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Temperature variation and its biological significance in fellfield habitats on a maritime Antarctic island

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Abstract: Temperatures within soil and plant habitats on Signy Island in the maritime Antarctic were measured during 1987. Four sites were monitored using minithermistors attached to a data logging system. Three main periods within the annual temperature cycle were identified. In spring/summer (November–March) there was much inter-day variation in maximum temperatures, but minimum daily temperatures were always close to 0°C. However, there were very few freeze-thaw cycles extending below the -0.5°C threshold during this period, and those that occurred were not severe. It is considered that freeze-thaw cycling is unlikely to be a significant factor in organism survival during summer. All sites showed a long period of relatively mild subzero temperatures during autumn (March–May). This may be of importance in promoting cold-hardiness of organisms living in these ecosystems before the decline to lower winter temperatures. Minimum winter temperatures varied markedly between sites; lowest temperatures occurring in areas where there was little insulating snow cover. Within site temperature variation was generally small, confirming the validity of the use of small numbers of probes to monitor environmental temperatures in such habitats.

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Introduction

It has long been recognized that meteorological air temperatures bear little relation to the temperatures of the microhabitats inhabited by Antarctic terrestrial organisms (Chambers 1966, Longton & Holdgate 1967). For this reason many investigations have collected microclimate data from microhabitats biologically relevant although these have often been limited by the technology available (Chambers 1966, Longton & Holdgate 1967, Walton 1982). Modern microclimate instrumentation permit the relatively easy collection of large data sets, particularly of environmental temperatures (Smith 1988) and has been successfully used in studies of the ecology of individual species or groups of organisms (Kappen 1985, McKay & Friedmann 1985, Smith 1988, Pickup 1990a, 1990b, Davey 1991a).

In spite of the present potential for accurate temperature determinations misconceptions concerning the prevailing temperature regime in the maritime Antarctic continue to persist, particularly in relation to the number and severity of freeze-thaw cycles. In this paper we make use of extensive microclimate temperature data collected from a range of terrestrial habitats at Signy Island in the maritime Antarctic to reconsider the temperature regimes to which organisms are exposed. We also provide a general framework upon which future temperature measurement protocols can be based and with which results can be compared.

Materials and methods

The study was based at sites on Jane Col, Factory Bluffs and close to the British Antarctic Survey station on Signy Island, South Orkney Islands. The Jane Col site is a recently deglaciated fellfield situated 150 m a.s.l. and consists mainly of frost-sorted soil polygons up to 1.5 m in diameter with very little macrovegetation, although small patches of the moss *Ceratodon* occur around the edges of the polygons. In contrast, the Factory Bluffs plateau site is a more developed fellfield situated 110 m a.s.l. and supports a dense vegetation reflecting the pattern of periglacially sorted circles. The dominant plants are the lichens *Usnea* and *Himantormia* and the moss *Andreaea* with occasional patches of bare soil in the centre of the sorted circles. Both these sites have been extensively studied as part of the British Antarctic Survey Fellfield Ecology Research Programme (FERP) (British Antarctic Survey 1981, 1982). The station site consists of carpets and turves of several moss species, including *Drepanocladus*, *Chorisodontium* and *Polytrichum*, lichens and the alga *Prasiola*, on a northwest facing slope at an altitude of 20 m a.s.l. *c.* 100 m from the station.

Temperature data at all sites were collected using Squirrel (Grant Instruments Ltd, Cambridge, UK) 8-bit data loggers (Smith 1988). Type, position, recording resolution and recording interval of the thermistors varied slightly between sites (Table I). All thermistors were placed horizontally in the soil. Positions of thermistors were checked regularly, although

Table I. Details of type (all YSI I-18920 U), depth below soil/vegetation surface, recording resolution, recording intervals and the percentage of data missing for thermistors used in this study at Signy Island. Key to sites: JCC= Jane Col polygon centre, JCE= Jane Col polygon edge, FBU= Factory Bluffs *Usnea*, FBA= Factory Bluffs *Andreaea*, SD= Station site *Drepanocladus*.

