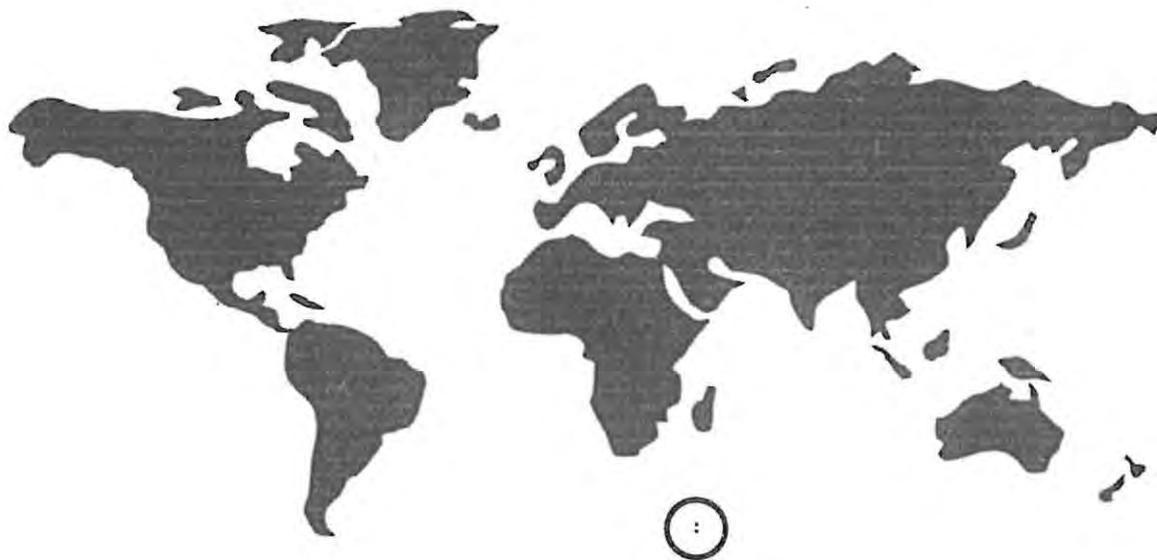


**PRODUCTION ECOLOGY OF
BRYOPHYTE VEGETATION AT
MARION ISLAND (SUB-ANTARCTIC)**

**BY
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**SUBMITTED IN FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
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ABSTRACT

The world's tundra regions can be considered as the last unexploited terrestrial biome on the earth's surface. Bryophytes contribute significantly to primary production and nutrient cycling in tundra habitats but received considerably less attention than the vascular plants during research for the Tundra Biome Project of the International Biological Programme in the 1970s. The IBP synthesis recognised this and called for more bryophyte production data and improved methodology in future studies. The synthesis also identified the need for more information on within-site variability, energy/chlorophyll relationships and mineral nutrient studies where tundra bryophyte production patterns are concerned.

Marion Island in the sub-Antarctic has an oceanic "tundra" type of vegetation, and the island offers the characteristics of an ideal "natural laboratory" for conducting fundamental ecological research particularly in the field of primary production and energy flow. Studies at Marion Island paralleled those of the IBP but also concentrated on the vascular component of the vegetation. Bryophytes contribute up to 60% of the biomass and 90% of plant cover in the mires that dominate the well-vegetated coastal plain of Marion Island. Following the termination of IBP research therefore, it was decided to extend these studies during the 1980s by measuring growth and characterising the major factors influencing growth patterns in Marion Island bryophytes.

In this thesis information is given on the physical and biotic environment of Marion Island. Data is presented on the cover, biomass, seasonal and annual production values, and turn-over rates (decomposition) of 15 bryophyte species found across the full range of habitat types at Marion Island. An analysis is also made of growth-associated variables viz. soils, climate, plant energy, chlorophyll, water and mineral nutrient contents.

Production was found to be related broadly to moisture-related variables, overlain by nutrient factors in some instances. Higher absolute production figures were obtained than at other tundra sites and interesting phenological data are discussed. The results suggest that decomposition is controlled mainly by tissue degradability factors and that decomposition is more significant than production in controlling biomass accumulation. A model is given for production/decomposition patterns across the range of habitat conditions at Marion Island.

Several growth measurement techniques were tested and recommendations are made concerning methodology for future bryophyte production studies. By reference to ecological data collected during the study, Marion Island is positioned in its bioclimatic/biogeographic context with other tundra regions of the world.

Information from the chapters on energy content, chlorophyll levels, water relations and mineral nutrient content contributes to an understanding of these factors in bryophyte growth physiology. The final conclusions emphasize the need for further research in these areas, but also for more work in the field of conservation ecology in threatened areas of the tundra biome.

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Special thanks are due to the head of my university department, Prof CEJ Botha, for understanding during my absences and assistance at various stages of the mainland-based work. Warmest thanks go also to my supervisor, Prof RA Lubke, for his patience, encouragement and help on many occasions. I am indebted to Mr Kent Cassels for assistance with computing and to Ms HJ Kew and support staff in the Rhodes University Botany Department for administrative assistance.

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Finally I would like to thank my wife for her assistance with the diagrams, and her consideration during my absence on the field-work phase of the project and her forbearance during the writing-up of the thesis.

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CHAPTER ONE

STUDY BACKGROUND AND OBJECTIVES

Marion Island (46° 54'S 37° 45'E) is one of several small islands included in the sub-Antarctic botanical zone (Greene & Greene, 1963; R Smith, 1984). This zone lies in the circum-Antarctic Southern Ocean, to the south of the principal continental land masses (Figure 1.1). The sub-Antarctic islands have long been recognised as of exceptional biogeographical interest (Hooker, 1847; Darwin, 1872; Good, 1949). The islands support anomalous and depauperate floras which however, offer unique insights into patterns of evolution and migration in the southern hemisphere (van Zinderen Bakker, 1967). The presence of pollen-preserving peat bogs renders the islands of importance in palaeoecological studies that attempt to trace the ebb and flow of the Antarctic ice sheet and the pattern of climatic change in the southern hemisphere during the Quaternary period.

Due to their geographical isolation, species poverty and harsh climatic conditions, the sub-Antarctic islands have relatively simple ecosystems, that often show little human interference (Holdgate & Wace, 1961). This makes them ideal "natural laboratories" for fundamental ecological research, for example in the field of primary production and energy flow within ecosystems (van Zinderen Bakker, 1971).

Following the establishment of a permanent weather station on Marion Island by the South African government in 1948, it became possible for scientific research teams to

