

From Bryophyte Ecology 1982
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Chapter 5

Bryophyte Vegetation in
Polar Regions

Rimmer
EFR 446/646

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5.1 INTRODUCTION: THE PHYSICAL BACKGROUND

No universal agreement exists as to the limits of the Arctic and Antarctic, but these areas are generally regarded as tundra in the broad sense of 'treeless regions beyond climatic timberlines' (Webber, 1974). The present account considers the low and high Arctic (Fig. 5.1) as defined by Bliss (1979), and the sub-Antarctic and Antarctic zones (Fig. 5.2) of Greene (1964a) and Holdgate (1964, 1970). These regions include most of the polar tundra, but exclude certain lands such as the Falkland Islands where the absence of arboreal vegetation may be attributable to oceanic as well as polar features of the climate.

The regions under discussion are diverse in topography and climate. Arctic lands encircle a polar ocean (Fig. 5.1), and the terrain ranges from folded mountains, often high and imposing, to rugged uplands on igneous Precambrian rocks and extensive flat-bedded plains and plateaus. Except in Greenland, glaciation is now localized and confined to the mountains. The principle Antarctic land mass is centred over the Pole and is surrounded by ocean (Fig. 5.2), which reaches a minimum width of c. 1000 km between the Antarctic Peninsula and Cape Horn. Islands, both those fringing the continent and others widely scattered in the ocean, though small in area, are highly significant in terms of Antarctic terrestrial biology, as over 98% of the continent lies buried in ice. Even South Georgia, a sub-Antarctic island at latitude 54°S, is heavily glaciated. Thus, vegetation is restricted to the almost universally rugged terrain of coastal regions and the islands, and to nunataks penetrating the inland ice sheet.

Differences between Arctic and Antarctic in the extent of glaciation, and distribution of land and sea, result in comparable variation in climate. Short, cool summers are the most consistent feature but, latitude for latitude, the summers are colder in the southern hemisphere than in the

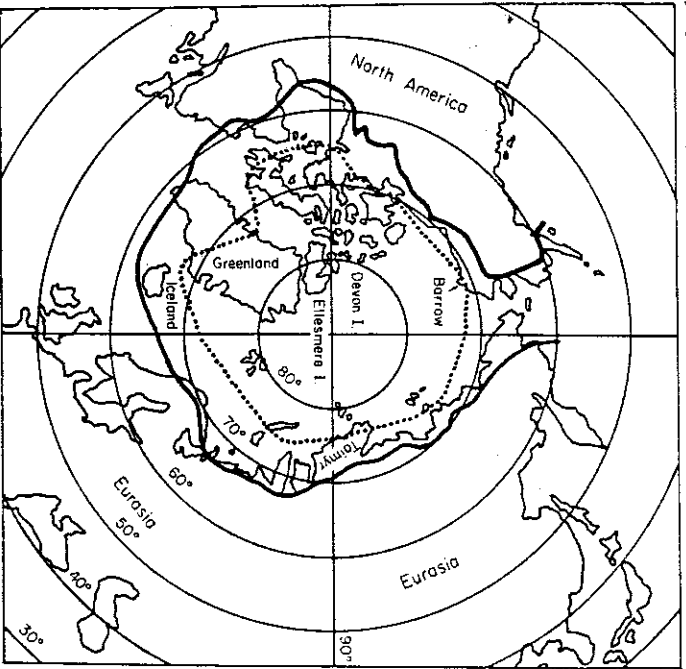


Fig. 5.1 Northern circumpolar region showing the southern boundaries of the low Arctic (solid line) and high Arctic (dotted line). After Bliss (1979).

north (Table 5.1). Mean monthly air temperatures in mid summer exceed 10°C at some low Arctic sites. They are normally above 3°C in the high Arctic, but remain below this value in the polar desert region of the USSR (Alexandrova, 1970) and throughout the Antarctic zone. Means exceed 0°C for one or two months in summer near the west coast of the Antarctic Peninsula and on Antarctic islands in the South Atlantic, i.e. in the maritime Antarctic of Holdgate (1964), but are below freezing throughout the year elsewhere in the Antarctic zone, i.e. in continental Antarctica. Prolonged winter frost and snow cover is a feature of most polar climates, but oceanic influences reduce the annual temperature range in the maritime Antarctic (Table 5.1), and on sub-Antarctic islands, some of which have mean monthly air temperatures above 0°C throughout the year.

Precipitation is moderate to low (Table 5.1), with the notable exception of the sub-Antarctic islands. Moderate precipitation, low evaporation rates, impeded drainage due to permafrost, and extensive spring run-off combine to produce waterlogged conditions over extensive areas of the low Arctic plains. Water is also freely available in many maritime Antarctic

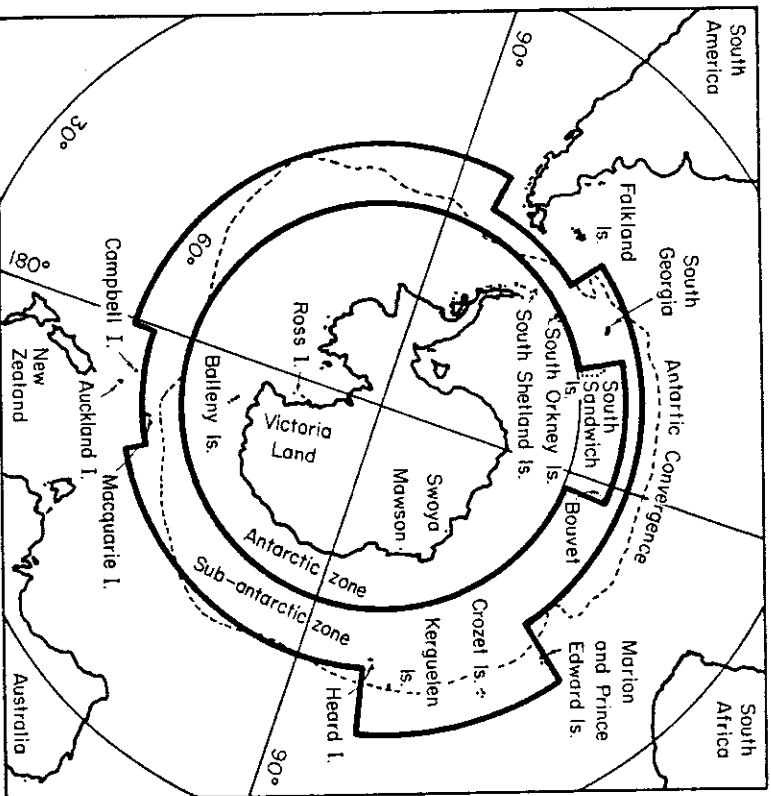


Fig. 5.2 Southern circumpolar region showing the boundaries of the sub-Antarctic and Antarctic zones. After Greene (1964a).

Table 5.1 Air Temperatures and precipitation in polar regions. Data from Anonymous (1978), Bliss (1979), Holdgate (1964), Thompson (1967).

	Mean air temperature, warmest month (°C)	Mean air temperature, coldest month (°C)	Mean annual precipitation (cm rainfall equivalent)
High Arctic	1 to 6	-43 to -27	7 to 20
Low Arctic	6 to 11	-33 to -24	10 to 64
Sub-Antarctic	3 to 8	2 to 2	93 to 258
Maritime Antarctic	1 to 3	-11 to -8	c. 40
Coastal sites in continental Antarctica	-7 to 0	-40 to -26	16 to 43

habitats. In contrast, aridity is a major limiting factor for biological activity throughout much of the high Arctic and in continental Antarctica. In the latter the influence of low precipitation is enhanced by the absence of rain, and by sub-freezing air temperatures throughout the summer. Aridity and cold are commonly accentuated by strong winds, while cloud cover also depresses ground level temperatures, particularly at oceanic localities.

Except on sub-Antarctic islands, which lie at only moderate latitudes, the maximum intensities of incoming solar radiation are lower in polar than in temperate regions, but total daily amounts of solar radiation in mid summer are similar due to increased day length (Gates, 1962). This regime may favour efficient energy utilization by plants, as relatively little radiation is received at intensities far above saturation levels for photosynthesis (Warren Wilson, 1966).

Extensive pleistocene glaciation, combined with harsh climatic conditions and a consequent predominance of physical weathering processes in more recent times, have resulted in the prevalence of immature, primarily mineral soils which may be poor in available nutrients, particularly nitrogen, except in coastal areas (Tedrow, 1977). However, upward water movement results locally in toxic concentrations of salts at the surface in arid regions. The soils are poorly stratified, with little incorporation of organic matter, although extensive superficial peat deposits occur in the wetlands. Permafrost is extensive, except on sub-Antarctic islands. Soil instability, resulting from solifluction and frost-induced phenomena, imposes further limitations on the establishment of closed plant cover, but presents conditions exploitable by pioneer communities. Only locally do soils approach the degree of development normal in temperate regions.

Arctic phanerogamic vegetation can be considered under three headings: wetlands, mesic communities and polar desert. Wetlands occupy level or gently sloping ground with impeded drainage, and support well-developed swards of graminoids over-topping mosses and herbs such as *Polygonum viviparum* and *Saxifraga hirculus*. A variety of vegetation types occurs under mesic conditions, including further graminoid-dominated communities, dwarf shrub heaths, and associations of cushion plants, notably *Dryas integrifolia*, with mosses and lichens. Taller scrub formed by species of *Betula* and *Salix* occurs locally. Mosses, lichens, perennial herbs and suffrutescens perennials such as *Salix arctica* are also conspicuous, with plant cover either continuous or discontinuous. In contrast, bare ground predominates in the polar deserts, where cover of scattered vascular plants and cryptogams totals less than 15%. The proportion of ground occupied by closed vegetation decreases northwards. Thus, wetland and mesic communities predominate in the low Arctic, while much of the high Arctic is occupied by polar desert. The transition is gradual, however, as polar desert is extensive in elevated or exposed

habitats in the low Arctic, and occasional stands of luxuriant vegetation extend almost to the northern limits of land.

Much of the vegetation at low altitudes on sub-Antarctic islands is physiognomically similar to that in the low Arctic. Dwarf shrub heaths are absent, but suffrutescens perennials in the genus *Acaena* are abundant, both in almost pure stands and in association with grasses. Mires and bogs are also widespread, but a number of distinctive southern hemisphere vegetation types also occur, notably herbfield and coastal tussock grassland (Jenkin and Ashton, 1970). Open communities reminiscent of Arctic deserts are widespread under exposed conditions and at higher elevations, where large cushion-forming flowering plants are another distinctive feature.

The sub-Antarctic and Antarctic zones are clearly demarcated, as only two native species of vascular plants occur in the latter. Cryptogamic communities are variable, extensive and often luxuriant in the maritime Antarctic, but are strikingly depauperate in the continental region. Antarctic vegetation is sometimes referred to as polar desert by analogy with that in the high Arctic. This term is appropriate for continental Antarctica, but its application to the maritime Antarctic is misleading in view of the favourable conditions of water availability.

Bryophytes are highly significant in polar ecosystems in terms of aerial cover, species richness, phytomass and production. An indication of the numbers of species involved is provided by the following figures, all of which will be subject to revision, probably upward, following further taxonomic study: Arctic Alaska, 415 mosses and 135 hepatics (Steere and Inoue, 1978; Steere, 1978a); Northern Ellesmere Island, Canadian high arctic, 166 mosses and 43 hepatics (Brassard, 1971a, 1976; Schuster, 1959); sub-Antarctic island of South Georgia, 111 mosses and 27 hepatics (Greene, 1973; Grolle, 1972); Antarctic zone, 85 mosses and 14 hepatics (Greene, 1968; Grolle, 1972; Steere, 1961). Phytogeographical relationships and possible origins of polar bryophyte floras are discussed in the above papers and in Robinson (1972), Schofield (1972) and Vitt (1979).

