THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: XVI. PEAT O_2-UPTAKE IN A MOSS TURF RELATIVE TO EDAPHIC AND MICROBIAL FACTORS

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ABSTRACT. Aerobic respiration by intact, field-fresh peat cores from the Maritime Antarctic moss turf community at SIRS 1, Signy Island, was monitored by measuring the rate of oxygen consumption through two growing seasons and two winters. The moisture content and temperature of the peat, and its bacterial, yeast and fungal microflora were monitored concurrently. The two mosses studied, *Polytrichum alpestre* and *Chorisodontium aciphyllum*, showed different respiratory responses to abiotic and microbial factors. Moisture and the availability of suitable substrates were more important than temperature for regulating peat O_2-uptake. Adjustment for Q_{10} was irrelevant during the metabolically-active spring period owing to the prolonged stability of peat temperature at 0 to 1°C. Log-transformation of the data improved the correlation between O_2-uptake and microbial population size. No multiple regression equation adequately accounted for $> 60\%$ of variation in *Polytrichum* peat O_2-uptake or $> 76\%$ peat for *Chorisodontium* peat.

INTRODUCTION

The Signy Island terrestrial reference sites (SIRS) were established to facilitate a study of both energy and nutrient cycling and of community interactions occurring within the Antarctic bryophyte ecosystems (Tilbrook, 1973). The study included attempts to balance measures of production and decomposition (Davis, 1981). The rate of peat respiration has been used as a measure of decomposition at Signy Island and in a range of other tundra sites. It has been measured either as CO_2 release (Flanagan and Veum, 1974) or O_2-uptake (Bunnell and others, 1977). The two methods have been compared on a latitudinal transect of Antarctic sites dominated by *Polytrichum alpestre* during a summer season (Wynn-Williams, 1984). The microflora associated with the mosses and their decomposition and respiration-rate at these sites was measured concurrently (Wynn-Williams, 1985). The SIRS were included in this transect to relate the detailed two-year (1975–77) seasonal study reported here to the Maritime Antarctic in general.

The aim of the present study was to determine the changes in the rate of peat O_2-uptake and associated variables with increasing depth away from the moss-bearing surface, and with the time elapsed after the spring thaw, which initiates the Antarctic growing season (Wynn-Williams, 1980). I predicted that rate of peat O_2-uptake would be more dependent on moisture and substrate quality and availability than on temperature. Microbial respiration is the main component of Antarctic peat respiration (Wynn-Williams, 1984), so its association with changes in yeast, fungal and bacterial populations was analysed concurrently to identify the dominant contributors.

Materials and Methods

Climate

The climate of Signy Island is cold, humid and windy with a high but seasonal incidence of precipitation as snow in winter and as rain or snow in summer (Collins and others, 1975). The micro-climate of the SIRS has been fully described by Walton (1982). From April to November the SIRS are usually snow covered. Mean monthly air temperatures during the period of study ranged from +2.2°C (February) to −15°C (June) with annual mean air temperature around −3.4°C. The peat of the SIRS is frozen throughout its depth (*c.* 30 cm) in winter (March–November), but it thaws in summer. Cycles of freezing and thawing occur regularly throughout the spring and summer with up to 64 such cycles occurring in the surface layers of a moss turf in one year. During spring, up to 20 d after thaw (Wynn-Williams, 1980), and again during late summer the peat and moss temperatures remain relatively stable at *c.* 0°C for 2–3 weeks and 1–2 weeks respectively (Walton, 1982).

Site

The site is a relatively dry moss turf community on a north-west facing slope on Gourlay Peninsula referred to as SIRS 1 and described fully by Tilbrook (1973). Its flora is dominated by the mosses *Polytrichum alpestre* Hoppe and *Chorisodontium aciphyllum* (Hook f. et Wils.) Broth., which grow in pure and mixed stands. Lichens, including *Alectoria chalybeiformis* (L.) Gray, *Sphaerophorus globosus* (Huds.) Vain., *Usnea antarctica* Du Rietz and *Ochrolechia frigida* (Sw.) Lynge, are also common on the site. Peat has accumulated to the average depth of 24 cm (Davis, 1981).