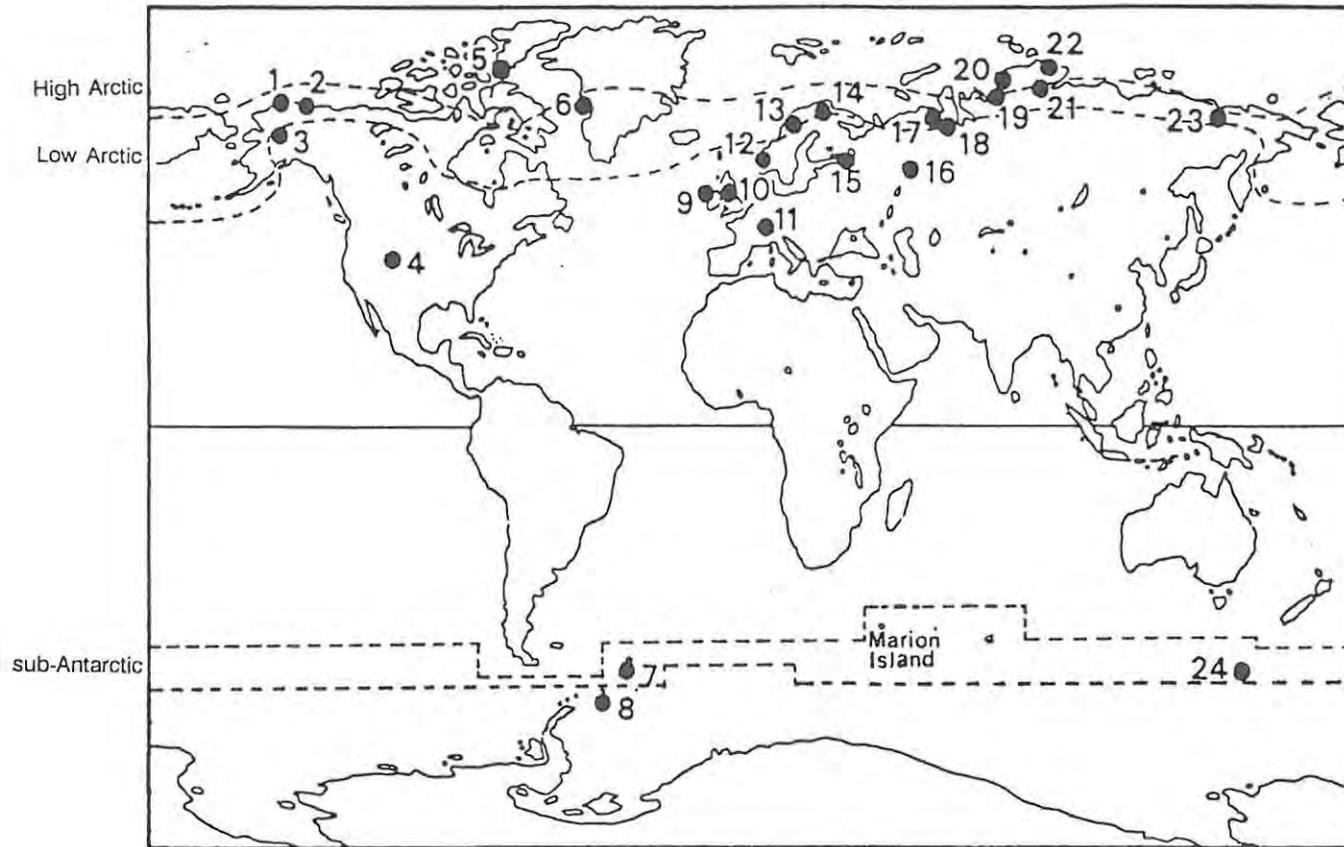


Figure 1.1

Position of Marion Island in relation to the sub-Antarctic zone, and locations of sites studied during the International Biological Programme, Tundra Biome Project.

The IBP Tundra Biome sites. 1. Point Barrow; 2. Prudhoe Bay; 3. Eagle Summit; 4. Niwot Ridge; 5. Devon Island; 6. Disko Island; 7. South Georgia; 8. Signy Island; 9. Glenamoy; 10. Moor House; 11. Mt Patscherkofel and Hoher Nebelkogel; 12. Hardangervidda; 13. Stordalen (Abisko); 14. Kevo; 15. Lammin-suo; 16. Petchora; 17. Sivaya Maska; 18. Harp; 19. Agapa; 20. Tareya; 21. Ary-Mas; 22. Maria Pronchitsheva Bay; 23. Kolyma; 24. Macquarie Island.

be accommodated at the island for periods longer than the ship-borne collecting visits that had previously been the rule. As early as 1952, Prof EM van Zinderen Bakker of the botany department at the University of the Orange Free State began to seek support for botanical research at Marion Island. His efforts led to the "First Biological and Geological Expedition to Marion and Prince Edward Islands" in 1965, and initiated a new era of annual visits by biologists conducting research on all aspects of ecosystem functioning (Condy, 1978).

Paralleling developments in the bipolar "Tundra Biome Project" of the International Biological Programme 1964-75 (Bliss, 1977), basic research into energy flow in the Marion Island ecosystem was begun in the early 1970s. Standing crop and primary production are standard measures of comparison between plant communities, and studies on these aspects of the terrestrial vegetation types at Marion Island concentrated initially on the vascular plants (Huntley, 1972; V Smith, 1976, 1977).

Bryophytes are however an important component of vegetation in "tundra" type habitats and contribute significantly to primary production in such ecosystems (Kallio & Karenlampi, 1975; Wielgolaski, Bliss, Svoboda & Doyle, 1981; Longton, 1984, 1988). On Marion Island, mosses and hepatics contribute approximately 25% of the total lowland biomass, increasing locally to 60% in *Agrostis* mires which may have over 90% bryophyte cover (V Smith, 1977, 1978; Gremmen, 1981). Above 300m altitude, cryptogams dominate the sparse fellfield vegetation.

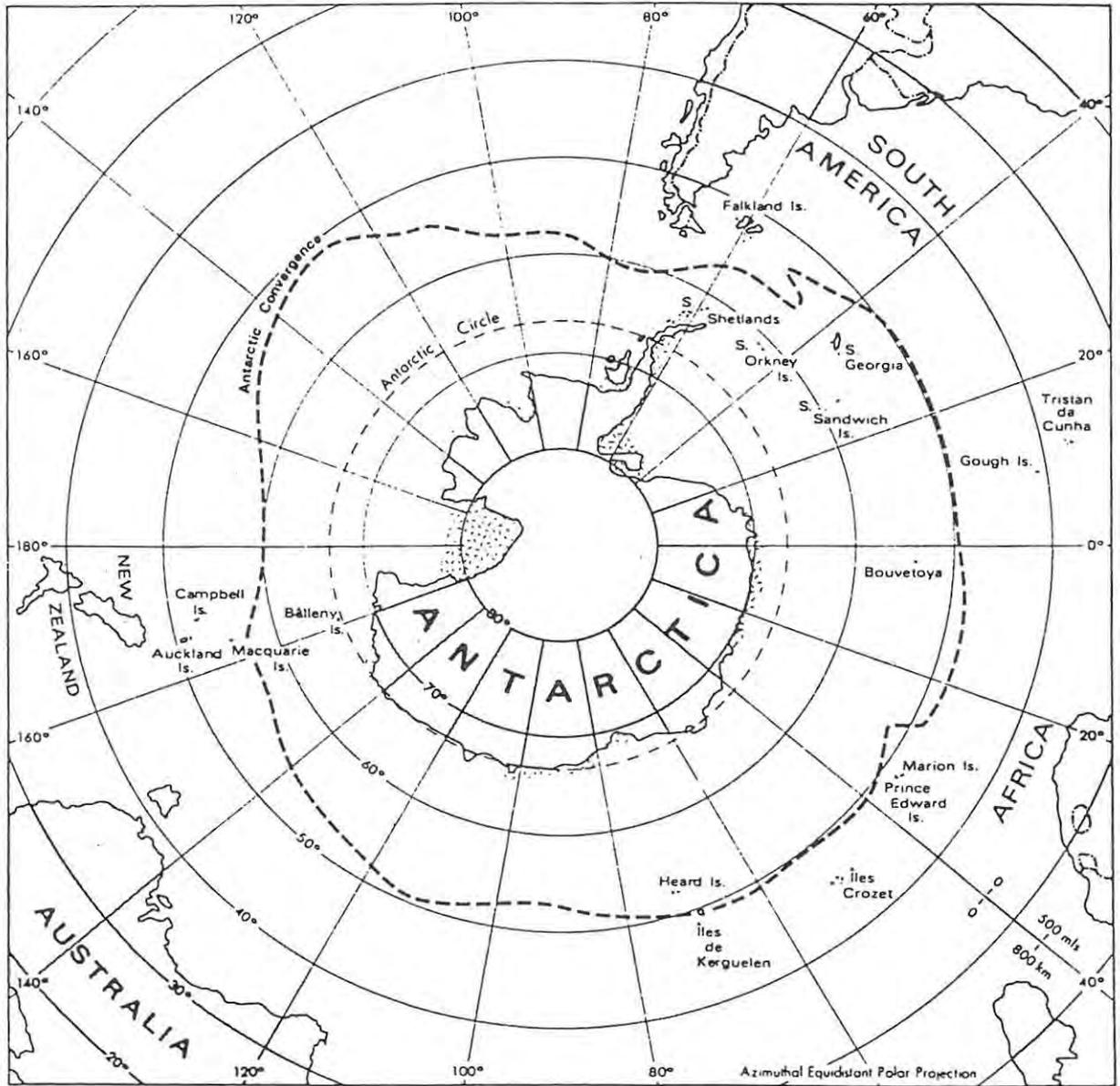


Figure 1.2 Position of Marion Island in relation to Antarctica, the southern continents and the Antarctic convergence.

Bryophytes are important in nutrient cycling in tundra habitats due to their highly adsorptive properties (Oechel & Sveinbjornsson, 1978) and because they often support large numbers of epiphytic nitrogen fixing bacteria (Alexander, Billington & Schell, 1978; Smith & Russell, 1982). There is some evidence that they may also be of direct importance in the food chain as a source of food for vertebrate (Arctic) and invertebrate grazers (V Smith, 1977; Block, 1985; Davidson, 1985; Gerson, 1985; Smith & Walton, 1985).

For these reasons the Marion Island plant ecology research plan for the years 1978-83 proposed in part:

- 1) "the initiation of studies on the primary production of mosses" (SASCAR, 1978) and consideration of the following question: "How does the primary producer component function and what are the inputs into a primary production sub-model?" (SASCAR, 1981)
- 2) "autecological studies of selected dominant species" (SASCAR, 1978).

Following preliminary studies at Marion Island by N Gremmen and VR Smith in 1974, the author assumed responsibility in 1980 for the execution of the bryophyte production project. This was carried out under the aegis of the Institute for Environmental Sciences, University of the Orange Free State, and while the author was on sabbatical from the department of Plant Sciences at Fort Hare University, Ciskei.

It was determined that the project should result primarily in the definition of a set of

annual production values for representative bryophyte species on Marion Island. These values would, in the first instance be necessary basic inputs for the model of ecosystem functioning being prepared during the early 1980s by biological researchers at Marion Island (SASCAR, 1981).