British and other national scientific activities in the Antarctic since IGY, and IBP investigations in the Arctic, have recently begun to elucidate the ecological relationships of polar bryophytes. Community studies have received detailed attention in the maritime Antarctic, while some aspects of bryophyte autecology are further advanced in the Arctic. Relationships between the physical environment and the distribution of cryptogamic life-form types stand out particularly clearly in the Antarctic in the absence of extensive vascular plant cover, and they have been embodied in a hierarchical classification of the vegetation as discussed on p. 139. No comparable classification of Arctic or sub-Antarctic bryophyte vegetation has yet been formulated. This may reflect either the greater emphasis

Table 5.2 Bryophyte life-forms in polar regions (after Gimmingham and Birse, 1957).

Small cushion	Systems with main shoots radiating in dome-shaped colonies; each colony < 5 cm in diameter. Branches adopting the same direction of growth as the main shoots. High spatial density of shoots and branches resulting in compact colonies.
Large cushion	Systems with main shoots radiating in dome-shaped colonies; many colonies > 5 cm in diameter. Branches adopting the same direction of growth as the main shoots. Spatial density of shoots and branches normally lower, and the colonies frequently looser, than in small cushions.
Short turf	Systems with main shoots parallel and erect. Branches erect, of indeterminate growth. Colonies loose or compact, > 2 cm tall.
Tall turf, branches erect	Systems with main shoots parallel and erect. Branches erect, of indeterminate growth. Colonies loose or compact, > 2 cm tall.
Tall turf, branches divergent	Systems with main shoots parallel and erect. Branches divergent, of determinate growth. Colonies loose or compact, > 2 cm tall.
Carpet	Systems with distal portions of shoots parallel and erect or ascending, derived from a prostrate, basal region of partially denuded stems. Colonies loose or compact.
Mat	Systems of prostrate or ascending shoots, interweaving to form compact colonies.
Wetf	Systems of long, often robust, erect ascending shoots, interweaving and forming loose colonies.
Canopy	Systems of sympodial shoots, at first stoloniferous, later becoming erect. Erect portion dendroid: unbranched and bearing scale leaves below, with abundant branches above, the branches bearing photosynthetic leaves and forming loose canopies.

placed on cryptogamic community ecology by students of Antarctic botany, or intrinsic difficulties arising from the wide range of species and vegetation types present in the Arctic. Steere (1978b) doubts whether it is feasible to define formal bryophyte communities in the Arctic because of the gradual and subtle changes in species composition which occur in response to gradients in water availability and other environmental variables. In the present account, Arctic and sub-Antarctic vegetation is described under the informal headings of wetland, mesic and dry ground communities. Attention is paid to the contribution of bryophytes both to vegetation with a significant vascular plant component and to essentially cryptogamic communities. It is hoped that this account will assist in the development of a comprehensive classification of polar vegetation which takes due account not only of flowering plants, but also of bryophytes and

the other major groups of cryptogams. Two possible approaches have been outlined by Bliss (1979) and Longton (1979a).

An attempt is also made to describe relationships between bryophyte life-form and environment in the Arctic and sub-Antarctic, in order to complement the Antarctic work, the life-form types considered here being outlined in Table 5.2. It should be noted that certain terms such as bryophyte carpet are commonly used less precisely than defined in Table 5.2, while many accounts of polar vegetation make no mention of life-form. The present assignment of life-form to species in areas not studied by the author must therefore be regarded as tentative. The term life-form is employed in preference to growth form, as used in recent Antarctic literature (Gimmingham and Smith, 1970; Longton, 1979a), for reasons discussed elsewhere in this volume by Mägdefrau (p. 49).

5.2 BRYOPHYTE VEGETATION IN THE ARCTIC

The widespread notion that bryophytes are abundant in Arctic vegetation is only partially true, and applies particularly to wet, low Arctic tundra. Steere (1978b) describes the landscape in the coastal plain province of Alaska as 'an almost unbroken expanse of bog, marshy meadows and fens' in which 'bryophytes - and particularly *Sphagnum* - may become the dominant and continuous vegetation over large areas, usually associated with grasses, carices and *Eriophorum*'. However, the abundance of bryophytes, as of flowering plants, varies broadly within the Arctic in relation to water availability, on both a local and a regional basis. Thus, considerable differences in abundance and species composition occur between the dry summits of ice-wedge polygons and the wet troughs between them (Steere, 1978b), while the high Arctic polar desert in places contrasts strongly with wetlands in the low Arctic in 'the extremely restricted development of the bryophyte vegetation' (Schuster, 1959).

The contribution of bryophytes to the plant cover of the Truelove Lowland region of Devon Island is considered by Vitt and Pakarinen (1977) and other reports on the Canadian IBP Tundra Biome investigations in Bliss (1977a). Truelove Lowland supports more extensive closed vegetation than is common at its latitudes of 76°N (Bliss, 1977b), and a representative selection of wetland, mesic and polar desert communities is developed in the Lowland and surrounding plateau region. In addition, Brassard (1977b), Holmen (1955) and Steere (1978a) have listed bryophyte associations from high Arctic localities in northern Ellesmere Island, Peary Land, north Greenland, and Arctic Alaska respectively, while comprehensive accounts of bryophyte vegetation have been presented for Iceland (Hesselbo, 1918), northern Swedish Lapland (Mårtensson, 1956) and south-east Spitzbergen (Philippi, 1973), the last based on methods of

the Zurich-Montpellier School. The following account is based largely on the papers cited above, supported by the present author's observations on northern Ellesmere Island and in low Arctic localities on the west coast of Hudson's Bay. Prominence is given to the diverse, well-documented bryophyte vegetation of Truelove Lowland which is summarized in Table 5.3.

5.2.1 Wetlands

Bryophytes are abundant in the Arctic wetlands. Four different meadow communities are recognized in Truelove Lowland (Table 5.3), each of which comprises stands of graminoids and other vascular plants rooted in an almost closed bryophyte understory. Significant breaks in the moss cover occur principally on hummocks or disturbed areas. The dominant mosses generally assume the tall turf life-form, and include pleurocarps such as *Drepanocladus* spp. as well as *Cinclidium arcticum* and other acrocarps. Other life-forms are represented more sparingly: for example, *Seligeria polaris* forms short turfs on small stones in relatively open areas of the frost boil meadow type. Over 40 species of bryophyte have been recorded in the meadow communities of Truelove and the nearby Sparbo-Hardy Lowlands of Devon Island. *Riccardia pinguis* was the only hepatic present at high frequency, while *Sphagnum* was represented only by the local occurrence of *S. orientale*.

A comparable bryophyte stratum, comprising largely tall turfs of peat-forming mosses, both acrocarpous and pleurocarpous, occurs in wetlands throughout the Arctic. Wetlands reach their most extensive development in the low Arctic where, as in Alaska, species of *Sphagnum* are prominent. *Lophozia* spp. and other hepatics are also frequent in low Arctic wetlands, both as isolated stems among mosses, and in small mats on eroding peat surfaces. However, isolated stands of sedge meadow extend in damp hollows to beyond 82°N in both Ellesmere Island and Peary Land, and here the bryophyte layer is represented principally by a *Drepanocladus brevifolius* community described by Brassard (1971b) and Holmen (1955). A detailed account of mire vegetation in the Torneträsk area of Lapland is provided by Sonesson (1967, 1969, 1970a, 1970b) and Sonesson and Kviller (1980).

5.2.2 Mesic communities

Five mesic communities have been described from the Truelove Lowland region (Table 5.3), including graminoid-moss tundra with the vascular plant cover dominated by *Hierochloa alpina* and *Luzula confusa*, dwarf shrub heath with abundant *Cassiope tetragona*, and three fellfield types dominated by *Dryas integrifolia* and other cushion-forming species. Mosses form an important component of all these vegetation types, which differ from most of the wet meadows in the greater abundance of lichens.

Table 5.3 Plant communities in the vicinity of Truelove Lowland, Devon Island, Canadian High Arctic.

Habitat – plant community types	Topographic position	Plant cover	Examples of representative species		
			Vascular plants	Bryophytes	Lichens
<i>Weiland communities</i>					
Wet sedge-moss meadow	By lowland streams and ponds: on peat often > 30 cm deep	Homogeneous vascular plant cover and abundant mosses	<i>Carex stans</i> (D) <i>Hierochloa paucifolia</i> (C)	<i>Calliergon giganteum</i> (D – tall turf) <i>Drepanocladus revolvens</i> (D – tall turf) <i>Meesia triquetra</i> (D – tall turf)	—
*Hummocky sedge-moss meadows	Level ground in lowlands: on peat often 10–15 cm deep	Vascular plants and mosses abundant. Hummocky relief due to differential growth of the latter	<i>Carex stans</i> (D) <i>Salix arctica</i> (C) <i>Saxifraga hirculus</i> (C)	<i>Cinclidium arcticum</i> (D – tall turf) <i>Drepanocladus revolvens</i> (D – tall turf) <i>D. brevifolius</i> (C – tall turf)	—
*Frost boil sedge-moss meadow	Level ground in lowlands: little or no peat formation	Frost boils cover c. 50% of ground, their surfaces usually covered by blue-green algae, mosses and scattered sedges, with <i>Seligeria polaris</i> on small stones. Continuous plant cover in intervening areas	<i>Eriophorum triste</i> (D) <i>Carex membranacea</i> (D) <i>Carex arctica</i> (C) <i>Polygonum viviparum</i> (C)	<i>Drepanocladus revolvens</i> (D – tall turf) <i>Campylium arcticum</i> (C – tall turf) <i>Dirichum flexicaule</i> (C – tall turf) <i>Seligeria polaris</i> (C – short turf)	—

Table 5.3 Continued. Plant communities in the vicinity of Truelove Lowland, Devon Island, Canadian High Arctic.

