

THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: XVII. PEAT O₂-UPTAKE IN A MOSS CARPET RELATIVE TO EDAPHIC AND MICROBIAL FACTORS

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ABSTRACT. Oxygen-uptake by intact, field-fresh peat cores from the maritime Antarctic moss carpet community at SIRS 2, Signy Island, was monitored through two growing seasons and two winters. Concurrent measurements included the moisture content and temperature of the peat, and its bacterial, yeast and fungal microflora. The two interspersed cryptogamic species studied, *Calliergon* (moss) and *Cephaloziella* (liverwort), differed in the response of their rate of O₂-uptake to edaphic and microbial factors. At high water content, conditions became microaerophilic in *Calliergon* peat and anaerobic in *Cephaloziella*. The stabilising effect of the water resulted in slow responses to thermal and other changes, and was contributory to the poor correlations between the rate of peat O₂-uptake and potentially-regulatory variables in *Cephaloziella*. However, the moisture content of *Calliergon* carpet was less extreme, and the hypothesis that the rate of O₂-uptake was more dependent on moisture and substrate availability than temperature was supported. The ruderal fungal and yeast population was associated with O₂-uptake although not as conspicuously as in the moss turf at SIRS 1. No single multiple regression accounted > 58% of the variation in peat O₂-uptake in the wet moss carpet or > 76% in the drier moss turf. The difference probably reflected the anaerobic component of peat decomposition at SIRS 2, emphasizing the need for measurements of anaerobic respiration to balance its C-cycling budget.

INTRODUCTION

The moss carpet site at the Signy Island terrestrial reference sites (SIRS 2) was established in 1970 for studies of a wet Antarctic bryophyte ecosystem relative to a drier moss turf community (Tilbrook, 1973). It has been described by Collins and others (1975), and comparison with a transect of *Drepanocladus uncinatus* sites on the Scotia Ridge islands and Antarctic Peninsula indicates that it is typical of such communities in the maritime Antarctic (Wynn-Williams, 1984). Peat respiration has been used to assess decomposer activity in tundra sites either as CO₂-release (Flanagan and Veum, 1974) or O₂-uptake (Bunnell and others, 1977), both of which were measured on the Antarctic Peninsula transect. The associated microfloras were monitored concurrently (Wynn-Williams, 1985a) as microbial respiration has been shown to be the main component of Antarctic peat respiration (Wynn-Williams, 1984).

The aim of the present study was to investigate the main abiotic and microbial variables affecting peat O₂-uptake at SIRS 2. Preliminary observations suggested that substrate quality and moisture availability were more influential than temperature. Changes in the effects of these variables with time elapsed after thaw and with increasing depth were monitored over a two-year period (1975-77). Emphasis was placed on the limitations of measurement of O₂-uptake rate for determining peat respiration in a moss carpet, part of which became anaerobic during saturation. This investigation contrasted with a parallel study of an adjacent drier, more aerobic moss turf at SIRS 1 (Wynn-Williams, 1985b) and served to stress the need for anaerobic

determinations of decomposer activity to balance the budget for C-cycling at SIRS 2 (Davis, 1981).

MATERIAL AND METHODS

Climate

The overall climate at SIRS 2 was similar to that described for SIRS 1 (Wynn-Williams, 1985*b*), and local differences have been described by Walton (1982). Its hollow topography and wetter conditions cause SIRS 2 to freeze and thaw later each year than SIRS 1. This higher water content, generally at least twice that of SIRS 1, also dampens temperature fluctuations, lowers their maxima, and decreases the number of freeze-thaw cycles per annum (e.g. in 1972, from 64 at dry SIRS 1 to 18 at wetter SIRS 2) (Walton, 1982). Snow cover is generally much deeper at SIRS 2 than SIRS 1 and therefore persists longer. This has an insulating effect as well as acting as a thermal sink. The net result of these influences is a longer growing season at SIRS 2 than at SIRS 1 but the difference varies from year to year (Wynn-Williams 1980; Walton, 1982).

