PREDICTION OF NET PRIMARY PRODUCTION IN TWO ANTARCTIC MOSSES BY TWO MODELS OF NET CO_2 FIXATION

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Abstract. Deficiencies in a previously published multiple regression model (model *1*) have been examined. The model was designed to predict rates of net CO_2 exchange (*PN*) in two Antarctic mosses, *Polytrichum alpestre* and *Drepanocladus uncinatus*. In model *1* the relationship between *PN* (when moss water content was optimum) and the environmental variables, radiant flux density (*R*) and temperature (*T*) was described by quadratic functions. Model *1* equations fit the data only poorly, particularly when *R* is equal to zero, between 50 and 200 $\mu E\, m^{-2}\, s^{-1}$ and above 700 $\mu E\, m^{-2}\, s^{-1}$. An alternative (model *2*) is presented which is based on the same data but uses a series of regression equations relating *PN* to ln *R* at 5-degree intervals between -10 and 30°C when $R > 0$, with linear interpolation between these intervals. A regression of ln *PN* on ln *T* is used when $R = 0$. The equations employed in model *2* give a better fit to the raw data. By comparing predictions from the two models when used with environmental data recorded in these moss communities on Signy Island, maritime Antarctic, it was shown that model *1* performed inadequately under normal field conditions. Over a six-day summer period the total CO_2 fixation predicted from model *2* was 25% greater than from model *1*. Predicted net primary production for *Polytrichum alpestre* by model *2* was in the lower end of the field range (342–647 g dry matter per m^2 per year). The value of multiple regression models for predicting photosynthesis in mosses growing in polar regions is discussed.

Models of photosynthesis used in ecosystem studies take a number of forms, e.g. Grace and Woolhouse (1970), Kershaw and Harris (1971) and Miller and Tieszen (1972). However, a common feature is that their ability to predict net photosynthesis in the field depends upon (1) the precision and range of data used to formulate equations employed in the models, and (2) the goodness of fit of the equations to those data.

Predictive equations are frequently based upon multiple regression analysis (Grace and Woolhouse, 1970; Kershaw and Harris, 1971; Callaghan, Collins and Callaghan, 1978; Collins and Callaghan, 1980) because it is possible to account for the effect of a number of variables acting simultaneously and to assess the goodness of fit from the coefficient of determination (r^2: which gives the proportion of variance in the data accounted for by the variables in the equation). Multiple regression equations have been reported to account for 86–93% of the variation in CO_2 exchange in the lichen *Cetraria nivalis* (L.) Ach. (Kallio and Kärenlampi, 1975), 52–68% in the heather *Calluna vulgaris* L. Hull (Grace and Woolhouse, 1970) 76–83% in four tundra species (Tieszen, 1975) and 61–67% in the mosses *Drepanocladus uncinatus* (Hedw.) Warnst. and *Polytrichum alpestre* Hoppe (Collins and Callaghan, 1980). They are therefore considered to be reasonable predictors of CO_2 exchange of plants in the field. However, in using a model based on multiple regression equations relating net CO_2 fixation of two mosses from Signy Island, maritime Antarctic, to variations in radiant flux density and temperature, Collins

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and Callaghan (1980) noted that there was poor correspondence between predicted and observed rates of CO_2 exchange. This occurred at both low temperatures and low radiant flux densities even though the observed rates were those used in developing the equations. The errors were attributed mainly to the use of a quadratic equation to describe the relationship between net CO_2 fixation and radiant flux density. Consequently significant errors may arise when predicting net primary production at Signy Island as low light levels and low temperatures are the norm under snow and at night. This was acknowledged by Collins and Callaghan (1980) who hence obtained estimates of photosynthesis under snow by interpolation directly from the physiological data presented by Collins (1977).

The aims of this paper are (1) to re-analyse the data of Collins (1977) used by Collins and Callaghan (1980), to produce a model which would not suffer from the lack of fit associated with the quadratic relationship and hence could be used over the full range of temperature and radiant flux densities encountered, and (2) to compare simulated patterns of net photosynthesis at Signy Island, using climatic data for that island, predicted by the model of Collins and Callaghan (1980) (referred to here as model *1*) and by the model developed in the present paper (referred to as model *2*).

DATA

Net CO_2 fixation rates for two moss species (*Polytrichum alpestre* and *Drepanocladus uncinatus*) collected from Signy Island, transported to the UK at a temperature of 4°C and cultured under controlled conditions were obtained by Collins (1977) using an infrared gas analyser. Samples of both mosses were kept at two temperature regimes in order to establish if thermal history affected net photosynthesis. There was a 'cold' regime of -5°C during the night (12 h) and 5°C during the day, and a 'warm' regime of 0–5°C at night (12 h) and 10–15°C throughout the day. Measurements were made over a range of radiant flux densities (R) from 0 to 1010 $\mu E\,m^{-2}\,s^{-1}$ and a range of temperatures (T) from -10 to 30°C, at 5-degree intervals (except for some measurements at -7 and -2.5°C) with the moss held at optimal water content (700% of dry weight in *D. uncinatus* and 400% in *P. alpestre*). *P. alpestre* showed a significantly different response to light and temperature depending on the temperature pre-treatment, but *D. uncinatus* did not (Collins, 1977). Data for *P. alpestre* 'cold' and 'warm' adapted material are therefore given and analysed separately, but for *D. uncinatus* the data have been combined.