Habitat – plant community types	Topographic position	Plant cover	Examples of representative species		
			Vascular plants	Bryophytes	Lichens
Hummocky graminoid meadow	Coastal, recently emerged areas	Graminoids and bryophytes abundant	<i>Arctagrostis latifolia</i> (D) <i>Dupontia fischeri</i> (D)	<i>Orthothecium chryseum</i> (C – tall turf) <i>Drepanocladus revolvens</i> (C – tall turf) <i>Cinclidium arcticum</i> (C – tall turf) <i>Calliergon giganteum</i> (C – tall turf) <i>Meesia triquetra</i> (C – tall turf)	—
Tidal salt marsh	10–30 m wide strip along coast	Continuous turf: mosses and lichens a very minor component	<i>Puccinellia phryganoides</i> (D)	—	—
<i>Mesic and dry ground communities</i>					
Raised centre polygons	Beach ridge margins and dry meadows	Scattered vascular plants, bryophytes and lichens	<i>Alopecurus alpinus</i> (D) <i>Dryas integrifolia</i> (D) <i>Salix arctica</i> (D)	<i>Aulacomnium turgidum</i> (C – tall turf) <i>Ditrichum flexicaule</i> (C – tall turf) <i>Polytrichum alpinum</i> (C – tall turf)	<i>Cladonia pocillum</i> (C) <i>Certraria nivalis</i> (C) <i>Lecanora epibryon</i> (C)
*Dwarf shrub heath-moss	Among rock outcrops	Cover averages 37% for vascular plants and 14% for bryophytes	<i>Cassiope tetragona</i> (D) <i>Dryas integrifolia</i> (C) <i>Saxifraga oppositifolia</i> (C)	<i>Racomitrium lanuginosum</i> (D – mat) <i>Hypnum revolutum</i> (C – mat) <i>Ditrichum flexicaule</i> (C – tall turf) <i>Hylocomium splendens</i> (C – mat)	<i>Certraria nivalis</i> (C) <i>Thamnolia vermicularis</i> (C) <i>Dactylina arctica</i> (C)
Graminoid-moss	Near summit of rocky slopes	Bare rock gives greatest cover. Cover of cryptogams exceeds that of vascular plants	<i>Hierochloa alpina</i> (D) <i>Luzula confusa</i> (D)	<i>Polytrichum juniperinum</i> (C – tall turf) <i>Racomitrium lanuginosum</i> (D – mat) <i>Hylocomium splendens</i> (C – mat) <i>Polytrichum juniperinum</i> (C – tall turf)	<i>Alectoria ochroleuca</i> (D) <i>Umbilicaria vellea</i> (D)
*Cushion plant moss	Mid to lower slopes of raised beaches and other lowland areas	Plant cover approaches 100% with mosses and lichens contributing 30–50%	<i>Dryas integrifolia</i> (D) <i>Carex rupestris</i> (C) <i>Saxifraga oppositifolia</i> (C) <i>Salix arctica</i> (C)	<i>Tortella arctica</i> (D – tall turf) <i>Oncophorus wahlenbergii</i> (D – tall turf) <i>Schistidium holmenianum</i> (D – tall turf)	<i>Certraria nivalis</i> (C) <i>Lecanora epibryon</i> (C)
*Cushion plant lichen	Crests and upper slopes of raised beaches, limestone pavement and rock outcrops: little winter snow cover, well drained and relatively warm in summer	Vascular plant cover c. 20% moss and lichen cover c. 40–45%	<i>Carex nardina</i> (C) <i>Dryas integrifolia</i> (C) <i>Salix arctica</i> (C) <i>Saxifraga oppositifolia</i> (C)	<i>Distichium capillaceum</i> (C – short turf) <i>Encalypta rhaptocarpa</i> (C – short turf) <i>Hypnum bambergeri</i> (C – mat or carpet) <i>Myurella julacea</i> (C – mat or short turf)	<i>Alectorea pubescens</i> (D) <i>Rhizocarpon geographicum</i> (C) <i>Thamnolia subbliformis</i> (C) <i>Umbilicaria arctica</i> (C)
<i>Polar desert communities</i>					
*Moss-herb (polar desert)	Dry plateau areas. Plant cover best developed in troughs of polygons, and between and under frost shattered rock fragments	Total plant cover 2–7%: mosses predominant	<i>Draba corymbosa</i> (M) <i>Papaver radicum</i> (M) <i>Saxifraga oppositifolia</i> (M)	<i>Distichium capillaceum</i> (C – short turf) <i>Ditrichum flexicaule</i> (C – short turf) <i>Hypnum bambergeri</i> (D – mat or carpet) <i>Mnium lycopodioides</i> (M – single stems among rocks)	<i>Alectorea nigricans</i> (M) <i>Perusaria dactylina</i> (M) <i>Polyblastia bryophila</i> (M)

Table 5.3 Continued. Plant communities in the vicinity of Truelove Lowland, Devon Island, Canadian High Arctic.

Habitat – plant community types	Topographic position	Plant cover	Examples of representative species		
			Vascular plants	Bryophytes	Lichens
<i>Bryophyte-dominated communities</i> Herb-moss snowbed	Small areas in lee of rocks: snow persists until July	Bryophyte cover exceeds that of vascular plants	<i>Oxyria digyna</i> (C) <i>Ranunculus sulphureus</i> (C) <i>Saxifraga cernua</i> (C)	<i>Bryum cryophyllum</i> (D – large cushion) <i>Bryum pseudotriquetrum</i> (D – tall turf or large cushion) <i>Cinclidium arcticum</i> (D – tall turf or large cushion) <i>Philonotis fontana</i> var. <i>pumila</i> (D – tall turf or large cushion)	—
<i>Scorpidium scorpioides</i> community	Submerged in shallow calcareous pools	Almost continuous moss cover	—	<i>Scorpidium scorpioides</i> (D – mat or carpet) <i>Scorpidium turgescens</i> (C – mat or carpet) <i>Calliergon giganteum</i> (C – mat)	—
<i>Schistidium alpicola</i> community	Submerged in swiftly-flowing streams	Discontinuous moss cover	—	<i>Schistidium alpicola</i> var. <i>rivularis</i> (C – small cushion) <i>Blindia acuta</i> (C – short turf)	—
<i>Aplodon wormskjoldii</i> community	Dung of musk ox	Continuous moss cover	—	<i>Aplodon wormskjoldii</i> (C – tall turf) <i>Bryum</i> spp. (C – tall turf) <i>Splachnum</i> spp. (tall turf) <i>Tetraplodon</i> spp. (tall turf) <i>Voitia hyperborea</i> (tall turf)	—
<i>Desmatodon-Funaria</i> community	Disturbed ground around lemming burrows	Discontinuous moss cover	—	<i>Desmatodon heimii</i> var. <i>arctica</i> (D – short turf) <i>Desmatodon leucostoma</i> (D – short turf) <i>Funaria polaris</i> (C – short turf)	—
Community of small acrocarpous mosses	Disturbed ground on sides of ice wedges	Discontinuous moss cover	—	<i>Ceratodon purpureus</i> (C – short turf) <i>Dicranella crispa</i> (C – short turf) <i>Leptobryum pyriforme</i> (C – short turf) <i>Psilopilum cavifolium</i> (C – short turf) <i>Stegonia latifolia</i> (C – short turf)	—
<i>Racomitrium lanuginosum</i> community	Dry sites among rocks	Extensive cover of mosses and lichens	—	<i>Racomitrium lanuginosum</i> (D – mat)	<i>Rhizocarpon</i> spp. (C) <i>Umbilicaria vellea</i> (D)

Additional, undescribed bryophyte communities occur, particularly on rock outcrops.

*Major communities in terms of area occupied.

D = dominant, C = common, M = minor component

Data from Bliss *et al.* (1977), Muc and Bliss (1977) and Vitt and Pakarinen (1977), with additional information from D.H. Vitt (personal communication).

Mosses are particularly abundant in the graminoid tundra, dwarf shrub heath, and in a closed cushion plant-moss community (Table 5.3), and the range of life-forms is wider than in the wetlands. Tall turfs are again represented, for example by *Polytrichum juniperinum* in the graminoid tundra, but short turf- and mat-forming species are also prominent, particularly in the drier habitats. Examples include mats of *Racomitrium lanuginosum*, a dominant moss in both dwarf shrub heath and graminoid tundra, and *Encalypta rhaptocarpa*, a short turf-forming species occurring commonly in the cushion plant-lichen community.

A similar range of life-forms occurs in association with *Cassiope* and *Dryas* elsewhere in the Arctic. Abundant tall turfs of *Aulacomnium* spp. occur in *Cassiope* heath on northern Ellesmere Island where a varied bryophyte assemblage, including mats of *Abietinella abietina* and the hepatic *Arnellia fenica*, with short turfs of *Encalypta alpina*, occurs among hummocks of *Dryas integrifolia* (Brassard, 1971b). In Peary Land, mats of *Hypnum revolutum* predominate in the bryophyte component of *Cassiope* heath, with *Aulacomnium turgidum* present only in the moister places (Holmen, 1955). Mats of *Hylocomium splendens* with tall turfs of *Aulacomnium turgidum* and *Tomentohypnum niens* are reported as the dominant bryophytes in a *Dryas*-sedge-moss tundra in the Taimyr region (Maiveyeva *et al.*, 1974).

At some low Arctic sites, the dwarf shrub heathlands support bryophyte communities resembling those of heaths in boreal and temperate regions. In Iceland, the wet-forming mosses *Pleurozium schreberi* and *Hylocomium splendens* are prominent, as well as tall turfs of *Dicranum* spp. with mats of such leafy hepatics as *Fruillania tamarisci*, *Lophozia* spp. and *Ptilidium ciliare* (Hesselbo, 1918). In addition, the canopy-forming moss *Climacium dendroides* occurs in association with wets of *Hylocomium* and *Rhytidadelphus* spp. and a wide range of other bryophytes on mesic, grassy slopes. Wet-forming mosses are also abundant in birch woodland, the presence of which indicates that not all Icelandic lowland vegetation is truly Arctic in character.

5.2.3 Polar desert

The dry polar desert soils support fellfields dominated by cushion-forming flowering plants and mosses, and other open communities comprising scattered vascular plants and cryptogams among which short, compact life-forms again generally predominate. Mats or carpets of *Hypnum bambergeri*, and short turfs of *Distichum capillare* and *Dicranum flexicaule*, are among the characteristic mosses of the dry plateau areas around Truelove Lowland (Table 5.3), while Brassard (1971b) lists a wide range of small acrocarpous mosses as constituents of a *Bryum-Encalypta* community on dry plains of sand, silt or clay in northern Ellesmere Island.

Similar communities occupy dry ground in the low Arctic. In Iceland, large stones on dry rocky flats in montane regions support scattered mats, small cushions and short turfs of such mosses as *Andreeva rupestris*, *Dicranoweisia crispata*, *Racomitrium fasciculare* and *Schistidium apocarpum*, and a similar assortment of life-forms is represented in an open, pioneer community on porous substrata in the extensive young lava fields (Hesselbo, 1918).

5.2.4 Bryophyte-dominated communities

The bryophyte assemblages so far considered form an integral part of plant communities also comprising vascular plants and often lichens. Additional bryophyte communities may be recognized in habitats such as rock faces where significant vascular plant cover has failed to develop, or in small areas where the habitat differs markedly from the norm for a major community, e.g. on muskox dung within a sedge meadow. Examples occur locally in sheltered sites where snow persists until well into July. As well as an unusually short growing season with freely available water, such sites are characterized by shelter from wind, well developed, protective winter snow cover, and often an accumulation of sand or organic debris blown into the hollows over the winter snow. Distinctive assemblages of both vascular plants and bryophytes may be found under such conditions. Mårtensson (1956) has noted, however, that many bryophytes which are characteristic of late snow areas in the low alpine belt of the Torneträsk area occur more widely in the high alpine region.

Late lying snowbeds on Truelove Lowland support luxuriant, large cushions and tall turfs of *Bryum cryophyllum*, *Philonotis fontana* var. *pumila* and other mosses, in which are rooted scattered herbaceous flowering plants (Table 5.3). The hepatic *Anthelia juratzkana* is characteristic of late snowbeds throughout the Arctic, for example in Peary Land (Holmen, 1955) and on Spitzbergen (Phillippi, 1973), and it is one of the few hepatics to assume dominance in Arctic plant communities. Holmen noted, however, that a covering of sand deposited by melting snow restricts the bryophyte vegetation of some late snow areas: *Polytrichum alpinum* and *Timmia australica* were considered two of the mosses best able to overcome this stress, and *P. alpinum* is also dominant in some snow bank vegetation on northern Ellesmere Island (Brassard, 1971b).