Site

SIRS 2, described fully by Tilbrook (1973), is a wet moss carpet community situated in a shallow basin 360 m south-west of the SIRS 1 slope on Gourlay Peninsula. Its flora is dominated by the mosses *Calliergon sarmentosum* (Wahlenb.) Kindb., *Drepanocladus uncinatus* (Hedw.) Warnst. and *Calliergidium austro-stramineum* (C. Muell.) Bartr., and the liverwort *Cephaloziella varians* (Gottsche) Steph. Unlike the *Polytrichum alpestre* at SIRS 1, none of these species has rhizoids. This community grows on peat 4–20 cm deep (mean 12 cm), which is always wet and occasionally waterlogged. Below a 0.5–1.0 cm layer of growing shoots there is a 3–4 cm layer of dark brown decomposing stems, below which the peat is more amorphous and changes from yellow-brown to dark brown on exposure to air. The site is frequently disturbed by non-breeding brown skuas (*Catharacta skua*).

The pH of peat expressate (or a 1:1 slurry if necessary) was monitored in detail during 1978–79. Corrections for the dilution were made using empirical equations derived for the 1978–79 summer data, where y = peat expressate pH and x = 1:1 slurry pH. For a *Calliergon*-dominated stand (75% *Calliergon*, 20% *Drepanocladus*, 5% *Calliergidium*) (R. I. Lewis Smith, pers. comm.), $y = 0.85x \pm 0.60$ (within the range $x = 4.63$ to 5.57). For a *Cephaloziella*-dominated stand (68% *Cephaloziella*, 22% *Calliergidium*, 10% *Calliergon*) $y = 0.65x \pm 1.59$ (within the range $x = 4.70 \pm 5.43$). Dilution corrections for winter data were based on a direct ratio derived from winter 1979 data. The ratios of expressate pH to 1:1 slurry pH were 0.91 and 0.93 for *Calliergon* and *Cephaloziella* respectively.

The E_h status of the peat was assessed qualitatively using silver-plated stakes.

Sampling, respirometry, microbial enumeration and analyses

The procedures were as described for SIRS 1 by Wynn-Williams (1985*b*). O_2 -uptake was expressed in $\mu l h^{-1}$ dry weight (d.w.) of peat. The standard error of the determination was rarely $> 13\%$ of the mean *Calliergon* or $> 11\%$ for *Cephaloziella*. Microbial counts were expressed as colony-forming units (CFU) $\times 10^{-2} g^{-1}$ d.w. The standard error of their mean viable microbial counts was generally *c.* 36% of the mean for *Calliergon* and 27–37% of the mean for *Cephaloziella*.

The growing season was divided into spring (elapsed time after thaw, $ET = 0-19$ d) and summer ($ET > 19$ d up to winter freeze-up). As for SIRS 1, depths were integrated into three horizons analyzed separately: 1-3 cm, 1-6 cm and 1-12 cm.

RESULTS

Abiotic Variables

Mean monthly air temperatures during 1975-77 were near the average for 1951-80 except for a colder winter in 1975. Ground temperature at sampling was measured from the onset of spring thaw which commenced on 28 October 1975 and 18 November 1976 and which reached 12 cm depth by mid-December in both years. During the unfrozen period, peat temperatures at sampling varied between 0 and 10°C. Surface temperatures were the most variable having a maximum diurnal range of 0 to c. 14°C in summer (Walton, 1982). There was no significant correlation of mean temperature with depth.

Water content fluctuated between 460 and 2550% d.w. in *Calliergon* and between 30 and 2400% in *Cephaloziella*. In *Cephaloziella* peat it remained high during winter and decreased significantly with ET ($P < 0.01$) but not with depth. Conversely in *Calliergon*, moisture content decreased with depth ($P < 0.001$) but not the ET . Both communities were slow to drain in spring, and *Cephaloziella* remained waterlogged by meltwater for much of the growing season.

