BRYOPHYTE DIVERSITY AND TERRESTRIAL PLANT ECOLOGY IN THE SUBANTARCTIC : HEARD ISLAND, A CASE STUDY

Dana Michelle Bergstrom

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School of Biological Sciences, Macquarie University.

MACQUARIE UNIVERSITY

HIGHER DEGREE THESIS (PhD)

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Certificate of originality

I hereby declare that the data and information in this thesis have not been submitted elsewhere for any other degree. Except where expressly acknowledged to the contrary in the text or acknowledgements all the work is my own.

Dana Bergstrom

Dana Michelle Bergstrom

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ABSTRACT

This study examines various aspects of terrestrial vegetation on subantarctic Heard Island. A major phytosociological study was conducted focussing on the bryophyte component of the flora. A revised annotated checklist for the Heard Island bryoflora, comprising 42 moss taxa and 12 liverwort taxa is presented. Heard Island's bryophyte and vascular plant floras are small compared with those of other subantarctic islands.

General environmental conditions that affect plants on Heard Island are outlined and ecological amplitude of major taxa are described. Hypotheses concerning ecological strategies of major taxa are proposed. Many taxa on Heard Island such as *Azorella selago* and *Dicranoweisia* spp. exhibit wide ecological amplitude. Patterning of vegetation in a variety of feldmarks was examined and a model concerning bryophyte establishment and maintenance of bare areas is presented.

This study has identified five major vegetation types on Heard Island, based on floristic diversity as well as the relationship between vegetation and environmental characteristics. The dominant vegetation type is open *Azorella* cushion vegetation. A highly significant feature is that bryophytes are major components of most vegetation on Heard Island and in many cases are the dominant component, such as in closed bryophyte vegetation on shallow stable ground.

Taxa in the most abundant vegetation types (*Azorella* cushion and other vegetation; feldmark vegetation on shallow stable ground; feldmark vegetation on labile ground) are generally effective tolerators of stress or disturbance. More competitive taxa are absent, allowing tolerators, such as *Azorella*, *Pringlea antiscorbutica* and mosses such as *Dicranoweisia* spp. and *Ditrichum immersum* to be more significant elements of the vegetation on Heard Island than on other subantarctic islands such as Marion and Prince Edward Islands.

Heard Island's position within the subantarctic is reviewed. It is the island within the Kerguelen Province on which the effects of the last glacial maximum are persisting longest. It is still emerging from extensive glaciation. With the current significant ice-retreat, new areas for colonization are being revealed. At present the island can be interpreted as an 'archipelago' with small islands of icefree land separated by glaciers, each requiring separate colonization events in order for vegetation to become established.

ACKNOWLEDGEMENTS

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Dr Rod Seppelt and Prof Riclef Grolle assisted with the identification of bryophyte specimens. Aspects of Chapter 3 relevant to mosses have been published by Bergstrom and Seppelt (1988). Ideas expressed in the discussion were my own but have been extensively discussed with Dr Rod Seppelt prior to publication.

Thanks to the many members of the 1986/87 ANARE to Heard Island who assisted with logistics and fieldwork. Field leader for the ANARE was Rod Ledingham, whose forethought, planning, superb organizational ability and pro-science attitude made the expedition incredibly effective and successful (and enjoyable).

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A special thankyou to my family, the Selkirk family and friends for their enthusiasm and support. I dedicate this work to my Mum, Natalie, and her "purple 'ats".

Finally and most importantly, to my supervisor, Dr Patricia Selkirk, a simple but heartfelt 'thanks' for her encouragement, guidance, friendship and endless support.

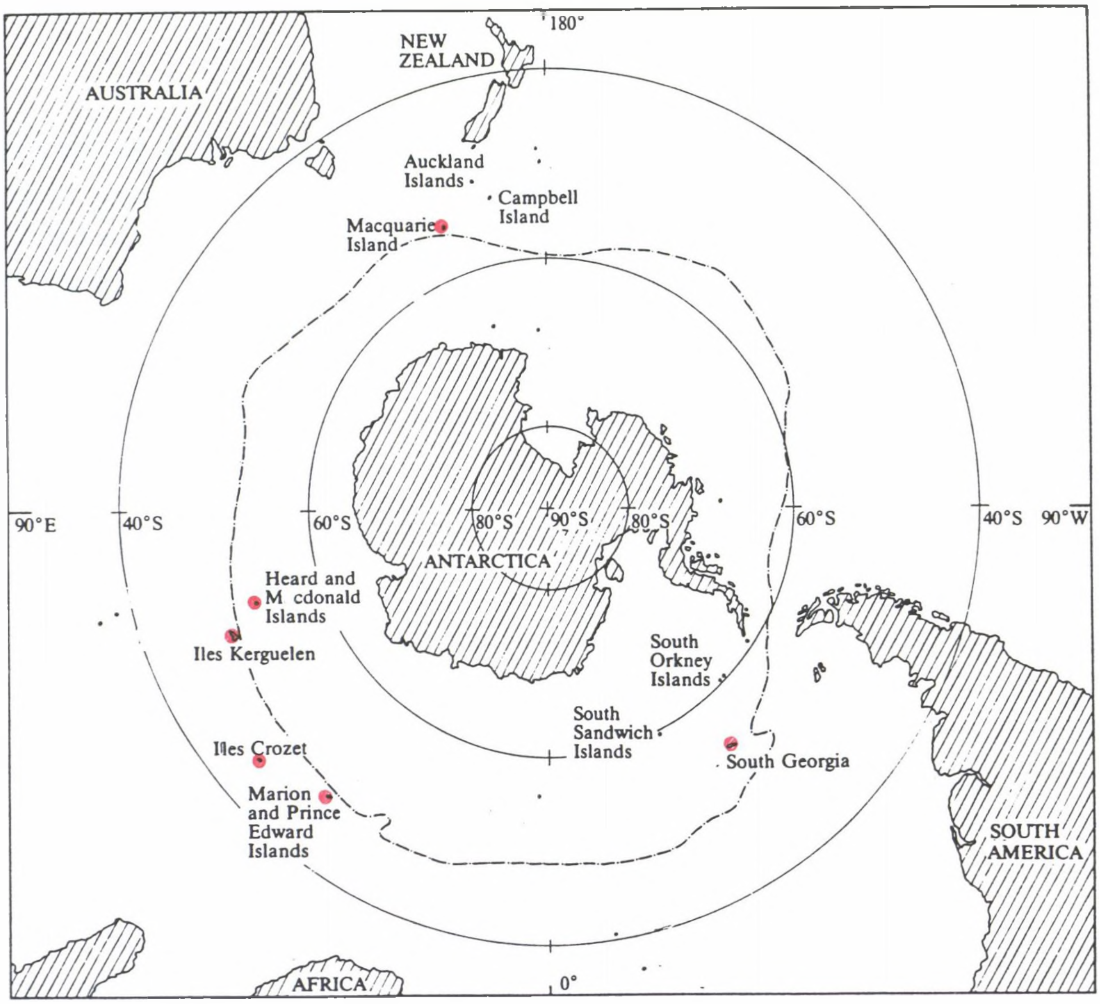


Figure 1.1 Antarctica and the Southern Ocean, showing location of subantarctic islands and Antarctic Convergence (dashed line). Based on the map of Antarctica and adjacent continents (Division of National Mapping, Australia, 1978)

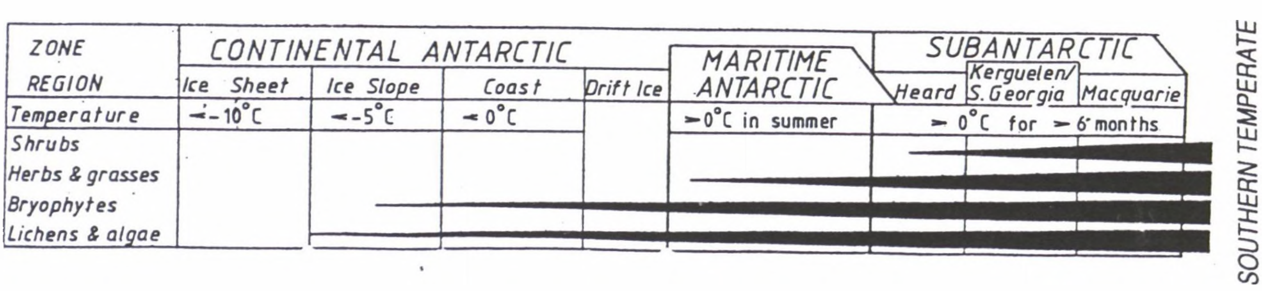


Figure 1.2 Latitudinal arrangement of phytogeographic zones and regions. Generalized occurrence of plants within each region is shown by width of solid bars. The term 'shrub' has been loosely interpreted to include low growing suffrutecent herbs such as *Acaena* spp. Medium sized and tall shrubs do not occur. (From Pickard & Seppelt, 1984.)

CHAPTER ONE

Introduction and description of environments

1.1 Introduction to the Subantarctic Zone and to this project

1.1.1 Subantarctic Zone

There are six subantarctic islands or island groups in the Southern Ocean (Fig 1.1). All are oceanic islands close to the Antarctic Convergence, an oceanic boundary where cold Antarctic waters from the south sink below warmer subantarctic waters from the north (Selkirk *et al.*, 1990). Heard and McDonald Islands and South Georgia are south of the Antarctic Convergence; Marion and Prince Edward Island, Iles Crozet, and Macquarie Island lie to the north; Iles Kerguelen lie on the mean position of the Convergence.

Pickard & Seppelt (1984) reviewed phytogeographic subdivisions of Antarctica and adjacent oceans and adopted a zonation of the subantarctic area based on previous schemes by Skottsberg (1905) and Korotkevich (1966). They divided the subantarctic zone into three regions: Heard (Heard Island & McDonald Island); Kerguelen/South Georgia (Kerguelen, Marion & Prince Edward, Crozet and South Georgia); Macquarie Island. The division is dependent on generalized occurrence of shrubs, herbs and grasses, bryophytes, and lichens and algae (Fig 1.2).

Wace (1965) proposed using the limit of tree or woody shrub growth to separate the subantarctic zone from the temperate zone. He suggested that four plant communities characterized the subantarctic zone:

A. closed herbfield communities in which large leaved perennial herbs are conspicuous;

B. communities of pedestal forming tussock grasses, especially on the coast;

C. soligenous mires in which peat forming plants are Bryales and Juncales (not Sphagna or cushion forming plants);

D. fjaeldmark (feldmark) or wind desert communities composed of flowering plants with compact mat or cushion growth form.

In principal component analyses of climate, edaphic and vegetation parameters French & Smith (1985) described subantarctic ecosystems as being qualitatively different from subarctic and Antarctic ecosystems. They included in their study data from South Georgia, Marion and Macquarie Islands. The distinguishing characteristics they reported were extreme oceanicity associated with wind as an important climatic factor, animal influence and geographical isolation.

French & Smith (1985) reported that "general climatic wetness, together with strong winds, applies a significant chill- factor to the vegetation, so that it resembles that of much higher latitudes in the Northern Hemisphere". They estimated that latitudinal differences between northern and southern hemispheres with equivalent vegetation types can be as much as 20 to 30 degrees. It is interesting to illustrate this with Heard Island: it is of comparable latitude to the city of Liverpool in Great Britain (53°) but has vegetation devoid of trees as does arctic tundra. Subantarctic climates provide growing conditions conducive to high primary production (long growing season, absence of very cold temperatures, substantial nutrient input from the marine ecosystem) and peat accumulation (retardation of decomposition by waterlogging and the absence of a warm summer) (Smith & French, 1988).

Soil nutrient balance is modified by salt spray and at some sites by manuring by seals and seabirds. In coastal sites this impact is striking due to large numbers of animals concentrated in very small areas on very small islands (French & Smith, 1985).

Geographical isolation of subantarctic terrestrial ecosystems and, in many instances, their relatively recent origin cause their biota to be species poor (French & Smith, 1985; Smith & Steenkamp, 1990). Many vascular species on subantarctic islands exhibit wide ecological amplitude and there is the tendency of some species to form specialized communities, often peculiar to a single subantarctic island or island group. Small floras allow for many 'vacant niches' which can be exploited by introduced species (Smith & French, 1988).

A major feature of subantarctic and other subpolar islands such as Signy Island, is the overwhelming importance of bryophytes in terrestrial ecosystems, not only as primary colonists but as important components of mature vegetation communities (Smith & French, 1988). They are highly significant in terms of surface cover, species richness, phytomass and production (Longton, 1982).

Subantarctic terrestrial ecosystems do not have indigenous macroherbivores and, considering the substantial annual primary production of many plant communities, this has a marked effect on ecosystem structure and function. Energy flow and nutrient cycling is controlled by detritivores rather than herbivores, fungi and bacteria (Smith, 1987a; Smith & Steenkamp 1990) Insects are the dominant detritivores in the subantarctic (Smith 1987a).

1.1.2 Introduction to the project

Knowledge of Heard Island terrestrial vegetation and ecosystems is at a rudimentary stage. Previously, little attention had been paid to bryophytes in studies of vegetation on Heard Island despite their importance in extreme environments (Smith 1982). The primary objective of this project was to document the bryophyte flora and to investigate the role of bryophytes within vegetation communities on Heard Island. While on the island an additional aim developed, namely to document small scale vegetation patterning in feldmark environments.

With analysis of data collected on the island, it became apparent that variation in bryophytes reflected variation in vegetation overall. What began as a 'bryophyte' study, focussing on one component of the vegetation developed into a major phytosociological study of Heard Island vegetation.

As part of this study a new vegetation classification scheme for Heard Island is presented, based on floristic diversity as well as the relationship between vegetation and environmental characteristics. A general framework of environmental conditions affecting vegetation on the island is provided and initial hypotheses as to ecological strategies of major taxa are proposed.

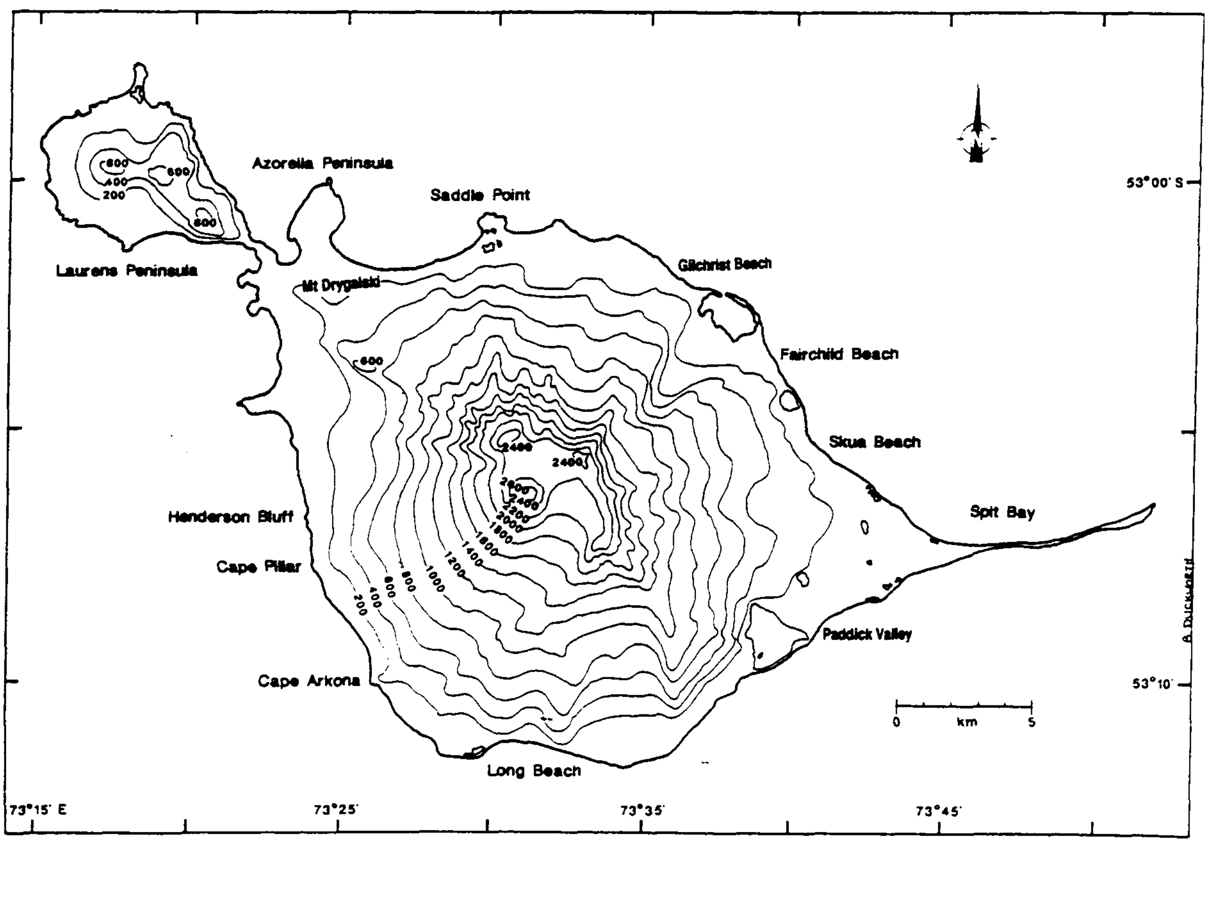
Finally, the position of Heard Island within the Subantarctic Zone, with regard to terrestrial ecosystems is re-examined in light of this study and other recent studies. Fieldwork conducted on Marion and Prince Edward Islands and on Macquarie Island was relevant to this comparison, as well as to the interpretation of patterning within feldmark.

This chapter reviews Heard Island physiography, geology, origin and climate and summarizes previous significant vegetation studies on the island. Comprehensive descriptions of major ice-free areas available for vegetation are provided. There are brief descriptions of Marion and Prince Edward Islands and Macquarie Island. A comparison of the island's physical characteristics is made with the other subantarctic islands.

1.2 Heard Island

1.2.1 Geology, origin and physiography

Heard Island (53°05'S, 73°30'E) is part of the Australian External Territory of Heard and McDonald Islands. It is approximately 4850km SE of southern Africa, 4350km SW of Western Australia and 1650km N of the Antarctic continent (Fig 1.1). The McDonald Island group, 38 km west of Heard Island, consists of 3 very small islands (total area 4.8 km^2): McDonald Island, Flat Island and Meyer Rock. The closest land mass is the Iles



<u>Figure 1.3</u> Heard Island showing place names common in the text. Based on Heard Island 1:50 000 topographical map (Divison of National Mapping, 1986).

Kerguelen, approximately 440 km to the north west.

Included in this volume (back cover pocket) is the current 1:50 000 topographical map (Map 1) and the current 1:50 000 satellite projection of the island (Map 2). These maps should be referred to in conjunction with the rest of this chapter. Figure 1.3 showing common names referred to in the text is based on the topographical map.

Heard Island is 42 km long on a NW - ESE axis. A large, glaciated, active volcano, Big Ben, 2475 m in altitude, 20 km in diameter, dominates the landscape. Figure 1.4 compares N-S profiles of Heard Island with Marion & Prince Edward and Macquarie Island. This illustation highlights the sheer size of Heard Island. The massive height and bulk of Big Ben has considereable influence on the island such as maintenance of the ice cap and infuence on local climate. The island is almost circular in outline but is modified by Laurens Peninsula to the north west and a low lying sand and cobble spit to the east. The surface area of Heard Island is 385 km^2 (DASETT, 1990).

Heard Island, McDonald Island and Iles Kerguelen are interpreted as subaerial portions of the mid-oceanic Gaussberg - Kerguelen Ridge. Heard Island's volcanic rocks have intruded through and accumulated on ocean floor crust which has a thick upper layer of pelagic sediment (Clarke *et al.*, 1983; Quilty *et al.*, 1983). Three geological units have been recognized (Fig 1.5) (Lambeth, 1952; Clarke *et al.*, 1983; Barling, 1990): lowermost limestones and mafic intrusions; the intermediate Drygalski Formation; and the uppermost lavas. Cliffs on the south coast of Laurens Peninsula and behind First Beach (Hoseason Beach) expose a unit of folded, pelagic limestones with minor chert, intruded by dolerites and gabbros (Clarke *et al.*, 1983). These rocks form the foundation for the rest of the island. Nanofossils and foraminifera from outcrops and beach cobbles indicate that these sediments are of Late Paleocene to Oligocene age (60 - 25 million years ago)(Quilty *et al.*, 1983). Terrestrial plant microfossils were also found in sediments of Late Eocene-mid Oligocene age (see section 1.2.3).

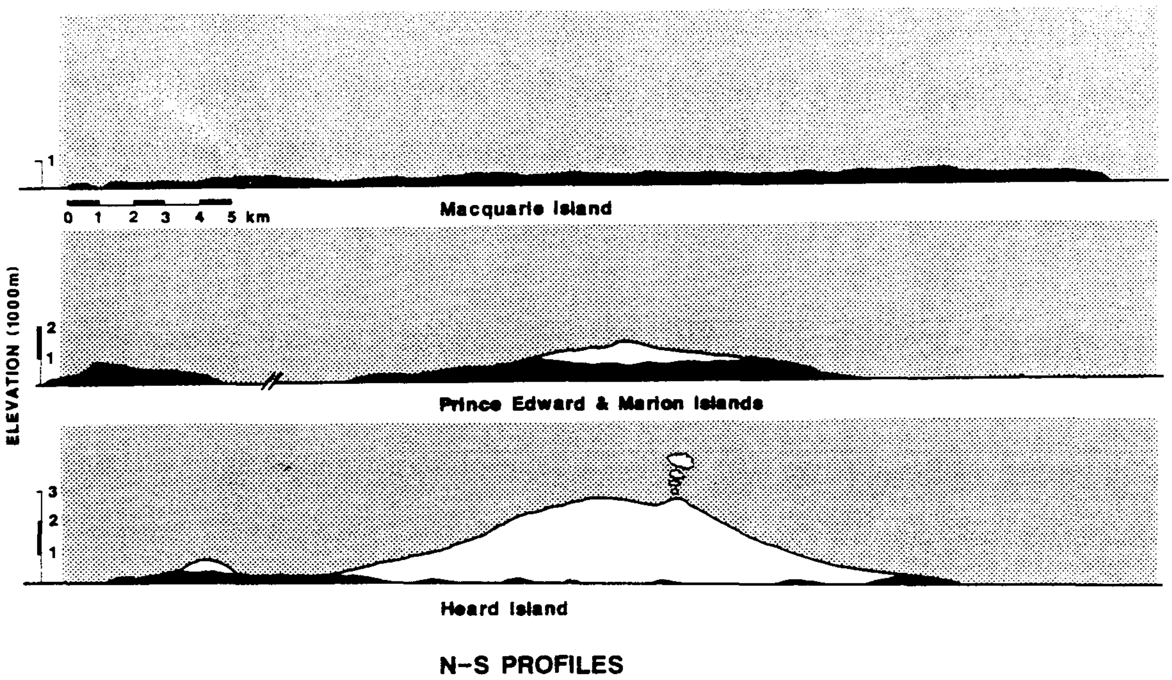


Figure 1.4 North-South profile diagram of Heard Island, Marion and Prince Edward Islands and Macquarie Island. Black areas are ice-free, white areas ice-covered.

The Drygalski Formation consists of clastic deposits and basaltic lavas. It occurs over most of Laurens Peninsula and on the east and south coast of the island and forms a plateau which rises to about 300m. The clastic deposits include conglomerates, sandstone and mudstones (Lambeth, 1952; Clarke *et al.*, 1983). Fossil deposits indicate that the Drygalski Formation was formed, at least in part, during the Late Miocene-Early Pliocene (10 - 3 million years ago) (Quilty *et al.*, 1983).

The bulk of Heard Island consists of basaltic lava. No more than 1 million years ago, the final phase of volcanism began and the Big Ben volcano was built upon the older plateau. Other more recent formations such as small scoria cones have developed in the last 10,000 years (Clarke *et al.*, 1983). Both pahoehoe and aa lava flows are evident (Lambeth, 1952). Pahoehoe lava consists of flat or undulating flows with smooth or ropy texture. Through these flows are lava tunnels or tubes. Aa lava flows are covered in loose clinker fragments piled up in heaps 5 - 20 m high. An eruptive phase of Big Ben began in January 1985. A basaltic lava flow, discovered on the southern flank of Mawson Peak was probably a result of the 1985 eruption (Wheller, 1987). The presence of a lava lake in the summit crater indicates continuing volcanic activity.

Glaciation on Heard Island may have occurred as early as the Miocene (Quilty *et al.*, 1983). The island's position south of the Antarctic Convergence would have ensured major glaciation events during cooling episodes of the Pleistocene. The last glacial maximum occurred approximately 18 000 years ago (Climap, 1976) and today Heard Island is still severely glaciated. Considerable glacial retreat has been recorded since 1948 (Allison & Keage, 1986). Allison & Keage (1986) estimated that in 1980 approximately 80% of Heard Island was ice covered with glaciers descending from 2,400m to sea level. These glaciers are clearly evident on Map 2. Major glaciers are up to 7 km long with areas exceeding 10 km^2 (Allison & Keage, 1986).

High-energy coastal environments and active glaciers on Heard Island have resulted in

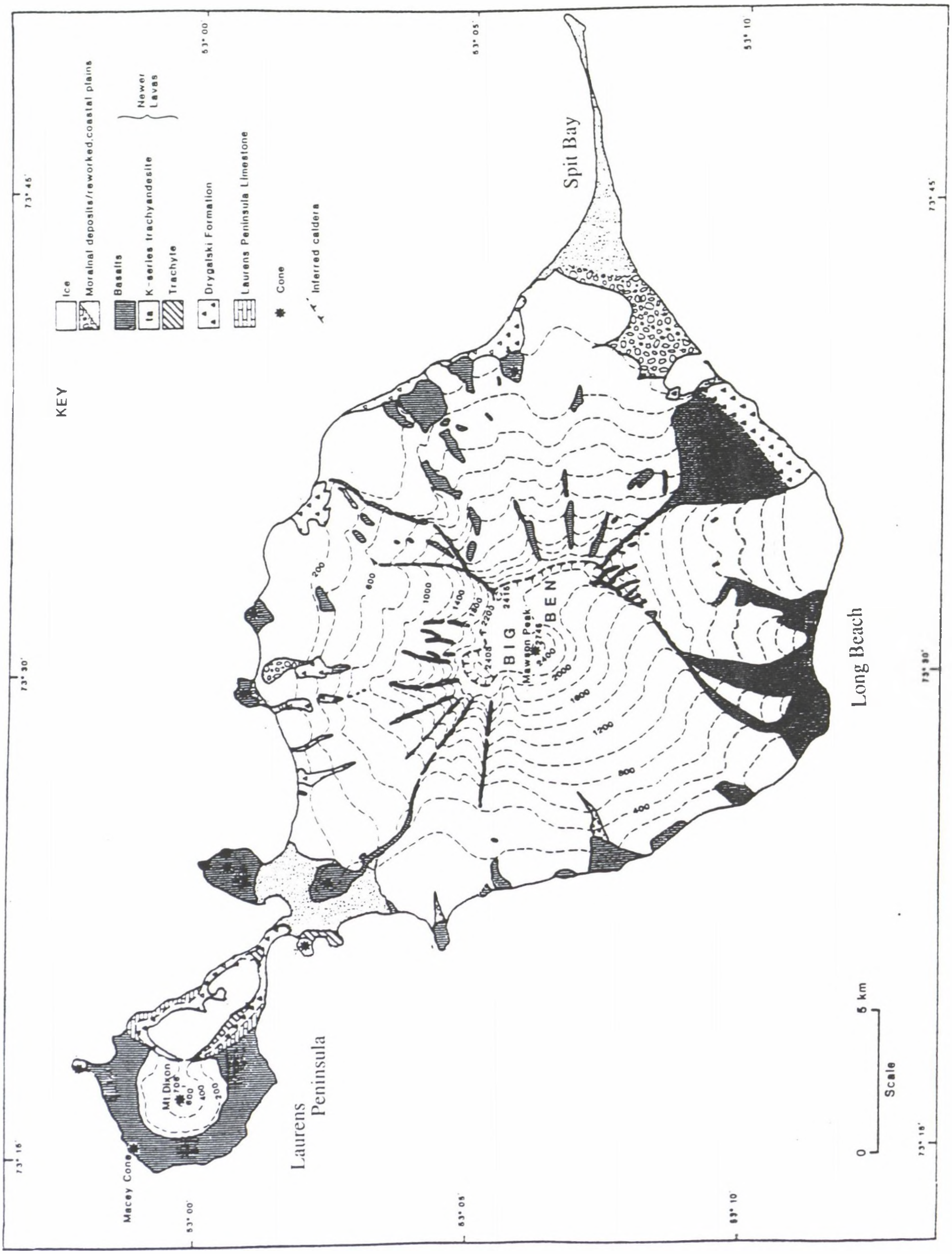


Figure 1.5 Geological units on Heard Island. Contour intervals 200m (After Barling 1990).

rapid geomorphological processes. Allison & Keage's (1986) analysis of 1980 airphotographs indicated prograding of northern and eastern coastlines, a result of large sediment output either from glacial erosion or marine or fluvial working of the retreating coastal ice cliffs. Recent coastal retreat is now evident on the northern and eastern side of Heard Island, including the northern side of Spit Bay (Bergstrom, 1987a; Keage 1987). With glacial retreat, many previous tidewater glaciers, particularly east coast glaciers have become grounded. Consequently, entrapment and deposition of glacial sediment in many coastal lagoons has significantly reduced sediment output carried in long shore drift (Keage 1987). Most dramatic, in terms of glacial retreat, has been the Compton Glacier. It has decreased in area by over 20% since 1948. The snout has retreated 1600 m from its previous tidewater position and the proglacial lake has expanded markedly. In 1988 the spit, marking the once tide-water position of the glacier had been breached in 3 places and the lake will soon develop into a major embayment (R. Kirkwood pers comm).

Associated with glaciation, glacial moraines are a major landscape feature on Heard Island. Some low lying moraine is extensively vegetated. The expansive glaciation on Heard Island leaves limited ice-free areas (see Map 1 & Map 2).

The largest ice-free area is Laurens Peninsula (Fig 1.3) with only limited ice caps on Mt Dixon, Anzac Peak and Mt Olsen. The bulk of the western half of the peninsula consists of non-glaciated lava flows and scoria cones interspersed with fluvial deposits and occasional tarns. Descending from Mt Dixon there are talus slopes. The eastern part of Laurens Peninsula is dominated by the plateau of Anzac Peak and Mt Olsen which is edged by steep scarps and bluffs. There are three areas of morainic deposits on Laurens Peninsula: to the north at Sydney Cove, to the east at the rapidly retreating Jacka Glacier and to the south at the base of Anzac Peak.

The northern end of the peninsula is capped by Red Island, an eroded scoria cone connected to the rest of the peninsula by an isthmus. The lagoon on the isthmus is one of only three non-proglacial lagoons on the island.

Laurens Peninsula extends to Mt Aubert de la Rue in the south-east where it is connected to a severely eroded scoria cone (Mt Andrée& Kildakey Head), Azorella Peninsula and the rest of the island by an extensive isthmus, the Nullabor. Azorella Peninsula is completely ice-free, has three prominent scoria cones and is covered in extensive lava flows. The Nullabor is flanked to the east by the Baudissin Glacier and to the south by the ice free Mt Drygalski. South of Mt Drygalski is the extensive Pageos Moraine system. The moraine systems consist of terminal moraines from the small Schmidt Glacier and lateral moraines from the extensive Vahsel Glacier.

Scattered around the north coast and the south west coast are small isolated ice-free areas. They consist of either scoria cones such as Saddle Pt or exposed bedrock and moraine such as Cape Pillar.

The Long Beach region including Cape Labuan on the south coast consists of extensive moraines and fluvial deposits flanked by the Gotley Glacier to the west and by high cliffs and talus slopes to the north and east. A significant beach terrace abuts Manning Lagoon.

A major ice free fringe on the east coast runs from the northerly Gilchrist Beach (to the north-east) to the southerly Cape Lockyer. In 1948 both Compton Glacier and Browns Glacier were tide water glaciers. Today moraines are associated with both glaciers but the most expansive moraine systems are those associated with the Stephenson and Winston Glaciers: Dovers Moraine and Paddick Valley.

Small raised beach terraces up to 5 m alt. also occur between Gilchrist Beach and Spit Bay. Extending from the oldest moraine line at Dovers Moraine is a more expansive raised beach terrace which culminates in the sand and cobble Elephant Spit.

There does not appear to be a permafrost at low altitude on Heard Island. A variety of periglacial processes and features was observed including stone bank lobes, terraces, patterned and sorted ground, frost heaving, nubbin formation and ground raking. Wind and water erosion are also important influences on small scale landscape forming processes.

There are no major river systems on Heard Island. Proglacial lakes and melt water streams are fed by glaciers and ice-cored moraines. Of the three non-glacial lagoons, Red Island and Manning Lagoons are permanent and Scho les Lagoon is ephemeral. Both non-glaciated lavas and moraines are generally very porous and drainage is rapid. However in some areas drainage is impeded, resulting in small pools or tarns. Numerous pools form an extensive network such as on the coastal terrace adjacent to Dovers Moraine (Whin am, 1989).

Little has been recorded about the soils on Heard Island. Most are poorly developed, mineral skeletal soils ranging from silts and sands to gravels and boulders. In some areas such as young lava flows and scoria cones no appreciable soil formation has occurred. Coastal organic soils are generally very shallow although *Azorella selago* peats are extensive in some places. In the Spit Bay region peats are up to 2 m deep.

1.2.2 Climate

Allison & Keages' (1986) review of Heard Island climate is summarized below. "Heard Island stands in the zone of strong and persistent westerly circulation, its climate depending largely on characteristics of the surrounding Antarctic surface waters. Temperatures at sea level are remarkably constant both diurnally and annually, closely matching sea surface temperatures. Snow or rain falls on most days" (Allison & Keage 1986).

An ANARE (Australian National Antarctic Research Expedition) station provided routine meteorological observations between February 1948 and December 1954. Monthly

Month	Station Level Pressure (mb)	Mean Temp °C	Mean Daily Max °C	Mean Daily Min °C	Relative Humidity %	Precip-itation mm	No of days of precipitation	Wind m/sec
Jan	994.5	3.2	5.2	1.5	89	139	27	7.2
Feb	998.8	3.4	5.2	1.7	88	145	25	7.6
Mar	999.9	3.0	4.8	1.2	86	146	27	7.7
April	997.5	2.5	4.2	0.7	87	158	27	8.1
May	994.5	1.4	3.1	−0.4	85	148	25	8.4
June	989.9	−0.2	1.4	−2.3	83	95	23	8.3
July	992.6	−0.4	1.3	−2.5	84	94	21	8.8
Aug	994.1	−0.6	1.2	−2.7	83	57	21	9.3
Sept	992.7	−1.1	0.8	−3.3	81	67	20	9.3
Oct	992.7	−0.1	1.5	−2.0	87	100	20	8.5
Nov	991.5	0.7	2.3	−0.8	84	100	21	9.0
Dec	994.1	2.2	4.1	0.7	88	132	24	7.3
Mean	994.4	1.2	2.9	−0.7	85	115	23	8.3

Table 1.1. Monthly climatic means 1948-1954. (From Allison & Keage, 1986).

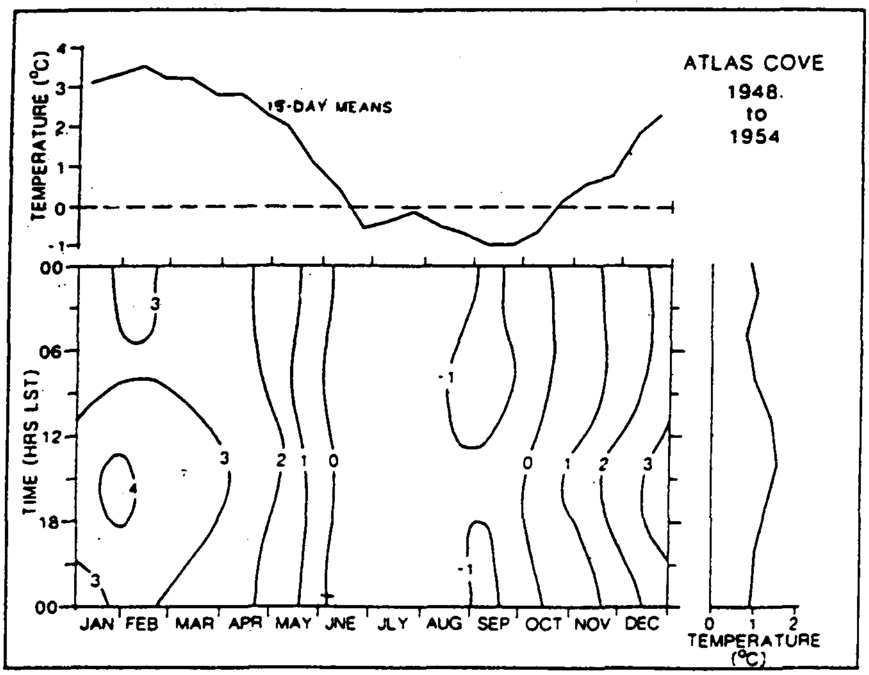


Figure 1.6 A thermo-isopleth diagram from Atlas Cove, from 15-day means of three-hourly temperatures 1948-1954. (From Allison & Keage, 1986).

climatic means are shown in Table 1.1. A thermo-isopleth diagram from Atlas Cove, from 15-day means of three-hourly temperatures 1948-1954 (Fig 1.6) shows stability in temperatures. Seasonal range is 4.5°C. The warmest period (+3.5°) is early February, the coldest (-1.0°C) September. Diurnal temperature range is very small. Mean air temperature is slightly below zero from late June to early October. During this period there is extensive snow cover at low altitudes followed by a spring melt.

Mean cloudiness is greater than 80%. Mean annual precipitation at Atlas Cove during 1948-1954 was 1380 mm. Precipitation is highest during autumn and summer. Relative humidity remains high (85%) throughout the year with a slight decrease in winter. Mean wind speed recorded at Atlas Cove was 8.3 m/s with 25% of the winds from the southwest and 75% from directions within the SSW-NW sector. However local topography affects local climate significantly and extreme climatic events have been observed. For example on the 11th April 1992 rising air, cooling on the windward side of Big Ben caused heavy precipitation. On the leeward side however, dry air descended warming at an adiabatic dry rate of 1.0°C/ 100m producing a very warm, foehn wind with local temperatures in the vicinity of Spit Bay Hut Creek peaking at 21.6°C, the highest maximum ever recorded (Green, 1992).

The considerable glacial retreat on Heard Island has been attributed to recent warming in the Southern Hemisphere (Allison & Keage, 1986) which is averaging approximately 0.25°C per decade (Jones, 1988).

1.2.3 Past and present vegetation of Heard Island

Plant microfossils have been recorded from both limestone and Drygalski Formation sediments spanning the Late Eocene to Early Pliocene (Quilty *et al.*, 1983). The Tertiary flora included a variety of ferns, a podocarp and a small herbaceous angiosperm component and was described as low scrubby fernbush vegetation (Quilty *et al.*, 1983). The Tertiary climate associated with this flora was described as cold and wet. The

Table 1.2 Heard Island vascular plant flora (from DASETT, 1990). Appendix 1 lists all species referred to in this thesis, with authorities.

ANGIOSPERMS, Dicotyledons

Apiaceae
Azorella selago
Brassicaceae
Pringlea antiscorbutica
Callitrichaceae
Callitriche antarctica
Caryophyllaceae
Colobanthus kerguelensis
Portulacaceae
Montia fontana
Ranunculaceae
Ranunculus biternatus
Rosaceae
Acaena magellanica

ANGIOSPERMS, Monocotyledons

Poaceae
Deschampsia antarctica
Poa annua
Poa cookii
Poa kerguelensis

Table 1.4 Estimated surface area covered by substantial vegetation for some major ice-free areas on Heard Island. Areas are underestimates calculated from planar projections.

REGION	surface area (km^2)
LAURENS PENINSULA	7.0
AZORELLA PENINSULA	1.6
MT DRYGALSKI	0.5
LONG BEACH	2.2
PADDICK VALLEY	0.6
SPIT BAY	2.3

composition of the Heard Island microflora is similar to the fossil flora on Iles Kerguelen (Cookson, 1947, Quilty *et al.*, 1983). Dettman (1986) described the Kerguelen Miocene flora recorded by Cookson (1947) as a cool temperate *Podocarpus*/Araucarian rainforest with dicksoniaceous ferns and herbaceous angiosperms.

The present vegetation on Heard Island is vastly different from this, dominated by herbaceous angiosperms and bryophytes. Now the vascular flora is small, comprising only 11 species, all angiosperms, (Hughes, 1987; Scott, 1988, 1989) (Table 1.2). All of these species have been recorded from other subantarctic islands or island groups. All vascular species from the island have also been recorded on Iles Kerguelen. Five of the 11 species (*Acaena magellanica, Azorella selago, Callitriche antarctica, Poa annua* and *Ranunculus biternatus*) have been recorded from all other subantarctic islands or island groups (Greene and Walton, 1975).

Although bryophytes are important components of vegetation on Heard Island, they have received little attention in previous vegetation studies on the island. Most have concentrated on the vascular plant component. Clifford (1953) reported only 17 moss taxa (10 considering present day revision). This study however, records 44 moss taxa and 12 liverwort taxa present on the island (Table 1.3)(see Chapter 3).

Vegetation on Heard Island occurs on suitable substrates in ice free areas, generally below 400m alt. Substantially vegetated areas are generally below 200m alt. and are shown on Map 2. From the September 1988, multispectral Spot I satellite image of Heard Island, the surface area occupied by substantial vegetation was estimated to be 20 km^2. This is approximately 5% of the total surface area of Heard Island. Table 1.4 presents surface area covered by substantial vegetation for the major ice-free areas on the island.

Jenkin (1980) briefly described five vascular plant communities on Heard Island. In a

Table 1.3 Bryophtye flora of Heard Island. (From Chapter 3)

MOSSES

Andreaeaceae
Andreaea acuminata
Andreaea mutabilis
Polytrichaceae
Polytrichum alpinum
Polytrichum piliferum
Psilopilum australe
Grimmiaceae
Grimmia immerso-leucophaea
Grimmia sp.
Schistidium apocarpum
Schistidium falcatum
Schistidium sp.
Racomitrium crispulum
Racomitrium lanuginosum
Ditrichaceae
Ditrichum conicum
Ditrichum immersum
Ditrichum subaustrale
Ceratodon purpureus
Seligeriaceae
Blindia contecta
Blindia robusta
Verrucidens microcarpus
Verrucidens tortifolius
Dicranaceae
Dicranella sp.
Dicranoloma billardieri
Dicranoweisia antarctica
Dicranoweisia brevipes
Dicranoweisia breviseta
Pottiaceae
Pottia heimii
Tortula geheebiaeopsis
Tortula robusta
Orthotrichaceae
Muelleriella crassifolia, subsp.*acuta*
Bryaceae
Bryum dichotomum
Bryum psuedotriquetrum
Bryum sp. 1.
Bryum sp.2.
Bryum sp.3.
Pohlia wahlenbergii
Pohlia sp.
Trichostomum sp.
Bartramiaceae
Bartramia patens
Philonotis cf *angustifolia*
Amblystegiaceae
Amblystegium serpens
Drepanocladus uncinatus
Brachytheciaceae
Brachythecium austro-salebrosum
Brachythecium paradoxum

Liverworts

Codoniaceae
Fossombronia australis
Marchantiaceae
Marchantia berteroana
Cephaloziellaceae
Cephaloziella exiliflora
C. varians
Jungermanniaceae
Cryptochila grandiflora
Jungermannia coniflora
Geocalycaceae
Pachyglossa fissa
Pedinophyllopsis abdita
Gymnomitriaceae
Herzogobryum atrocapillum
H. vermiculare
Lophocoleoideae sp.
Scapaniaceae
Blepharidophyllum densifolium

preliminary study, Hughes (1987) expanded this to six vascular plant community categories. The communities were described on the basis of various combinations of vascular plant taxa, physiognomic and microtopographical features. Scott (1988) defined 6 mappable vegetation categories based on Hughes'(1987) scheme as well as recognising a close relationship between a number of vascular plant communities and the animal and bird populations using them. In doing so she provided more detailed descriptions of the vascular plant communities. A summary of the six vascular plant community categories follows. In Chapter 7 a new vegetation classification scheme is presented. Figure captions include vascular plant community categories according to Hughes' (1987) scheme and in parentheses, the new vegetation classification descriptions resulting from this study:

Poa cookii maritime grassland (Fig 1.7) is described as being characteristic of nutrient-enriched, biotically influenced environments (Hughes, 1987; Scott, 1988). This community is dominated by the small tussock grass *Poa cookii*, (Hughes, 1987). *Callitriche antarctica* and *Montia fontana* are also reported from this community.

Pool complex (Fig 1.8) occurs in areas where drainage is impeded. *Callitriche antarctica* is described as the indicator species (Hughes, 1987; Whinam, 1989). Whinam (1989) delineated eight ecological groups within this community depending on extent of cover by *Azorella selago* and a mixture of other species. Areas which can be categorized as pool complex vegetation most often occur inland of a narrow fringe of maritime grassland on coastal flats. These areas are subjected to seasonal disturbance by wallowing moulting elephant seals. The extent of pool complex vegetation at altitudes higher than the coastal flats is limited (Scott, 1988).

Meadow community category encompasses vegetation dominated by one of either two species: *Poa cookii*, and at some sites at the eastern end of the island, *Deschampsia antarctica* (Fig 1.9). Meadow communities are reported from moist environments where the water table is close to the surface. Usually bryophytes are common, as are the vascular plants *Montia fontana* and

Figure 1.7 *Poa cookii* maritime grassland, Oil Barrel Point, Spit Bay. (Open *Poa cookii* stand on nutrient enriched, animal disturbed beach).

Figure 1.8 Pool complex, Atlas Cove. (Surrounding pools - Open *Azorella* & *Poa cookii* vegetation on nutrient enriched, peaty lava, interspersed with pools. On pool edge - Sparse *Callitriche* vegetation on nutrient enriched pool edge.)

Figure 1.9 *Acaena* herbfield on slope and meadow growing in the drainage line at the base of the slope. Purple plant (a) - *Acaena magellanica*; light yellow grass on slope (p)- *Poa cookii*; yellow grass in drainage line (d) -*Deschampsia antarctica*. (closed *Acaena* vegetation on wet moraine slope and closed bryophyte and *Deschampsia* vegetation in drainage line; foreground - open *Azorella* cushion vegetation on moraine)

Figure 1.10 Herbfield with *Pringlea* dominant, Spit Bay Hut Creek. (Closed *Pringlea* stand on maritime slope).

Acaena magellanica. *Callitriche antarctica* and *Colobanthus kerguelensis* sometimes occur (Scott, 1988).

Herbfield is also described as being dominated by one of either two species: *Pringlea antiscorbutica* (Fig 1.10) and *Acaena magellanica* (Fig 1.9)(Hughes, 1987; Scott, 1988). *Acaena* has only been recorded from the eastern end of the island (Scott, 1988). Herbfield has been reported from a variety of situations such as sheltered moraine slopes and gullies. Stands can be monospecific or mixed, with *Azorella* and *Poa cookii* being subsidiary species. *Pringlea* can colonize scree slopes, landslip surfaces and recently deposited moraines. It is also common along gravelly stream margins (Hughes, 1987; Scott, 1988).

Cushion carpet vegetation is dominated by *Azorella selago*. In this vegetation category individual cushions of *Azorella* coalesce into continuous carpets. Hughes (1987) described cushion carpet communities (Figs 1.11 & 1.12) occurring in locations of moderate to high wind exposure. This type of vegetation is the most widespread on Heard Island , occurring throughout the altitudinal range of vegetation. Scott (1988) has recognized 5 sub-categories; dense cushion carpet, patchy cushion carpet, *Azorella/Poa cookii* "network" vegetation, "*Azorella* mossfield" and vegetated cliff edges and ledges. Dense cushion carpet (Fig. 1.11) is described as almost completely dominated by *Azorella* with sporadic occurrence of *Poa cookii*, *Poa kerguelensis*, *Colobanthus kerguelensis* and bryophytes. Dense cushion carpet gives way to patchy cushion carpet (Fig. 1.12) in areas of increased wind exposure. Both can occur on coastal flats and slopes and are usually well drained. *Azorella/Poa cookii* "network" vegetation occurs in dense cushion carpet on a variety of slopes, and from a distance presents a network appearance. Scott (1988) suggested that the hummocky appearance appeared to be the result of moderate to high burrowing activity of Antarctic prions with nutrient enrichment of the soil encouraging

Figure 1.11 Dense cushion carpet, Manning Lagoon, Long Beach.(Foreground - Closed *Azorella* cushion vegetation on peaty moraine. Midground on left - Closed *Poa cookii* grassland vegetation on nutrient enriched, peaty moraine).