Collins (1977) presented the CO_2 fixation results as smoothed response curves fitted by eye to the data points. In this form it is difficult to assess visually the goodness of fit of the response curves fitted by regression analysis. The data are therefore given in full in the appendix of the present paper and the response of net CO_2 fixation (expressed as $mg\,m^{-2}\,h^{-1}$) to varying radiant flux density at two selected temperatures, 0 and 5°C, is plotted in Fig. 1. The results in the appendix differ in two ways from those used by Collins and Callaghan (1980) to generate multiple regression equations. Firstly, net CO_2 fixation rates at 2000 $\mu E\,m^{-2}\,s^{-1}$ have been omitted. It was not possible to produce light levels greater than 1010 $\mu E\,m^{-2}\,s^{-1}$ in the laboratory, so the CO_2 fixation rates for those levels were assumed by Collins and Callaghan to be equal to or greater than the rates of 1000 $\mu E\,m^{-2}\,s^{-1}$ depending on temperature. This method seems dubious as it is not known if photoinhibition occurs at higher radiation levels. Secondly, errors in five of the 385 data points have been detected and corrected. Whilst these were sufficiently obvious to be detected, they had little effect on the regression equations due to the large amount of data with which they were combined.

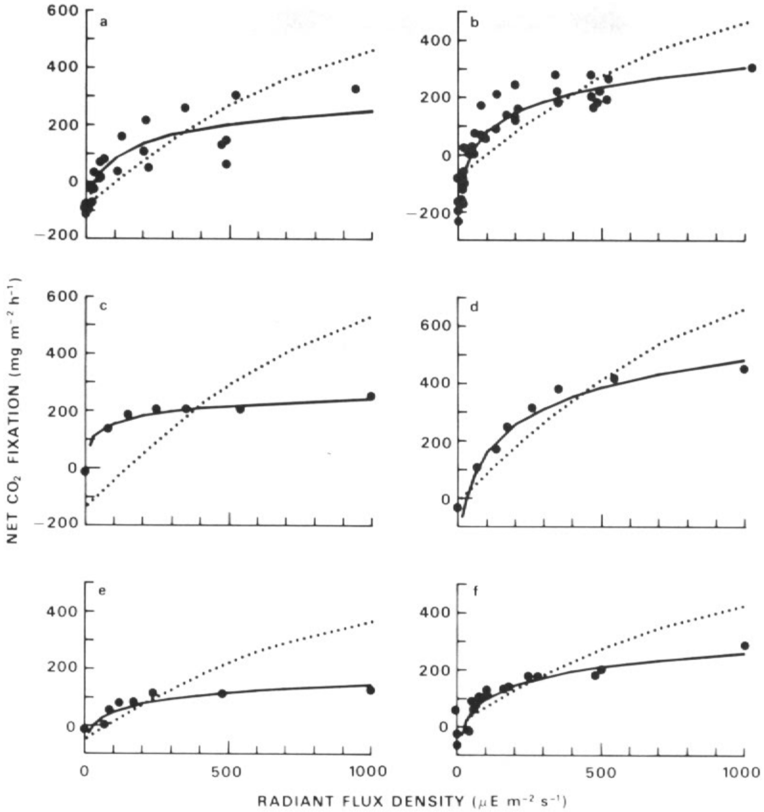

Fig. 1. Relationship between net CO_2 fixation rate and radiant flux density for *Polytrichum alpestre* 'cold' adapted at 0°C (a) and 5°C (b), 'warm' adapted at 0°C (c) and 5°C (d), and *Drepanocladus uncinatus* at 0°C (e) and 5°C (f). Fitted curves are from multiple regression (equation (1); dotted line) and from logarithmic curve fit (equation (4); solid line).

Prediction of Net Photosynthesis by Multiple Regression (model *I*)

Multiple regression analysis in which net CO_2 fixation (*PN*) at optimal water content was regressed against R, R^2, T and T^2 (equation (1), Table I) (where [illegible] $= R + 2\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$ and $T = T + 12$°C) accounted for 65% of the variance in the data from *Polytrichum alpestre* 'cold' adapted material (Table I), 61% in *P. alpestre* 'warm' adapted and 67% in *Drepanocladus uncinatus* (Collins and Callaghan, 1980). The curves relating net CO_2 fixation to radiant flux density at 0 and 5°C generated from the derived multiple regression equations for the two species and temperature pre-treatments are shown in Fig. 1 as dotted lines. Despite the reasonably high r^2 values the curves fit only poorly to the data. Large deviations occur at zero radiant flux density, between 50 and 200 $\mu\mathrm{E\,m^{-2}\,s^{-1}}$ and above 700 $\mu\mathrm{E\,m^{-2}\,s^{-1}}$. In addition, at low temperatures, the net photosynthesis compensation points are shifted markedly to the right (i.e. toward higher radiant flux densities, Fig. 1a, c, e). The relationship between net CO_2 exchange in the dark and temperature is shown in Fig. 2. The curves generated by equation (1) (dotted lines) are again not representative of the response exhibited by the mosses. The fitted curves indicate positive CO_2 fixation at temperatures between 7 and 20°C in *P. alpestre* 'warm' adapted and between 5 and

Table I. Multiple regression equations relating net CO_2 fixation (PN) to radiant flux density (R) and temperature (T), under optimal water conditions, in *Polytrichum alpestre* 'cold' adapted material, and the values of r^2 (coefficient of determination) and F (variance ratio) used for examining the goodness of fit and the significance of the regression.

$$PN = a + bT + cT^2 + dR + eR^2 \qquad \text{equation (1)}$$

$$PN = a + bT + cT^2 + d\ln(R+1) \qquad \text{equation (2)}$$

$$PN = a + bT + cT^2 + d\ln(R+1) + eRT \qquad \text{equation (3)}$$

Equation	r^2	*d.f.**	*F*	*P*
(1)	0.650	4/213	98.9	$\ll 0.01$
(2)	0.741	3/204	194.4	$\ll 0.01$
(3)	0.875	4/203	356.9	$\ll 0.01$

* Degrees of freedom (d.f.) are expressed as d.f. for regression/d.f. for residuals.

