Temperature Relationships of Antarctic Vegetation

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Temperature relationships of Antarctic vegetation

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Introduction

The extremely impoverished nature of the vascular flora in Antarctic regions has long been recognized and contrasted with the richness of comparable latitudes in the northern hemisphere. Rudmose Brown (1906), for example, reported finding no vascular plants on the South Orkney Islands (lat. 61° S), whereas over 100 species were then known from Spitzbergen (lat. 79° N). Even today only two native species of flowering plant are known from these islands and the neighbouring area of the Antarctic Peninsula, while no island even in the Sub-Antarctic zone, in latitudes as low as 50° S, rivals Spitzbergen in the richness of its flora (Greene & Greene 1963). Further south still the ice capped interior of the Antarctic is barren of flowering plants, its nunataks supporting only a meagre cryptogamic flora (Siple 1938; Greene 1964*a*; Bowra, Holdgate & Tilbrook 1966).

The vegetation now established in Antarctic regions may have resulted from the action of biogeographical as well as ecological factors. The oceanic barriers to the dispersal of land plants to the Antarctic are very great, and the floristic poverty of coastal areas may well result in part from their isolation combined with the relatively short time available for colonization since recession of the former more extensive ice sheets (Nicholls 1964). This isolation is intensified by the additional barrier of the west wind belt, whose strong circumpolar airstreams and associated ocean currents must reduce the chance of airborne or waterborne propagules being carried south to the Antarctic. Even if the problems of dispersal are overcome, however, the environmental conditions within Antarctic regions are unfavourable for the establishment of many land plants, due to the low temperatures, the shortage of available water in many areas, and, locally, to intense competition from large and densely packed sea-bird colonies.

It is clear, therefore, that the relative importance of these ecological and biogeographical factors in determining the nature and distribution of the flora must be assessed if the relationships between Antarctic vegetation and its environment are to be fully understood. Temperature is undoubtedly one of the most important ecological factors, and the present paper reviews data on the temperature regimes in Antarctic regions, paying particular attention to the microclimate at plant level and around fumaroles on the South Sandwich Islands. In addition, the distribution and performance of native and alien plants is discussed in relation to variations in the temperature regime in an attempt to determine how far the extreme cold should be regarded as limiting the further spread and development of vegetation in the Antarctic.

Temperature regimes at plant level

Annual air temperature regimes at stations in southern circumpolar regions, summarized by Holdgate (1964*a*), demonstrate a progressive cooling of the climate from the Sub-Antarctic southwards into the Maritime Antarctic and finally into Continental Antarctica. On South Georgia, a typical Sub-Antarctic island, mean monthly air temperatures range from 0 to 7 °C during 8 months of the year, rarely falling below −5 °C in winter, while on Signy Island, South Orkney Islands, air temperatures normally average only 0 to 2 °C for one or two summer months. In Continental Antarctica air temperatures are even lower, mean monthly values remaining below freezing, and falling to −40 °C or lower in winter.

It is well known, however, that temperatures at plant level in polar environments, as elsewhere, may often be higher than those recorded by standard meteorological methods (Siple 1938; Warren Wilson 1957), and recent investigations have attempted to determine how far this is true in Antarctic regions. Temperatures in vegetation have been reported by Matsuda (1964) at East Ongul Island in Continental Antarctica, by Holdgate (1964*a*) and Tilbrook (personal communication) on Signy Island, and by Longton & Greene (1967, this Discussion, p. 295) on South Georgia. These reports, together with additional unpublished data for several Maritime Antarctic stations, have confirmed that Antarctic vegetation exists in a relatively favourable microclimate due principally to the effects of an insulating snow blanket in winter, and of absorbed solar radiation in summer.

Temperatures in vegetation under winter snow cover may be considerably higher than those above the snow, fluctuating slowly with long-term changes in external air temperature while diurnal fluctuation is eliminated. Conditions at plant level appear to be influenced by the depth of snow cover, however, as well as by air temperature. Winter temperatures near the surface of a *Polytrichum alpestre* bank on South Georgia during the winter of 1961 were normally between 0 and 0·5 °C, rarely falling below −2 °C, but a minimum of −20 °C was recorded during the same winter in a moss cushion on East Ongul Island, at a time when air temperature was −40 °C. On Signy Island, where air temperatures are intermediate between those at the previous localities, readings down to −10 °C were recorded in a moss colony under 6 cm of snow, whereas at the same time, when air temperature was −14 °C, the temperature in other mosses under 85 cm of snow was as high as −2 °C.

During summer, solar radiation frequently heats the surface of soil and of bryophyte colonies to levels greatly above air temperature by day, but at night heat loss by radiation may cause an inversion so that soil and vegetation surfaces are cooler than the surrounding air. Wide and rapid diurnal fluctuations in temperature thus occur, particularly in clear weather, and considerable warming of the plants also takes place at times during light overcast conditions. On cloudy days, however, temperatures near the surface of the vegetation may differ little from air temperature.