Site	Thermistor type	Depth (cm)	Recording resolution (°C)	Recording interval (min)		Lost data (%)
				Summer	Winter	
JCC	mini (3 cm)	0	0.40	10	30	8
JCC	mini	3	0.40	10	30	
JCE	mini	0	0.40	10	30	
FBU	mini	0	0.28	5	5	4
FBU	mini	3	0.28	5	5	
FBA	micro (3 mm)	1	0.28	5	5	6
FBA	mini	5	0.28	5	5	
SD	mini	1	0.40	no data	5	0
SD	mini	5	0.40	no data	5	

there was no evidence of frost-heaving. The percentages of data lost at each site during measurement periods are also indicated in Table I; the missing data were usually due to either operator error or battery failure. All logged data in this paper were collected during 1987; in most cases this represents only part of a longer data set, although data for the station site are available for April–November 1987 only. Temperature probes were calibrated against standard meteorological mercury thermometers.

On 3, 11 and 19 February 1990 spot temperatures were measured at the soil surface of 60 polygons on Jane Col. Using a microthermistor attached to an electronic thermometer (accuracy 0.1°C) all measurements were taken within 30 min.

Air temperatures were also recorded in a Stevenson's screen 1.5 m above ground level at the station using standard maximum and minimum thermometers as part of synoptic meteorological observations.

Results

The annual temperature variations at the soil surface in the centre of a polygon on Jane Col (Fig. 1) indicate the typical pattern over the year in the habitats under investigation. Also included in Fig. 1 is the depth of snow on this site through the year. Three main periods within the annual temperature cycle are evident. Firstly, spring/summer (November–March) when day temperatures may be high, although with much day-to-day