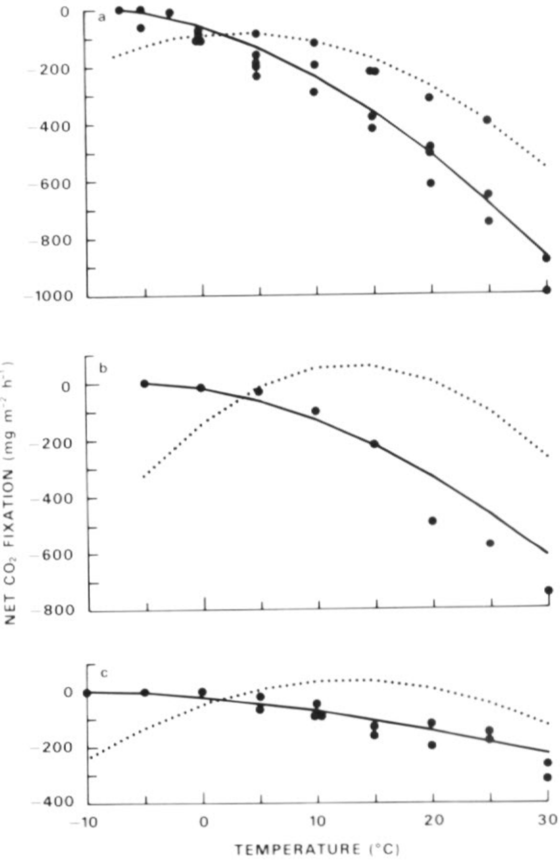

Fig. 2. Relationship between net CO_2 fixation rate and temperature when radiant flux density is zero in *Polytrichum alpestre* (a) 'cold' adapted, (b) 'warm' adapted and (c) *Drepanocladus uncinatus*. Fitted curves are from multiple regression (equation (1); dotted line) and from an inverse power curve fit (equation (5); solid line).

Table II. Predicted rates of net CO_2 fixation ($mg\ m^{-2}\ h^{-1}$) in two mosses from equation (1) in relation to temperature and radiant flux densities ($R/\mu E\ m^{-2}\ s^{-1}$) in excess of 1 000 $\mu E\ m^{-2}\ s^{-1}$

	Polytrichum alpestre				*Drepanocladus uncinatus*	
	'Cold' adapted		*'Warm' adapted*			
R	*5°C*	*10°C*	*5°C*	*10°C*	*5°C*	*10°C*
1 000	457	428	650	716	416	444
1 500	479	450	715	780	444	472
2 000	335	306	599	664	353	381
2 500	24	−5	303	369	144	171

20°C in *D. uncinatus* (Fig. 2b, c). Furthermore, net CO_2 production in the dark ccording to equation (1) increases with decreasing temperature below 5°C in *P. alpestre* 'cold' adapted and below 10°C in *P. alpestre* 'warm' adapted and in *D. uncinatus*. This clearly contradicts the dark respiration response to temperature (Fig. 2).

At high radiant flux densities, predicted rates of net CO_2 fixation using equation (1) are higher than the observed rates (Fig. 1). However, as the relationship between photosynthesis and light is described by a quadratic equation, increasing radiant flux densities lead eventually to a decline in photosynthesis as shown in Table II. Predicted peak CO_2 fixation occurs at about 1500 $\mu E\,m^{-2}\,s^{-1}$ and then declines, becoming negative in *P. alpestre* 'cold' adapted at temperatures above 9°C. Such radiant flux densities occur frequently during the summer. Between 12 November 1969 and 17 March 1970 the radiant flux density exceeded 1000 $\mu E\,m^{-2}\,s^{-1}$ on 47 of the 82 days (i.e. 57%) for each of which 24 hourly radiation values were recorded. In those 47 days the average number of hours with a radiant flux density greater than 1000 $\mu E\,m^{-2}\,s^{-1}$ was 3.3 $h\,d^{-1}$ (range 1–8 h). The mean for the whole period (82 d) was 1.9 $h\,d^{-1}$. As CO_2 fixation rates were not measured at such high radiant flux densities, it is best not to extrapolate beyond 1000 $\mu E\,m^{-2}\,s^{-1}$ using equation (1).

Confining predictions to within the range of temperature and radiant flux density for which laboratory data are available will reduce errors. Another way would be to improve the fit of the equation to the observed rates. This has been attempted with *P. alpestre* 'cold' adapted as described below. The photosynthesis-light response curves (Fig. 1) suggest that net CO_2 fixation increases as a function of the logarithm of the radiant flux density rather than as a quadratic function. In addition, Collins (1977) indicated that the optimum temperature for photosynthesis increased with increasing radiant flux densities. These properties were incorporated step-wise into the multiple regression by regressing PN firstly on T, T^2 and $\ln(R+1)$ and secondly on T, T^2, $\ln(R+1)$ and RT (equations (2) and (3) respectively; Table I). Each step increased r^2 by approximately 0.1 so that equation (3) accounted for 88% of the variance. Despite these improvements both equations (2) and (3) were inadequate at low temperatures. Both gave positive rates of fixation at and below −7°C and overestimated dark respiration at temperatures below 5°C. It was decided, therefore, that an alternative to the multiple regression model was required for species growing at Signy Island where mean temperatures of *P. alpestre* and *D. uncinatus* are below 5°C for approximately 70% and 90% of the summer (November to April) respectively (Walton, 1977).