After occasional determinations of pH in 1975–77 had suggested slight seasonal trends, regular monitoring was carried out in 1978–79. When present, peat expressate was used to determine pH, but as the peat dried out a 1 : 1 slurry was used. Corrections for this dilution were made using the following empirical equations derived for the 1978/79 summer data, where y = peat expressate pH and x = 1 : 1 slurry pH. For the *Polytrichum*-rich stands (60% *Polytrichum*, 20% *Chorisodontium*, 20% lichens, R. I. Lewis Smith, pers. comm.), $y = 0.63x + 1.51$ (within the range $x = 4.03$ to 4.92). For *Chorisodontium*-rich (65% *Chorisodontium*, 25% *Polytrichum*, 10% lichens) stands, $y = 0.70x + 1.91$ (within the range $x = 3.83$ to 4.78). Dilution corrections for winter data were made using the same empirical quotient (derived for winter 1979 data) for both communities, where the quotient of expressate pH/1 : 1 slurry pH = 0.93. The E_h status of the peat was assessed qualitatively using silver plated stakes (Wynn-Williams, 1980; Davis, 1981). As compression in such shallow peat banks is slight owing to low decomposition rates (Fenton, 1980) and relatively low water content, the peat is mainly aerobic (Wynn-Williams, 1980).

Sampling

Sampling began in March 1975 and was repeated each month throughout the following austral winter and summer. It was reduced in frequency during 1976 and was ended in March 1977. Field samples were collected at *c.* 1200 h local time on each occasion. The time of the initial spring thaw in each successive layer of the profile was recorded.

Details of sampling techniques and subsequent sample treatments are given in Wynn-Williams (1979). Eight replicate peat cores (2.7 cm diameter, 12 cm deep) for respirometry and four cores for microbial enumeration were collected randomly from

areas rich in the required moss cover. The surface layer of green shoots (0–1 cm) was removed, and the remainder sectioned into four zones: 1–3, 3–6, 6–9 and 9–12 cm below the surface respectively. These zones were used for respiration measurement and microbial studies. Results are presented for mean depths (i.e. 2.0, 4.5, 7.5 and 10.5 cm). The core sections were not homogenized but were inserted directly into tightly fitting cones which were inserted into the base of special Gilson respirometry flasks. These were shaken to maximize CO_2-uptake by KOH solution in the annular well of the flasks.

When the peat was not frozen, the temperature throughout the profile was measured at the time of sampling using a thermistor thermometer (Edale Instruments).

Respirometry

Within 3 h of sampling, the oxygen uptake rate of peat core sections was measured using a Gilson respirometer permitting a detection limit of $\pm 0.5\ \mu l\ h^{-1}$ (Wynn-Williams, 1979). After one hour of equilibration at field temperature the rate of O_2-uptake was constant. Frozen cores in winter were monitored at a standard +5°C. The value of Q_{10} and Respiratory Quotient for this community were measured by the procedure described by Wynn-Williams (1984).

O_2-uptake was expressed in $\mu l\ h^{-1}\ g^{-1}$ dry weight (d.w.) of peat. The standard error between cores was rarely $> 16\%$ of the mean for *Polytrichum* or 13% for *Chorisodontium*.

Microbial enumeration

The microbiological procedures are given in Wynn-Williams (1979). Despite the considerable underestimation of the absolute size of viable microbial populations of tundra peat by plate counts (Martin and others, 1982), they are justified for detecting relative fluctuations of the ruderal saprophytic microbial groups prevailing in moss peat subjected to freeze–thaw and wet–dry stress. Counts were expressed as colony-forming units (CFU) $\times 10^{-2}\ g^{-1}$ d.w.

The standard error of mean viable microbial counts between cores was in the range 32–43% of the mean for *Polytrichum* and 27–39% of the mean for *Chorisodontium*.

Analyses

Analyses were applied to relate peat O_2-uptake to abiotic (moisture, temperature, time elapsed after thaw (*ET*) and depth) and microbial factors. Initially, relationships between the variables were examined by Spearman rank correlation analysis. This showed statistically significant relationships between O_2-uptake and all variables except temperature. To analyse O_2-uptake in relation to sets of abiotic and microbial variables, I used stepwise multiple regression analysis. Preliminary plots of scatter diagrams indicated $\log_e$ transformation of both O_2-uptake and microbial variables to comply more closely with the assumption of linearity and homogeneity of variance in the regression analysis.