Secondly, in addition to knowledge of the quantitative aspects of plant production, it is at least as important to have an understanding of the role of the factors controlling production processes. Therefore, to implement proposal 2 above, and in parallel with plant ecological investigations elsewhere in the tundra biome, studies were made of various properties of bryophytes that were hypothesized to correlate with growth:

- 1) Energy (calorific) content - an alternative to biomass as a measure of standing crop (Forman, 1968)
- 2) Chlorophyll content - "representing a measure of the size of the assimilatory apparatus which can be correlated with the rate of dry matter production" (Sestak, Catsky & Jarvis, 1971)
- 3) Water content - the principle factor controlling growth in bryophytes (Gimingham & Smith, 1971; Proctor, 1981)
- 4) Nutrient status - potentially a limiting factor in dry matter production, especially in bryophytes of oligotrophic and supertrophicated (biotically influenced) habitats (Vitt & Pakarinen, 1977).

Thirdly, these figures would allow comparison of the ecosystem at Marion Island, with other polar alpine habitats. Such indices of plant performance would help define the

bioclimatic/biogeographic relationships of Marion Island ecosystem with other "tundra" type ecosystems, especially the other sub-Antarctic islands (Figure 1.2). They would also add to the understanding of the role played by these factors in the eco-physiology of bryophytes in general.

Fourthly, the study of a large number of species with varied growth forms, from a broad range of habitats would offer a unique opportunity for the testing and evaluation of a full spectrum of growth measurement techniques. The results would therefore allow recommendations to be made concerning appropriate field methods to be applied during future studies of bryophyte production.

With regard to extrinsic properties affecting bryophyte growth, rather than carry out an extensive substrate survey during the course of this investigation, it was decided that use would be made of the comprehensive previous work of Gremmen (1975) and V Smith (1978) with regard to edaphic factors.

In respect of climatic parameters, apart from incidental measurements, no long term microclimate recordings had been made at Marion Island. This is partly because the expensive equipment necessary for such work has not been available to researchers in the Marion Island biology programme. Such studies were a major part of the research effort at other tundra sites (Romanova, 1971; Sonesson, Wielgolaski & Kallio, 1975; Courtin & Labine 1977; Walton, 1977; Dingman, Barry, Weller, Benson, Le Drew & Goodman, 1980).

However, for the purposes of the bryophyte production investigation, the lack of such studies at Marion Island has not been considered critical for the following reasons. Firstly, the most vegetationally diverse habitats at Marion Island are situated on the eastern coastal plain, where the majority of biological research has taken place. The scientific base station is sited in this same area (Figure 4.) and includes a South African Weather Bureau primary weather station which continuously monitors many of the parameters recorded during microclimatic studies, including solar radiation and "grass minimum" temperatures. Secondly, due to its extreme oceanicity, Marion Island shares with Macquarie Island the distinction of having probably the most isothermal climate on earth (Fabricius, 1957). Certain parameters e.g. temperature and humidity are therefore extremely constant and less likely to influence growth patterns to the same extent as the other environmental or intrinsic factors which were studied during the course of the project.

Finally, it was realised that information on decomposition would be necessary to give a more complete picture of production/biomass relationships. Such data were rarely if ever collected for bryophytes during the IBP studies. It was anticipated that the Marion Island study would provide "annual shoot production" and standing crop (biomass) data equivalent to that obtained at most IBP sites, and that indirect decomposition data could be calculated from biomass turnover ratios. However, due to time constraints, a separate decomposition project using direct methods of measurement could not be carried out by the author. This work was scheduled for inclusion at a later stage of the overall ecosystem study.

To achieve the above objectives, the author commenced accumulating literature on tundra bryophyte production in 1980 before beginning field work at Marion Island in September of that year. This visit lasted for eight months until May 1981, during which period the following activities took place:

- 1) Familiarization with the bryoflora including collecting trips to various parts of Marion and Prince Edward Islands.
- 2) A survey of bryophyte communities using a pre-publication copy of Gremmen's (1981) vegetation survey, in order to select the most important species for growth trials.
- 3) Application of eight different growth measurement methods to sixteen species during a six month summer growth trial period (including monthly stem increment measurements).
- 4) Chlorophyll analyses were carried out on the island while additional plant material was collected for later energy and mineral determinations on the mainland.
- 5) Subsidiary projects (tussock grass leaf litter-fall rates, and moss-epiphytic cyanobacterial nitrogen fixation) were also undertaken. Some time was also spent perfecting a microclimate monitoring station at one of the growth plots, which was however only used effectively during the nitrogen fixation study (Smith & Russell, 1982). Trials were also conducted on an inexpensive method for measuring photosynthetic CO₂ gas exchange of bryophytes in the field (Russell, 1988b).

A further period of six weeks, including another short collecting visit to Prince Edward Island, was spent at Marion Island in April-June 1982. This time was spent harvesting the full year growth plots that had been established at the beginning of 1981, using the most successful measurement techniques as determined during the earlier six month study. In addition, preliminary experiments on bryophyte CO₂ exchange were carried out using laboratory apparatus at the base station (reported elsewhere).

Titles of papers which have resulted in total or in part from work carried out by the author at Marion Island include:

- Verwoerd, W.J., Russell, S. & Berruti, A. 1981. Volcanic eruption on Marion Island. *Earth & Planetary Science Letters* 54:153-156.
- Smith, V.R. & Russell, S. 1982. Acetylene reduction by bryophyte-cyanobacterial associations on a sub-Antarctic island. *Polar Biology* 1:153-157.
- Russell, S. 1984. Growth measurement in bryophytes. *J. Hattori Bot. Lab.* 56:147-157.
- Russell, S. 1985. Bryophyte production at Marion Island. In: W.R. Siegfried, D.R. Condy & R.M. Laws (eds). *Antarctic Nutrient Cycles and Food Webs*. Berlin: Springer Verlag.
- Seppelt, R.D. & Russell, S. 1986. *Fissidens bryoides* Hedw., new to the moss flora of subantarctic Prince Edward Island. *Lindbergia* 12:57-59.
- Russell, S. 1987. Water relations and nutrient status of bryophyte communities at Marion Island Sub-Antarctic.. In: T. Pocs, T. Simon, Z. Tuba & J. Podani (eds), *Proceedings of the IAB conference of bryoecology, Budapest-Vacratot, Hungary, 5-10 Aug. 1985. Symposia Biologica Hungarica* 35:39-57.

- Russell, S. 1988a. Measurement of bryophyte growth 1. Biomass (harvest) techniques: 249-257. In J. Glime (Ed.), *Methods in Bryology*. Nichinan, Japan: Hattori Bot. Lab.
- Russell, S. 1988a. Measurement of bryophyte growth 2. Gas exchange techniques: 259-273. In: J.Glime (Ed.), *Methods in Bryology*. Nichinan, Japan: Hattori Bot. Lab.
- Russell, S. 1990. Bryophyte production and decomposition in tundra ecosystems. *Bot. Jl. Lin. Soc.* 104:3-22.
- Russell, S., Cooper, J. & Voisin, J. Who named sub-Antarctic Marion Island? *Polar Record* (in press).

Many aspects of the information collected during the 1980-81 and 1981-82 field seasons have not been addressed in the above papers and have relevance for lacunae in knowledge of tundra bryophyte production ecology such as within-site variability, energy and chlorophyll relations etc., that have been pinpointed by Holdgate (1977), Wielgolaski (1981), R Smith (1984) and Longton (1988). A more detailed analysis of the data has therefore been undertaken for presentation in this thesis.

Specific aspects of the study e.g. biomass and production, energy, chlorophyll, water relations, and nutrient status, are treated in separate chapters which emulate independent articles and therefore have their own inclusive literature review sections. For the same reason, cross referencing between chapters is not exhaustive, but conclusions drawn from all the studies are synthesised in chapter 9, and a reassessment of the overall project objectives as stated above is included in the conclusion (chapter 10).

CHAPTER TWO

PHYSICAL ENVIRONMENT**2.1 Introduction**

Comprehensive descriptions of the physical environment of Marion Island have been given in Van Zinderen Bakker et al (1971), Gremmen (1981) and V. Smith (1985). A brief outline is presented here, with particular reference to features of the physical environment that are of relevance for the ecology of bryophyte vegetation at the island.

2.2 Geography and geology

The Prince Edward Islands comprise Marion Island and its smaller neighbour, Prince Edward Island. Marion Island has an area of 290km² and lies 20km SSW of Prince Edward Island which has an area of 94km². The islands lie approximately 1800km SSE of the southern tip of the African continent and 2300km north of the Antarctic (Figure 1.2). The group is 7500km distant from southern South America, from whence the majority of immigrant biota have arrived through the agency of the predominantly westerly winds and ocean currents.