Prediction of Net Photosynthesis by Regression and Linear Interpolation (model 2)

An alternative to multiple regression was developed by fitting a logarithmic curve to the relationship between net CO_2 fixation under optimal water conditions and radiant flux density at each 5-degree temperature interval for which measurements were made (Fig. 3, Table III). The relationship is linear from 10 to 1000 $\mu E\,m^{-2}\,s^{-1}$ (2.40–6.91 on the transformed scale), but a sharp discontinuity occurs at zero light intensity (zero on the transformed scale, Fig. 3). For this reason the fitted regression lines were calculated with the data at zero radiant flux density excluded. The relationship between net CO_2 fixation and radiant flux density on a linear scale derived from the logarithmic regression is given in Fig. 1 (solid line) to show the better fit compared with the multiple regression equation (1).

CO_2 fixation at zero light intensity in relation to temperature is shown in Fig. 2. This is described by an inverse power curve (equation (5), Table IV) as shown by the solid line.

Coefficients describing the relationship between CO_2 fixation and radiant flux density (where $R > 0$) are given in Table III and for CO_2 fixation and temperature (where $R = 0$) in Table IV. The photosynthesis results for *Polytrichum alpestre* 'cold' adapted material collected at $-2.5°C$ are not included in Table III because fewer measurements were made than at other temperatures and they are out of step in the 5-degree sequence of results.

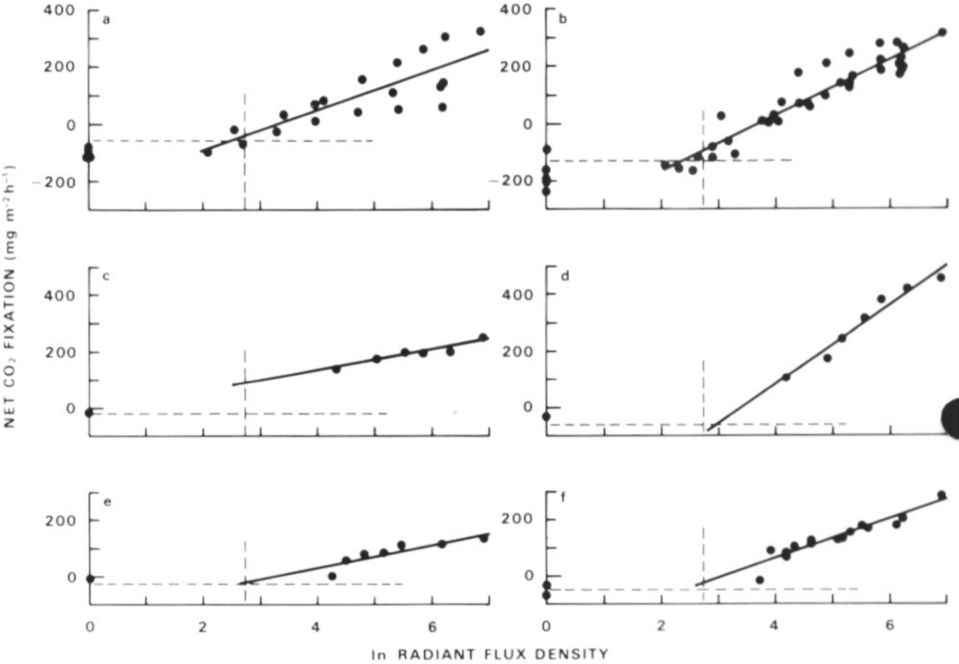

Fig. 3. Relationship between net CO_2 fixation rate and the natural logarithm of radiant flux density ($\ln(R + 1)$) for *Polytrichum alpestre* 'cold' adapted at 0°C (a) and 5°C (b), 'warm' adapted at 0°C (c) and 5°C (d), and *Drepanocladus uncinatus* at 0°C (e) and 5°C (f). Solid line is fitted regression with data at zero radiant flux density excluded. Horizontal dashed line denotes predicted rate of CO_2 exchange at zero light intensity using equation 5. Vertical dashed line denotes a radiant flux density of approximately 15 $\mu E\,m^{-2}\,s^{-1}$.

Table III. Regression equation relating net CO_2 fixation (PN) of two mosses to radiant flux density (R) at constant temperature and under optimal water conditions. The coefficients (a, b) of the equations obtained at temperatures ranging from −10 to 30°C are given. – denotes not determined.

$PN = a + b \ln (R + 1)$ equation (4)

Temperature °C	*Polytrichum alpestre*				*Drepanocladus uncinatus*	
	'Cold' adapted		*'Warm' adapted*			
	a	*b*	*a*	*b*	*a*	*b*
−10	–	–	–	–	0.0	0.0
−7	0.0	0.0	–	–	–	–
−5	−26.8	12.6	0.0	0.0	−9.1	6.3
0	−237.3	70.4	−13.7	36.9	−134.0	40.5
5	−367.6	97.3	−481.0	139.7	−218.8	69.4
10	−520.1	124.4	−735.2	200.1	−397.8	118.0
15	−647.1	126.1	−963.7	236.7	−449.7	122.1
20	−1005.6	180.3	−1055.4	256.8	−797.4	189.5
25	−1198.7	201.0	−2405.5	465.7	−747.3	159.4
30	−1705.8	264.2	−1906.2	339.3	−843.4	162.1

Table IV. Regression equation relating net CO_2 fixation (PN) of two mosses to temperature (T) when radiant flux density equals zero and under optimal water conditions. Coefficients (a, b) of the equation are also shown.