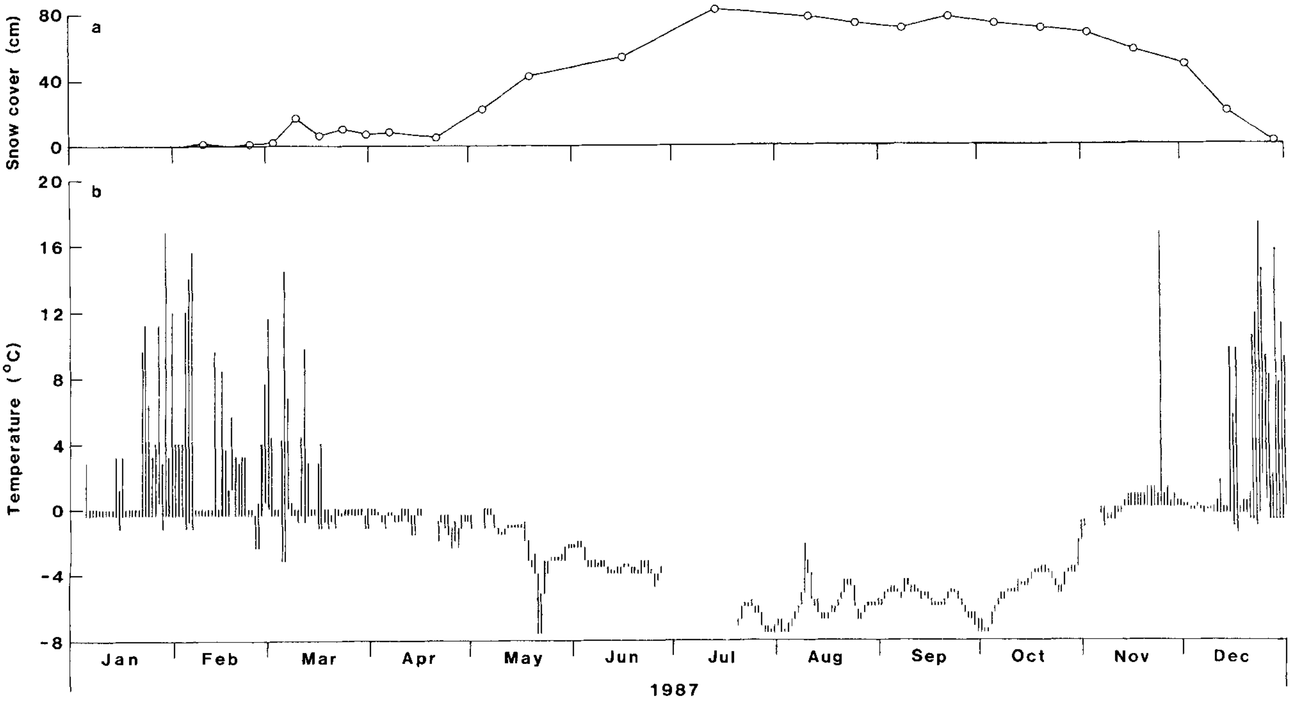

Fig. 1. a. Depth of snow cover, and **b.** daily temperature ranges (maximum and minimum values) during 1987 at the soil surface in the centre of a polygon at Jane Col, Signy Island.

Table II. Number of short-term freeze-thaw cycles per month at various sites on Signy Island during 1987. Key to sites: JCC= Jane Col polygon centre, JCE= Jane Col polygon edge, FBU= Factory Bluffs *Usnea*, FBA= Factory Bluffs *Andreaea*, SD= Station site *Drepanocladus*, Air= macrometeorological data. Figures indicate the number of short-term freeze-thaw cycles, F= point of main winter freeze, T= point of main spring thaw, *= no data available.

	-0.5 to 0.5°C										-2.0 to 0.5°C									
Site	JCC	JCC	JCE	FBU	FBU	FBA	FBA	SD	SD	Air	JCC	JCC	JCE	FBU	FBU	FBA	FBA	SD	SD	Air
Depth (cm)	0	3	0	0	3	1	5	1	5	-	0	3	0	0	3	1	5	1	5	-
January	2	0	6	8	0	*	*	*	*	11	0	0	0	0	0	*	*	*	*	1
February	5	0	5	7	0	3	0	*	*	14	2	0	1	2	0	0	0	*	*	6
March	7F	0	4F	7	0	6	0	*	*	20	2	0	2	2	0	1	0	*	*	14
April	0	0F	0	5	4	1	0F	0F	0	14	0F	0F	0F	4	4	1	0F	0	0	10
May	0	0	0	2F	1F	1F	0	0	0	8	0	0	0	1F	1F	1F	0	0	0	6
June	0	0	0	0	0	0	0	0	0F	5	0	0	0	0	0	0	0	0	0	2
July	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0F	0F	5
August	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	5
September	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	6
October	0	0	0	T10	T0	T0	0	0	0	11	0	0	0	T4	T0	T0	0	0	0	8
November	*	*	*	5	0	2	T0	T0	0	25	*	*	*	0	0	0	T0	T0	0	14
December	T10	T3	T8	0	0	1	0	*	*	20	T0	T0	T1	0	0	0	0	*	*	11
Total	25	4	24	46	5	14	1	1	1	148	5	1	5	14	5	4	1	1	1	79

variation, and temperatures rarely fall far below 0°C at night. Secondly, autumn (March–May) when temperatures are stable around 0°C. Thirdly, winter (May–November) when temperatures fall well below 0°C.

Fig. 1 also suggests that very few freeze-thaw cycles occur in this habitat. A wider investigation of freeze-thaw cycles at all the study sites (Table II) demonstrates that whilst the temperature may fluctuate about 0°C there are very few freeze-thaw cycles to below 2°C outside the winter freeze period. Closer examination of the data indicated that when the minimum daily temperature traversed the 0°C threshold there was no oscillation around 0°C and hence only one freeze-thaw cycle in any 24 h period.