Vegetation resembling the snowpatch community of Truelove Lowland in the abundance of large cushion-forming mosses such as *Bryum cryophyllum* and *Philonotis* spp. is widely distributed on stony or marshy ground by permanently flowing rivers and streams (Brassard, 1971b; Hesselbo, 1918; Holmen, 1955). Bryophytes are only sparsely developed on rocks submerged in streams in some high Arctic regions (Holmen, 1955), but communities with abundant *Hygrohypnum* and *Schistidium*

spp. have been reported from Truelove Lowland (Table 5.3) and elsewhere, particularly by waterfalls (Brassard, 1971b; Holmen, 1955; Steere, 1978b). *Scapania* and *Fomitella* are among other genera characteristic of such habitats in low Arctic regions (Hesselbo, 1918; Mårtensson, 1956). *Scorpidium scopioides* and other mat or carpet-forming pleurocarpous mosses, including *S. turgescens* and species of *Calliergon* and *Drepanocladus*, are widely distributed in shallow calcareous ponds.

Boulders, cliffs and other rocky habitats at high Arctic sites are commonly too dry to support an abundance of bryophytes. Rapid weathering of sedimentary rock is another limiting factor (Brassard, 1971b). Vitt and Pakkarinen (1977) note that small cushion-forming acrocarps are rare in calcareous conditions on Devon Island, but that such species as *Amphidium lapponicum*, *Andreea rupestris*, *Dicranoweisia crispula* and *Grimmia torquata* are common on acidic rock outcrops. Similar communities occur in other high Arctic sites (Brassard, 1971b; Holmen, 1955). In contrast, small mat- and turf-forming species appear to predominate in the open vegetation found in sheltered rock crevices. Examples include the *Cyrtomitium hymenophylloides* community of northern Ellesmere Island, where associated species include *Fissidens arcticus*, *Isoperlygium pulchellum*, *Pohlia cruda* and *Myurella* spp., and an assemblage of *Leskeella nervosa*, *Seligeria* spp. and other mosses from Alaska (Brassard, 1971b; Steere, 1978b). Cliff vegetation is best developed at oceanic low Arctic sites where many communities resemble those of temperate montane regions (Hesselbo, 1918; Mårtensson, 1956).

The Arctic is notable for the number of bryophyte communities associated with substrata enriched in nutrients by animal activity. Most striking is the assemblage comprising members of the Splachnaceae, with *Bryum* spp. and other mosses at later stages in succession (Webster and Sharp, 1973), found on faeces, bone and other animal remains. It occurs throughout the Arctic, and a wide range of splachnaceous mosses may be represented. Brassard (1971b) regards six such species, and a comparable number of other acrocarpous mosses, as characteristic of an *Aplodon wormskjoldii* community in northern Ellesmere Island. Seventeen members of the Splachnaceae have been recorded in Alaska (Steere, 1978a), but not all are restricted to animal remains. In Scandinavia, the spores of splachnaceous mosses characteristic of dung have been shown to differ from those of related species growing on soil or as epiphytes, and the attraction of insects to coprophilous species, possibly by odours or secretions from the enlarged and brightly coloured hypophysis, has been demonstrated experimentally. These and other factors which suggest the evolution of entomophily within the Splachnaceae have been discussed by Koponen (1978) and Koponen and Koponen (1978); see also Chapter 9, pp. 312-315.

Bird perches and the mouths of lemming burrows also support distinctive bryophyte communities, composed, at least in the high Arctic, of short turf-forming acrocarps. Several of the species associated with lemming burrows are apparently Arctic endemics, e.g. *Desmatodon leucostoma* and *Funaria polaris* (Steere, 1978b; Vitt, 1975). In contrast, the cosmopolitan *Bryum argenteum* is among the mosses colonizing sites habitually frequented by birds in several areas. Mårtensson (1956) has noted that certain mosses with southern distribution patterns extend to alpine sites in the Tornaträsk area only around bird perches.

Short turf-forming acrocarps are also prominent in successional communities on ground disturbed by ice action and other factors. Examples include a community on the sides of ice-wedge polygons on Truelove Lowland (Table 5.3), and an assemblage of such cosmopolitan weeds as *Bryum argenteum*, *Ceratodon purpureus*, *Funaria hygrometrica* and *Marchantia polymorpha* on ground disturbed by man and other animals in Alaska (Steere, 1978b).

A final community type which should be mentioned is the moss 'heath', generally dominated by species of *Racomitrium*, notably *R. lanuginosum*. The latter is widespread throughout the Arctic: it is a frequent component of dwarf shrub heath and other vascular plant communities, and may become dominant in dry rocky sites, as on Truelove Lowland (Table 5.3). Extensive areas of *Racomitrium* 'heath' are characteristic of certain islands where porous volcanic soils occur in an oceanic climate characterized by strong winds, frequent precipitation, and generally high relative humidity with frequent fog. The combination of strong winds and porous substrata restricts vascular plant cover, and bryophytes, whose colonies can absorb and retain precipitation, and even water from a saturated atmosphere (Tallis, 1959), predominate. Thus, large tracts of stony ground on Iceland support a closed *Racomitrium lanuginosum* 'heath', often with only scattered phanerogams and a small admixture of other bryophytes (Hesselbo, 1918), and a similar community on exposed hillsides forms the principal vegetation of Jan Mayen. A second bryophyte community, in which *Drepanocladus uncinatus* may predominate (E. V. Watson, personal communication), is developed extensively in parts of Jan Meyen thought to experience particularly frequent precipitation and mist (Russell and Wellington, 1940), and similar communities dominated by *D. uncinatus* and *Racomitrium* spp. occur on Spitzbergen (Philippi, 1973).

5.3 BRYOPHYTE VEGETATION IN THE MARITIME ANTARCTIC

5.3.1 Classification

A vegetation classification for the maritime Antarctic has been developed

by Holdgate (1964), Gimingham and Smith (1970) and Longton (1967). In this hierarchical scheme (Table 5.4), the basic unit, the sociation, is recognized by aerial cover of the dominant or codominant species, and sociations are grouped within associations, defined by the floristic similarity of the component sociations and the high constancy of a group of characteristic species, following Poore (1962). Associations are included within subformations on the basis of life-form of the community dominants, and two formations are recognized according to the dominance of vascular plants or cryptogams.

The classification has been generated subjectively and there is intergradation between the vegetation units at all levels. However, quantitative analysis of quadrat data from Signy Island, South Orkney Islands (Fig. 5.2), provided strong support for a number of the units recognized (Smith and Gimingham, 1976). The classification has been applied successfully in describing vegetation at several maritime Antarctic localities (Allison and Smith, 1973; Lindsay, 1971; Longton and Holdgate, 1979; Smith and Corner, 1973), and notably in Smith's (1972) detailed account of Signy Island. More recently, the classification has been extended to parts of continental Antarctica (Longton, 1973a; Nakanishi, 1977; Seppelt and Ashton, 1978). Literature on Antarctic plant communities is reviewed by Longton (1979a), who lists the sociations so far recognized.

5.3.2 Vascular plant and lichen communities

Vegetation developed under the cold oceanic conditions prevailing in the maritime Antarctic is almost entirely cryptogamic. The two native species of flowering plants only become abundant locally in small stands of the grass and cushion chamaephyte formation (Table 5.4). In contrast, vegetation dominated by mosses, lichens and, locally, algae is extensive and often luxuriant. The crustaceous lichen subformation (Table 5.4) is widely distributed on boulders and rock faces, particularly in dry exposed situations and on sea cliffs, but also around pools and in other wet habitats. *Buellia*, *Caloplaca*, *Placopsis*, *Xanthoria*, with *Verrucaria* low on marine cliffs, are among the prominent genera. Bryophytes are generally rare or absent. Mosses, particularly small cushion-forming species of *Andreaea*, *Dicranoweisia* and *Grimmia*, are more prominent in some stands of the fruiticose and foliose lichen subformation. These communities, in which species of *Himantornia*, *Umbilicaria* and *Usnea* generally predominate, cover extensive areas on cliffs, scree slopes and other exposed, rocky habitats. Small moss cushions are most frequent as associates of the macrolichens on the moister rocks, and the green alga *Prasiola crispa* may become abundant where water trickles over rock surfaces.

Table 5.4 Outline of a classification of vegetation in the Antarctic zone (After Longton, 1979a).

Antarctic nonvascular cryptogam tundra formation
Crustaceous lichen subformation
<i>Buellia</i> – <i>Lecanora</i> – <i>Lecidea</i> association: 2 sociations
<i>Caloplaca</i> – <i>Xanthoria</i> association: 10 sociations
<i>Placopsis contortuplicata</i> association: 3 sociations
<i>Verrucaria</i> association: 5 sociations
Fruiteose and foliose lichen subformation
<i>Usnea</i> – <i>Umbilicaria</i> association: 15 sociations
Short moss turf and cushion subformation
<i>Andreaea</i> association: 6 sociations
<i>Bryum antarcticum</i> – <i>B. argenteum</i> association: 4 sociations
<i>Bryum incomplexum</i> association: 5 sociations
<i>Ceratodon</i> association: 3 sociations
<i>Pohlia nutans</i> association: 2 sociations
<i>Pohlia austro-georgica</i> association: 1 sociation
<i>Sarcocaulum glaciale</i> association: 1 sociation
<i>Tortula</i> – <i>Grimmia antarctici</i> association: 6 sociations
Tall moss turf subformation
<i>Campylopus</i> association: 2 sociations
<i>Polytrichum alpestre</i> – <i>Chorisodontium aciphyllum</i> association: 6 sociations
<i>Polytrichum alpinum</i> – <i>Pohlia nutans</i> association: 7 sociations
Bryophyte carpet and mat subformation
<i>Brachythecium</i> association: 1 sociation
<i>Calliergidium austro-stramineum</i> – <i>Calliergon sarmentosum</i> – <i>Drepanocladus uncinatus</i> association: 6 sociations
<i>Cephalozia badia</i> association: 1 sociation
<i>Cryptochilia grandiflora</i> association: 2 sociations
<i>Marchantia</i> association: 1 sociation
Moss hummock subformation
<i>Brachythecium austro-salebrosum</i> association: 1 sociation
<i>Bryum algens</i> – <i>Drepanocladus uncinatus</i> association: 3 sociations
Alga subformation
<i>Prasiola crispa</i> association: 1 sociation
<i>Nostoc</i> association: 1 sociation
Snow alga subformation
<i>Chlamydomonas nivalis</i> association: 2 sociations
Antarctic herb tundra formation
Grass and cushion chamaephyte subformation
<i>Deschampsia antarctica</i> – <i>Colobanthus quitensis</i> association: 4 sociations

5.3.3 Short moss turf and cushion subformation

Mixed communities comprising fruticose and foliose lichens, with small cushions of *Andreea* spp. and other mosses, in places intergrade with essentially bryophytic vegetation in the *Andreea* association of the short moss turf and cushion subformation (Table 5.4). The latter is characteristic of stones, gravel and sand on level ground or gentle slopes, principally on acidic substrata, at sites covered by winter snow. Small cushion-forming mosses predominate, principally *Andreea depressinervis*, *A. gainii*, *A. regularis* and locally *Racomitrium austro-georgicum*. Mats of *Drepanocladus uncinatus* are also widespread, and small areas on Signy Island support an *Andreea*-hepatic socrition in which *Barbilophozia hatcheri*, *Cephalozia varians*, *Herzogobryum teres*, *Hygrolobidium isophyllum* and *Pachygloussa dissitifolia* form mixed mats up to 50 cm in diameter (Smith, 1972). Bryophyte cover may be high, particularly at the moister sites where moss cushions coalesce to give a closed sward. Lichens are present and become abundant in drier areas. They include epipetric species such as *Usnea antarctica*, and other, principally crustose forms, which grow epiphytically on the mosses. Solifluction and frost heave may disrupt the moss cover, and Smith (1972) describes hillsides on Signy Island where the *Andreea*-lichen socrition occurs as narrow strips parallel with the slope, on coarse, relatively stable substrata, which alternate with strips of mobile clay almost devoid of vegetation.