On South Georgia diurnal temperature fluctuations of over 30 degC were recorded in summer near the surface of a *P. alpestre* turf, the mean of 3-hourly readings reaching 10 °C during 2-week periods in high summer, although temperatures frequently fell to around or slightly below freezing by night. Moss surface temperatures during the summer at

East Ongul Island showed a similar pattern, but were considerably lower than on South Georgia, doubtless a result of the lower air temperatures and the sun's position lower on the horizon. Nevertheless, a maximum temperature of 19 °C was recorded at the surface of a moss cushion, and a mean of 4 °C was given by 6-hourly readings during the first 2 weeks of January 1962.

No data for moss surface temperatures over extended periods are available for the Maritime Antarctic, but it is clear from the available results that widely oscillating temperatures are characteristic of this area also. Diurnal fluctuations of 15 degC have been noted at a depth of 2·5 cm in *Polytrichum alpestre–Dicranum aciphyllum* turf on Signy Island, while daily maximum temperatures at this depth averaged 5 °C over a 75-day period between January and March 1962. The rapidity of the fluctuations is emphasized in figure 24, which indicates a rise from 0 to 19 °C during 2 h at a depth of 2 to 3 mm in *P. alpestre* turf on Signy Island. Lesser fluctuations as clouds pass over the sun are also indicated, while temperature changes at a depth of 2·5 cm were slower and more steady than those nearer the surface, reaching a lower maximum, due to delay in heat conduction through the turf.

The temperatures indicated in figure 24 are by no means the highest recorded in Maritime Antarctic vegetation. On Galindez Island, Argentine Islands, at 14.00 h on 18 February 1965, five thermistor readings taken 2 to 3 mm deep in a dry mat of *Drepanocladus uncinatus* against a rock face gave an exceptionally high mean of 30 °C, at a time when the air temperature of 7·8 °C was also unusually high. A mean of only 23·2 °C was recorded, however, in a wet mat of the same species less than 1 m away and with a similar aspect and slope. Similar point-to-point variations in temperature have been noted elsewhere, Holdgate (1964*a*) reporting interspecific differences and suggesting that the highest temperatures occur in species whose colonies have a relatively large air content and little percolating meltwater. Measurements in turfs of the grass *Deschampsia antarctica* and in cushions of the herb *Colobanthus crassifolius* confirm that they are also warmed substantially by solar radiation (Holtom & Greene 1967, this Discussion, p. 323).

Aspect is another important factor influencing the extent to which plants are warmed by radiation. Its effects are shown dramatically by the results of two series of thermistor readings taken 2 to 3 mm deep in cushions of a *Grimmia* on Deception Island, one series for plants on north-facing and the other for plants on south-facing rocks. The readings were taken at 11.00 h on 9 December 1964, when air temperature was 0·4 °C, the mean for cushions on north-facing rocks being 11·2 °C, while those in south-facing situations were frozen solid and had a mean temperature of 0 °C.

Strong and gale force winds are characteristic of many Antarctic areas, and may lower plant temperatures through removing the layer of air that has been warmed by the plants, by increasing the rate of evaporation when the vegetation is wet, and by reducing winter snow cover. The effects of wind on Antarctic vegetation do not appear to have been investigated in detail, and may be reduced compared with those in other areas as the plants are typically low lying, and thus occupy a layer of relatively still air near the ground. Nevertheless, Antarctic plants are in general likely to experience more favourable temperature regimes in sheltered than in exposed habitats, although Föhn winds are known to bring about local increases in temperature.