The growing season was divided into spring ($ET = 0$–19 d) and summer ($ET \geqslant 20$ d up to winter freeze-up). Depths were integrated into three horizons, analysed separately: 1–3 cm, immediately beneath the green shoots, and including the majority of the saprotrophs such as yeasts; 1–6 cm, including additionally more decomposers of macromolecules such as cellulose; and 1–12 cm, a horizon representative of a major portion of the whole peat profile.

Results

Abiotic variables

Mean monthly air temperatures during 1975–77 were near the average for 1951–80 except for a colder winter in 1975. Corresponding seasonal changes in ground temperature, depth of thaw and water content of *Polytrichum* and *Chorisodontium* peat have been illustrated in Wynn-Williams (1982). Temperature at sampling was measured from the onset of spring thaw, which commenced on 17 October 1975 and on 12 November 1976. Thawing exceeded 12 cm depth by the end of November in both years. During the unfrozen period, mean $\pm$ SE peat temperatures at sampling were 2.0 ± 2.9 for *Polytrichum* and 1.8 ± 3.3 for *Chorisodontium*. Surface temperatures were the most variable, but there was no significant correlation between mean temperature and depth. Typical diurnal patterns of variation in peat temperature (maximal summer range of 0°C to *c.* 23°C) are given in Walton (1982).

Water content fluctuated between 370 and 1140% d.w. in *Polytrichum*, and 350 and 800% d.w. in *Chorisodontium*. It decreased significantly ($P < 0.01$) throughout the growing season in both communities but was independent of depth down to 12 cm over the total growing season as a whole. However, during spring alone, moisture increased with depth in *Polytrichum*. High moisture was recorded in winter (mean *c.* 760% d.w.) decreasing to *c.* 500% d.w. in the first 20–30 days after spring thaw. Ice formation at the end of summer restricted drainage, and high moisture values were quickly re-established.

The fluctuations of peat pH in *Polytrichum* and *Chorisodontium* communities over two growing seasons and a winter are shown in Fig. 1. Peat pH values were higher at the beginning of the first growing season than at the beginning of the second. This trend was exaggerated by a slight decrease in diluent pH during the first season but was confirmed in the second. In both summer seasons pH was within the range 3.8–4.5. The pH stabilized in winter and changed markedly only at times of freeze and thaw.

During the course of the study, silver plated stakes embedded in the peat never showed signs of blackening. This indicated that aerobic or microaerophilic conditions prevailed all year round throughout the peat profile (Wynn-Williams, 1980).

Subdivision of seasons. The combination of O_2-uptake data from winter, when the ground was frozen and both respiration and growth were insignificant (Wynn-Williams, 1982), with data for the growing season was not valid. The use of thawed winter cores to simulate spring activities has been reported elsewhere (Wynn-Williams, 1982). Subsequent analyses here were therefore restricted to the growing season comprising spring and summer only.

Correlation analyses. Preliminary Spearman rank correlation analysis of microbial data for the 1–12 cm horizon showed the number of bacteria able to grow on NA medium correlated closely with yeasts and fungi, and to a lesser extent with bacteria able to grow on CPSA medium. The latter was used for most of the later stages of the survey as it gave improved colonial morphology and pigmentation. Rank correlation analysis also showed statistically significant relationships between O_2-uptake and all biotic and abiotic variables except temperature.

Correlation between rate of O_2-uptake and microbial groups in *Polytrichum* peat was not demonstrable in the metabolically-responsive 1–3 cm layer adjacent to the primary producers. This was due partly to reduced replication on eliminating data from depths 3–6, 6–9 and 9–12 cm, and partly to the variability of moisture content and nutrient-availability near the surface. Correlations were more evident on combining the data from the 1–3 with the less variable 3–6 cm level, which included more