The *Andreea* association is commonly replaced on calcareous substrata by the *Tortula-Grimmia* association. The dominant mosses again assume the small cushion life-form, but short turf-forming species of *Encalypta*, *Pohlia*, *Pohlia* and other genera may also be present, as well as mats of *Brachythecium* and *Drepanocladus* spp. Species of *Amblystegia*, *Cephalozia* and *Pseudoleskea* have been recorded as scattered stems among the more abundant mosses, while lichens become frequent only in the drier sites. The *Tortula-Grimmia* association is particularly well developed on relatively dry sandy or gravelly soils around local outcrops of marble on Signy Island. Here, moss cover may reach 100% in small stands of vegetation supporting several species not recorded on the prevalent acidic substrata (Smith, 1972).

The remaining associations within the short moss turf and cushion subformation are all characteristic of particularly arid habitats or, in the case of the *Pohlia austrogeorgica* association, occur as temporary colonizers of unstable soils. Those communities dominated by species of *Bryum* or *Sarcocaulum* (Table 5.4) occur primarily in continental Antarctica, while the *Ceratodon* and *Pohlia nutans* associations are well represented on porous, volcanic substrata in the maritime Antarctic, notably on Deception Island, South Shetland Islands, and on the South

Sandwich Islands. For example, volcanic ash and scoria on level ground and gentle slopes on Candlemas Island support extensive turfs of *Pohlia nutans*, which form a crust c. 1 cm deep. Much of the moss is moribund and colonized by a species of *Lepraria* and other crustose lichens, which may be so frequent as to give the vegetation a whitish-green colour when viewed from a distance. The *Pohlia nutans*-*Lepraria* socrition comprises species-poor, short, open turfs of *Polytrichum* spp., only 1-2 cm high and frequently intermixed with *Pohlia nutans*, being the principal associates.

Short turf- and small cushion-forming mosses are also characteristic of rock crevices, together with mats of both mosses and hepatics. On Signy Island, crevices on acidic and on base-rich rocks usually support mosses characteristic of the *Andreea* and *Tortula-Grimmia* associations respectively, while additional bryophytes include species of *Barrania*, *Dicranoweisia*, *Isopterygium*, *Plagiothecium*, *Barbilophozia*, *Metzgeria* and *Pachygloussa* on siliceous rocks, and of *Amblystegia*, *Barbula*, *Diurnodon*, *Pseudoleskea* and *Sarcocaulum* under base-rich conditions (Smith, 1972). These communities have not yet been formally grouped into sociations and associations.

5.3.4 Tall moss turf subformation

The tall moss turf subformation (Table 5.4) is characteristic of mesic substrata, often on gentle to moderately steep rocky slopes. Of particular interest are communities in the *Polytrichum alpestre*-*Chorisodontium actinophyllum* association which form raised banks commonly overlying 1-2 m of ombrogenous peat, and extending continuously for as much as 50 m. The surface of the banks is hummocky or undulating, and the underlying peat shows permafrost below 20-30 cm. Uptake of water from melting ice above the permafrost layer is considered important in irrigating the shoot apices. *C. actinophyllum* prefers wetter conditions than *P. alpestre*, and is often dominant in shallow banks on level ground, while on the drier slopes either species may occur singly or in mixed turf. Lichen encrustation is widespread on the higher, more windswept parts of the banks.

Smith (1979) has pointed out that peat in the *Polytrichum-Chorisodontium* banks is unusual in being largely unhumified, and in developing under conditions that are neither waterlogged nor anaerobic. He attributes its formation to permafrost, and to slow decomposition in the active layer due to a very low pH and an unusually poor microbial flora. Decomposition of material above the permafrost has been estimated as only 2% per year (Baker, 1972). The growth of *P. alpestre* in the Antarctic and elsewhere is compared by Longton (1974b, 1979b).

Polytrichum alpinum is a frequent component of many vegetation types in the maritime Antarctic, but only locally becomes dominant. In particular, the *P. alpinum* association replaces the *P. alpestre*-

Chorisodontium aciphyllum association on recent volcanic substrate on the South Sandwich Islands and on many of the South Shetland Islands. On these loose-textured soils *P. alpinum* forms circular colonies up to 1 m in diameter and 20–30 cm in height, but deep peat deposits do not occur. *Polytrichum piliferum*, *Chorisodontium aciphyllum*, a tall form of *Pohlia nutans* and mats of *Drepanocladus uncinatus* have all been recorded as codominant with *Polytrichum alpinum*. Several species of *Campylopus* may be abundant in stands of the *Campylopus* association, but this vegetation type is confined to the vicinity of fumaroles on the South Sandwich Islands.

5.3.5 Bryophyte carpet and mat subformation

Bryophyte carpets have so far been recorded widely only in the maritime Antarctic. They comprise pleurocarpous mosses, or less commonly leafy hepatics, occurring as closely packed, almost parallel, erect shoots connected to a basal prostrate layer of partially denuded stems (Gunningham and Smith, 1970; Longton, 1967). Some species typically form carpets in wet habitats, and mats under drier conditions. Communities in the *Calliergidium austro-stramineum* – *Calliergon sarnentosum* – *Drepanocladus uncinatus* association are widespread, and may cover extensive areas in permanently moist or wet habitats on level or gently sloping ground at low altitudes, particularly on seepage slopes receiving meltwater throughout the summer. The carpet-forming mosses commonly occur in continuous stands overlying soligenous peat up to 15 cm deep. Other life-forms are seldom abundant, although mats of *Cephalozia varia* may occur on the surface of the mosses. Lichens are rare except for crustose species on stones. A striking feature of many moss carpets are 'fairy rings' up to 20 cm in diameter composed of white, moribund shoots, associated with fungal infection (Longton, 1973b).

Carpets of an unidentified species of *Brachythecium* occur in similar habitats on the South Sandwich Islands, where the fumaroles support a range of hepatic-dominated communities also placed in the bryophyte carpet and mat subformation (Longton and Holdgate, 1979). Luxuriant carpets of *Cypriochila grandiflora*, and locally of *Triandrophyllum subrifidum*, occupy finely divided ash and scoria around many of the fumarole vents. Tall turfs of *Pohlia nutans* and species of *Campylopus* are frequent associates, while crustose lichens are abundant on projecting stones. Shallow, compact mats of *Cephalozia badia* were recorded around a single fumarole. Conversely, a species of *Marchantia* is widespread in the fumarole vegetation, and becomes abundant locally both there, and at well insulated sites in the South Orkney Islands not influenced by current volcanic heat and moisture.

5.3.6 Moss hummock subformation

The margins of melt water streams, wet rock ledges subjected to dripping water, and other flushed sites in contact with moving water form the typical habitat for the remaining major terrestrial bryophyte vegetation type, the moss hummock subformation (Table 5.4). The life-forms represented have been described by Smith (1972) as 'a tall compact cushion (*Bryum algens*), a tall loose cushion (*Brachythecium austro-salebrosum*), or a deep undulating carpet (*Drepanocladus uncinatus*)'. The large cushions may attain heights of 20 cm, and frequently coalesce to form a closed, hummocky stand. Communities in the moss hummock subformation are widely distributed, but are seldom extensive, and may intergrade with those dominated by carpet-forming mosses as distance from flowing water increases.

5.3.7 Pattern and succession

Cryptogamic vegetation is extensive at favourable locations in the maritime Antarctic, as indicated in Table 5.5 for Signy Island, which has an area of 17 km² and a maximum elevation of 281 m. It can be seen that 30% of the land surface is exposed from snow and ice in summer. Some 13% supports closed bryophyte vegetation, principally in the tall moss turf, and bryophyte carpet and mat subformations. Additional closed vegetation occurs within the short moss turf and cushion subformation, and less than 26% of the exposed land surface lacks either open or closed macroscopic plant cover. Table 5.5 also emphasizes the limited role of phanerogams.

The relationships between topography and life-form of the dominant cryptogams are indicated in outline in Fig. 5.3, which represents diagrammatically the distribution of major vegetation types across an idealized, well-vegetated valley. Carpet-forming mosses cover large areas on the lower slopes and valley floor, particularly in areas below late snow beds, with large cushion mosses occurring locally by streams. Mesic, often steeper, rocky slopes support banks of tall turf-forming acrocarps, while short moss turfs and small cushions occur principally on more exposed, elevated slopes of sand, gravel and scree. Lichen communities occupy boulders, cliffs and even more windswept slopes of scree and gravel, with crustose lichens particularly prominent on coastal cliffs. The highest, most exposed cliffs and scree slopes are largely devoid of vegetation.

A more detailed discussion of pattern within and between bryophyte communities on Signy Island has been presented by Smith (1972) who recognized four major types, namely environmental, zonal, morphological and sociological pattern. Of these, environmental pattern is the most widespread. It develops in response to interacting, and sometimes intersecting gradients in several environmental factors, and results in a

Table 5.5 Extent of major vegetation types on Signy Island, South Orkney Island (Data from Tibbrot, 1970).

	Area occupied (km ²)	% total snow-free surface
Crustaceous lichen subformation or bare ground	4.25	26
Fruiteose and foliose lichen and short moss turf and cushion subformations		
Cover > 50%	3.5	21
Cover < 50%	5.0	30
Tall moss turf subformation	1.0	6
Bryophyte carpet and mat and moss hummock subformations		
Cover > 50%	1.25	7.5
Cover < 50%	0.75	4.5
Grass and cushion chamaephyte subformation	0.0001	< 0.001
Biologically formed organic soil	0.65	4.0
Penguin nests and seal wallows	0.1	0.6
Other bird nests	0.0005	< 0.005

mosaic of communities in which different cryptogams assume dominance. An example discussed by Smith occurs on low knolls in coastal districts (Fig. 5.4). The thin mantle of sandy and gravelly soil on the windswept summits of the knolls supports a sociation dominated by the fruiteose lichen *Usnea antarctica*. In more sheltered locations below the summit, subject to shallow snow accumulation in winter, this gives way to a community dominated by other lichens and *Andreaea depressinervis*, while slopes receiving deeper snow accumulation, and moist level ground at the foot of the knoll, support stands of *Drepanocladus uncinatus* and *Polytrichum alpinum*. The gradual nature of the transition between the three communities, and the wide ecological amplitude of certain of the species, is emphasized in Fig. 5.4, though the mosaic of communities associated with environmental pattern is not well illustrated by the transect data.

Less complex, zonal patterns of plant distribution in response to environmental gradients are not frequent on Signy Island, and are best exemplified by coastal lichen communities. However, clear zonal patterns are associated with the gradients of temperature and moisture around fumaroles on the South Sandwich Islands (Longton and Holdgate, 1979), which give rise to concentric distributions of plant communities. An example is described in Table 5.6.