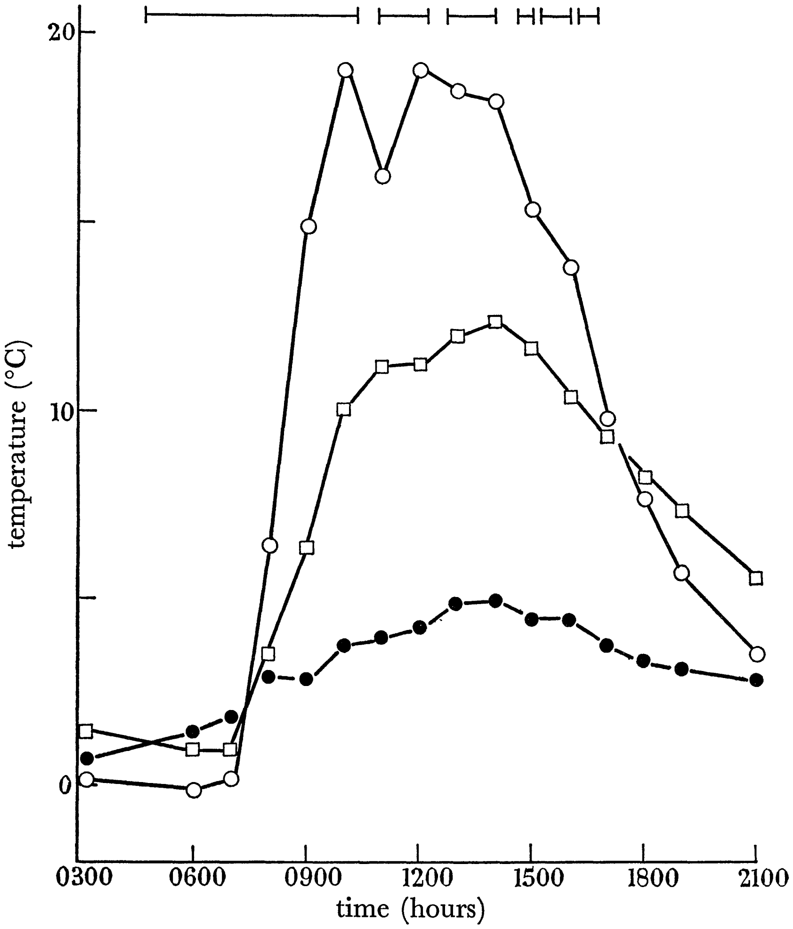

Figure 24. Temperature fluctuations in a turf of *Polytrichum alpestre* on Signy Island on 31 January 1965, recorded by thermistors. The turf was on a north-east facing slope at an altitude of 20 m. The meteorological screen was 100 m distant and near sea level.

Key. ○, 2 to 3 mm deep in turf; □, 2·5 cm deep in turf; ●, met. screen; ⊢⊣, period of sunshine.

PLANT DISTRIBUTION AND PERFORMANCE IN RELATION TO TEMPERATURE GRADIENTS

It is clear from the considerations discussed above that if low temperatures are important in limiting plant growth in Antarctic regions the best performance would be expected in localities with relatively high air temperatures combined with long periods of sunshine during summer. At each site aspect and degree of slope are seen to be important factors acting on plant temperatures during summer, while sheltered situations are likely to be more favourable than exposed ones during both summer and winter, although snow may lie longer in the former thus shortening the growing season. One obvious approach to analysing the role of temperature in limiting Antarctic vegetation is thus to examine plant distribution and performance in relation to those factors considered to influence the micro-environment.

Herbacious phanerogams are widespread and abundant on Sub-Antarctic islands, twenty-four native species having been recorded on South Georgia, where they predominate in much of the vegetation at altitudes up to *ca.* 250 m on the sheltered north-east coast (Greene 1964*b*). Scattered individuals of several species reach altitudes well over 350 m, however, including plants of *Colobanthus crassifolius* and *Deschampsia antarctica*, the only native species of vascular plants recorded in the Antarctic zone. On South Georgia these two taxa are widespread at low altitudes, becoming frequent or abundant on slopes with varying aspect, and moreover they flower and fruit freely (Holtom & Greene 1967, this Discussion, p. 323).

Farther south *C. crassifolius* and *D. antarctica* are widespread on islands of the Scotia Ridge and near the north-west coast of the Antarctic Peninsula, but in this area they only locally become dominant in small stands of vascular plant communities. They are most frequent below 100 m altitude in sites well exposed to solar radiation on relatively steep slopes with a northerly aspect and sheltered by high ground to the south, although scattered individuals may occur elsewhere in cryptogam dominated vegetation (Holdgate 1964*a*; Longton 1967, this Discussion, p. 213).

Where the vascular plants occur more frequently in different situations there are often other features of the habitat suggesting a particularly favourable temperature regime. For example, *D. antarctica* is locally abundant on gentle south-facing ash slopes on Candlemas Island, South Sandwich Islands, on ground possibly warmed by fumarolic activity, while the grass may also be locally frequent in cryptogamic communities occupying level, relatively exposed ground on parts of the Argentine Islands, with scattered plants in south-facing situations, in an area where strong winds are much less frequent than in most Antarctic localities (Longton 1967, this Discussion, p. 213). On Signy Island it was noted that the vascular plants often occur in gullies where deep snow may lie in winter and conditions are normally moist in summer, though they appear to be relatively tolerant with regard to water supply further south.

C. crassifolius and *D. antarctica* are known to flower and set seed at least during some seasons throughout their Antarctic range, but their reproductive performance is less efficient in parts of the Maritime Antarctic than on South Georgia. Holtom & Greene (1967, this Discussion, p. 323) have shown, however, that both inflorescence maturity and seed size in *D. antarctica* are greater on the Argentine Islands and at other localities near the west coast of the Antarctic Peninsula than at the more northerly South Orkney Islands and South Shetland Islands. They relate this to the greater duration of summer sunshine in the former areas.