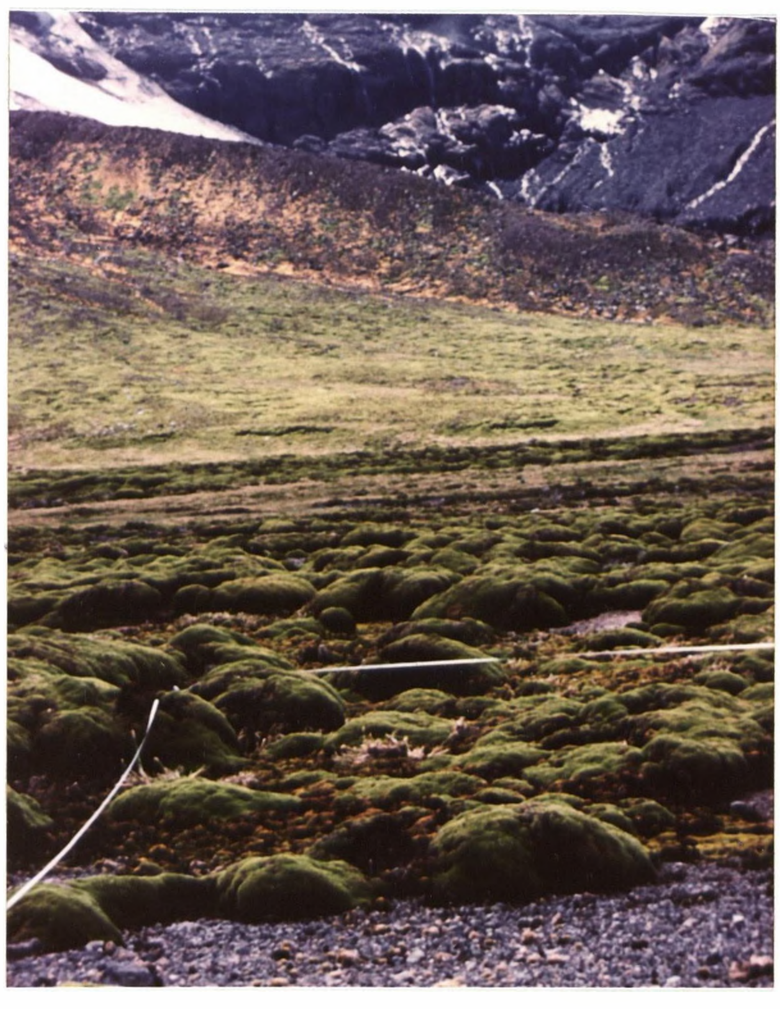


Figure 1.12 Patchy cushion carpet, near Deacock Moraine, Long Beach region. (Foreground - Open *Azorella* and *Dicranowesia* vegetation on moraine. Yellow vegetation on moraine below snow - Closed *Blindia* vegetation on stable moraine slope).

Figure 1.13 Feldmark, inland from Manning Lagoon, Long Beach.
(Open *Azorella* and moss vegetation on stable moraine.)

colonization by *Poa cookii*. *Azorella* mossfield vegetation consists of dense carpets of bryophytes between *Azorella* cushions. In some cases bryophytes dominate.

Feldmark communities are characterized by less than 50% vegetation cover (Fig 1.13). Hughes (1987) described feldmark having high relative vascular plant diversity but low species abundance, with predominant plants being *Azorella*, *Poa kerguelensis*, *Colobanthus kerguelensis*, *Pringlea*, bryophytes and lichens. Scott (1988) recorded feldmark on well-drained areas of high altitude/high wind exposure, areas of recent glacial retreat, flat valleys likely to be subject to cold air drainage, and geologically recent lava flows.

Scott (1988) recorded examples of utilization by either birds or seals of all vegetation communities on Heard Island.

1.2.4 Fauna

Three species of seals breed on Heard Island (DASETT, 1990): the southern elephant seal (*Mirounga leonina*), the Antarctic fur seal (*Arctocephalus gazella*) (Fig 1.7) and the Subantarctic fur seals (*A. tropicalis*). Leopard seals (*Hydrurga leptonyx*) make summer visits to the island.

Thirty species of birds have been recorded at Heard Island, of which 19 species breed on the island. These include four species of penguins, twelve species of petrels and prions, the subantarctic skua (*Catharacta lonnbergi*), 2 species of albatross, one gull species, two species of terns, an endemic cormorant (*Phalacrocorax atriceps*) and the lesser sheathbill (*Chionis minor*) (DASETT, 1990).

Brown (1964) recorded 25 species of insects including 5 species of collembola, and 3 species of wingless flies and a wingless moth *Pringleophaga heardensis*. However, the invertebrate flora is at present in a state of review. There may however be over 80 invertebrate species on the island. There appear to be at least 11 species of collembola, 4 weevil species, one species of spider, up to 30 species of mites, and a land snail (P. Greenslade, pers.comm, 1992). Eleven species of tardigrades have been recorded including 3 newly described species (W. Miller, pers.comm.1992).

1.3 Marion and Prince Edward Island.

1.3.1 Geology, origin and physiography

Marion Island (46°54'S, 37°45'E) and it s smaller neighbour, Prince Edward Island, 22 km to the north (Fig 1.1), are 1800 km SSE of the Cape of Good Hope. The islands are coalescing shield volcanoes situated near the centre of the West Indian Ridge (Verwoerd, 1971). Potassium argon dates of volcanic rock from Marion Island have indicated an age of 450 000 years (McDougall, unpublished data 1985, in Verwoerd, 1990a). A small eruption occurred on the west coast of Marion Island in 1980 (Verwoerd *et al.*, 1981).

Two distinct volcanic stages have been documented on the islands. The first stage produced fine grained compact basalts, generally grey in colour ('old grey lavas'), with some stratified tuffs and pyroclastic deposits. The second stage produced strongly vesicular black lavas, which dominate the islands' landscape and over 100 scoria cones. 'Young black lavas' have been dated at a maximum of 15 000 + 8 000 years BP (McDougall, 1971).

A permanent ice-cap is present on Marion Island above 1000m (see Fig 1.4). Striated platforms, moraines and glacially polished grey lava outcrops and ridges indicate former, more extensive glaciation. The black lavas show no evidence of glaciation. Prince Edward Island does not have a permanent ice-cap and evidence of past glaciation has not been found (Verwoerd, 1990b).

1.3.2 Climate

Detailed accounts of climate for the Marion and Prince Edward Islands have been given by

Schulze (1971) and Gremmen (1982). The average temperature is around 5°C with small diurnal (mean 1.9°C) and seasonal (4.1°C) ranges. Frosts occur on average of 55 days/yr. Mean annual precipitation is >2500mm/yr, distributed fairly evenly throughout the year and falling mainly as rain. However snow can fall at any time and there is generally a snow cover at low altitudes for a few weeks in winter. Cloudiness is approximately 30 % and relative humidity is high (mean 80%).

1.3.3 Vegetation.

Palynological evidence for a Quaternary vegetation on Marion Island has been obtained from organic rich basal sediments associated with interglacial deposits. The pollen spectra indicated a floral assemblage similar to that present today (Scott & Hall 1983).

Two major vegetation studies have been conducted on Marion Island: by Huntley (1971) and by Gremmen (1982). Thirty eight vascular plant species have been recorded from Marion and Prince Edward Islands, 15 of which are considered as alien (Bergstrom & Smith, 1990). Seventy two moss species, 35 liverwort species and approximately 100 lichen species have also been recorded from the islands (Smith, 1987a).

Gremmen (1982) has recorded 41 plant communities to association or sub-association level. These communities can be grouped into six community complexes (Smith, 1987a):

The salt spray (*Crassula moschata*) complex is restricted to shore-zone areas strongly affected by wind-blown sea spray.

The 'biotic' (*Callitriche antarctica- Poa cookii*) complex consists of a variety of communities which are influenced by trampling and manuring by animals. Most occur on the coastal zone near colonies of seals and penguins. Inland communities belonging to this complex occur near bird colonies and burrows.

The *Acaena magellanica - Brachythecium* complex forms at mire and lowland slope sites where there is substantial lateral subsurface water movement. It includes vegetation communities of springs, flushes and drainage lines.

The mire/grassland and bog (*Juncus scheuchzerioides- Blepharidophyllum densifolium*) complex is dominated by bryophytes and monocotyledonous flowering plants and occurs on wet peat.

Fernbrake communities (*Blechnum penna-marina* complex) dominate well drained lowland slopes.

Fjaeldmark (feldmark) (*Andreaea- Racomitrium crispulum* complex) is found on rocky areas strongly exposed to wind, dominating the vegetation above 300m altitude but can occur at lower altitudes. This complex is characterized by *Azorella selago*, bryophytes and lichens.

The Marion Island biota has been affected by the introduction of mice and cats. Extensive populations of mice are now present on the island (Crafford, 1990; Smith & Steenkamp, 1990). A sustained cat eradication program has been in operation since 1987 and numbers have been reduced considerably (W Bester, personal communications).

1.4 Macquarie Island

1.4.1 Geology, origin and physiography

Macquarie Island (54°30'S, 158°57'E) is approximately 1130km SW of New Zealand and 1580km SSE of Tasmania. The island is elongate in shape, 34 km long and at maximum 5.5 km wide. It rises steeply from sea level to an undulating plateau, 200m to 350m in altitude with a few higher peaks rising to 440m alt.(see Fig 1.4).

Macquarie Island is an emergent portion of the mid-oceanic Macquarie Ridge complex which is part of the boundary between the Australian and Pacific tectonic plates. The rocks of Macquarie Island were formed by crustal accretion during sea-floor spreading, most likely during the Oligocene (Willamson, 1978, 1988). The island is estimated to have emerged between 80 000 and 300 000 years ago. "Fault movement on a monumental scale must have been responsible for its uplift" (Selkirk *et al.*, 1990).

There are three geological components on the island: pillow basalts and basalt flows, volcaniclastic sediments and sediments of marine origin deposited in the interstices of the volcanic and volcaniclastic rocks. Pillow basalts make up the bulk of the island (Christodoulou *et al.*, 1984).

There is no present ice cap on Macquarie Island and there does not appear to have been any major glaciation in the past (D. Adamson, pers.comm, 1993). Present landscape features are mainly the results of interplay between faulting, uplift, sea-level change, erosion and periglacial processes (Selkirk *et al.*, 1990).

1.4.2 Climate

Climate on the island is uniformly cool, wet and windy; at the Meteorological Station (6m a.s.l) the mean annual temperature is 4.7°C, (Jacka *et al.*, 1984), mean annual precipitation is 893mm and mean wind speed is 8.3m/sec (Löffler, 1983). Temperature records (1948-86) have shown a 1C° warming trend (twice the global average), with an acceleration between 1966-1986, (Adamson *et al.*, 1988).

Climate on the plateau is more severe than that summarized for the meteorological station. Mallis (1988) reported the annual precipitation for the northern end of the plateau to be 42% greater than at the Meteorological Station. There is a drop in air temperature of approximately 1C° per 100m increase in altitude (Jenkin, 1975) and wind speeds are greater too (Selkirk *et al.*, 1990). Löffler (1983) estimated there would be frost on approximately 170 days per year at an altitude of 200m.

2.4.3 Vegetation

Late Pleistocene and Holocene vegetation histories have documented past plant communities as being similar to those found on the island today (Selkirk *et al.*, 1983; Bergstrom, 1987b; D.R. Selkirk *et al.*, 1988). At present 45 non-woody vascular plant species, 83 moss species, 51 liverwort species and 119 lichen species have been reported from the island. Selkirk *et al.*, (1990) have produced a comprehensive review of the vegetation on Macquarie Island. They modified a vegetation classification scheme designed by Taylor (1955). A number of vegetation types can be recognized, based on dominant vascular plant species:

Tall tussock grassland is dominated by *Poa foliosa* and occurs on all coastal slopes up to about 330 m altitude, on flats on the coastal terraces where the water table is low, and on some protected inland slopes and plateau upland flats.

Short grassland includes areas dominated by species of *Agrostis*, *Luzula*, *Uncinia* and *Deschampsia* or *Festuca*. Short grassland communities are widespread on inland slopes.

Fernbrake communities are fairly rare on Macquarie Island occurring mainly on the east coast on some valley sides, steep slopes or sheltered valley floors. They are usually dominated by closed stands of *Polystichum vestitum*. At one locality *Blechnum penna-marina* dominates fernbrake.

Mire communities in which the water table is close to or at the surface are generally dominated by bryophytes. Seepage-flush areas can be dominated by *Juncus scheuchzerioides*, *Montia fontana* and the moss *Breutelia pendula*.

Herbfield in which the rosette *Pleurophyllum hookeri* is often found, can occur in many situations such as raised coastal terraces, protected valleys and inland slopes. Its distribution may be restricted by strong winds and water logging of soils.

Feldmark vegetation occurs extensively on the island plateau, generally above 200m altitude. Vegetation cover is extremely variable (Selkirk & Seppelt, 1984; Selkirk *et al.*, 1990). Feldmark areas are usually characterized by *Azorella selago* and the mosses *Andreaea* spp., *Ditrichum strictum* and *Racomitrium crispulum*.

Areas omitted from this scheme include salt spray zones and animal influenced areas. At salt spray zones such as headlands and coastal rocks and beaches, communities including

Figure 1.14 Summary of the geology and origin of the subantarctic islands. (From, Laws, 1978: Williams, 1988; Selkirk *et al.*, 1990; Verwoerd, 1971; Giret, 1986; Lambeth, 1952; Quilty *et al*,. 1983)

SUMMARY OF GEOLOGY AND ORIGIN OF ISLANDS IN THE SUBANTARCTIC ZONE

OCEANIC
mainly volcanic origin

CONTINENTAL

South Georgia
Detached block, mainly Jurassic - early Cretaceous greywackes.

SEA FLOOR ACCRETION

Macquarie Island
(Ophiolite complex, emergent portion of Macquarie Ridge. Rocks mainly basalts, volcanic sediments and marine sediments. Emerged between 90 000 and 300 000 years ago)

SUBAERIAL VOLCANIC ACCUMULATION

Marion and Prince Edward Islands
Shield volcanoes on the Mid-Indian Ocean Ridge 250 000 - 500 000 years old

Iles Crozet
Emerging volcanics and plutonics on the oceanic Crozet Plateau. Miocene origin.

Iles Kerguelen
Volcanics and plutonics on the Kerguelen- Gaussberg Ridge. Initial subaerial magmatic activity in the Eocene.

SUBAERIAL LIMESTONE BASE

Heard Island
Evidence of emerged marine limestones in late Eocene- early Oligocence. Subsequent volcanic accumulation.

Colobanthus spp., *Cotula plumosa, Crassula moschata* and *Poa annua* can be found. On coastal flats where seals wallow *Callitriche antarctica* and *Poa annua* can be found. *Poa cookii* is common near penguin rookeries.

One of the major features of Macquarie Island vegetation is its complexity, with many communities intermixing and many being difficult to define (Selkirk *et al.*, 1990). Macquarie Island's ecosystem has been influenced by the introductions of number of animal species including mice, cats, black rats, rabbits, and wekas (Selkirk *et al.*, 1990).

1.5 Comparison of Heard Island physical environments with Marion and Prince Edward Islands, and other subantarctic islands

Figure 1.14 summarizes geology and origin of islands in the subantarctic zone. Heard Island, like most of the subantarctic islands and island groups, is of oceanic volcanic origin (rather than of continental origin) with basalt being the predominant rock type. When considering vegetation niche variation, geologies on Heard and the other volcanic islands can, generally, be considered as similar. For example, the unglaciated clinker lava flows and the scoria cones on Heard Island are of comparable structure to the young black lavas on Marion and Prince Edward Islands.

All of the oceanic subantarctic islands are on high points of ocean ridges or plateaux. Heard Island is distinct in having a partially emerged limestone sequence between the ocean crust and the volcanic accumulations.

The islands of 'oceanic origin', including Heard Island have been isolated from continental land masses since their formation. Consequently all flora and fauna on these oceanic islands, have arrived via transoceanic dispersal.

With respect to emergence above sea, the 'oceanic origin' islands can be divided into two groups: Quaternary emergence (Macquarie, Marion and Prince Edward Islands) and

Tertiary emergence (Heard, Crozet and Kerguelen). Giret (1987) reported the first magmatic phase on Iles Kerguelen to have begun between 40 to 26 million years ago. Lignites have yielded evidence of a Tertiary flora on Iles Kerguelen (Cookson, 1947). The first evidence of a terrestrial flora and hence emerged land on Heard Island is argillaceous limestones with microfossils of Late Eocene - mid Oligocene, (48- 30 Ma.)(Quilty *et al.*, 1983). This implies that both Heard Island and Iles Kerguelen had emerged at comparable times, both subsequently being colonized by plants during the Tertiary.

Although the time of emergence above sea can distinguish between the subantarctic islands of 'oceanic origin', more recent geological and geomorphological processes, specifically, Pleistocene glaciation and post-glacial volcanic activity are of greater significance when considering the development of present day terrestrial vegetation. It has been suggested that during glacial maxima the Antarctic Convergence would have moved northward, a result of an extended Antarctic ice sheet. This would have had the effect of lowering the mean land temperatures at some of the subantarctic islands (Walton, 1984). Heard, Marion, Ile de la Possession (Iles Crozet) and Grand Terre (Iles Kerguelen) were glaciated to some extent (Allison & Keage, 1986; Verwoerd, 1990a; Giret, 1986). The other oceanic subantarctic islands including McDonald Island, Macquarie Island and Prince Edward Island were generally too low lying to sustain considerable permanent ice (Selkirk *et al.*, 1990; Verwoerd, 1990b). Glaciation has the effect of reducing the area of land available and also the range of habitats available for vegetation. The bulk of the Heard Island and Iles Kerguelen Tertiary floras were destroyed during the Pleistocene cooling events, although *Pringlea antiscorbutica* and *Lyallia kerguelensis* are suggested as relict species (Young and Schofield, 1973). With warming however, the reverse occurs: land formerly unavailable to vegetation by glaciation is available for colonization when glaciers retreat.

Being south of the present position of the Antarctic Convergence, Heard Island is still extensively glaciated. Marion Island, which is north of the Antarctic Convergence and Grand Terre, which lies on the mean position of the Antarctic Convergence, have relatively small permanent remnant ice caps (in comparison to overall island size). The glacial moraines, on Marion Island and Grand Terre, in terms of vegetation habitat can be considered advanced models of those presently on Heard Island.

Heard Island and all other subantarctic islands south of the Indian Ocean have had Holocene volcanic activity (Verwoerd *et al.*, 1990). In particular both Heard Island and Marion Island have both had post-glacial volcanic accumulation, either lava flows or scoria or cinder cones. This allows for comparison of colonization of new ground under their different climatic regimes.

Heard and McDonald Islands generally have a more severe climate than the other 'oceanic origin' subantarctic islands. The significant component in relation to vegetation on these islands is the temperature regime with mean summer temperatures around 3°C on Heard and McDonald, compared with mean summer temperatures around 7°C on most of the other subantarctic islands (Marion and Prince Edward, Crozet, Kerguelen and Macquarie) (reviewed in Selkirk 1992). Heard Island has a distinct winter with temperatures below zero and considerable snow cover to low elevations.

In the Southern Hemisphere recent warming is most marked at the islands in the 45°-55°S zone (which incorporates the subantarctic islands), averaging approximately 0.25°C per decade (Jones, 1988). If this rate is maintained then in about 100 years Heard Island will have a climatic regime similar to other subantarctic islands such as Marion and Macquarie Islands. If the rate of warming increases then this will occur sooner.

1.6 Summary

Heard Island is part of the the Subantarctic Zone which incorporates six islands or island groups. Vegetation on subantarctic islands is devoid of trees and can generally be characterized by four plant communities; closed communities in which large-leaved perennial herbs are conspicuous, tussock grasslands, soligenous mires and feldmark. Bryophytes are important components of subantarctic terrestrial ecosystems. Major factors influencing subantarctic ecosystems include extreme oceanicity, geographic isolation and local animal disturbance. Subantarctic floras are generally species poor.

Within this chapter a detailed introduction to Heard Island's geology, origin, physiography, climate, flora and fauna is provided. Brief descriptions of Marion and Prince Edward Islands and Macquarie Island are also provided.

Comparison of Heard Island physical environments with other subantarctic islands is made. Heard Island, like the majority of subantarctic islands is of 'oceanic' volcanic origin. Like Iles Kerguelen, emergence above sea occurred during the Tertiary. Both Heard Island and Iles Kerguelen consequently developed Tertiary floras, the majority of which were destroyed with Pleistocene glaciation.

Being south of the Antarctic Convergence, climate on Heard Island is generally more severe than the majority of subantarctic islands. In addition, Heard Island is still extensively glaciated. However with present day climatic warming land removed from former vegetation by glaciation is available for colonization with glacial retreat. Glacial moraines on other subantarctic islands such as Grand Terre, Iles Kerguelen, can be considered advance models of those presently on Heard Island. Similarly post-glacial volcanic activity has occurred on all subantarctic islands south of the Indian Ocean. Comparison of volcanic accumulations on Heard Island and for example Marion Island can allow for comparison of colonization of new ground under their different climatic regimes.

With present warming in the Southern Hemisphere, Heard Island will have a similar climatic regime to other subantarctic islands such as Marion and Macquarie Islands in about 100 years.

The primary aim of this project is to document the bryophyte flora and to investigate the role of bryophytes within vegetation communities on the Heard Island. A major phytosociological study of the islands' vegetation is presented along with a new vegetation classification scheme for Heard Island, based on floristic diversity as well as the relationship between vegetation and environmental characteristics. A general framework of environmental conditions affecting vegetation on the island is provided and initial hypotheses as to ecological strategies of major taxa are proposed. The study concludes with a re-examination of the position of Heard Island within the Subantarctic Zone with regard to terrestrial ecosystems.

CHAPTER TWO

Vegetation survey methods

2.1 General survey details

The basis of this study is a vegetation survey conducted on Heard Island during the 1986/1987 Australian National Antarctic Research Expedition (ANARE) to Heard Island. Field work was also conducted on Marion and Prince Edward Islands (1987) and Macquarie Island (1988). On Heard Island, a stratified random sampling approach was adopted in selecting field sites. A total of 475, 1 x 1 m quadrats were surveyed during the eight week field period. Sites were chosen to cover as many visibly distinct vegetation types as possible. Locations of field sites are marked on Map 1 (back of thesis). Most of the quadrats (400) were either part of 10 random quadrats in a series of 10 x 10 m areas, sampling recognizable landscape unit/ vegetation types or, were contiguous or non-contiguous transects over distinct landscape features (such as creeks). The remainder of the samples were isolated quadrats.

In each quadrat the following habitat characteristics were noted:

1. location
2. geomorphological description, (moraine, clinker lava, lava flow, or sand), and general notes on the topography.
3. altitude
4. general slope of the quadrat (although in clinker lava sites such values are meaningless, due to the irregularity of the sites).
5. aspect.
6. unconsolidated substrate depth up to 100 cm. A metal pole, 1 cm in diameter was probed into the ground.

7* availability of water, rated on a subjective 5 - point scale ranging from 1 (very dry) to 5 (free surface water).

8* exposure to wind, rated on a subjective 5 - point scale ranging from 1 (very protected) to 5 (very exposed).

9* availability of light, rated on a subjective 5 - point scale ranging from 1 (exposed to full light conditions) to 5 (deep shade).

(* these scales are exponential scales)

Table 2.1 Braun-Blanquet (1932) scales of vegetation cover.

scale	cover value %
+	sparse
1	<5 %
2	5 - 20
3	20 - 50
4	50 - 75
5	75 - 100

Each quadrat was classified into one of Hughes (1987) vascular plant community categories.

In each quadrat, cover values using Braun-Blanquet (1932) scale (Table 2.1) were recorded for all vascular plants, bryophytes (as a collective unit), bare ground and rock (either non-consolidated or bedrock). Braun-Blanquet cover values (+ - 5) were transposed to a scale, 1-6,to facilitate numerical analysis. These values are termed 'modified' Braun-Blanquet values in the text. Notes on the individual cover values for major bryophyte species were also taken. Small samples of all bryophyte taxa were collected from each quadrat for indentification in Australia. Notes on lichens were made but due to the hardness of basalts on Heard Island few collections were made. Lichen data is not presented in this work.

Quadrat data has been stored in a data base (dBase III Plus). In the studies presented in Chapters Four, Five, Six and Seven the moss taxon list (see Table 1.3) was reduced from 43 to 36 taxa, as a number of species were treated as species complexes: *Verrucidens* spp. complex (combining *V. microcarpa* and *V. tortifolia*); *Dicranoweisia* spp. complex (combining *D. antarctica, D. brevipes* and *D. breviseta*); *Brachythecium* spp. complex (combining *B. austro-salebrosum* and *B. paradoxum.* The liverwort taxon list remained at 12.

Working in such a remote locality as Heard Island presents inherent logistical difficulties. Available field time was short. Transport between ice-free areas was by helicopter, commonly grounded by unfavorable weather. Access within major ice free areas was generally by foot over difficult terrain. It was necessary to conduct fieldwork opportunistically: a consequence of this is uneven sampling. I was fortunate to be able to conduct field work in three major ice-free areas on the island, the north-western regions of Laurens Peninsula, Azorella Peninsula and Mt Drygalski, the eastern region of Spit Bay and the southern region of Long Beach. Within these regions five geographic zones were defined (see Fig. 2.1). Time spent in each of these regions was however uneven and this is reflected in the number of quadrats sampled from each region (Fig. 2.1.). Additional 'grab-bag' collections were made at small, isolated, ice free areas to the south and north when visits were possible. Visits to these areas were mostly of very short duration (15 min) and the collection strategy was to collect as many different taxa as possible. Specific details of methods applicable to particular aspects of this study are found at the beginning of relevant chapters.

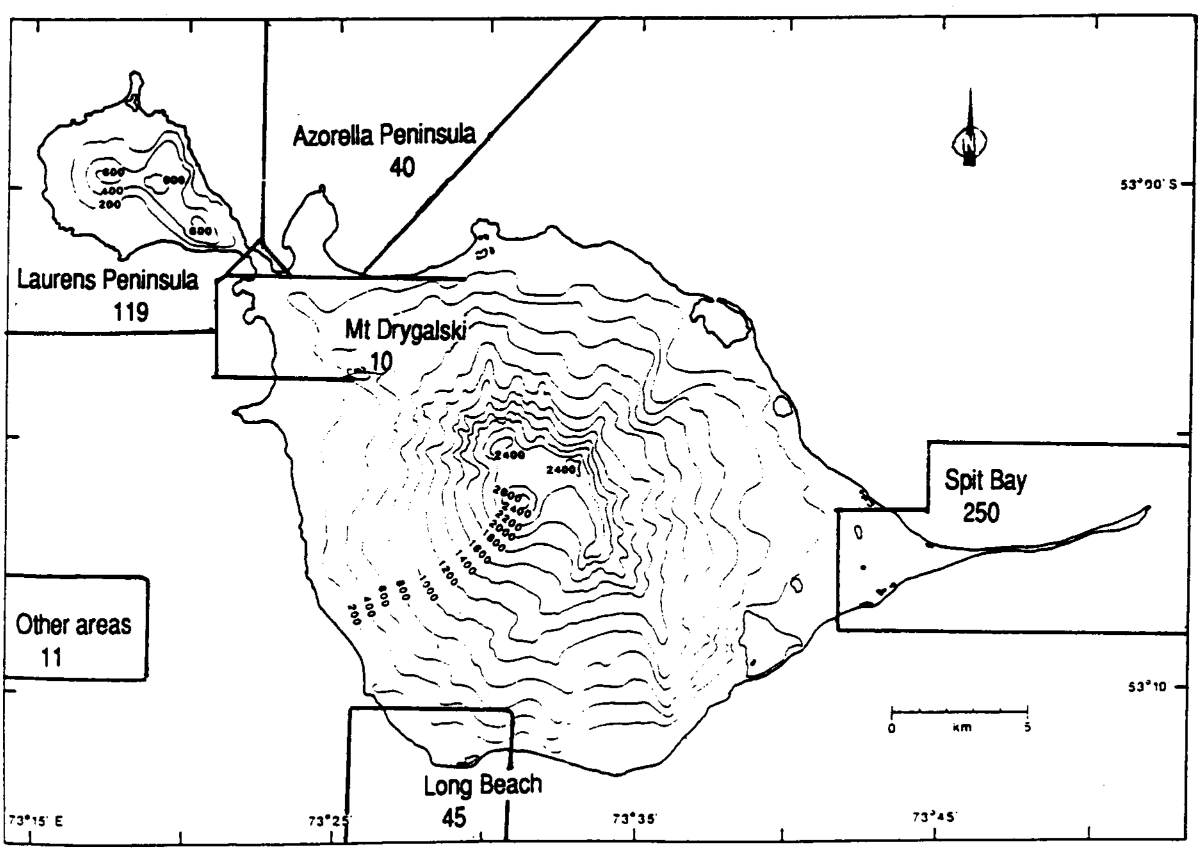


Figure 2.1 Areas on Heard Island where field work was conducted. Boundaries define geographic zones. Figures indicate number of quadrats surveyed within each of zone (total number of quadrats - 475).

CHAPTER THREE

The bryoflora of Heard Island: revised checklist, annotations and phytogeographical considerations.

3.1 Introduction

In this chapter the range of bryophytes on Heard Island is examined, and their phytogeographical relationships considered. The list of taxa recorded from the island is extended from 13 moss and 0 liverworts taxa to 44 moss and 12 liverwort taxa.

Three previous publications have reported moss species from Heard Island. Mitten (1885) recorded two species collected by the *Challenger* Expedition of 1884. Four species were collected by the Deutsche Südpolar Expedition of 1901-03 (Brotherus, 1906). Clifford (1953) reviewed these descriptions and examined material collected by the British, Australian & New Zealand Antarctic Expedition (BANZARE) of 1929 and by the Australian National Antarctic Research Expeditions (ANARE) of 1947 to 1952, enumerating 17 species (10 considering present day revision). There are no previous publications reporting liverwort species from Heard Island.

Dr Rod Seppelt and Prof Riclef Grolle assisted with the identification of specimens.
The aspects of this chapter relevant to mosses (Sections 3.2, 3.3.1, 3.3.3, and parts of 3.1 and 3.3 have been published by Bergstrom and Seppelt (1988). Ideas expressed in the discussion were my own but have been extensively discussed with Dr Rod Seppelt prior to publication.

3.2 Collections

Collections examined for the present checklist are those made by J. Jenkin (in 1980), H.F. Heatwole (in 1983), J.M.R. Hughes (in 1985), D.M. Bergstrom (in 1986), and J.J. Scott (in 1986 and 1987). All recent collections have been or will be lodged in the herbarium of the Australian Antarctic Division, Kingston, Tasmania (ADT). Collections examined by Clifford (1953) have not been located.

3.3 Annotated species list of bryophyte taxa recorded from Heard Island

Species marked with an asterisk (*) are new records.

3.3.1 Mosses

Andreaeaceae

Andreaea acuminata Mitt.

Andreaea mutabilis Hook. f. et Wils.

Polytrichaceae

Polytrichum alpinum (Hedw.)Mitt.

Polytrichum piliferum Hedw.

Psilopilum australe (Hook. f. et Wils.) Mitt.

Grimmiaceae

Grimmia immerso-leucophaea (C. Muell.) Kindb.

The reviews of *Grimmia* and *Schistidium* from South Georgia (Bell, 1984) and Patagonia (Deguchi, 1984) are relevant to the interpretation of Heard Island material. Morphological variation is pronounced and establishing the correct identity of all specimens will require more detailed study. Capsules show persistent columellae.

Grimmia sp.

Without capsules but differing in leaf morphology from fertile specimens of *G. immerso-leucophaea*.

**Schistidium apocarpum* (Hedw.)BSG.

**Schistidium falcatum* (Hook.f.& Wils.) van Zanten

**Schistidium* sp.

Similar to *G. immerso-leucophaea* in leaf morphology. Capsules lack persistent columellae.

Racomitrium crispulum (Hook.f.et. Wils.) Hook.f.et. Wils.

**Racomitrium lanuginosum* (Hedw.) Brid.

Ditrichaceae

**Ditrichum conicum* (Mont.) Par.

**Ditrichum immersum* van Zanten

Ditrichum subaustrale Broth.

Ceratodon purpureus (Hedw.)Brid.

In extreme environments the leaf morphology of *C.purpureus* is variable. As with Antarctic material (Seppelt 1986), taxonomic reassessment of at least some of the specimens attributed to *C. purpureus* from Heard Island may be required.

Seligeriaceae

Blindia contecta (H.f. et W) C.Muell

Reported by Clifford (1953) but not recorded since.

**Blindia robusta* Hampe.

**Verrucidens microcarpus* (Mitt.)van Zanten

Verrucidens tortifolius (Hook.f.et.Wils.) Reim.

Dicranaceae

**Dicranella* sp.

Small, barren plants with uncertain affinity, awaiting comparative study.

Dicranoloma billarderii (Brid. ex anon) Par.

The taxonomy of *Dicranoloma* requires revision.

**Dicranoweisia antarctica* (C.Muell.) Par.

A very variable species. The usually distinct, coloured alar cells separate this from the other *Dicranoweisia* species reported.

**Dicranoweisia brevipes* (C.Muell.) Card.

Alar cells often scarcely differentiated from adjacent cells of the leaf base and not inflated or coloured as in *D. antarctica.*

**Dicranoweisia breviseta* Card.

This species and *D. brevipes* seem doubtfully distinct. *D. brevipes* is smaller in size, has shorter leaves and the male gametangia are positioned below the perichaetia. In *D. breviseta,* male gametangia occur in short lateral branches. However, in specimens we have examined the gametoecial arrangement is variable. The relationship with *D. antarctica* also needs further assessment.

Pottiaceae

**Pottia heimii* (Hedw.) Feurnr.

**Tortula geheebiaeopsis* (C.Muell.)Broth.

Tortula robusta Hook. et Grev.

This species was reported from the ANARE collections (1947-52) by Clifford (1953). Since the specimen could not be located at MEL, Lightowlers (1985) considered this record as 'doubtful'. This species was not recorded amongst these collections.

Orthotrichaceae

**Muelleriella crassifolia* (Hook.f.et.Wils).Dus., subsp.*acuta* (C.Muell.) Vitt.

Bryaceae

**Bryum dichotomum* Hedw.

**Bryum pseudotriquetrum* (Hedw.) Meyer, Scherb., et Geartn.

The extreme morphological variation in this species has been discussed by Seppelt and Kanda (1986).

*Bryum sp. 1.

Similar in appearance to *B. pseudotriquetrum* but with a border of 1-4 rows of elongate cells distinct from adjacent lamina cells.

*Bryum sp.2.

Similar to *B. pseudotriquetrum* but with an auricle of large quadrate cells distinct from adjacent cells of the lamina.

*Bryum sp.3.

Small plants similar in size to *Bryum argenteum* and with leaves generally less than 1mm long. *Bryum* sp. 3. is readily distinguished by leaves having the costa excurrent into a short mucro or percurrent, the cells hexagonal to elongate rhomboid and all lamina cells chlorophyllose.

*Pohlia wahlenbergii (Web. et Mohr) Andrews

*Pohlia sp.

The margin of leaves in this species is slightly denticulate, and the base almost auriculate.

Pottiaceae

? *Trichostomum* sp.

Assignation of this taxon is not firm. Lanceolate leaf, widest below the middle. Costa excurrent into a short mucro. Cells below, narrow and elongate without papillae, becoming more or less quadrate and densely papillose with elongate papillae towards the tip. The outer abaxial layer of cells over costa scarcely differentiated. Section of costa has adaxial and abaxial stereid bands, cut stem exudes oil.

Bartramiaceae

Bartramia patens Brid.

Three species *B. papillata*, *B. diminutiva* and *B. robusta* have been reported from Heard Island (Mitten 1885; Brotherus 1906; Clifford 1953). There is considerable variation in vegetative characters. Dixon (1926) discussed the relationship between *B. patens* and *B. papillata* and considered them doubtfully distinct except that the inflorescence is dioicous in *B. papillata* and synoicous in *B. patens*. Robinson (1975) gave *B. diminutiva* as a synonym of *B. patens*. Matteri (1985) considered *B. robusta* a variety of *B. patens*. We consider all previous records of *Bartramia* from Heard Island to be forms of *B. patens*.

Philonotis cf *angustifolia* Kaal.

Lanceolate leaves with irregularly rectangular papillose cells. Upper margin dentate.

Amblystegiaceae

Amblystegium serpens Hook. f. et Wils.

Drepanocladus uncinatus (Hedw.) Warnst.

Brachytheciaceae

**Brachythecium austro-salebrosum* (C.Muell.) Par.

The taxonomy of this species has been discussed at length by Newton (1979). The record of *B.* cf. *salebrosum* of Clifford (1953) may belong here.

**Brachythecium paradoxum* (Hook.f.et Wils) Jaeg.

3.3.2 Liverworts

Codoniaceae

**Fossombronia australis* Mitt.

Marchantiaceae

**Marchantia berteroana* Lehm. et Lindenb.

Cephaloziellaceae

**Cephaloziella exiliflora* (Tayl.) Dovin

**C. varians* (Gottsche) Steph.

Jungermanniaceae

**Cryptochila grandiflora* (Lindenb. et Gottsche)

**Jungermannia coniflora* Schiffn.

Geocalycaceae

Pachyglossa fissa (Mitt.) Herz. & Grolle.

Table 3.1 Phytogeographical distribution of Heard Island moss species. Data from Ando (1979); Bell (1984); Bell and Greene (1975); Brotherus (1906); Clark and Lightowlers (1983); Clifford (1953); Crum and Anderson (1981); Deguchi (1984); Delarue (1988); Gremmen (1982); Hébrard (1970); Ireland (1982); Ireland *et al.* (1987); Lightlowlers (1985); Magill (1981); Matteri (1977, 1985); Mitten (1885); Newton (1973, 1979); Ochi and Ochyra (1985); Ochyra and Bell (1984); Ochyra *et al.*(1986); Sainsbury (1955); Scott and Stone (1976); Selkirk *et al.*(1990); Seppelt and Russell (1986); Smith (1978); R.I.L. Smith (1984b); Vitt (1976, 1979); Wijk *et al.* (1959-1969); Zanten (1971).

Distribution:	South America	Maritime Antarctica	South Georgia	Africa	Marion Island	Prince Edward Island	Ile Crozet	Ile Kerguelen	Heard Island	Australia	Macquaric Island	New Zealand	Auckland Islands	Northern Hemisphere
Andreaeaceae														
Andreaea acuminata	+	−	+	−	+	+	+	+	+	+	+	+	+	−
Andreaea mutabilis	+	−	−	−	−	−	−	−	+	−	+	+	+	+
Polytrichaceae														
Polytrichum alpinum	+	+	−	−	−	−	−	−	+	+	+	+	−	+
Polytrichum piliferum	+	+	+	+	+	−	−	−	+	+	−	−	−	+
Psilopilum australe	−	−	−	+	−	−	−	−	+	+	+	+	−	−
Grimmiaceae														
Grimmia immerso-leucophaea	+	−	+	−	+	+	+	+	+	−	−	−	−	−
Schistidium apocarpum	+	+	+	−	−	−	−	−	+	+	+	+	−	+
Schistidium falcatum	+	+	+	−	+	−	−	+	+	−	−	−	−	−
Racomitrium crispulum	+	+	+	+	+	+	+	+	+	+	+	+	+	−
Racomitrium lanuginosum	+	+	+	+	+	−	+	+	+	+	+	+	+	+
Ditrichaceae														
Ditrichum conicum	+	−	−	+	+	+	+	+	+	−	−	−	−	−
Ditrichum immersum	−	−	−	−	+	−	+	−	+	−	−	−	−	−
Ditrichum subaustrale	−	−	−	−	−	−	−	+	+	−	−	−	−	−
Ceratodon purpureus	+	+	+	+	+	−	−	−	+	+	+	+	+	+
Seligeriaceae														
Blindia contecta	+	−	−	−	−	−	−	+	+	−	−	+	+	−
Blindia robusta	+	−	−	−	−	−	−	−	+	+	+	+	−	−
Verrucidens microcarpus	−	−	−	−	+	+	−	+	+	−	−	−	−	−
Verrucidens tortifolius	−	−	−	−	−	−	−	−	+	−	+	−	−	−
Dicranaceae														
Dicranoloma billarderii	+	−	−	+	+	−	+	+	+	+	+	+	+	−
Dicranoweisia antarctica	−	+	+	+	−	−	−	−	+	+	+	+	+	−
Dicranoweisia brevipes	+	−	−	−	−	+	−	−	+	−	−	−	−	−
Dicranoweisia breviseta	+	−	−	−	+	+	−	−	+	−	−	−	−	−
Pottiaceae														
Pottia heimii	+	−	+	+	−	−	−	−	+	+	+	+	−	+
Tortula geheebiaeopsis	−	−	+	−	−	−	−	+	+	−	−	−	−	−
Tortula robusta	+	−	+	−	−	−	−	−	+	−	−	−	−	−
Orthotrichaceae														
Muelleriella crassifolia	+	+	+	−	+	+	+	+	+	−	+	+	+	−
Bryaceae														
Bryum dichotomum	+	+	−	−	+	−	+	−	+	+	+	+	+	+
Bryum pseudotriquetrum	−	+	+	+	−	−	−	−	+	+	+	+	+	+
Pohlia wahlenbergii	+	+	−	+	−	−	−	−	+	+	+	+	+	+
Bartramiaceae														
Bartramia patens	+	+	+	−	+	+	−	+	+	+	+	+	+	−
Philonotis cf. *angustifolia*	−	−	−	−	+	−	+	−	+	−	−	−	−	−
Amblystegiaceae														
Amblystegium serpens	+	−	−	+	−	−	−	−	+	+	+	+	+	+
Drepanocladus uncinatus	+	+	+	+	+	+	+	+	+	+	+	+	−	+
Brachytheciaceae														
Brachythecium austro-salebrosum	+	+	+	−	+	−	−	+	+	−	−	−	−	−
Brachythecium paradoxum	+	−	−	+	+	−	+	+	+	+	−	+	−	−

Pedinophyllopsis abdita (Sull.) Schuster et Inoue

Gymnomitriaceae

**Herzogobryum atrocapillum* (Hook. f. et Tayl) Grolle

**H. vermiculare* (Schiffn) Grolle

*Lophocoleoideae sp.

Scapaniaceae

**Blepharidophyllum densifolium* (Hook.) Angstr. ex Mass.

3.3.3 Summary Notes on Clifford's 1953 checklist

Of the 17 moss species reported by Clifford (1953), 10 species have been retained in this checklist. Seven species have been either reduced or changed due to synonomy: *Bartramia papillata*, *B. diminutiva* and *B.robusta* = *B. patens* (see annotations); *Blindia tortifolia* and *Dicranoweisia grimmiaceae* = *Verrucidens tortifolius*; *Grimmia insularis* = *Blindia contecta*; *Racomitrium nigritum* = *R. crispulum* (Wijk *et al*, 1959-69). As stated earlier the record of *Brachythecium* cf *salebrosum* may be the same as this record of *B. austro-salebrosum*. As Clifford's specimens can not be located at MEL, this can not be verified.

3.4. Discussion

3.4.1 Phytogeography

Table 3.1 records the phytogeographical distribution of the 35 moss taxa named to species level. The list of inter-regional relationships will certainly be incomplete due to the uncertain status of some taxa and the incomplete knowledge of the moss flora of areas such as Prince Edward Island and Iles Kerguelen. Despite these problems there are significant discernible patterns worthy of examination. Critical phytogeographical comparisons of the liverwort flora however are not possible at present. There have not been thorough liverwort surveys on most subantarctic islands and there is great difficulty in identification of sterile liverwort material.

Bryophytes have not been recorded in the fossil record from Heard Island but are components of almost all modern terrestrial ecosystems. It is likely that they were components of the Heard Island Tertiary flora (see 1.2.3).

The sporadic, 'island building' vulcanism on Heard Island is most likely to have destroyed only local plant communities, not the island's entire biota. Volcanic activity would have eventually increased the area available for vegetation establishment.

The flora of Heard Island has been subjected to climatic change, including substantial cooling episodes. The mid volcanic phase (Late Miocene-Early Pliocene) was accompanied by glaciation (Clarke *et al*, 1983) and there were many cooling cycles during the Pleistocene (Fink & Kukla, 1977). The formation of glaciers and a possible ice cap on Heard Island would have reduced the area of land available for vegetation and also the range of habitats available for vegetation establishment.

With major cooling episodes during the Pleistocene large portions of the flora on Heard Island and Iles Kerguelen became extinct; for example there are no current records of pteridophytes on Heard Island. It has been suggested that two angiosperms, *Pringlea antiscorbutica* and *Lyallia kerguelensis*, present on Iles Kerguelen are relicts from the Tertiary Kerguelenian flora. Fossil pollen of these species has been found in sediments from Iles Kerguelen, dating from the latter part of the last glacial episode (Young & Schofield, 1973). Only *Pringlea* is present on Heard Island today.

Polar bryophytes today possess physiological attributes such as desiccation and frost tolerance, but such features are widely distributed amongst bryophytes generally (Longton, 1988). Some bryophytes now on Heard Island may have survived past glacial as well as volcanic disturbances to the island and be relicts of the Tertiary flora.

I propose six species of moss as potential Tertiary survivors due to their restricted world distribution. *Ditrichum immersum, D. subaustrale, Philonotis angustifolia, Verrucidens microcarpa, V. tortifolius* are endemic to subantarctic islands and a sixth, a subspecies of *Muelleriella,* is endemic to the Kerguelen region. *Ditrichum subaustrale* is known only from Heard Island and Iles Kerguelen; perhaps having evolved from a related species which could have arrived at some stage since the Tertiary. *Muelleriella crassifolia* is found in supralittoral zones on all the subantarctic island groups, the Antarctic Peninsula and the southernmost coastal regions of New Zealand and South America. There are two subspecies within this distributional areas (Vitt, 1976): *M. crassifolia* subsp. *acuta* found only on Iles Kerguelen, Iles Crozet and now Heard Island, and *M. crassifolia* subsp. *crassifolia* found throughout the remainder of the species' range with a stepped cline from the New Zealand region to South America and then Marion Island. Vitt (1976) suggested that in relatively recent times there has been little gene exchange and lack of long distance dispersal between populations of *M. crassifolia* in the Kerguelen region and those in other regions. Thus the subspecies *M. crassifolia* subsp. *acuta* has probably either evolved in the Kerguelen region after formation of these islands during the Miocene or perhaps in coastal areas of East Antarctica and dispersed to the Kerguelen region.

Other moss species are probably more recent arrivals, particularly *Brachythecium austro-salebrosum, Dicranoweisia brevipes, Dicranoweisia breviseta, Grimmia immerso-leucophaea, Schistidium falcatum, Tortula geheebiaeopsis,* and *Tortula robusta,* which occur in southern South America and on up to five subantarctic island groups. These species are absent from Australasia and geologically young Macquarie Island. Such a distribution may reflect an island hopping dispersal pattern from South America, in the direction of the prevailing westerly wind.

Nine species (*Andreaea mutabilis, Amblystegium serpens, Bryum pseudotriquetrum, Ceratodon purpureus, Drepanocladus uncinatus, Pohlia wahlenbergii, Polytrichum alpinum, Polytrichum piliferum, Pottia heimii*) have bipolar disjunct distributions, occurring in cool-temperate to polar regions in both hemispheres. Schofield (1974) suggested that bipolar disjunct species reflect very long distance dispersal events from the Northern Hemisphere, either during or post Pleistocene.

Psilopilum australe, *Andreaea acuminata*, *Bartramia patens*, *Blindia contecta*, *B. robusta*, *Dicranowesia antarctica*, *Brachythecium paradoxum*, *Dicranoloma billarderii*, and *Ditrichum conicum* occur on two or more southern continental land masses as well as some of the subantarctic island groups. *Bryum dichotomum*, *Racomitrium lanuginosum*, *Racomitrium crispulum* and *Schistidium apocarpum*, have widespread or cosmopolitan distributions.

Andreaea acuminata, *Drepanocladus uncinatus*, *Racomitrium crispulum* and *R. lanuginosum* are the only moss species which occur on all the subantarctic island groups.

3.4.2 Size of Flora

The Heard Island extant moss and liverwort flora is small compared with that of other subantarctic islands (Macquarie Island has 85 moss and 51 liverwort taxa; Marion Island 81 moss and 31 liverwort; South Georgia ca 175 moss and 85 liverwort taxa) (Selkirk *et al.*, 1990; Seppelt & Russell, 1986; Smith, R.I.L. 1984a). Despite the relatively large size of Heard Island, there is only limited surface area available for vegetation (see Table 1.4 & Map 1). This ensures a limited number and restricted range of habitats and limitation of the bryophyte diversity. During the last forty years there has been major glacial retreat on Heard Island (see 1.2.1). With continued global warming of the atmosphere, glacial retreat will continue, exposing further habitats and permitting other species to colonize the island. The diaspores for these species may already be present on the island. The huge expanse of Big Ben may act as a sink for airborne particles. Meltwater could then supply diaspores to newly exposed habitats.

3.5 Summary

A revised annotated checklist of the bryoflora for Heard Island is presented. Only 10 moss taxa had been previously recorded from the island. This has been expanded to 42 moss taxa and 12 liverwort taxa. Phytogeographical distribution of the 35 moss taxa named to species level was examined. These taxa were divided into two distinct components, potential Tertiary relicts and more recent arrivals. The more recent arrivals can be grouped into species restricted to South America and the subantarctic islands, bipolar disjunct species, Southern Hemisphere species or widespread/cosmopolitan species.

All flora has reached Heard Island via some form of transoceanic dispersal (see Section 8.2.1). The size of the moss flora is small compared with that of other subantarctic islands. Heard Island is more than 80% ice covered and the paucity of the flora reflects restricted diversity and limited availability of suitable habitats.