Morphological pattern is associated with the life-form of individual species and is commonly exhibited only by species of *Polytrichum*, notably

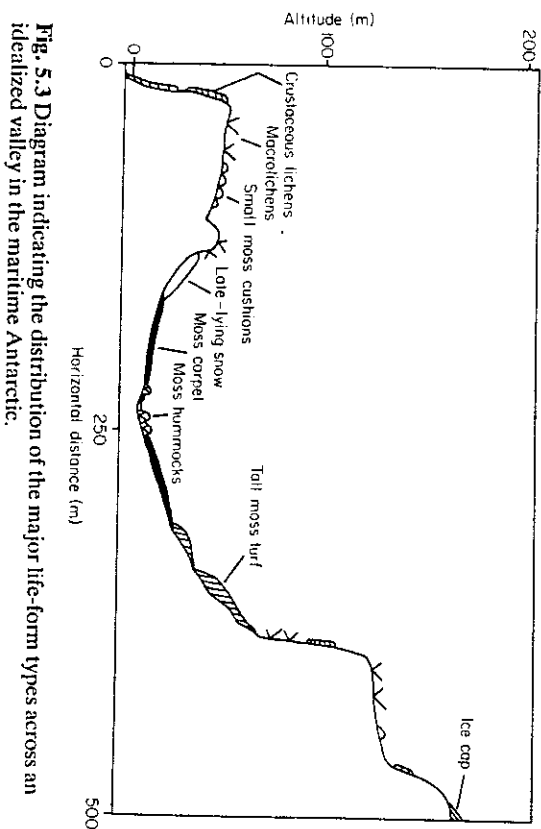


Fig. 5.3 Diagram indicating the distribution of the major life-form types across an idealized valley in the maritime Antarctic.

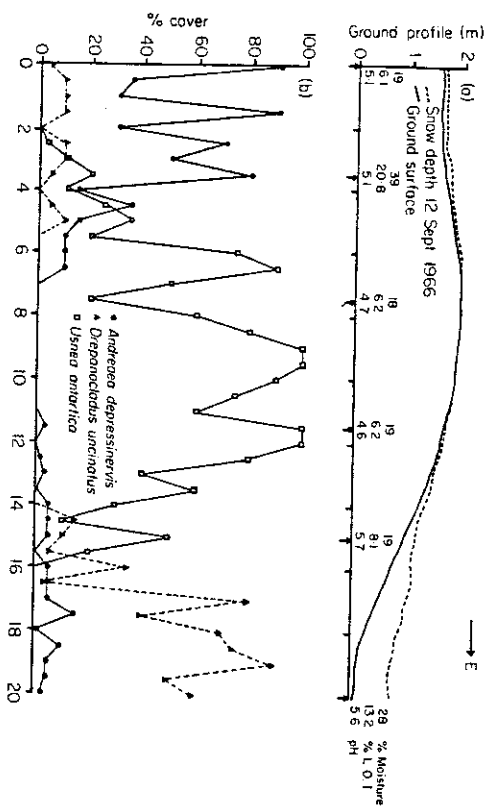


Fig. 5.4 Relationships between ground profile, soil data and winter snow cover (a) and % cover of the principal species (b) along a transect across a low knoll on Signy Island, South Orkney Islands. Arrows indicate positions where soil data were obtained. L.O.I. is loss on ignition. Redrawn from Smith (1972).

Table 5.6 Zonation of vegetation around a fumarole on Bellingshausen Island, South Sandwich Islands. (From Longton and Holdgate, 1979.)

Zone	Approximate distance from vents	Dominant species	Notes
1	0–30 cm	Algae and a small dicranoid moss	Glistening areas of algae, together with abundant turfs of a small dicranoid moss, scattered stems of <i>Bryum sp.</i> and taller turfs of <i>Campylopus spiralis</i> .
2	30–150 cm	<i>Campylopus spiralis</i>	Turfs of <i>Campylopus spiralis</i> dominant. <i>Cryptochila grandiflora</i> and <i>Marchantia berteriana</i> frequent. <i>Polytrichum alpinum</i> and <i>Pohlia nutans</i> recorded as associates.
3	150–270 cm	<i>Cryptochila grandiflora</i>	<i>Cryptochila grandiflora</i> increased in frequency to form a luxuriant, closed, bright orange stand. <i>Campylopus spiralis</i> and <i>Marchantia berteriana</i> abundant in central areas, dying out further from the vent, where <i>Psilopilum antarcticum</i> recorded as an associate. Basidiomycete fruiting bodies scattered throughout.
4	270–390 cm	<i>Cryptochila grandiflora</i> and mosses	<i>Cryptochila grandiflora</i> became drier and dark reddish brown in colour, being interspersed with large areas of <i>Racomitrium crispulum</i> and other mosses including <i>Drepanocladus uncinatus</i> and <i>Pohlia nutans</i> . Basidiomycetes persisted.
5	390–570 cm	<i>Cryptochila grandiflora</i> and <i>Usnea antarctica</i>	<i>Cryptochila grandiflora</i> very dark brown and dry, forming an open community with <i>Usnea antarctica</i> . <i>Psilopilum antarcticum</i> frequent. <i>Polytrichum alpinum</i> and <i>Racomitrium crispulum</i> recorded as associates.
6	> 570 cm	<i>Usnea antarctica</i>	Abundant <i>Usnea antarctica</i> on bare stones, with less common cushions and turfs of <i>Dicranoweisia sp.</i> , <i>Pohlia nutans</i> and <i>Polytrichum alpinum</i> as well as small mats of <i>Lophocolea secundifolia</i> and <i>Cephaloziella sp.</i>

Temperature readings 2.5 cm deep in the vegetation on a cloudy day in late summer ranged from 38°C at the junction between zones 1 and 2 to 7°C in zone 6.

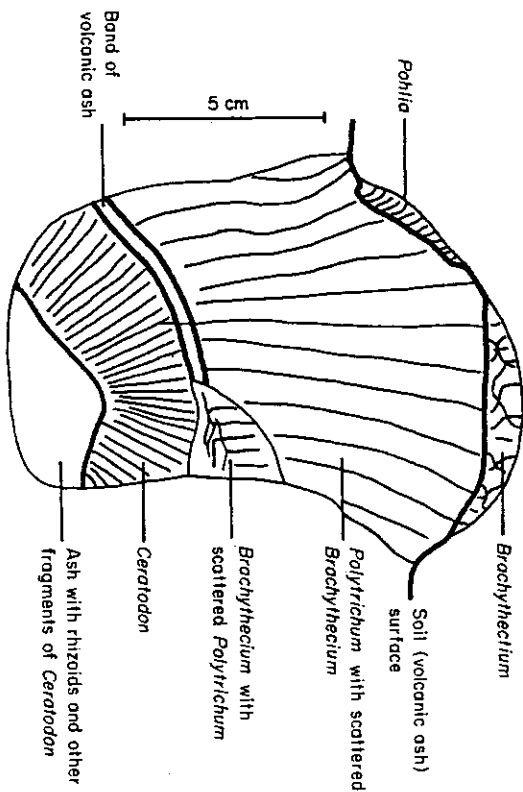


Fig. 5.5 Diagram of a circular colony of *Polytrichum alpinum* on Signy Island, South Orkney Islands, exhibiting morphological pattern. Redrawn from Smith (1972). (a) Area outside *Polytrichum* colony; (b) Scattered young shoots of *Polytrichum* arising from rhizomes; (c) Living, green *Polytrichum* 1–5 cm tall; (d) Dying, brown *Polytrichum*; (e) Moribund, black *Polytrichum*; (f) Thin layer of decaying *Polytrichum* peat colonized by bryophytes and lichens; (g) Peaty soil with occasional bryophytes, often heavily encrusted with lichens.

Fig. 5.6 Profile from a stand of the *Polytrichum alpinum* socrasion on Candlemas Island, South Sandwich Islands. Redrawn from Longton and Holdgate (1979).

P. alpinum. On level ground, *P. alpinum* tends to form circular stands which gradually expand as underground rhizomes grow outwards from the periphery and give rise to aerial shoots. Translocation of photosynthate from older shoots along rhizomes to young growing points has been demonstrated in Arctic *P. alpinum* (Collins and Oechel, 1974). On Signy Island individual colonies may reach 1 m or more in diameter but peripheral expansion of the larger examples is usually accompanied by progressive death of plants from the centre outwards followed by colonization of the decaying *Polytrichum* remains by other species (Fig. 5.5). In some cases *P. alpinum* may eventually re-invade the central region so that a cyclic succession is established.

A somewhat different pattern of cyclic succession involving *P. alpinum* was demonstrated on a slope of volcanic ash on Candlemas Island by observations on the living vegetation combined with analysis of the shallow peat deposits beneath (Longton and Holdgate, 1979). Here, *P. alpinum* forms large hummocky turfs up to 15 cm in diameter, associated with similar turfs of *Pohlia nutans* and mats of *Brachythecium* and *Drepanocladus* spp. The larger turfs are subject to lichen encrustation and ultimately to severe wind erosion which leaves areas of bare mineral soil. A cushion-forming species of *Ceratodon* is the principal colonizer of the bare areas, and shoots of *P. alpinum* are common in the larger cushions. The peat profiles suggest that re-establishment of *P. alpinum* frequently occurs in areas initially invaded by *Ceratodon* (Fig. 5.6).

Sociological pattern as understood by Smith (1972) arises as a result of successional processes involving the invasion of one community by species characteristic of a second. An example is provided by the banks of *Chorisodontium aciphyllum* and *Polytrichum alpestre*, whose development has been discussed by Collins (1976) and Smith (1972, 1979). It was suggested that the banks may be initiated either through colonization by *P. alpestre* of cushion-forming mosses on slopes, or by *C. aciphyllum* invading carpet-forming mosses on moist level ground followed by the establishment of *P. alpestre* on the higher, relatively dry areas of the *Chorisodontium* turfs. Eventually, peat formation results in the upper parts of the banks being blown clear of snow in winter, thus initiating cyclic succession involving the mosses and epiphytic lichens, which become established following erosion of the surface layer of moss.

Sociological pattern of the type occurring where *P. alpestre* and *C. aciphyllum* are actively invading communities dominated by other mosses appears to be surprisingly uncommon in Antarctic vegetation. Smith (1972) noted that the cryptogamic communities on Signy Island are seldom affected by competition from adjacent communities, and that once established, most appear to be climax units showing little evidence of seral succession. This view is supported by radiocarbon dates ranging from

several hundred to 5000 years for the base of *Polytrichum-Chorisodontium* banks (Smith, 1979). Similarly, analysis of peat profiles beneath the living vegetation on Candlemas Island suggested that all the major bryophyte community types had developed independently of each other. Thus there is some evidence that succession in Antarctic cryptogamic vegetation may be primarily cyclic rather than directional (Longton and Holdgate, 1979).

5.4 BRYOPHYTE VEGETATION ON CONTINENTAL ANTARCTICA

Vegetation in continental Antarctica contrasts strongly with that in the maritime Antarctic in its sparsity, and in the restricted diversity of bryophyte species and life-form types. Bare rock, scree and gravel predominate in unglaciated areas. Crustose, fruticose and foliose lichens are all locally abundant. Bryophyte vegetation is restricted to the short moss turf and cushion subformation, which occurs most extensively on sandy and gravelly soils and is seldom well developed on rock. Perhaps surprisingly, the range of algal communities is wider than in the maritime Antarctic, particularly in semi-terrestrial vegetation in and beside melt water streams. It is possible that low temperatures prevent the growth of carpet and hummock-forming mosses and that algae flourish due to reduced competition from bryophytes. Vegetation is best developed at localized coastal sites but mosses, lichens, algae and also micro-organisms and invertebrates occur on inland nunataks as far as 84°S to 87°S (Cameron *et al.*, 1971; Janetschek, 1970; Wise and Gressitt, 1965).

The dominant mosses may vary between sites. Thus communities in the *Bryum antarcticum-B. argenteum* and *Sarcocnurum* associations have been reported from Cape Hallett (Rudolph, 1963) and McMurdo Station (Longton, 1973a) in southern Victoria Land (Fig. 5.2), while the *Bryum incomplexum* and *Ceratodon* associations are represented at Swoya Station on East Ongul Island (Matsuda, 1968; Nakanishi, 1977). The moss communities recently reported from Mawson Station (Seppelt and Ashton, 1978) are dominated by *Bryum algens*, and thus recognition of a *B. algens* association, additional to those listed in Table 5.3, may become necessary. It is possible, however, that the apparent diversity of *Bryum*-dominated vegetation results in part from differences in taxonomic interpretation.