Silver-plated stakes embedded in *Cephaloziella* peat were intensely blackened under wet conditions by anaerobic sulphide production to within 2 cm of the surface. Those in micro-aerophilic *Calliergon* peat were discoloured in patches only (Wynn-Williams, 1980; Davis, 1981).

The changes of peat pH in *Calliergon* and *Cephaloziella* during 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 year but was confirmed in the second. In both summer seasons, pH was within the range 4.2-5.4 and only changed markedly at the time of thaw.

Seasons. In winter, the ground was frozen and both respiration and growth were insignificant (Wynn-Williams, 1982). Analyses 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 to correlate closely with yeasts, fungi and bacteria capable of growth on CPSA medium. The latter was used for later stages of the survey. Rank correlation analysis also showed statistically significant relationships between O₂-uptake and all biotic and abiotic variables except temperature.

Scatter diagrams generated during parametric correlation analysis of these data showed that log_e-transformation of both O₂-uptake and microbial variables complied more closely with assumptions of linearity and homogeneity of variance.

As indicated by preliminary non-parametric analysis, O₂-uptake rate of the 1-12 cm horizon of both *Calliergon* and *Cephaloziella* peat decreased significantly with increasing depth (Table I). O₂-uptake in *Calliergon* peat also decreased with ET , and increased with moisture and log-fungi. However, correlation of O₂-uptake with any other variable was not demonstrable. All components of the microflora of *Calliergon* peat decreased with depth and were inter-correlated. Only fungi decreased with depth in *Cephaloziella* peat, and only bacteria and yeasts were intercorrelated.

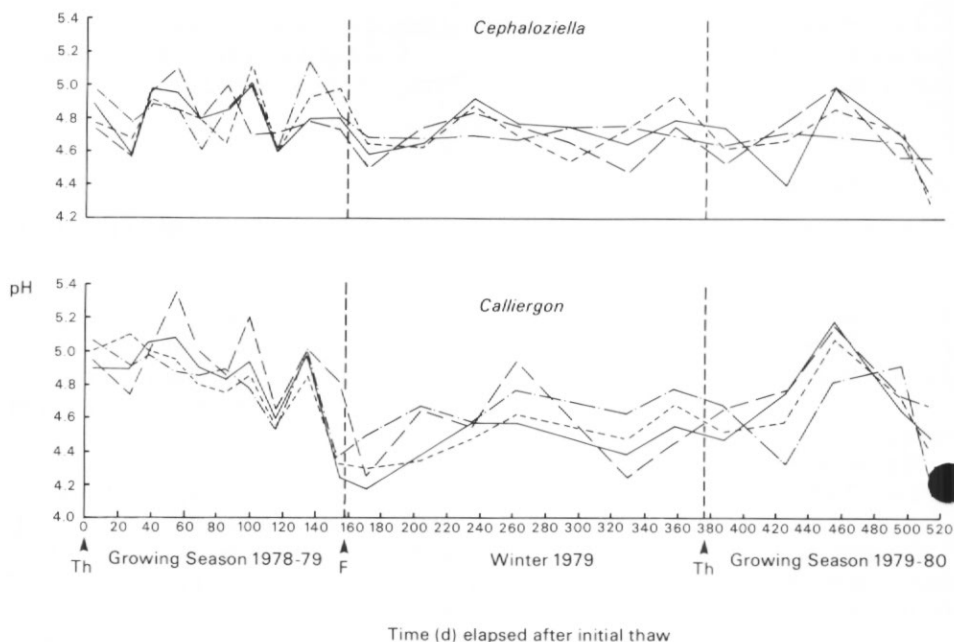


Fig. 1. Seasonal fluctuations in the pH of peat expressate from four horizons of *Calliergon* and *Cephaloziella* stands at SIRS 2. ···· 1-3 cm, ---- 3-6 cm, — 6-9 cm, -- 9-12 cm. Th = Thaw; F = Freeze-up.