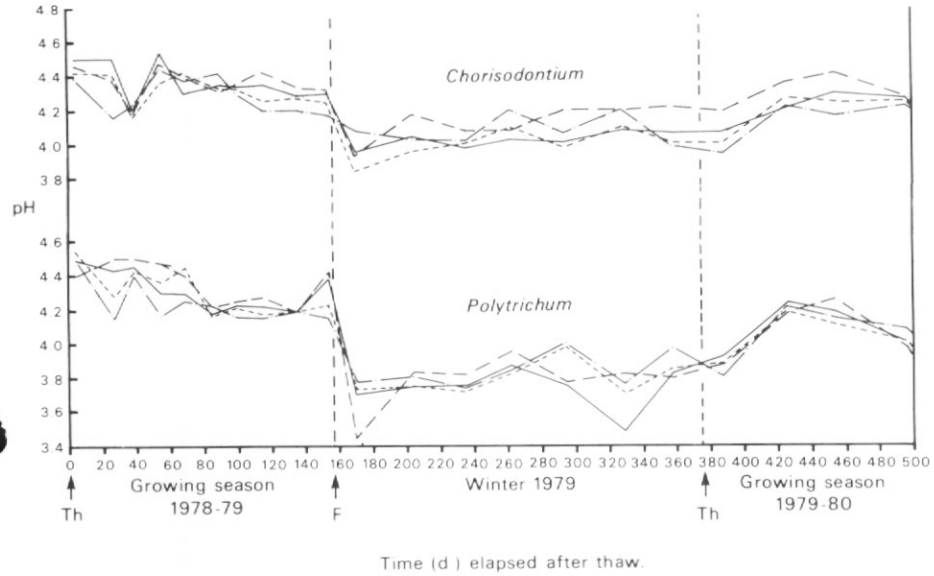

Fig. 1. Seasonal fluctuations in the pH of peat expressate from four horizons of *Polytrichum* and *Chorisodontium* stands at SIRS 1. –·–· 1–3 cm, - - - 3–6 cm, —— 6–9 cm, — — 9–12 cm. Th = Thaw; F = Freeze-up.

macromolecule-decomposition (Wynn-Williams, 1980). On combining the data from all four depths, peat respiration was shown to correlate with all microbial groups. Such correlations were less evident in *Chorisodontium* due in part to less replication of data.

As indicated by preliminary non-parametric analysis, O_2-uptake in the 1–12 cm horizon of *Polytrichum* peat was associated with *ET* (possibly its component of decreasing moisture), depth and microflora (Table I). Yeasts showed the closest correlation but all groups were inter-correlated. These trends were not as clear in *Chorisodontium* peat where O_2-uptake decreased markedly with greater depth and decreasing yeasts and fungi which were all inter-correlated. These observations led to the use of multiple regression analysis to determine the dominant factors associated with peat O_2-uptake.

Multiple regression of O_2-uptake rate on abiotic and microbial variables

In *Polytrichum* communities, environmental and microbial changes associated with *ET* were more influential than those linked with depth in accounting for variation in $\log_e$-transformed peat respiration (Table II). The converse was true for *Chorisodontium* (Table III). The influence of moisture on log O_2-uptake was only apparent in *Polytrichum* peat.

On including all abiotic variables, the comprehensive range of factors changing with depth and *ET* made them the dominant correlates in both communities. The inclusion of moisture with depth accounted for little or no additional variation in the O_2-uptake. Although the correlation of all microbial groups with peat O_2-uptake was similar (Table I), the yeasts predominated in multiple regressions (Tables II and III) and largely represented the covariates fungi and bacteria. Therefore, including elapsed time

Table I. Percentage of variation accounted for ($100\ r^2$) in inter-correlations between moss turf peat O_2-uptake at SIRS 1 and associated biotic and abiotic variables