Variation in community structure is also evident. At McMurdo Station *Bryum argenteum* and *Sarcocnurum glaciale* typically form widely scattered short, compact turfs nesting among stones or with their surfaces flush with the surrounding substrate. Other species form small cushions which may give continuous cover over several square metres in particularly favourable sites. At Swoya Station the moss vegetation reaches 5–9 cm in

depth, and Matsuda (1968) has estimated the age of the larger *Bryum incomexum* cushions as c. 100 years on the basis of rhizoid banding. Development of the moss cover at Mawson begins with small cushions, less than 1 cm in diameter, which in some cases have living shoots all over the surface and are blown around by the wind (Seppelt and Ashton, 1978). Larger colonies become sedentary and anchored to the ground by rhizoids. Complex vegetation may be built up by coalescence of the cushions and by young colonies growing over older ones, often of the same species. The older cushions become convoluted and longitudinal sections reveal cores of sand, gravel and small stones, features attributed by Seppelt and Ashton to differential frost action resulting from the relatively high water content of the moss cushions and the substrate immediately below. Cushions with similar mineral cores, and others with hollow centres, have been observed in strands of *Bryum* and *Ceratodon* spp. on Deception Island in the maritime Antarctic, and again attributed to frost action (Longton, 1967). The older colonies of many mosses in continental Antarctica become colonized by lichens or more locally (Matsuda, 1968) by algae.

5.5 BRYOPHYTE VEGETATION IN THE SUB-ANTARCTIC

The sub-Antarctic as understood here (Fig. 5.2) comprises a series of isolated islands characterized by rugged terrain and a cool, oceanic climate (Table 5.1). Descriptions of the vegetation have been provided for Macquarie Island (Taylor, 1955), Marion and Prince Edward Islands (Huntley, 1971) and South Georgia (Greene, 1964b) and these, combined with the author's observations on South Georgia, form the basis of the present account.

Tall turf-forming mosses predominate in the bryophyte stratum of most planerogamic vegetation at low altitudes, at least on South Georgia. The extensive wetlands support communities dominated by graminoids, which physiognomically resemble comparable Arctic vegetation. On South Georgia, *Calliergon sarmmentosum*, *Drepanocladus uncinatus* and *Tortula robusta* are abundant in the continuous bryophyte understorey in large areas of mire dominated by the sedge *Rostkovia magellanica*. Stands of *Sphagnum fimbriatum* up to 20 m in diameter are locally frequent in *Rostkovia* mire, while conspicuous, circular colonies of *Philonotis acicularis* are interspersed among other mosses at some flushed sites. Comparable communities, although without *Sphagnum*, occur on the other islands and wetland vegetation may comprise principally bryophytes with only scattered vascular plants. For example, on Marion and Prince Edward Islands, some flushes support an assemblage of mosses dominated

by *Breweria integrifolia* and *Bryum laevigata*, while the leafy hepatic *Blepharidophyllum densifolium* assumes dominance in lowland bogs.

Mesic sites in the lowlands support grassland and herbfield, the most conspicuous component of the latter being large forbs such as *Conium plamosa* or suffrutescent perennials in the genus *Acaena*. The vascular plants reach heights up to 25 cm. Herbfields are to some extent the counterpart of heaths, from which they differ principally in the absence of ericoid shrubs. Heaths occur in the southern temperate zone but not in the sub-Antarctic. The most widespread mesic communities on South Georgia form an intergrading series ranging from swards of *Acaena magellanica* through mixed stands in which *A. magellanica* and the caespitose grass *Festuca contracta* are both abundant to areas of *Festuca* grassland. Stands of *A. magellanica* occur principally on steep scree slopes, and the creeping, woody stems are usually embedded in a closed turf of *Tortula robusta*. On more gently sloping ground, where *F. contracta* is abundant, *T. robusta* is largely replaced by other large acrocarps, particularly *Polytrichum alpinum*: other prominent mosses include *Chorisodontium aciphyllum*, *Conostomum australe* and *Psilopitium trichodon*. The bryophyte layer in *Festuca* grassland is generally discontinuous, as the mosses are interspersed among macrolichens, notably *Cladonia* spp., and areas of bare ground.

It is noteworthy that the association of *Acaena magellanica* and *Tortula robusta* on South Georgia may be found both on scree slopes and in wet flushes. Similarly, Huntley (1971) records *A. magellanica* as dominant in flushes and in some mesic sites on Marion and Prince Edward Islands, with *Drepanocladus uncinatus* and *Rhynchostigium brachyperygium* the principal bryophyte associates in both cases.

Tussock grassland dominated by species of *Poa* is a distinctive feature of coastal sites in south temperate and sub-Antarctic regions, where it may form an almost continuous zone along shorelines, and ascend to at least 750 m altitude on cliffs subjected to wind-blown spray. *Poa flabellata* is the principal component on South Georgia where it forms tussocks reaching 1.0 m in diameter and 1.5 m in height, each comprising a stool bearing a dense crown of leaves. Tall turf-forming mosses, particularly *Chorisodontium aciphyllum*, *Polytrichum alpestre* and *P. alpinum*, are abundant in the more open stands. *P. alpestre* locally forms extensive banks resembling those in the maritime Antarctic, particularly where *Poa flabellata* has been overgrazed by introduced herbivores.

A wider range of bryophyte life-form types is represented in essentially cryptogamic communities of rock and scree, which predominate in South Georgian vegetation at elevations above 250 m. Here, the exposed mineral soils support open fellfields in which short turfs, small cushions and mats formed by species of *Andraea*, *Dicranoweisia*, *Grimmia*, *Polytrichum* and

Racomitrium are prominent, in association with lichens and scattered vascular plants. Small cushion-forming mosses, including species of *Andreaea*, *Bindia* and *Dicranoweisia* are widespread on rock faces, while sheltered crevices and ledges support a further range of cushions, turfs and mats. Genera represented here include *Barrania*, *Brachythecium*, *Dicranum*, *Distichum*, *Drepanocladus*, *Pohlia*, *Polytrichum* and *Racomitrium*.

Concerning vascular plants, the South Georgian felfields frequently support small cushions of *Colobanhus guttensis* but lack the large compact cushions of *Azorella selago* which are a conspicuous feature of comparable vegetation on some of the other islands. On Macquarie, Marion and Prince Edward Islands, individual cushions of *A. selago* may exceed 50 cm in diameter and they frequently support epiphytic mats of *Racomitrium*, *lanuginosum* and cushions of *Dirichium strictum*. The latter is dominant in the more exposed felfields on these islands, where its cushions may become dislodged by the wind and develop as spherical, mobile 'moss balls' up to 8 cm in diameter. This process, and successional relationships in the felfield communities, have been discussed by Ashton and Gill (1965), Handley (1971) and Seppelt and Ashton (1978).

Finally, it may be noted that, as in other areas, particularly rich and luxuriant bryophyte assemblages are to be found on sub-Antarctic islands on rocks in the spray zone of waterfalls and in other permanently wet habitats.

5.6 BENTHIC COMMUNITIES

Attention should also be drawn to the bryophyte communities occurring submerged at depths up to 10 m in polar lakes. Such vegetation appears to be widespread in both Arctic and Antarctic regions (Light and Heywood, 1973, 1975; Mårtensson, 1956; Persson, 1942; Welch and Kalf, 1974), particularly under oligotrophic conditions where little incoming radiation is absorbed by phytoplankton (Priddle, 1980a, b). Individual moss stems may reach 40 cm in length in these benthic communities, whose luxuriance in continental Antarctica contrasts strongly with the sparsity of the terrestrial vegetation (Light and Heywood, 1975). Genera recorded submerged in polar lakes include *Bryum*, *Calliergon*, *Campyllum*, *Dicranella*, *Distichum*, *Drepanocladus*, *Fornitulis* and *Marsupella*. In several cases, the submerged plants showed larger leaves and longer internodes than terrestrial material of the same species (Priddle, 1979). A detailed study of benthic bryophytes on Siny Island has shown that positive net photosynthesis occurs during all except the three darkest months of the year, although the lake surfaces are frozen for 8–12 months annually. It was confirmed that the mosses have unusually low light

compensation points, and an estimate of 40 g m⁻² was obtained for net annual production in closed stands (Priddle, 1980a, b). This relatively low figure suggests that the luxuriance of some benthic communities may result from stability rather than rapid growth.

5.7 ENVIRONMENTAL RELATIONSHIPS OF POLAR BRYOPHYTE VEGETATION

5.7.1 Temperature

One of the most striking conclusions to be drawn from recent biological investigations in the Arctic and Antarctic is that polar environments are diverse in the extreme, and that generalizations concerning environmental relationships of polar biota should therefore be undertaken with caution. The regions considered here include some having mean temperatures in mid summer around 10°C and freely available water in many habitats, others where mean summer temperatures remain below 3°C with water again freely available, and yet others which experience extremes of both cold and aridity. Differences in these and other climatic, edaphic and biotic variables are reflected in the diversity of tundra vegetation.

The influence of environment on the distribution of plant life-forms has long been recognized. Thus, the timber-line marking the southern boundary of the Arctic as understood here corresponds closely with the mean summer position of Arctic frontal systems (Bryson, 1966), and is no doubt determined largely by the contrast in summer climate to the north and to the south of the fronts. Of the various factors involved, low summer temperature has traditionally been regarded as the most significant. Similarly, low summer temperature is thought to be the most important single factor determining the essentially cryptogamic facies of Antarctic vegetation. This is due to the relatively mild winters, the free availability of water and mineral nutrients in many maritime Antarctic habitats, the restriction of the two native phanerogams to sheltered, well-insolated sites, and the poor performance of vascular plants in experimental introductions to the Antarctic (Edwards, 1979; Longton, 1979a; Longton and Holdgate, 1967).

That temperature is important in restricting the number of species able to colonize polar regions is also demonstrated by the floras of sites influenced by geothermal heat. Many hot springs on Iceland and Greenland are surrounded by concentrically zoned vegetation comparable with that around fumaroles on the South Sandwich Islands (Table 5.6), and support a wide range of mosses and hepatics not recorded elsewhere on these islands (Halliday *et al.*, 1974; Hesselbo, 1918; Lange, 1973). On the South Sandwich Islands, also, 19 bryophytes have been recorded only from

the fumaroles. Several, including *Campylopus* spp. and *Cryptochila grandiflora* (Table 5.6), are locally abundant at these highly localized sites of volcanic heat and moisture but are unknown elsewhere in the Antarctic zone. Summer temperature again appears to be a key factor (Longton and Holdgate, 1979).

The influence of temperature on bryophyte distribution within the polar regions is difficult to assess, since temperature seldom varies in isolation from other factors. Thus, increasing latitude is generally accompanied by decreases in both temperature and water availability. It may be noted, however, that some arid sites in northern Ellesmere Island have, for their latitude, both unusually warm summers and rich floras of vascular plants and of bryophytes (Brassard, 1971b; Savile, 1964). Concerning aspect, the luxuriant banks of tall turf-forming mosses in the maritime Antarctic are characteristic of north- and north-west facing slopes which benefit most strongly from radiant heating. Similarly, Steere (1978b) notes a contrast between the floras of some north- and south-facing slopes in Alaska, the former comprising principally of Arctic mosses, while the latter includes many species of temperate affinity. Again, however, the drier nature of the south- compared with the north-facing slopes make interpretation difficult.