A description of the islands' geology has been given in Verwoerd (1971) and generalised geological features are shown in Figure 2.1. The islands lie close to a diffuse and incompletely understood part of the world's mid-ocean ridge system in the south west Indian Ocean. The islands are entirely volcanic in origin and their active seismicity and associated volcanism is



Plate 1

Sterile species of *Bryum* colonizing recently ejected volcanic ash from Kaalkoppie, November, 1981.

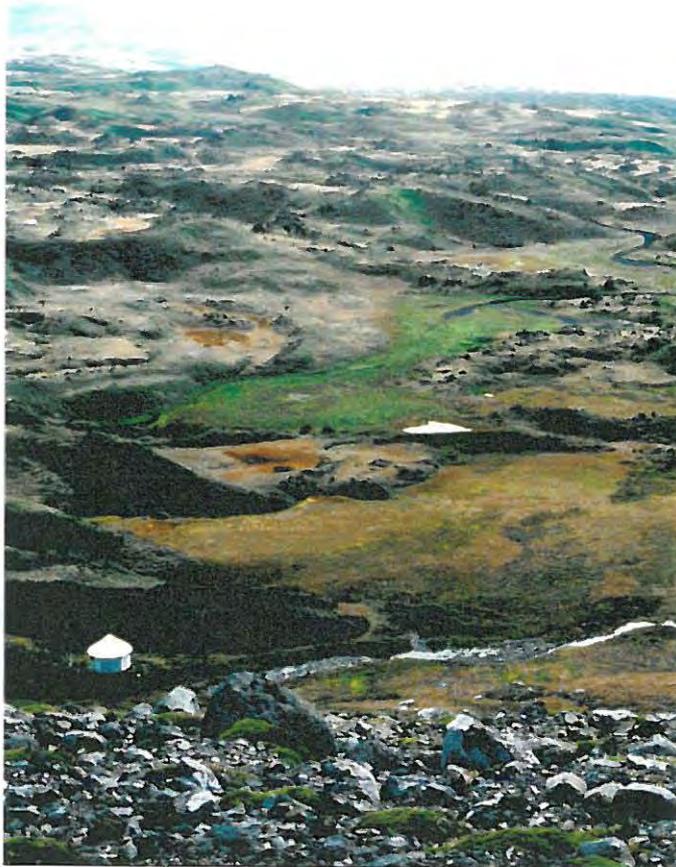


Plate 2

General view of part of the Eastern Coastal Plain at Marion Island, from Long Ridge looking north west to show habitat types.

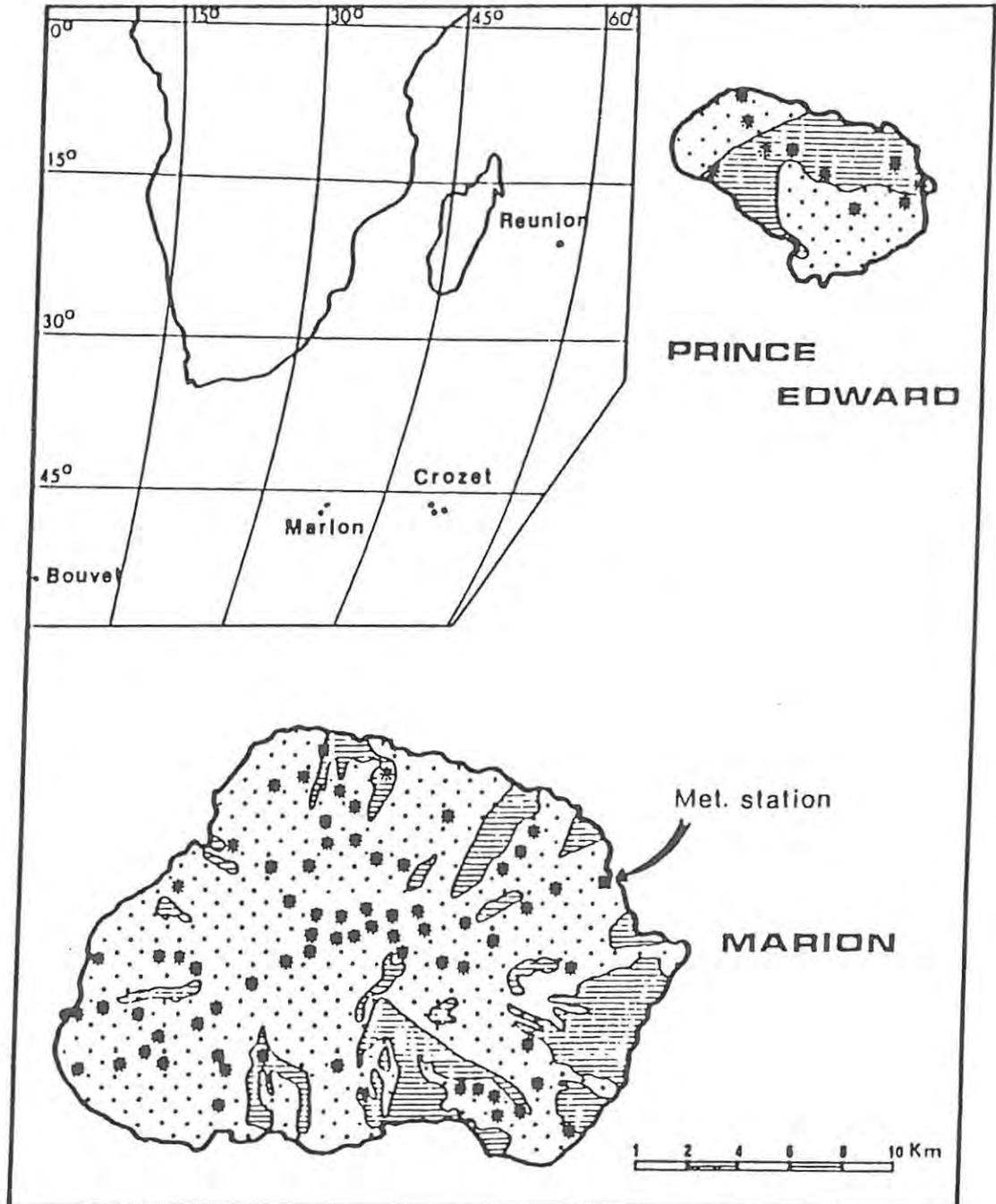


Figure 2.1

Location and generalised geology of Marion and Prince Edward Islands. Older succession ruled; younger volcanics stippled. Asterisks denote tuff and scoria cones of younger succession.

probably related to instability along transcurrent wrench faults forming part of the ridge system in this area (Prince Edward and Malagasy fracture zones).

The islands probably emerged more than half a million years ago, as some of the lavas have been age-dated at over 500 000 years (Smith & Verwoerd, 1985). Rocks are fine grained (often glassy) basalts and trachybasalts, with a characteristic grey colour in hand specimen in the older series (dated at >100 000 years), and a fresher black colour in lavas of a more recent volcanic phase which began approximately 15 000 years b.p. Typical oceanic basalt (Hawaiian type) volcanism continues to the present day (Verwoerd, Russell & Berruti, 1981) and freshly ejected lava and ash provide substrata that are rapidly colonised by bryophytes e.g. Bryum species (Plate 1).

Major glaciation of the islands took place after the Pleistocene grey lava eruptive period, but before the Holocene black lava phase. Glaciation was contemporaneous with major "ice age" events in the northern hemisphere. Ice-free refugia are postulated to have existed at the island during this period, and the ice cover began to recede, beginning about 10 000 years ago. Morainic deposits occur at the islands, and cores in post-glacial peat deposits have been dated back to 7 000 years b.p. (Gribnitz et al, 1987).

Pedogenesis at Marion Island has been influenced by glacier retreat, ash falls, new lava flows and mass movement (slumping) on unstable slopes (phenomena that are continuing at the present day). The soils at exposed sites tend to be thin lithosols with low plant nutrient status due to their youthfulness and poorly advanced state of decomposition. In the lowlands, peats of more

than 2m in depth may develop under mires which form in areas of impeded drainage. Detailed information on Marion Island soils is given in V Smith (1978) and basic characteristics of substrata in 510 vegetation relevees are given in Gremmen's (1981) phytosociological survey of the island's vegetation.

General features of the island's topography are mapped in Figure 2.2 and diagrammatised in Figure 2.3. A view of the general environment at Marion Island is also shown in Plate 2. The physiography is dominated by features resulting from the volcanic eruptive episodes. A central mountainous region ascends to 1200m and encloses a small permanent ice cap in a basin below the highest peaks. Spurs and valleys descend to a bounding coastal plain that varies in width from ½-4km, and lies generally at an altitude of less than 100m. Convexly rounded, glaciated outcrops of grey lava tend to form exposed ridges and plateaux. These are interdigitated with rugged expanses of black lava forming broad vales that are often "submerged" at lower altitudes by thick accumulations of peat. Cones (up to 1000m in height) of porous volcanic scoria having a characteristic reddish colour and supporting little vegetation, also occur throughout the island.