			Chorisodontium ($n = 19$)†							
Polytrichum ($n = 34$)†	Units	Range of data‡	$\log_e R$ 1.46–4.14	*ET* 0–339	*D* 2.0–10.5	*M* 347–800	*T* −0.3–10.0	$\log_e Y$ 58–25336	$\log_e F$ 202–30330	$\log_e B$ 47–46630
$\log_e$ respiration ($\log_e R$)	$\mu l\ h^{-1}$	1.36–4.03		−13	−59	4	< 1	37**	20*	31*
Elapsed time (*ET*)	d	0–335	−28***		N.V.	−45**	23*	−32**	−2	−1
Depth (*D*)	cm	2.0–10.5	−23**	N.V.		−2	−1	−56***	−16	−52***
Moisture (*M*)	% dry wt	370–1142	−15*	−38***	−1		−25*	23*	1	< 1
Temperature (*T*)	°C	0–13.0	2	< 1	−3	−4		−9	< 1	< 1
$\log_e$ yeasts ($\log_e Y$)	CFU × 10^{-2} g^{-1} dry wt	26–6905	43***	−4	−57***	10	1		11	38**
$\log_e$ fungi ($\log_e F$)	CFU × 10^{-2} g^{-1} dry wt	109–12210	33***	< 1	−48***	2	7	48***		42**
$\log_e$ bacteria ($\log_e B$)	CFU × 10^{-2} g^{-1} dry wt	57–64860	37***	−15*	−12*	4	5	25**	38***	

Results are from 1–12 cm horizon during the growing season.
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.V., not valid; −, negative correlations.
† Number of peat-core section mean data incorporated.
‡ Before transformation.

Table II. Regression coefficients and percentage of total variation (100 R^2) in $\log_e$-transformed respiration data accounted for by multiple regression of 16 different combinations of variables in the 1–12 cm peat profile of *Polytrichum* stands at SIRS 1 during two growing seasons. The variables comprised time elapsed after thaw (*ET*), depth and moisture, excluding and including microbial data

Excluding $\log_e$-microbial data				*Including $\log_e$-microbial data*						
Regression Coefficient, b			100 R^2	*Regression Coefficient, b*						100 R^2
ET	*Depth*	*Moisture*	*Overall*	*ET*	*Depth*	*Moisture*	*$\log_e$–Yeast*	*$\log_e$–Fungi*	*$\log_e$–Bacteria*	*Overall*
−0.007**	—	—	28**	−0.005**	—	—	0.21*	0.15	0.07	65***
—	−0.12**	—	23**	—	0.007	—	0.27*	0.04	0.17*	53***
—	—	0.002*	15**	—	—	0.001	0.22	0.47	0.16	57***
—	—	—	—	—	—	—	0.26*	0.03	0.17*	53***
—	−0.10**	0.002*	38**	—	−0.012	0.001	0.20	0.05	0.17*	56***
−0.005*	—	0.001	31*	−0.005*	—	−0.001	0.22*	0.16	0.06	65***
−0.006***	−0.10**	—	46*	−0.005**	0.021	—	0.24*	0.18	0.06	65**
−0.005*	−0.10	0.001	48***	−0.006*	0.032	0.001	0.27*	0.20	0.04	66***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
— Variable excluded.

Table III. Regression coefficients and percentage of total variation (100 R^2) in $\log_e$-transformed respiration data accounted for by multiple regression of 16 different combinations of variables in the 1–12 cm peat profile of *Chorisodontium* stands at SIRS 1 during two growing seasons. The variables comprised time elapsed after thaw (*ET*), depth, and moisture, excluding and including microbial data

Excluding $\log_e$-microbial data				*Including $\log_e$-microbial data*						
Regression Coefficient, b			100 R^2	*Regression Coefficient, b*						100 R^2
ET	*Depth*	*Moisture*	*Overall*	*ET*	*Depth*	*Moisture*	*$\log_e$–Yeast*	*$\log_e$–Fungi*	*$\log_e$–Bacteria*	*Overall*
−0.005	—	—	13	−0.002	—	—	0.16	0.12	0.13	45
—	−0.20***	—	59***	—	−0.19*	—	0.04	0.18	−0.11	62**
—	—	0.002	4	—	—	0.001	0.24	0.15	0.06	48
—	—	—	—	—	—	—	0.21	0.14	0.09	44
—	−0.20**	0.001	60**	—	−0.20**	0.001	< 0.001	0.16	−0.08	63**
−0.007	—	< 0.001	19	−0.003	—	< 0.001	0.18	0.13	0.10	51
−0.005*	−0.19*	—	68***	−0.009*	−0.30***	—	−0.29	0.11	−0.04	77**
−0.007*	−0.19***	−0.001	71**	−0.01*	−0.30**	−0.001	−0.25	0.13	0.08	78**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

(*ET*) and log yeast (log *Y*) only, 60% of the variation in log rate of peat O_2-uptake (*R*) in *Polytrichum* stands was given by

$$\log_e R = 0.978 - 0.005\ ET + 0.340 \log_e Y$$

where *R* was in $\mu l\ h^{-1}\ g^{-1}$ d.w., *ET* was in d, and *Y* was in CFU $\times 10^{-2}\ g^{-1}$ d.w. The inclusion of yeasts compensated for changes with depth due to covariation (Table I). Restriction of the data to the 1–6 cm peat horizon improved the response of log O_2-uptake to *ET* from 31% to 40%. Further restriction was detrimental.