Therefore, it is clear that the winter freeze is the major freezing event within these habitats, and may be the only one that can be expected to cause significant mortality in the populations. Monthly minimum temperatures for the winter months are given in Table III along with the approximate snowcover at each site. Two points emerge from these data. Firstly, within these sites there is little variation in temperature in relation to depth within the soil/plant profile in the upper layers where most organisms are found. The benefits of a motile organism moving deeper into the substratum to avoid freezing are therefore likely to be limited. Secondly, there is considerable variation in minimum temperatures between sites because of the differing amounts of insulating snowcover on the sites. This is particularly evident in the case of the *Usnea* site which had very little snowcover and was exposed to temperatures well below those experienced at the other sites. The exposure/elevation of the site may be of some lesser significance, for example the Jane Col site (150 m a.s.l.) was exposed to lower minimum temperatures than the station site (20 m a.s.l.), although both experienced deep snow cover. Some melting and recrystallization of the snow to form ice layers was observed during late winter at the Jane Col and station sites. The depth and extent of these layers were not

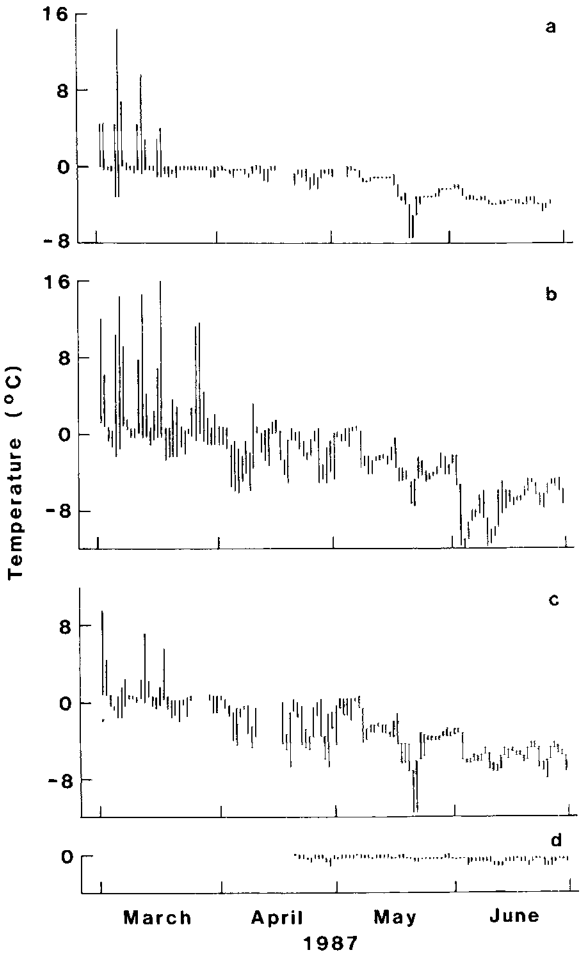

Fig. 2. Daily temperature ranges at four sites on Signy Island during late summer early winter 1987; **a.** Jane Col soil surface at polygon centre; **b.** Factory Bluffs surface of *Usnea* carpet; **c.** Factory Bluffs *Andreaea* carpet at 1 cm depth; **d.** Station site *Drepanocladus* carpet at 1 cm depth.

Table III. Monthly absolute minimum temperatures (°C) and mean depth of snow cover (cm) at various sites on Signy Island during the winter and spring of 1987. Key to sites as Table II. JC refers to both Jane Col sites.