Parallel trends are seen in the growth and reproduction of bryophytes. On South Georgia many species are widespread and abundant on south as well as north-facing ground and produce sporophytes throughout the north-east coastal area (Longton 1966*a*; Longton & Greene 1967, this Discussion, p. 213). In the Maritime Antarctic, however, certain bryophyte communities, notably those dominated by tall turf forming mosses, are especially typical of slopes with a northerly aspect, and moss carpet communities are also least developed on south-facing ground. Moreover, there is a marked drop in the proportion of species normally producing capsules, and several individual taxa have been found to fruit much more freely on South Georgia than in the Antarctic zone. For example, capsules of *Polytrichum alpinum* are widespread and abundant on parts of South Georgia, but have been seen only in widely scattered localities on the South Sandwich Islands and near the Antarctic Peninsula. This effect is more likely to result from temperature differences than changes in photoperiod with increasing latitude in view of the marked increase in the reproductive success of this species on South Georgia (lat. 53° 30′ to 55° S) compared with the much colder South Sandwich Islands (lat. 56° 15′ to 59° 30′ S).

There is also evidence that the reproductive performance of Antarctic mosses, as well as flowering plants, may be influenced to some extent by solar radiation. For example, male inflorescences in *P. alpinum*, although widely distributed, are seen most frequently on north-facing slopes, while several species have been recorded in fruit on north-facing rock ledges on the Argentine Islands, although they are abundant but apparently without capsules on the cloudier Signy Island to the north (Longton 1966*a*).

In Continental Antarctica there is a continuation of this pattern. In the Heimefrontfjella, Bowra *et al.* (1966) described the richest vegetation, and the only bryophytes, as occurring on ledges and crevices low down on north-facing slopes. Similarly, Siple (1938) noted that in the Edsel Ford Ranges plants were most common in sites exposed to the north, and that most of the lichens that predominated in the flora were dark coloured and thus particularly efficient at absorbing radiation.

In general, therefore, it is clear that penetration form the Sub-Antarctic into Maritime and finally Continental Antarctic regions leads to a progressive reduction in the variety and abundance of bryophytes and of native vascular plants, the latter being unknown in Continental Antarctica. This trend may be interrupted by local variations in certain climatic factors, as several species appear to be most frequent, and reproductively most successful, in sites well exposed to solar radiation and in other areas likely to experience particularly favourable temperature regimes.

FUMAROLE VEGETATION

Recent volcanicity is characteristic of many areas in the Antarctic with active sites at present occurring on Ross Island in McMurdo Sound, on Deception Island and Penguin Island in the South Shetland Islands, and on a number of the South Sandwich Islands. Observations on the biology of such locally warmed areas have been made by Janetschek (1963), who reported a soil flora of fungi, bacteria and blue green algae, but no macroscopic plants, at 3600 m altitude on Mount Erebus, Ross Island, while during March 1964 detailed studies were carried out by the present authors on the rich bryophyte vegetation around fumaroles on four of the South Sandwich Islands, i.e. Bellingshausen, Candlemas, Leskov and Visokoi (Baker *et al.* 1964).

The fumaroles on the South Sandwich Islands occur on gentle slopes of volcanic ash or on steeper slopes strewn with lava boulders, and show considerable variation in form. The hottest areas usually coincide with a series of vents which occur either as narrow elongated openings up to 15 cm long among the ash, or in deep fissures up to 50 cm wide between boulders. The vents frequently emit steam, but in some cases they are not clearly defined, steam rising diffusely over an area of ground. Whatever their form, however, a local warming of the ground is characteristic of fumarolic areas, and as the emission of steam is frequently accompanied by condensation of water droplets on to the surrounding ground a moisture gradient is established corresponding to the gradient of decreasing temperature radiating outwards from the vents. The areas thus affected support more or less clearly zoned vegetation comprising luxuriant and varied bryophyte communities in striking contrast to the dry barren slopes of ash and lava that occur extensively elsewhere on these islands (figure 25).