In *Chorisodontium* stands (Table III), peat O_2-uptake was not conspicuously associated with changes in moisture, but log O_2-uptake decreased markedly (59% of variation) with increasing depth. Changes with *ET* were not as influential but yeasts were again conspicuously associated with increasing respiratory activity. Therefore, on excluding fungal and bacterial data as before, the optimal equation accounting for 76% of variation in log rate of peat O_2-uptake (*R*) in *Chorisodontium* stands was

$$\log_e R = 7.305 - 0.312\ D - 0.009\ ET - 0.306 \log_e Y$$

where the units for *R*, *ET* and *Y* are as above, and *D* is in cm.

Restricting the data to the 1–6 cm horizon improved the response of log O_2-uptake to *ET* from 13% (not significant) to 32% ($P < 0.05$), and to moisture from 4% (not significant) to 16% ($P < 0.05$). In both stands, the effect of moisture was largely subsumed within the composite variables *ET* and *D*.

Discussion

Decreasing O_2-uptake by field-fresh peat with increasing depth was a trend common to both *Polytrichum* and *Chorisodontium* stands. However, a decrease in O_2-uptake with elapsed time after the thaw was only demonstrable in *Polytrichum* peat. This was due partly to the non-linearity of seasonal changes (Wynn-Williams, 1980). The determination of the dominant regulatory factors for field-fresh peat O_2-uptake was hindered by the limits of variation in temperature and to a lesser extent the range of moisture occurring on sampling occasions. The influence of field temperature was not apparent in the present survey owing to small scale of variation between measurements on sampling occasions. The duration of high (> 10°C) summer ground temperatures at Signy Island was generally short (Walton, 1982), and the period of maximum field-fresh peat O_2-uptake occurred in spring at temperatures close to freezing-point (Wynn-Williams, 1980). However, a Q_{10} value of 3.0 has been determined *in vitro* for *Polytrichum*-dominated peat at Signy Island (Wynn-Williams, 1984). Predictions of peat O_2-uptake based on this survey therefore refer to typical field temperature conditions rather than the full potential of the system.

A geographically broader survey of *Polytrichum* stands (Wynn-Williams, 1984) indicated the range of moisture recorded in the present survey to be frequently within the optimal range for peat O_2-uptake and therefore not necessarily rate-limiting. This was evident for *Chorisodontium*, and the association between O_2-uptake and moisture in *Polytrichum* peat was weak.

Factors associated with *ET* and depth other than temperature and moisture were apparently regulatory for peat O_2-uptake. The availability of respiratory substrates was a potential factor but was difficult to quantify due to the complex requirements of the heterogeneous peat microflora. Supplements of *Polytrichum* peat *in vitro* with potential substrates indicated that they may, on occasion, be rate-limiting (Wynn-Williams, 1982). These studies *in vitro* suggested that the exponential multiplication of the saccharolytic microflora reflected substrate availability. The correlations

between peat O_2-uptake and microbial CFU counts in the present field survey are taken to reflect the unquantifiable availability of suitable respiratory substrates. The close correlation between O_2-uptake and yeasts in both stands was therefore important.

The optimal regression equations differed between the two stands. *ET* was more influential than depth in *Polytrichum* but not in *Chorisodontium*. Up to 66% of the total variation in peat O_2-uptake for *Polytrichum* and 78% for *Chorisodontium* was accounted for by the equations. Other than error variation, the residue was attributable to biotic and abiotic factors not incorporated. These included redox conditions (Wynn-Williams, 1980), pH (Fig. 1), inorganic nutrients, and non-microbial respiration.