Multiple regression of O_2 -uptake on abiotic and microbial variables

Table II shows that a maximum of 62% of the variation in respiration by *Calliergon* peat was accounted for by the combined effect of abiotic and microbial variables. The changes associated with depth were more influential than those of ET , due mainly to moisture, which explained only part of the influence of ET . The influence of temperature was not demonstrable from these field data. Moisture accounted for 21% of variation in O_2 -uptake. A combination of microbial with abiotic data explained 50% of the variation, of which fungi were the main influence, although yeasts and bacteria were co-variates. On including only log-fungi in the regression, the optimal equation for *Calliergon* ($100 R^2 = 58\%$, $P < 0.001$) was

$$\log_e R = 0.074 - 0.008 ET + 0.066 D + 0.450 \log_e F,$$

where R was in $\mu\text{l h}^{-1} \text{g}^{-1}$ dry wt., ET in d, D in cm and F in $\text{CFU} \times 10^{-2} \text{g}^{-1}$ dry wt.

Restriction of the horizon to 1-3 cm obscured these trends but correlation of O_2 -uptake with ET , fungi and moisture was demonstrable in the 1-6 cm horizon.

Error variation obscured most trends in *Cephaloziella* peat except for 49% ($P < 0.01$) of the variation in O_2 -uptake rate being associated with increasing depth, given by

$$\log_e R = 3.090 - 0.077 D.$$

Inclusion of other variables, abiotic or microbial, attenuated this relationship.

Table I. Percentage of variation accounted for (100 r^2) in inter-correlations between the rate of O₂-uptake in moss carpet peat at SIRS 2 and associated biotic and abiotic variables.

<i>Calliergon</i> (n = 26)†	Units	Range of data‡	<i>Cephaloziella</i> (n = 11)†							
			$\log_e R$ 1.93-3.49	<i>ET</i> 0-349	<i>D</i> 2.0-10.5	<i>M</i> 358-2381	<i>T</i> 0-7.0	$\log_e Y$ 53-20330	$\log_e F$ 30-1510	$\log_e B$ 57-35600
\log_e respiration ($\log_e R$)	$\mu\text{l h}^{-1}$	0.47-3.78		-5	-44*	< 1	< 1	6	19	15
Elapsed time (<i>ET</i>)	d	0-341	-19*		1	37*	5	19	-20	11
Depth (<i>D</i>)	cm	2.0-10.5	-27**	< 1		-14	-1	-31	-64**	-19
Moisture (<i>M</i>)	% dry wt	462-2552	21*	-1	-47*		-21	1	29	-1
Temperature (<i>T</i>)	°C	0-10.1	11	-7	-9	1		< 1	-1	2
\log_e yeasts ($\log_e Y$)	CFU $\times 10^{-2}$	31-28280	1	32**	-43***	22*	< 1		3	67**
\log_e fungi ($\log_e F$)	g ⁻¹ dry wt									
	CFU $\times 10^{-2}$	29-4630	32**	1	-83***	32**	10	53***		1
	g ⁻¹ dry wt									
\log_e bacteria ($\log_e B$)	CFU $\times 10^{-2}$	133-92970	7	7	-31**	1	18*	27**	44***	
	g ⁻¹ dry wt									

Results are for the 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 O_2 -uptake rate data accounted for by multiple regression of 16 different combinations of variables in the 1–12 cm peat profile of *Calliergon* stands at SIRS 2 during two growing seasons. The variables comprised time elapsed after thaw (*ET*), depth and moisture, excluding and including microbial data.