$PN' = a + bT'$ equation (5)

where $PN' = \ln (-1 . PN) + 1)$
$T' = T + 6$ with *P. alpestre* 'warm' adapted
$T' = T + 8$ with *P. alpestre* 'cold' adapted
$T' = T + 11$ with *D. uncinatus*

Polytrichum alpestre				*Drepanocladus uncinatus*	
'Cold' adapted		*'Warm' adapted*			
a	*b*	*a*	*b*	*a*	*b*
0.361	1.76	−0.353	1.89	−0.537	1.61

There are two advantages of this analysis over the multiple regression analysis. Firstly, values of zero are obtained for the coefficients of equation (4) at −10, −7 and −5°C (Table III) depending on species and treatment, and the curve generated by equation (5) passes through the origin at these temperatures (Fig. 2). Hence, as temperature declines towards these lower temperature limits for which activity can be detected, predicted rates of net CO_2 fixation approach zero. Below these temperatures all activity is assumed to cease. Secondly, using equation (5), dark respiration can be predicted over the full temperature range.

The main disadvantage is that, for positive radiant flux densities and temperatures other than those for which CO_2 exchange data were collected, net photosynthesis rates cannot be predicted directly from the regression equations. When this occurs prediction is made by linear interpolation from the values calculated using R and equation (4) at the temperature intervals immediately above and below the temperature for which PN is being predicted. In addition, another potential source of error arises at low, but positive, radiant flux densities, because under these conditions equation (4) yields a greater rate of loss of CO_2 than the loss rate in the dark given by equation (5) (Fig. 3). When this happens *PN* is predicted from equation (5) rather than equation (4). However, in practice, this rarely occurs as the minimum light level measurable in the field, with the equipment available, was approximately 15 $\mu E\,m^{-2}\,s^{-1}$ (indicated by the vertical dashed line in Fig. 3). Hence the switch from predicting *PN* by equation (4) to equation (5) occurs when equation (5) yields the lower value.

COMPARISON OF PREDICTED PATTERNS OF NET CO_2 FIXATION

The diurnal pattern of net CO_2 exchange in each species and pre-treatment has been predicted for selected dates (see Table V) during the austral summer of 1969–70 from Signy Island climatic data of E. P. Wright (T. V. Callaghan, pers. comm.). These were the dates for which Collins and Callaghan (1980) predicted patterns of net photosynthesis using model *1*, so that a comparison of predictions from the two models was possible. Field measures of radiation were converted to radiant flu[illegible] densities by taking 1 $cal\,cm^{-2}\,min^{-1}$ as equivalent to 1 449 $\mu E\,m^{-2}\,s^{-1}$ (Collins and Callaghan, 1980). Detailed analyses of the temperature and radiation data and notes on the equipment employed are given in Collins and Callaghan (1980).

Predicted patterns of CO_2 fixation are shown in Fig. 4a, b, c for *Polytrichum alpestre* 'cold' adapted on 16 November 1969 and 8 January 1970, and 'warm' adapted on 14 March 1970 respectively. The total net CO_2 fixation on each of these dates and on the dates examined by Collins and Callaghan, but not included in Fig. 4, are given in Table V. These results show marked differences depending on the model used. All these differences can be attributed to the multiple regression models being an inadequate description of the response in net CO_2 fixation of the mosses as determined by the laboratory study of Collins (1977). The main ways in which the rates predicted by model *2* differ from those of model *1* are:

Table V. Comparison of predicted daily total net CO_2 fixation ($mg\,m^{-2}$) of two mosses by multiple regression (model *1*; equation (1)) and by regression and linear interpolation (model *2*; equations (4) and (5)) on selected dates at Signy Island. Figures in parentheses denote lower and upper 95% confidence limits.

	Model 1	*Model 2*
Polytrichum alpestre		
'Cold' adapted		
15 November 1969	2 505	2 521 (2 366–2 672)
16 November 1969	− 341.4	1 078 (914–1 237)
21 December 1969	3 412.7	3 174 (3 000–3 345)
8 January 1970	2 045.8	3 328 (3 085–3 568)
14 March 1970	1 191.2	2 093 (1 954–2 231)
Polytrichum alpestre		
'Warm' adapted		
8 January 1970	6 703.7	9 564 (9 333–9 794)
14 March 1970	− 616.5	3 389 (3 245–3 533)
Drepanocladus uncinatus		
21 December 1979	3 946.3	3 347 (3 182–3 513)
8 January 1970	4 758.0	5 406 (5 199–5 612)