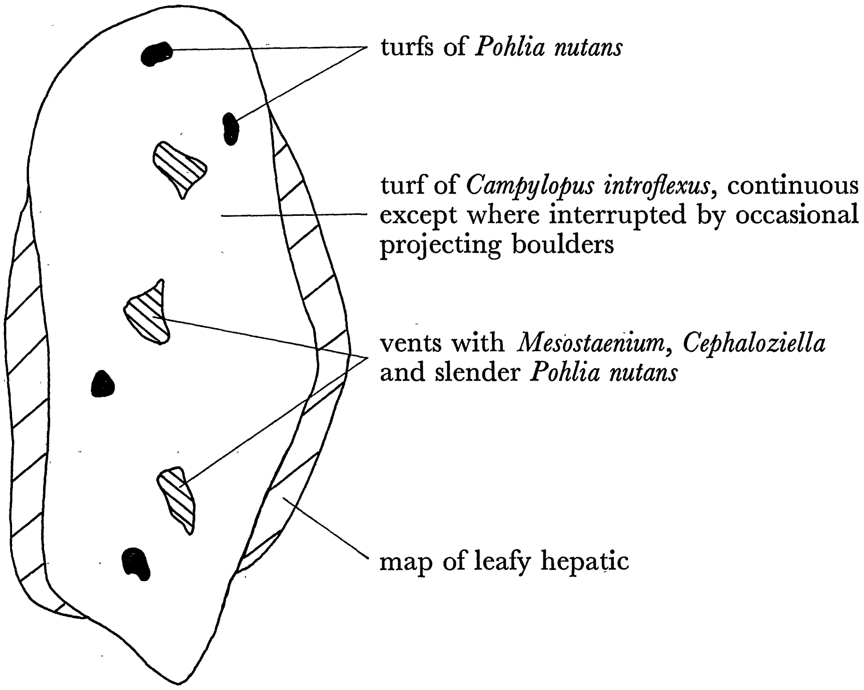

FIGURE 25. Sketch map of the vegetation surrounding a fumarole complex on Candlemas Island. The strip of vegetation is approximately 10 m long by 5 m wide, and is surrounded by almost completely bare ground.

Although zonation is a characteristic feature of the fumarole vegetation some intergradation takes place, and the species dominant in one zone may occur less frequently as associates in adjacent ones. Moreover, details of the communities vary from place to place. On Candlemas Island continuous areas of vegetation up to 20 m in diameter surround many of the fumaroles and up to four zones can be distinguished. The innermost zone, occupying the vents, has *Pohlia nutans* and species of *Cephaloziella* and the gelatinous alga *Mesotaenium* as the most frequent taxa, while on ash slopes varying proportions of *Pohlia nutans* and a large leafy hepatic resembling species of *Alicularia* frequently predominate in the second zone, being largely replaced by *Campylopus introflexus* among lava boulders. The *Campylopus* zone is in places surrounded by a narrow belt of a small leafy hepatic (figure 25), while outer zones dominated by *Polytrichum alpinum* surrounded by a short turf of *Pohlia nutans* with abundant *Lepraria* and other crustose lichens are frequently developed on volcanic ash.

More extensive areas of vegetation surround several of the fumaroles on Bellingshausen Island, and up to five zones are developed. Gelatinous algae are again characteristic of the vents, while species abundant in surrounding areas include *Campylopus introflexus*, *Pohlia nutans*, a green dicranoid moss and the hepatic resembling *Alicularia*. In contrast to Candlemas Island, however, species of *Brachythecium* and *Drepanocladus* are often extensive on warm moist peripheral ground, in some cases giving way to outer zones dominated by *Polytrichum alpinum* and finally by *Pohlia nutans* and lichens.

Further slight modifications in the vegetation surrounding fumaroles were recorded on Leskov and Visokoi Islands, but an increase in the vigour of certain widespread species, and the presence of additional taxa, are features common to the fumarole vegetation on the four islands examined. *Pohlia nutans*, for example, normally forms only short, partially moribund turfs up to 2 to 3 cm tall on Candlemas Island, both on unheated ground and in the peripheral zones in fumarolic areas, but around the vents it occurs in vivid green, densely packed turfs up to 10 cm deep. Conditions here appear to be optimum, as only scattered, slender, distantly leaved stems of this species were normally seen within the vents. Increased moisture may be largely responsible for the vigorous growth of *P. nutans* near the fumaroles as it also forms luxuriant turfs in occasional moist hollows on unheated ground.

Campylopus introflexus is the most striking example of a taxon restricted to the fumarolic areas. This species was recorded on all four islands where fumaroles were examined, but is not known elsewhere in the Antarctic or Sub-Antarctic botanical zones, its nearest reported station being the Falkland Islands. Several of the other characteristic fumarole species, including a number of hepatics, are also unknown in the Antarctic zone, and as these species were not recorded in moist hollows on unheated ground it may be concluded that low temperature is the principal factor limiting their distribution in the South Sandwich Islands.

TABLE 14. TEMPERATURES IN THE VEGETATION AROUND A FUMAROLE ON CANDLEMAS ISLAND

species	zone	distance from vents (cm)	number of readings	temperature (°C)		
				maximum	minimum	mean
**Mesotaenium* sp.	1	nil	1	—	—	18·0
Pohlia nutans (slender form)	1	nil	5	17·0	13·5	15·6
hepatic resembling *Alicularia*	2	30–60	5	16·0	14·5	14·9
**Pohlia nutans* (tall form)	2	30–60	10	17·0	13·0	14·2
Polytrichum alpinum	2	30–60	5	14·5	11·5	12·9
Pohlia nutans (tall form)	3	120–150	5	14·5	10·0	12·4
**Polytrichum alpinum*	3	120–150	5	11·0	9·5	10·3
**Pohlia nutans* (short form)	4	270–300	5	7·5	8·5	7·9

* Most abundant species in each zone. Readings taken on a cloudy day when air temperature was 0·0 °C.