	Minimum monthly temperatures (°C)									Snow cover (cm)			
Site	JCC	JCC	JCE	FBU	FBU	FBA	FBA	SD	SD	JC	FBU	FBA	SD
Depth (cm)	0	3	0	0	3	1	5	1	5				
April	-2.4	-2.0	-2.4	-6.2	-4.8	-6.7	-5.6	-1.2	-0.4	5	1	2	*
May	-7.6	-7.2	-8.0	-7.6	-6.2	-11.5	-9.8	-0.8	-0.4	30	7	15	*
June	-4.8	-4.4	-4.8	-12.3	-10.4	-7.3	-7.3	-1.2	-0.8	50	6	25	> 50
July	-7.6	-7.6	-8.4	-17.1	-14.8	-11.8	-11.5	-2.8	-2.4	60	6	25	> 50
August	-7.6	-7.6	-8.0	-16.0	-13.4	-10.9	-10.1	-3.2	-2.8	80	3	25	> 50
September	-7.2	-6.8	-7.6	-16.5	-14.6	-7.3	-7.0	-4.8	-4.4	80	2	23	> 50
October	-7.6	-7.6	-8.0	-16.8	-15.4	-11.5	-10.1	-5.6	-5.6	75	1	20	*
November	*	*	*	-1.4	0.3	-0.6	-0.3	-0.4	-0.4	65	0	0	*
December	-2.0	-2.0	-2.0	-0.3	0.3	-0.8	0.3	*	*	20	0	0	*

Table IV. Temperature variations between 60 polygons on Jane Col, Signy Island within a 30 minute period around midday on the dates stated.

Date	Weather conditions	Temperature (°C) Min	Mean (sd)	Max
3.2.90	Overcast	4.3	5.8 (1.0)	7.6
11.2.90	Overcast	4.2	5.1 (0.5)	6.2
19.2.90	Sunny	8.9	12.8 (1.4)	15.0

quantified.

The period of autumnal thermal stability observed in Fig. 1 also occurred at the other sites (Fig. 2). The degree of stability at each site was again correlated with the depth of snow cover, variation being smallest at the Jane Col and station sites where snow cover was greatest, although some stability was evident even at the *Usnea* site where snow depth was minimal.

Daily mean temperatures at the soil/plant surface for the Jane Col and Factory Bluffs sites during the summer (Fig. 3) demonstrate the general pattern of temperature variation within these habitats when the sites are clear of snow. Little variation in surface temperature was observed between probes within sites or between sites during the latter half of the summer. However, there was marked variation between the soil and *Usnea* sites in early summer, possibly because of the higher water content of the soils at this time. The lack of within-site variation was confirmed by the wider study of 60 polygons on Jane Col during 1990 (Table IV). Very little temperature variation was observed between polygons, especially on the overcast days.