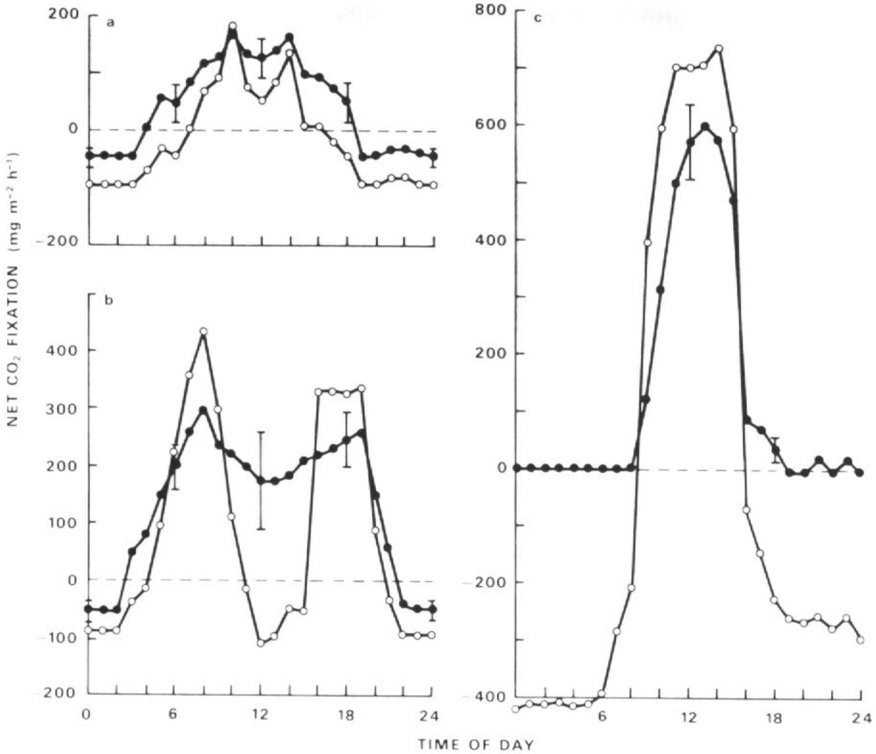

Fig. 4. Predicted patterns of net CO_2 fixation for *Polytrichum alpestre* 'cold' adapted material on Signy Island using model *1* (○——○) and model *2* (●——●). (a) 16 November 1969, (b) 8 January 1970, (c) 14 March 1970. Error bars denote 95% confidence limits at 0.00 h, 06.00 h, 12.00 h and 18.00 h.

(1) peak daytime photosynthesis is lower (e.g. Fig. 4c), because model *1* overestimates net CO_2 exchange at high radiant flux densities (Fig. 1);
(2) net photosynthesis is positive for a greater part of each day (e.g. Fig. 4a), because the multiple regression equation displaces the light compensation point at low temperatures towards high light intensities (Fig. 1a, c, e);
(3) at low night temperatures dark respiration is less (Fig. 4c), because with the multiple regression model dark respiration increases as temperature decreases (Fig. 2);
(4) the range of values is smaller, because of the combined effect of (1) and (3). In addition, short-term fluctuations in the day are less marked because fluctuations in light intensity at higher radiant flux densities have little effect with model *2* but a large effect with model *1* as the multiple regression equation does not plateau (Fig. 1);
(5) the depression around 13.00 h is less marked (Fig. 4b), because with model *1* the use of radiant flux densities in excess of 2000 $\mu E\ m^{-2}\ s^{-1}$ has a greater effect on predicted rates of net CO_2 fixation than supraoptimal temperatures (Table II).

The combined effects of the above differences sometimes cancelled each other out so that there was no significant differences between daily total net CO_2 fixation predicted by the two models, e.g. *P. alpestre* 'cold' adapted on 15 November 1969

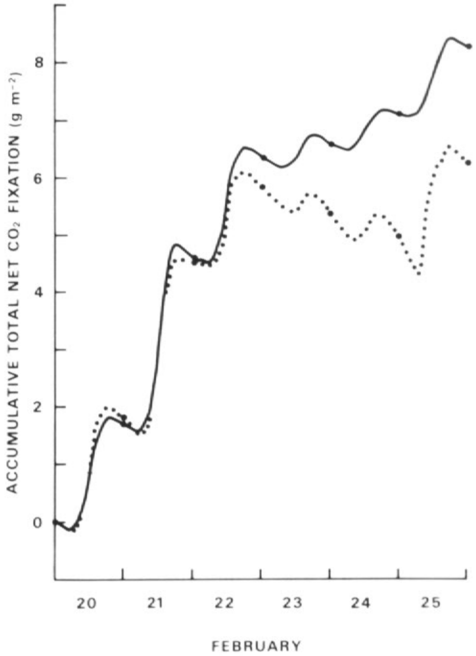

Fig. 5. Predicted cumulative total of fixed CO_2 for *Drepanocladus uncinatus* between 20 and 25 February 1970 at Signy Island. Solid line by model *2*, dotted line by model *1*.

(Table V). However, significant differences in daily total did occur and these varied in magnitude and direction depending on the temperature and radiant flux density (Table V). Over a number of days these differences may therefore cancel out. This is examined in Fig. 5 where the accumulated total net CO_2 fixation predicted by the two models is compared for the period 20–25 February 1970. Over the first three days, where temperatures were generally above zero and daytime radiant flux densities were up to 1000 $\mu E\, m^{-2}\, s^{-1}$, the two models yielded similar results. Thereafter, on 23 and 24 February, model *2* predicted a higher rate of fixation which left a difference at the end of the period amounting to nearly 25% of the total predicted by model *2*. The divergence in predictions was caused by two days of sub-zero temperatures and radiant flux densities $<300\, \mu E\, m^{-2}\, s^{-1}$. Under these conditions the multiple regression model would underestimate the rate of CO_2 fixation during the day, and overestimate the loss of CO_2 during the night. As such temperatures and radiant flux densities are common at Signy Island the model of Collins and Callaghan (1980) will be inadequate for a large part of the austral summer.