An investigation of the temperatures within and around fumaroles on the South Sandwich Islands was carried out to determine whether zonation of the vegetation could be related to this factor. Readings were taken at a depth of 2·5 cm in the bryophyte colonies using a thermistor or mercury thermometer, and air temperatures at a height of 1·5 m were also measured using the same instruments, dry and shaded. It was found that although conditions became progressively cooler from the inner to the outer zones of each fumarole complex (table 14) a considerable degree of local variation existed between comparable vegetation (table 15). The hottest fumaroles were noted on Bellingshausen Island, and temperatures of at least 70 °C, the upper limit of the thermistor probe available, were recorded several times in fumes and air within the vents. On Candlemas Island the vegetation frequently extended to the centre of the vents, but on Bellingshausen Island it had an inner limit where temperatures among the mosses ranged from an extreme of

TABLE 15. SUMMARY OF TEMPERATURE RECORDS FROM SOUTH SANDWICH ISLANDS FUMAROLES

(*a*) Candlemas Island

fumes or air in vents	limits of vegetation	Algae–hepatics–*Pohlia* (slender form) zone, in vents	*Pohlia* (tall form)–hepatics or *Campylopus* zone	*Brachythecium*–*Drepanocladus* zone	*Polytrichum* zone	*Pohlia*–lichen zone
no data	no data	17·0–16·1–13·5 (6)	17·0–14·0–12·5 (20)*	absent	14·5–11·3–9–5 (10)	8·5–7·9–7·5 (5)
23·0–21·4–20·0 (5)	no data	no data	20·5–12·9–8·0 (20)*	absent	9·5–7·7–6·0 (13)	absent
no data	no data	23·5–21·8–20·0 (5)	16·5–12·5–7·5 (12)*	absent	8·0–6·9–5·0 (5)	9·5–8·1–6·5 (5)
no data	no data	29·5–20·8–11·0 (3)	20·0–15·8–9·0 (20)†	absent	absent	absent

(*b*) Bellingshausen Island

fumes or air in vents		limits of vegetation	Algae–hepatics–*Pohlia*, near vents	tall hepatics, *Pohlia*‡ away from vents	*Brachythecium*‡–*Drepanocladus*	*Polytrichum* zone	outer zones with lichens
over 70–62 (4)	at 2·5 cm depth	61–37–15 (7)	38–32–26 (7)	11·5–10–9 (4)	37–17 (2)	8 (1)	7–5 (2)
	at 5 cm depth	over 70–53–31 (7)	53–37–21 (11)	21–16–11 (6)	39–32–20 (3)	9·5 (1)	11–9–8 (3)

The data show the maximum, mean and minimum temperatures (°C) at 2·5 cm depth in each zone of four fumaroles on Candlemas Island and maximum, mean and minimum temperatures in comparable zones around seven fumaroles on Bellingshausen Island together with the number of readings in each zone (in brackets). Results from different fumaroles on Bellingshausen Island have been grouped, but measurements at 2·5 cm and 5 cm depth are shown separately. A single reading in a small dicranoid moss in a fifth fumarole on Candlemas Island was 55 °C.

* Vegetation comprising predominantly *Pohlia* or hepatics.
† Vegetation comprising predominantly *Campylopus*.
‡ These vegetation types are characteristic of different fumaroles.

61 °C to a surprisingly low minimum of 15 °C, with a mean of 37 °C for ten sites. The highest temperatures recorded in vegetation on Candlemas Island was 55 °C below a dicranoid moss, while mean values for the outer zones of vegetation were as low as 7 °C.

Observations in the largest colony of *Deschampsia antarctica* on Candlemas Island, situated approximately 15 m from a vent and outside the area of continuous vegetation surrounding it, suggest that the heating effects of the fumaroles may extend beyond the limit of the zoned vegetation. Five temperature readings in the grass turfs ranged from 5·5 to 6·5 °C, the mean of 6·0 °C being 4 degC above the air temperature then prevailing under a continuous cloud canopy. At distances of 25 and 75 m, from the nearest vent, however, most temperatures in bryophyte vegetation under similar weather conditions were between 0·5 and 4·0 °C, with a maximum of 6·0 °C, the mean for a series of twenty readings only being 2·3 °C at a time when air temperature remained at zero.