In general, the youthful landscape has a poorly developed surface drainage pattern. Impeded drainage leads to mire formation, as seen elsewhere in areas of recently glaciated terrain, e.g. the "muskegs" of northern North America. Shallow rills ("drainage lines") may form in the centre of mires, and springs ("flushes") often occur at breaks of slope on the more impervious grey lavas. Much drainage water is diverted underground in hollow subterranean channels ("lava tubes") which are common in the black lava areas. These lava tubes may account for the low frequency of perennial surface streams observed at Marion Island, notwithstanding the high

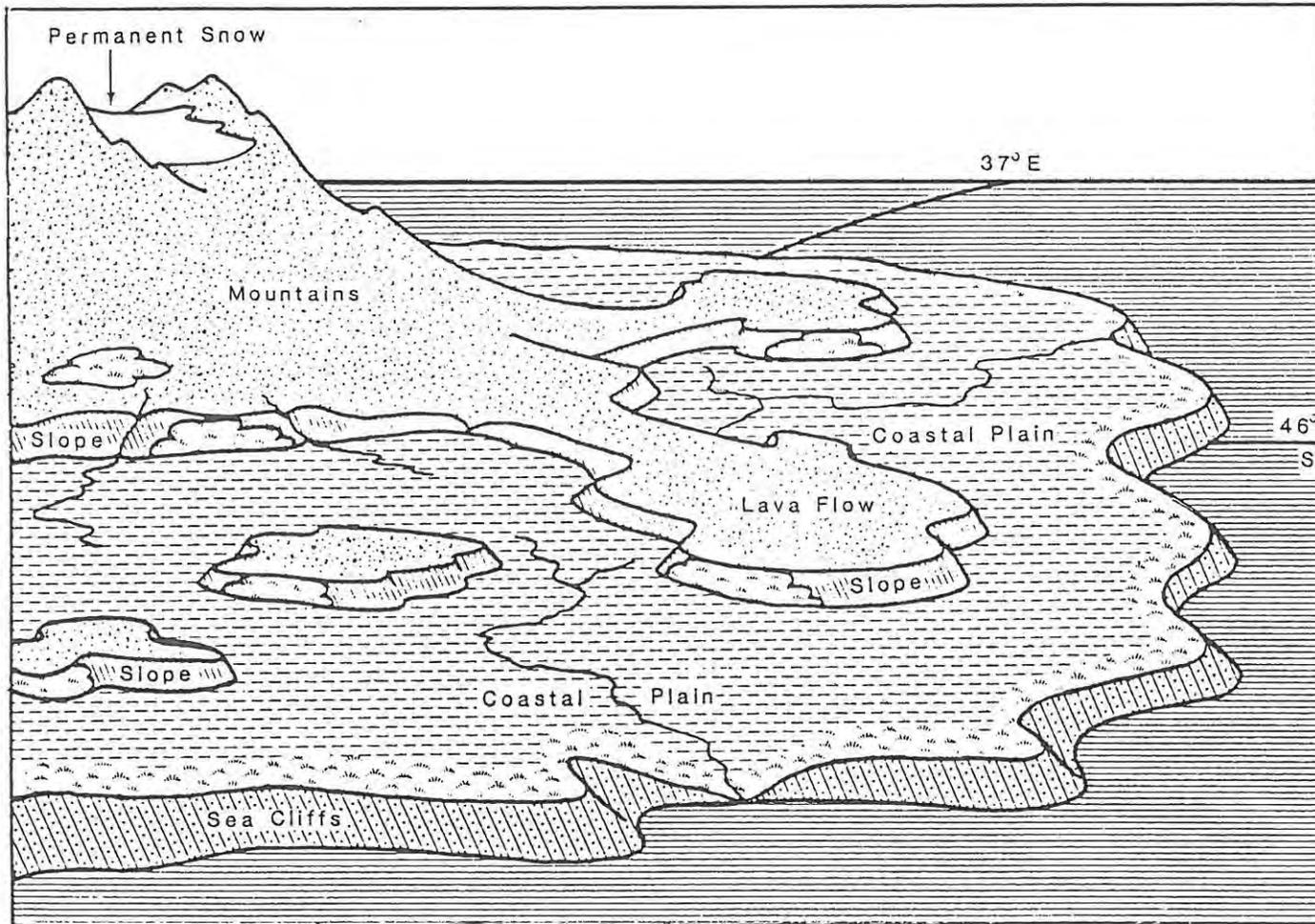


Figure 2.3 Generalised physiography of Marion Island

rainfall received at this station.

2.3 Climate

Discussions of the climate of the sub-Antarctic zone and of Marion Island in particular have been given in Fabricius (1957) and Schulze (1971). Comparisons of the Marion Island climate with other polar "tundra" regions and in relation to plant ecological parameters, are given in Gremmen (1981), French & Smith (1985) and Smith & French (1988).

A weather station has existed at Marion Island since 1948, and the climatic data available since that time represents a relatively complete and accurate set by sub-Antarctic standards, especially in respect of the early years (Venter, 1957). Individual climatic parameters are given in Table 2.1, and are further discussed below. A Walter type climate diagram for Marion Island is presented in Figure 2.4 to allow comparison with other sites for which comparable data exist (Walter & Lieth, 1967).

2.3.1 Cloudiness

High humidity due to the oceanic situation, and orographic influences of the island's mountainous landmass contribute to frequent and high levels of cloud cover at Marion Island. On average, the sky is 75% obscured by cloud throughout the year.

2.3.2 Sunshine duration

Marion Island is the northernmost of the sub-Antarctic islands, but despite its relatively low

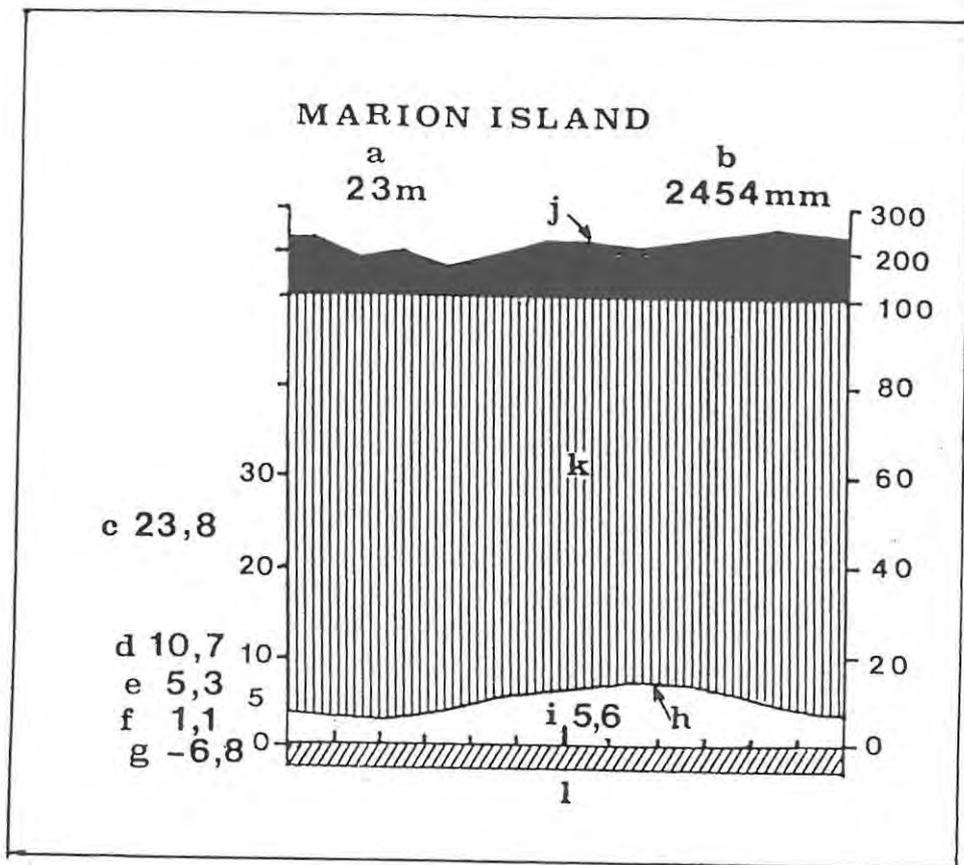


Figure 2.4

Walter climate diagram for Marion Island.

a = altitude (m); b = mean rainfall (mm); c = abs. max. temp. °C; d = mean daily max. hottest month; e = mean daily temp. range; f = mean daily min. coldest month; g = abs. min. temp.; h = mean monthly temp. curve (one scale interval = 10°C); i = mean annual temp.; j = mean monthly rainfall > 100mm (scale reduced to 1/10); k = humid period; l = months, from July to June.

latitude (46°S) it receives very little sunshine due to the cloudy conditions. From an average of approximately five hours per day in summer to less than two hours per day in winter, the island receives only 29% of the total sunshine hours possible at this latitude. On average no days occur with full sunshine, and this contributes to a relatively narrow diurnal temperature range and low evapotranspiration demands compared with other polar sites.