To test if these deficiencies are likely to cause significant errors in predicting net primary production of mosses growing under Signy Island conditions, total organic matter production of *P. alpestre* has been predicted, from both models, for the 1972–73 summer season using environmental data from a moss turf (Walton, 1977). In doing this it has been assumed that photosynthesis began on 26 November at about the time of the spring thaw. Prior to this date more than 10 cm of snow and ice covered the site and would have reduced activity to negligible levels. The end of the summer season is less easy to define. Tempertures were around 0°C throughout April 1973, at which time snow began to accumulate. However, its distribution was patchy and it was generally less than 10 cm in depth. Predictions have been made up

Table VI. Predicted organic matter production (g dry matter per m^2) of *Polytrichum alpestre* growing on Signy Island in the summer of 1972–3 from models *1* and *2*. Results are given as ten day totals. nd denotes not determined but assumed zero due to snow cover and low temperatures.

	Model 1		*Model 2*	
Date	*'Warm' adapted*	*'Cold' adapted*	*'Warm' adapted*	*'Cold' adapted*
15–26 Nov	30*	20*	nd	nd
26 Nov–5 Dec	37.51	25.73	37.38	20.45
6–15 Dec	25.26	12.26	37.51	15.37
16–25 Dec	40.92	12.62	48.85	15.41
26 Dec–4 Jan	34.07	14.73	43.79	15.22
5–14 Jan	9.19	12.54	19.09	12.36
15–24 Jan	15.01	14.81	22.83	13.69
25 Jan–3 Feb	32.13	13.47	42.71	14.91
4–13 Feb	23.44	9.71	32.72	11.50
14–23 Feb	11.88	6.79	24.76	10.73
24 Feb–5 Mar	−2.16	−2.49	15.25	4.72
6–15 Mar	−5.66	−4.60	11.11	1.54
6–25 Mar	−18.12	−12.21	3.07	−4.88
26 Mar–4 Apr	−23.67	−12.64	6.16	−2.22
5–14 Apr	−14.55	−6.59	10.35	2.37
15–24 Apr	−35.35	−11.40	5.16	1.64
25 Apr–4 May	−30.72	−12.14	6.71	0.43
Totals				
26 Nov–4 May	99.18	60.59	367.45	133.24
15 Nov–4 Apr	209.80	110.72	345.23	128.80

* Values estimated assuming low levels of activity below snow.

Mean net primary production calculated using five separate measurements of *Polytrichum alpestre* growing in pure stands at Signy Island: 475 ± 106 (range 342–647) g dry matter per m^2 per year (Davis, 1981).

to the end of April 1973. CO_2 fixation was converted to organic matter production using the constant 0.682 g dry matter per gram CO_2 given by Collins and Callaghan (1980). The results (Table VI) show that model *2* gives a consistently higher rate of production over periods of ten days or more. As a result the end of season total was between 1.2 and 3.7 times greater than that from model *1* depending on the temperature pre-treatment of the moss and the perceived length of season. It should be noted that although the same environmental data, analytical procedures and model were employed as were used by Collins and Callaghan (1980), the annual values are less than half of those in the latter paper. Annual rates of primary production for *P. alpestre* growing on Signy Island measured by harvesting and other methods vary from 342 to 647 g dry matter per m^2, with a mean of 475 g dry matter per m^2 (Davis, 1981). Predictions from both models are therefore low, but those of model *2* appear to provide a better estimate of the field situation.

DISCUSSION

Predictions made by model *1* and model *2* were compared. Errors were greatest when there was (1) a combination of low temperatures (<5°C) and low light levels (0–50 $\mu E\,m^{-2}\,s^{-1}$), and (2) a combination of high temperatures (>20°C) and high light levels ($>700\,\mu E\,m^{-2}\,s^{-1}$). Callaghan and others (1978) noted similar errors in multiple regression models of photosynthesis in *Hylocomium splendens* (Hedw.) B. & S. and

Polytrichum commune (L.) Hedw. Kallio and Kärenlampi (1975) suggested that multiple regression models may not be able to fully describe the relationship between photosynthesis and environmental variables in *Cetraria nivalis*. Any inadequacies may be gradually exaggerated as the number of variables incorporated is increased. For instance, when Grace and Woolhouse (1970) combined several equations, each relating photosynthesis in *Calluna vulgaris* to temperature, 'temperature prehistory', leaf age, and flowering index, to produce a single equation which incorporated the effect of variable light intensity too, there was a loss in forecasting precision.

Although photosynthesis models based on multiple regression equations are unikely to perform as well as models based on independent regressions of photosynthesis on each variable, as shown above, data are not always suitable for the latter type of analysis. Where environmental variables are not under the control of the experimenter and cannot be varied independently, as occurs when field observations are being made, multiple regression analysis may be of greater value. However, even though quadratic functions will often account for 50% or more of the variance it should not be assumed that they are the most suitable functions for describing the relationships in the data. As shown above, the combination of a logarithmic function of radiant flux density and a multiplicative temperature–irradiance interaction factor increased the coefficient of determination in a multiple regression analysis of *Polytrichum alpestre* photosynthesis data by more than 20% over that obtained with a quadratic function of irradiance (cf. equations (1) and (3) in Table I). In a similar analysis of the dependence of gross CO_2 fixation in *Hylocomium splendens* and *Polytrichum commune* on temperature, irradiance and state of hydration in the field, Callaghan and others (1978) used a quadratic function for the first two variables and a cubic function for the last. Although a significant regression was obtained in both cases, temperature did not account for a significant proportion of the variance in either and state of hydration was also not significant with *P. commune*. yet from their discussion it would appear that Callaghan and others (1978) suspected a relationship between gross photosynthesis and both of these variables. Possibly, this is a case where re-analysis might provide equations of greater predictive value, as Callaghan and others suggested.