CHAPTER FOUR

Distribution of bryophytes on Heard Island

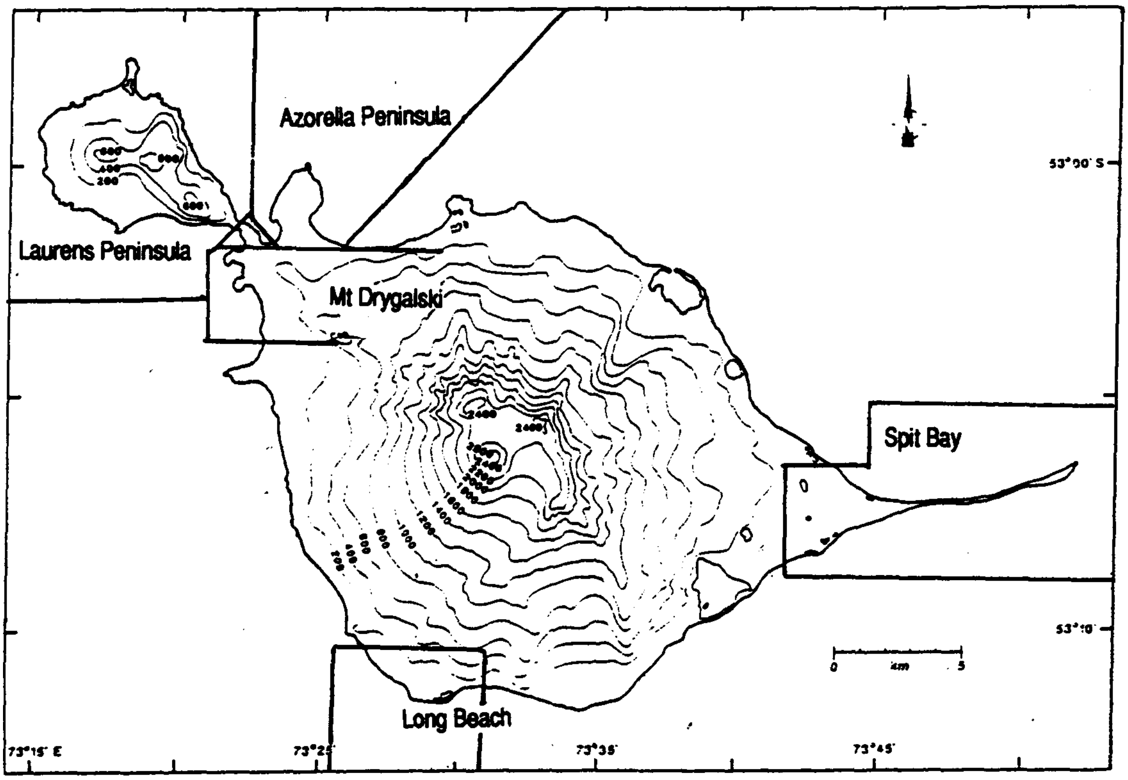
4.1 Introduction

Each species present on Heard Island has arrived as a result of a long distance dispersal event. Initial colonization processes would have involved propagule arrival, germination and establishment, followed by local dispersal.

Extensive glaciation during the Pleistocene would have reduced surface area and habitat diversity available for plants (see Sections 1.4.1 & 3.3.1). With an ameliorating climate during the Holocene these trends have been reversing. The areas presently available for plants on Heard Island are generally the result of landform building events; either glacial moraines exposed with the retreat of glaciers or non-glaciated lava flows or scoria cones. Colonization of most of these areas has occurred post last glacial maximum. Basal peats on the oldest terminal moraines at Dovers Moraine, Spit Bay have been C^{14} dated at 2120 $\pm$ 80 yr BP (SUA 2810). Extensive vegetation has been recorded even on very young sites, exposed post 1947 (Scott, 1990). As tide water glaciers isolate major ice-free areas, each of these areas can be considered as individual islands and Heard Island an archipelago. Separate colonization processes would be required for each ice free region.

This study investigates the diversity of bryophytes within and between ice-free areas. In considering differences in diversity between geographic zones, it is acknowledged that the data will be incomplete. This is an unavoidable artifact of limited field time and is common to most, if not all vegetation surveys. For example, Nillsson & Nillsson (1982 & 1985) found that thoroughly executed censuses of vascular plants on Swedish islands recorded on average less than 80% of all species present. Additionally, no collections were made in

Figure 4.1 Map of Heard Island showing geographic zones.



vegetated areas north of Skua Beach or in Paddick Valley (see Fig. 1.3). However, some meaningful comparisons can be made.

4.2 Methods

4.2.1 Analysis of distribution

Within the three major regions in which the vegetation survey was conducted, five geographic zones were defined. These are presented again in Figure 4.1. Taxa lists for each of these zones were compiled and tabulated and were compared with lists from other zones. Sørensens's Index of Similarity (Schmitt & Slack, 1990) was calculated for each comparison where:

$$\text{Sørensen's Index} \quad I = \frac{2w}{m+n}$$

w = no. of species common between zones

m = no. of species in first zone

n = no. of species in second zone

Taxa lists for Saddle Point, Cape Gazert, Cape Pillar and Cape Arkona (see Fig. 1.3) were also compiled, but as field-time in these areas was very short they are not considered in the comparisons.

4.3 Distribution and Diversity

Table 4.1 records bryophyte taxa distribution and Table 4.2.a summarizes the number of taxa recorded from the five geographic zones. Table 4.2.b presents Sorrensen's Index of similarity for comparison between the zones. It can be seen that of the 48 bryophyte taxa being considered, 18 have been recorded from all five geographic zones. These represent a

Table 4.1. Distribution of bryophytes on Heard Island

LP - Laurens Peninsula
AP - Azorella Peninsula
MD - Mt Drygalski
LB - Long Beach
SB - Spit Bay
CG - Cape Gazert
SP - Saddle Point
CP - Cape Pillar
CA - Cape Arkona

	LP	AP	MD	LB	SB	CG	SP	CP	CA
Amblystegium serpens		+	+						
Andreaea acuminata	+		+	+	+		+		
Andreaea mutabilis	+	+	+	+				+	+
Bartramia patens	+	+	+	+	+		+		+
Blindia robusta	+		+	+	+				
Brachythecium spp.	+		+	+	+			+	
Bryum dichotomum	+				+				
Bryum pseudotriquetrum	+	+	+	+	+	+			
Bryum sp. 1	+				+				
Bryum sp. 2	+	+			+				
Ceratodon purpureus	+	+	+	+	+		+	+	+
Dicranella sp.	+		+	+	+				+
Dicranoloma billarderii	+		+	+					
Dicranoweisia spp.	+	+	+	+	+	+	+	+	+
Ditrichum conicum	+			+	+			+	
Ditrichum immersum	+	+	+	+	+	+	+	+	+
Ditrichum subaustralae	+			+	+				
Drepanocladus uncinatus	+	+	+	+	+	+		+	
Grimmia immerso-leucophaea		+	+	+	+		+		+
Grimmia sp.					+				
Muelleriella crassifolia	+	+	+	+	+			+	
Philonotis angustifolia	+			+	+				
Pohlia wahlenbergii	+	+	+	+	+			+	
Pohlia sp.	+	+	+	+	+				
Polytrichum alpinum	+	+	+	+	+				
Polytrichum piliferum				+	+				
Pottia heimii	+			+	+			+	
Psilopilum australe	+		+	+	+				
Racomitrium crispulum	+	+	+	+	+	+	+	+	+
Racomitrium lanuginosum	+			+					
Schistidium apocarpum	+	+	+	+	+		+	+	+
Schistidium falcatum	+	+			+				
Tortula andersonii					+				
Tortula geheebiaeopsis	+				+				
Trichostomum sp.	+	+	+	+	+			+	+
Verrucidens spp.	+		+	+	+		+		
Blepharidophyllum densifolium	+		+	+	+				
Cephaloziella exiliflora	+	+	+	+	+				
Cephaloziella varians	+	+	+	+		+			
Cryptochila grandiflora	+		+	+					
Fossombronia australis	+	+	+	+	+	+	+	+	
Herzogobryum atrocapillum	+			+	+		+		
Herzogobryum vermiculare	+		+	+					
Jungermannia coniflora	+			+	+				
Lophocoleoideae sp.	+	+						+	
Marchantia berteroana				+	+				
Pachyglossa fissa	+	+	+	+	+		+		
Pedinophyllopsis abdita	+	+	+	+	+	+	+	+	+

group of widespread taxa within which a core of five, *Dicranoweisia* spp., *Ditrichum immersum*, *Racomitrium crispulum*, *Trichostomum* sp., *Pedinophyllopsis abdita*, can reasonably be described as ubiquitous in ice-free areas of Heard Island. These taxa were recorded from all ice free areas from which collections were made. Widespread distribution of species between ice free zones could represent multiple colonization events (at least one at each ice free area) or colonization of one ice free zone followed by 'island hopping' to one or many of the other ice free zones.

Tables 4.1 & 4.2. a & b illustrate the high degree of similarity in taxa diversity, between the ice free areas in general, and between the major ice free regions of Laurens Peninsula, Long Beach and Spit Bay in particular. . However, not all species occur in all regions. For example *Grimmia immerso-leucophaea* and *Marchantia berteroana* have not been recorded from Laurens Peninsula (occurring only at Long Beach and Spit Bay). The possibility of such conspicuous species being overlooked is remote and suitable habitats for these species appear to exist on Laurens Peninsula. It is most likely that propagules of these species have not arrived, or have not established on Laurens Peninsula. Similarly, *Racomitrium lanuginosum* was not recorded from Spit Bay. The Sorrensen's Index of similarity is highest (0.88) in comparisons of moss taxa between Laurens Peninsula & Long Beach and between Laurens Peninsula & Spit Bay. The similarity index is slightly lower for comparison between Long Beach with Spit Bay (0.83). This may suggest that a sizable proportion of the moss taxa arrived and established on Laurens Peninsula and then 'island hopped' in an easterly and/or southerly direction along prevailing winds.

Azorella Peninsula and the Mt Drygalski zone have significantly lower moss species diversity than the other regions (19 & 23 respectively) which is reflected with some of the lowest Sorrensens's Index values for the survey (eg. Azorella Peninsula vs Spit Bay, I = 0.63). This is most likely due to the smaller surface areas of these regions or lower habitat diversity. The possibility of lower habitat diversity can be illustrated on Azorella Peninsula. Two conspicuous species, *Polytrichum piliferum* and *Philonotis angustifolia*

Table 4.2.a. Number of bryophyte taxa recorded from each of the five geographic regions on Heard Island.

	MOSSES	LIVERWORTS	TOTAL
Laurens Peninsula	31	11	42
Azorella Peninsula	19	7	26
Mt Drygalski	34	8	31
Long Beach	28	11	39
Spit Bay	32	8	40

Table 4.2.b. Sorrensen's Index of similarity for mosses (above diagonal line) and liverworts (below diagonal line) between geographic zones on Heard Island.

MOSSES

	LP	AP	MD	LB	SB
Laurens Peninsula (LP)		0.64	0.81	0.88	0.88
Azorella Peninsula (AP)	0.77		0.76	0.63	0.63
Mt Drygalski (MD)	0.84	0.66		0.86	0.73
Long Beach (LB)	0.90	0.66	0.84		0.83
Spit Bay (SB)	0.84	0.66	0.62	0.84	

LIVERWORTS

were not recorded from this area. Twenty seven out of a total of 28 occurrences of *P. piliferum* were from moraines. Moraines are not present on Azorella Peninsula. The absence of this taxon may reflect the absence of moraine habitats from the area. Similarly, 14 out of 15 occurrences of *P. angustifolia* from elsewhere on the island had a water scale rating of 4 or 5 (mean 4.6 - very wet) (see 2.2.). On Azorella Peninsula water is present in the form of pool complexes, but these are intensively used by elephant seals as wallows. Whinam (1989) reported that bryophytes, sensitive to disturbance, are absent from areas of heavy animal impact. Again, absence of suitable habitat may explain the absence of this species from Azorella Peninsula.

4.4 Summary

A vegetation survey of Heard Island consisting of 475 quadrats was conducted over 5 geographical zones; Laurens Peninsula, Azorella Peninsula, Mt Drygalski, Long Beach and Spit Bay. The opportunistic nature of the field work has resulted in an uneven distribution of quadrats between zones. Additional collections were also made from remote Saddle Point, Cape Gazert, Cape Pillar and Cape Arkona. Ice free areas on Heard Island are separated from each other by glaciers. With this situation Heard Island is comparable to an archipelago and ice free areas to small islands.

Of the 48 bryophyte taxa whose distribution was considered there appeared to be a group of 18 which were widespread. These taxa were recorded from the five geographic zones. Five of these taxa were ubiquitous, being recorded from all areas where collections were made. Taxa with widespread intra-island distribution represent either multiple individual long distance dispersal and colonization events or single long distance dispersal and colonization events followed by local 'island hopping' dispersal to other zones.

Absence of some conspicuous species from particular zones appeared to reflect situations where either propagules had not arrived or restricted habitat variety prevented establishment of species.

CHAPTER FIVE

The diversity of bryophytes within Heard Island vegetation units

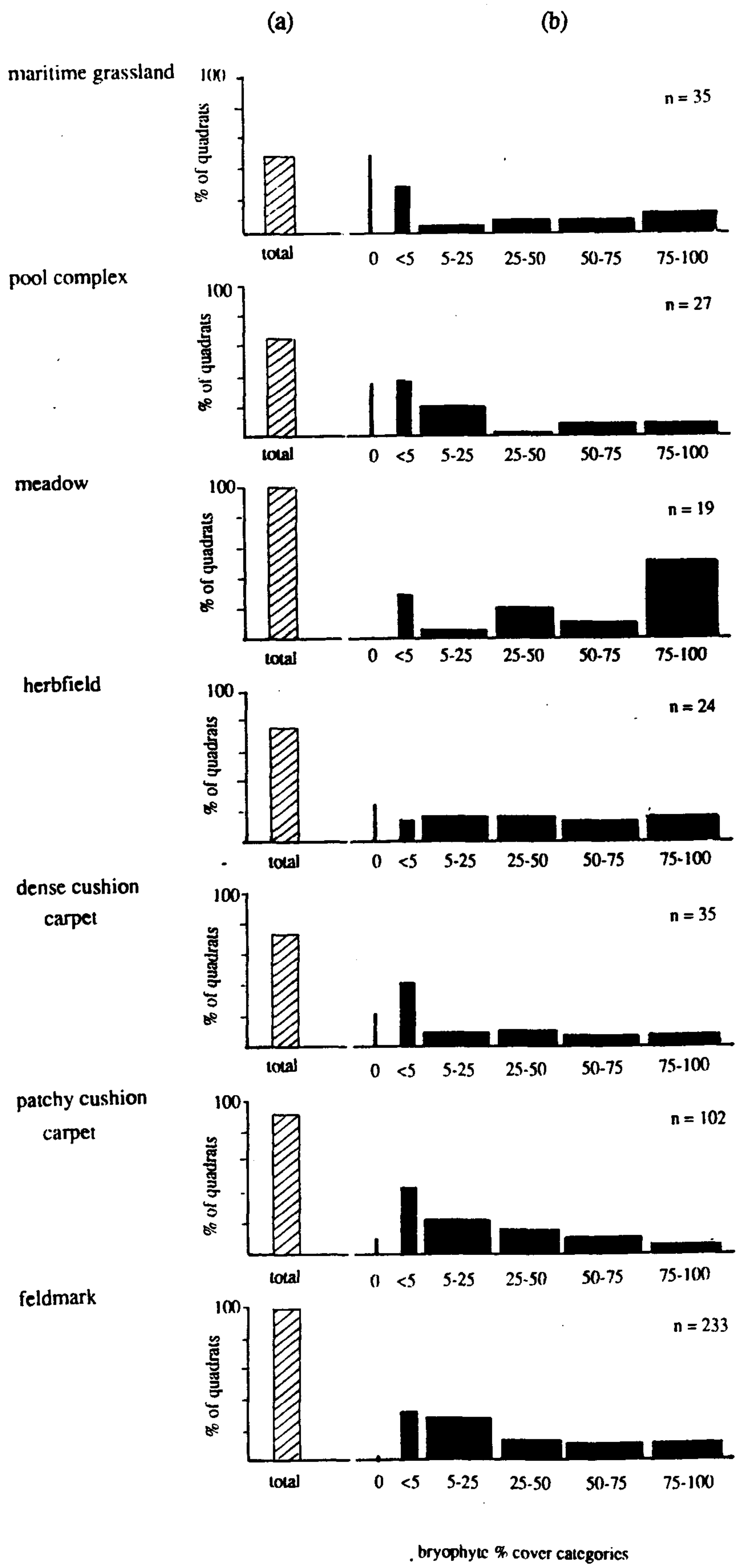
5.1 Introduction

This chapter documents the general vegetation survey conducted on Heard Island. In particular it examines the diversity of bryophyte taxa within common vegetation and landscape units on Heard Island. Previous plant community studies on the island have focused on the vascular plant component, generally amalgamating all bryophytes into the single taxon 'bryophytes' (Hughes, 1987, Whinam, 1989) or a small number of collective groups (Scott, 1990). Total bryophyte cover is a useful measure but the difficulty with this approach is that information on plant community complexity and species richness is not gathered. In this study both total bryophyte cover and floristic details were recorded from sites examined.

As this is an introductory study of the bryophyte component of Heard Island vegetation a semi quantitative approach has been taken. Such an approach provides descriptions and classification of common vegetation; enables comparison with vegetation data from other regions; establishes an initial framework for considering spatial relationships of species and vegetation types; reveals efficiently the principal directions of variation within the vegetation complex; and permits the generation of working hypotheses concerning the role of environmental factors influencing the vegetation (Birks 1973).

Details of the survey are provided in Chapter 2. Information pertaining to the two analyses is in Sections 5.3.1 and 5.3.2. Although the initial aim of the study was to investigate bryophyte assemblages and their role within major vegetation or landscape features, the study also revealed information on the structure and complexity of major vegetation types

Figure 5.1. a Percentage of quadrats from which bryophytes were recorded for all sites categorized into Hughes' (1987) vascular plant categories.
Figure 5.1.b Percentage of total quadrats in which bryophytes contributes particular % cover.



on the island.

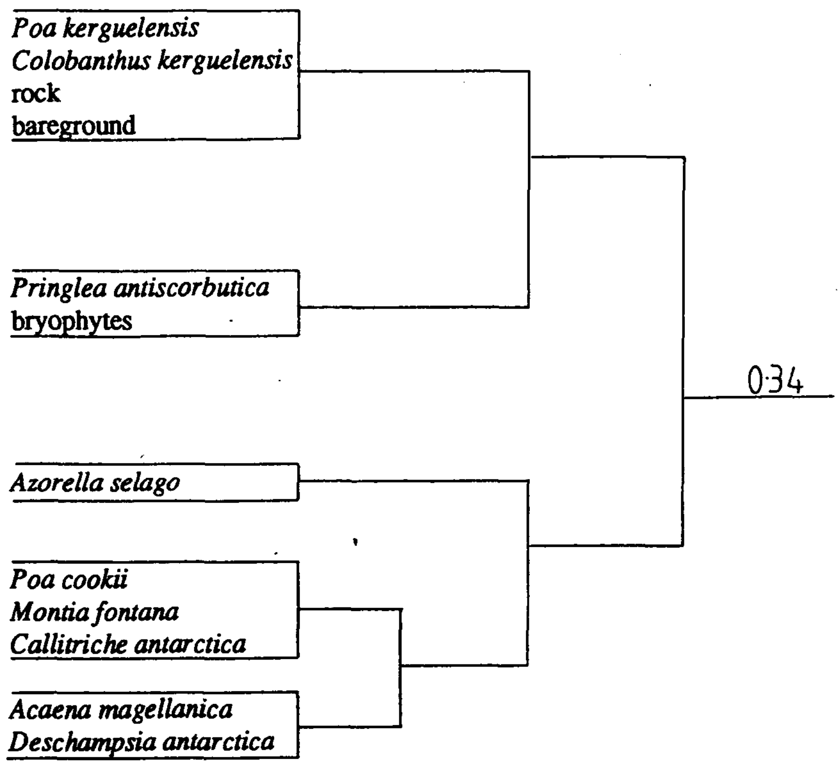
5.2 Bryophytes in Hughes' (1987) vascular plant categories.

Vegetation at each site surveyed, and the surrounding area (approximately 2000 m^2) was categorized into one of Hughes' (1987) six vascular plant communities: feldmark, cushion carpet, herbfield, meadow, pool complex and maritime grassland (see Section 1.3.3). Hughes' survey was very preliminary, examining a total of only 30, 1m^2 quadrats and 12 transects. Bryophyte taxa were not recorded from cushion carpet or maritime grassland communities. Bryophytes were reported to occupy only between 1 and 25% vegetation cover in the other four vascular plant communities (feldmark, pool complex, herbfield and meadow).

In contrast, this present study included an examination of 475, 1 m^2 quadrats. This survey shows that Hughes' data under-represents the bryophytic components of the vegetation. Figure 5.1a shows that bryophytes are present in sites which represent examples of all vascular plant community categories, although bryophytes were not recorded from all 475 quadrats studied. Of sixty quadrats that had no bryophytes present, the greatest proportion were in maritime grassland (17/35).

A substantial proportion of quadrats, (158/475) had bryophyte cover of 25% or more. Many quadrats (51/475) had bryophyte cover between 75 - 100%. These quadrats occurred across the range of community categories and included 10 of the 19 quadrats classified as meadow (Fig 5.1). Cover is a significant measure of the relative importance of a component within a particular vegetation unit, but it is not the only useful measure. This is particularly relevant to the feldmark community category where by definition, total vegetation cover is generally low. In such communities bryophytes may be the most prominent component yet have low cover values. Other measures such as species richness can provide insight in such situations and will be presented later in the chapter.

Figure 5.2 Dendrogram showing taxon classification from preliminary TWINSPAN analysis based on Braun-Blanquet cover values.



5.3. Ordination and classification analyses

5.3.1. TWINSPAN Classification analysis

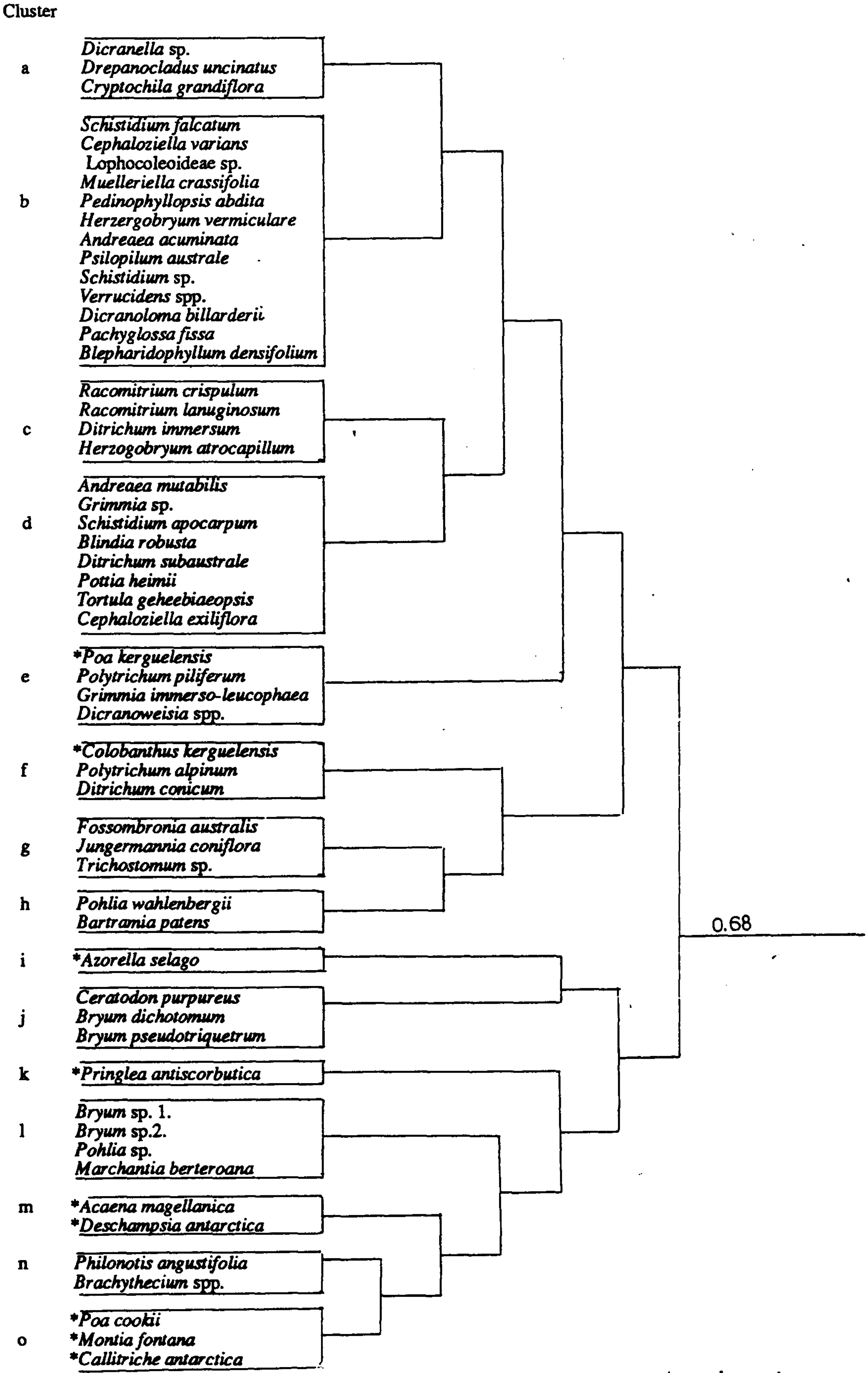
TWINSPAN is a polythetic divisive method of ordination and classification. The analysis constructs an ordered two way table of taxa and sites by identification of differential (discriminating) species. Sites are classified first and taxa second using the site classification as a basis. Levels of division are determined by the coherence of the ecological groupings obtained. An 'indicator' ordination is performed, in which highly preferential taxa or 'indicator' taxa within ecological groupings are identified and ranked.

One of the advantages of TWINSPAN is that cover values can be used in the analysis. A preliminary analysis of the vegetation survey data set was performed using the Braun Blanquet cover values for all vascular species recorded and total bryophyte cover. Bare ground and rock cover values (see Section 2.2.1) were also included with bare ground and rock being considered as taxa. A dendogram showing the taxon classification is presented (Fig. 5.2), but the cumbersome two way table of taxa vs sites of all 475 quadrats is not presented. Although this classification is successful with regard to most of the vascular species, it is inadequate with regard to the bryophyte component of Heard Island vegetation.

The primary split in the dendogram accounted for 34% of variance in the data. The first cluster of species, *Poa kerguelensis*, *Colobanthus kerguelensis*, rock and bare ground reflect forms of harsh, feldmark environments, indicative of extensive bare ground and exposed unvegetated rocky areas. The second classification in the top half of the dendogram is ineffectual because of the treatment of bryophytes as a single widespread, all encompassing species. No interpretation can be applied to this clustering.

The lower half of the dendogram include species which commonly associate in non-feldmark environments as well as *Azorella selago*. The classification of *Azorella* by itself

Figure 5.3 Dendogram showing TWINSPAN taxon classification of both bryophyte and vascular plant taxa, based on presence/absence data.



* vascular species

is discussed later in this section. In the second clustering in the lower half on the dendogram, *Poa cookii*, *Montia fontana* and *Callitriche antarctica* are species found in areas of nutrient enrichment.

The final clustering, *Deschampsia antarctica* and *Acaena magellanica* reflect vegetation which would be included in either meadow or herbfield vegetation categories. Vegetation incorporating these species was not extensively sampled during this survey. All quadrats were in the Spit Bay region and at the sites there were continuums between areas in which *Deschampsia* was significant and others in which *Acaena* was significant.

A TWINSPAN analysis of the full data set, including bryophyte taxa, was conducted using presence/absence data only. Figure 5.3. presents the dendogram of the taxon classification. The most obvious and striking feature of this figure is that with the inclusion of bryophyte taxa the dendogram is far more extensive. However, the vascular plants, indicated by an * (except for *Pringlea antiscorbutica*) are generally in a similar positions compared with Figure 5.2. This implies that there have not been significant changes to the classification of these taxa with the reduction of data from cover values to presence/ absence levels. Collection of cover value information for bryophytes was not possible as the bryophyte taxa had not been established at the time of fieldwork. I believe also that it would be most impractical to collect cover value information for all bryophyte taxa because important and prominent species complexes such as *Dicranoweisia* spp. can only be distinguished from other species by microscopic examination.

There are 15 taxon clusters in total (a-o)(Fig 5.3.). These clusters indicate that there are distinct suites of bryophyte taxa within the vegetation units on Heard Island. That is, there are bryophyte taxa which commonly occur together. Nine of the 15 clusters contain bryophytes only. The remaining clusters contain either vascular species only or vascular and bryophyte taxa.

The primary split in the dendrogram is far stronger with the inclusion of bryophyte taxa compared with Figure 5.2., accounting for 68% of variance in the data. This implies that there is a stronger division of taxa when bryophyte diversity data is included in the analysis than when vascular species only are included. Of the eight clusters in the top half of the dendrogram, all except 'e' and 'd' contain bryophyte taxa only. The remaining two clusters contain *Poa kerguelensis* as part of one cluster and *Colobanthus kerguelensis* as part of another closely related cluster.

As with the preliminary analysis (Fig 5.2.) *Azorella* is classified by itself and is not associated with other taxa in the lower half of the dendrogram. This is of interest and relates to two aspects of *Azorella*'s distribution. Firstly in areas categorized as patchy cushion carpet and dense cushion carpet vegetation communities by Hughes (1987) the dominance of this species in terms of both extensive cover and stature of this species is outstanding. Cushions of *Azorella* can reach heights of above 1 m and groups of plants can coalesce to cover many square metres (see Fig 1.11). These features make *Azorella* the largest and most dominant plant on Heard Island. The second aspect of the ecology of *Azorella*, reflected in its isolated position on the dendrogram, is that apart from being dominant in some vegetation types the species exhibits wide ecological amplitude, occurring with the majority of both vascular plants and bryophytes. Cushion size, however, may be very small (only a few centimetres in diameter) in some environments.

As well as 15 taxon clusters, 15 ecological groups (Groups 1-15) were delineated in the TWINSPAN analysis of the 475 quadrats. These groups contain between 13 and 67 quadrats. The frequency of occurrence of taxa in each of these 15 groups is shown in Table 5.1. The TWINSPAN taxon clusters of Figure 5.3. are maintained in this table.

There are a number of salient features to the table. The ubiquitous nature of *Azorella* is highlighted, occurring in all 15 groups. *Azorella* was recorded from 80% (379/475) of all quadrats in this study. Six other species/species complexes can be classified as having

Table 5.1 Frequency of occurrence of taxa in each of the 15 TWINSPAN groups expressed as a percentage of the total number of quadrat/group. TWINSPAN taxon clusters (see Fig 5.3) indicated by letter (a-o).

Cluster	Taxon	TWINSPAN groups 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
a	*Dicranella* sp.	12	22	28	10		3			9		22				
a	*Drepanocladus uncinatus*	56	31	68	50	7				18	18	61	54			
a	*Cryptochila grandiflora*		2	5									8			
b	*Schistidium falcatum*		4	5	2				3					3		
b	*Cephaloziella varians*		17	40	44	7								7		
b	Lophocoleoideae sp.			7	8	60								7		
b	*Muelleriella crassifolia*		2	3	2	7								22		
b	*Pedinophyllopsis abdita*	6	83	60	73	80							8			
b	*Herzogobryum vermiculare*	6	9	5	6											
b	*Andreaea acuminata*		26	3	4		2		3	2						
b	*Psilopilum australe*		22	22	6											
b	*Schistidium* sp.		4													
b	*Verrucidens* spp.	18	54	5	2		3									
b	*Dicranoloma billarderii*	12	17	5	2											
b	*Pachyglossa fissa*	6	66	12	21											
b	*Blepharidophyllum densifo*	6	84	12	6	14										
c	*Racomitrium crispulum*	62	46	33	85	87	5	22			6					
c	*Racomitrium lanuginosum*		4		6	7										
c	*Ditrichum immersum*	31	61	43	96	93	3	11								
c	*Herzogobryum atrocapillum*	18	26	5	19	73										
d	*Andreaea mutabilis*	**	20	35		7				7						
d	*Grimmia* sp.	25		3												
d	*Schistidium apocarpum*	75	9	8	4		3									
d	*Blindia robusta*	62	61	12			3				6					
d	*Ditrichum subaustrale*		6	12	8	7	3			2						
d	*Pottia heimii*	12		3		7			3							
d	*Tortula geheebiaeopsis*		2	3					3							
d	*Cephaloziella exiliflora*	6	24	10	15		3		12	14		4				
e	**Poa kerguelensis*	1	19	5	54	73	94	89	90	5				7		
e	*Polytrichum piliferum*		4				6	50	16	18						
e	*Grimmia immerso-leucophae*	56	20	3	10		43	72	10	5						
e	*Dicranoweisia* spp.	31	85	70	94	13	87	83	83	63	31	9		7		
f	**Colobanthus kerguelensis*		28	3	52	47	81	78	83	5	56	35	8	64		
f	*Polytrichum alpinum*	18	39	45	50	20	76	55	50	81	12	65	8			
f	*Ditrichum conicum*		54	30	8		30	28	43	47		30				
g	*Fossombronia australis*	6	54	50	38		37		33	54	62	70	85	17		
g	*Jungermannia coniflora*		4	12			2			2		26	8			
g	*Trichostomum* sp.		2	3	2		2				6					
h	*Pohlia wahlenbergii*	69	15	38	4		7		40	7		26	15			
h	*Bartramia patens*	56	56	70	65		21	5	70	49	50	70	15	3		
i	**Azorella selago*	6	93	85	98	86	**	77	67	88	94	**	23	75	69	**
j	*Ceratodon purpureus*		7	28		13	2	61	72	67	56	48	8	34		
j	*Bryum dichotomum*			3			2	17	6	5	19		69			
j	*Bryum pseudotriquetrum*		17	40	10		16		63	56	56	74				
k	**Pringlea antiscorbutica*		16	15	12	27	7		20	2	6	26		46		9
l	*Bryum* sp. 1.			5					3	2		4		3		
l	*Bryum* sp.2.			18					3			4		11		
l	*Pohlia* sp.	12	36	3	6		2	5	33	46	56	48	61	7		
l	*Marchantia berteroana*	31							13	16		65		7		
m	**Acaena magellanica*									30	31	74	54		4	27
m	**Deschampsia antarctica*									2	6	48	69			
n	*Philonotis angustifolia*									2	6	17	38			
n	*Brachythecium* spp.	6	4	8					3	2	12	17	54	3		
o	**Poa cookii*		13	25	4		3	5	10	7	93	78	64	78	96	9
o	**Montia fontana*		2								50	9		28	13	
o	**Callitriche antarctica*			3							69	56	23	34	35	
	number of quadrats/group	17	54	40	51	15	67	18	30	42	16	23	13	31	22	22

** = 100%

TWINSPAN taxa clusters [yellow] = 50-75% [red] = 75-100%

* vascular species

Figure 5.4 Number of bryophyte and vascular plant taxa in each of the 15 TWINSPAN ecological groups.

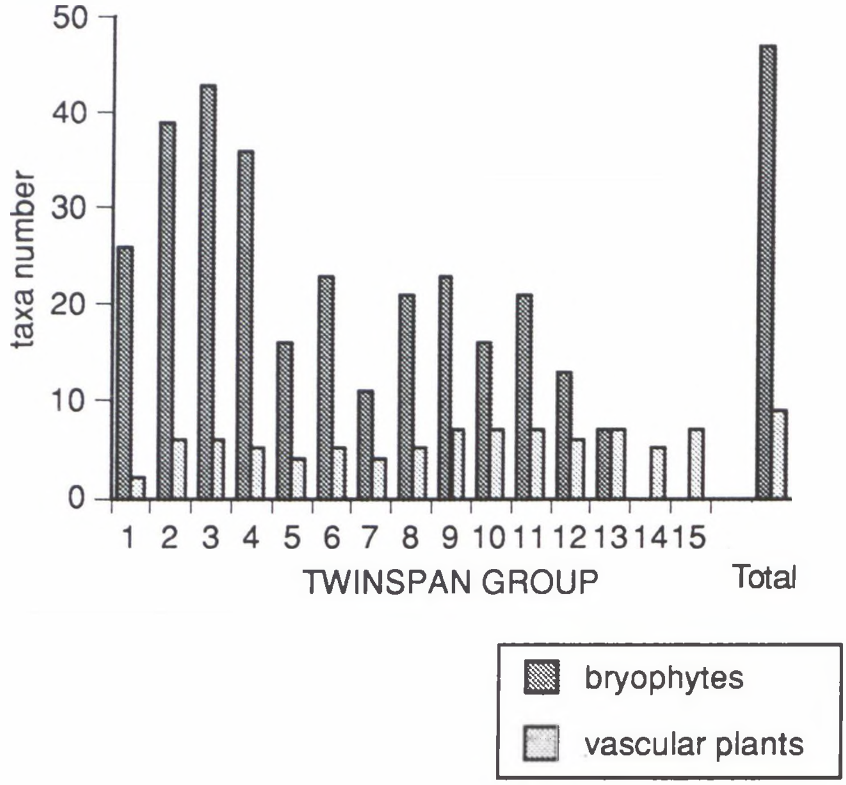


Table 5.2 Correlation coefficients with corresponding probability values for environmental parameters and total bryophyte and *Azorella selago* cover vs DECORANA eigen vector scores (axes co-ordinates). Significant correlation outlined in red.

		Axis 1	Axis 2	Axis 3	Axis 4
Altitude	r	0.48	0.07	0.29	0.26
	p	0.0001	0.14	0.001	0.0001
rock cover	r	0.40	0.25	0.27	0.10
	p	0.0001	0.0001	0.0001	0.03
substrate depth	r	0.43	0.14	0.15	0.22
	p	0.0001	0.002	0.0008	0.0001
water scale	r	0.19	0.45	0.17	0.13
	p	0.0001	0.0001	0.0003	0.007
wind scale	r	0.06	0.40	0.24	0.12
	p	0.18	0.0001	0.0001	0.006
bryophyte cover	r	0.41	0.42	0.09	0.24
	p	0.0001	0.0001	0.05	0.0001
Azorella cover	r	0.11	0.05	0.19	0.29
	p	0.01	0.21	0.0001	0.0001

r - correlation coefficient
p - probability value

wide ecological amplitude: the bryophytes *Dicranoweisia* spp, *Polytrichum alpinum*, *Fossombronia australis*, *Bartramia patens* and *Ceratodon purpureus* and the vascular species *Poa kerguelensis* and *Colobanthus kerguelensis*. Interestingly *Dicranoweisia* spp.and *Ceratodon purpureus* were also recorded as having widespread distributions on the island (see Table 4.1).

Taxa in cluster a generally occur between groups 1-4 and 9-12. Clusters b, c and d have particularly strong frequencies of occurrence in groups 1-5 (Table 5.1). Clusters e-l are generally widespread across the groups with a number of common taxa (taxa with high frequencies of occurrence). Clusters m, n, and o with the exception of *Poa cookii* are generally confined to groups 10 - 15.

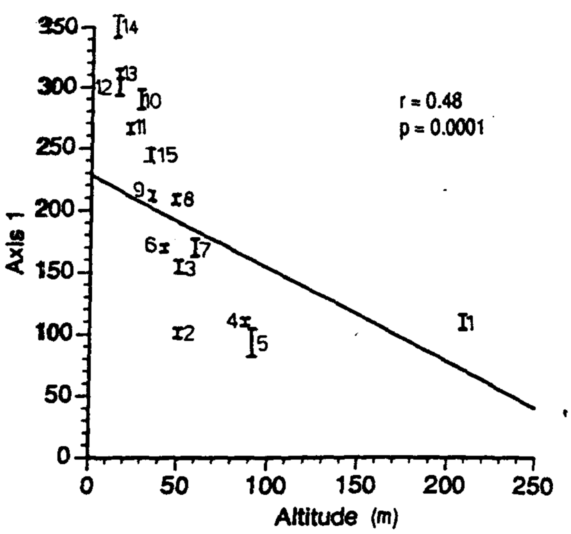
Bryophyte species richness (Fig. 5.4.) is particularly high in groups 1 - 4 and relatively low in groups 7, 12 and 13. Bryophyte taxa are absent from groups 14 and 15. Vascular species richness is less varied, highlighting Scott's (1990) observation that one of the features of Heard Island's vegetation is the small number of vascular species occupying a large range of habitats. However group 1 contains only two vascular species, *Poa kerguelensis* and *Azorella selago*. Table 5.1 and Figure 5.4 re-emphasises the five-fold difference in species number between bryophyte and vascular plants on Heard Island.

5.3.2 DECORANA analysis

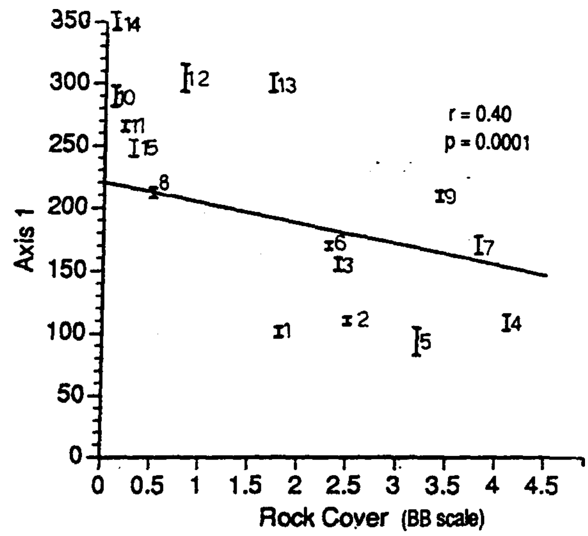
Bryophyte and vascular plant presence/absence data from the vegetation survey was ordinated using detrended correspondence analysis (DECORANA). The DECORANA ordination is a measure of association between taxa based on a correlation matrix . Its output is in the form of co-ordinates (eigen vectors) for four axes. Each quadrat has its own set of co-ordinates. Each axis has a eigen value which is proportional to variance in the data (Hill and Gauche, 1980). In this study DECORANA Axis 1 had an eigen value of 0.40 accounting for 40% of the variance in the data. Axis 2 had an eigen value of 0.22, accounting for 22% of variance in the data. Axis 3 and Axis 4 accounted for only 15% and

Figure 5.5 Environmental parameters and total bryophyte cover vs Axis 1. (Rock and bryophyte cover values are expressed as modified Braun-Blanquet values [see Section 2.1]). Superimposed on the regression lines are mean point (± standard error) for each of the 15 TWINSPAN ecological groups

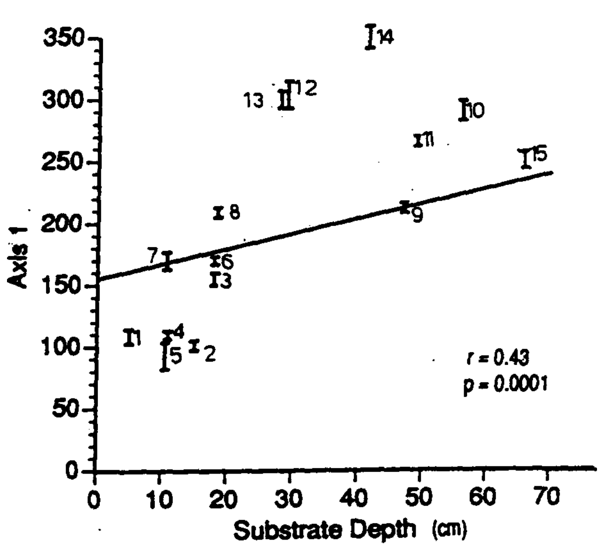
a. Altitude vs Axis 1



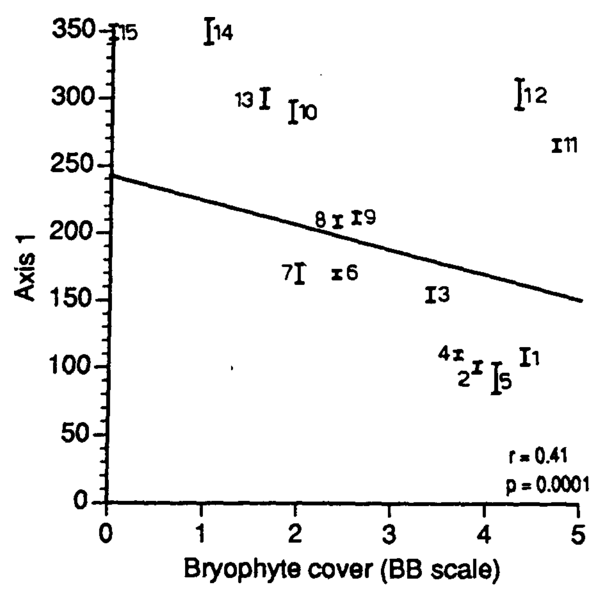
b. Rock cover vs Axis 1



c. Unconsolidated substrate depth vs Axis 1



d. Total bryophyte cover vs Axis 1



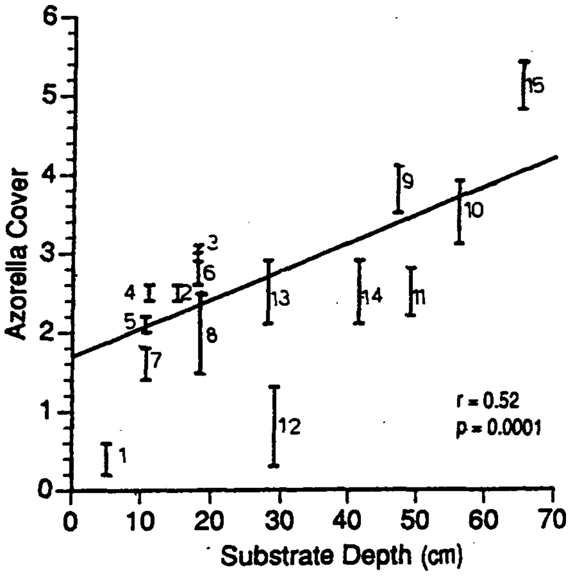
14% of a variance in the data respectively.

Once the DECORANA ordination is established, the aim is then to relate the axes which account for the highest proportion of the variance, to environmental gradients or parameters in order to establish hypotheses as to the role of environmental factors in influencing the vegetation. In this survey eight quantitative or semiquantitive parameters were recorded for each quadrat (see Section 2.1.). The parameters were then correlated with the DECORANA eigen vector scores (the axes co-ordinates).

Of the eight parameters measured, significant correlations were found between 5 parameters and vector scores of either Axis 1 or Axis 2. Significant correlations were found between Axis 1 and altitude, rock cover and substrate depth. Significant correlations were found between Axis 2 and water availability and exposure to wind (Table 5.2). Significant correlation between some of these parameters and Axis 3 and Axis 4 were also found (Table 5.2), but as these axes accounted for such a small percentage of variance in the total data set (15% and 14 %) they were not considered further. Since no significant correlations were found between axis vector scores and light intensity, aspect or slope of the sites, correlation coefficients (r) and probabilities (p) for these parameters are not presented. Correlation coefficients between the five significant environmental parameters, total bryophyte cover and *Azorella* cover (the most widespread species on the island) were also calculated (Table 5.2).

The strongest correlation was recorded between Axis 1 and altitude ($r = 0.48$ $p = 0.0001$). With decreases in Axis 1 values, altitude increased (Fig 5.5.a.). The changes with altitude most likely reflect a number of changing environmental components. One of these is temperature: on Macquarie Island, Selkirk *et al*,. (1990) reported that there is a 2° temperature drop for every 200 m increase in altitude. However, I believe that on Heard Island increase in altitude most significantly affects nutrient levels. An increase in altitude means a move away from the coast, generally away from gross disturbance and manuring

Figure 5.6 *Azorella selago* cover vs unconsolidated substrate depth.(Cover values are expressed as modified Braun-Blanquet values [see Section 2.1]). Superimposed on the regression lines are mean point (+ standard error) for each of the 15 TWINSPAN ecological groups



by seals and sea birds and from immediate salt deposition.