Much of the point-to-point variation within similar vegetation around the fumaroles may be associated by fluctuations in volcanic activity. Thus between 8 and 10 March the temperature 1 m from a vent on Candlemas Island rose from 9·5 to 18·0 °C, but in a comparable site on Bellingshausen Island the temperature dropped from 25·0 to 21·4 °C during the same period (table 16). Moreover, in the Candlemas Island fumarole the rise of 8·5 degC, which followed a fall of 4·5 degC between 7 and 8 March, was accompanied by an increase in temperature of only 3·3 degC at a point beside the vent (table 16). Volcanicity on the islands is also known to alter in vigour over longer periods. For example, geysers reported active on Candlemas Island in 1962 (Holdgate 1963) were inactive when examined several times in March 1964, while a significant difference in the position of fumarolic areas on Bellingshausen Island, and in the amount of steam being emitted, was also noted between 1962 and 1964.

TABLE 16. FLUCTUATIONS IN THE TEMPERATURES NEAR TWO FUMAROLES IN MARCH 1964

			date and time						
		distance from vent	7 Mar.	8 March		9 March		10 March	
locality	site	(m)	16.00	10.45	16.00*	09.00	10.15	09.30*	15.30
Candlemas Island	1. *Pohlia nutans* (tall form)	0·01	14·4	11·1	13·3	—	14·4	15·5	16·6
	2. *Polytrichum alpinum*	1·0	14·0	10·0	9·5	—	13·0	14·0	18·0
	3. *Polytrichum alpinum*	1·5	13·3	11·1	11·7	—	10·5	10·5	13·3
	4. *Polytrichum alpinum* outside continuous area of vegetation around fumarole	20·0	6·0	2·5	6·0	—	3·0	2·0	5·0
	5. *Polytrichum alpinum* as 4	50·0	—	3·0	4·5	—	4·0	3·0	4·0
Bellingshausen Island	1. hepatic resembling *Alicularia*	1·6	—	—	25·0	24·5	—	21·4	—
	2. *Pohlia nutans* (tall form) and hepatic resembling *Alicularia*	3·3	—	—	15·5	14·7	—	13·3	—
	3. *Pohlia nutans* (short form) and crustose lichens	6·3	—	—	11·5	8·3	—	8·3	—

* The observation on Candlemas Island on the afternoon of 8 March, was made at 15.30 h and on Bellingshausen Island at 16.00 h. On 10 March, the morning reading on Candlemas Island was at 09.30 and on Bellingshausen at 10.00 h.

Temperatures are shown in degC. There was continuous cloud cover during the period of observation, daily maximum air temperature being between 0 and 3 °C.

Major variations in the intensity of fumarolic activity may at times prove lethal to the vegetation. Thus, abundant dead bryophytes were seen near one of the hottest vents on Bellingshausen Island where sulphur was subliming on to the mosses and neighbouring rocks. Moreover, extensive areas of *Campylopus introflexus* and other bryophytes near some of the fumaroles on Candlemas Island were brown and moribund in March 1964, though showing signs of recovery through the production of abundant new shoots, suggesting that there had been a temporary period of adverse conditions.

It seems clear, therefore, that the fumarole vegetation experiences temperature fluctuations due to variations in volcanic activity, possibly accompanied on clear sunny days by diurnal fluctuations resulting from absorbed solar radiation. Summer temperatures in the vegetation near the vents are likely to have a higher mean value than those in vegetation away from the fumaroles as, however, are winter minima. Moreover, winter snow cover over vegetation in the inner zones would be expected to have a shorter duration than on neighbouring unheated ground, if indeed it forms at all, while moisture supply is also particularly favourable near the fumaroles. Thus since these areas support bryophytes not recorded elsewhere on the South Sandwich Islands, while widely distributed species may be more vigorous near the fumaroles, it may be concluded that ecological rather than dispersal factors are the more limiting as far as the development of rich, luxuriant vegetation in these islands is concerned.

Discussion

When contrasting the flora of Arctic and Antarctic regions it is clearly pertinent to compare the temperature regimes in the two areas. Pepper (1954) pointed out that although summer air temperatures at stations in the Maritime Antarctic may generally be lower than at comparable latitudes in Greenland and the Canadian Arctic archipelago, winter conditions are frequently colder at the Arctic stations. The latter point is emphasized by observations from more continental localities in the Arctic such as those quoted by Scholander, Flagg, Hock & Irving (1953), who reported that mean monthly air temperatures at Umiat (lat. 69° 25′ N) in eastern Alaska ranged from −28 to −39 °C for the 4 months December to March 1951–52. Willow and alder bushes as well as phanerogam-dominated tundra occur around Umiat, however, suggesting that a wide range of Arctic vascular plants could survive winter conditions in the Maritime Antarctic, where mean monthly air temperatures rarely fall below −15 °C, though it is by no means clear what proportion of the southern cool temperate and Sub-Antarctic floras could do so. However, eight species of vascular plants, including the cosmopolitan weeds *Poa annua* and *P. pratensis*, as well as temperate zone species from the Falkland Islands, are known to have remained alive through at least one winter in this area (Corte 1961; Holdgate 1964; Longton 1966*b*), while, in addition, *Acaena adscendens* and *Rostkovia magellanica*, transplanted from South Georgia to Signy Island as rhizomes in moss turf by one of the present authors in April 1964, produced shoots at the latter station in the summer of 1965–65. Nevertheless, *Poa annua* and *P. pratensis* are the only aliens so far known to have survived two or more full years in the Antarctic, and even they have so far formed only small populations.