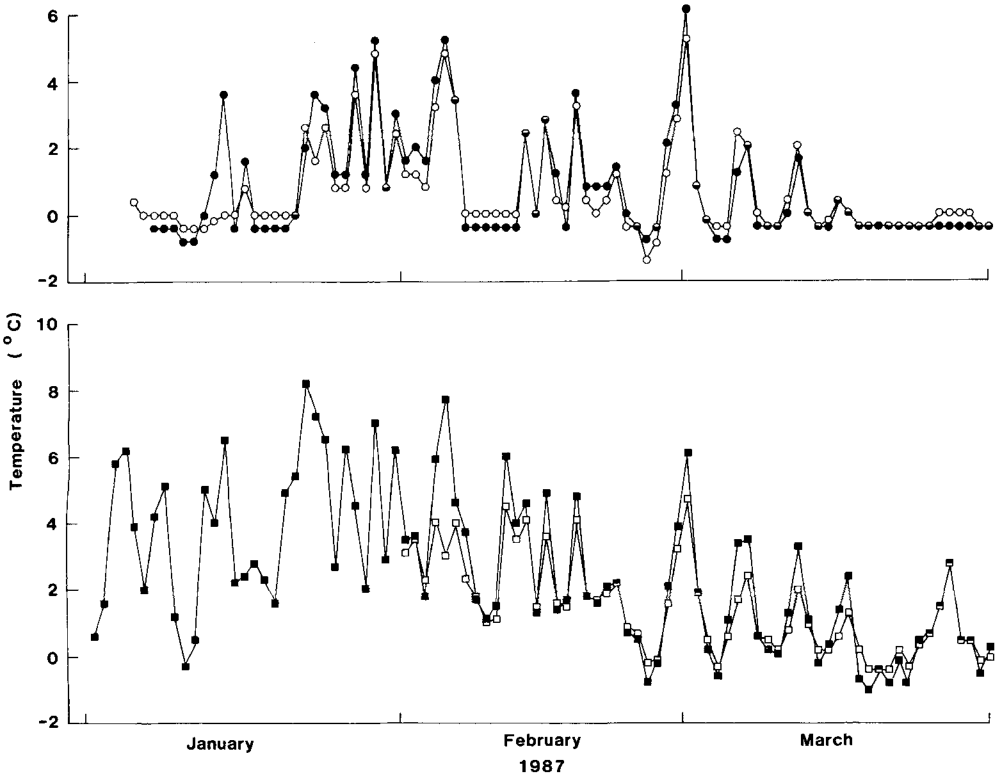

Fig. 3. Daily mean temperatures at four sites on Signy Island during summer 1987. ○ Jane Col, soil surface at centre of polygon; ● Jane Col, soil surface at edge of polygon; ■ Factory Bluffs surface of *Usnea* carpet; □ Factory Bluffs *Andreaea* carpet at 1 cm depth.

Discussion

Terrestrial vegetation and soils in this area of the maritime Antarctic were exposed to very few freeze-thaw cycles in 1987. Such overnight freezing that does occur is restricted to the soil/vegetation surface and to only a few degrees below zero; temperatures that are not sufficiently severe to cause freezing damage to even the most susceptible Antarctic organisms (Block 1990, Hawes 1990). Furthermore, whilst localized ice formation undoubtedly occurred, this was often restricted to surface water and much of the habitat was left icefree, and, hence, many of the freeze-thaw events that were recorded may not have affected the microorganisms within the vegetation/soil. Such conditions compare favourably with the local air temperatures, which often undergo severe daily freeze-thaw cycles, and conditions in continental Antarctica where a combination of lower night temperatures and a lack of water to buffer temperature changes can result in wide diel temperature fluctuations (MacNamara 1973, Kappen 1985, McKay & Friedmann 1985, Smith 1988). A similar increase in freeze-thaw cycles in drier habitats has been observed on Signy Island (Longton 1988). However, it appears unlikely that the occurrence of freeze-thaw cycles during the icefree months is a major factor in the survival and growth of the organisms living in wet terrestrial habitats of the maritime Antarctic.

Of greater severity, and therefore of greater potential biological significance, are the absolute minimum temperatures reached during the Antarctic winter. These are often below the temperatures known to cause death in many Antarctic organisms (Block 1990, Hawes 1990, Davey 1991b), and may significantly reduce the size of soil populations that survive until the spring thaw. The results presented here prompt consideration of two factors, apart from the air temperature, that may affect the minimum soil temperature experienced by organisms. Of greatest importance is the depth of snow that covers the site during the winter. This acts as a thermal blanket, protecting the underlying habitats from the effects of declining air temperatures and, in general, the deeper the snow covering the site the less severe the winter temperatures experienced at, or near, the soil surface. Therefore, the large-scale topography of any site, and hence the potential for snow to settle and remain on the surface, may become a significant factor in the suitability of an area for colonization. Similar results have been reported from other sites on Signy Island (Walton 1982, Longton 1988) and from South Georgia (Heilbronn & Walton 1984) suggesting that snow depth should be more regularly recorded as part of microclimatic studies. The elevation of the site also appears to be significant, although requiring further observations to determine its degree of importance.

It is clear from the results presented that, within the upper layer investigated, depth within the soil/vegetation is not an important factor in determining the minimum winter temperature. Such results are similar to previous studies of moss carpets on Signy Island, where little temperature variation with depth was reported during winter (Walton 1982, fig. 6). Hence, the hypothesis that organisms may be protected from the effects of winter by being buried in the soil may be discounted within the upper zone of the profile containing most living organisms, provided that snow can accumulate on the site.