<i>Excluding log_e-microbial data</i>				<i>Including log_e-microbial data</i>						
<i>Regression Coefficient, b</i>			<i>100 R² Overall</i>	<i>Regression Coefficient, b</i>						<i>100 R² Overall</i>
<i>ET</i>	<i>Depth</i>	<i>Moisture</i>		<i>ET</i>	<i>Depth</i>	<i>Moisture</i>	<i>log_e-Yeast</i>	<i>log_e-Fungi</i>	<i>log_e-Bacteria</i>	
-0.006*	—	—	19*	-0.005	—	—	-0.12	0.45*	-0.03	58***
—	-0.13**	—	27**	—	0.02	—	-0.27**	0.64*	0.09	53**
—	—	0.001*	21*	—	—	0.001	-0.29**	0.50**	-0.02	56**
—	—	—	—	—	—	—	-0.27**	0.60***	-0.09	53**
—	-0.07	0.001	33*	—	0.09	0.001	-0.30**	0.65**	-0.01	58**
-0.006*	—	0.001*	40**	-0.004	—	0.001	-0.16	0.41*	0.001	59*
-0.006**	-0.13**	—	46***	-0.56	0.06	—	-0.10	0.54*	0.04	58**
-0.006	-0.10	0.001	47**	-0.005	0.11	0.001	0.15	0.57*	0.03	62**

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

DISCUSSION

The location of SIRS 2 in a shallow basin restricted its drainage. This permitted greater accumulation of inorganic nutrients than at the better-drained SIRS 1 (P. Christie, pers. comm.). The percentages of total N, P and K in the moss carpet (SIRS 2) were up to 4, 11 and 4 times greater respectively than in the moss turf (SIRS 1). They were therefore unlikely to be rate-limiting for respiration or growth at this oligotrophic site (Wynn-Williams, 1985b). This contrasted with 'biotic' sites (enriched by seals and sea-birds), such as at Marion Island, sub-Antarctic, where the main regulator of the bacterial flora was the high level of NH₄-N (accounting for 44% of variation in bacterial counts), while the total influence of NO₃-N, P, moisture and pH amounted to only 19% of the remaining variation (Smith and Steyn, 1982). Moreover, the higher pH of the Signy Island moss carpet compared with that of the moss turf permitted the growth of a broader range of microbes (Wynn-Williams, 1985a).

Although moisture was itself a major factor affecting O₂-uptake rate, especially when the peat was drier, the occasional build-up of anaerobic conditions in saturated peat (Wynn-Williams, 1980) restricted O₂-uptake *in situ* at SIRS 2. However, the respirometric conditions exposed O₂-limited sections of peat to an aerobic atmosphere. The respiration rate measure when the peat was saturated was therefore the potential O₂-uptake of a microflora acclimatised to reduced P_{O₂}. On such occasions, it therefore over-estimated true field O₂-uptake but reflected the activity of the aerobic microflora.

The estimates of O₂-uptake rate for the drier aerobic SIRS 1 (Wynn-Williams, 1985b) were probably *c.* 50% in excess of the true field rate for such tundra peat (Peterson and Billings, 1975). The similarity between R.Q. values Q_{CO_2/O_2} determined for wet *Drepanocladus* carpets and adjacent drier *Polytrichum* turf, on a transect including Signy Island (Wynn-Williams, 1984) indicated O₂-uptake rate to be an adequate measure of peat respiration rate in both stands. However, when conditions were anaerobic in peat beneath *Cephaloziella*, the O₂-uptake was much less than for adjacent microaerophilic *Calliergon* and *Drepanocladus* peat (Wynn-Williams, 1980). Nevertheless, decomposer activity, as indicated by loss in tensile strength of cotton strips, was very similar in both anaerobic *Cephaloziella* peat and aerobic *Polytrichum* peat (Wynn-Williams, 1980). This implied that O₂-uptake was only part of the peat respiration at SIRS 2, of which microbial activity constituted *c.* 85% (Wynn-Williams, 1984). The incomplete determination of respiration in saturated peat using an aerobic system was confirmed by the demonstration of significant methanogenesis at SIRS 2 (Harrington and Wynn-Williams, 1984). However, its extent was considerably less than at a comparable Arctic mire at Stordalen (Svensson and Rosswall, 1984). The occurrence of both aerobic and anaerobic decomposition partly explained the more rapid turnover of respiratory substrates at SIRS 2 than SIRS 1 (Davis, 1981).