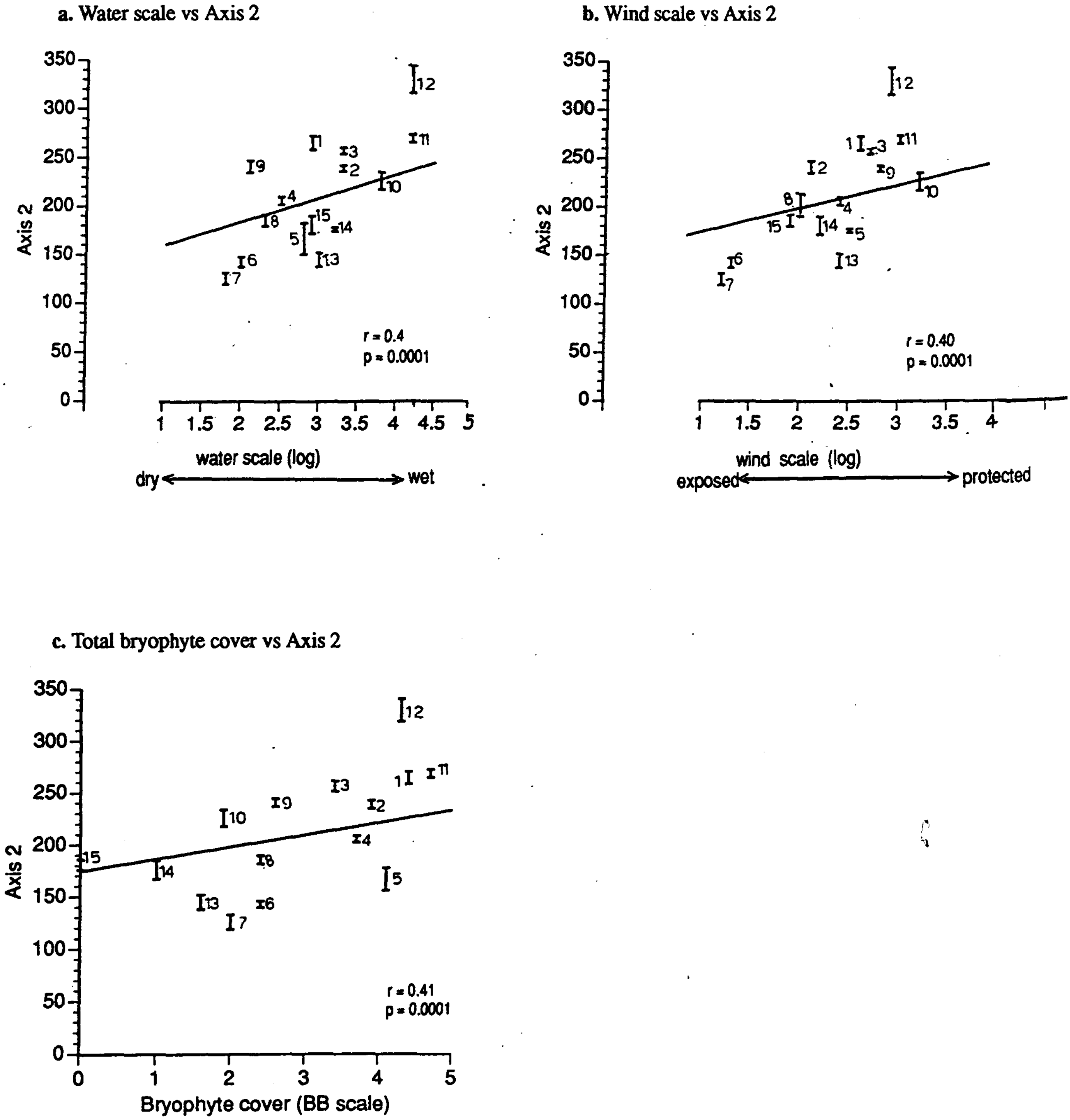
Rock cover, the amount of either exposed unconsolidated rock or bedrock decreased with increasing values in Axis 1 (Fig 5.5.b.). Conversely depth of unconsolidated substrate increased with increasing values of Axis 1 (Fig 5.5.c.) . Both were strongly correlated with the axis (rock, r= 0.4 p=0.0001; substrate depth, r= 0.43 p= 0.0001) (Table 5.2).

In addition, total bryophyte cover was significantly correlated with Axis 1 (Table 5.2). Total bryophyte cover per quadrat decreased with increasing Axis 1 vector scores (Fig 5.5.d.). *Azorella* cover was not significantly correlated with Axis 1.

Overall variance in the data expressed in Axis 1 appears to reflect changes associated with gradient), the amount of exposed rock and the depth of unconsolidated substrate. Total bryophyte cover increased with increasing altitude (and hence distance from coastal influences), increasing rock cover and decreasing substrate depth. Increase in rock cover may increase habitat variety available for bryophytes. Reduction in substrate depth may reduce habitat availability for vascular plants with extensive root systems such as *Azorella selago*. This appears to be the case; *Azorella* cover was significantly correlated with substrate depth (Fig 5.6). *Azorella* cover decreased with a decrease in substrate depth. Both high rock cover and low unconsolidated substrate depth would decrease potential competition from vascular plants.

Axis 2 showed significant correlations both with water and wind exposure scales (Table 5.2). With an increase in Axis 2 vector scores there was an increase in available moisture and a trend from exposed to protected sites (Figs 5.7.a. & 5.7.b.). Water stress is directly related to evaporative potential and hence to the level of wind exposure. Bryophyte cover also increased with increases in Axis 2 vector scores (Fig.5.7.c.) Total bryophyte cover appears to be greatest in areas of high water availability and low exposure to wind. Interestingly, however, only 6% of all quadrats surveyed had an exposure scale of 4 or 5

Figure 5.7. Environmental parameters and total bryophyte cover vs Axis 2. (Rock and bryophyte cover values are expressed as modified Braun-Blanquet values [see Section 2.1]). Superimposed on the regression lines are mean point (+ standard error) for each of the 15 TWINSPAN ecological groups



(very protected). This is indicative of Heard Island being very windswept (mean windspeed at Atlas Cove 8.3m m/s).

Smith and French (1988) in a principal component analysis of climate, edaphic and vegetation parameters from South Georgia, Marion, Macquarie and Signy Islands reported that the three main environmental influences on vegetation were;" (a) distance from sea, and altitude, (the two are inevitably confounded to some degree in the field), (b) amount *and source* of nutrient input from sea-spray or from vertebrate manuring, (c) wind exposure and/ or osmotic stress" (Smith and French, 1988 p. 42). Basic as the parameter measurements in this survey are, it appears that the trends are in line with those on other subantarctic islands. Future detailed work in this area should confirm these trends.

The correlation of rock cover and substrate depth with DECORANA Axis 1 in this study and the relationship with bryophyte cover (increased bryophyte cover with increased rock cover and decreased substrate depth) may be specific to Heard Island although Smith and French (1988) did report that cushion forming species, including bryophytes, were responsible for initiation of peat formation on new rock substrates.

5.4 Details of ecological groups

In this section major features of the 15 ecological groups, delineated in the TWINSPAN analysis, are described.

TWINSPAN Group 1 n= 17 quadrats

mean altitude: high >200 m alt
moisture: mesic
wind exposure: medium
mean substrate depth: 5 cm
mean rock cover: 37%
mean bare ground cover: 10%
mean total bryophyte cover: 47%
mean *Azorella* cover: 1%
geomorphology: exclusively moraine, 'boulder scree'

TWINSPAN indicator species: *Andreaea mutabilis* & *Schistidium apocarpum*
Community categories: overwhelmingly feldmark

Notes: Group 1 is a somewhat detached group consisting of quadrats from one local area,Deacock Moraine, Long Beach. The group is characterized by a predominance of bryophytes, high in both total bryophyte cover and species richness (26 taxa, Fig. 5.4). In some quadrats bryophyte cover exceeded 80%. The ground is stable, rocky moraine with minimal skeletal soil development. This is highlighted by the two indicator species, the mosses *Andreaea mutabilis* and *Schistidium apocarpum* being rock colonizers. Lichens including *Usnea* sp.were also abundant on exposed rock. In areas where a thin peaty layer, (2-5cm) had developed lush turves and carpets dominated by any/and *Dicranoweisia* spp, *Blindia robusta* and *Drepanocladus uncinatus* could be found. Only two vascular species, *Poa kerguelensis* and *Azorella selago* were recorded, both with sparse cover.

TWINSPAN Group 2 n= 54

mean altitude: medium, 50 m alt
moisture: mesic
wind exposure: medium
mean substrate depth: 15 cm
mean rock cover: 11%
mean bare ground cover: 18%
mean total bryophyte cover: 35%
mean *Azorella* cover: 16%
geomorphology: lavas and stable moraines
TWINSPAN indicator species: *Blepharidophyllum densifolium* & *Verrucidens* spp

Community categories: predominately feldmark

Notes: Group 2 consists of quadrats in which bryophytes are overwhelmingly the dominant component, both in terms of cover and diversity (40 taxa, Fig. 5.4). Thirty three quadrats had lush bryophyte carpets, exceeding 50% cover. Stability of habitat appeared to be an important factor and shallow substrate depth reduced competition from *Azorella*. Major bryophyte species included *Blindia robusta*, *Ditrichum immersum*, *Dicranoweisia* spp.and *Bartramia patens* as well as the indicator taxa. This group included sites in the Mt Drygalski area, on Deacock Moraine, Long Beach, on lavas on Laurens Peninsula as well as sites on limestone moraine at the southern base of Anzac Peak.

TWINSPAN Group 3 n= 40 quadrats

mean altitude: medium 50 m alt
moisture: mesic
wind exposure: medium
mean substrate depth: 18 cm
mean rock cover: 13%
mean bareground cover: 20%
mean total bryophyte cover: 27%
mean *Azorella* cover: 23%
geomorphology: varied, lava scoria and flows, moraines and sand.
TWINSPAN indicator species: *Drepanocladus uncinatus*

Community categories: continuum between dense cushion carpet, patchy cushion carpet and feldmark

Notes: Group 3 represents a continuum from dense to patchy cushion carpet to feldmark categories. As with Group 2 bryophyte diversity is very high (42 taxa, Fig. 5.4). The main distinguishing feature between this group and Group 2 is an increase in prominence of *Azorella* in some quadrats. *Dicranoweisia* spp. and *Ditrichum immersum* were the most abundant bryophyte taxa, *Blindia robusta* being less conspicuous. Carpets of *Drepanocladus uncinatus* were also recorded. The presence of this species is a good indication of mesic conditions. Ten sites in Group 3 had *Poa cookii* present, perhaps reflecting slightly higher nutrient status. Sites were recorded from either stable lava or moraine or sand such as on a stream bank. Group three included sites from all major vegetated regions as well as from Capes Pillar, Arkona and Gazert.

TWINSPAN Group 4 n=51 quadrats

mean altitude: high, 90 m alt
moisture: mesic
wind exposure: medium to exposed
mean substrate depth: 11 cm
mean rock cover: 15%
mean bare ground cover: 22%
mean total bryophyte cover: 33%
mean *Azorella* cover: 11%
geomorphology: predominately lava scoria and flows
TWINSPAN indicator species: *Dicranoweisia* spp. and *Bartramia patens*
Community category: patchy cushion carpet and feldmark

Notes: Group 4 contains quadrats similar in species composition to Groups 2 & 3. Bryophyte species richness is fairly high (34 taxa, Fig. 5.4). Sites are predominantly on lava and are more exposed and drier than those represented in the previous two groups.

Azorella cover is low. Sites included areas at the base of Macey Cone (see Section 6.2), the higher scoria slopes of Corinth Head, lava ridges SW of Cape Cartright and higher slopes of Deacock Moraine.

TWINSPAN Group 5 n= 15

mean altitude: high, 90 m alt
moisture: mesic
wind exposure: exposed
mean substrate depth: 10 cm
mean rock cover: 25%
mean bare ground cover: 23%
mean total bryophyte cover: 45%
mean *Azorella* cover: 5%
geomorphology: predominantly scoria
TWINSPAN indicator species: *Herzogobryum atrocapillum* & *Lophocolea* sp.1.
Community category: feldmark

Notes: Group 5 with very exposed scoria sites, represents a more extreme version of Group 4. Bryophyte species richness is low although total bryophyte cover is high, suggesting reduced habitat variety. *Azorella* cover is low, again reflecting shallow substrate depth. Most of the sites are high slopes on Macey Cone (see Section 6.1).

TWINSPAN Group 6 n=67 quadrats

mean altitude: medium, 40 m alt
moisture: predominantly xeric
wind exposure: exposed
mean substrate depth: 18 cm
mean rock cover: 18%
mean bare ground cover: 39%
mean total bryophyte cover: 11%
mean *Azorella* cover: 20%
geomorphology: exclusively moraine
TWINSPAN indicator species: *Fossombronia australis*
Community category: generally patchy cushion carpet and feldmark

Notes: The majority of sites in Group 6 are from patchy cushion carpet/ feldmark continuums in the Dovers Moraine area, Spit Bay. The sites are generally characterized by small *Azorella* cushions with occasional clusters of small moss polsters, surrounded by windswept gravel. In some sites there is evidence of frost raking and nubbin formation running parallel with the prevailing wind direction. The indicator species for this group is *Fossombronia australis* which colonizes the edges of, or spaces between branches of

Azorella cushions. *Azorella, Poa kerguelensis, Colobanthus kerguelensis, Dicranoweisia* spp. and *Polytrichum alpinum* were recorded from most of the 67 quadrats in this group (Table 5.1).

TWINSPAN Group 7 n=18 quadrats

mean altitude: medium 60 m alt
moisture: predominantly xeric
wind exposure: exposed
mean substrate depth: 10 cm
mean rock cover: 38%
mean bare ground cover: 37%
mean total bryophyte cover: 7%
mean *Azorella* cover: 8%
geomorphology: exclusively moraine
TWINSPAN indicator species: *Ceratodon purpureus* & *Polytrichum piliferum*
Community category: feldmark

Notes: This group represents a continuum from Group 6 with most sites again occurring in the Dovers Moraine area. Quadrats in Group 7 are all feldmark on moraines. Most sites are extremely exposed and xeric. Many sites showed indication of periglacial activity such as nubbins, frost raking and sorted pavement. There was little vegetation, either bryophytes or vascular plants. Species diversity is low (Fig. 5.4). The indicator species *Ceratodon purpureus* and *Polytrichum piliferum* as well as *Poa kerguelensis* and *Polytrichum alpinum* were often found growing in gravel and fines and appeared to tolerate surface movement.

TWINSPAN Group 8 n=30 quadrats

mean altitude: medium, 50 m alt
moisture: xeric to mesic
wind exposure: exposed to protected
mean substrate depth: 18 cm
mean rock cover: 40%
mean bare ground cover: 11%
mean total bryophyte cover: 15%
mean *Azorella* cover: 14%
geomorphology: exclusively moraine
TWINSPAN indicator species: *Poa kerguelensis* & *Colobanthus kerguelensis*
Community category: patchy cushion carpet and feldmark

Notes: Group 8 is another variation of Group 6 occurring in drainage lines and beside streams. The sites are wetter than the previous groups and this is indicated by a higher number of Bryaceae taxa (Table 5.1) in the quadrats. The sites were exclusive to the

Dovers Moraine area, Spit Bay.

TWINSPAN Group 9 n=42 quadrats

mean altitude: medium low, 35m alt
moisture: xeric to hydric
wind exposure: exposed to medium
mean substrate depth: 47 cm
mean rock cover: 5%
mean bare ground cover: 14%
mean total bryophyte cover: 19%
mean *Azorella* cover: 43%
geomorphology: predominantly moraine
TWINSPAN indicator species: *Polytrichum alpinum*
Community category: mixed

Notes: Group 9 consists of quadrats, spanning all vascular plant community categories except maritime grassland categories. However the common features of the sites are that they are generally on moraines and common taxa include *Azorella* (with high cover values) and the indicator species *Polytrichum alpinum*. Unconsolidated substrate depth is high with a mean of 47cm being an underestimation as many sites had depth of greater than the limit of measurement (100cm). The majority of sites were in the Dovers Moraine area.

TWINSPAN Group 10 n=16 quadrats

mean altitude: low, 30 m alt
moisture: hydric
wind exposure: medium to protected
mean substrate depth: 56 cm
mean rock cover: 0%
mean bare ground cover: 12%
mean total bryophyte cover: 11%
mean *Azorella* cover: 32%
geomorphology: predominantly moraine
TWINSPAN indicator species: *Montia fontana*
Community category: Predominantly pool complex & patchy cushion carpet

Notes: This group contains quadrats on or near impeded drainage areas on moraine substrates close to the coast. This is reflected by *Montia fontana* being the indicator species. The sites generally have large or coalescing cushions of *Azorella* with deep unconsolidated substrate or peat depths exceeding 100 cm at many sites. Many cushions flank pools. Nutrient status of the sites was high, manifested by the presence of *Poa cookii* and *Callitriche antarctica* in the majority of quadrats. The source of nutrient enrichment was the wallows of elephant seals. Bryophytes consisted mainly of small cushions of *Dicranoweisia* spp. at the edge of *Azorella* cushions, *Polytrichum alpinum* growing in gravel, *Fossombronia australis* growing beside or in *Azorella* cushions and *Brachythecium* spp.growing in moist or wet areas at the edge of pools. The sites had wide distribution including areas in Dovers Moraine, Long Beach and Atlas Cove.

TWINSPAN Group 11 n=23 quadrats

mean altitude: medium to low, 20 m alt
moisture: hydric
wind exposure: medium to protected
mean substrate depth: 50 cm
mean rock cover: 0%
mean bare ground cover: 3%
mean total bryophyte cover: 56%
mean *Azorella* cover: 16%
geomorphology: exclusively moraine
TWINSPAN indicator species: *Marchantia berteroana*
Community category: mixed but meadow and herbfield dominant

Notes: Group 11 consists mainly of wet sites of meadow and herbfield categories. Vegetation cover is high and total bryophyte cover is very extensive. Major vascular species include mats of *Acaena magellanica* and tufts of *Deschampsia antarctica* and *Poa cookii*. *Azorella* occurred in all quadrats in this group, although not a dominant species in terms of cover. Major bryophyte species include mats of *Marchantia berteroana* lush carpets of *Drepanocladus uncinatus* and turves of *Bryum pseudotriquetrum.* Many sites had peat depth exceeding 100 cm. Sites classified into this group were from Sydney Cove, Long Beach and Dovers Moraine areas.

TWINSPAN Group 12 n=13 quadrats

mean altitude: low, 15 m alt.
moisture: mesic
wind exposure: medium
mean substrate depth: 30 cm
mean rock cover: 7%
mean bare ground cover: 1%
mean total bryophyte cover: 50%
mean *Azorella* cover: 7%
geomorphology: exclusively moraine
TWINSPAN indicator species: *Brachythecium* spp.
Community category: Predominantly meadow

Notes: Group 12 consists mainly of quadrats classified as meadow with *Deschampsia antarctica* being present. *Azorella* cover and abundance is very low in this group. In comparison with Group 11 sites were drier and mean substrate depth considerably shallower. The indicator taxa *Brachythecium* spp. often occurred as thick carpets.

TWINSPAN Group 13 n=31 quadrats

mean altitude: low, 15 m alt
moisture: xeric to mesic
wind exposure: medium
mean substrate depth: 28 cm
mean rock cover: 12%
mean bare ground cover: 23%
mean total bryophyte cover: 7%
mean *Azorella* cover: 20%
geomorphology: predominantly moraine
TWINSPAN indicator species: *Colobanthus kerguelensis*
Community category: mixed but predominantly coastal

Notes: Quadrats in Group 13 are generally salt affected coastal sites, including maritime grassland, pool complex and low lying patchy cushion carpet at Atlas Cove, Spit Bay region and Sydney Cove. Also included in this group are sites from the supralittoral zone at Atlas Cove. *Colobanthus kerguelensis* as an indicator species I believe denotes small scale xeric conditions. Bryophyte species richness is low. One notable feature is the presence of *Muelleriella crassifolia* in all the supralittoral sites. A high occurrence of *Poa cookii* throughout the sites may reflect a high nutrient status, perhaps blown in from local animal disturbance sites.

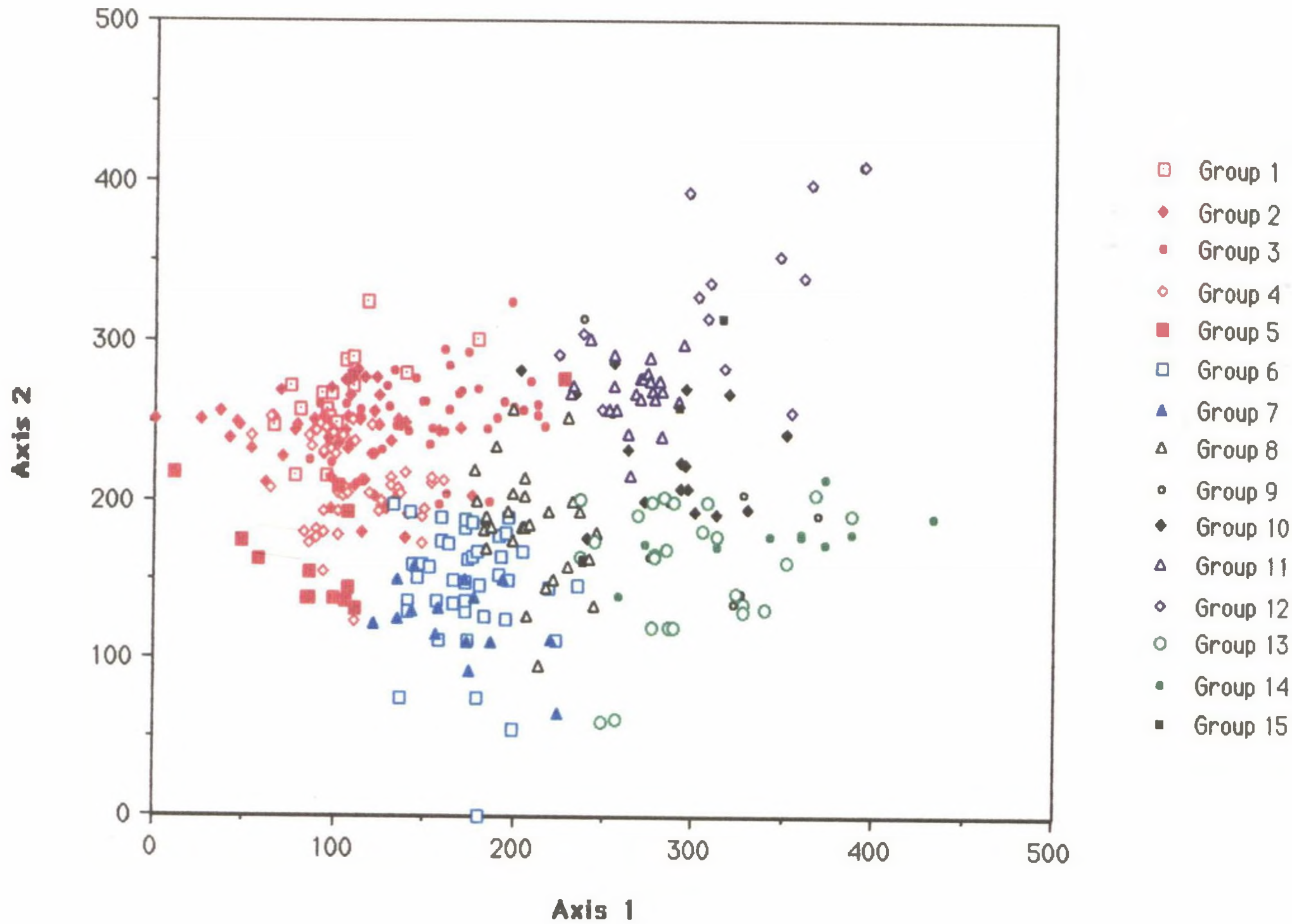
TWINSPAN Group 14 n=21 quadrats

mean altitude: low, 13 m alt
moisture: mesic
wind exposure: exposed
mean substrate depth: 41 cm
mean rock cover: 1%
mean bare ground cover: 27%
mean total bryophyte cover: 0%
mean *Azorella* cover: 21%
geomorphology: predominantly moraine
TWINSPAN indicator species: *Poa cookii*
Community category: predominantly maritime grassland

Notes: Group 14 consist of coastal sites near penguin colonies and seal wallowing areas at

Figure 5.9 DECORANA Axis 1 vs Axis 2. Each quadrat surveyed is represented by an individual DECORANA co-ordinate. In addition the quadrats are indentified according to their TWINSPAN ecological group classification (Groups 1-15) and to one of the five Amalgamated groups (by colour):

Amalgamated Group I - red
Amalgamated Group II - blue
Amalgamated Group III - black
Amalgamated Group IV - purple
Amalgamated Group V - green



Spit Bay, seal wallowing areas at Atlas cove and an area approximately 500m inland from Long Beach. *Poa cookii* was the dominant species. No bryophyte taxa were recorded in these quadrats, possibly due to animal disturbance and toxic nutrient levels.

TWINSPAN Group 15 n=22 quadrats

mean altitude: medium, 33m alt
moisture: mesic
wind exposure: exposed
mean substrate depth: 65 cm
mean rock cover: 0%
mean bare ground cover: 6%
mean total bryophyte cover: 0%
mean *Azorella* cover: 68%
geomorphology: moraine or sand
TWINSPAN indicator species: *Pringlea antiscorbutica*
Community category: predominantly cushion carpet

Notes: Group 15 sites have very high *Azorella* cover and little else. Unconsolidated substrate depths exceeded 100 cm at many sites. Sites were recorded from areas of Dovers Moraine, Long Beach, Atlas Cove and southern side of Laurens Peninsula. An indicator species of *Pringlea antiscorbutica* is not conclusive.

5.5 Discussion

It is apparent that various TWINSPAN ecological groups are similar both on a floristic and structural basis. Although data was examined at a quadrat level many of the sites were sampled in close proximity to each other, such as part of 10 random quadrats in a 10 x 10 m area. Interestingly many of these quadrats are separated into different groups on the basis of different species composition. These sites are in essence reflecting small scale mosaic patterning.

Figure 5.9 plots DECORANA Axis 1 vs Axis 2 for mean values for the 15 TWINSPAN groups. Related groups have been linked into a total of five amalgamated groups. Amalgamated Group I (Groups 1-5) contains groups categorized as feldmark communities in which bryophytes play a major role both in terms of species diversity and cover.

Amalgamated Group II (Groups 6 & 7) contains quadrats ranging from feldmark to cushion carpet categories in which bryophytes play a minor role, generally having low total cover and diversity. Closely related to this is Amalgamated Group III in which *Azorella* has generally dominant cover (Groups 8, 9, 10 & 15). Amalgamated Group IV (Groups 11 & 12) contains many sites classified as herbfield or meadow and represents mainly seepage zones. The last complex, Amalgamated Group V (13 & 14) contains coastal and/or nutrient enriched sites. In Chapter 7, this model will be expanded and a revised classification scheme for Heard Island vegetation will be presented.

This study has included an examination of bryophyte assemblages in the most visually recognizable vegetation types on Heard Island. It has revealed that the bryophyte component is significant in most vegetation on Heard Island and in some vegetation it is the most significant component in terms of both total cover and species diversity. One aspect of the vegetation ecology which this survey has only just touched on is differences in controlling environmental factors for bryophyte taxa and vascular plant taxa in many situations. For example, the scale of the quadrats ($1m^2$) could cover many different bryophyte niches. Some sites on Deacock Moraine had *Andreaea mutabilis* on exposed xeric rocks, two forms of *Dicranoweisia* spp; a black wet form and a drier green form, and also *Bartramia patens* growing in low light conditions in very protected, small crevices in the same quadrat. This is an area which warrants further study.

5.6 Summary

This chapter documented the general vegetation survey spanning common vegetation/ landscape features on Heard Island. Particular attention was given to the bryophyte component of the vegetation in terms of both total cover and taxon diversity.

Quadrats surveyed were categorized into one of the six vascular plant community categories described by Hughes (1987). This study found that bryophytes were present in all vascular plant vegetation categories and a substantial proportion of quadrats (158/475) had bryophyte cover of 25% or more, thus showing that Hughes' preliminary work under-represented the bryophyte component of the vegetation.

Data was classified using two way indicator analysis (TWINSPAN). A preliminary analysis was conducted using Braun Blanquet cover values for vascular plant species and for a single category 'total bryophytes'. A final analysis was conducted on the full data set, including bryophyte taxa, where the data was in presence/absence form only. There was no significant change to the classification of vascular plants with reduction of the data from cover values to presence/ absence levels. However, the inclusion of bryophyte taxa in the final analysis yielded significant information.

Fifteen taxon clusters (groupings of taxa which commonly occur together) were resolved, indicating that there are distinct suites of bryophyte taxa within Heard Island vegetation. A core of taxa with wide ecological amplitude was also identified. Fifteen ecological groups were also discerned from the quadrats.

Data was ordinated using detrended correspondence analysis (DECORANA). Of the eight parameters measured, significant correlations were found between 5 parameters and vector scores of either DECORANA Axis 1 or Axis 2. Overall variance in the data expressed in Axis 1 appeared to relate to changes associated with altitudinal variation (change in nutrient status, salt levels and perhaps temperature gradient), the amount of exposed rock and the depth of unconsolidated substrate. Axis 2 showed significant correlations both with water and wind exposure scales. With an increase in Axis 2 vector scores there was an increase in available moisture and a trend from exposed to protected sites.

Total bryophyte cover was also correlated with DECORANA Axes 1 and 2 and hence with the five environmental parameters. Total bryophyte cover increased with increasing altitude (and hence distance from coastal influences), increasing rock cover and decreasing substrate depth. It is most likely that an increase in rock cover could increase habitat variety available for bryophytes. Shallow substrate depth may reduce habitat availability for vascular plants with extensive root systems such as *Azorella selago*. Both high rock cover and low unconsolidated substrate depth would decrease potential competition from vascular plants. Total bryophyte cover also appeared to be highest in areas of high water availability and low exposure to wind.

Major features of the 15 ecological groups delineated in the TWINSPAN analysis were described in detail. It was apparent that various groups could be linked on the basis of structural and floristic similarity. Five amalgamated groups were identifed:

Amalgamated Group I contains quadrats categorized as feldmark with high bryophytes species diversity and cover;

Amalgamated Group II contains quadrats ranging from feldmark to cushion carpet categories in which bryophytes play a minor role, generally having total low cover and diversity;

Amalgamated Group III contains quadrats in which *Azorella* is generally dominant cover;

Amalgamated Group IV contains mainly quadrats classified as herbfield or meadow and represent mainly seepage zone sites;

Amalgamated Group V contains coastal and/or nutrient enriched sites.

CHAPTER SIX

Vegetation patterning in feldmark on Heard Island and other subantarctic islands

6.1 Introduction

Bare areas, lacking macroscopic vegetation, are a major feature of feldmark environments on all subantarctic islands. Small scale vegetation patterning is also common. Division between vegetated and bare areas, in many settings, is not random. R.I.L.Smith (1984a), in a major review of terrestrial plant biology in the subantarctic and Antarctic, listed five major environmental factors (moisture regime; drainage pattern; soil nutrient status; stability and texture of substratum; exposure to wind) which control patterning in vegetation.

A number of previous studies have documented patterning in subantarctic feldmarks. On South Georgia, Greene (1964) reported cryptogamic communities above 250 m altitude. Bryophyte communities were present on rock faces, ledges and sheltered crevices. Scattered turves of bryophytes were recorded on the summit of scree slopes, on glacial outwash plains and on moraines, with extensive swards growing on stable, hydric surfaces. Heilbronn & Walton (1984) described grasses, *Acaena tenera* and the occasional bryophyte growing in the fines of actively sorted stone stripes.

Huntley (1971) reported *Azorella* cushions scattered within loose aggregations of rocks and pebble pavements in feldmarks on Marion and Prince Edward Islands. Various bryophyte taxa could be found growing on the *Azorella* cushions, and others on boulders. Gremmen (1982) detailed an *Andreaea-Racomitrium crispulum* complex in feldmarks on Marion and Prince Edward Islands. He reported some bryophyte communities growing between large scoria boulders. Other areas had only fragmentary vegetation stands. Gremmen suggested that cryoturbatic processes prevented the establishment of many species in these areas.

This study documents vegetation patterning at a variety of feldmark sites on Heard Island and also on Marion and Prince Edward Islands. Particular attention is given to the distribution of the bryophyte component in predominantly bare areas. Vegetation survey protocol on Marion and Prince Edward Islands followed that for Heard Island (see Section 2.1).

Two of the five major environmental factors delimited by R.I.L.Smith (1984a) appeared to be most significant in controlling patterning; these were water availability and substrate stability. A hypothesis concerning both the process of colonization of bare areas by bryophytes and maintenance of patterning was developed. This hypothesis was tested on Macquarie Island, examining in detail surface layer propagule banks and surface stablility. A model is presented.

6.2 Heard Island sites

6.2.1 Macey Cone, Laurens Peninsula

Macey Cone is a small scoria cone on the western side of Laurens Peninsula (see Fig 1.3). Distinct patterning of vegetation exists in feldmark on and around the cone. Figure 6.1 shows an aerial image of the area. Three distinct zones are discernible and are outlined on the overlay. A transect through these zones is also indicated (overlay - Fig 6.1) and a profile diagram of this transect is shown (Fig 6.2).

Zone One extends from the crater lip to approximately 30 m down the slope on the south-facing and to some of the east-facing side of the cone. The general slope of Zone One was 30°. In some areas rocks or ash/sand and small amounts of vegetation had slipped.

Figure 6.2 Profile diagram of the transect on southern face of Macey Cone, Heard Island showing the division into three zones.

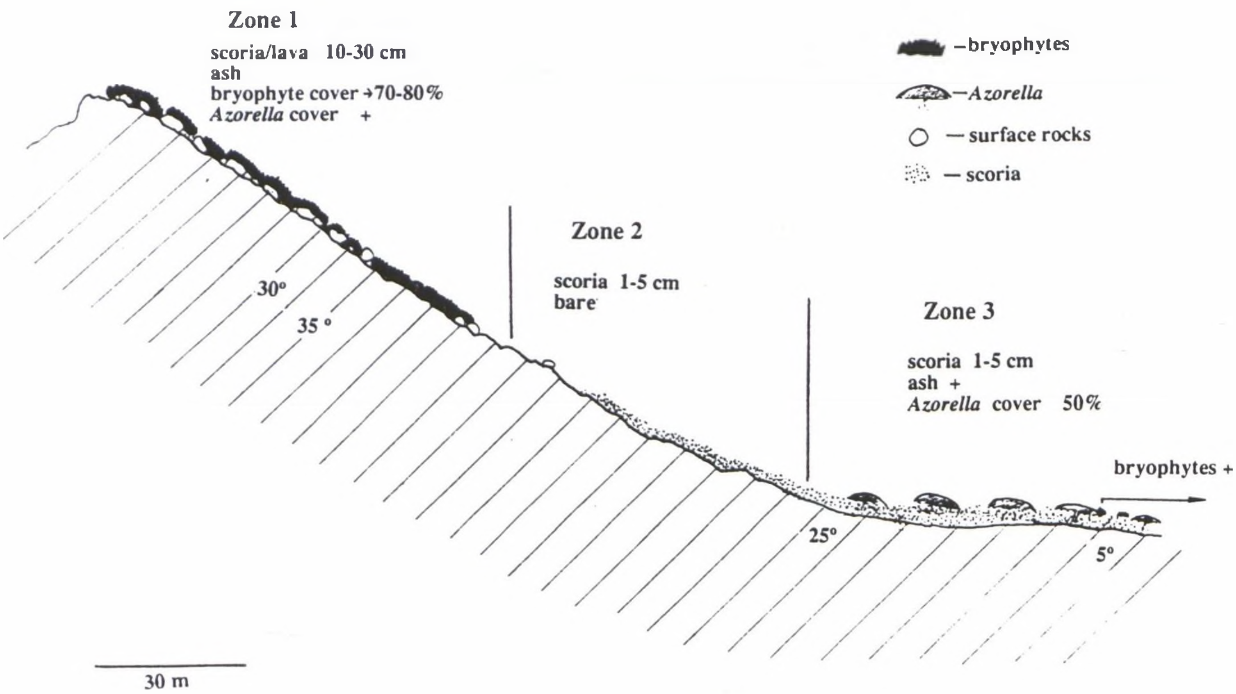


Figure 6.1 Aerial photograph of Macey Cone and surrounds, Heard Island. Cone height is 124 m. Bright green - *Azorella* cushion vegetation; olive green - bryophyte dominated vegetation.

Figure 6.1 overlay Three zones distinct on the face of the cone and the ridges at the base of the cone. Dashed line indicates the position of the transect. See Fig 6.2 for detail of transect.

100m

The significant feature of this zone was the extensive bryophyte cover. Plants were growing over lava, on the scattered large scoria rocks (>30 cm in diameter) and in ash/sand. On the lava at the crater lip, cover was approximately 30% and lichens including *Usnea* sp. were also present. In the centre of Zone One the bryophyte cover was generally in excess of 75% (Fig 6.3).

Bryophyte species richness was, however, very poor with a total of only eight taxa being recorded from the 10, 1 m^2 quadrats surveyed in the zone. The dominant taxon was *Dicranoweisia* spp. occurring as either cushions or turves (Fig 6.3). Other moss taxa recorded were *Ditrichum immersum*, *Racomitrium crispulum* and occasionally, *Polytrichum alpinum*. There were four liverwort taxa; *Pedinophyllopsis abdita*, Lophocoleoideae sp., *Herzogobryum atrocapillum* and *Blepharidophyllum densifolium*. The liverworts were generally found growing through moss cushions and turves.

Small cushions of *Azorella* and occasional plants of *Poa kerguelensis* were also present in Zone One. *Azorella* cushions were low in profile and limited in size by very shallow substrate depths. Cushions larger than in 20 cm in diameter were found only in areas where a deep sandy, peaty layer had collected, such as behind rocks, or in crevices.

Zone One was very exposed to the wind yet the surface and sub-surface was mesic. The cushions of moss were growing into the wind, with wind driven mist being an important source of moisture. Quadrats surveyed from this zone were classified into group 5 in the TWINSPAN analysis (see Section 5.4).

Zone Two, midway down the cone side was bare of macroscopic plants (Fig 6.2). The steep (35°) and very unstable surface layer was comprised entirely of loose scoria particles ranging from 1-5 cm.

Zone Three, towards the base of the cone, was marked by a lessening of slope to 25° (Figs

Figure 6.3 Detail of Zone One, Macey Cone, Heard Island, looking down the slope. White tape defines a 10 x 10 m area. Yellow brown turves and cushions are mainly *Dicranoweisia* spp. and *Ditrichum immersum*. Bright green, low lying cushions are *Azorella selago*.

Figure 6.4 An example of the small series of ridges below Macey Cone, running parallel to the Macey Cone transect. Area marked by tape is 20 x 5 m. Light covered patch in foreground is bare ground covered with penguin feathers, blown in from coastal colonies.

6.1 & 6.2). The predominant plants were cushions of *Azorella*. In the upper part of this zone, cushions were between 15-30 cm. Coarse scoria (1-5 cm), rolling down from Zone Two had accumulated behind the cushions.

Lower down the zone, the slope reduced considerably to 5°. In this area, *Azorella* cushions up to 100 cm in diameter were recorded. Bryophytes could be found in this part of Zone Three (Fig 6.2), growing in *Azorella* cushions and in fines (ash/sands) collected around the cushions, and on large scoria boulders which had rolled from the top of the cone. Total bryophyte cover was minimal. Taxa included the mosses found in Zone 1, as well as *Bartramia patens* and *Ditrichum conicum*. Liverwort taxa, *Fossombronia australis*, *Pedinophyllopsis abdita*, Lophocoleoideae sp. and *Cephaloziella varians* were also recorded. Quadrats from this area were classified into TWINSPAN group 4 (see Section 5.4).

At the base of the Macey Cone there are a number of small ridges, approximately 5 m in height, running parallel to the transect (Fig 6.1). These ridges have somewhat similar vegetation patterning to that on Macey Cone but on a smaller scale (Fig 6.4). Vegetation on top and on the higher slopes of these ridges consisted of small cushions of *Azorella*, surrounded by lush cushions and turves of mosses. Bryophytes were the dominant component of the vegetation in terms of total cover. Lower down the slopes the bryophyte component diminished leaving predominantly *Azorella* cushions surrounded by bare ground.

6.2.2 Dovers Moraine, Spit Bay

South of Stevensons Lagoon is a series of lateral moraine ridges and valleys (Fig 6.5). There is a small coastal fringe of extensive vegetation between the lagoon and the hut at Spit Bay. The vegetation within this area is generally a mixture of nutrient enriched *Poa cookii* vegetation, *Pringlea* herbfield vegetation and patchy *Azorella* cushion vegetation.

Inland from the coastal fringe the moraine is speckled with feldmark vegetation (Fig 6.5). The total cover of this vegetation is exceedingly low, with small cushions of *Azorella* being predominant.

In the first valley system south of the lagoon, an example of small scale patterning on moraines is documented. On the north-facing side of the valley, at an altitude of approximately 45 m, a small drainage line runs between two small hillocks (Fig 6.6 & 6.7.a).

On either side of the drainage line the surface of the 25° slope was sorted, comprising rocks generally between 4-20 cm in diameter (Fig 6.7.a & b). They were angular with smooth corners. There was however, occasional large rocks or erratic boulders. Subsurface there was a layer of sand and gravel which was very moist and considerably colder than ambient day-time air temperature. The slope was dynamic, with many rocks leaving scar marks up to 50 cm, having moved down slope.

Vegetation on the slope consisted of scattered cushions of *Azorella*, principally between 30-60 cm in diameter. There were also scattered plants of *Poa kerguelensis* and *Colobanthus kerguelensis*, but the density of these plants was extremely low. Bryophytes too, were also notably sparse. Five moss taxa were recorded in the vicinity. *Grimmia immerso-leucophaea* could be found on a few rocks, *Dicranoweisia* spp. complex, *Polytrichum alpinum*, *Racomitrium crispulum* and *Ceratodon purpureus* could be found growing in sand which had collected behind and around *Azorella* cushions. *Dicranoweisia* could also be found as small sprigs growing between branches of *Azorella* cushions.

In contrast to the rest of the slope, the small drainage line was considerably vegetated and in particular with turves and cushions of mosses (Fig 6.6). Moss taxa recorded growing on the slope were also found here, as well as *Bryum pseudotriquetrum*, *Pohlia wahlenbergii* and *Brachythecium* spp.

Figure 6.5 Aerial photograph of a small part of Dovers Moraine adjacent to Stevensons Lagoon (top lefthand corner). Valley site indicated by <-. Small green dots in the general vicinity of site are *Azorella* cushions. To the east of valley site is the coastal strip of extensive vegetation. Distinguishable in this area are the dark green patches of closed *Pringlea* monsospecific vegetation on coastal moraine) (p).

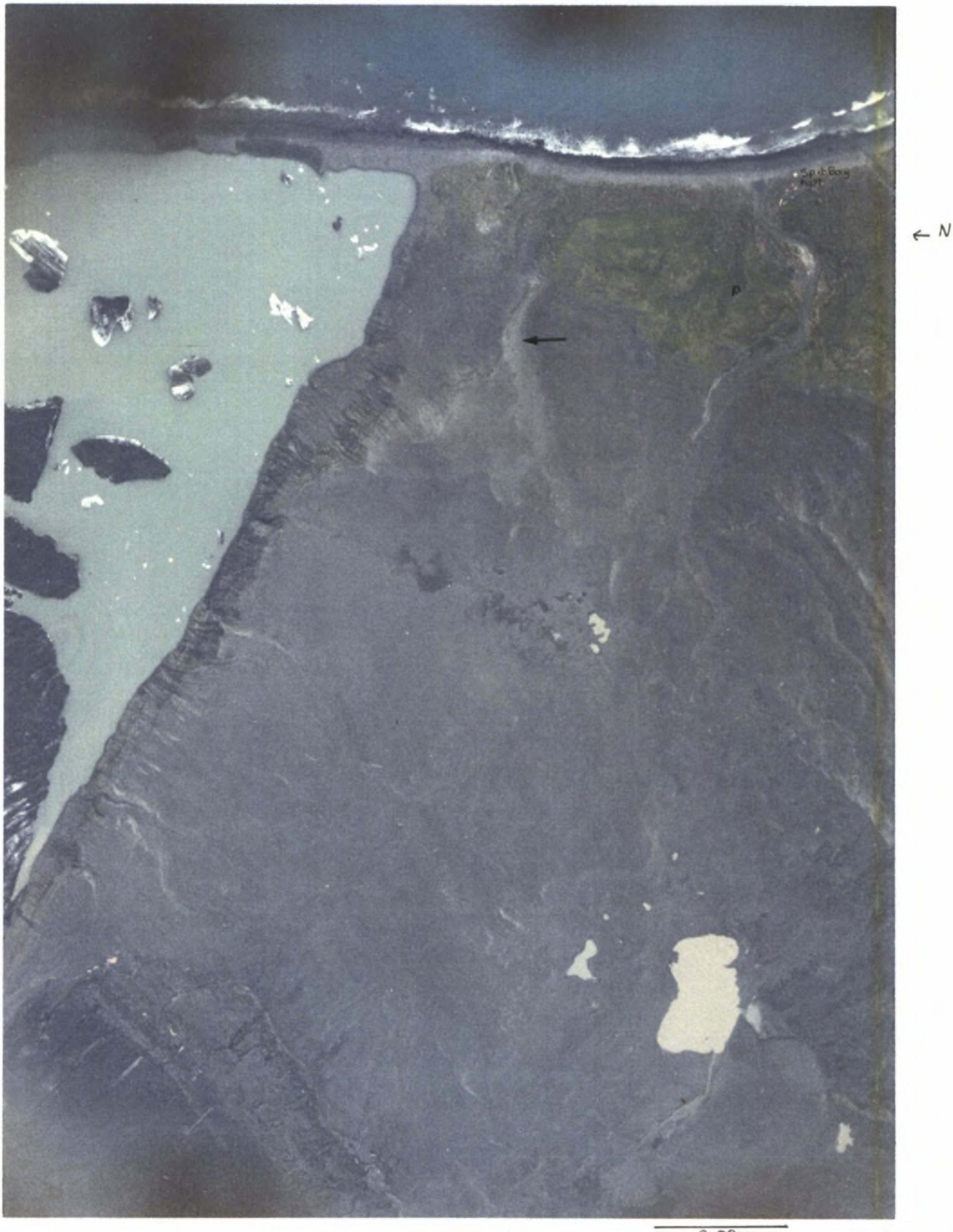


Figure 6.6 Feldmark site on Dovers Moraine showing drainage line on right hand side of photograph. Light green cushion plants are *Azorella*, olive green plants are bryophytes, generally *Dicranoweisia* spp. complex. Yellow poles-1 m scales.

Figure 6.7.a left. Detail of drainge line and adjacent areas, Dovers Moraine, Heard Island. Pole scales- 1 m.

Figure 6.7.b below. Detail of surface of slope adjacent to drainage line. Pole in *Azorella* cushions indicates reference point for Fig. 6.7.a.

Figure 6.8 Moss turves growing in drainage line, Dovers Moraine, Heard Island. Scale 5 cm lens cap.

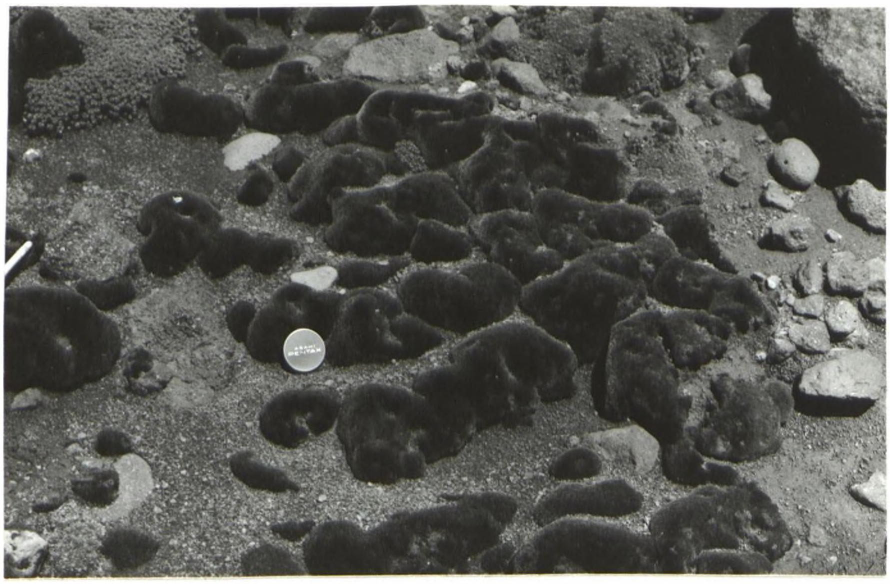
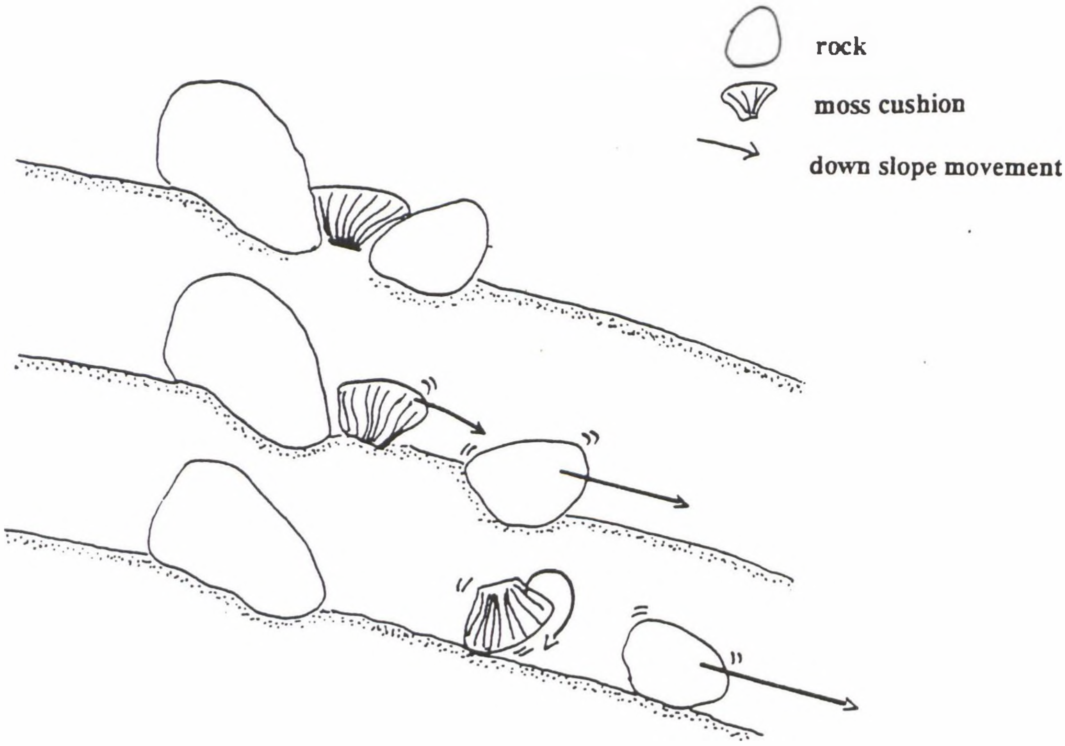


Figure 6.9 Process of dislodgement of moss cushions, evident in the drainage line, Dovers Moraine, Heard Island.