Bryophyte microclimates throughout the polar regions are more favourable for plant growth and survival than indicated by the air temperature data in Table 5.1. Relationships between summer temperatures and carbon assimilation in mosses are explored in Collins (1977), Longton (1974a) and Oechel and Sveinbjörnsson (1978).

5.7.2 Life-form and water relations

Among bryophytes, it is clear that relatively compact turfs, mats and small cushions predominate in polar regions, with carpets also widespread in the Antarctic. The looser life-forms described by Gimingham and Birse (1957) from temperate regions, notably the welt and the canopy (Table 5.2), are of local occurrence only in the low Arctic. The latter types are typical of sheltered, humid habitats under trees and shrubs, and would hardly be expected to prosper under open, windswept polar conditions, especially as welts have few anchoring rhizoids and are easily disrupted by wind. Schofield (1972) noted that species such as *Hylacomium splendens*, which form welts in boreal forest regions, normally occur as mats in the Arctic, where many other pleurocarps occur as tall turfs. Among species assuming the latter life-form, the pleurocarps can best be described as 'tall turfs branches erect', and the acrocarps and *Sphagnum* spp. as 'tall turfs, divergent branches' (Table 5.2).

Habitat relationships of the life-form types have been better documented in the Antarctic than in the Arctic, but several parallels between the two regions may be drawn, and it is clear that water avail-

ability is of utmost importance in determining distribution patterns in each case. Thus small, compact cushions and short turfs predominate in particularly dry, exposed habitats, both on rocks and on soil. These are the major bryophyte life-forms in continental Antarctica and in the Arctic polar desert, being locally abundant also on porous, volcanic substrata in areas of higher precipitation in Iceland and in the maritime Antarctic. In addition, they are among the most frequent pioneers in successional sequences on moraines and disturbed ground.

Small acrocarpous mosses are also well represented in some mesic habitats in the Arctic, in which mats and tall turf-forming acrocarps are also abundant. The latter predominate under similar conditions in the Antarctic, where mats are less common than might be expected. Tall turf-forming mosses, particularly pleurocarps and *Sphagnum*, form a high proportion of the bryophyte stratum beneath the graminoids of wetland communities in the low Arctic and on South Georgia. Carpet-forming mosses largely replace the turfs on seepage slopes in the maritime Antarctic. The family Amblystegiaceae is well represented in both types of habitat, and a careful comparison of these carpet and turf-forming pleurocarps would be of interest. It is possible that the carpet form (p. 144) results in part from the pressure of winter snow on essentially erect-growing but weak-stemmed mosses lacking protection and support from vascular plants. Finally, it is of interest that large, loose cushions appear to be characteristic of stream banks and other sites influenced by flowing water in both northern and southern polar regions, while the contribution of hepatics to the vegetation cover is disproportionately low in relation to the numbers of species recorded.

Aggregation of bryophyte shoots into colonies may substantially enhance capillary uptake and retention of externally held water, and thus indirectly affect the internal water content of the plants. By comparing rates of water uptake and loss in individual shoots and in portions of intact colonies representing several common mosses on Signy Island, Gimingham and Smith (1971) were able to demonstrate that the most widespread life-form types differ in their degree of influence on water relations in a manner corresponding with their habitat preferences. Thus, small compact cushions from dry habitats showed the greatest effect of life-form in reducing evaporation rates, and also possessed a marked ability to hydrate rapidly when provided with water either at the base or at the upper surface. These effects were least marked in the case of carpets and large cushions from wet habitats. Anomalous results were given by *Polytrichum alpinum*, which extends into dry habitats despite forming tall, loose turfs with a relatively weak capacity for retaining external water. This may be attributable to the partially endohydric nature of *P. alpinum* which, compared with ectohydric species, may have greater access to soil water and

higher internal resistance to water loss due to cuticularization and ability to fold leaf margins over lamellae and leaves against stems in dry conditions.

Mosses of wet meadows in the low Arctic may benefit from close to optimal conditions of hydration throughout the summer, as a result both of precipitation and freely available ground water (Oechel and Sveinbjörnsson, 1978; Vitt and Pakarinen, 1977), and the same may apply in many habitats in the sub-Antarctic and maritime Antarctic (Collins, 1977). In contrast, the scattered mosses of the polar deserts are largely dependent upon melt water derived from ground ice and late-lying winter snow. Under the arid conditions prevailing in these areas it is doubtful whether resistance to the loss of externally held water as a result of compact life-form is sufficient to prevent periodic desiccation of the predominantly ectohydric mosses, which have little resistance to the loss of internal water. Bryophytes are generally regarded as poikilohydrous, however, with an ability to withstand a considerable degree of cytoplasmic dehydration (Hinschri and Proctor, 1971). The adaptive value of compact growth forms may thus principally lie in extending periods when the plants are sufficiently hydrated to achieve significant rates of net photosynthesis in habitats with a low and intermittent supply of water.

5.7.3 Light

Polar bryophytes appear to be well adapted to the prevailing summer conditions of long days or continuous illumination at relatively low intensities as the light intensities required for compensation and saturation of net photosynthesis are depressed at low temperatures (Longton, 1974a; Oechel and Sveinbjörnsson, 1978). Field experiments have confirmed that positive net assimilation is sustained for 24 h per day in some Alaskan mosses under favourable conditions in early summer (June) when the lightest 'nights' occur (Oechel and Collins, 1973). Maximum light intensities during summer may have an inhibitory effect on photosynthesis in some Alaskan mosses (Oechel and Sveinbjörnsson, 1978), and direct insolation may lower chlorophyll content and alter the chlorophyll *a:b* ratio in *Bryum antarcticum* in southern Victoria Land (Rastorfer, 1970). Otherwise, there is little evidence that either continuous illumination in summer, or lack of shade from vascular plants, have seriously deleterious effects on polar bryophytes. Kallio and Valanne (1975) have shown that rates of photosynthesis in temperate and boreal forest bryophytes may be reduced by cultivation in continuous light as compared with alternating light and darkness, due to reduction in chlorophyll content and to ultrastructural modifications. However, these effects were not well marked in the Arctic moss *Dicranum elongatum*. In *Racomitrium lanuginosum*, Arctic and temperate strains showed contrasting responses suggestive of ecotypic adaptation to polar conditions in the former. Both

Arctic and boreal forest populations of *Pleurozium schreberi* showed reduced net photosynthesis after cultivation in continuous light, however, and this could be one factor responsible for the restricted distribution of *P. schreberi*, and possibly other mosses, in the Arctic.

5.7.4 Wind and snow

The effects of wind and snow on polar vegetation are powerful, and they may be inter-related as wind largely controls the distribution of snow cover. Wind is important through its cooling and desiccating effects. It also acts as an agent of erosion, particularly in winter when particles of sand and hard snow driven by strong winds can cause severe abrasion of frozen vegetation. Even thin snow cover gives protection from these effects, while deeper snow provides insulation from minimum temperatures and repeated freezing and thawing (Longton, 1979b; Matsuda, 1968). Thus many polar bryophyte communities are characteristic of habitats protected by winter snow (Smith, 1972), but conversely bryophyte vegetation decreases with winter snow cover in some areas (Holmen, 1955). Late-lying snow banks are of great importance in providing moisture for surrounding vegetation in summer although unusually prolonged snow may damage the plants below. Light summer snowfall accumulating in sheltered hollows may also be significant in the water relations of mosses in arid regions.

Effects of wind and snow on bryophyte distribution patterns are most evident in the high Arctic and in continental Antarctica, where snow cover is discontinuous in winter, and water of extreme scarcity. Thus, the scattered short turf- and cushion-forming mosses of the latter region have, at several stations, been reported principally from the vicinity of late-lying snow on lee slopes (Seppelt and Ashton, 1978). The important influence of wind and snow on moss distribution is indicated by the observation that near Swoya Station (Fig. 5.2), where the winds are predominantly from the north-east, the mosses are most frequent on south-west-facing slopes (Matsuda, 1968), despite the more favourable summer temperature regime that may be expected under conditions of stronger insolation on slopes of northerly aspect.

5.7.5 Edaphic and biotic factors

While the distribution of bryophyte life-form types appears to be controlled largely by water relations, habitat preferences at the level of genera and species are strongly influenced by pH and other chemical features of the substrate. Many bryophytes show a strong affinity for either acidic or base-rich conditions, for reasons discussed in Longton (1980). The preferences of the *Andreadea* and the *Tortula-Grinnia* associations of the short moss turf and cushion subformation for siliceous and calcareous substrata respectively in the maritime Antarctic have already been noted

(p. 142). The effect may be extremely localized, as cushions of *Grimmia* spp., *Tortula* spp. and other calcicoles occur around deposits of limpet shells left by gulls on otherwise acidic soil. Steere (1978b) gives similar examples of distribution patterns in lithophytic bryophytes in Alaska apparently being determined by the calcium content of the rocks, and the distribution of *Sphagnum* spp. and other bryophytes in the wetland communities on peat varies according to the base status of the ground water (Mårtensson, 1956).

The general level of the major nutrients in maritime Antarctic soils is unlikely to be seriously limiting for plant growth, due to the marine influence and the presence of large bird and seal colonies (Allen and Heal, 1970). Similarly at Barrow, Alaska, Oechel and Sveinbjörnsson (1978) found that watering with a dilute nutrient solution resulted in no increase in moss growth or photosynthesis.

In contrast, many soils of inland regions in the high Arctic and in continental Antarctica are strongly deficient in certain nutrients. This applies particularly to available nitrogen, due to the limited extent of microbial activity (Tedrow, 1977). Nitrogen fixation by blue-green algae associated with tundra mosses has recently been demonstrated (Alexander, 1975) and could be important in the early development of the soils. Other elements may occur in high or even toxic concentrations in polar desert soils due to lack of leaching or in extreme cases to prevalence of upward water movement. Steere (1978b) noted that Arctic desert soils are apt to be calcareous due to the low rate of leaching and that this is reflected in the bryophyte flora. Ujolini (1970, 1977) has suggested that there is 'an inverse relationship between pedologic development and life succession' in continental Antarctica because of the high salt content of the most highly developed soils.

The distribution of bryophyte communities associated with lemming burrows and other sites of animal activity in the Arctic (p. 138) could well be controlled in part by concentrations of available nitrogen. Similarly, the most luxuriant vegetation on inland nunataks in continental Antarctica occurs in the vicinity of seabird colonies (Llano, 1965), and again availability of nitrogen could be the key factor. It is not always clear, however, to what extent such distributions reflect nitrophily in the species concerned, as opposed to low nitrogen levels in areas not under strong biotic influence. Experimental studies have shown that a wide range of nitrogen sources is capable of supporting *Bryum algens* on Ross Island (Schofield and Ahmadjian, 1972).

In conclusion, it may be stated that Arctic and Antarctic bryophytes survive, and often thrive, in environments marked by severity not only of temperature but also of several other major factors. Space constraints do not permit a detailed consideration of recent studies on the adaptations of

bryophytes to polar environments, or of the contribution of bryophytes to polar ecosystems, to be presented here. Reviews of these topics may be found on Oechel and Sveinbjörnsson (1978), Longton (1980) and Smith (in press).

ACKNOWLEDGMENTS

This account is an outgrowth from work supported by the British Antarctic Survey, United States Antarctic Research Programme, National Research Council of Canada and University of Manitoba Northern Studies Committee, to whom grateful acknowledgment is made. I also thank Dr D.H. Vitt for comment and criticism of a large section of the manuscript.

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