komarkova and others, 1985), it is much scarcer and less widespread as a result of its considerably narrower ecological amplitude. Smith and Stephenson (1975) commented on the tolerance of *D. antarctica* to adverse situations on South Georgia, where its rapid growth and development and its colonization of fluvio-glacial detritus and moraines, permit it to behave as a pioneer species. The restricted distribution of both angiosperm species on the South Orkney Islands (Greene and Holtom, 1971; Smith, 1972) and on the South Shetland Islands (Lindsay, 1971) indicates that neither has been able to extensively colonize the more exposed northern coasts of these groups, where radiation receipt is theoretically greatest. Instead, most vascular plant sites occur on north-facing slopes to the south of high mountain ranges, protected from the more humid and exposed conditions which prevail on the windward side of the islands. Tieszen and others (1980) noted that graminoid leaf temperatures are closely coupled to air temperature in the Arctic tundra but the data presented here, and by Edwards (1972), suggest this not to be true in the Antarctic, possibly the result of differences in canopy structure or microtopography. The aspect of the sites is not only important in increasing temperatures of both grass and pearlwort but is also critical in determining the length of the growing season.

On the South Orkney Islands *D. antarctica* was able to recommence growth rapidly after becoming free of snow, although Gannutz (1970) reported that at Palmer Station, Anvers Island (64° 46' S, 64° 07' W), the grass was completely inactive for some time following the spring melt and was brown in colour due to the absence of chlorophyll as a result of winter die-back. On Signy Island, however, activity, as indicated by new root growth, was observed within ten days of a major melt in September, prior to fresh snowfalls which deeply buried the plants. Tallwin and Smith (1977) noted that the vulnerability of overwintering green shoots to wind and snow abrasion was reduced in *Festuca contracta* by a large amount of standing dead leaves, but this probably does not apply to *D. antarctica* which has a more prostrate growth form and carries less than 15% of its dry weight as attached dead leaves for the majority of the growing season (Edwards, 1973). Some isolated clumps of grass and pearlwort did appear yellowish in November on Signy Island but most of the larger populations still contained much chlorophyll, particularly in the youngest two leaves, although the longer leaves, which may have projected above the snow for periods during the winter, appeared dead. The overall brown effect noted by Gannutz seems to indicate a greater abundance of standing dead leaves, which may be due to the ground remaining colder longer at Palmer Station, or an earlier removal of protective snow cover.

Walton (1982) recorded a minimum temperature of  $-26.5^{\circ}\text{C}$  at the surface of a moss bank on Signy Island and illustrated the pattern of isotherms in the moss-peat profile for a winter's day. These show that beneath 10 cm of snow cover vegetation temperatures still fluctuated between  $-15$  and  $-20^{\circ}\text{C}$ , but that beneath 27 cm of snow these changes are considerably damped. Previous measurements on Signy Island (Edwards, 1972) indicated that temperatures did not go below  $-10^{\circ}\text{C}$  in grass beneath 30 cm of snow, even when air temperatures were below  $-20^{\circ}\text{C}$ , and a depth of 50 cm or more snow ensured that temperatures at plant level were maintained between  $-2$  and  $-6^{\circ}\text{C}$ . For most of the winter larger swards of *D. antarctica* and *C. quitensis* are covered with between 20 and 30 cm of snow and so would only occasionally be exposed to temperatures lower than  $-10^{\circ}\text{C}$ . Many of the smaller sites, often comprising only a few clumps of grass, accumulate deep snow drifts and would probably never be subjected to temperatures below  $-6^{\circ}\text{C}$ . Plants growing in such sites experience a considerably shortened growing season of around 75–90 days,

which inhibits their reproductive development and reduces the possibility of producing viable seed. The larger swards tend to become snow-free for short periods from September onwards and in some years it is possible that their growing season could extend to c. 150 days.