The drainage line surface consisted mainly of sand between the occasional boulder or *Azorella* cushion with only a few medium sized rocks (5-20 cm in diameter) in contrast to adjacent slope. Most likely medium sized rocks had been washed away from the drainage line during times of heavy water flow, such as after snow fall. In many places the sand became the tread of small, irregular, terracettes with substantial turves of *Dicranoweisia* making up the riser (see Fig 6.8). *Dicranoweisia* also grew as substantial cushions between rocks and on the surface of *Azorella* cushions. Other taxa grew in fines, next to and on rocks and on *Azorella* cushions.

There was some evidence of surface movement along the drainage line. It was apparent that moss cushions growing between rocks had been dislodged as the rock lower down the slope had moved. This process is illustrated in Fig 6.9.

6.3 Marion and Prince Edward Islands sites

6.3.1 Kaalkopie lava flow, Marion Island

In 1980 a small volcanic eruption occurred at Kaalkoppie, on the east coast of Marion Island (Verwoerd *et al*, 1981). Three small cinder cones and a small aa lava field were formed. When the area was visited in May 1987, patterning was evident in the distribution of colonizing plants. In some areas such as on the inner slope of the smaller crater, there were considerable stands of thick, fertile, carpets of *Racomitrium lanuginosum*. Other areas were bare.

Of particular interest was the patterning of vegetation on the lava field. The field was generally 1.5 m to 3 m higher than the surrounding ground and could be classified into two distinct elements. Most of the field consisted of hummocks and hollows (1-1.5 m high), composed of loose, black, small (1-3 cm) basalt clinker fragments (Fig 6.10). These fragments formed a thick mantle over the second element of the field: a solid flow. The solid flow was exposed in a number of a places, in particular at surface cracks (Fig 6.11)

Figure 6.10 Hummocks and hollows of small clinker fragments on the Kaalkoppie lava flow, Marion Island. *Racomitrium lanuginosum* dominated vegetation patterns on the tops of hummocks. Transect site in foreground.(↑)

Figure 6.11 Cracks in the Kaalkoppie lava field. Pencil as scale, 15 cm long with 2 cm scale markings (<-). Mosses growing on rock walls and on sections of rock, emergent from the clinker fragments.

Figure 6.12.a Tuffaceous terracing on the rim of Kent Crater, Prince Edward Island.→ indicates location of transect.

and at the edge of the flow.

Vegetation, predominantly the moss taxon *Racomitrium lanuginosum*, but also *Bryum argenteum*, *Ceratodon purpureus*, *Ditrichum stric :tum*, *Pohlia* sp. and the grass *Agrostis magellanica* was restrictd to only a few niches. Mosses were growing on the rock walls and ledges within the protected lava cracks, and on exposed areas of solid lava (Fig 6.11). *Racomitrium lanuginosum* and occasionally other moss taxa could be found growing in small patches on top of the clinker hummocks (Fig 6.10).

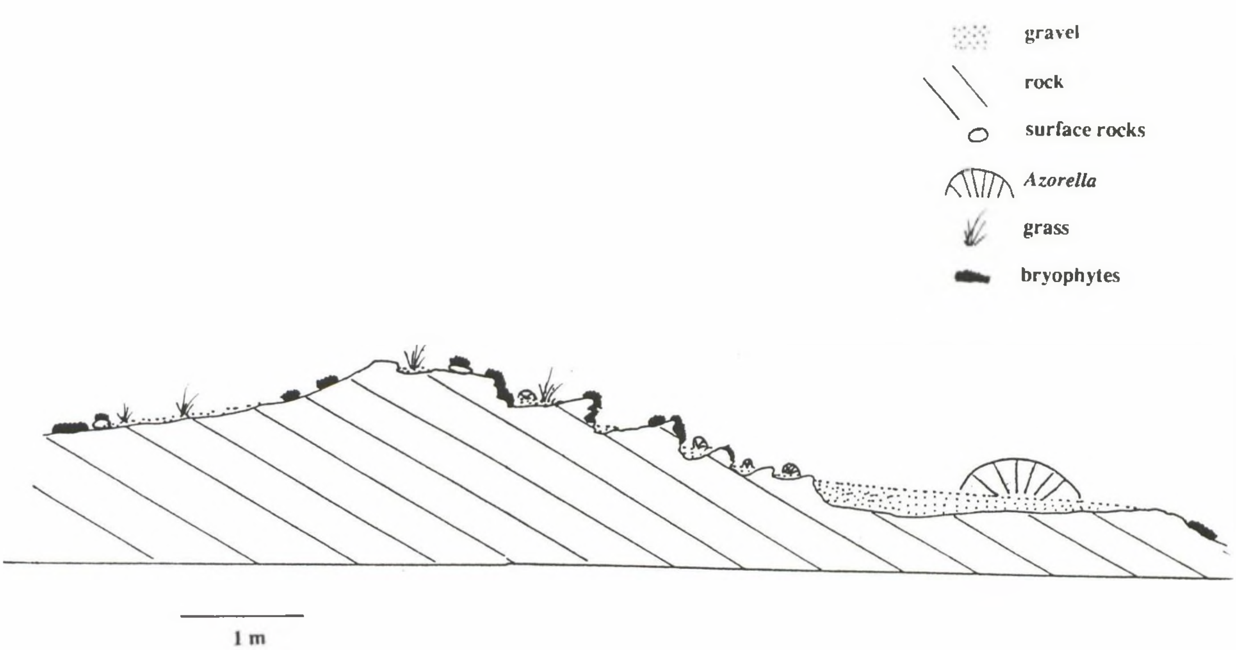
The striking feature of the vegetation was that an extensive rhizoidal matting system was holding the *Racomitrium* patches tightly to the surface. This matting system bound clinker fragments, both immediately below the gametophores and for approximately 10 cm around the patch. A 1 m transect along which upright matches were placed at 10 cm intervals was established from the top to bottom of a hummock (Fig 6.10). After one week, the matches were still upright, however total transect length had compacted by 1 cm. Although far from being conclusive, the transect data suggested that there was movement occurring within the bare hollows compared with the vegetated hummock tops.

6.3.2 Kent Crater, Prince Edward Island

Kent Crater is a double ringed surtseyan tuff cone on the north western coast of Prince Edward Island (Verwoerd & Chevallier, 1987). There is substantial patterning of vegetation on the northern and eastern sectors of the crater rim (Fig 6.12.a). Weathering of the tuffaceous rim has created a series of terraces. The terrace risers are exposed tuffaceous rock, including layers of soft accretionary lapilli (Verwoerd & Chevallier, 1987). The treads are lined with vertically sorted pavement with a surface cover of gravel (particle size generally 0.5-2 cm in diameter) (Fig 6.12.b). A series of eight contiguous 1 m^2 quadrats laid across the upper-most terraces on the NNE part of the crater rim was studied. A profile diagram of these quadrats is shown in Figure 6.13.

Figure 6.12.b Cushions of *Azorella* growing in the pavement in the treads. Mosses growing on exposed tuffaceous rock of Kent Crater.

Figure 6.13 Profile diagram of rim of Kent Crater, Prince Edward Island, show the distribution of bryophytes and vascular plants.



On the terraces, there is clear demarcation between the distribution of flowering plants and bryophytes. Significantly, bryophytes were growing only on the exposed tuffaceous rock or on large rocks positioned on the pavement. Bryophytes were not growing within the gravel pavement. *Dicranoweisia* spp. complex was the predominant bryophyte taxon on the terraces. Other taxa recorded were *Racomitrium crispulum*, *Ditrichum strictum* and *Clasmatocolea vermicularis*.

Cushions of *Azorella* and tufts of *Agrostis magellanica* were growing in the gravel pavement. Cushion size was restricted by the depth of the gravel. The largest cushion recorded being 60 cm in diameter; gravel depth adjacent to this cushion exceeded 30 cm.

6.4 Discussion of patterning and establishment of hypothesis

6.4.1 Discussion

This study has documented differential patterning in vegetation at a number of selected sites from three subantarctic islands. Although, at a glance, the selected feldmark sites appeared to be considerably varied, there were a number of interlinking factors between them.

One basic, yet considerably important feature of some feldmark environments, observed at Macey Cone (Heard Island) and Kent Crater (Prince Edward Island) was the limitation of the size of *Azorella* cushions due to the depth of the substrate: shallow substrate resulting in small cushions. This was also noted in the general vegetation survey of Heard Island (see Fig 5.6) where a significant correlation was found between *Azorella* cover and substrate depth. Hence the competitive ability of *Azorella* was curtailed in some environments.

A factor which contributed to the success of the bryophyte component of vegetation in particular environments was their ability to exploit ombrotrophically derived moisture. The

Table 6.1 Summary of the presence and absence of bryophytes at the four feldmark study sites.

	BRYOPHYTES PRESENT	BRYOPHYTES ABSENT
Macey Cone		
ZONE 1	lava large scoria (>30 cm)* ash/sand*	
ZONE 2		scoria (1-5 cm)*
ZONE 3	ash/sand *Azorella* cushion large scoria (>30 cm)	scoria (1-5 cm)*
Dovers Moraine		
SLOPE	large rocks (>20 cm) fines behind cushions *Azorella* cushions	rocky surface * (4-20 cm)
DRAINAGE LINE	sand risers* on large rocks on cushions	sand treads*
Kaalkoppie		
SOLID LAVA	walls, ledges, exposed areas	
CLINKER	tops of hillocks	sides of hillocks* hollows*
Kent Crater		
RISER	tuffaceous outcrops	
TREAD	large rocks	sorted pavement*

* possible moving surfaces

bryophytes in Zone One on Macey Cone, on the top of clinker hummocks at Kaalkoppie, and on the treads on Kent Crater, all depended on, to a large degree, ombrotrophic sources of moisture, in particular, wind driven mist.

A most significant feature of the feldmarks studied concerns the distribution of vegetation in relation to substrate characteristics. A range of substrates was recorded across the selected feldmark sites. In Table 6.1 these substrates are classified into those with bryophytes present and those with bryophytes absent. Asterisks indicate substrates which showed evidence of surface movement. Bryophytes were recorded growing on a number of stable surfaces as well as on only two potential moving surfaces: sand and large scoria rocks. In contrast, substrates devoid of bryophytes were all considered to be moving surfaces, predominantly with surface particles in the size range of 1-20 cm.

6.4.2 Hypothesis

The patterning at the selected sites, suggests that if moisture is available in feldmark environments, and propagules are present in the substrate, then surface movement is a critical factor contributing to the establishment or non-establishment of bryophytes. It appears that some moving substrates may either bury or damage propagules or young plants and hence prevent establishment. Continual disturbance may maintain bare areas.

The hypothesis has the following components. In bare areas in feldmark:

1. the surface is moving
2. there are viable bryophyte propagules present on the surface and within the in the top 5cm of the substrate
3. with exposure of the bryophyte propagules, the provision of moisture and the cessation of movement of the substrate, the propagules will germinate and establish

6.5 Testing the hypothesis on Macquarie Island

6.5.1 Feldmark on Macquarie Island

In order to test the hypothesis, substrates were probed for viable propagules and surfaces inspected for movement in bare areas in feldmark on Macquarie Island.

Feldmark occurs extensively above 200 m alt. on Macquarie Island. Vegetation cover is extremely variable (Selkirk & Seppelt, 1984; Selkirk *et al.*, 1990). Many of the feldmark areas are terraced. Well-developed terraces generally consist of vegetated risers dominated by *Azorella selago*, the grass *Agrostis magellanica* and the moss *Racomitrium crispulum*. Vegetation cover on the risers can be extensive, up to 100%. In contrast the treads are commonly covered in stones, gravel and fines and are either devoid of vegetation or are sparsely covered with cushion and turf-forming mosses and associated liverworts, such as *Ditrichum strictum, Andreaea mutabilis, Racomitrium crispulum* and *Jamesoniella colorata*. Selkirk *et al.* (1988) examined terraces on non-windward slopes and interpreted their features as dynamic, with wind, moisture, hillslope, slope stability and vegetation affecting terrace form.

6.5.2 Sites

Four terrace sites (A-D), spanning two treads and the intermediate riser, were established on the northern plateau on Macquarie Island. Details of the sites are presented in Table 6.2 and Table 6.3. Site locations are shown in Figure 6.14. Vegetation on the risers at all four sites exceeded 70% and was growing over thick mantles of peat. The treads had 5% or less vegetation cover, generally small cushions of *Ditrichum strictum* and *Andreaea* spp. (Figs 6.15 & 6.16). Evidence of solifluction activity was present at Sites A, C and D.

Two non-terraced sites were also surveyed. Site E was an extensive, steep (15°) SW facing slope immediately above the Sandy Bay/ Bauer Bay track junction (Fig 6. 14). The surface consisted of a 10 cm deep layer of heterogeneous particles, ranging from sand to

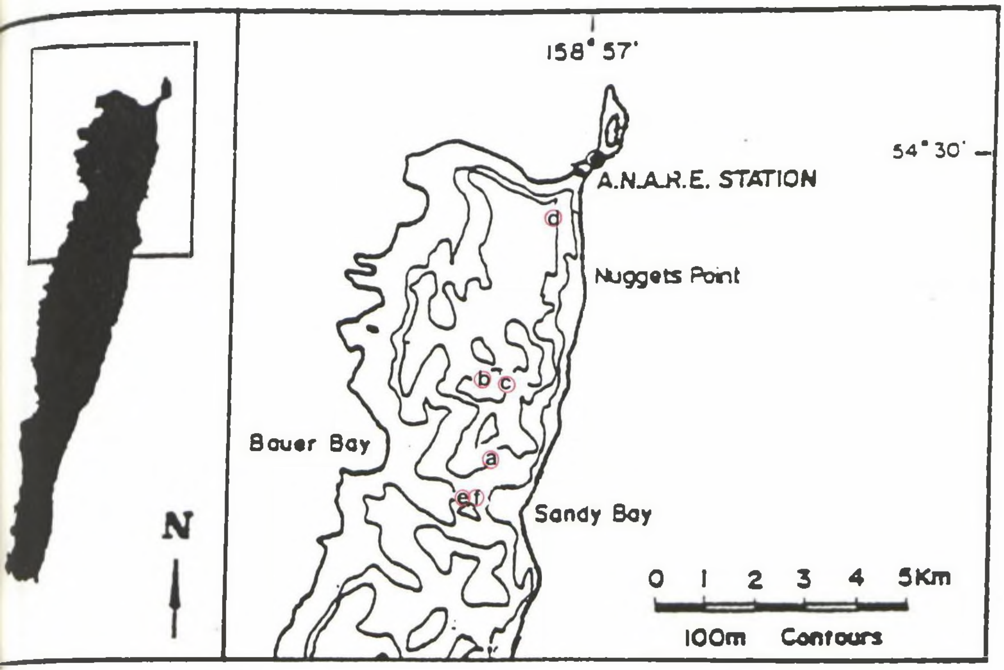


Figure 6.14 Location of terrace sites and other soil core collecting sites on the north plateau on Macquarie Island.

a - Site A, south-west slope of Hill 277
b - Site B, west side of Mt Power
c - Site C, east side of Mt Power
d - Site D, north side of North Mountain
e - Site E, south-west slope Sandy Bay/ Bauer Bay Track Junction
f - Site F, north of Site E

Figure 6.15 Terrace Site C, east side of Mt Power on Macquarie Island. Tread (t) with cushions of *Andreaea* spp. and *Ditrichum strictum* and riser (r) dominated by the *Agrostis magellanica* and *Racomitrium crispulum*.

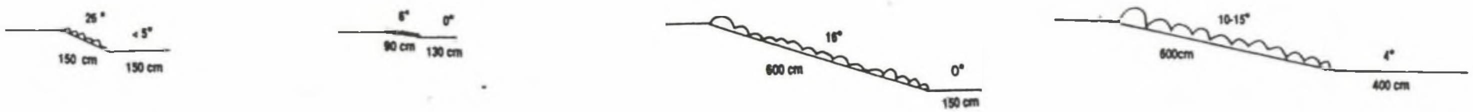
Figure 6.16 Detail of riser at Terrace Site B, west side of Mt Power, Macquarie Island showing turves of *Racomitrium crispulum*. Area defined by 1 m^2 yellow quadrat.

Figure 6.17 Site E of Macquarie Island. Soil core was sampled mid slope, adjacent to 1 m yellow pole.

Table 6.2 Details of the four terrace sites on Macquarie Island.

TERRACES	SITE A	SITE B	SITE C	SITE D

PROFILE



TERRACES	SITE A	SITE B	SITE C	SITE D
Aspect of hillslope	SW	W	E	N
Slope along length of terrace	16°	5°	2°	0°
RISERS				
Vegetation cover	95%	75%	100%	100%
Peat depth	20 cm	30 - 40 cm	30 -40 cm	50 - 60cm
Dominant species	*Azorella selago* *Agrostis magellanica* *Racomitrium crispulum* *Polytrichum alpinum* *Breutelia pendula*	*Azorella selago* *Racomitrium crispulum*	*Agrostis magellanica* *Racomitrium crispulum*	*Azorella selago* *Agrostis magellanica*
Other species	*Acaena magellanica* *Luzula crinita* *Cephaloziella exiliflora* *Jamesoniella colorata* *Lepidozia* sp. 15 moss species (Table 6.3) *Buellia mawsoni* *Usnea* sp.	*Agrostis magellanica* *Cephaloziella exiliflora* *Isotachis* sp. *Jamesoniella colorata* *Lepidozia* sp. *Lophocolea bidentata* 9 moss species (Table 6.3)	*Acaena magellanica* *Azorella selago* *Luzula crinita* *Grammitis poepigiana* *Cephaloziella exiliflora* *Jamesoniella colorata* *Isotachis* sp. *Lophocolea bidentata* *Plagiochila* sp. 8 moss species (Table 6.3)	*Acaena magellanica* *Luzula crinita* *Pleurophyllum hookeri* *Hypnum cupressiforme* *Polytrichum alpinum* *Racomitrium crispulum* *Jamesoniella colorata*
TREADS				
Surface	irregular gravel and rocks up to 20cm poorly defined polygons (20cm diameter)	fines, irregular gravel and rocks up to 5cm in size.	fines, gravel and rocks to 7cm stone polygons 20cm in diameter.	gravel and rocks up to 10cm stone polygons, 20cm in diameter.
Sub-surface	heterogeneous mixture of gravel, rocks and clay.	heterogeneous mixture of gravel and fines.	gravel and fines	heterogeneous mixture of gravel and fines.
Vegetation cover	5%	<5%	<5%	<5%
Species	*Azorella selago* *Agrostis magellanica* *Jamesoniella colorata* 6 moss species (Table 6.3)	*Azorella selago* *Agrostis magellanica* *Jamesoniella colorata* 6 species of moss (Table 6.3)	*Ditrichum strictum* *Andreaea* sp.	*Andreaea* sp. *Ditrichum strictum* *Racomitrium crispulum*

rocks up to 10 cm across overlying a clay layer. The slope was generally bare except for occasional cushions of *Ditrichum strictum* and tufts of *Racomitrium crispulum* and *Agrostis magellanica* (Fig 6.17) (Table 6.4).

Site F was an east-facing hollow to the north of Site E (Fig 6.14). The surface slope of 10-15°, consisted mainly of sand and small gravel particles. The hollow was devoid of plants but there was an adjacent drainage line. The mosses listed in Table 6.4 were growing in this drainage line as were occasional flowering plants including *Agrostis magellanica*, *Cerastium fontanum* and *Luzula crinita.*

6.5.3 Propagule germination trials

To probe the bare feldmark substrates for viable propagules, 5.5 cm long cores of the substrate were collected from each of the treads surveyed at Sites A, B,C & D and in the middle of the bare areas at Sites E & F. Soil cores were transported back to Sydney, divided into subsamples and cultured in laboratory conditions for 280 days. Details of the protocol are presented in Appendix 1. At the end of the time period, germinated taxa were identified. Comparisons were then made with the species recorded from adjacent vegetation in the field.

Successful germination of bryophyte propagules occurred in all soil core samples and in all but 2 subsamples. In these two subsamples, a 3.5 -5.5 cm deep sample from Site D and a 3.5 -5.5 cm deep subsample from Site F, fungal growth was vigorous and the lack of germination appeared to be due to pathogenic interaction with fungi rather than an absence of bryophyte propagules.

Total shoot number for some subsamples exceeded 500, in particular 1.5 -3.5 cm deep and 3.5 -5.5 cm deep subsamples from Sites B and C. Shoot number however, did not appear to be a reliable indicator of propagule number. Factors such as the water holding capacity of a particular volume of soil (0 -0.5 cm deep sample vs. 3.5 -5.5cm deep) seemed to

Table 6.3 Moss taxa recorded from treads and risers at the four terrace sites (Sites A-D) as well as germinated taxa from soil cores.

Species	Riser	Tread	Soil Cores
Site A, south-west slope of Hill 277			
Andreaea acuminata	+		
Andreaea acutifolia	+	+	
Andreaea gánii	+	+	
Bartramia patens	+		+
Breutelia sp.	+		
Bryum sp.	+		
Campylopus sp.	+		
Ceratodon purpureus	+	+	
Dicranoloma billardieri	+		
Ditrichum punctulatum	+		
Ditrichum strictum	+	+	+
Grimmia sp.	+		
Philonotis scabrifolia	+		
Polytrichum alpinum	+	+	
Racomitrium crispulum	+	+	
Isopterygium limatum			+
Pohlia sp. 1			+
Pohlia sp.2			+
Tortula andersonii			+
Tortula rubra			+
Bryoerythrophyllum aff.			+
Unknown			+
Total	15	6	9
Site B, west side of Mt Power			
Andreaea acuminata	+		+
Campylopus clavatus	+		
Ditrichum punctulatum	+	+	
Ditrichum strictum	+	+	+
Polytrichum alpinum	+		
Psilopilum australe	+	+	
Racomitrium crispulum	+	+	
R. lanuginosum	+		
Dicranales sp.	+		
Andreaea gánii		+	
Bartramia patens			+
Ditrichum brevirostre			+
Isopterygium limatum			+
Pohlia sp. 1			+
Pohlia sp.2			+
Ptychomnion aciculare			+
Tortula andersonii			+
Tortula rubra			+
Total	9	5	10
Site C, east side of Mt Power			
Bartramia patens	+	+	
Campylopus clavatus	+		
Ditrichum punctulatum	+		
Ditrichum strictum	+		+
Polytrichum alpinum	+		
Psilopilum australe	+		
Racomitrium crispulum	+		
Verrucidens sp.	+		
Andreaea sp.		+	
Funariaceae			+
Pohlia sp. 1			+
Tortula andersonii			+
Tortula rubra			+
Bryoerythrophyllum aff.			+
Total	8	2	6
Site D, north side of North Mt			
Hypnum cupressiforme	+		
Polytrichum alpinum	+		
Racomitrium crispulum	+	+	
Andreaea sp.		+	
Ditrichum strictum		+	+
Bartramia patens			+
Bryum sp.			+
Ditrichum strictum			+
Isopterygium limatum			+
Ptychomnion aciculare			+
Pohlia sp. 1			+
Tortula andersonii			+
Total	3	3	8

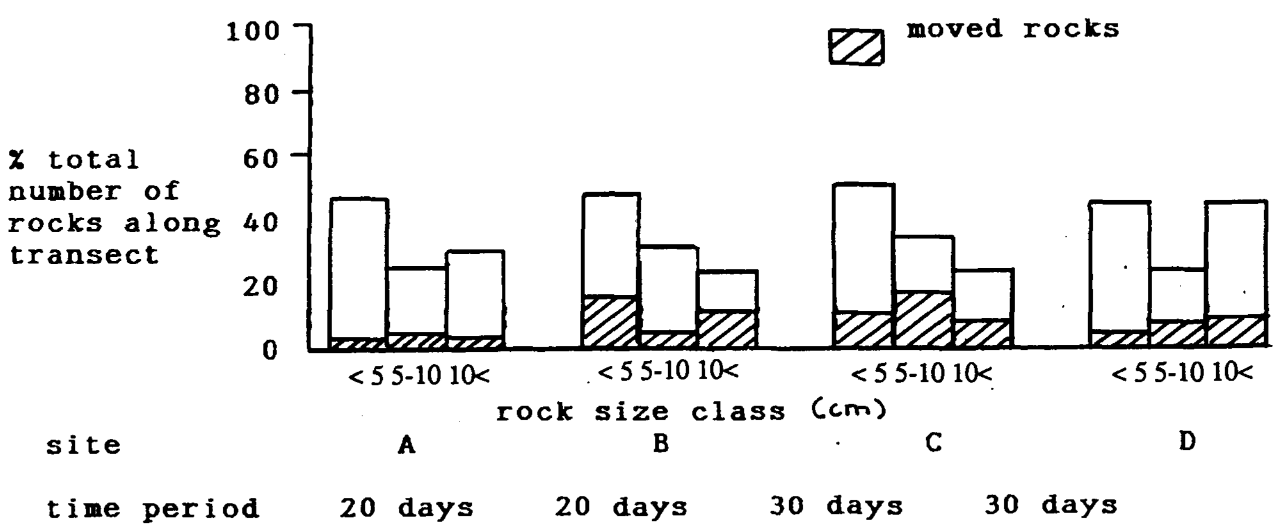
Table 6.4 Moss taxa recorded adjacent (within 2 m) to Sites E & F as well as germinated taxa from gravel cores.

	adjacent vegetation	gravel core
Site E		
Ditrichum strictum	+	+
Racomitrium crispulum	+	
Bartramia patens		+
Ceratodon purpureus		+
Pohlia sp. 1		+
Pohlia sp. 2		+
Tortula andersonii		+
Total	2	6
Site F		
Bartramia patens	+	+
Breutelia pendula	+	
Ceratodon purpureus	+	
Ditrichum strictum	+	
Hypnum cupressiforme	+	
Polytrichum alpinum	+	
Racomitrium crispulum	+	
Pohlia sp. 1		+
Tortula andersonii		+
Total	7	3

Table 6.5 Summary of surface movement data from feldmark terrace Sites A-D, Macquarie Island.

Site	A	B	C	D
Total number of rocks on transect	153	103	123	140
% rocks on transect that moved	5%	28%	3%	16%
max displacement of rocks from transect line (cm)	1.4 ±0.2	2.1 ±0.5	5.0 ±0.5	3.0 ±0.5
% of painted transect unaccounted for	4%	7%	10%	13%
slope across transect	16°	6°	0°	4°
number of rocks moved up slope	3	22	23	5
number of rocks moved down slope	4	5	15	14

Figure 6.18 Total number of rocks and number of moved rocks along the transects at Sites A-D, Macquarie Island. Rocks also classified into rock size classes.



influence the success of various subsamples. Also it was impossible to distinguish whether growth was from one or many propagules.

Table 6.3 compares the moss taxa recorded on the risers and the treads at the terrace Sites A, B, C, & D with the taxa successfully cultured from the respective substrate cores. Table 6.4 compares species lists of vegetation adjacent to Sites E and F with taxa germinated from the substrate cores. A total of 15 taxa were germinated in the propagule trials. Seven of these occurred in substrate cores from 3 or more of the 6 sites. Twenty one moss taxa were recorded in the field surveys, either on the risers and/or the treads at terrace sites or in adjacent vegetation at Sites E and F. Only 5 of the 21 taxa were germinated in the trials.

6.5.4 Surface movement

To examine surface movement, a 1 m transect, constructed by painting a blue line along the surface particles, was established across a tread at each of the terrace sites (A-D) (for details of protocol see Appendix 2). The transects were at right angles to the direction of greatest slope on the tread. The sites were photographed initially and then re-photographed after a period of between 20 and 30 days. Rotation, burial and displacement events were identified by comparing the two sets of photographs.

Table 6.5 and Figure 6.18 summarize data collected on surface movement after the elapsed time period (20 - 30 days). Between 5 and 33% of the total number of rocks along each transect line moved. Between 4 and 13% of the painted rocks along the transect length were unaccounted for. Maximum displacement of rock from the transect line ranged from 1.4 $\pm$0.2 cm to 5.0 $\pm$ 0.5 cm. Table 6.5 also records rock sizes along each transect.

6.5.5 Discussion of the Macquarie Island study

The above study has shown the presence of viable bryophyte propagules to a depth of 5.5 cm in relatively bare feldmark sites on Macquarie Island. Germination requirements of 15 species were met, including exposing propagules from subsurface layers, providing moisture, and the stabilization of the substrate surface. Five of the 15 germinated species *Andreaea acuminata*, *Bartramia patens*, *Ceratodon purpureus*, *Ditrichum punctulatum* and *Ditrichum strictum* were recorded in adjacent feldmark vegetation at the sites. Local vegetation is the most probable source of propagules for these species. Attempts to germinate propagules of *A. acuminata* and *D. strictum* were previously unsuccessful (Bergstrom & Selkirk, 1987). The absence of germination of other local taxa can not be used to suggest an absence of propagules in the substrate cores, as the warm moist laboratory conditions may not have met the germination requirements of other feldmark species.

Ten of the 15 taxa germinated in the trials were not recorded in the vicinity of the sites. Most of these species such as *Ditrichum brevirostre*, *Isopterygium limatum*, *Ptychomnion aciculare* and *Tortula rubra* are components of short grassland or herbfield vegetation associations but not feldmark (Selkirk *et al.*, 1987, R.D. Seppelt pers comm, 1992). The presence of these taxa in the germination trials indicates transport of propagules from other areas on the island to the feldmark uplands; while their absence from both vegetated and non-vegetated areas at these feldmark sites is presumably due to environmental conditions being not favorable for the germination and establishment of such species.

These results are in contrast with During & ter Horst's (1983) examination of propagule banks in Dutch chalk grasslands in which they reported that only bryophyte species present above ground were represented in the bryophyte propagule bank. This contrast most likely reflects the extremely windy conditions on Macquarie Island which can blow propagules from lower altitudes to upland sites. Selkirk (1984) trapped and then successfully cultured, wind blown bryophyte fragments and gemmae from a number of species, such as *Tortula rubra* and *Ulota phyllantha* at altitudes above 200m on Macquarie Island, despite such species being consistently found growing only at low altitudes. Similarly, R.I.L.Smith (1987) germinated local taxa from feldmark propagule banks on Signy Island (Maritime

Antarctic), and he recorded exotic species as well: evidence of long distance wind dispersal in high latitude environments.

The hypothesis suggests that if there are viable bryophyte propagules in the bare areas in feldmark then some factor or factors are preventing them from either germinating and/or establishing. Surface movement appears to be the likely disturbing factor in many cases. Selkirk *et al.* (1988) interpreted features of terrace sites as 'dynamic'. This study shows that this is indeed the case at an individual rock level (Table 6.5) with between 5 and 33% of rocks on a 1 m transect line moving during a time period of between 20 and 30 days. Rocks were moved up to 5 cm away from the transect line. There was no apparent pattern in direction of movement (Table 6.5) nor did movement appear to be related to rock size.

Stone polygons, observed at Sites A, C & D are indicative of frost heaving, which is the most probable cause of the movement at the Macquarie Island terrace sites. These sites, however were visited in wet, cyclonic weather conditions when it was observed that run-off from the risers flooded the terraces treads caused movement as well as provided water for ice formation. Gale force winds are also responsible for blowing or rolling small rocks along the surface. Thus a number of environmental factors contribute to movement of the surface layers of the treads in terraced areas.

6.6 Discussion

This study has documented patterning at a number of feldmark sites, and examined the distribution of three major components: bare areas, the vascular plants and bryophytes.

The distribution of bryophytes was of considerable interest. Bryophytes were recorded growing on stable surfaces, on large moving rocks and on possibly moving sand (Table 6.1). Bryophytes were absent from moving substrates with intermediate surface particle size (1-5 cm). At the Macquarie Island terrace sites, occasional cushions of *Ditrichum*

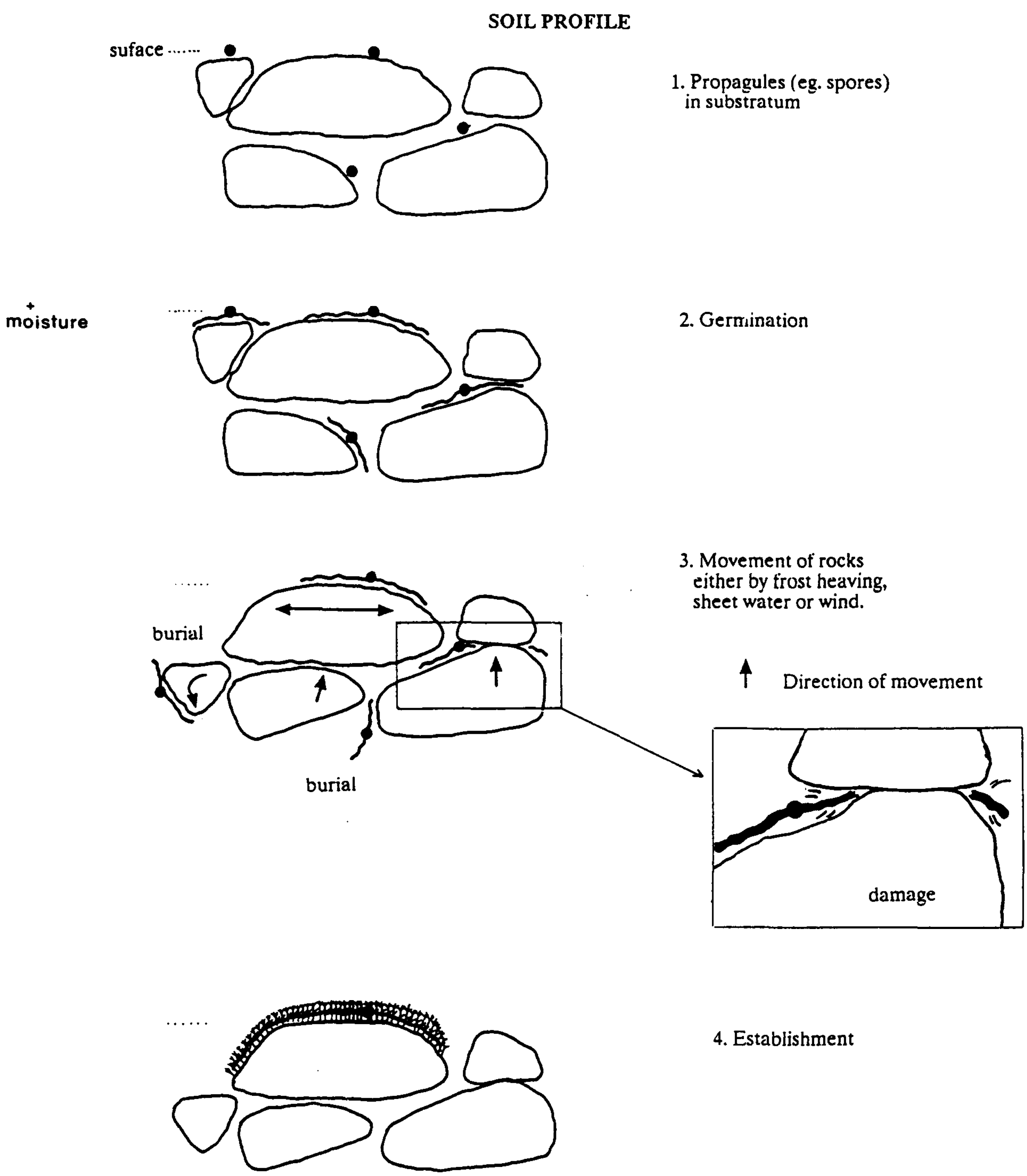


Figure 6.19 Model for successful colonization and retardation of bryophytes in feldmarks.

strictum and *Andreaea* spp. were present on the treads. These plants were, however, on relatively stable fines close to the risers or growing on top of large rocks present on the surface.

The Macquarie Island germination trials have shown that viable bryophyte propagules are present in the top 5.5 cm of substrates in feldmark. Three conditions were met during these trials: propagules from subsurface layers were uncovered, moisture was amply available, the substrate surfaces were stabilized.

Figure 6.19 presents a model for both successful colonization and non establishment of bryophytes on the Macquarie Island terraces. In part 1 of the sequence, propagules are shown to be present throughout the soil profile. In part 2, germination of propagules occur in an adequate water regime. If drought conditions prevail, then germination requirements will not be met. R.I.L.Smith (1987) reported that increasing the nutrient supply in germination trials of soil cores from Maritime Antarctic feldmarks did not increase the number of species or increase productivity in germinating propagules.

In Part 3 (Fig 6.19), bryophyte establishment is curtailed in some microhabitats due to either burial and/or damage of propagules or germinating protonema by surface particles. As a result bare areas are maintained. Germination of bryophyte propagules may be successful if protonemal growth becomes attached to larger rocks. Washburn (1973) reports that large rocks are differentially sorted to the top of frost heaving surfaces. Gremmen (1982), Selkirk *et al.* (1988) and Selkirk *et al.* (1990) all reported fines being washed away during sheet flow in feldmark areas. Large rocks have a greater chance of 'floating' in a periglacially active substrate, or in areas subjected to water run off. They may be subjected to displacement (or lateral movement) but are less likely to be buried or rolled (Fig.6.19), thereby reducing the chance of damage to surface protonema. The surface of a large rock can be considered a small scale version of a stable bed rock surface.

This model can be used to explain most of the patterning of bryophytes observed at the selected sites on Heard, Marion and Prince Edward Islands. Areas in which bryophytes were absent generally had surface particles of intermediate size (Table 6.1), which are more prone to rolling. The cause of surface movement does not have to be restricted to water wash or periglacial activity but can also include movement on steep slopes such as in Zones Two and Three at Macey Cone or by wind as on the Macquarie Island terraces. Bryophytes on large moving scoria rocks in Zone One at the top of Macey Cone can be explained by means of successful colonization events depicted in the model.

Movement of the substrate was restricted by rhizoidal matting on the tops of clinker hummocks at Kaalkoppie. As the rhizoidal mats of *Racomitrium lanuginosum* extended beyond the gametophores (see Section 6.3.1) this may be a method of increasing the surface area available for colonization by the species.

Bryophytes were also recorded on possible mobile sands/ash in Zone One of Macey Cone and in the drainage line of the Dovers Moraine site (see Section 6.2 & Table 6.2). Protonemal and eventually rhizoidal matting may bind and stabilize fines. Disruption as a result of, for example, down wash may then move the matted block as a whole entity rather than disrupt and damage individual filaments. This may help explain the formation of mobile 'moss balls' reported from many alpine, subantarctic, and Antarctic localities (Huntley, 1971; Gremmen, 1982; Mägdefrau, 1987; Seppelt & Ashton, 1978). I believe that a spherical ball of moss is an extension of a cushion habit. Some of these 'moss balls' have formed around rocks (extending the establishment phase in the model). Others have a centre of fines.

Heilbronn & Walton (1984) reported the formation of small steps by flowering plants in sorted stripes in feldmarks on South Georgia. They suggested that mobile areas were stabilized by extensive root systems, the greater the volume of soil held, the less likely the chance of frost heaving. Also, the formation of steps would probably lead to a change in the microclimate around the plant in relation to wind exposure and snow lie. These ideas can be applied at a smaller scale, to the moss terracettes on sand in the drainage line in Dovers Moraine, with rhizoidal matting stabilizing fines.

In many areas there was clear demarcation between the bryophyte component and the flowering plant component. Heilbronn & Waltons'(1984) concepts are of considerable relevance to cushions of *Azorella* which were the most abundant plants on the moraine slopes adjacent to the Dovers Moraine drainage line. They represented 'stable' islands and had been colonized by bryophytes. A similar scenario has been documented for *Phleum alpinum* in South Georgia (Heilbronn & Walton 1984). *Azorella*, with its deep root system was more successful in coping with the movement on the moraine slope than were bryophytes. This pattern was also observed at the base of Macey Cone (Zone Three) and on the treads at Kent Crater. The major deep tap root system of *Azorella* can occupy a volume of soil comparable to the above ground shoot system. Such an extensive root system would be able to stabilize surrounding mobile substrates. Also, Gradwell (in Heilbronn & Walton, 1984) reported that frost heave was inversely proportional to plant diameter in some cases, as plants shaded the ground and altered the immediate heat balance, reducing the frequency of needle ice formation.

Azorella can be described as a successful colonizer of moraine slopes and other unstable ground. Scott (1990) has also reported *Azorella* as a major component of many recently exposed, low altitude moraines on Heard Island. Seeds are abundant on many substrates on Heard Island. It can be predicted that seedlings would need to have deep and rapid growth to avoid damage resulting from substrate movement.

Azorella was not successful in all feldmark environments. For example, Zone Two of Macey Cone appeared to be too unstable for its establishment. But more importantly this study has illustrated that shallow substrates appeared to restrict growth of *Azorella* cushions (Zone One Macey Cone, risers at Kent Crater). In these areas bryophytes were more successful in terms of total cover, due to lack of competition from vigorous vascular plants.

This study shows that surface movement is a critical factor contributing to establishment or non establishment of bryophytes in feldmarks. This however, should not be considered the only factor. At other sites bryophyte non establishment may be due to other factors such as damage caused by particle abrasion in very windy sites. Inhibition by allelopathic means may also be significant in a few sites on Heard Island. On coastal moraines adjacent to Spit Bay Hut Creek (see Map 1) vegetation is dominated by *Pringlea antiscorbutica*, grading from feldmark to closed stands of *Pringlea*. Bryophytes were notably absent from the vicinity of *Pringlea* plants, suggesting allelopathic inhibition.

6.7 Summary

Patterning in vegetation was described from a number of selected sites in feldmark areas on Heard, Marion and Prince Edward Islands. In many areas there appeared to be demarcation between the bryophyte component and the vascular plant component of the vegetation. Patterning in bryophyte distribution appeared to reflect relative substrate stability. A hypothesis was established, suggesting that if moisture was available and viable bryophytes propagules were present in the substrate, movement of the surface was a critical factor contributing to the establishment or non establishment of bryophytes in particular feldmark environments. The hypothesis was tested at feldmark sites on Macquarie Island and the requirements of the hypothesis were met.

A model representing both successful colonization events and maintenance of bare areas in feldmarks was developed. Bryophytes were successful at colonizing stable ground but were generally unsuccessful at colonizing mobile areas of intermediate particle size. In these environments movement resulted in either burial and/or damage of propagules or young plants.

Azorella selago was a successful colonizer of moraine slopes and other unstable ground in feldmarks on Heard Island and Prince Edward Island. *Azorella* however, was not successful in all feldmark environments. Shallow substrate appeared to restrict the growth of cushions. In such areas bryophytes were more successful in terms of total cover reflecting lack of competition from vigorous vascular plants.

CHAPTER SEVEN

Aspects of Heard Island terrestrial plant ecology

7.1 Introduction

The study of terrestrial plant ecology on Heard Island is in its infancy. The vascular plant communities presented by Hughes (1987), modified from Jenkin (1980) have provided a sound basis for subsequent studies. The categories are subjective broad units, visually recognizable, based on physiognomic, microtopographic and some floristic features. There are a number of inherent problems with this classification scheme, generally in terms of scope (limited to vascular plants only), some difficult terminology and insufficient floristic detail.

This chapter seeks to extend the interpretations of Heard Island vegetation ecology combining three ecological approaches defined below, which include aspects of structural form, plant species strategies and species diversity. A new vegetation classification scheme for Heard Island is presented along with a general framework of environmental conditions, and species ecological amplitude. Information is integrated from this and other Heard Island studies and extrapolated from relevant studies on other subantarctic islands.

There are numerous approaches to the study of vegetation ecology and subsequent interpretation. Three useful, successful and somewhat different approaches have been presented by Specht (1970), Grime (1979) and Huston (1979). Specht (1970) presented a scheme in which vegetation was classified and compared on the basis of structural form, defined by life form, height and projected foliage cover of the tallest stratum. Life forms include trees, shrubs and hummock grasses.

Grime' s general approach (the Competitor-Stress tolerator-Ruderal [C-S-R] model) examines species density in relation to interspecific competition, environmental stress and disturbance. This approach examines plant strategies, defined as "a grouping of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology " (Grime, 1979 p.1). Environmental stresses are described as those which restrict photosynthetic production and while disturbance is associated with the destruction of total or partial biomass.

Huston (1979) presented a species diversity hypothesis based on differences in the rates at which populations of competing species approach competitive equilibrium. He suggested that most communities exist in a state of nonequilibrium, competitive equilibrium being prevented by disturbance and stress. There are three main scenarios in his model:

- under high stress or disturbance species diversity is low as the rate of species recovery compared with the rate of population reduction is low;
- under conditions of infrequent reductions in populations, an increase in the population growth rate of competitors also leads to low diversity as competing species approach competitive equilibrium (resulting in reduction or exclusion of less competitive species);
- under intermediate conditions of disturbance or stress, species diversity is at its highest as a dynamic balance may be established between the rate of competitive displacement and the frequency of population reduction.

7.2 Variations in environmental components that affect Heard Island plants

Following are descriptions of the major environmental components that presently affect plants on Heard Island.

Animal-derived nutrients: In identifying patterns of variation in the climates, soils and vegetation on some subantarctic islands, Smith & French (1988) recognized changes in soil chemistry, caused by manuring by seals and seabirds, as a major component affecting vegetation. Heard Island was not considered in their study, however as with other subantarctic islands, animal-derived nutrients are a major component of soil variation. Initially the source of these nutrients is the surrounding Southern Ocean.

A nutrient gradient is apparent on the island, diminishing away from coastal, seal and bird breeding, resting and hauling-out areas. Areas affected by direct manuring by seals, penguins, cormorants and giant petrels are generally devoid of vegetation, reflecting in most cases a combination of toxic nutrient levels and physical damage to plants. In some areas, such as the periphery of a Gentoo penguin rookery, inland of Spit Bay Hut (Map 2) scorching of plants by guano is evident. The soils within and immediately surrounding penguin rookeries should be recognized as ornithogenic soils. Walton (1984) characterized ornithogenic soils in Antarctica as having a pH of 7.1-7.4, high organic matter content and high nitrogen and phosphorous levels. Nitrogen is present mainly in the form of ammonia and uric acid, reflecting the high protein diets of penguins. The same conditions are likely to exist on Heard Island.

Volatilization of ammonia from penguin rookeries and subsequent deposition on vegetation downwind has been reported on both Macquarie Island (Jenkin, 1975) and on Marion Island (Lindebloom, in Gremmen, 1982). Areas adjacent to penguin and giant petrel rookeries support lush growth of *Poa cookii*, blue-green in colour, indicative of high nitrogen levels. However, Smith & Steenkamp (1990) reviewing substantial nutrient-related studies on Marion Island conducted by Smith during the 1980s stated that "although seabird and seal manuring is an important source of nutrients at some (mainly shore zone) areas, most plant communities are not affected by this and pools of available nutrients are small". Both Heard Island and Marion Island are relatively small, roughly circular islands with snow covered mountainous interiors and coastal, animal occupied areas. There is every possibility that nutrient pools in most vegetated areas on Heard Island are also small.

One factor in which Heard Island vegetation may differ considerably from Marion Island is the direct, small scale, nutrient input associated with burrowing petrel nests. Scott (1988) reported petrel nests in most vegetation types on Heard Island. Petrel numbers on Marion Island have in the past been severely reduced by predation from introduced cats on the island. Van Aarde (1979) estimated that in 1975 cats killed 450 000 petrels. Heard Island, fortunately, does not have any introduced mammals.

Smith & Steenkamp (1990) also reported that on Marion Island inputs of N, P, and K through biological fixation are negligible. Lower temperatures on Heard Island compared with Marion Island suggested that nutrient input through biological fixation may be very low.

Dissolved nutrients from parent rock

Various gradients can be predicted with respect to dissolved nutrients from parent rock on Heard Island. Unglaciated lava would be likely to yield more dissolved nutrients than moraine debris as limited physical destruction of these rocks would have occurred. In volcanic areas on the island, ash, scoria and clinker lava deposits may yield relatively more nutrients than ropy or smooth lava flows due to the greater surface area available for weathering. However, whether dissolved nutrients from parent rock is of any consequence to plants needs to be determined. Leaching may reduce the availability of dissolved mineral nutrients. Greenfield (1992) reported that mineral-N and probably other nutrients reaching recently formed or exposed Antarctic fellfield (feldmark) soils would be largely lost by drainage if not microbially scavenged beforehand. However significant amounts may be retained in highly vesicular basalts due to physical entrapment in pores.