The decrease in peat respiration with increasing depth in both *Calliergon* and *Cephaloziella* stands may reflect the high moisture content, and therefore restricted O₂-diffusion, in SIRS 2 peat. The saturation of the *Cephaloziella* carpet with concomitant anaerobiosis throughout most of its profile probably obscured changes in respiration with elapsed time. Its high moisture content also has a thermal stabilizing effect, which may be contributory to the inability to demonstrate a significant influence of temperature using the field data, despite the known Q_{10} of 2.5 for the stand. This was, however, mainly due to O₂-uptake rates being higher at 0°C during the spring flush than at temperatures of up to 10°C in mid-summer (Wynn-Williams, 1980). However, Svensson (1980) showed temperature to account for *c.* 80% of the variations in CO₂-production at the comparable Stordalen mire (Abisko,

Sweden). Moreover, Q_{10} values in Stordalen mire increased markedly with decreasing temperature to values at least twice those of SIRS 2.

The increase in respiration with increasing moisture in *Calliergon* was not apparent in saturated *Cephaloziella* where factors other than moisture and temperature were regulatory. A multiple regression incorporating moisture and temperature accounted for only 21% of the variation of respiration in *Calliergon*, and the regression was insignificant for *Cephaloziella* data. This contrasted with equivalent values in similar sites obtained by Svensson (1980) at Stordalen (69%), and by Flanagan and Veum (1974) at Hardangervidda, Norway (67%) and Barrow, Alaska (63%). This discrepancy was partly explained by the smaller proportion of respiration detected by O_2 -uptake in waterlogged peat relative to CO_2 -release, which includes some anaerobic respiration.

Covariation complicated the detection of regulatory factors. Moisture, pH and nutrients are covariates with respect to C-loss (Svensson, 1980) and fungal mycelium length (Dowding and Widden, 1974). Moreover, the high percentage of organic matter in peat obscured part of the relationship of moisture with respiration and microbial counts, both expressed on a basis of dry weight, which was equivalent to a basis of potential substrate.

Despite inter-correlation between microbial groups, O_2 -uptake rate correlated conspicuously with yeasts and fungi, although not as strongly as at SIRS 1 (Wynn-Williams, 1985b). The yeasts and 'sugar fungi' represented the zymogenous, saprophytic tundra microflora, readily detected by plate counts (Lund and Goksøyr, 1980). This group was responsive to edaphic and nutritional changes. Changes in the availability of respiratory substrates were not measured because their diversity relative to microbial requirements is highly complex. However, their availability was implied by changes in O_2 -uptake and microflora and depth and *ET* which could not be adequately explained by the main physical factors.

The availability of respiratory substrates was probably maximal during spring when nutrients would be released from cells damaged during freeze-thaw cycles (Morley and others, 1983) which result in peaks of peat respiration and exponential yeast growth *in vivo* and *in vitro* (Wynn-Williams, 1980, 1982).

No single multiple regression equation accounted for > 58% of variation in peat O_2 -uptake at SIRS 2, especially in the often waterlogged *Cephaloziella* stand. However, moisture was more influential than temperature, and saprophytic yeasts and fungi were closely associated with changes in the rate of O_2 -uptake. A broader spectrum of the microflora will be involved in maintaining the 'basal' rate (Wynn-Williams, 1982), which would include the slower decomposition of macromolecules. In the more frequently anaerobic *Cephaloziella* carpet, factors changing with increasing depth predominated. The maximum amount of variation in peat O_2 -uptake rate at SIRS 2 explained by the multiple regressions was 44–58% relative to 66–78% at SIRS 1 (Wynn-Williams, 1985b). The difference probably reflected the anaerobic component of peat decomposition at SIRS 2, which was not measurable by aerobic means.

The anaerobic characteristics of C-loss at SIRS 2 merit specific investigation of anaerobic respiration, fermentation and methanogenesis to complete an energy budget for such a wet cryptogamic community.

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