A non-linear decrease in peat O_2-uptake with depth, steeper near the surface (Wynn-Williams, 1980), was confirmed by close correlation and linearity between log-transformed O_2-uptake and depth. This paralleled the non-linear decrease in P_{O_2}, also steeper near the surface, suggesting the presence of microaerophilic conditions which may become rate-limiting for aerobic respiration.

Edaphic factors

Except for the transition during freeze-up, changes in pH were gradual in both communities, but showed occasional irregularities both with *ET* and depth. Hence, although the mean pH of a tundra site may affect its intrinsic respiratory and microfloral characteristics (Heal and others, 1981; Holding, 1981), changes in pH with depth and time were unlikely to exert a significant effect within SIRS 1.

Correlation between peat respiration and nutrients such as nitrogen, phosphorus and potassium is of limited value unless the requirements of the extant population are known. In Antarctic mineral soils where the N content is low, such as on the Antarctic continent near Syowa Station, respiration correlates with total N (Ino and others, 1980). However, Allen and others (1967) considered that the supply of all major nutrients in moss turf at Signy Island, including potassium which is the least abundant, to be in excess of requirements for plant growth and therefore probably also for microbial activity at SIRS 1. Bailey and Wynn-Williams (1982) showed that, although % total N, % loss on ignition, % moisture and pH (negative) inter-correlated in a *Polytrichum–Chorisodontium* turf at Signy Island, % P correlated independently ($P < 0.05$) with viable bacteria. However, fungi correlated better with the factors grouped above. Analyses for N, P and K at SIRS 1 in 1978–80 (P. Christie, pers. comm.) showed that total N was less variable at 0–9 cm than at 9–12 cm and a winter accumulation of total N was not apparent. Total P (% d.w.) was larger and more variable at depths > 6 cm and there was a gradual winter accumulation of total P at SIRS 1 and soluble P at a comparable site nearby (Northover and Allen, 1967). However, there was no sharp response of P to thawing or freeze-up at SIRS 1. Potassium did not show consistent seasonal variation at SIRS 1 although it was more abundant in the 0–3 cm horizon than at 3–12 cm. None of these nutrients followed strictly the same trend as peat respiration and microbial populations so that edaphic and microclimatic variables are more likely to be regulatory, as Allen and others (1967) concluded for cryptogam development. The elimination of these variables left moisture, temperature, respiratory substrate and respiratory biomass as the main potential factors of the trends with depth and *ET*.

Abiotic factors

On a transect of *Polytrichum* sites on islands of the Scotia Arc and on the Antarctic Peninsula, Wynn-Williams (1984) found that correlation was not demonstrable between O_2-uptake and field temperature, with or without transformation of the data. This was borne out by the present detailed study at one of these sites, SIRS 1. The Q_{10} value of 3.0 shown for *Polytrichum* peat at SIRS 1 (Wynn-Williams, 1984) was similar to Arctic sites. However, the duration of high field temperatures was brief, only 25% of the growing season having a ten-day mean ground temperature (at 1.5 cm) of 5°C or over and only 4% at 6.8°C or over (Walton, 1977). During the metabolically active spring period the ground temperature remained at *c.* 0°C so that the influence of temperature was minimal. Its influence was similarly limited in mineral soil on Ongul Island, Antarctica (Ino and others, 1980). These findings contrasted with northern tundra sites where a broader range of temperature accounts for 40% of variation in respiration at Barrow and 81% at Hardangervidda (Flanagan and Veum, 1974).

High rates of respiration at increased moisture content and low positive temperatures, as in spring at Signy Island, were common at other tundra sites such as Point Barrow and Hardangervidda (Flanagan and Veum, 1974). However, comparison of respiration rates at moisture contents differing with depth and *ET* suggests that, as long as there is *c.* 400–1100% (d.w.) moisture present and the ground temperature is positive, respiration at SIRS 1 will be regulated by other factors.

In addition to their moisture component, both *ET* and depth represent increasing remoteness from the potential source of soluble respiratory substrates, either in time after the spring flush or in distance from the autotrophic and microfaunal layer. Therefore the strong association of O_2-uptake with *ET* and depth relative to a weaker correlation with moisture alone and no demonstrable correlation with temperature implied that respiratory substrate was a major regulator of O_2-uptake and microbial multiplication.