Geographic isolation may have severely restricted the spread of vascular plants to the

Antarctic, and additional controlled experimental introductions of alien species into both north-facing and potentially less favourable habitats in the Antarctic Peninsula area will be necessary to determine to what extent vascular plants could thrive under the prevailing climatic conditions. It would be of particular interest to compare the performance of species already adapted to conditions in the high Arctic with those from the southern lands nearest to the Antarctic Peninsula that may, in the absence of continuous land connexions in the post-glacial era, have been denied the opportunity for southward migration accompanied by progressive adaptation to more severe environments. In the meantime, however, the severaly restricted distribution of *Colobanthus* and *Deschampsia* communities to sites apparently enjoying a particularly favourable temperature regime, and the failure of most alien species so far introduced to survive more than a few years, suggests that the vegetation over much of the Maritime Antarctic might retain a principally cryptogamic facies even if dispersal barriers were to become ineffective, although additional species of vascular plant could well become established locally.

The observations summarized in the present paper suggest that the abundance and performance of bryophytes as well as vascular plants in Antarctic regions can be related to variations in the temperature regime, exposure to solar radiation during summer being a particularly important factor. The effects of temperature and other ecological variables are difficult to distinguish, but the present authors agree with Rudmose Brown (1906) in suggesting that the general character of the vegetation on the South Orkney Islands and at other stations near the north-west coast of the Antarctic Peninsula, where water availability is not a serious limiting factor, may be determined largely by the short, cool and generally cloudy summers. Observations on the South Sandwich fumaroles, and the report by Heal, Bailey & Latter (1967, this Discussion, p. 191) that spores of microorganisms reach Signy Island in a viable condition, suggest that a richer cryptogamic flora would probably develop in these areas if conditions were warmer. In view of the continuous land connexion with Maritime areas the even greater restriction of the flora and vegetation in Continental Antarctica can clearly be attributed principally to ecological factors, of which low temperatures and aridity are probably the most important.

The native vascular plants and many of the bryophytes in the Antarctic Peninsula sector belong to species that are also widely distributed in southern temperature regions. Cardot (1908) considered the mosses to represent a largely post-glacial immigrant flora. Several species have been grown successfully under cool greenhouse conditions in Birmingham, indicating that Antarctic populations retain the capacity to survive under a warmer temperature regime than they normally experience in the field. The plants established in the Antarctic, however, are clearly cold tolerant, if not to the same extent as many Arctic species, as they regularly survive temperatures continuously near or below 0 °C for several months each year. This tolerance is well shown by specimens of *Dicranum aciphyllum*, *Drepanocladus uncinatus*, *Pohlia nutans* and a species of *Cephaloziella* from Signy Island, which after being allowed to thaw at room temperature following storage in a deep freeze at −15 °C for 3 years, resumed growth which has been maintained in a cool greenhouse in Birmingham for 12 months.

Antarctic plants must also withstand rapid diurnal fluctuations in temperature of as much as 30 degC, and indeed, the short periods of warming by solar radiation are clearly of utmost importance in permitting a significant amount of metabolic activity and growth. Even so, the summer temperatures in Antarctic vegetation may normally be lower than the optimum for many physiological processes in temperate plants. According to Gates (1965), for example, the optimum temperature for photosynthesis in many temperate species is between 25 and 30 °C, and, although such temperatures are undoubtedly attained on occasions in some types of Antarctic vegetation, they are seldom sustained for long periods. Gates also noted, however, that photosynthesis in certain Arctic species is most rapid at temperatures as low as 15 °C, while Mooney & Billings (1961) showed that optimum temperatures for photosynthesis may be considerably lower in Arctic than in alpine populations of the same species. Moreover, Antarctic marine algae grow and reproduce in an environment where maximum temperatures only marginally exceed 0 °C.

It will thus be of the greatest interest to determine how far terrestrial Antarctic plants, both of endemic and widely distributed taxa, are physiologically adapted to their environment in this and other ways. Such investigations should be stimulated by the experimental studies of Holtom & Greene (1967, this Discussion, p. 323), who show that South Georgian populations of *Colobanthus crassifolius* and *Deschampsia antarctica* grew and reproduced more successfully under a temperate regime of 5 °C by night and 20 °C by day than under continuous temperatures at either the lower or the higher level. The latter, indeed, ultimately proved lethal.

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