Many vegetated areas on Heard Island, particularly in the eastern part of the island, around Spit Bay, appeared to be free draining. On Macquarie Island, Buckney & Tyler (1974) reported that there was little contribution of nutrients to lake, tarn and pond waters by surrounding rocks.

Most lavas on Heard Island are alkali basalts (DASETT, 1990) as are the lavas on Marion Island (Verwoerd, 1971). However, in an extensive plant ecological study on Marion Island, Gremmen (1982) recorded most sites having acidic pH levels. This included feldmark sites with skeletal mineral soils and low humic levels.

Unusually high levels of titanium and related elements have been reported from lavas on Mt Dixon, Laurens Peninsula (DASETT, 1990). Whether this has any influence on local vegetation is unknown. Whether the limestone deposits have any bearing on local vegetation compared with basalts is also not clear at present. There appears to be no distinct suite of limestone plant species. Quadrats surveyed on limestone moraines at the base of Anzac Peak, Laurens Peninsula (Fig 7.1) had similar bryophyte species composition to lava sites in the same area and were classified into the same TWINSPAN taxon group (Group 2, see Section 5.4). In Eastern Australia, basalt and limestone areas in the Blue Mountains have similar bryofloral components (A. J. Downing, pers comm 1992).

Figure 7.1 Closed bryophyte and *Azorella* vegetation on limestone moraine polygons. Southern base of Anzac Peak, Laurens Peninsula.

Sea-salt: Deposition of sea-salt on subantarctic islands can occur in a number of ways. In heavy storms, waves can splash directly onto coastal margins such as lava cliffs. Airborne sea-spray can be incorporated into winds blowing over land and air borne sea-salt particles can be 'scavenged' from the atmosphere and deposited on land in precipitation (Mallis, 1988). On other subantarctic islands deposition gradients appear to be related to the direction of the prevailing wind and settling mist (Mallis, 1988; Smith, 1987b).

Similar deposition patterns are evident on Heard Island. Supra-littoral zones are evident on coastal margins. Also, halophytes such *Muelleriella crassifolia* subsp.*acuta* occur some distance inland on the south and south-western sides of Laurens Peninsula, and in the Long Beach region (regions that receive the brunt of the prevailing winds), but can only be found on beach side rocks in the more sheltered, Spit Bay region.

In a study of the chemical composition of precipitation falling on Marion Island, Smith (1987b) recorded inputs of Na, N, K, Ca and Mg. Most of the inorganic N had probably been volatilized from nearby penguin rookeries. No P was added via precipitation and the only source of nutrients for plant growth were from weathered volcanic parent rock and mineralization of organic matter.

Water availability: An extreme range of availability of water exists on Heard Island. Many factors contribute to the variation. Although snow or rain falls on most days, this can be very localised. Although no objective data is yet available, expeditions have reported that the eastern ice-free areas, such as the Spit Bay region may have a generally less severe climate, with reduced cloud cover and reduced precipitation than the north-western and southern sides of the island. The controlling factor appears to be forced uplift of westerly or south-westerly moist air bodies over Big Ben (Ledingham, 1987).

Extensive snow cover in winter will provide spring melt waters but the significance to vegetation is unknown. Input can be affected by local topography. Depressions in landform can allow accumulation of snow or ice, which on melting provides free water for local vegetation. Scott (1988) reported 'meadow' vascular plant communities in areas below late lying snow banks.

Another major input of water is melt-water from glaciers, feeding creeks and out-wash lakes, and more importantly from ice-cored moraines such as in areas of Dovers Moraine, in the Spit Bay region. In summer, in some areas, constant subsurface lateral water flow is available to deep rooted plants such as *Azorella selago.*

Water output (loss of moisture) from land on Heard Island is mainly influenced by evaporation rates and drainage rates. Most areas across the island are subjected to, at times, strong, drying winds. Very exposed areas could be described as wind deserts, with any precipitation being blown away or rapidly evaporated. In some areas wind-driven mist may be the only source of moisture making the environments suitable for ectohydric bryophytes but not endohydric vascular plants.

Considerable variation in drainage rates can be found on Heard Island. A large proportion of ice-free moraines, scoria lavas and aeolian areas are free draining. A number of environmental features however, contribute to reduced drainage rates. Moisture may still be available to bryophytes as opposed to vascular plants on substrates, such as scoria, with high porosity. For example, Greenfield (1992) suggests that high microporosities of vesicular basalt Antarctic fellfield (feldmark) soils may retain moisture as well as mineral nutrients and that this may explain the occurrence of *Racomitrium* spp and other mosses on surface dry scoria on Maritime Deception Island.

Solid beds of smooth, pahoehoe lava, such as near the ANARE base can present a non-porous bedrock plane. Weathering in some areas, such as on the moraines directly behind Manning Lagoon (Long Beach region) or on the lavas near the alluvial flats, south of Anzac Peak (Laurens Peninsula) has yielded clay particles which increase the water holding capacity of the substratum. Accumulation of peat also improves the water holding capacity of the substrate.

In areas of impeded drainage, small pools or tarns occur, fed by local catchment areas. Whinam (1989) stated that pools at elevations above coastal plains are generally oriented parallel to lava ridges, suggesting that geomorphological characteristics are contributing to the pool formation. On coastal plains and beach terraces a different situation exists. Animal activity, in particular seal wallowing, contributes to reduced drainage with seals depositing excrement, carcasses and nasal mucus (Whinam, 1989) as well as moulted hair and skin. In the wet, anaerobic conditions it appears that such deposits are not decomposed. On Macquarie Island preserved seal hair and skin fragments from a wallow, have been found in sediments dated at 8510± 550 yrs BP (Bergstrom, 1987b). Seals also compress the substrate and destroy dam walls of small wallows (Whinam, 1989).

Other areas of open water include melt water streams. Wet areas but without open water include seepage zones and drainage lines. Subsurface lateral water flow would be expected to be better oxygenated than with stagnant water and may also be enriched with leached nutrients.

Substrate depth: Substrate depth, and hence volume available for vascular plant root systems varies considerably in ice-free areas on Heard Island. There are large areas of solid lava, which are either bare or thinly covered with cryptogamically derived peaty layers. Rocky areas such as clinker lava flows, and scoria cones present a range of substrate depths. In between large rocks and amongst bed rock there are areas where sediment has accumulated. Wind deposition of sediment is a major landscape forming process on Heard Island. Deep (> 50cm) unconsolidated substrates can generally be found on moraines, talus slopes and aeolian deposits and on beach terraces.

Peat deposits, derived mainly from *Azorella selago* cushions can be found on moraines and on lavas. Peat depths up to 2 m have been measured on moraines in the Spit Bay region. There are a few areas of saturated peats on Heard Island such as near the creekline draining into Sydney Cove, Laurens Peninsula, and moraines directly behind Manning Lagoon, Long Beach region. In such areas anaerobic conditions may be present, which inhibit root growth in some species. Smith (1987b) reported, that on Marion Island, waterlogging of island peats serves to buffer the temperature range experienced by plant roots and soil microorganisms.

Particle abrasion: Particle abrasion of plants is a major environmental disturbance on Heard Island. Ventifacts are evident in many exposed areas such along the Spit, demonstrating the constant presence of windblown particles. Particles will include sand and ash as well as snow and ice.

Considerable variation in exposure to windblown particles occurs. Aeolian deserts such as the Nullabor (Map 1) and other exposed areas are subjected to far more particle abrasion than protected gullies. On a microtopographical level, vegetation on lee sides in rocky areas will be less subjected to particle abrasion.

Surface movement: There are five main causes of surface movement in ice- free areas on Heard Island: gravity; cryoturbation; fluvial and fluvioglacial activity; melt of ice cored moraines; aeolian activity. All these processes can cause considerable reworking of the land surface.

Gravity can operate on unstable moraine slopes, talus slopes and scoria cone slopes causing down slope creep. Frost heaving and cryoturbation require two factors, moisture and below freezing temperatures. Evidence of frost raking and nubbin formation is often found between cushions of *Azorella selago* on moraine sediments. Sorted stripes occur on scoria and ash/sand sediments at the northern base of Mt Dixon. On the limestone moraines at the southern base of Anzac Peak there are stone polygons up to 8 m in diameter.

Fluvial activity associated with melting of winter snow will considerably affect surface structure over a wide area of topography. On a smaller scale, but of equal significance is surface movement caused by precipitation runoff during summer (peak growing season for plants).Apart from removal or burial of established plants by fluvial sediment, germinating propagules of plants can be dislodged and destroyed.

Fluvioglacial activity results generally in the removal of habitat suitable for terrestrial plants, although some redeposition of eroded stream bank sediment will occur. Entrapment of sediment is occurring in coastal glacial lagoons (see Section 1.2.1). This redeposition forms new substrates and is available for colonization by terrestrial plants.

Even though moraine material provides some insulation, melt of ice cores does occur on Heard Island in mid-summer. Slumping of surface material and burial of bryophyte vegetation occurred in 1987 in the higher areas above 60 m alt. to the east of King Creek on Dovers Moraine.

Removal and deposition of sediment is a major landscape altering process on Heard Island. With constant severe winds, particles including small rocks, gravel and ash/sand are highly unstable in many exposed areas.

Animal disturbance: The level of disturbance by animals on Heard Island ranges from no activity to very heavy trampling (Fig 7.2) and is parallel with the range of animal derived nutrients (see above, p. 92). Scott (1988) provides descriptions of habitats used by both seals and seabirds. Whinam (1989) notes intensive use of coastal vegetation by penguins and seals and reports destruction of *Poa cookii* tussocks by giant petrels.

Figure 7.2 Destroyed vegetation resulting from trampling and probably nutrient toxicity by elephant seals, Atlas Cove, Heard Island. (vegetation type: open *Azorella* and *Poa cookii* vegetation in animal disturbed area

General climate characteristics: Relative temperature gradients which may affect plant physiology exist on the island. As mentioned above, the eastern ice-free areas are reported to have milder climatic conditions than the north-western and southern areas. This appears to influence phenological stages in the vascular flora. In early December 1986 at Atlas Cove, *Pringlea antiscorbutica* and *Azorella selago* plants had flower buds within the rosette and cushion respectively. *Poa cookii* was in flower but stamens were not mature. Plants growing in the Spit Bay region, appeared to be at least two weeks more advanced in development. *Azorella* flowers were open, *Pringlea* flower heads were well elevated above the rosette and *Poa cookii* stamens had emerged with ripe pollen.

Variation in local temperatures in relation to microtopographic features occur. Valleys between lateral moraines can be subject to cold drainage. On a small scale, stones in polar regions can absorb more heat than fines, this can then be radiated to the surrounding environment. In moist fines, energy is utilized in evaporation, lowering temperature (Aleksandrova, 1988).

The snow regime can also influence microclimate. In Russian polar deserts, three major effects have been reported: snow cover can provide an insulating protective cover; snow is blown away from raised areas as well as from the tops of exposed parts of slopes and is deposited in depressions and low lying areas; the disappearance of snow can extend vegetative growth periods and contribute significantly to the amount of total heat received by plants (Aleksandrova, 1988). Similar effects can be expected in vegetated areas on Heard Island.

The annual growth period of the majority of terrestrial plants on Heard Island is restricted by winter snowfalls. Leaves of *Azorella selago* and *Acaena magellanica* are seasonally senescent (although on *Azorella* the leaves remain within the cushion; Ashton & Gill, 1965). This means that these plants can not resume growth until new leaves are active. Bryophytes, however can resume growth as soon as free water is available.

Plants are exposed to a long photoperiod during the summer months. Adamson (1991) has reported some photoinhibition among a variety of plants on Macquarie Island. Similar conditions are likely to exist on Heard Island. Nevertheless, damage to plants would not be severe compared with continental Antarctic plants as even in mid-summer there is a night recovery period. On Marion Island there is a 5-6 fold increase in daily radiation from mid-winter to mid-summer due to higher sun angles and longer day lengths (Smith , 1987b).

The effect of consistently cold conditions on plant reproduction on Heard Island is unknown at present.

Table 7.1 Major influences that affect plants on Heard Island.

STRESS -restricts photosynthetic production

animal derived nutrients

+		0		-
seal and sea bird areas	adjacent to seal and sea bird areas	burrowing bird nests	skua pools	inland, high altitudes

dissolved nutrients from parent rock

+	0			-
		lava sediments	lava	moraine, leeched zones

sea salt

+		0		-
coastal	northern and southern regions		eastern regions	inland

water availability

+		0		-
pools and lakes	seepage zones, melt waters, edges of pools	protected gullies, lava areas with clay soils	most ice-free areas, free draining lava and moraine	wind deserts

substrate depth

+		0		-
peat deposits on moraine	moraines, talus slopes aeolian deposits		rocky areas	solid lava

temperature

high	0	low
sheltered areas		cold drainage areas

DISTURBANCE -partial or total destruction of biomass

particle abrasion

protected	0	disturbed
sheltered gullies, rocky hummocks		exposed areas, aeolian deserts rocky ridges

surface movement

protected	0	disturbed
flat dry areas bed rock	mild slopes	cryotubatic areas steep slopes tallus slopes

animal disturbance

protected	0		disturbed
inland, high altitudes	burrowing bird nests	adjacent to seal and sea bird areas	seal and sea bird areas

OTHER INFLUENCES

General climatic characteristics

winter snow
consistent cold conditions
long summer photoperiod

Invertebrate interactions

nutrient cycling at detritus level

Invertebrate interactions: On Marion Island herbivory is insignificant. Most energy flow and nutrient cycling occurs through the detritus level. The main mediators for nutrient mineralization are soil macro-invertebrates (Smith & Steenkamp, 1990). Microcosm studies on Marion Island (Smith & Steenkamp, 1992) have shown that the rate of nutrient release from plant litter is enhanced by invertebrates including moth lavae and weevil lavae and adults. These types of macro-invertebrates are also found on Heard Island and it is likely that they play a similar role.

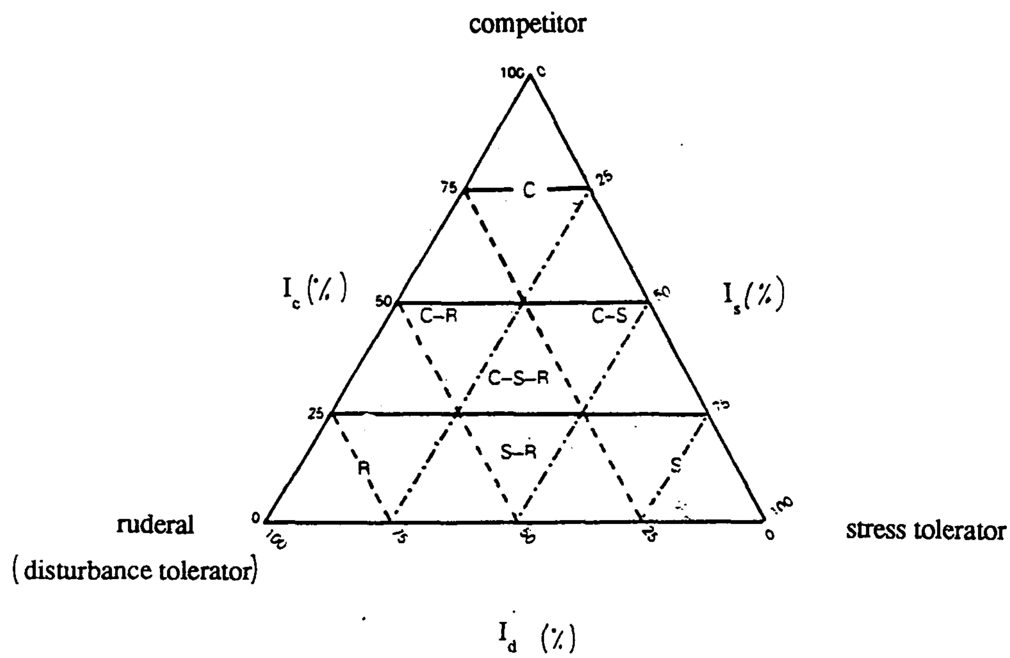
Summary: Table 7.1 lists major influences that affect plants on Heard Island and categorises them as "disturbance" or "stress" in the sense of Grime (1979), or as "other influences". It is clear however, that stress and disturbance are interlinked since disturbance creates stresses for plants, and at times the categories are difficult to separate clearly. For example, a drop in temperature to below zero on Heard Island may have many consequences. There may be cryoturbation of the substrate. This may lead to damage of root hairs of vascular plants (a disturbance event) which in turn exerts a stress via reduced mineral and water uptake. A freezing event may have different consequences for different plants. Frost damage to young shoot tips or seedlings may occur in vascular plants (disturbance) yet freezing in bryophytes may be equated to desiccation (water stress) (Longton, 1988).

Factors such as nutrient availablity can have diametrically opposite effects. For example, lack of nutrients can inhibit plant growth, while excess nutrients can be toxic. A subjective scale is presented in Table 7.1 for some environmental factors, with 0 the midline (the parameter perhaps being termed 'abundant') with - and + extremities or with an arbitrary scale ranging from sheltered to exposed.

Table 7.2 Primary strategies of response by plants to environmental factors (Grime, 1977).

Intensity of disturbance	Intensity of stress	
	LOW	HIGH
LOW	Competitors	Stress-tolerators
HIGH	Ruderals	(no viable strategy)

Figure 7.3 Model for expressing equilibrium between competition, stress and disturbance within a triangular area. I_c - relative importance of competition; I_s - relative importance of stress; I_c - relative importance of disturbance (after Grime, 1974).



7.3 Life form, ecological amplitude and strategies of major plant species on Heard Island

In Grime's (1974) C-S-R model (see Section 7.1.2), three possible primary strategies of plant species in relation to environmental factors are suggested. These are described in Table 7.2. For example, taxa which are present in conditions of low stress and low disturbance can be categorized as competitors. In conditions of continual severe stress in highly disturbed environments, rapid recovery of vegetation is prevented (Grime *et al.*, 1988).

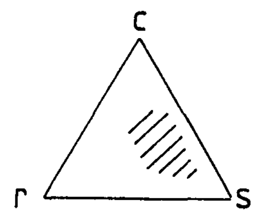
This model suggests that vegetation in a particular environment, at a particular time reflects an equilibrium between the intensities of stress, disturbance and competition (Grime *et al.*, 1988). This equilibrium can be expressed within a triangular area, as illustrated in Figure 7.3.

Following are descriptions of life form, ecological amplitude and ecological strategies of abundant or significant terrestrial plant taxa on Heard Island. Bryophyte life forms are after Gimingham and Birse, (1957). Taxa are listed according to their position in the TWINSPAN dendogram classification (see Fig. 5.3). For each of the major taxa a subjective triangular model along the C-S-R principles is presented. These models relate to Heard Island.

7.3.1 *Drepanocladus uncinatus*

Life form: ranges from moss carpets to mats.

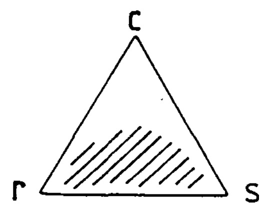
Ecological amplitude: *Drepanocladus uncinatus* was recorded generally in mesic to hydric sites, on both lava and moraine. Lush carpets were recorded in areas of lateral surface drainage. In drier sites the species grew in a tighter mat form.



Notes: Hébrard (1970) reported the genus *Drepanocladus* as occurring preferentially on acidic environments on Iles Crozet and Iles Kerguelen.

7.3.2 *Racomitrium crispulum*

Life form: moss turves.

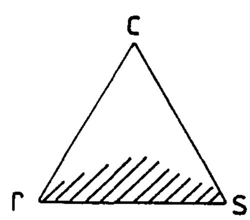


Ecological amplitude: *Racomitrium crispulum* is a wide ranging species on Heard Island. It was recorded in dry to mesic sites and from coastal to 250 m altitude. Monoculture turves of the species were usually found growing in gravel/ash/sand substrates. Often the species was a component of mixed turves, and this could be on a variety of substrates such as thin peaty layers over lava. Although the species is widespread, total cover in any one area was not high.

Notes: Hébrard (1970) reports *Racomitrium* spp. to be restricted to siliceous environments on Iles Kerguelen and Crozet. This may match the substrate range of *R. crispulum* on Heard Island although siliceous environments have not yet been identified. On Macquarie Island, *R. crispulum* is a major component of vegetation in feldmark terraces where extensive turves of the species occur on terrace risers (see Section 6.5). Comparable turves were not found on Heard Island.

7.3.3 *Ditrichum immersum*

Life form: moss cushion and turve.



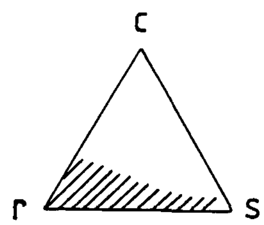
Ecological amplitude: The species occurred as cushions and turves both in exposed sites with wind driven mist the predominant moisture source and mesic sites. The species generally occurs in areas with stable substrates, often away from the coast.

At some sites *Ditrichum immersum* cushions and turves would coalesce to form extensive bryophyte turves with other taxa such *Dicranoweisia* spp.

Notes: Although recorded elsewhere on Heard Island *Ditrichum immersum* was particularly abundant in the northern and southern ice free areas on Heard Island. Hébrard (1970) reported the genus, *Ditrichum* to occur preferentially on acidic environments on Iles Crozet and Iles Kerguelen. However, on Heard Island, *Ditrichum immersum* was recorded growing on limestone derived moraine on the southern side of Laurens Peninsula as well as at other sites,. Moist, limestone derived moraines are likely to be alkaline.

7.3.4 *Poa kerguelensis*

Life form: small tufted grass, generally less than 20cm high.

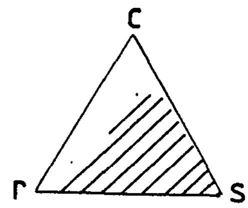


Ecological amplitude: This species is considerably widespread but very rarely forms extensive stands (although some swards, with a cover of greater than 50% were recorded at the base of Macey Cone, Laurens Peninsula. Generally the species occurs as sporadic tufts.

Of the 163 records of *P. kerguelensis* from quadrats in the vegetation survey (Chapter 5) 154 of these had cover values of 5% or less. The species was prevalent in gravels and sands. It was commonly growing in xeric, exposed conditions, although it also grew on stream banks. The species could be found in relatively unstable substrates such as in areas of frost heaving, ice cored moraines, stream banks and appears to possess characteristics of a ruderal species. The species was not recorded in environments of increased nutrient status or animal disturbance.

Notes: Hughes' (1987) report of *Poa kerguelensis* only from feldmark categories on Heard Island is an under representation of distribution of the species. The species is widely distributed in Hughes' cushion carpet category. Scott (1990) also recorded *P. kerguelensis* in areas of similar conditions as described above, and included sites recently exposed by glacial recession, post 1947.

7.3.5 *Dicranoweisia* species complex

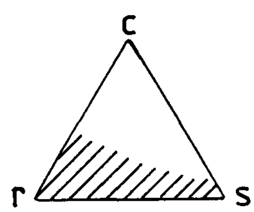


Life form: moss cushion and turf including an aquatic, black, loose turf in creeks.

Ecological amplitude: *Dicranoweisia* species complex is the most abundant bryophyte taxon on Heard Island. It exhibits wide ecological amplitude being recorded from most vegetated areas with the exception of very high animal disturbance and lush vegetated areas inundated with surface water flow. The taxon appears to be a successful stress tolerator. Extensive turves of *Dicranoweisia* spp. occur, similar to those of *Ditrichum immersum*. In bryophyte dominant areas, cover dominance or co-dominance of this taxon suggests that on a bryophytic level *Dicranoweisia* spp. is competitively successful. However, the relative cover of the taxon is reduced in areas of extensive stands of *Azorella*.

Notes: *Dicranoweisia* spp. occurs on Marion and Prince Edward Islands in environments similar to those it occupies on Heard Island (eg see Section 6.3.2). It, however, does not appear to play such a dominant role as on Heard Island. Perhaps other bryophytes such as *Ditrichum strictum*, which have not be recorded provide diffuse competition for the taxon.

7.3.6 *Colobanthus kerguelensis*



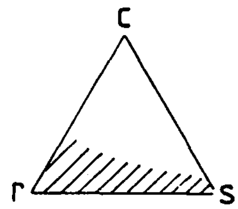
Life form: very small, low growing flowering cushion plant.

Ecological amplitude: *C. kerguelensis* is another species with very wide ecological amplitude. The species generally grows in gravel or ash/sand. It was recorded from most vegetated areas, excepting high altitude, rocky habitats and areas of extensive animal disturbance.

Notes: Scott (1990) reported *Colobanthus* as well as *Poa kerguelensis* and *Azorella* growing in crevices between rocks and in the lee of boulders on well drained moraines on Heard Island. These micro-habitats are likely to be areas of either greater moisture availability or of protection from wind exposure.

7.3.6 *Polytrichum alpinum*

Life form: open carpet moss.

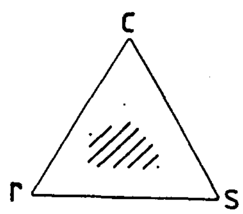


Ecological amplitude: *Polytrichum alpinum* exhibits wide ecological amplitude on Heard Island, similar to *Colobanthus kerguelensis* and *Poa kerguelensis*. The species usually grows as small loose open carpets in gravel or ash/sand or as a single stem growing between branches of *Azorella*. Total cover of the species is generally small. It appears able to tolerate extreme xeric conditions as well as relatively unstable substrates such as areas of frost heaving.

Notes: This species exhibits similar ecological amplitude on Marion and Prince Edward Islands, Macquarie Island (R. Seppelt, pers comm) and in alpine N.S.W. The extensive rhizomes and rhizoidal matting of this species, along with the root systems of *Colobanthus kerguelensis* and *Poa kerguelensis* may contribute significantly to the stabilization of bare ground on Heard Island.

7.3.7 *Bartramia patens*

Life form: Single moss stems to loose moss carpets.

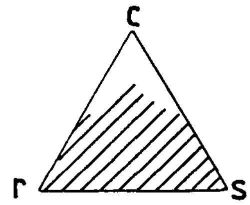


Ecological amplitude: *Bartramia patens* is a widespread species on Heard Island. Although not extensive in cover, it is particularly prevalent in moist microhabitats that have low light levels, such as in between rocks.

Notes: As on Heard Island, *B. patens* is usually found in sheltered or shaded habitats on Macquarie Island (R. Seppelt, pers comm). Hébrard (1970) reported the *Bartramia* genera to occur preferentially on acidic environments on Iles Kerguelen and Iles Crozet.

7.3.8 *Azorella selago*

Life form: cushion, with extensive tap root system with contractile roots (Ashton & Gill, 1965).

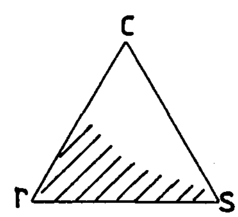


Ecological amplitude: *Azorella selago* is the most widespread, abundant and dominant plant species on Heard Island. It was recorded in 80% of all quadrats surveyed in this study and occurred in all of the 15 ecological groups delineated. It can generally be found throughout the range of environments in which terrestrial plants occur: from coastal beaches up to 400 m altitude; from protected to exposed sites. In some areas it can be found in a semi-aquatic environment, such on the edge of Spit Bay Hut Creek. As discussed in Chapter 6 (see Section 6.6) *Azorella* can be described as a successful colonizer of moraine slopes and other unstable ground. Shallow substrates appear to restrict the growth of *Azorella* cushions while other limiting factors appear to be very steep slopes and extreme environments which also limit all other plant growth on the island. *Azorella* can clearly be described as a 'tolerator' and considering its dominance of vegetated areas on Heard Island, a relatively successful competitor in the majority of areas.

Notes: *Azorella* dominated vegetation can be found on all subantarctic island groups other than South Georgia (Greene & Walton, 1975).

7.3.9 *Pringlea antiscorbutica*

Life form: perennial suffrutescent herb, up to 60 cm tall.

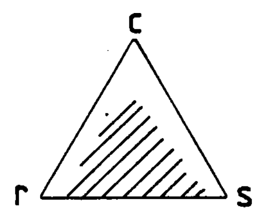


Ecological amplitude: *Pringlea* is widespread on Heard Island, occurring from coastal environments to the extreme limits of plant growth at higher altitudes. Hughes (1987) reported *Pringlea* occurring at low frequencies in all her vascular plant community categories. She described the species as an "opportunistic species which colonizes newly disturbed areas such as landslides and recently deposited moraines". Scott (1988) reported the species growing along edges of gravelly streams, lakes, old river terraces and on scree slopes, and also reported monospecific stands on sheltered moraine slopes and luxuriant growth adjacent to penguin colonies. *Pringlea* is an effective ruderal species. It appears to occur preferentially on gravel or ash/sand substrates with most occurrences in morainic debris of which many are ice-cored and/or unstable.

Notes: Young and Schofield (1973) suggested that on Iles Kerguelen, "*Pringlea* is tolerant of low temperatures and high winds, but that it requires a continuous supply of moisture and good drainage." This statement appears most apt with reference to the species distribution on Heard Island. They also reported from microfossil studies that *Pringlea* was present on Iles Kerguelen during the last glacial maximum and suggested that the species is a remnant of a Tertiary Kerguelen flora.

7.3.10 *Poa cookii*

Life form: small tussock grass.



Ecological amplitude: *Poa cookii* is widespread on Heard Island, occurring from coastal to high altitudes. The species is an effective indicator of nutrient enriched soil conditions. Extensive stands occur near seals and sea bird areas.

Notes: Similar patterns of distribution of this species have been reported on Marion and Prince Edward Islands (Gremmen, 1982).

7.3.11 Notes on other taxa

The following species, although not as significant as those listed above, are significant or characteristic components of some vegetation on Heard Island.

Andreaea mutabilis and *Schistidium apocarpum*: these species are rock colonizing bryophytes commonly growing in stable areas and on large scoria boulders or rocks in moraine. Many recordings of these species were from high altitude sites such as on Deacock Moraine, Long Beach region.

Pedinophyllopsis abdita: this species is a common liverwort in the northern and southern regions of Heard Island. It was recorded from a range of coastal to high altitude, mesic environments, but generally not in sites with significant nutrient enrichment. It grows as a mat or as single stems entangled with other plants.

Blepharidophyllum densifolium: this liverwort species was generally recorded from stable mesic rocky feldmark sites similar to *Pedinophyllopsis abdita.*

Herzogobryum atrocapillum: this very tiny, threadlike liverwort species was recorded mainly from mesic scoria and stable rocky moraines with high bryophyte cover. Single stems were commonly found interwoven with other bryophytes.

Blindia robusta: extensive lush stands of this moss can be found on moraine, cliffs and lava on the eastern and southern sides of Heard Island.

Polytrichum piliferum: this moss was recorded only from moraines on Heard Island. It generally grows in gravel, or fines and appears to tolerate xeric conditions and unstable substrates, anchoring to the substrate with rhizoidal mats.

Fossombronia australis: This liverwort is very widespread on Heard Island but was never recorded as abundant at any particular site. It was generally seen growing in gravel at the edge of *Azorella* cushions or growing between branches of *Azorella* with its rhizoids anchored in a mixture of humic material such as abscised leaves and accumulated wind blown sediment. In this microhabitat it can be described as an epiphyte.

Ceratodon purpureus: this moss species, like *Fossombronia*, is widespread but never very plentiful on Heard Island. It was most commonly found growing in gravel, and spanned a large range of environments from xeric exposed moraines to flush zones. This species is, however, far more widespread and abundant on Heard Island than on Macquarie Island.

Bryum pseudotriquetrum: this moss is another widespread but not abundant bryophyte on Heard Island. It was often recorded as single stems amongst *Azorella* cushions, but could also be found in hydric zones such as at the edge of glacial lakes and streams or in meltwater areas in generally unvegetated ice-cored moraines. Scott (1988) reported *B. pseudotriquetrum* with *Pohlia wahlenbergii* colonizing areas exposed to spray from waterfalls.

Acaena magellanica: this suffrutescent herb has been recorded from the southeast ice-free areas on Heard Island, between Fifty-one Glacier and Fairchild Beach (Scott, 1988). This species most often grows on moist slopes, generally in association with other species such as *Azorella* and *Poa cookii*. Scott (1988) also reported the species growing with *Pringlea*.

Deschampsia antarctica: This grass species has been noted in the eastern areas of Heard Island growing in drainage lines and springs (Hughes, 1987: Scott, 1988).

Brachythecium species complex: these mosses are generally confined to areas of lateral water flow such as on slopes below springs or in areas of melt water drainage from ice-cored moraines. Scott (1990) reported *Bracythecium* spp. to be growing on wet cliff ledges below waterfalls.

Callitriche antarctica and *Montia fontana*: these small herbs are restricted to nutrient enriched, moist environments such as the edges of seal wallows (Hughes, 1987;

Whinam, 1989, Scott, 1989). *Montia* appears to have a restricted distribution on the island (Scott, 1988).

7.4 A new Heard Island vegetation classification scheme

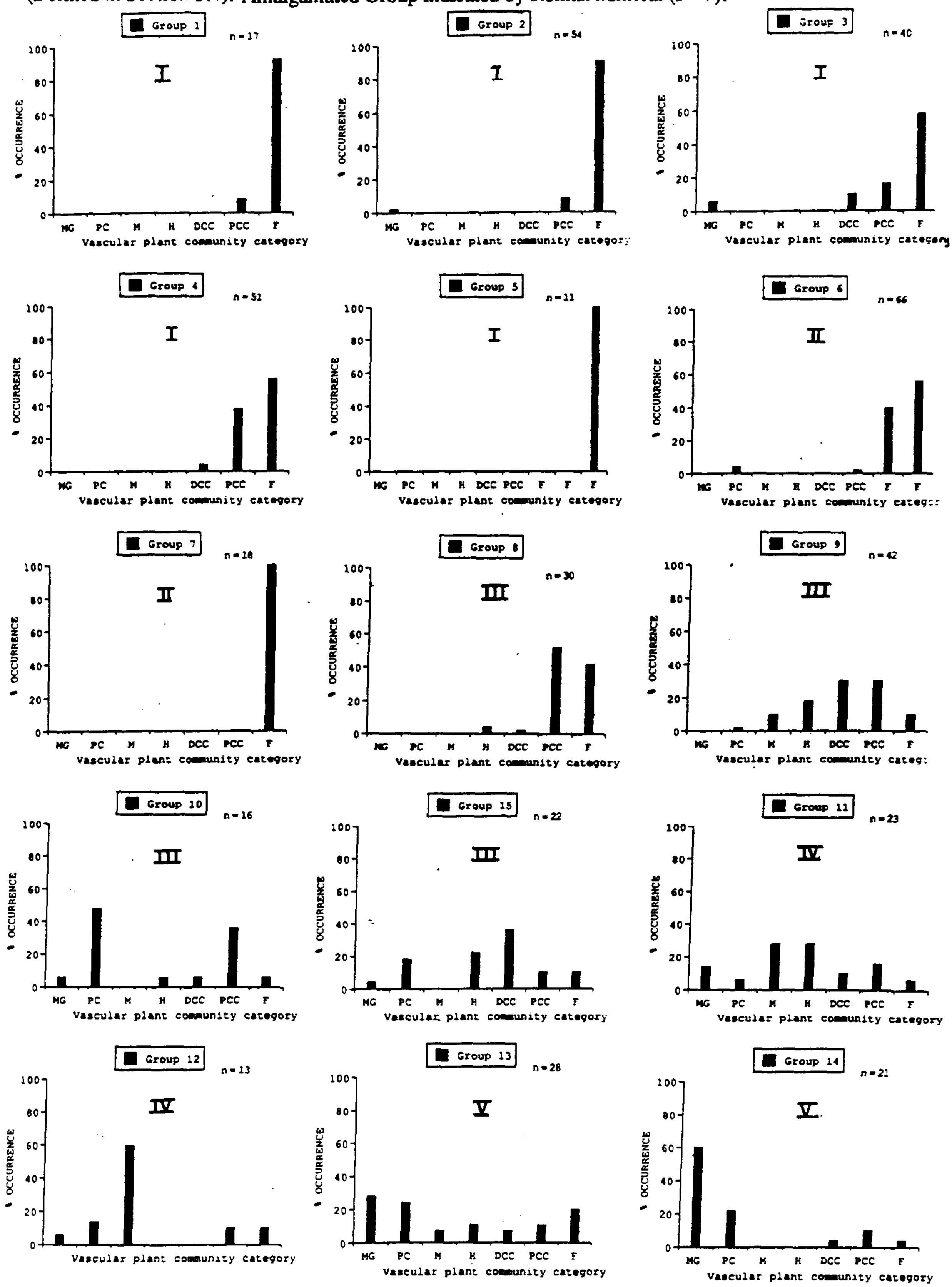
7.4.1 Difficulties with Hughes' (1987) vascular plant communities

Hughes' (1987) vascular plant community categories are sound subjective, visually recognizable, broad units. Her scheme is essentially structurally based, which is a reflection of the limited state of knowledge of Heard Island vegetation at the time. There are a number of difficulties with this scheme primarily to do with the scope and terminology.

The major difficulty is that the categories are 'vascular plant communities'. Bryophytes have been lumped into a single taxon. This study has shown that bryophytes are a major component of Heard Island vegetation and that bryophyte diversity is at least five times greater than that of vascular plants on the island (53 bryophyte species, 11 vascular species recorded so far). There are distinct suites of bryophytes within different vegetation types on Heard Island (see Chapter 5). It is neither realistic nor theoretically sound to separate or isolate vascular plant communities from Heard Island vegetation communities as a whole.

Complications arise when comparing Hughes' terminology with vegetation descriptions from other subantarctic islands and elsewhere. In particular, there is difficulty with the terms 'cushion carpet', 'meadow' and 'herbfield'. The term 'cushion carpet', although beautifully descriptive to people studying vegetation on Heard Island, is difficult to interpret without prior knowledge of the situation. Both flowering plants and mosses grow in the cushion habit. If one is told that *Azorella* is the cushion plant, then the term 'cushion carpet' could also be interpreted as monospecific stands of *Azorella*, which is generally not the case.

Figure 7.4 Frequency of Hughes' vacular plant categories in each of the 15 TWINSPAN Ecological Groups (Defined in Section 5.4). Amalgamated Group indicated by Roman numeral (I - V).



MG = **maritime grassland**
PC = **pool complex**
M = **meadow**
H = **herbfield**
DCC = **dense cushion carpet**
PCC = **patchy cushion carpet**
F = **feldmark**

Meadow is a awkward term to apply to the subantarctic as it generally implies cultivation. The term herbfield also presents problems in interpretation. Hughes (1987) uses the term to describe vegetation dominated by *Pringlea* or *Acaena.* A definition of a herb is a "flowering plant whose stem above ground does not become woody or persistent" (Macquarie Dictionary, 1982). Applying such a definition to Heard Island flora presents complications. All grass species on the island could be considered herbs. In contradiction to the definition, *Pringlea antiscorbutica* and *Acaena magellanica* are both perennial species and possess a small amount of woody growth; *Azorella* also possesses a small amount of woody growth. If *Pringlea* and *Acaena* are considered herbs then *Azorella* could also be considered a herb too, despite it being of cushion form. Also, the term herbfield also, does not take in to account the bryophytic component of the vegetation.

This study has identified floristic variation in Heard Island vegetation presenting the opportunity to progress beyond Hughes'(1987) scheme. In the general vegetation survey (Chapter 5) 475 quadrats surveyed were ordinated and classified into 15 ecological groups based on floristic composition. These groups, in turn, were amalgamated into five larger groups after examining a variety of parameters pertaining to each group (see Section 5.4). Additionally individual quadrats were classified into Hughes' community categories. Figure 7.4 shows the frequency of Hughes' (1987) vascular plant community categories in each of the 15 TWINSPAN groups. The groups are arranged according to their amalgamated group. Groups 1, 2, 5 and 7 consist of sites which were classified as predominantly feldmark units. Quadrats from Group 7 are quite distinct from those in Groups 1,2, and 5. Conseqently, Group 7 was classified into Amalgamated Group II. Groups 3,4, 6 and 8 include a mixture of feldmark, patchy and dense cushion carpet classified quadrats, with occasional other units such as maritime grassland. The remaining groups show quadrat groupings from a variety of units.

7.4.2 The new scheme

One of the features of small, subantarctic island floras including that of Heard Island is that taxa, particularly vascular plant taxa exhibit wide ecological amplitude (Smith & French, 1988; Scott, 1990). The difficulty with describing subantarctic vegetation is in trying to find middle ground between floristic and/or structural accuracy and in trying to cope with the myriad of small-scale vegetation mosaics. Vegetation schemes can end up being too broad (such as Hughes, 1987), too rigid (elements become difficult to classify) or too detailed (trends are lost). To try and avoid such problems, I wish to present an open ended, flexible scheme which can be expanded in the future when more information is available.

The scheme has two main elements, a nomenclature format, and an identification of principal directions in variation in vegetation on the island. I reject the concept of clear-cut definable vegetation communities on Heard Island, preferring to interpret the vegetation as reflecting various gradients and inter-gradings or continuums. Figure 7.5 (p. 125) is a plot of co-ordinates for two axes (AXIS 1 & 2) from the DECORANA ordination of floristic data from the 475 quadrats surveyed. (see Section 5.3). The graph shows a general scattering of points with significant outliers. The outliers can be interpreted as showing the extremes of variation in particular directions in the vegetation.

Table 7.3 Nomenclature format for the new Heard Island vegetation classification scheme.

Component I cover description	**Component II** vegetation description co/dominant taxa	**Component III** vegetation	**Component IV** environmental description
sparse (< 50%)	turves	vegetation	shallow
open (50 - 75%)	grassland	subcategory:-	deep
closed (> 75%)	cushion	monospecific	stable
	low growing		labile
	feldmark		mesic
	mire (water logged)		hydric/wet
	moss		xeric/dry
	bryophyte		nutrient enriched
	lichen		aerobic
	algae		anaerobic
	network		rocky
			peaty
	Azorella		exposed (windy)
	Poa cookii		sheltered (not windy)
	Pringlea		animal disturbed
	Acaena		supralittoral
	Deschampsia		maritime
	Drepanocladus		
	Dicranoweisia		ground
	Ditrichum immersum		area/s
	Blindia		zone/s
			field/s
			slope
			steep slope
			moraine
			lava
			smooth lava
			ropey lava
			clinker lava
			scoria
			ash/sand
			alluvium
			creek bank
			beach terrace
			terrace
			beach
			scree
			lake edge
			spring
			seepage
			pool
			pool edge
			wallow
			snow bank

7.4.3 The Heard Island vegetation nomenclature format

The format proposed for Heard Island vegetation descriptions has four components which are listed sequentially (Table 7.3). Component I is vegetation cover description, of which there are three possibilities: *closed* (cover > 75%); *open* (cover 50-75%); *sparse* (cover < 50%). Cover is defined as the substrate area covered by vegetation. Area size in which cover is evaluated can be defined when appropriate. In this study descriptions generally apply to areas of approximately 2000 m^2.

Component II includes vegetation structure or dominant or co-dominant taxa. Multiple terms can be used from Component II. Most terms are self-explanatory, but one which is unusual is the term 'network' coined by Scott (1988). She described *Poa cookii*/*Azorella* "network" vegetation in which vegetation exhibits a hummocky local topography in which *Azorella* forms the mounds and *Poa cookii* or *Pringlea* grow along the troughs. This patterning can also occur with *Acaena* growing along the troughs. The resultant patterning exhibits a network or honeycomb appearance (Fig 7.5). I suspect that the patterning is caused by the periphery species growing at the perimeter junctions of coalescing *Azorella* cushions.

The Component III - "vegetation" has as 'sub-category' to allow for the identification of monospecific vegetation.

Component IV consists of simple environmental descriptions. Multiple terms can be used from Component IV. Environmental characteristics have been included in the description as they are particularly relevant to some vegetation types on the island. The pool of terminology in Components II & IV can be expanded and can therefore incorporate information from further studies of the island's terrestrial environments.

The aim of this format is to allow accurate, unambiguous descriptions of Heard Island vegetation. The most detailed descriptions will include terms from all components. For

Table 7.4 Frequency of occurrence of taxa in each of the 15 TWINSPAN groups expressed as a percentage of the total number of quadrat/group. TWINSPAN taxon clusters (see Fig 5.3) indicated by letter (a-o).

Cluster	Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
a	*Dicranella* sp.	12	22	28	10		3			9		22				
a	*Drepanocladus uncinatus*	56	31	68	50	7				18	18	61	54			
a	*Cryptochila grandiflora*		2	5									8			
b	*Schistidium falcatum*		4	5	2				3					3		
b	*Cephaloziella varians*		17	40	44	7								7		
b	Lophocoleoideae sp.			7	8	60								7		
b	*Muelleriella crassifolia*		2	3	2	7								22		
b	*Pedinophyllopsis abdita*	6	83	60	73	80							8			
b	*Herzogobryum vermiculare*	6	9	5	6											
b	*Andreaea acuminata*		26	3	4		2		3	2						
b	*Psilopilum australe*		22	22	6											
b	*Schistidium* sp.		4													
b	*Verrucidens* spp.	18	54	5	2		3									
b	*Dicranoloma billarderii*	12	17	5	2											
b	*Pachyglossa fissa*	6	66	12	21											
b	*Blepharidophyllum densifo*	6	84	12	6	14										
c	*Racomitrium crispulum*	62	46	33	85	87	5	22			6					
c	*Racomitrium lanuginosum*		4		6	7										
c	*Ditrichum immersum*	31	61	43	96	93	3	11								
c	*Herzogobryum atrocapillum*	18	26	5	19	73										
d	*Andreaea mutabilis*	**	20	35		7				7						
d	*Grimmia* sp.	25		3												
d	*Schistidium apocarpum*	75	9	8	4		3									
d	*Blindia robusta*	62	61	12			3				6					
d	*Ditrichum subaustrale*		6	12	8	7	3			2						
d	*Pottia heimii*	12		3		7			3							
d	*Tortula geheebiaeopsis*		2	3					3							
d	*Cephaloziella exiliflora*	6	24	10	15		3		12	14		4				
e	**Poa kerguelensis*	1	19	5	54	73	94	89	90	5				7		
e	*Polytrichum piliferum*		4				6	50	16	18						
e	*Grimmia immerso-leucophae*	56	20	3	10		43	72	10	5						
e	*Dicranoweisia* spp.	31	85	70	94	13	87	83	83	63	31	9		7		
f	**Colobanthus kerguelensis*		28	3	52	47	81	78	83	5	56	35	8	64		
f	*Polytrichum alpinum*	18	39	45	50	20	76	55	50	81	12	65	8			
f	*Ditrichum conicum*		54	30	8		30	28	43	47		30				
g	*Fossombronia australis*	6	54	50	38		37		33	54	62	70	85	17		
g	*Jungermannia coniflora*		4	12			2			2		26	8			
g	*Trichostomum* sp.		2	3	2		2				6					
h	*Pohlia wahlenbergii*	69	15	38	4		7		40	7		26	15			
h	*Bartramia patens*	56	56	70	65		21	5	70	49	50	70	15	3		
i	**Azorella selago*	6	93	85	98	86	**	77	67	88	94	**	23	75	69	**
j	*Ceratodon purpureus*		7	28		13	2	61	72	67	56	48	8	34		
j	*Bryum dichotomum*			3			2	17	6	5	19		69			
j	*Bryum pseudotriquetrum*		17	40	10		16		63	56	56	74				
k	**Pringlea antiscorbutica*		16	15	12	27	7		20	2	6	26		46		9
l	*Bryum* sp. 1.			5					3	2		4		3		
l	*Bryum* sp.2.			18					3			4		11		
l	*Pohlia* sp.	12	36	3	6		2	5	33	46	56	48	61	7		
l	*Marchantia berteroana*	31							13	16		65		7		
m	**Acaena magellanica*									30	31	74	54		4	27
m	**Deschampsia antarctica*									2	6	48	69			
n	*Philonotis angustifolia*									2	6	17	38			
n	*Brachythecium* spp.	6	4	8					3	2	12	17	54	3		
o	**Poa cookii*		13	25	4		3	5	10	7	93	78	64	78	96	9
o	**Montia fontana*		2								50	9		28	13	
o	**Callitriche antarctica*			3							69	56	23	34	35	
	number of quadrats/group	17	54	40	51	15	67	18	30	42	16	23	13	31	22	22

** = 100%

TWINSPAN taxa clusters [yellow] = 50-75% [orange] = 75-100%

* vascular species

example, one of the most outstanding features of Heard Island vegetation is the dominance of *Azorella*. If one wishes to discuss all areas in which *Azorella* is dominant, then a general description '*Azorella* cushion' vegetation could be used (Components I & IV have not been defined as cover and environmental conditions on a large scale are varied). However, if vegetation at a particular site is being described, open *Azorella* cushion vegetation on dry moraine would be an example of an accurate description which takes advantage of all four components. I recommend that the full vegetation description be underlined. If comparing Heard Island vegetation with all other vegetation types it should be stressed that all vascular plant and bryophyte taxa on Heard Island at present can be decribed structurally as 'low growing plants', and hence all vegetation as 'low growing vegetation'.

7.4.4 Principal directions of variation within vegetation on Heard Island.

During the TWINSPAN analysis, 15 ecological groups were delineated on the basis of an ordination and classification of presence/absence taxa data (see Section 5.2). These groups have been described in detail in Section 5.4. After comparison of floristic and structural components, five amalgamated groups were created. These groups are illustrated in Figure 7.5.a overlying DECORANA axes co-ordinates for all 475 quadrats.