The maximum deviations between predicted and observed rates of gaseous exchange reported by Callaghan and others (1978) and by Grace and Woolhouse (1970) occurred under conditions of high rates of net photosynthesis and/or high rates of dark respiration (i.e. in mid-morning or mid-afternoon and during the night). It was at these times that maximal deviations were encountered in the present study. As these are common features of Antarctic and Arctic conditions it is recommended that due caution is exercised when employing multiple regression models to predict net gaseous exchange of mosses growing in polar regions.

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APPENDIX

Measured rates of CO_2 fixation (PN/mg m^{-2} h^{-1}) under controlled conditions of temperature (T/°C) and radiant flux density (R/μE m^{-2} s^{-1}).

PN	*R*	*PN*	*R*	*PN*	*R*	*PN*	*R*
P. alpestre		0	3	37	108	158	209
'cold' adapted		−67	0	78	59	133	202
		0	0	68	52	133	202
at −7°*C*				12	52	122	202
0	1 000	*at* −2.5°*C*		33	30	242	200
0	495	24	1 000	−24	26	135	174
0	202	24	495	−73	14	207	135
0	84	24	209	−22	12	90	131
0	52	24	77	−98	7	49	101
0	21	12	17	−79	0	66	97
0	0	12	9	−89	0	66	83
		0	3	−110	0	173	80
		−12	0			69	60
						0	57
at −5°*C*				*at* 5°*C*		22	52
50	1 000	*at* 0°*C*		305	1 010	0	49
0	495	327	941	259	523	0	43
111	488	305	523	188	519	−110	26
0	209	144	488	219	495	−67	23
100	202	61	488	177	488	23	20
44	84	133	475	200	475	−88	17
0	77	259	348	166	475	−124	17
22	52	49	219	276	465	−122	13
11	21	214	209	214	348	−171	12
0	17	111	202	180	348	−158	9
0	9	158	122	276	340	−155	7

PN	R
−92	0
−166	0
−195	0
−200	0
−237	0
at 10°C	
361	1 000
305	523
244	519
190	500
207	488
199	488
155	475
226	348
178	325
142	215
146	205
200	202
111	202
214	174
107	135
56	113
199	91
71	90
24	78
24	50
111	45
−135	45
−85	43
−219	26
−203	17
−244	10
−248	9
−119	0
−200	0
−293	0
at 15°C	
200	1 000
189	697
133	500
144	475
73	453
78	348
133	320
44	210
24	205
177	202
−22	174
−145	104
0	75
−98	75
0	73
−219	47
−334	45
−210	31
−356	21
−265	19
−366	16
−379	10
−298	9
−353	3
−222	0
−222	0
−382	0
−423	0
at 20°C	
312	1 010
156	523
89	488
33	488
138	480
78	475
11	348
46	320
−44	203
45	202
0	202
0	202
−115	200
−134	174
−172	120
−334	80
−155	73
−245	59
−423	45
−298	35
−431	17
−321	0
−497	0
−513	0
−621	0
at 25°C	
312	976
0	530
145	523
0	488
0	475
−89	350
45	348
−166	215
−99	205
−223	174
−267	120
−331	90
−334	87
−311	65
−464	52
−356	35
−597	17
−400	0
−663	0
−757	0
at 30°C	
189	941
33	523
−221	523
−78	348
−376	205
−390	174
−486	108
−535	87
−663	38
−884	0
−1002	0
P. alpestre 'warm' adapted	
at −5°C	
0	1 000
0	500
0	250
0	150
0	75
0	0
at 0°C	
250	1 000
200	540
200	350
200	250
180	150
140	75
−14	0
at 5°C	
450	1 000
413	545
379	350
310	260
241	175
172	135
103	65
−34	0
at 10°C	
600	1 000
586	515
483	360
334	215
256	160
156	95
78	70
33	55
19	30
−103	0
at 15°C	
600	1 000
578	515
445	335
311	200
200	140
100	90
67	80
22	70
−222	0
at 20°C	
700	1 000
530	530
501	345
334	210
233	150
100	90
0	65
−489	0
at 25°C	
800	1 000
488	465
222	300
22	175
−244	105
−577	0
at 30°C	
400	1 000
250	500
100	350
−50	250
−200	150
−450	75
−750	0
D. uncinatus	
at −10°C	
0	1 000
0	500
0	250
0	150
0	75
0	0
at −5°C	
30	1000
30	500
30	250
30	150
10	75
−5	0
at 0°C	
130	1 000
113	480
113	235

PN	*R*
80	170
79	120
56	90
0	70
− 11	0
at 5° C	
280	1 000
201	500
180	480
167	275
169	250
135	170
134	165
124	100
112	100
100	75
79	65
68	65
89	50
− 22	40
− 34	0
− 67	0
at 10° C	
450	1 000
357	500
245	480
301	330
212	250
284	235
279	235
223	175
112	90
67	65
89	50
11	40
45	30
− 56	0
− 89	0
− 89	0
at 15° C	
500	1 000
250	1 000
411	500
203	480
333	315
169	250
266	180
156	180
211	135
100	120
44	90
111	80
− 33	55
44	50
0	30
− 134	0
− 155	0
at 20° C	
500	1 000
480	1 000
442	485
358	480
292	450
335	310
269	250
246	250
225	230
213	175
213	175
168	165
112	120
78	110
90	90
67	90
0	70
− 67	60
− 67	50
− 123	0
− 202	0
at 25° C	
350	1 000
300	1 000
222	500
250	480
155	320
168	250
168	250
133	240
123	175
89	170
67	130
22	120
− 33	90
− 123	60
− 179	50
− 157	0
− 178	0
at 30° C	
250	1 000
168	480
56	240
22	180
− 67	120
− 56	120
− 234	50
− 268	0
− 314	0