2.3.3 Solar radiation

Average annual total radiation receipt at Marion Island is $1.272 \text{ kJ cm}^{-2} \text{ day}^{-1}$ based on five years data given in Schulze (1971). A slightly higher figure of $1.326 \text{ kJ cm}^{-2} \text{ day}^{-1}$ from four year's data in the 1950s is given by Fabricius (1957), and $1.414 \text{ kJ cm}^{-2} \text{ day}^{-1}$ was recorded at the Marion Island weather station in 1979, the year before this project was commenced. These levels of radiation are low by world standards due to the high incidence of cloudiness at this station. However, summer days may receive as much as $3.766 \text{ kJ cm}^{-2} \text{ day}^{-1}$ due to the long day length and the sun's high position at solstice. A large component of diffuse radiation is also transmitted by the cloud cover (Fabricius, 1957)(see also Figure 2.5).

In winter, a radiation receipt of only $0.418\text{-}1.255 \text{ kJ cm}^{-2} \text{ day}^{-1}$ is normal. On average there is a five-fold increase in daily radiation receipt from winter to summer, and this might be expected to have significant consequences for the course of plant growth during the year. Selected curves for daily radiation recorded during the author's nitrogen fixation studies at Marion Island are shown in Figure 2.5. These demonstrate the effect that cloud cover has on total energy received at the surface.

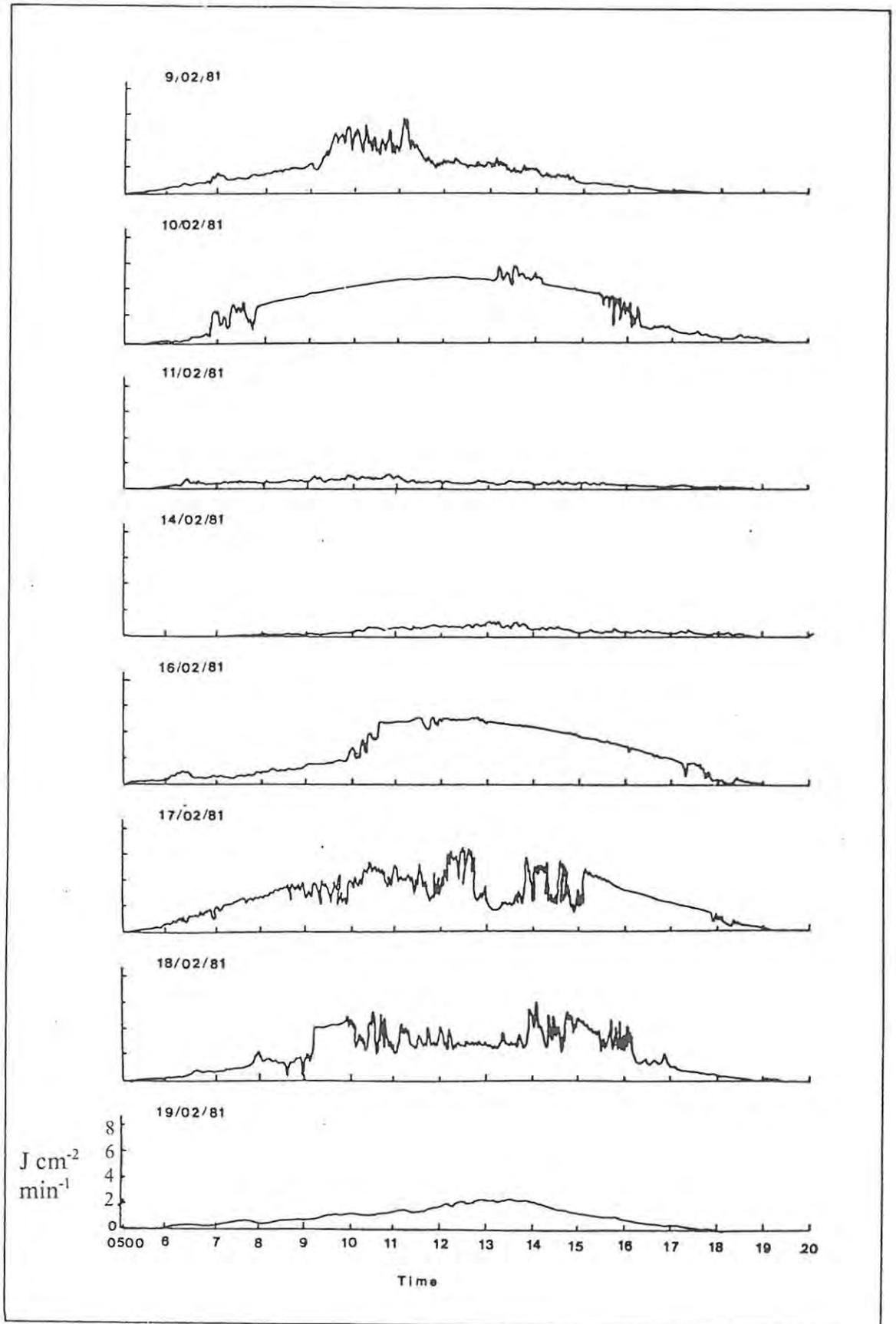


Figure 2.5

Daily solar radiation curves recorded at the Marion Island meteorological station during early February, 1981.

2.3.4 Temperature

The Prince Edward Islands are situated 1800km from the nearest landmass and the temperature of the surrounding body of seawater therefore strongly influences the islands' climate. The sub-Antarctic surface water has a mean temperature of circa 5°C which drops to around 3°C where it converges with Antarctic water 250km to the south Deacon (1984). Air temperature at Marion Island is concordant with the temperature of the sub-Antarctic surface water at approximately 5°C. Cold water of the Weddell Sea "gyre" is subject to maximum radiative warming at the time of the summer solstice. This current feeds the Bouvet Current which in turn brings the summer warm water to influence Marion Island at a later stage in the season. This lag phase buffers the effect of December maximum radiation receipt at the island, causing a delay of two months until February when maximum temperatures are experienced (Figure 2.6).

The oceanic influence also leads to an extremely small fluctuation ($\pm 2.5^{\circ}\text{C}$) of the mean monthly temperature about the annual mean of 5.7°C. This confers on Marion Island, the distinction of having one of the most isothermal climates on earth. Measured at ground level, the so called "grass minimum" temperature shows an annual mean of 1.2°C (Schulze, 1971) and rarely falls below 0°C (Figure 2.6). Soil temperatures also remain above zero for most of the year especially under vegetation cover (Smith, 1985). Temperature conditions can therefore be expected to be favourable for bryophyte growth the whole year round.

The temperature data presented by Fabricius (1957) covers the period 1948-56, during which time the mean temperature at Marion Island was 5.4°C. Schulze gave an average of 5.5°C for the period 1961-65. Mean temperature calculated in the same way $\{(annual\ max+annual\ min)/2\}$ from S. A. Weather Bureau data for the years to 1987, gives a mean monthly figure of 5.7°C.