The five amalgamated groups represent principal variation in vegetation on Heard Island and encompass major vegetation types. The direction of this variation is illustrated by arrows on Fig. 7.5.a. Also superimposed on the axes are gradients for which significant correlations were identified (see Section 5.3). With increases in Axis I values, altitude and rock cover decreases and substrate depth increases. With increases in Axis 2 values, water availability increases and wind exposure decreases. Table 7.4 again lists freqency of occurence of taxa, and Figure 7.6 gives total taxa number for each of the TWINSPAN groups (ordered according to their position in the five amalgamated groups). The five major vegetation types on Heard Island can be described as:

Azorella cushion vegetation

Feldmark vegetation on shallow stable ground

Feldmark vegetation on labile ground

Coastal and other vegetation in nutrient enriched areas

Closed vegetation in wet sheltered areas

Azorella cushion vegetation

Azorella is the most abundant species in terms of biomass and distribution on Heard Island. The dominant vegetation type on Heard Island is *Azorella* cushion vegetation - Amalgamated group III (under Hughes' 1987 - cushion carpet). There is a large degree of overlap with this vegetation type and all other vegetation types (Fig 7.5.a) indicating that there are continuums within the vegetation from *Azorella* cushion vegetation to other vegetation types.

One extreme form of this vegetation type is closed *Azorella* cushion vegetation (Fig 7.7) (Twinspan group 15) in which *Azorella* approaches competitive equilibrium with continuous expanses of coalescing cushions (see Section 7.1. p.91), outcompeting most, and in some cases, all other taxa. Taxon diversity is exceedingly low (Table 7.6) with no bryophytes and only up to three other vascular plant species present (*Pringlea*, *Acaena* & *Poa cookii*). The conditions which allow for the formation of this vegetation appear to be deep unconsolidated substrate and mesic, exposed conditions without particularly enriched nutrient levels. Burrowing petrels may, however, elevate nutrient levels to some extent. Peat accumulation in some areas is considerable.

Most other sites included in *Azorella* cushion vegetation, including most quadrats in TWINSPAN Groups 8 and 9, can be described as open *Azorella* cushion vegetation, where single or coalescing cushions are interspersed with open ground (Fig 7.8). In this vegetation *Azorella*, again, is the dominant species. Other taxa are either growing on or in the periphery of its cushions or in microhabitats within the vegetated area such as on rocks, in shallow gravel which does not allow extensive *Azorella* growth, or in areas with increased, small scale

Figure 7.6 Total number of taxa for bryophytes and vascular plants in each of the 15 TWINSPAN groups.

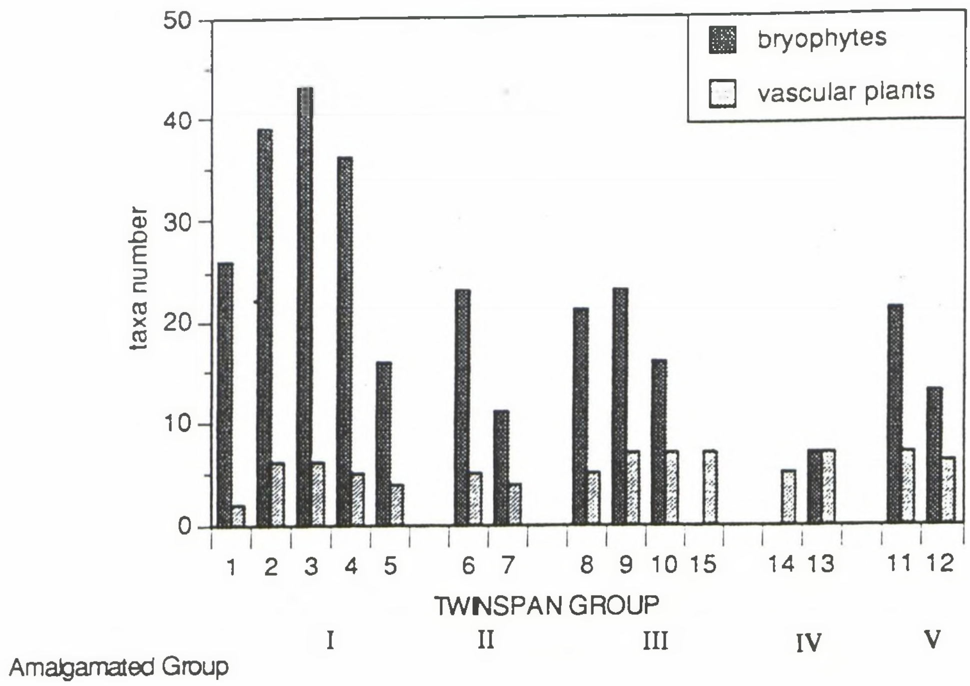
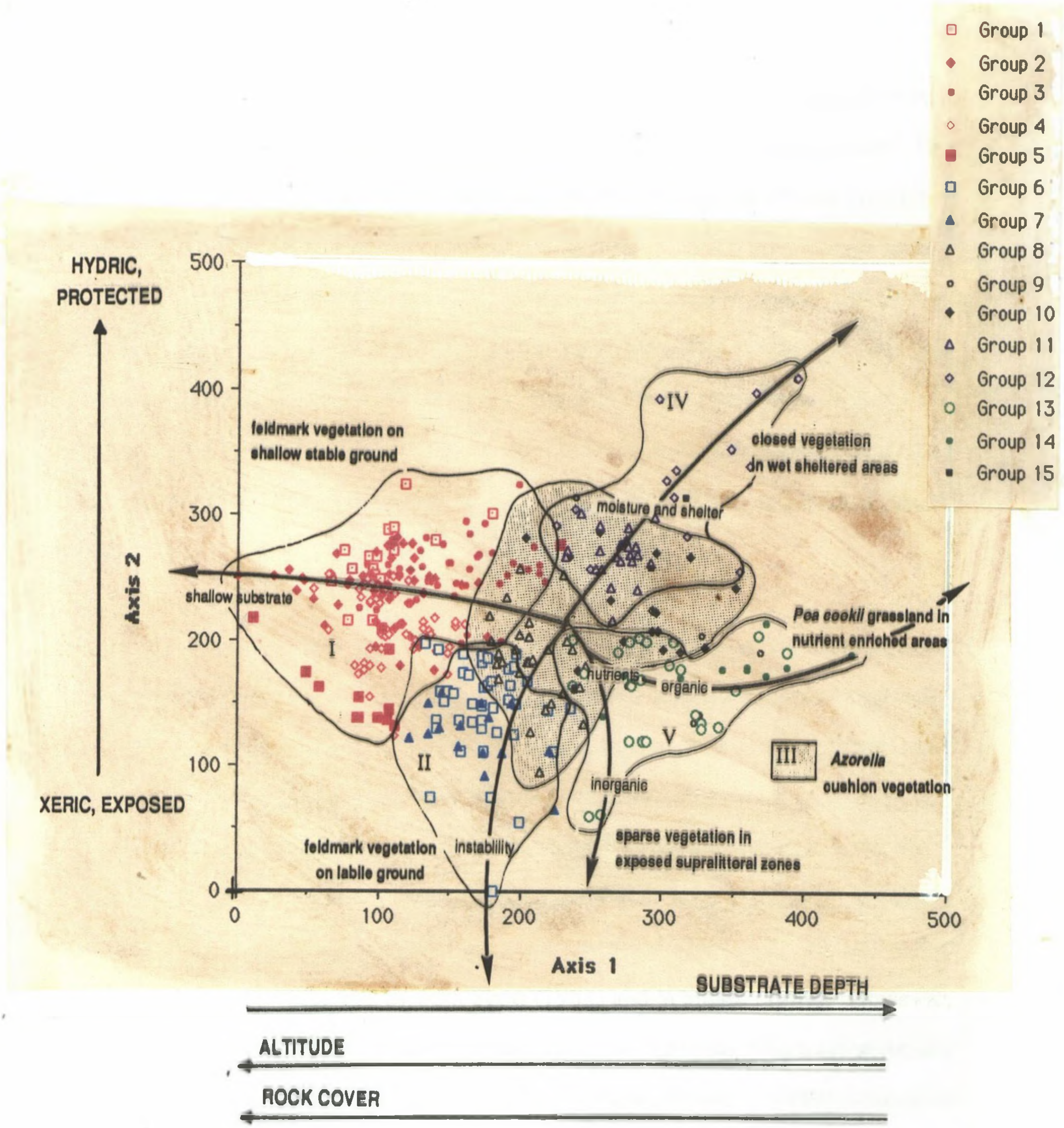


Figure 7.5 DECORANA Axis 1 vs Axis 2

Figure 7.5.a Overlay. Five Amalgamated Groups (I - V) with directions of variation indicated by axes and arrows.



vegetation which exceeds 50% cover on Heard Island, Open *Azorella* cushion vegetation is by far the most abundant and it occurs on a variety of substrates including clinker lava which has substantial peat accumulation between the lava fragments and on moraine.

Included in open *Azorella* cushion vegetation there is vegetation which would have been previously described within Hughes' 'pool complex vascular plant communities'. This includes quadrats which are classified into TWINSPAN group 10 and consist of coalescing cushions over deep peat and unconsolidated substrate, interspersed by seal wallows and pools. *Callitriche antarctica, Montia fontana* and *Poa cookii* and also the alga *Prasiola crispa*, which are indicators of nutrient enriched (animal induced) conditions, grow at the edge of these pools. The vegetation within these areas can be divided into two types. The first would be described as open *Azorella* cushion vegetation interspersed with pools and the second as open vegetation on nutrient enriched pool or wallow edges.

I do not believe that a distinct 'pool complex' vascular plant community category (Hughes, 1987) can be recognised on Heard Island. Water bodies occur amongst a variety of vegetation types. Pools, wallows and tarns are significant landscape features in some areas and there is a variety of geomorphological processes controlling their formation and maintenance (see section 7.2.- water availability). If the water body is subjected to animal activity and consequential nutrient enrichment then open vegetation on nutrient enriched pool or wallow edges will be likely to occur (described above). Edge vegetation has been described by both Scott (1988) and Whinam (1989). However, around these water bodies there can be various types of vegetation which are generally controlled by other environmental factors. For example, Whinam (1989) delineated seven ecological groups in a TWINSPAN analysis of vegetation around water bodies on Heard Island. Three of these groups could be described as variations of *Azorella* cushion vegetation interspersed with pools (see Fig 7.9). Another could be described as

Figure 7.7 Closed *Azorella* cushion vegetation on moraine. Pageos Moraine, Mt Drygalski region, Heard Island.

Figure 7.8 Open *Azorella* cushion vegetation on moraine, inland of Manning Lagoon, Long Beach region, Heard Island.

Figure 7.9 Closed *Azorella* cushion vegetation interspersed with pools. Dovers Moraine, Spit Bay region, Heard Island.

Figure 7.10 Closed *Poa cookii* vegetation interspersed with pools, Atlas Cove, Azorella Peninsula, Heard Island.

closed *Poa cookii* stands interspersed with pools (Fig.7.10). There would be different environmental factors controlling these two types of vegetation.

Feldmark vegetation on shallow stable ground

There are at least three major types of feldmark vegetation on Heard Island. Previously these vegetation types would have been lumped together on the basis of generally low total cover. The first type of feldmark, feldmark vegetation on shallow stable ground includes the majority of quadrats in Amalgamated group I. The majority of these sites are in rocky, moraine or scoria areas. Bryophytes are the dominant vegetation component in this vegetation. The liverworts *Pedinophyllopsis abdita*, *Pachyglossa fissa* and *Blepharidophyllum densifolium* and other members of Taxon Cluster B (see Table 7.4) appear to be generally restricted to this type of feldmark. Species diversity within the TWINSPAN groups included within this vegetation type can be exceedingly high particularly in the bryophyte component, (Fig. 7.6).

The majority of sites can be described as being of intermediate stress. These sites reflect Huston's (1979) concept of non-equilibrium (see Section 7.1). Species diversity is at its highest when a dynamic balance exists between the rate of competitive displacement between taxa and the frequency of population reductions. Substrates are too shallow and rocky to allow effective competition from *Azorella*, although the species is present at many sites (see Section 6.7). Sites are generally away from the coast, suggesting that the pool of nutrients available would be low. However, on scoria sites, nutrients and water may be available to small rootless plants due to the high porosity of the substrate. (see Section 7.2)

Sites are of medium to high exposure and are generally mesic with wind-driven mist a major source of water. Greenfield (1992) has reported that mosses and lichens in Antarctic fellfields (feldmarks) obtain most of their N from precipitation. A similar situation can be anticipated on Heard Island. There is generally moderate to low disturbance which would allow the establishment and maintenance of the high bryophyte component (see Section 6.7). A high bryophyte species diversity may also reflect a greater variety of micro-habitats available within the mesotopography. Similar patterns have been reported in high arctic uplands in Canada (Lafarge- England, 1989).

Within this vegetation type there exists a continuum from sparse bryophyte feldmark vegetation on shallow stable ground (Fig 7.11) to closed, bryophyte vegetation on shallow stable ground (Fig 7.12). The latter vegetation included quadrats classified into TWINSPAN groups 2 & 3 and areas described from the middle of Zone One on Macey Cone (Section 6.2.1).

Feldmark vegetation on labile ground

The second type of feldmark, typified by Amalgamated group II can be described as feldmark vegetation on labile ground, the term 'labile' being defined as meaning 'apt to change' (Macquarie Dictionary, 1992). Areas in which this vegetation occurs include areas such as ice-cored moraines and areas subjected to periglacial activity and exposed wind deserts, described under 'surface movement disturbances' in Section 7.2.. A high level of disturbance (and in some areas surface water stress) is reflected in low species diversity (Fig 7.6) and, in more extreme examples of this vegetation, low bryophyte diversity (TWINSPAN group 7). Such vegetation includes the Dovers Moraine sites described in Section 6.2.2. Feldmark vegetation on labile ground is characterized by scatterings of *Azorella* cushions and other low growing vascular species (Fig 7.13) including *Poa kerguelensis* and *Colobanthus kerguelensis*. Abundance of bryophytes is very low and their distribution is confined to sheltered and moderately stable microhabitats. Species include those which are prevalent in gravels such as *Polytrichum* spp. and *Ceratodon purpureus*, the ubiquitous *Dicranoweisia* spp. and species which are associated with *Azorella* cushions such as *Fossombronia australis*.

Figure 7.11 Foreground: Sparse bryophyte feldmark vegetation on shallow, stable lava slope (s). Background: closed bryophyte vegetation on shallow, stable lava slope (c), Macey Cone, Laurens Peninsula, Heard Island.

Figure 7.12 Closed, bryophyte vegetation on shallow stable ground. Foreground - closed, bryophyte and *Azorella* vegetation on shallow clinker lavas (c). Top right hand corner closed *Blindia* vegetation on shallow stable clinker lava (b). South of Anzac Peak, Laurens Peninsula approx 15m alt

Figure 7.13 Sparse feldmark vegetation on labile moraine slope. Dovers Moraine, Spit Bay region, Heard Island.

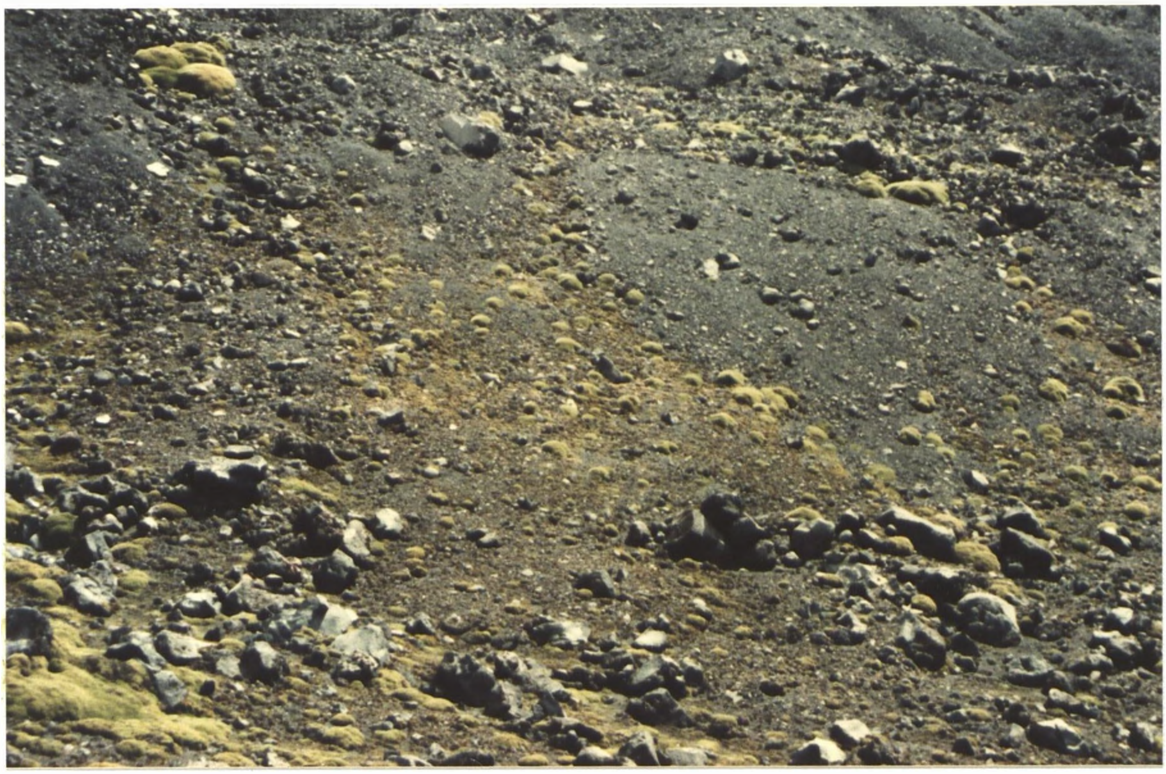


Figure 7.14 Sparse vegetation in exposed supralittoral zone on ropey lava. Atlas Cove, Azorella Peninsula.

Coastal and other vegetation in nutrient enriched areas

The third type of feldmark occurs in association with Amalgamated group V. The major direction in variation in this group appears to reflect coastal environments and the associated input of nutrients. In this environment there are both inorganic and organic nutrient inputs. Inorganic nutrient input reflects salt-laden coastal areas. The most extreme example would be sparse vegetation in exposed supralittoral zones . The most significant example of this on Heard Island is on ropey lava in the vicinity of the ANARE station on Azorella Peninsula (Fig 7.14). The vegetation consists of scatterings of the mosses *Muelleriella crassifolia* var *acuta* and *Pottia heimii* on lava and small *Azorella* cushions and the occasional tuft of *Poa cookii* growing in areas where gravel has accumulated.

In areas such as in seal breeding areas or near penguin or giant petrel colonies (see Section 7.2.1 - animal derived nutrients) organic nutrient input from animals is high and stands of *Poa cookii* occur. *Poa cookii* grassland vegetation in maritime areas (modified from Scott, 1988) (both of open and closed structure) (Fig 7.15) is the most appropriate description for much of this vegetation. Sites adjacent to bird colonies are not necessarily maritime, although generally of low altitude and are better described as closed *Poa cookii* grassland vegetation in nutrient enriched areas (Fig 7.16), or in some cases stands. Sites with less nutrient enrichment generally support mixed vegetation such as open *Poa cookii* and *Azorella* vegetation in maritime areas or open *Poa cookii* and *Pringlea* vegetation in maritime areas.

Closed vegetation in wet sheltered areas

The final variation in vegetation identified in the analysis include sites classified into Amalgamated group IV (TWINSPAN groups 11 & 12) and reflect sheltered areas with water near or at the surface. This included sites which would previously have been classified as meadow or herbfield. Vegetation in these areas was generally of closed structure. Only a small number of sites of this vegetation type was surveyed so variation at the moment is not well defined. In seepage areas total bryophyte cover including *Bryum*

Figure 7.15 Open *Poa cookii* grassland vegetation in animal disturbed maritime area. Oil Barrel Point, Spit Bay region, Heard Island.

Figure 7.16 Closed *Poa cookii* vegetation on nutrient enriched slope.- (P), south of Gilchrist Glacier, Laurens Peninsula, Heard Island. Mid ground - Closed *Azorella* cushion vegetation - (A).

Figure 7.17 Closed bryophyte & *Deschampsia* vegetation in wet seepage area. Dovers Moraine, Spit Bay region, Heard Island. (B) -bryophytes (mainly the moss *Drapanocaldus*); (D) - *Deschampsia*; (A) - *Acaena*.

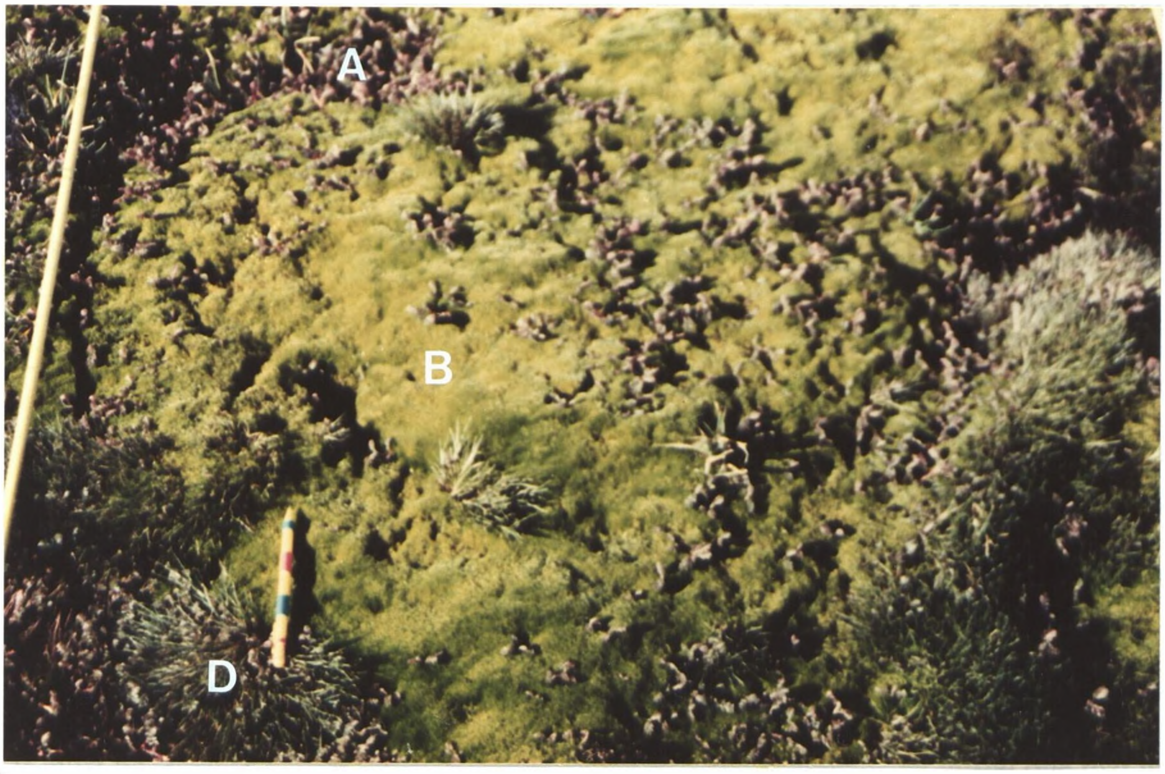


Figure 7.18 Mid-ground: Closed *Pringlea* monospecific vegetation on moraine slope. Creek adjacent to Spit Bay Station.

pseudotriquetrum, *Marchantia berteroana* and *Drepanocladus uncinatus* was high, as was the cover of the grass, *Deschampsia antarctica*. This vegetation can be described as closed bryophyte & *Deschampsia* vegetation in wet sheltered areas (Fig 7.17). More mixed vegetation was observed which also included *Azorella*, *Acaena* and *Poa cookii* (closed bryophyte and low growing vegetation in wet sheltered areas). Some areas in which peat depth was significant may also be termed mires, although these areas were not extensive.

Table 7.6 lists vegetation descriptions for a number of variations within the vegetation types described here. It is by no means exhaustive but it does include new interpretations of vegetation described by Hughes (1987), Scott (1988) and Whinam (1989) as well as types identified in this analysis. Scott (1988), in particular, provided detailed vegetation descriptions and distribution information.

It must be stressed that the new vegetation classification scheme is an initial one that will be refined when more information is available, with future vegetation studies of the island. The scheme is limited by the extent of the vegetation survey. Fieldtime was restricted and not all vegetated areas on Heard Island were studied. Unlike Hughes' scheme, this study has identified some of the major directions in variation within the vegetation. However, I do not believe that all directions in variation have been identified (again consequence of the limitations of the survey). For example, this survey did not collect sufficient data on closed *Pringlea* monospecific vegetation (Fig. 7.18). In Table 7.6, I have placed this vegetation type at the end of Amalgamated Group III, which is predominantly *Azorella* cushion vegetation. When more information is available on *Pringlea* in the future, the inclusion of a sixth major vegetation type on the Heard Island may be warranted.

Table 7.6 Vegetation on Heard Island. Vegetation descriptions are generally organized into collections which would occur within area defined by one of the Amalgamated groups shown in Figure 7.5. Notes include old terminolgy and source. H = Hughes (1987); S = Scott (1988); W = Whinam (1989).

Vegetation type	Notes and source
Feldmark vegetation on shallow stable ground - Amalgamated group I	
sparse feldmark vegetation on shallow stable ground	Fellfield; S
open bryophyte & *Azorella* vegetation on shallow stable ground	
open bryophyte vegetation on stable rocky ground	
closed bryophyte vegetation on shallow stable ground	
closed bryophyte vegetation on shallow stable scoria slope	
closed *Dicranoweisia* vegetation on shallow stable ground	
closed *Blindia robusta* vegetation on shallow ground	
Feldmark vegetation on labile ground - Amalgamated group II	
sparse feldmark vegetation on labile ground	Fellfield; H,S
sparse feldmark vegetation on labile, moraine slopes	Fellfield;H,S
Pringlea feldmark vegetation on labile scree slopes	Herbfield; S
***Azorella* cushion vegetation** - Amalgamated group III	
closed *Azorella* cushion vegetation	Dense cushion carpet; H,S
open *Azorella* cushion vegetation	Patchy cushion carpet; H,S
closed *Poa cookii* &*Azorella* network vegetation	Terminology from S
closed *Azorella* & *Pringlea* network vegetation	Terminology from S
closed *Azorella* & *Acaena* network vegetation	*Acaena* confined to eastern & southern areas
open *Azorella* and bryophyte vegetation	*Azorella* mossfield; S
open *Azorella* cushion vegetation interspersed with pools	Pool complex; H. *Azorella* dominant pool complex; S, W.
open *Azorella* & *Poa cookii* vegetation in maritime areas	
open vegetation on nutrient enriched, wet pool edges	Pool complex; H, S, W
open *Azorella* & *Dicranoweisia* vegetation	
closed *Azorella* & *Dicranoweisia* vegetation	
open *Poa kerguelensis* vegetation	
open *Pringlea*, *Azorella*, *Poa cookii* vegetation on labile slopes	Herbfield; S
closed *Pringlea* stands on moraine slopes	Herbfield; S
closed *Pringlea* vegetation in sheltered wet areas	Herbfield; S
open *Pringlea* & *Acaena* vegetation on sheltered, mesic slopes	Herbfield; S

Vegetation type	Notes and source
closed vegetation in wet shelterd areas - Amalgamated group IV	
closed bryophyte & *Deschampsia* vegetation in wet, sheltered areas	Meadow; H, S
closed bryophyte & *Deschampsia* vegetation in seepage areas	Meadow; S
closed bryophyte vegetation in wet areas	
closed *Drepanocladus* vegetation in wet areas	
closed bryophte & low growing vegetation in wet, shelterd areas	Meadow; H, S
closed *Acaena* vegetation on mesic slopes	Herbfield; S
Coastal and other vegetation in nutrient enriched areas - Amalgamated group V	
sparse feldmark vegetation in exposed, supralittoral zones	
open *Poa cookii* grassland vegetation in maritime areas	Terminology similar to S: tussock grassland; H
open *Poa cookii* & *Azorella* vegetation in maritime areas	
open *Poa cookii* & *Pringlea* vegetation in maritime areas	
closed *Poa cookii* grassland vegetation in nutrient enriched areas	Meadow; H: *Poa cookii* grassland; S
closed *Poa cookii*, *Pringlea* & *Acaena* vegetation on slopes	Herbfield; S
open *Poa cookii* vegetation in wet, snowbank areas	Herbfield; S
closed *Poa cookii* vegetation in wet, seepage areas	Meadow; S
closed *Poa cookii* vegetation interspersed with pools	Pool complex; H, S, W
closed, *Poa annua* vegetation in animal disturbed, seepage areas	Meadow; S
open vegetation on nutrient enriched, wet pool edges	Pool complex; H, S, W
closed *Poa cookii* vegetation interspersed with pools	Pool complex; H

7.5 Summary

A new vegetation classification scheme along with a general framework of present environmental conditions on Heard Island has been presented. An analysis of major environmental stresses and disturbances and other environmental conditions affecting vegetation on Heard Island has been made. Life form, ecological amplitude and initial hypotheses as to strategies (based on Grime's (1974) C-S-R model) for abundant or significant terrestrial plant taxa on the island have been described.

Hughes' (1987) vascular plant community categories for Heard Island were discussed and then used as a starting point for a new vegetation classification scheme. A new open-ended scheme based on the premise that vegetation on the island reflects various gradients and intergradings was proposed. The new scheme has a flexible nomenclature format.

The five major vegetation types on Heard Island were recognised and described:

Azorella cushion vegetation

Feldmark vegetation on shallow stable ground

Feldmark vegetation on labile ground

Coastal and other vegetation in nutrient enriched areas

Closed vegetation in wet sheltered areas

Azorella cushion vegetation is the dominant vegetation type on Heard Island. Variations within *Azorella* cushion vegetation were described, including closed *Azorella* cushion vegetation, open *Azorella* cushion vegetation and open *Azorella* cushion vegetation interspersed with pools. Overlap between *Azorella* cushion vegetation and other vegetation types was noted.

An increase in altitude, rock cover and a decrease in substrate depth supports feldmark vegetation on shallow stable ground. Bryophytes are the dominant component of this vegetation type and bryophyte species diversity can be exceedingly high.

Feldmark vegetation on labile ground includes vegetation growing in areas subjected to surface movement disturbances. A high level of disturbance is reflected by low species diversity. Feldmark vegetation on labile ground is characterized by scatterings of *Azorella* cushions and other low growing vascular species including *Poa kerguelensis* and *Colobanthus kerguelensis*. Abundance of bryophytes is very low.

Coastal and other vegetation in nutrient enriched areas reflects variation in coastal environments and the associated input of nutrients. It includes both inorganic and organic nutrient inputs. Areas of inorganic nutrient input include salt-laden coastal areas, the most extreme example being sparse vegetation in exposed supralittoral zones. In areas with organic nutrient inputs, vegetation is usually dominated by *Poa cookii*, with the most common vegetation being open *Poa cookii* grassland vegetation in nutrient-enriched maritime areas.

Closed vegetation in wet sheltered areas included vegetation dominated by hydrophylic bryophyte taxa, *Deschampsia antarctica* and *Acaena magellanica*.

CHAPTER EIGHT

Discussion

8.1 Recapitulation of significant aspects of this study

This chapter identifies and summarizes the most significant aspects of this study. After consideration of the results of this study, Heard Island terrestrial ecosystems are placed within the general context of the Subantarctic Zone.

8.1.1 Heard Island physiography

Using Spot satellite imagery it has been calculated that approximately 20 km^2 or 5% of land area is substantially occupied by vegetation on Heard Island. Surface areas occupied by substantial vegetation in each major ice-free region on the island were also calculated (see Table 1.3). Major landform features of the ice-free areas were described in Section 1.3.1.

8.1.2 Heard Island bryophyte diversity and biogeography

A revised annotated checklist of 44 moss taxa and 12 liverwort taxa from Heard Island was presented (Section 3.2). Previously only 10 moss taxa had been recorded from the island. The bryoflora on Heard Island is small compared with that of other subantarctic islands..

Phytogeographical distributions of 35 moss taxa named to species level were examined. These taxa were divided into two distinct components, potential Tertiary relicts and more recent arrivals. The more recent arrivals could be grouped into species restricted to South America and the subantarctic islands, bipolar disjunct species, Southern Hemisphere or widespread/ cosmopolitan species.

8.1.3 Distribution and diversity of bryophytes on Heard Island - the archipelago concept

Ice free areas on Heard Island are separated from each other by glaciers. This situation is described as comparable to an archipelago with the ice free areas comparable to small islands. In a vegetation survey of five major ice-free areas, the distribution of 48 bryophyte taxa was considered. There appears to be a group of 24 widespread taxa. Taxa with widespread intra-island distribution represent either multiple individual long distance dispersal and colonization events or, single long distance dispersal and colonization events followed by local 'island hopping' dispersal to other regions on Heard Island.

Absence of some conspicuous species from particular regions was either a result of propagules not having arrived there or restricted habitat variety having prevented their establishment.

Similar situations have been recorded with members of the vascular plant flora, including *Ranunculus biternatus* and *Poa annua* (Scott, 1989).

8.1.4 The diversity of bryophytes within vegetation on Heard Island

A major phytosociological survey spanning common vegetation and landscape features was conducted. Particular focus was placed on the bryophyte component of the vegetation both in terms of diversity and of total cover. It was found that previous studies (Hughes, 1987) had under - represented the bryophyte component of the vegetation.

Taxon diversity data of bryophyte and vascular plants from 475 quadrats, was ordinated using detrended correspondence analysis (DECORANA). Of eight quantitative and semi-quantitative parameters measured, significant correlations were found between five parameters and vector scores for two axes (Axis 1 & Axis 2). Overall variance in the data expressed in the first axis (Axis 1) was significantly correlated with altitudinal variation (reflecting changes in nutrient status, salt levels and perhaps temperature gradient), the amount of exposed rock and the depth of the substrate. Overall variance expressed in the second axis (Axis 2) showed significant correlation with water availability and exposure to wind.

It was also found that total bryophyte cover on Heard Island increased with increased altitude, increased rock cover and decreased substrate depth. Total bryophyte cover also appeared to be highest in areas of high water availability and low exposure to wind.

Site taxon diversity data was also ordinated and classified using two way indicator analysis (TWINSPAN). Fifteen taxon clusters were resolved indicating that there are distinct suites of bryophyte taxa within Heard Island vegetation. A core of taxa with wide ecological amplitude was also identified.

Fifteen taxon clusters, as well as 15 ecological groups were delineated with the analysis. These groups were described in detail. It was apparent that certain groups could be linked on the basis of structural and floristic characteristics. Five amalgamated ecological groups were discerned and these became the basis for a new Heard Island vegetation classification scheme. Significantly, the analysis identified two feldmarks types which were clearly distinguishable on the basis of bryophyte taxon diversity.

8.1.5 Vegetation patterning in feldmark on Heard Island and other subantarctic islands

Patterning in vegetation was described from a number of feldmark areas on Heard Island and on Marion and Prince Edward Islands. In many areas there was spatial separation between the bryophyte component and the vascular plant component of the vegetation as well as between vegetated areas and bare areas. Patterning in bryophyte distribution at the sites studied appears to reflect relative substrate stability. A hypothesis was established suggesting that if moisture was available and viable bryophyte propagules were present in the substrate, then surface movement was a critical factor to the establishment or non-establishment of bryophytes in particular feldmark environments.

The hypothesis was tested at feldmark sites on Macquarie Island. It was found that viable bryophyte propagules were present in the the top 5cm of soil in bare areas in feldmarks. The propagules included both local feldmark taxa as well as taxa from other vegetation types, which were likely to have been transported to the feldmark sites by wind. Surface rocks in bare areas were shown to have moved significantly during a 30 day study period. A model representing both successful colonization events and maintenance of bare areas in feldmarks, was developed. The model suggests that bryophytes are successful at colonizing stable ground but are generally unsuccessful at colonizing mobile areas of intermediate particle size. In these environments, movement results in either burial and/or damage of propagules or young plants.

Information on the ecological strategy of *Azorella selago* was also gained in this part of the study. *Azorella* was observed to be a successful colonizer of moraine slopes and other unstable ground in feldmarks on Heard Island and Prince Edward Island. *Azorella* however, was not successful in all feldmark environments. Shallow substrates appeared to restrict the growth of cushions. In such areas bryophytes were more successful in terms of total cover reflecting lack of competition from vigorous vascular plants.

8.1.6 A new Heard Island vegetation classification scheme and a general framework of present environmental conditions

A new vegetation classification scheme and a general framework of environmental conditions for Heard Island was presented. Major environmental stresses and disturbances and other environmental conditions affecting vegetation on the island were documented. Life form and ecological amplitude for major terrestrial plant taxa on the island were described and initial hypotheses as to ecological strategies utilized by taxa were presented.

Hughes' (1987) vascular plant categories were evaluated and then used as a starting point for a new vegetation classification scheme. The new scheme is open-ended and based on the premise that Heard Island vegetation reflects various gradients and intergradings or continuums. The new scheme has two components:

a flexible nomenclature format

identification of principal directions in variation in the vegetation.

Information on taxon diversity (bryophytes in particular), significant environmental parameters, plant ecological strategies and amplitude were incorporated into the new classification scheme, as was the model for bryophyte colonization and maintenance of bare areas.

Five major, low growing, vegetation types on Heard Island were defined:

Azorella cushion vegetation

Feldmark vegetation on shallow stable ground

Feldmark vegetation on labile ground

Coastal and other vegetation in nutrient enriched areas

Closed vegetation in wet sheltered areas

It is predicted that a sixth major vegetation type, based on vegetation in which *Pringlea antiscorbutica* is dominant, may be defined in the future when more data on this species is collected.

There are a number of noteworthy features of the new scheme. The scheme can be pitched at different levels of complexity . It can allow for broad vegetation description which encompasses a range of situations as well as being able to cope with small scale mosaic patterning. When the nomenclature format is used to its maximum, the scheme allows for very detailed, unambiguous descriptions of vegetation which take into account the relationship between vegetation and environmental characteristics.

Table 8.1.a) Number of taxa for some subantarctic and other Southern Ocean islands (excluding taxa considered as introduced by humans). (After Gremmen, 1982:Vitt, 1979; R.I.L Smith, 1984, 1993; Hughes, 1987; Scott, 1988; Delarue, 1988; Selkirk, *et al.*,1990). { } number of mosses and liverwort taxa respectively.

	NUMBER OF TAXA	
	Bryophytes	Vascular plants
AUCKLAND ISLANDS	145+{145,?}	168
MACQUARIE ISLAND	134 {83,51}	41
MARION ISLAND	120 {80,35}	25
PRINCE EDWARD	54 {29,25}	21
HEARD ISLAND	54+{42,12}	11
ILES KERGUELEN	130 {85,45}	29
ILES CROZET	110 {70,40}	28
Sth GEORGIA	260 {175,85}	29
Sth ORKNEYS	62 {50,12}	2
Sth SHETLANDS	52 {42,10}	2
ANTARCTIC PENINSULA	50 {45,5}	2

Table 8.1.b Total surface area, estimated surface area free from permanent ice and distance from nearest continental land mass for some island. (After Gremmen, 1982:Vitt, 1979; R.I.L Smith, 1993; Delarue, 1988; Selkirk, *et al.*,1990).

	Total surface area (km^2)	Area free from permanent ice (km^2)	Distance from closest continental land mass (km)
AUCKLAND ISLANDS	600	600	305 (New Zealand)
MACQUARIE ISLAND	120	120	1130 (New Zealand)
MARION ISLAND	290	285	1840 (South Africa)
PRINCE EDWARD	44	285	1840 (South Africa)
HEARD ISLAND	385	80	4350 (Australia)
ILES KERGUELEN	7205	6500	4160 (South Africa)
Sth GEORGIA	3600	1440	2000 (South America)

8.2 Comparison of Heard Island flora and terrestrial ecosystems with those of Marion and Prince Edward Islands, and other subantarctic islands

Subantarctic island ecosystems have been identified as being qualitatively different from subarctic and Antarctic ecosystems. Data from South Georgia, Marion and Macquarie Islands was included in an analysis of climate, edaphic and vegetation parameters by Smith & French (1985) who identified extreme oceanicity (associated with wind as an important climatic factor), animal influence and geographical isolation as distinguishing characteristics of the subantarctic. They also considered bryophytes to be overwhelmingly important in terrestrial ecosystems, not only as primary colonists but as important components of mature vegetation communities (Smith & French, 1988).

This study has confirmed that Heard Island ecosystems exhibit characteristics similar to those identified above. However there are inter-island differences, highlighted in the following comparison of Heard Island with other subantarctic islands.

8.2.1 Flora

A most significant feature of Heard Island in comparison with other subantarctic islands, is its considerably smaller flora in terms of both the vascular plant and bryophyte components (Table 8.1.a.). There are many factors which have contributed to this. These factors can be categorized according to the stage of the colonization process in which they are most significant: dispersal, colonization or establishment (Table 8.2).

Geographic isolation has been identified as a major factor affecting the size of floras in the subantarctic (French & Smith, 1985; Seppelt & Hughes, 1988). Distance from a continental land mass appears to be more of a barrier to the dispersal of vascular plants than to bryophytes. In Table 8.1.b. distance from the nearest continental land mass is given for some subantarctic islands. Macquarie Island has, for example, an indigenous vascular flora with a high affinity with New Zealand (31/41 taxa) and is almost twice the number of

Table 8.2 Factors affecting flora size on Heard Island

<table>
<tr><th>DISPERSAL</th><th>COLONIZATION</th><th>ESTABLISHMENT</th></tr>
<tr><td rowspan="2">isolation</td><td>limited habitat availablity

-limited time available
-limited area available</td><td></td></tr>
<tr><td colspan="2">limited habitat variety

-limited geological variation
- severe climatic regime</td></tr>
</table>

vascular plant taxa compared with Marion Island despite having less than half the total surface area of Marion. Marion Island has limited southern African affinities (Selkirk *et al* 1990). Iles Kerguelen, six times larger in terms of surface area also has a smaller vascular flora than Macquarie Island.

Isolation however, does not appear to be a limiting factor affecting the size of the bryophyte component of subantarctic floras. Both Macquarie Island and Marion Island have similar sized bryophyte floras. Aerial dispersal, both jet streams and lower level wind systems and bird dispersal are the most plausible means of transoceanic dispersal in the subantarctic (Selkirk *et al*,1990). Van Zanten and Pócs (1981) estimated that there was a maximum spore diameter (25 μm) compatible with aerial transport of bryophytes. Bergstrom and Selkirk (1987) reported that of 60 Macquarie Island moss taxa for which spore measurements were available, 80% had spores below the 25 μm limit. However, there are very successful taxa on the island which have spores as well as vegetative propagules above this size limit, for example, *Muelleriella crassifolia* (40- 80 μm). It appears that bryophyte propagule size is not necessarily restrictive in terms of potential long distance dispersal in the subantarctic where wind speeds are regularly high.

However, propagule size an order of magnitude greater, within the size range of seeds and vascular plant vegetative propagules may be restrictive. Also the greater surface area offered by seeds may have a greater probability of collecting water molecules in moist air currents, subsequently becoming heavier and dropping out of the currents into the ocean. It follows that the further away an island is from a continental land mass the smaller the chance of wind dispersed colonists and therefore the smaller vascular plant diversity.

Similarly, if external transport of propagules by birds (on feathers or in mud on feet) is considered, larger seeds have a greater probability of being preened and removed before arrival.

Another factor which may be significant when considering bird dispersal is internal transport within the crop of a bird. Analysis of crop contents of birds (snow buntings) visiting subarctic Surtsey have revealed viable seeds. Birds have been observed grazing on vascular plants. Identification of the gravel within some of the crops suggested that the source of some seeds was the Scottish highlands, over 800 km away (Fridriksson pers. comm). It has been estimated that 64% of the vascular plant species that have colonized Surtsey since the island emerged in 1963 were the result of bird dispersal events (Fridriksson, 1992).

Long distance transport of propagules within the crop of birds appears to be an ideal method of dispersal in the subantarctic and should be investigated in the future. A bird's crop would provide a warm moist protective environment. But it may be that crops are emptied on first landfall by migratory birds such as arctic terns, albatross or skuas and that dispersal to islands further away from continental land masses such as Heard Island, is a result of island hopping birds, as they refill their crops. Satellite tracking of migratory patterns of non-breeding wandering albatross have documented birds travelling from off the eastern coast of Australia to the region of Iles Crozet and then to the region of Heard Island (Murray, 1992).

Despite a successful trans-oceanic dispersal event to a subantarctic island, establishment may still fail to occur if the arriving propagule does not land in a suitable habitat. Little habitat variety on an island reduces the chances of an arriving propagule reaching a suitable habitat and hence becoming establishment. Heard Island has a considerable total surface area (385 km^2) yet only approximately 70 km^2 is ice-free and available for colonization, compared with most of the 7200 km^2 of near-by Iles Kerguelen or 290 km^2 on Marion Island, both of which have considerably larger floras but limited ice-caps.

Time is also an important factor when considering habitat availability. Only six moss species (see Section 3.3) were identified in this study as potential Tertiary survivors. Of the vascular flora, *Pringlea antiscorbutica* is also a potential Tertiary survivor Interestingly, five of the six moss species identified, *Ditrichum immersum, D. subaustrale, Verrucidens microcarpa, V. tortifolius* and *Muelleriella crassifolia* subsp. *acuta* are, at present, generally restricted to one of the feldmark vegetation types on Heard Island. *Pringlea* is also a common species is some feldmarks. Many of these feldmark habitats can be described as epilithic biotopes. Epilithic biotopes in the subantarctic include feldmark areas dominated by cryptogams, vertical rock faces, rocky shores and lava outcrops (Chown, 1989).

Chown (1989, 1992) argued that many subantarctic epilithic biotopes would have been exposed during Pleistocene glaciation. These areas could therefore, have been refugia for plants and animals during that time. Time available on Heard Island for colonization of any continuously exposed, epilithic biotopes is roughly equivalent to the time since the island's emergence (48- 30 MA) from the sea. However, as 80% of Heard Island is ice-covered at present, then the extent of available refugia during the last glacial maximum, would have been very limited. Stonehouse (1989) suggested that the paucity of high latitude species, in comparison with temperate and tropical species, is partially due to lack of time and that most high latitude habitats and communities are new. Most ice-free land on Heard Island can be considered relatively new and the majority of terrestrial biota the result of relatively recent colonization events.

Marion Island and Grand Terre, Iles Kerguelen were also extensively glaciated during the Pleistocene, but since climatic amelioration has proceeded further on these islands since the last glacial maximum, they have both more extensive surface area and had longer time for colonization than has Heard Island. All vascular species present on Heard Island are present on Iles Kerguelen. Considering the close proximity of Kerguelen to Heard (440 km to the NW), it is highly likely that Iles Kerguelen is the source population for many, if not all of these species.

In examining intra-island distribution of bryophytes on Heard Island (Chapter 3) it was argued that the absence of taxa from a particular area may reflect either one of two possibilities: either that propagules had not arrived in the area or that restricted habitat variety prevented successful colonization and establishment. The same arguments apply on an inter-island scale. Habitat variety is dependent on many variables (see Section 7.2) but in general, it appears that inter-island habitat variation in the subantarctic and other high latitude southern environments can be broadly divided into either/and geologically and climatically derived variation.

It appears that geologically derived variation appears to be more significant to bryophyte components of floras and climatic variation to vascular plant components. South Georgia, being of continental origin (see Figure 1.13), presents a greater number of different substrate compositions to potential plant colonizers than are available on the subantarctic islands of 'oceanic origin'. There is a variety of sedimentary formations, some interspersed with igneous plutons and sills, pillow lava and stratified breccias as well as other plutonic complexes present on the island (summarized in Laws, 1978). This habitat variety due to the varied geology may explain the very large bryophyte flora (260 taxa) compared with the other subantarctic islands (Table 8.1). Similarly the maritime antarctic South Orkney Islands with quite a varied geology including juxtaposed marbles and schist (R.I.L. Smith & Gimingham, 1976) have a bryophyte flora slightly larger than that of Heard Island despite a more severe climate.