The maximum production estimate of  $1700 \text{ g m}^{-2} \text{ yr}^{-1}$ , based on a growing season of 110 days, exceeds other estimates for *D. antarctica* made on Signy Island (Edwards, 1974). Growth analysis trials with tillers of the grass in native soil, and in vermiculite supplied with nutrient solution, carried out between 1967 and 1970 gave values for net assimilation of between  $0.2\text{--}0.4 \text{ g dm}^{-2} \text{ wk}^{-1}$ , equivalent to  $28\text{--}57 \text{ mg dry weight dm}^{-2} \text{ day}^{-1}$ , or  $700\text{--}1400 \text{ g m}^{-2}$  annual production for the sward described above. These assimilation rates are lower than those reported in the Arctic by Wilson (1966), yet the production estimates exceed the  $300\text{--}400 \text{ g dry weight m}^{-2}$  quoted for a tundra community (Lewis and Callaghan, 1976). However, the latter production was recorded during a shorter (60–70 day) growing season. Smith and Stephenson (1975) have also recorded high production of tillers and leaves of *D. antarctica*, and obtained assimilation rates of  $0.12\text{--}0.54 \text{ g dm}^{-2} \text{ wk}^{-1}$  with seedlings on South Georgia, more than double those recorded with *Festuca contracta* but similar to production reported for South Georgian *Phleum alpinum* by Callaghan and Lewis (1971).

It seems unlikely that *D. antarctica* has a substantially greater annual production than other polar species since the photosynthesis and respiration responses are not dissimilar to those reported for other arctic and sub-Antarctic graminoids (Tieszen, 1973; Tieszen and others, 1980; Mayo and others, 1977; Bate and Smith, 1983) and the predicted 24 hour totals of net  $\text{CO}_2$  incorporated are of the same order as those reported by Tieszen (1973) for arctic grasses. By physically separating and drying the different components, including roots, of the grass in a series of cores from a *D. antarctica* sward, collected over the 1969–70 growing season, a production estimate of  $390 \text{ g m}^{-2} \text{ y}^{-1}$  was obtained for this species on Signy Island (Edwards, 1973). This value is still greater than the above ground primary production of  $100 \text{ g m}^{-2} \text{ y}^{-1}$  reported for an Alaskan tundra vascular community (Tieszen, 1975) but is below the production estimate for vascular plants in a sub-Antarctic grassland (Walton and others, 1975), which increased at a rate of  $5.47 \text{ g m}^{-2} \text{ day}^{-1}$ .

From the data presented here, it is suggested that neither *D. antarctica* nor *C. quitensis* has developed any unique metabolic adaptations for survival under Antarctic conditions, since many arctic and alpine species show similar features. They are able to exist in maritime Antarctic regions because, through a combination of genetical, morphological and ecological strategies and their occupation of the more favourable habitats, they avoid the most severe environmental conditions. Bennett and others (1982) reported that in the increasingly harsh climates at high latitudes there is strong selection against species with diploid genomes and those with high DNA amounts; both *D. antarctica* and *C. quitensis* may be polyploids and both have very low DNA amounts. In the case of *D. antarctica* survival and spread is enhanced by a considerable tolerance to salt water spray, long periods of uprooting, and sub-zero temperatures during the growing season (Edwards, 1972). Transplant experiments (Edwards and Greene, 1973; Edwards, 1979) suggest that the few weeks following the major melt at the end of winter are an especially critical time. *Poa annua* and *P. flabellata*, non-indigenous species that can grow well and set seed during the summer on Signy Island (Edwards, 1979), suffered high mortality at this time, while the native species showed considerable die-back of older aerial parts. Komarkova and others (1985) suggest the cold growing season to be the main reason for the paucity of the vascular flora of the Antarctic, relative to Arctic regions, but the dispersal problems of Southern Hemisphere vascular species to Antarctic sites, coupled with

their lack of adequate frost tolerance, would seem to be more likely reasons why this continent remains colonised by only two species of flowering plant.

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