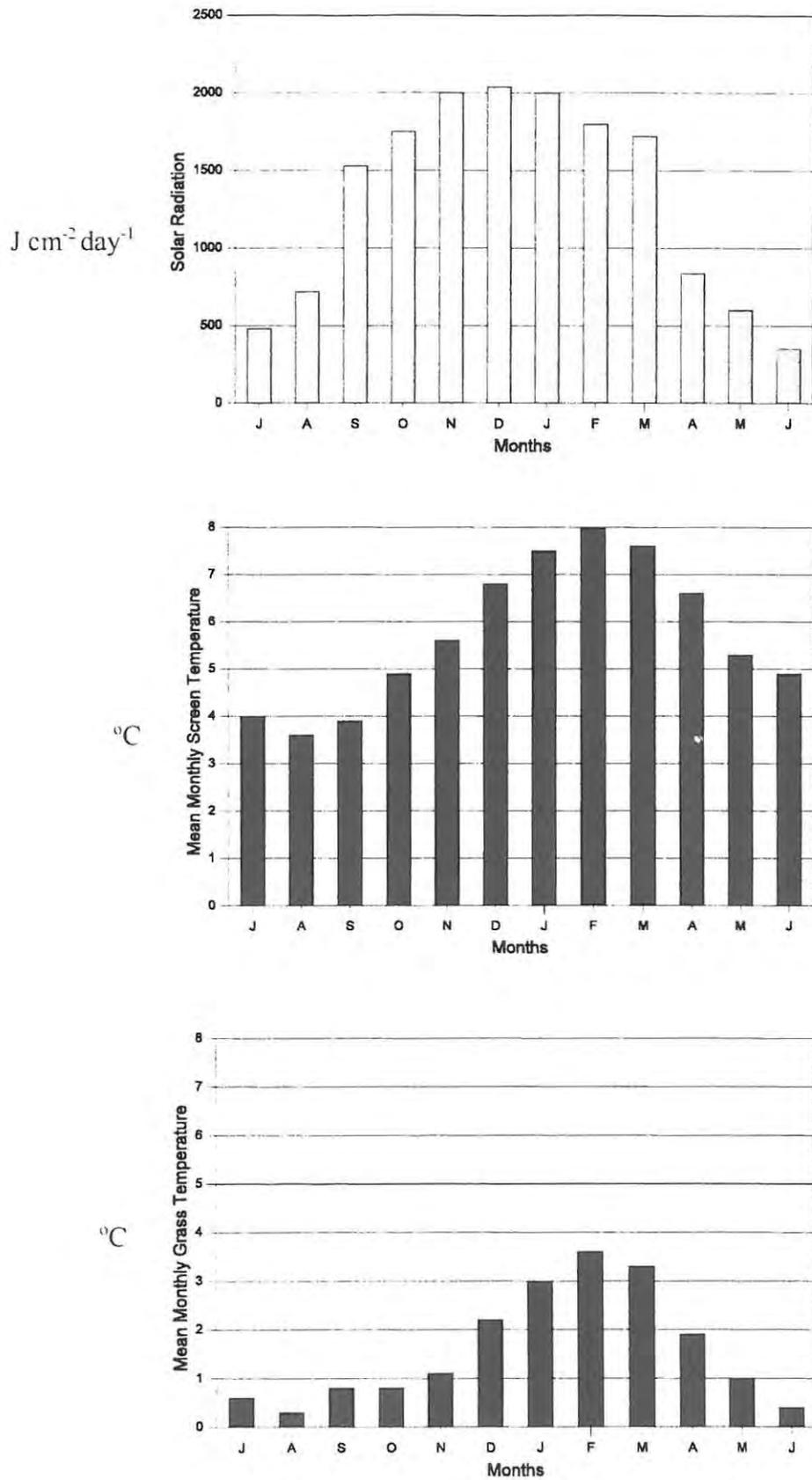


Figure 2.6 Annual March of solar radiation, screen temperature and grass minimum temperature at Marion Island.

Study of the temperature curve for the years 1951 to 1987 (Figure 2.7) reveals that this parameter remained fairly constant before 1977. In the ten years between 1977 and 1987 however, mean annual temperature rose significantly and the overall warming trend has continued into the 1990s (V. Smith, 1992). The above method of calculation overestimates the true value for mean annual temperature by about 0.3°C. However, the trend of increasing temperature at the well-buffered Marion Island site is significant in relation to wider evidence for global climatic warming, and correlates well with the observed shrinkage of the Marion Island ice cap in recent years.

2.3.5 Wind

The zone of maximum mean absolute wind force and maximum resultant windspeed (January) in the southern hemisphere, lies approximately midway between South Africa and the Antarctic continent (Vowinckel, 1957). Marion Island is situated closer to this zone than any other area of land except Bouvet Island. Marion Island experiences moderate gales on 107 days every year, and full gales on 43 days, with gusts of over 200km hr⁻¹ having been recorded.

This high and constant windiness has repercussions for plant ecology at Marion Island, in terms of evapotranspiration stress, removal of litter, and deposition of nutrient elements from salt spray. Mechanical abrasion and the deposition of particulate mineral matter are also factors that might be expected to affect cushion mosses of exposed fellfield habitats.

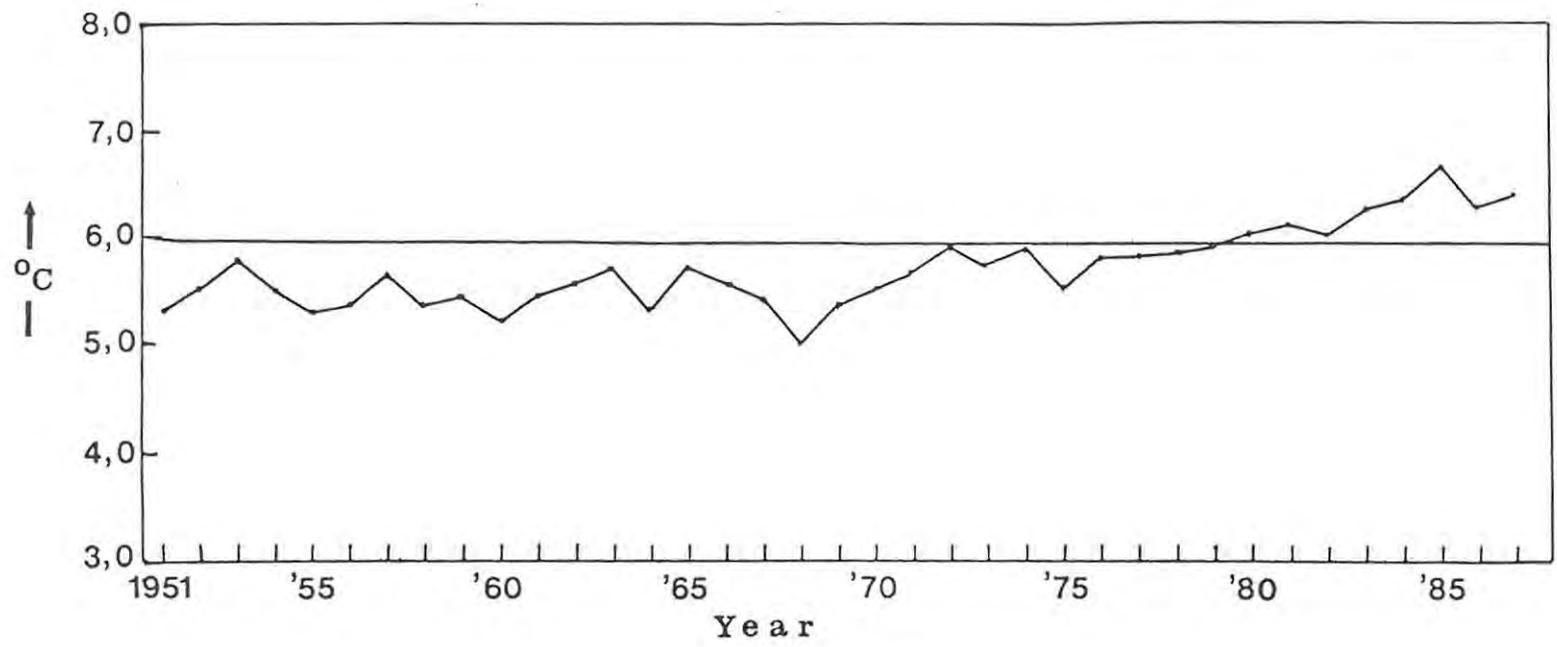


Figure 2.7 Mean annual temperature for Marion Island, from 1951-1987.

2.3.6 Relative humidity

Relative humidity is consistently high at Marion Island and generally remains above 80% at all times of day (Table 2.1). Periods of lower humidity do occur, although it is rare for RH to drop below 50% and such dry periods seldom last for more than 2-3 days (Gremmen, 1981).

2.3.7 Precipitation

Marion Island has the wettest climate in the sub-Antarctic zone with a mean annual rainfall of 2454mm and precipitation occurring on an average of six days out of every seven. Rainfall figures for other sub-Antarctic sites are shown in Table 2.2 for comparison. Notwithstanding the cool mean annual temperature, days on which snow occurs at Marion Island are few (83) and snow seldom lies for more than a week at sea level, even in mid-winter.

2.3.8 Evaporation

This parameter has not been measured directly at Marion Island but is of importance where ecological studies of poikilohydric plants such as bryophytes are concerned. Calculation of a potential evapotranspiration (PE) value for Marion Island according to the thermal formula of Holdridge (1971), results in a figure of 329mm yr⁻¹ (0.9mm day⁻¹). However, the Holdridge formula is more appropriately applied in temperate and tropical, continental conditions and is likely to underestimate the true evaporation value at a polar site by a significant margin. For example, the Holdridge PE figure for Macquarie Island

Table 2.2 Climatic data including "Indices of Hygrothermy" for some sub-Antarctic sites.

	precipitation (mm)	temperature (°C)	mean temp hottest month	mean temp coldest month	index of hygro-thermy
Stanley (Falklands)	668	5.7	9.3	2.2	53.6
Grytviken (S. Georgia)	1398	1.6	5.4	-2.1	29.8
Campbell Island	1451	6.7	9.2	4.4	202.5
Macquarie Island	1045	4.5	6.4	2.9	134.4
Heard Island	1381	1.1	3.3	-1.1	34.5
Kerguelen	1105	4.3	7.3	1.9	88
Marion Island	2454	5.6	7.9	3.4	311.5

is 277mm, but Loewe (1957), in a survey of sub-Antarctic evaporation conditions, gives a more realistic value of 442 mm yr⁻¹ for the same station.