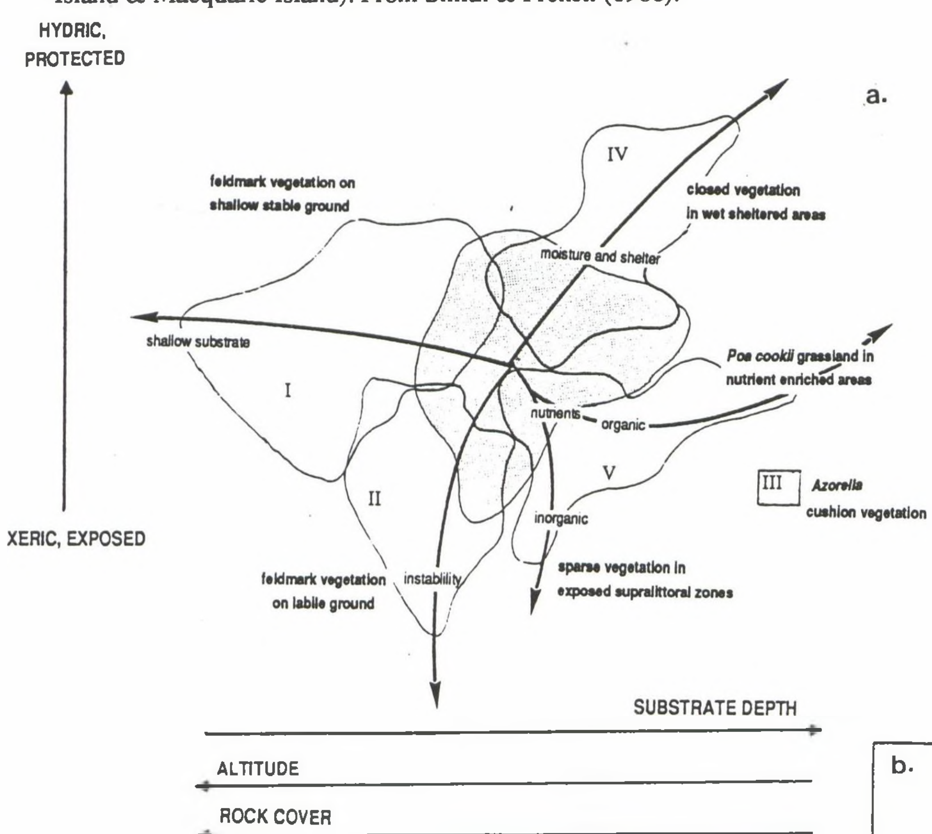
Climatic variation is a significant factor controlling the establishment stage. One of the most obvious regional trends evident in Table 8.1 is that the number of vascular plant taxa decreases zonally from temperate islands to subantarctic islands to the Maritime Antarctic. Of interest is Heard Island's small vascular plant flora compared with both Iles Kerguelen which lies on the Antarctic Convergence and with Prince Edward Island which has approximately half the surface area available for plant colonization (see Table 8.1.b).

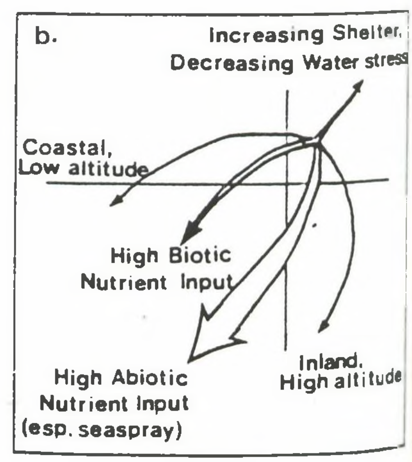
Table 8.3 The vascular flora of Heard Island and occurrence of these species on Marion Island, Iles Kerguelen and Macquarie Island. (From Hughes, 1987; Scott, 1988; Gremmen, 1982; Delarue, 1988; Selkirk *et al.*, 1990)

HEARD ISLAND	MARION ISLAND	ILES KERGUELEN	MACQUARIE ISLAND
Acaena magellanica	+	+	+
Azorella selago	+	+	!
Callitriche antarctica	+	+	+
Colobanthus kerguelensis	+	+	-
Deschampsia antarctica	-	+	-
Montia fontana	+	+	+
Poa annua	+	+	+
Poa cookii	+	+	+
Poa kerguelensis	-	+	-
Pringlea antiscorbutica	+	+	-
Rannunculus biternatus	+	+	+

! Orchard (1989) segregated Macquarie Island *Azorella* from *A. selago* to the endemic *A.macquariensis*

Figure 8.1.a The main directions of variation identified in vegetation on Heard Island (see Figure 7.5).
Figure 8.1.b General characteristics of subantarctic ecosystems (based on data from Sth Georgia, Marion Island & Macquarie Island). From Smith & French (1988).





On islands with more severe climates the availability of suitable vascular plant habitats is reduced and the limit of vascular plant distribution is approached. Germination of dispersed propagules may not occur as a result of low or freezing temperatures or reduced water availability. Establishment would also be prevented if flowering or fruit set was restricted. As mentioned above, all vascular plant taxa present on Heard Island are also present on Iles Kerguelen. It seems unlikely that propagules from other Kerguelen taxa have not arrived on Heard Island since the last glacial maximum.

Table 8.3 lists the vascular plant flora on Heard Island as well as the occurrence of these species on Iles Kerguelen, Marion and Prince Edward Islands and Macquarie Island. The majority of vascular plant species on Heard Island also occur on other subantarctic islands. For example, *Acaena magellanica* has been recorded from all subantarctic island groups and the genus *Azorella* has been recorded on all subantarctic islands groups except South Georgia (Greene & Walton, 1975).

8.2.2 Terrestrial ecosystems

Figure 8.1.a. illustrates the main directions of variation identified in vegetation on Heard Island. This variation fundamentally reflects the general characteristic of subantarctic ecosystems identified by Smith & French (1988) (Fig 8.1.b).

However, Seppelt and Hughes (1987) described Heard Island's vegetation as simple in comparison with that of Macquarie Island. Complexity in Macquarie Island vegetation is particularly enhanced by its relatively large vascular flora. The concept, however, of comparative simplicity in Heard Island vegetation can be extended to include the other subantarctic island groups as well. Most relevant comparisons can be made with the Marion and Prince Edward Islands, in particular Marion Island. Heard Island and Marion Island are of similar scale in terms of total surface area (Table 8.3), geologies are similar (Section 8.2) and their floras exhibit similar phytogeographic patterns (for example both islands lack the strong affinity of their vascular floras with a nearby land mass as opposed

Table 8.4 Comparison of vegetation types on Heard and Marion Islands.

HEARD ISLAND	MARION ISLAND	NOTES
Coastal and other vegetation in nutrient enriched areas		
- inorganic nutrient input eg. feldmark vegetation in exposed supralittoral zones	Salt-spray (*Crassula moschata*) complex	Occur in similar environments, however the major species on Marion Island, *Cotula plumosa* and *Crassula moschata,* are absent from Heard Island.
- organic nutrient input eg. closed *Poa cookii* vegetation in nutrient enriched areas	'Biotic' (*Callitriche antarctica-Poa cookii*) complex	Comparable range of vegetation and distribution on both island
Azorella cushion vegetation	*Azorella selago* community	Specialized dominant vegetation type on Heard Island. Similar vegetation types recorded on Marion but not as extensive.
Feldmark vegetation on shallow stable ground	fjaeldmark	Gremmen (1981) has described a number of variations within fjaeldmark on Marion Island including subassociations on deposits of large scoria and others on volcanic sands. Some stands were also reported to have relatively high bryophyte taxa diversity similar to feldmark vegetation on shallow stable ground on Heard Island. Cryogenic activity was also reported from some sites. Fjaeldmark on Marion Island could be classified in a similar fashion to feldmark on Heard Island.
Feldmark on labile ground	fjaeldmark	
Closed vegetation in wet sheltered areas eg. closed bryophyte and low growing vegetation in wet sheltered areas	*Acaena magellanica-Brachythecium* complex	Some wet closed vegetation in wet sheltered areas on Heard Island is comparable to *Acaena magellanica-Brachythecium* complex on Marion Island. However mire vegetation is not very developed on Heard Island.
	mire -grassland complex	Various grasses and sedges on Marion Island such as *Agrostis magellanica*, *Uncinia compacta* and *Juncus scheuchzeroides*, which are major elements of mire and bogs, are absent from Heard Island.
	fernbrake	*Blechnum penna-marina* the major component of fernbrakes on Marion Island, is absent from Heard Island.

to Macquarie Island and New Zealand).

There are a number of notable differences between Heard Island vegetation and that of Marion Island. Table 8.4 collates the major vegetation types for both islands. Some species, such as *Azorella selago* and *Pringlea antiscorbutica*, exhibit wider ecological amplitude than they do on other islands. There are unique specialized vegetation types on Heard Island. In some vegetation types, taxon variety is low with some elements absent compared with other subantarctic islands. There are some vegetation types on Marion Island which are not present on Heard Island.

French and Smith (1985) described one of the consequences of species-poor biota in the subantarctic as wide ecological amplitude of vascular plant species and the tendency of some species to form specialized communities which may be peculiar to a particular subantarctic island. On Heard Island, this is expressed most markedly by the omnipresent *Azorella selago* and the dominance of open and closed *Azorella* cushion vegetation. On Marion and Prince Edward Islands similar vegetation is present (Gremmen, 1982) but it is far less extensive, occurring generally in sheltered sites with high precipitation and free drainage. Most *Azorella* on Marion Island is restricted to feldmark areas. Similarly, the distribution and abundance of *Pringlea antiscorbutica* in vegetation on Heard Island, particularly the closed Pringlea stands on moraine slopes is considerable compared to Marion and Prince Edward Islands where its occurrence is sporadic.

Feldmarks (fjaeldmarks) on Marion and Prince Edward Islands are generally restricted to either uplands or exposed lowland areas whereas on Heard Island all vegetation is generally below 250 m in altitude. Gremmen (1982) described a number of variations of fjaeldmark including sociations with high bryophyte diversity on large scoria rocks. It appears possible to characterise Marion and Prince Edward Islands feldmarks (as has been done in this study for Heard Island), with a large proportion of the vegetation being classified as feldmark vegetation on shallow stable ground. One variation, closed bryophyte vegetation on shallow stable ground can be found on Marion Island, most often with *Racomitrium lanuginosum* the principal species, (e.g. in the young craters at Kaalkoppie, [see Section 6.3] or on the extensive lava flows in Santa Rosa Valley. However, extensive closed bryophyte vegetation on shallow stable ground with *Ditrichum immersum*, *Dicranoweisia* spp. or *Blindia robusta* as dominant taxa, as can be found on Heard Island, does not occur on Marion and Prince Edward Islands.

Comparable vegetation to sparse feldmark vegetation on labile ground occurs on the central highlands generally above 450m in altitude. Moraines at low altitude are generally covered in closed vegetation.

Variation in two directions was identified in coastal and other vegetation in nutrient enriched areas on Heard Island. The first was vegetation in areas with inorganic nutrient input such as in supralittoral zones. Similar environments occur on Marion and Prince Edward Islands, however, where vegetation is generally dominated by *Cotula plumosa* and *Crassula moschata* (Gremmen, 1982), species which have not been recorded from Heard Island. The second type of nutrient enriched vegetation occurred in areas with organic nutrient input. Comparable vegetation dominated by *Poa cookii* with similar distributions can be found on Heard Island and the Marion and Prince Edward Islands.

Open vegetation on nutrient enriched wet pool or wallow edge vegetation with *Callitriche antarctica* and *Montia fontana* is also present on Marion and Prince Edward Islands, although seal wallow areas are not as extensive as they are on Heard Island since beach areas are very small and there are no extensive raised terrace areas.

Drainage lines on Marion and Prince Edward Islands are generally occupied by *Acaena magellanica-Brachythecium* complex (Gremmen, 1982; Smith, 1987a). This complex is comparable to some forms of closed bryophyte and low growing vegetation in wet sheltered areas. on Heard Island.

The majority of lowland areas on Marion and Prince Edward Islands are occupied by mire-grasslands and bogs and fernbrakes (Smith, 1987a & b). Mires on Heard Island are very limited and poorly developed, reflecting the absence of some major peat accumulating taxa. Major peat accumulating species on Marion Island include the graminoids *Agrostis magellanica, Uncinia compacta, Juncus scheuchzerioides* and *Luzula crinita* and the liverwort, *Jamesoniella colorata.* The moss *Racomitrium lanuginosum* is also a major peat-forming plant on Marion Island but has limited distribution and cover on Heard Island. There are low altitude areas on Heard Island, such as at Sydney Cove (Laurens Peninsula), Dovers Moraine and on moraines in the Long Beach area which appear to be suitable habitats, in terms of impeded drainage, for extensive mire-grassland formation The peat forming species listed above, are present on most other subantarctic islands including Iles Kerguelen (see Gremmen, 1982 and Table 8.3) and it is unlikely that propagules of these major species have not arrived on Heard Island. It seems more probable that colonization and establishment by these species has been prevented by severe climatic conditions.

Similarly, fernbrake dominated by an extensive cover of *Blechnum penna-marina* (Table 8.4) occupies most free draining lava slopes on Marion and Prince Edward Islands. Smith (1987b) described a pattern of succession on rocky (lava) slopes on Marion Island. Firstly, rocky slopes are colonized by fjaeldmark species, mosses, lichens and mainly *Azorella.* These plants "initiate peat formation as well as acting as traps for fine, wind blown volcanic ash. The peaty material fills the crevices and porous structure of the lava". The plants establish a stable peat in which fernbrake elements can develop, which eventually extends as a closed carpet of *B. penna-marina.* On Heard Island, I believe similar processes occur on lava slopes. Initially, colonization is by bryophytes and lichens, mainly by species such as *Andreaea* spp, *Dicranoweisia* spp, *Racomitrium crispulum, Schistidium* spp, *Blindia robusta* and *Pedinophyllopsis abdita* and other taxa from clusters A - E (see Table 5.1). If sufficient moisture is available eventually closed bryophyte vegetation on shallow stable ground will develop with occasional small cushions of *Azorella* in areas where sediment or peat accumulation has occurred. Continual peat accumulation has not allowed colonization by *B. penna-marina* however, but extension of *Azorella* cushions, eventually developing into open or closed *Azorella* cushion vegetation such as on the west coast of Laurens Peninsula. These extensive lava slopes appear to be suitable habitats for fernbrake vegetation. Again, the probable explanation for the absence of fernbrake is prevention of colonization and establishment by severe climatic conditions.

The majority of vegetated areas on Heard Island are occupied by three of the five vegetation types: *Azorella* cushion and other vegetation; feldmark vegetation on shallow stable ground; feldmark vegetation on labile ground. Taxa occurring in these vegetation types are generally effective tolerators of stress or disturbance (see section 7.3). Taxa which are less effective stress or disturbance tolerators such as *Acaena magellanica* are restricted in their distribution. Absent from Heard Island are more competitive taxa such as *Agrostis magellanica* and *Blechnum penna-marina*. In the absence of these competitive taxa, tolerators such as *Azorella*, *Pringlea antiscorbutica* and mosses such as *Dicranoweisia* spp. and *Ditrichum immmersum* exhibit wider ecological amplitude and are more significant components of the vegetation on Heard Island than on other islands such as Marion and Prince Edward Islands where more effective competitors are present.

Selkirk (1992) has suggested that warming in the subantarctic may allow for increased species diversity and changes in species distribution. If severity of the climate is the factor restricting the colonization and establishment of more competitive elements in the vegetation it can be predicted that with an ameliorating climate these elements may be established on Heard Island in the future. There will most likely be subsequent development of vegetation such as mire-grasslands and fernbrakes in low altitude areas, relegating *Azorella* dominated and moss dominated vegetation to higher altitudes or to areas of higher stress or disturbance on the island. Currently, Marion and Prince Edward Islands can be considered older (in terms of ice-free areas available for colonization), warmer, smaller models of Heard Island. Marion and Prince Edward Islands can be used to predict future effects of climate change on Heard Island.

In reviewing phytogeographic subdivisions of Antarctica and adjacent oceans, Pickard & Seppelt (1984) adopted a zonation in which they divided the subantarctic zone into three regions on the basis of generalized occurrence of different vegetation structures : Heard (Heard Is & McDonald Is); Kerguelen/South Georgia (Kerguelen, Marion & Prince Edward, Crozet and South Georgia); Macquarie Island (see Fig 1.2). When considering the similarities in the vegetation between Heard Island and Marion and Prince Edward Islands, and the strong affinities of the vascular plant flora with Iles Kerguelen and Heard Island's 'oceanic origin', I believe the separation of Heard and MacDonald Islands into a separate region is not warranted. They should be considered as part of the Kerguelen Province (Marion and Prince Edward-Islands-Crozet-Kerguelen-Heard) proposed by Skottsberg (1960), with South Georgia in a Magellanic Province.

However, one factor on Marion Island and other islands in the Kerguelen Province that hopefully will not become common in the future on Heard Island, is the effect of alien plants and animals. At present, no animal or plant taxa are considered to be of alien status on Heard Island and sadly the Heard and MacDonald Islands are the only subantarctic island group to be in this position. Marion Island has had more than 15 plant taxa introduced through human activity. Two such aggressive species, *Agrostis stolonifera* and *Sagina apetala*,are currently showing rapid expansions of their distributions and are posing serious threats to the ecosystem of Marion Island (Bergstrom and Smith, 1990). Small floras allow for many 'vacant niches' which can be exploited by alien species (Smith & French, 1988). Selkirk (1992) has warned that in warmer conditions, substantial disturbance to subantarctic ecosystems can occur in the future by the establishment of vigorous alien plants or animals which could displace native species by competition or damage by grazing. Only maintained vigilance can reduce the threat of alien species to Heard Island.

8.3 Concluding remarks

It is only recently that significant information about Heard Island vegetation has become available (Hughes, 1987; Whinam, 1988; Scott, 1988 & 1990). This study has contributed significantly to this information. Heard Island's position within the subantarctic is now clear. It is the island within the Kerguelen Province on which the effects of the last glacial maximum are persisting longest. It is still emerging from extensive glaciation. With the current significant ice-retreat, new areas for colonization are being revealed. At present the island can be interpreted as an 'archipelago' with small ice-free islands separated by glaciers, each requiring separate colonization events in order for vegetation to become established.

Heard Island's vascular plant and bryophyte floras are small compared with those of other islands within the subantarctic zone. The lichen flora has yet to be examined. This study has outlined the general environmental conditions and described the ecological amplitude of major taxa on the island. Initial hypotheses concerning ecological strategies of major taxa have been proposed. In comparison with vegetation on other subantarctic islands, many taxa on Heard Island, such as *Azorella selago*, exhibit wider ecological amplitude, and there are unique, specialized vegetation types. Some vegetation types such as mire-grassland, and some vegetation elements present on other subantarctic islands are absent from Heard Island.

A highly significant feature on Heard Island is that bryophytes are major components of most vegetation and in many cases are the dominant component of the vegetation such as closed bryophyte vegetation on shallow stable ground.

This study has initially identified five major vegetation types based on floristic diversity as well as the relationship between vegetation and environmental characteristics. The dominant vegetation type is open *Azorella* cushion vegetation and the extent of this on the island, in a subantarctic context, is truly remarkable.

It is suggested that taxa in the most abundant vegetation types (*Azorella* cushion and other vegetation;, feldmark vegetation on shallow stable ground; feldmark vegetation on labile ground) are generally effective tolerators of stress or disturbance. Absent from Heard Island are more competitive taxa such as *Agrostis magellanica* and *Blechnum penna-marina*. Without these competitive elements, tolerators such as *Azorella*, *Pringlea antiscorbutica* and mosses such as *Dicranoweisia* spp. and *Ditrichum immersum* are more significant elements of the vegetation on Heard Island than on other islands such as Marion and Prince Edward Islands where more effective competitors are present.

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APPENDIX 1

Species mentioned in the text, * - recorded from Heard Island.

LICHENS

Buellia mawsoni Dodge

BRYOPHYTES, Mosses

Andreaeaceae

**Andreaea acuminata* Mitt.
Andreaea acutifolia Hook. f. et Wils.
Andreaea gainii Card.
**Andreaea mutabilis* Hook. f. et Wils.

Polytrichaceae

**Polytrichum alpinum* (Hedw.)Mitt.
**Polytrichum piliferum* Hedw.
**Psilopilum australe* (Hook. f. et Wils.) Mitt.

Grimmiaceae

**Grimmia immerso-leucophaea* (C. Muell.) Kindb.
**Schistidium apocarpum* (Hedw.)BSG.
**Schistidium falcatum* (Hook.f. et Wils.) van Zanten
**Racomitrium crispulum* (Hook.f.et. Wils.) Hook.f.et. Wils.
**Racomitrium lanuginosum* (Hedw.) Brid.

Ditrichaceae

Ditrichum brevirostre (R. Br ter.) Broth.
**Ditrichum conicum* (Mont.) Par.
**Ditrichum immersum* Van Zanten
Ditrichum punctulatum Mitt.
**Ditrichum subaustrale* Broth.
Ditrichum strictum (Hook. f. et. Wils.) Hampe.
**Ceratodon purpureus* (Hedw.)Brid.

Seligeriaceae

**Blindia contecta* (Hook. f. et Wils.) C. Muell
**Blindia robusta* Hampe.
**Verrucidens microcarpus* (Mitt.) Van Zanten
**Verrucidens tortifolius* (Hook.f.et.Wils.) Reim.

Dicranaceae

Campylopus clavatus (R. Br) Hook. f. et. Wils.
**Dicranoloma billardieri* (Schwaegr.)Par.
**Dicranoweisia antarctica* (C.Muell.) Par.
**Dicranoweisia brevipes* (C.Muell.) Card.
**Dicranoweisia breviseta* Card.

Pottiaceae

**Pottia heimii* (Hedw.) Feurnr.
Tortula andersonii Aongstr.
**Tortula geheebiaeopsis* (C.Muell.)Broth.
**Tortula robusta* Hook. et Grev.
Tortula rubra Mitt.

Orthotrichaceae

**Muelleriella crassifolia* (Hook.f.et.Wils).Dus., subsp.*acuta* (C.Muell.) Vitt.

Bryaceae

**Bryum dichotomum* Hedw.
**Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer et Scherb.
**Pohlia wahlenbergii* (Web. et Mohr) Andrews

Bartramiaceae

**Bartramia patens* Brid.
Breutelia pendula (Smith) Mitt.
**Philonotis* cf *angustifolia* Kaal.
Philonotis scabrifolia (Hook. f. et. Wils)

Ptychomitricaceae

Ptychomnion aciculare (Brid.) Mitt.

Amblystegiaceae

**Amblystegium serpens* Hook. f. et Wils.
**Drepanocladus uncinatus* (Hedw.) Warnst.

Brachytheciaceae

**Brachythecium austro-salebrosum* (C.Muell.) Par.
**Brachythecium paradoxum* (Hook.f.et Wils) Jaeg.

Plagiotheciaceae

Isopterygium limatum (Hook. f. et. Wils) Broth.

Hypnaceae

Hypnum cupressiforme Hedw.

BRYOPHYTES, Liverworts

Codoniaceae

**Fossombronia australis* Mitt.

Marchantiaceae

**Marchantia berteroana* Lehm. et Lindenb.

Cephaloziellaceae

**Cephaloziella exiliflora* (Tayl.) Dovin
**C. varians* (Gottsche) Steph.

Jungermanniaceae

**Cryptochila grandiflora* (Lindenb. et Gottsche) Grolle
Jamesoniella colorata (Lehm.) Spruce
**Jungermannia coniflora* Schiffn.

Geocalycaceae

**Pachyglossa fissa* (Mitt.) Herz. & Grolle
**Pedinophyllopsis abdita* (Sull.) Schuster et Inoue

Gymnomitriaceae

**Herzogobryum atrocapillum* (Hook.f et Tayl) Grolle
**H. vermiculare* (Schiffn.) Grolle
Lophocolea bidentata (L.) Dumort.

Scapaniaceae

**Blepharidophyllum densifolium* (Hook.) Angstr. ex Mass.

FERNS

Blechnaceae

Blechnum penna-marina (Poir.) Kuhn

Polypodiaceae

Grammitis poeppigeana (Mett.) Pic. Serm.

ANGIOSPERMS, Dicotyledons

Asteraceae

Cotula plumosa Hook. f.
Pleurophyllum hookeri Buchan.

Apiaceae

**Azorella selago* Hook.f.
Azorella macquariensis Orchard

Brassicaceae

**Pringlea antiscorbutica* R. Br.

Callitrichaceae

**Callitriche antarctica* Engelm. ex Hegel

Caryophyllaceae

**Colobanthus kergeulensis* Hook. F   Lyallia kerguelensis Hook. F.
Sagina apetala Ard.

Crassulaceae

Crassula moschata Forst. f.

Portulacaceae

**Montia fontana* L.

Ranunculaceae

**Ranunculus biternatus* Smith

Rosaceae

**Acaena magellanica* (Lam.) Vahl.

ANGIOSPERMS, Monocotyledons

Cyperaceae

Uncinia compacta R.Br

Juncaceae

Juncus scheuchzeroides Gaud.
Luzula crinita Hook.f. var *crinita*

Poaceae

Agrostis magellanica Lam.
Agrostis stolonifera L.
**Deschampsia antarctica* Desv.
**Poa annua* L.
**Poa cookii* (Hook. f.) Hook. f.
**Poa kerguelensis* (Hook. f.) Hook. f.

APPENDIX 2

Protocol for germination trials and surface movement experiments on Macquarie Island

Diaspore germination trials

Soil cores at each of the treads in Sites A, B,C & D and at Sites E & F (Fig. 6.14) were collected by pressing sterile plastic specimen jars (40mm in diameter, 55mm long) into the substratum. The cores were sealed in the field and then frozen for transport back to the laboratory in Australia (Sydney). The cores were collected in November 1988 and remained frozen for 30 days. In the laboratory the cores were removed and cut into 4 segments; the top 5mm, 5 - 15mm, 15 -35mm, 35 -55mm. Care was taken to keep disturbance of the segments to a minimum. The segments were placed in sealed petri dishes and allowed to thaw at 6° for 24hrs. The segments were then watered with a mist spray of deionized water and were sealed again with Parafilm. The dishes were cultured for 280 days at 22°C with a 14:10 hr light regime. At the termination of the experiment the germinated taxa were identified. For each of the terrace sites (A,B,C,D) taxa lists from the two treads were pooled. Comparisons were then made with the species recorded from adjacent vegetation in the field.

Surface Movement

A 1m transect was established across a tread at each of the sites A, B, C & D. The transects were perpendicular to the direction of greatest slope on the tread. At each end of the transect 3 steel pegs were driven into the substratum to a depth of approximately 300mm. Along the surface particles of each transect a light blue line was painted with fast drying acrylic paint. A light blue colour (which blended well with the colour of the rock) was chosen in an attempt to avoid differential heating and cooling of painted and non-painted rocks and also scavenging by birds. An effort was made to maintain the width of the painted line at 5mm.

At the end of the first survey period (20 days for Sites A & B, 30 days for sites C & D) the transects were again established by attaching a taut line to the steel pegs. The transects were then photographed at approximately 300mm intervals against this line in association with a scale. From the photographs, rotation of painted rocks, burial of painted rocks and displacement of painted rock from the line were recorded.

The number of such displacements and the size of the rocks that had moved were recorded. The direction of the displacement (either up or down slope) was recorded and in some cases it was possible to record, with a reasonable degree of accuracy, the distance that the rock had been displaced. In some areas of the transects, sections of the painted line could not be located. In these cases the distance in which the rocks were missing was measured and a total length of missing line was tallied for each transect. The total number of rocks along the transect were counted and a percentage of rocks moved per 1m transect was calculated.

LINDBERGIA 14: 184–190. Copenhagen 1988

The moss flora of Heard Island: revised checklist, annotations and phytogeographical considerations

Dana M. Bergstrom and R. D. Seppelt


DMB


RDS

Bergstrom, D. M. and Seppelt, R. D. 1988. The moss flora of Heard Island: revised checklist, annotations and phytogeographical considerations. – Lindbergia 14: 184–190.

A revised annotated checklist comprising 42 moss taxa for subantarctic Heard Island is presented. A summary of their phytogeographical distributions is provided.
All flora has reached Heard Island via some form of transoceanic dispersal. The size of the moss flora is small compared with other subantarctic islands. Heard Island is more than 80% ice covered and the paucity of the flora reflects restricted diversity and limited availability of suitable habitats.

D. M. Bergstrom, School of Biol. Sci., Macquarie Univ., NSW 2109, Australia. R. D. Seppelt, Antarctic Div., Channel Highway, Kingston, Tasmania 7150, Australia.

Тут представлен пересмотренный аннотированный перечень, содержащий 42 таксона мхов на субарктическом острове Херд. Приводится сводка их фитогеографического распространения.
Всякая флора достигла острова Херд через какую-либо форму трансокеанского распространения. Численность флоры мхов небольшая по сравнению с другими субарктическими островами. Остров Херд выше 80% покрыт льдом, и малое количество флоры отражает ограниченное разнообразие и ограниченное наличне подходящих местообитаний.

Introduction

Heard Island (53°05′S, 73°30′E) is a small volcanic island in the Southern Ocean, approximately 4850 km SE of southern Africa, 4350 km SW of Western Australia and 1650 km N of the Antarctic continent. More than 80% of Heard Island is covered with ice (Allison and Keage 1986). The landscape is dominated by the large, glaciated volcano, Big Ben, 2745 m in altitude. Vegetation occurs on suitable substrates in coastal pockets, generally below 400 m a.s.l.

The vegetation is dominated by herbaceous angiosperms and bryophytes. The vascular flora is small. Only eleven species, all angiosperms, have been reported (Hughes 1987, Scott 1989). This study records 42 moss taxa and there are about 12 liverwort taxa present on the island.

Three previous publications have reported moss species from Heard Island. Mitten (1885) recorded two species collected by the Challenger Expedition of 1873–1876. Four species were collected by the Deutschen Südpolar Expedition of 1901–03 (Brotherus 1906). Clifford (1953) reviewed these descriptions and examined material collected by the British, Australian and New Zealand Antarctic Expedition (BANZARE) of 1929 and by the Australian National Antarctic Research Expeditions (ANARE) of 1947 to 1952, enumerating 17 species.

Collections

Collections examined for the present checklist are those made by J. Jenkin (in 1980), H. F. Heatwole (in 1983), J. M. R. Hughes (in 1985), D. M. Bergstrom (in 1986), and J. J. Scott (in 1986 and 1987). All recent collections have been or will be lodged in the herbarium of the Australian Antarctic Division, Kingston, Tasmania (ADT). Collections examined by Clifford (1953) have not been located.

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Annotated species list of moss taxa recorded from Heard Island

Species marked with an asterisk (*) are new records.

Andreaeaceae

**Andreaea acuminata* Mitt.
**Andreaea mutabilis* Hook.f. et Wils.

Polytrichaceae

Polytrichum alpinum (Hedw.) Mitt.
**Polytrichum piliferum* Hedw.
Psilopilum australe (Hook.f. et Wils.) Mitt.

Grimmiaceae

**Grimmia immerso-leucophaea* (C. Muell.) Kindb.
The reviews of *Grimmia* and *Schistidium* from South Georgia (Bell 1984) and Patagonia (Deguchi 1984) are relevant to the interpretation of Heard Island material. Morphological variation is pronounced and establishing the correct identity of all specimens will require more detailed study. Capsules show persistent columellae.
**Grimmia* sp.
Without capsules but differing in leaf morphology from fertile specimens of *G. immerso-leucophaea.*
**Schistidium apocarpum* (Hedw.) B.S.G.
**Schistidium falcatum* (Hook.f. et Wils.) Zant.
**Schistidium* sp.
Similar to *G. immerso-leucophaea* in leaf morphology but capsules lack persistent columellae.
Racomitrium crispulum (Hook.f. et Wils.) Hook.f. et Wils.
**Racomitrium lanuginosum* (Hedw.) Brid.

Ditrichaceae

**Ditrichum conicum* (Mont.) Par.
**Ditrichum immersum* Van Zanten
Ditrichum subaustrale Broth.
Ceratodon purpureus (Hedw.) Brid.
In extreme environments the leaf morphology of *C. purpureus* is variable. As with Antarctic material (Seppelt 1986), taxonomic reassessment of at least some of the specimens attributed to *C. purpureus* from Heard Island may be required.

Seligeriaceae

Blindia contecta (Hook.f. et Wils.) C. Muell.
Reported by Clifford (1953) but not recorded since.
**Blindia robusta* Hampe
**Verrucidens microcarpus* (Mitt.) Zant.
Verrucidens tortifolius (Hook.f. et Wils.) Reim.

Dicranaceae

**Dicranella* sp.
Small, barren plants with uncertain affinity, awaiting further comparative study.
Dicranoloma billardieri (Schwaegr.) Par.
The taxonomy of *Dicranoloma* requires revision.
**Dicranoweisia antarctica* (C. Muell.) Par.
A very variable species. The usually distinct, coloured alar cells separate this from the other *Dicranoweisia* species reported.
**Dicranoweisia brevipes* (C. Muell.) Card.
Alar cells often scarcely differentiated from adjacent cells of the leaf base and not inflated or coloured as in *D. antarctica.*
**Dicranoweisia breviseta* Card.
This species and *D. brevipes* seem doubtfully distinct. *D. brevipes* is smaller in size, has shorter leaves and the male gametangia are positioned below the perichaetia. In *D. breviseta,* male gametangia occur in short lateral branches. However, in specimens we have examined the gametoecial arrangement is variable. The relationship also with *D. antarctica* needs further assessment.

Pottiaceae

**Pottia heimii* (Hedw.) Feurnr.
**Tortula geheebiaeopsis* (C. Muell.) Broth.
Tortula robusta Hook. et Grev.
This species was reported from the ANARE collections (1947–52) by Clifford (1953). Since the specimen could not be located Lightowlers (1986) considered this record as 'doubtful'. We have not recorded this species.

Orthotrichaceae

**Muelleriella crassifolia* (Hook.f. et Wils.) Dus. subsp. *acuta* (C. Muell.) Vitt.

Bryaceae

**Bryum dichotomum* Hedw.
**Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer et Scherb.
The extreme morphological variation in this species has been discussed by Seppelt and Kanda (1986).
**Bryum* sp. 1.
Similar in appearance to *B. pseudotriquetrum* but with a border of 1–4 rows of elongate cells distinct from adjacent lamina cells.
**Bryum* sp. 2.
Similar to *B. pseudotriquetrum* but the leaves possess an auricle of large quadrate cells distinct from adjacent cells of the lamina.
**Bryum* sp. 3.
Small plants similar in size to *Bryum argenteum* and

with leaves generally less than 1 mm long. It is readily distinguished from that species by leaves having the costa excurrent into a short mucro or percurrent, the cells hexagonal to elongate rhomboid and all lamina cells chlorophyllose.

**Pohlia wahlenbergii* (Web. et Mohr) Andrews

**Pohlia* sp.

The margin of leaves in this species is slightly denticulate, and the base almost auriculate.

Bartramiaceae

Bartramia patens Brid.

Three species *B. papillata, B. diminutiva* and *B. robusta* have been reported from Heard Island (Mitten 1885, Brotherus 1906, Clifford 1953). There is considerable variation in vegetative characters. Dixon (1926) discussed the relationship between *B. patens* and *B. papillata* and considered them doubtfully distinct except that the inflorescence is dioicous in *B. papillata* and synoicous in *B. patens*. Robinson (1975) gave *B. diminutiva* as a synonym of *B. patens*. Matteri (1985) considered *B. robusta* a variety of *B. patens*. We consider all previous records of *Bartramia* from Heard Island to be forms of *B. patens*.

**Philonotis* cf. *angustifolia* Kaal.

Lanceolate leaves with irregularly rectangular papillose cells. Upper margin dentate.

Amblystegiaceae

Amblystegium serpens Hook.f. et Wils.

Drepanocladus uncinatus (Hedw.) Warnst.

Brachytheciaceae

**Brachythecium austro-salebrosum* (C. Muell.) Par.

The taxonomy of this species has been discussed at length by Newton (1979). The record of *B.* cf. *salebrosum* of Clifford (1953) may belong here.

**Brachythecium paradoxum* (Hook.f. et Wills.) Jaeg.

Summary notes on Clifford's 1953 checklist

Of the 17 species reported by Clifford (1953), 9 species have been retained in this checklist. Seven species have been either reduced or changed due to synonomy: *Bartramia papillata, B. diminutiva* and *B. robusta* = *B. patens* (see annotations); *Blindia tortifolia* and *Dicranoweisia grimmiacea* = *Verrucidens tortifolius; Grimmia insularis* = *Blindia contecta; Racomitrium nigritum* = *R. crispulum* (Wijk et al. 1959–69). As stated earlier we suggest that the record of *Brachythecium* cf. *salebrosum* may be the same as our record of *B. austro-salebrosum*. As Clifford's specimens can not be located at MEL, this can not be verified.

Discussion

Heard Island is interpreted as a portion of the mid-oceanic Gaussberg – Kerguelen Ridge that emerges above sea level. The island's volcanic rocks have intruded through and accumulated on ocean floor crust which has a thick upper layer of pelagic sediment (Clarke et al. 1983, Quilty et al. 1983). This implies that Heard Island has been isolated from continental land masses since it was formed. If this is so, then all flora and fauna have arrived via transoceanic dispersal.

Plants existed on Heard Island during the Tertiary (Quilty et al. 1983). Plant microfossils have been recorded in sediments spanning the Late Eocene to Early Pliocene. The flora included a variety of ferns, a podocarp and a small herbaceous angiosperm component and was described as low scrubby fernbush vegetation (Quilty et al. 1983). The climate associated with this flora was described as cold and wet. The composition of the Heard Island microflora is similar to the fossil flora on Îles Kerguelen (Cookson 1947, Quilty et al. 1983). Dettman (1986) described the Kerguelen Miocene flora recorded by Cookson (1947) as a cool temperate *Podocarpus*/Araucarian rainforest with dicksoniaceous ferns and herbaceous angiosperms.

Major environmental changes have occurred on Heard Island since the Tertiary. There have been three main phases of volcanic activity (Clarke et al. 1983). Between the Late Miocene and Early Pliocene igneous rocks intruded into the pelagic limestone base of the island, then sporadic volcanism resulted in accumulation of basalts subaerially. Today, the latter formation is present in the form of a plateau which rises to about 300 m. No more than 1 million years ago the final phase of volcanism began and the Big Ben volcano was built upon the older plateau. Other more recent formations such as small scoria cones have developed in the last 10,000 yr (Clarke et al. 1983). The presence of a lava lake in the summit crater indicates continuing volcanic activity.

The sporadic, 'island building' volcanism on Heard Island is most likely to have destroyed local plant communities and not the island's entire biota. Today, bryophytes are principal colonizers of young lavas on Heard Island. Previous volcanic activity would have eventually increased the area available for vegetation establishment.

The type of environmental change which appears to have had a far greater influence on the flora of Heard Island has been climatic change, particularly cooling episodes. The mid volcanic phase (Late Miocene-Early Pliocene) was accompanied by glaciation (Clarke et al.

Tab. 1. Phytogeographical distribution of Heard Island moss species. Data from: Ando (1979); Bell (1984); Bell and Greene (1975); Brotherus (1906); Clark and Lightowlers (1983); Clifford (1953); Crum and Anderson (1981); Deguchi (1984); Delarue (1988); Gremmen (1982); Hebrard (1970); Ireland (1982); Ireland et al. (1987); Lightowlers (1985); Longton (1979); Magill (1981); Matteri (1977, 1985); Mitten (1885); Newton (1973, 1979); Ochi and Ochyra (1985); Ochyra and Bell (1984); Ochyra et al. (1986); Sainsbury (1955); Scott and Stone (1976); Selkirk et al. (in press); Seppelt and Russell (1986); Smith (1978); Smith (1984b); Vitt (1976, 1979); Wijk et al. (1959–1969); Zanten (1971).

Distribution:	South America	Maritime Antarctica	South Georgia	Africa	Marion Island	Prince Edward Island	Ile Crozet	Ile Kerguelen	Heard Island	Australia	Macquaric Island	New Zealand	Auckland Islands	Northern Hemisphere
Andreaeaceae														
Andreaea acuminata	+	–	+	–	+	+	+	+	+	+	+	+	+	–
Andreaea mutabilis	+	–	–	–	–	–	–	–	+	–	+	+	+	+
Polytrichaceae														
Polytrichum alpinum	+	+	–	–	–	–	–	–	+	+	+	+	–	+
Polytrichum piliferum	+	+	+	+	+	–	–	–	+	+	–	–	–	+
Psilopilum australe	–	–	–	+	–	–	–	–	+	+	+	+	–	–
Grimmiaceae														
Grimmia immerso-leucophaea	+	–	+	–	+	+	+	+	+	–	–	–	–	–
Schistidium apocarpum	+	+	+	–	–	–	–	–	+	+	+	+	–	+
Schistidium falcatum	+	+	+	–	+	–	–	+	+	–	–	–	–	–
Racomitrium crispulum	+	+	+	+	+	+	+	+	+	+	+	+	+	–
Racomitrium lanuginosum	+	+	+	+	+	–	+	+	+	+	+	+	+	+
Ditrichaceae														
Ditrichum conicum	+	–	–	+	+	+	+	+	+	–	–	–	–	–
Ditrichum immersum	–	–	–	–	+	–	+	+	+	–	–	–	–	–
Ditrichum subaustrale	–	–	–	–	–	–	–	+	+	–	–	–	–	–
Ceratodon purpureus	+	+	+	+	+	–	–	–	+	+	+	+	+	+
Seligeriaceae														
Blindia contecta	+	–	–	–	–	–	–	+	+	–	–	+	+	–
Blindia robusta	+	–	–	–	–	–	–	–	+	+	+	+	–	–
Verrucidens microcarpus	–	–	–	–	+	+	–	+	+	–	–	–	–	–
Verrucidens tortifolius	–	–	–	–	–	–	–	–	+	–	+	–	–	–
Dicranaceae														
Dicranoloma billarderi	+	–	–	+	+	–	+	+	+	+	+	+	+	–
Dicranoweisia antarctica	–	+	+	+	–	–	–	–	+	+	+	+	+	–
Dicranoweisia brevipes	+	–	–	–	–	+	–	–	+	–	–	–	–	–
Dicranoweisia breviseta	+	–	–	–	+	+	–	–	+	–	–	–	–	–
Pottiaceae														
Pottia heimii	+	–	+	+	–	–	–	–	+	+	+	+	–	+
Tortula geheebiaeopsis	–	–	+	–	–	–	–	+	+	–	–	–	–	–
Tortula robusta	+	–	+	–	–	–	–	–	+	–	–	–	–	–
Orthotrichaceae														
Muelleriella crassifolia	+	+	+	–	+	+	+	+	+	–	+	+	+	–
Bryaceae														
Bryum dichotomum	+	+	–	–	+	–	+	–	+	+	+	+	+	+
Bryum pseudotriquetrum	–	+	+	+	–	–	–	–	+	+	+	+	+	+
Pohlia wahlenbergii	+	+	–	+	–	–	–	–	+	+	+	+	+	+
Bartramiaceae														
Bartramia patens	+	+	+	–	+	+	–	+	+	+	+	+	+	–
Philonotis cf. *angustifolia*	–	–	–	–	+	–	+	–	+	–	–	–	–	–
Amblystegiaceae														
Amblystegium serpens	+	–	–	+	–	–	–	–	+	+	+	+	+	+
Drepanocladus uncinatus	+	+	+	+	+	+	+	+	+	+	+	+	–	+
Brachytheciaceae														
Brachythecium austro-salebrosum	+	+	+	–	+	–	–	+	+	–	–	–	–	–
Brachythecium paradoxum	+	–	–	+	+	–	+	+	+	+	–	+	–	–

1983) and there were many cooling cycles during the Pleistocene (Fink and Kukla 1977).

Severe climatic cooling events are accompanied by increases in frost frequency and duration, desiccation and reduced summer temperatures. On Heard Island, the formation of glaciers and a possible ice cap would have reduced the area of land available for vegetation and also the range of habitats available for vegetation establishment. There would have been increased seasonality and a resultant reduction in water availability (also contributing to physiological stress and reduced range of habitats).

The present climate on Heard Island has a distinct winter. There is a prolonged period of extensive snow cover followed by a spring melt. Free water in the summer growing season is limited. Such conditions would have been present during previous glacial events.

With major cooling episodes in the Pleistocene large portions of the flora on Heard Island and Îles Kerguelen became extinct; for example there are no current records of pteridophytes on Heard Island. It has been suggested that two angiosperms, *Pringlea antiscorbutica* and *Lyallia kerguelensis,* present on Îles Kerguelen are relicts from the Tertiary Kerguelenian flora. Fossil pollen of these species has been found in sediments from Îles Kerguelen, dating from the latter part of the last glacial episode (Young and Schofield 1973). Only *Pringlea* is present on Heard Island today.

Bryophytes have not been recorded in the fossil record from Heard Island but are components of almost all modern terrestrial ecosystems. It is likely that they were components of the Heard Island Tertiary flora. Polar bryophytes today possess physiological attributes such as desiccation and frost tolerance, but such features are widely distributed amongst bryophytes generally (Longton 1988). Some bryophytes now on Heard Island may have survived past glacial as well as volcanic disturbances to the island and be relicts of the Tertiary flora.

Size of flora

On Heard Island, the extant moss flora is small compared with that of other subantarctic islands (Macquarie Island has 85 species, Marion Island 81 species and South Georgia ca. 175 species) (Selkirk et al., in press; Seppelt and Russell 1986, Smith 1984a). The last glacial maximum occurred approximately 18,000 yr ago (Climap 1976). Despite recent climatic warming, 80% of Heard Island is still covered by ice, ensuring a limited number and restricted range of habitats and limiting the diversity of the bryoflora. During the last forty years there has been major glacial retreat on Heard Island (Allison and Keage 1986). With continued global warming of the atmosphere, glacial retreat will continue, exposing further habitats and permitting other species to colonize the island. The diaspores for these species may already be present on the island. The huge expanse of Big Ben may act as a sink for airborne particles. Meltwater could then supply diaspores to newly exposed habitats.

Phytogeography

Table 1 records the phytogeographical distribution of the 35 taxa named to species level. The list of interregional relationships will certainly be incomplete due to the uncertainty of the status of some taxa and the incomplete knowledge of the bryoflora of areas such as Prince Edward Island and Îles Kerguelen.

We suggest six species of moss as potentially Tertiary survivors, five of which *(Ditrichum immersum, D. subaustrale, Philonotis angustifolia, Verrucidens microcarpus, V. tortifolius)* are endemic to subantarctic islands and a sixth, a subspecies of *Muelleriella,* is endemic to the Kerguelen region. *Ditrichum subaustrale* is known only from Heard Island and Îles Kerguelen; perhaps it evolved from a related species which arrived at any stage since the Tertiary. *Muelleriella crassifolia* is found in supralittoral zones on all the subantarctic island groups, the Antarctic Peninsula and the southernmost coastal regions of New Zealand and South America. There are two subspecies within this range (Vitt 1976); *M. crassifolia* subsp. *acuta* found only on Îles Kerguelen, Îles Crozet and now Heard Island, and *M. crassifolia* subsp. *crassifolia* found throughout the remainder of the species' range with a stepped cline from the New Zealand region to South America and then Marion Island. Vitt (1976) suggested that in relatively recent times there has been little gene exchange and lack of long distance dispersal between populations of *M. crassifolia* in the Kerguelen region and those in other regions. Thus the subspecies *M. crassifolia* subsp. *acuta* has probably either evolved in the Kerguelen region or perhaps in coastal areas of East Antarctica and dispersed to the Kerguelen region after formation of these islands during the Miocene.

The remaining 27 determined species of the flora are probably more recent arrivals, particularly *Brachythecium austro-salebrosum, Dicranoweisia brevipes, D. breviseta, Grimmia immerso-leucophaea, Schistidium falcatum, Tortula geheebiaeopsis* and *Tortula robusta,* which occur in southern South America and on up to five subantarctic island groups. These species are absent from Australasia and geologically young Macquarie Island. Such a distribution may reflect an island hopping dispersal pattern from South America, in the direction of the prevailing westerly wind.

Nine species (*Andreaea mutabilis, Amblystegium serpens, Bryum pseudotriquetrum, Ceratodon purpureus, Drepanocladus uncinatus, Pohlia wahlenbergii, Polytrichum alpinum, P. piliferum, Pottia heimii*) have polar disjunct distributions, occurring in cool-temperate to polar regions in both hemispheres. Schofield (1974) suggested that bipolar disjunct species reflect very long distance dispersal events from the Northern Hemisphere, either during or post Pleistocene.

Psilopilum australe, Andreaea acuminata, Bartramia patens, Blindia contecta, B. robusta, Dicranoweisia antarctica, Brachythecium paradoxum, Dicranoloma billardieri, and *Ditrichum conicum* occur on two or more southern continental land masses as well as some of the subantarctic island groups. The remaining four species, *Bryum dichotomum, Racomitrium lanuginosum, R. crispulum* and *Schistidium apocarpum,* have widespread or cosmopolitan distributions.

Andreaea acuminata, Drepanocladus uncinatus, Racomitrium crispulum and *R. lanuginosum* are the only species which occur on all the subantarctic island groups.

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News and progress...

Hedenäs, L., Herben, T., Rydin, H. and Söderström, L. 1989. Ecology of the invading moss species *Orthodontium lineare* in Sweden: Spatial distribution and population structure. – Holarct. Ecol. 12: 163–172.

The moss species *Orthodontium lineare,* originally from the southern hemisphere, has been spreading in Europe during this century. We have monitored the distribution patterns of the species in Sweden.
The age distribution differed between localities due to variation in the proportion of colonies in old age classes. We attributed this to differences in colony mortality.
Although *O. lineare* had a high spore output in most localities, the colonies showed a clumped pattern, indicating strong neighbourhood effects in the colonization of new spots within the locality.
The regional distribution was uneven and markedly southwestern. The distribution was related to regional and local availability of suitable habitats (decaying wood in not-too-dense forests), and to a lesser extent to climatic variables.
Spore transport and establishment are suggested to be the limiting factors for colonization of suitable habitats of *O. lineare.*

L. Hedenäs, Dept of Botany, Univ. of Stockholm, S-106 91 Stockholm, Sweden. T. Herben, Botanical Inst. of the Czechoslovak Acad. of Sciences, CS-252 43 Průhonice, Czechoslovakia, H. Rydin, Inst. of Ecological Botany, Uppsala Univ., Box 559, S-751 22 Uppsala, Sweden. L. Söderström (reprint requests), Dept of Ecological Botany, Univ. of Umeå, S-901 87 Umeå, Sweden.

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