The peak in respiration at SIRS 1 in spring and the implied increase in the availability of respiratory substrates was associated with light freeze–thaw cycles (Wynn-Williams, 1982). These may not be extreme enough to freeze cells (Walton, 1982). Although the eutectic point of water in the surrounding soils may be −7°C (Morley and others, 1983), bacterial cells may supercool until they freeze at *c.* −16°C (Mazur, 1980). However, supercooling stresses cells, making their membranes 'leaky' (Macleod and Calcott, 1976). Morley and others (1983) concluded that two supercooling cycles were as detrimental to a soil pseudomonad as one true freeze–thaw cycle (−27°C to +23°C), although sensitivity varies among species (Nelson and Parkinson, 1978). The organic material thus leaked from cryptogamic, invertebrate and microbial cells, together with the remains of cells ultimately killed by supercooling stress and freezing may act as respiratory substrates, reflecting the biomass made available for decomposition (Jenkinson, 1976) during spring freeze–thaw cycles.

Correlation of O_2-uptake with depth and *ET* was construed to represent two types of relationship: First, parallel response to fluctuating substrate availability and moisture; second, constant respiration at a 'basal' level during more stable edaphic conditions. The basal level in spring was lower than in summer (Wynn-Williams, 1982). This may represent an increase in slower but more constant decomposition of insoluble material such as cellulose by fungi at times of decreased substrate availability.

Microbial factors

The abiotic variables also regulate the size of the microbial population and its composition (Wynn-Williams, 1985). However, respiration is not necessarily proportional to microbial biomass as many cells may be dormant. The microflora, especially ruderals such as yeasts and 'sugar fungi', respond to substrates by multiplication as well as respiration (Wynn-Williams, 1982). The predominance of yeasts in the multiple regression equations therefore reflects the availability of respiratory substrates. However, dormancy implies that microbial population-size, and consequently biomass, is not necessarily a regulator of respiration but will be a correlate.

The predominance at SIRS 1 of ruderals (fast growth-rate and high sporulation) such as yeasts and *Mortierella* would not have been predicted for the high stress and high disturbance situation of the terrestrial Antarctic (Pugh and Allsopp, 1982). However, these opportunists are probably sustained by the leaching of nutrients such as glucose and fructose from *Polytrichum* cells (Skre and others, 1975) and the availability of diverse dead cells as substrates. The decrease in yeast population with *M* at SIRS 1 was consistent with their exploitation of the spring flush (Wynn-Williams, 1982) and subsequent decline. Similar abundance of yeasts has been reported from Arctic tundra sites (Baker, 1974, Bab'yeva and Chernov, 1982) but their significance for respiration and implied decomposition of soluble substrates has not been demonstrated as emphatically as here.

Part of the bacterial and fungal contribution to O_2-uptake was probably subsumed within the more stable basal level of respiration associated with the decomposition of macro-molecules. Precise relationships may be obscured by the varying proportions of respiration due to microbial metabolism, growth and multiplication. Populations may also be disrupted by migration and leaching so that their exponential growth may not be detected in the field, unlike studies *in vitro* (Wynn-Williams, 1982). Finally, they may be grazed by invertebrates at such a rate as to preclude detection of any exponential growth (Clarholm, 1981; Wynn-Williams, 1983).

Peat respiration is not due entirely to the microflora, and Davis (1981) and Wynn-Williams (1984) have estimated their percentage contribution relative to moss tissue, algae and microfauna at SIRS 1. The latter concluded that the non-microbial contribution to peat respiration may be *c.* 17% which would account for some of error variation between the microflora and peat O_2-uptake here.

Conclusion

The use of sectioned cores exaggerated the rate of O_2-uptake by releasing nutrients and by artificially exposing cut surfaces for aerobic gas exchange as discussed by Wynn-Williams (1984). However, the importance of moisture, the implied importance of available respiratory substrates, and the elevation of temperature above freezing point emerged as the main potential regulators of peat O_2-uptake in the moss turf. Moreover, the predominant correlation of yeasts with high peat O_2-uptake shown *in vivo* here at SIRS 1 and at other similar sites (Wynn-Williams, 1984) and *in vitro* (Wynn-Williams, 1982) indicate this to be a feature of maritime Antarctic tundra.

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