A feature of all sites investigated in this study was the long period of relatively mild subzero temperatures in April and May compared with the much harsher temperatures experienced later in the winter. These were most noticeable in the wetter sites, which had the highest temperature buffering capacity. The effect of such an autumnal freeze pattern is to expose the organisms living in these habitats to an extended period of freezing and generally sublethal temperatures prior to the decline to minimum temperatures. This difference between dry and wet sites corresponds to that reported by Walton (1982) but in all three years of his measurements at the dry *Polytrichum* site there was no long mild period in April and May. Any extended mild period may at this time be of biological significance in two ways. Firstly, by simply reducing the length of the true winter period by two months (25–30%). The length of freezing period has been shown to be an important factor in the survival of algae (Hawes 1990), and for invertebrates survival is related to the product of time and temperature (Block 1990). Secondly, exposure to a period of low temperatures will aid in the acclimatization of the organisms to the approaching freeze. Young & Block (1980) showed that the Antarctic oribatid mite *Alaskozetes antarcticus* (Michael) requires one month at around 0°C to increase glycerol content, reduce gut nucleators and prepare for winter. Many other organisms also demonstrate increased potential for survival of low temperatures during winter (Cannon & Block 1988, Pickup 1990a, 1990b), and hence the period of change from 'summer' to 'winter' populations will be important in determining organism survival. Such observations also demonstrate the degree of thermal inertia within the environment and the amount of energy that has to be removed from the system as latent heat to allow freezing to occur.

The results highlight the difficulties in determining environmental cooling rates. Clearly the cooling rates observed during the autumnal freeze were very low; maximum recorded freezing rates during this period were 0.4°C in 3 h at the Jane Col and *Andreaea* sites and 0.4°C in 1 h at the drier *Usnea* site. Although much higher cooling rates occurred during the summer these usually started from high temperatures and did not encompass a freezing event without a marked slowing of the cooling rate. These observations suggest that freezing occurs slowly in wet terrestrial ecosystems providing time for chill-hardening of organisms (Levitt 1980). Such effects should be considered in the application of cooling rates to experimental systems.

Few biological investigators have apparently considered how representative the point measurements are of the generally prevailing conditions within a particular type of microsite. Whilst it is well documented that major topographical variations can lead to differences in environmental temperatures, for example north- and southfacing rock surfaces (Kappen 1985, Smith 1988), little previous consideration has been given to the extent of variation in temperature between visually similar sites over scales of centimetres, metres and kilometres. Comparison of the temperatures across a soil polygon has demonstrated that there are small, but consistent, increases in the range of temperatures experienced at the edge in comparison to the centre of the polygon. Likewise, comparison of spot temperatures between polygons at one site showed some variation between polygons, although these differences were not consistent between dates. Such observations are in agreement with the temperature data for two polygons during the summer of 1987–88 presented in Davey & Clarke (1991). Both within and between polygons the temperature variations observed were small, and it is doubtful if they were of any biological significance in comparison to the wide temperature variations experienced on a day-to-day basis. Again the water content of the soil is likely to be the most important factor in determining the susceptibility of sites to variation in temperature. Thus, the measurement of temperature changes in a small number of sorted polygons will provide representative data for other similar polygons within a site, limiting data collection without sacrificing biological relevance.

This study has highlighted some aspects of the temperature regime that may be generally applicable to the terrestrial ecosystems of the maritime Antarctic. The paucity of freeze-thaw activity at the soil surface when compared with the air or with habitats of continental Antarctica is consistent with many previous reports (reviewed in Longton 1988). Snowcover plays an important rôle in the insulation of the soil during winter and heterogeneity in the depth of snow leads to local variations in minimum temperatures. In addition, the inertia to freezing experienced during the autumn may significantly affect organism survival if it continues over a long period. Whilst it would be unwise to conclude that these features are universally applicable they are sufficiently consistent for any deviations from these conditions to be worthy of comment.

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