Similarly, a Holdridge PE figure of 377 is calculated for Los Evangelistas on the southern coast of Chile. This station has mean annual temperature and rainfall figures almost identical with those recorded at Marion Island and is one of the very few stations in the world with a similar climate diagram (Walter & Lieth, 1967). Evaporation for Los Evangelistas is given as 559mm yr⁻¹ in Muller (1982). Based on these examples therefore, the Holdridge value would seem to underestimate PE at hyperoceanic southern sites by a factor of approximately 50%. Potential evapotranspiration for Marion Island recalculated on this basis, would approximate 504mm yr⁻¹, which is closer to the value of 536 mm yr⁻¹ calculated by the Thornthwaite method (French & Smith, 1985) for the same site. This accords well with evaporation figures for the sub-Antarctic zone shown on global climatic charts.

The latter PE figure gives a PE ratio (precipitation:potential evapotranspiration) of 4.9:1. By comparison, the PE ratio for Macquarie Island is 2.1:1, which confirms the greater "wetness" of the Marion Island climate (associated with its higher elevation and concomitant orographic effects). In other respects Macquarie Island might be expected to have a similar evaporative demand to Marion Island, as a slightly lower radiation receipt at the former site is balanced by a somewhat higher degree of windiness.

2.4 Climatic indices and classifications

In the 1920s, J Amman (cited in Streeter, 1970), devised a simple "Index of Hygrothermy" for relating bryophyte distribution to the degree of "oceanicity" of a climate viz:

$$H = \frac{PT}{t_H - t_c}$$

Where:

- H = Index of Hygrothermy
- P = annual precipitation (cm)
- T = annual mean temperature
- t_H = mean temperature of the hottest month
- t_c = mean temperature of the coldest month

Using this coefficient, Greig-Smith (1950) calculated that a "least oceanic" site on the east coast of England for example would have H equal to about 35. Conversely, his most oceanic site in the British Isles was Kerry on the west coast of Ireland with $H = 184$. By comparison, the Index of Hygrothermy for Marion Island is 318. H values for some other sub-Antarctic sites are given in Table 2.2 for comparative purposes.

According to the climatic classification of Köppen (1931), Marion Island is designated "ET"; a tundra ice climate. The more detailed scheme of Troll & Paffen (1980) classifies

Marion Island as "I,4": a highly oceanic sub polar climate with moderately cold winters, poor in snow (coldest month -8 - +2°C), cool summers (warmest month 5 - 12°C), annual fluctuation <13°C, often <10°C, and supporting subpolar tussock grassland and moors.

2.5 Comparison of the Marion Island climate with other regions

Marion Island's sub-Antarctic climate differs from the climate of northern tundra e.g. in the sub-Arctic, by its higher mean monthly temperatures (above 0°C all year) and by its thermal constancy (northern sites show greater temperature ranges and extremes due to their chiefly continental locations). Due to high winds however, chill factor may be more important than screen temperatures suggest for plants at exposed and high altitude sites in the sub-Antarctic. This factor contributes to the occurrence at southern sites, of fellfield habitats with scanty vegetation and skeletal soils that show extensive cryo-nival ("periglacial") phenomena. Marion Island thus shows a variety of habitats encompassing the polar extremes of:

- 1) temperate oceanic sites at sea level and
- 2) fellfields at higher elevations, analagous in several respects to the polar deserts of the high Arctic.

Very few other places on earth have a climatic regime similar to that of Marion Island. Equatorial regions with higher rainfall include Amazonia, Central America, Zaire and the East Indies; but these areas also have far higher temperatures and thus evaporative demands (>10000mm yr⁻¹). Northern hemisphere oceanic sites with high rainfall include

Hawaii, Vancouver, Washington and Oregon. But these sites too, have higher temperatures and evaporation values (700mm yr^{-1} in the north western United States for example). The only other northern stations with a climate approaching that of Marion Island occur at the southern tip of Greenland, in Iceland and at the Aleutian Islands (all these however have significantly lower PE ratios due to the influence of warm ocean currents).

Related stations in the southern hemisphere include sites in the mountains of New Zealand, the New Zealand shelf islands e.g. Campbell Island, the Falkland Islands, other sub-Antarctic islands and the northernmost islands of the maritime Antarctic e.g. S. Orkney Islands. Their PE ratios are still smaller than for Marion Island however, due to lower rainfall in all cases. Grytviken at South Georgia for example, has a rainfall figure approximately 60% that of Marion Island, and 253 rain days per year against 308 at Marion Island (Fabricius 1957).

Climatically, the sites with the greatest similarity to Marion Island are found on the westerly coasts of the southern Chilean archipelago e.g. Guarello, Los Evangelistas and Bahia Felix (the "Isothermic tundra" of Pisano, 1983). Even this region tends to be slightly warmer than Marion Island except in the furthest south west where reliable weather records are not available.

This degree of wetness favours the development of bryophyte-rich communities at Marion

Island and might be expected to promote high growth rates due to the maintenance of bryophyte tissue in a continuous state of hydration. Pisano (1983) notes that Sphagnum bogs which occur in central southern Patagonia, are replaced by liverwort dominated mires in the wettest western zone. He suggests that the species of Sphagnum involved may require at least short periods of unsaturated conditions at the stem apex for optimum growth. This may also account for the prevalence at Marion Island, of liverwort bogs that are structurally and floristically almost identical with those of western Fuegia.

2.6 Microclimate

V Smith (1987) states that for Marion Island "very little is known regarding the microclimate of the main vegetation types or the climatic regime at higher altitudes." For the reasons stated in the introductory chapter, biologists at Marion Island have tended to rely on data from the weather station in their investigations. For some purposes these are adequate; for example during the author's fieldwork for a study of cyanobacterial nitrogen fixation in moss carpets at Marion Island, in situ measurements of solar radiation and "grass minimum" temperatures were virtually identical with weather station data for the same period (Smith & Russell, 1982).

Climatic factors which might be expected to deviate significantly from screen values at bryophyte microsites include humidity (due largely to wind effects) and temperature which may be strongly buffered by moisture content in hydric moss turves. Diurnal

temperature ranges in bryophyte colonies may vary according to differing albedos and thermal coefficients of plants and their substrates (e.g. rock versus peat) respectively.

R Smith (1988) has carried out a study of moss microsite temperature patterns in an area of coastal Antarctica. At the surface of saturated turves of the moss Ceratodon, a narrow daily temperature range was experienced. Below the surface of the turf e.g. at 10cm depth, temperature fluctuations were negligible. However, at the surface of cushions of the moss Schistidium only a few centimetres away, large diurnal temperature cycles of up to 55°C were recorded, associated with radiative heat build up under the influence of direct sunlight. Significant temperature differences were also found on different aspects of moss hummocks at the same site.

Spatial heterogeneity in surface temperatures could therefore have important consequences for bryophyte production patterns at the microsite level. However, such variations could be predicted to be more extreme at the coastal Antarctic site than at Marion Island, as deeper, waterlogged bryophyte turves would be expected to maintain more constant microsite temperatures at the latter site.

At Marion Island, Huntley (1971) recorded 24 hour temperature curves using thermistors placed 2cm below the colony surfaces of five plants that are relevant to this investigation (Figures 2.8 & 2.9). Brachthecium rutabulum from a fernbrake habitat showed a narrow diurnal temperature range (5°C), due to shading beneath a canopy of the flowering plant

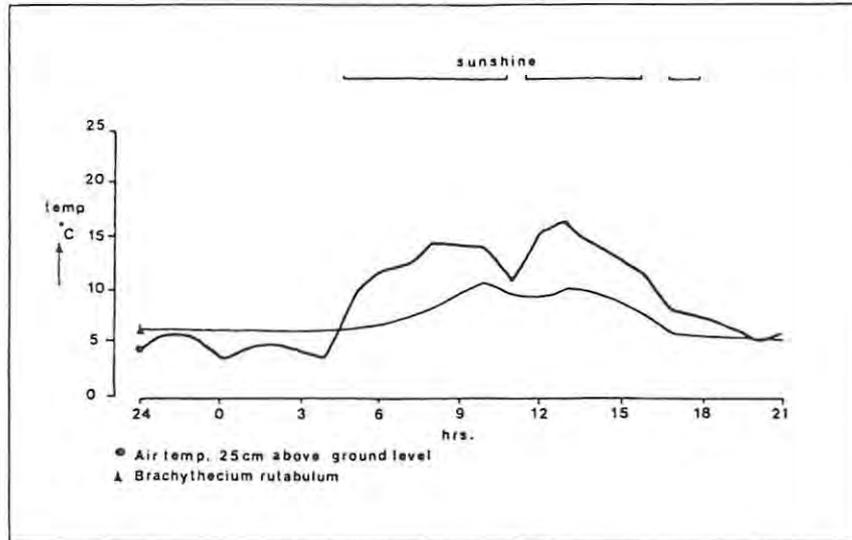


Figure 2.8 Diurnal temperature range in a colony of the slope/fernbrake moss *Brachythecium rutabulum* at Marion Island (Huntley, 1971).

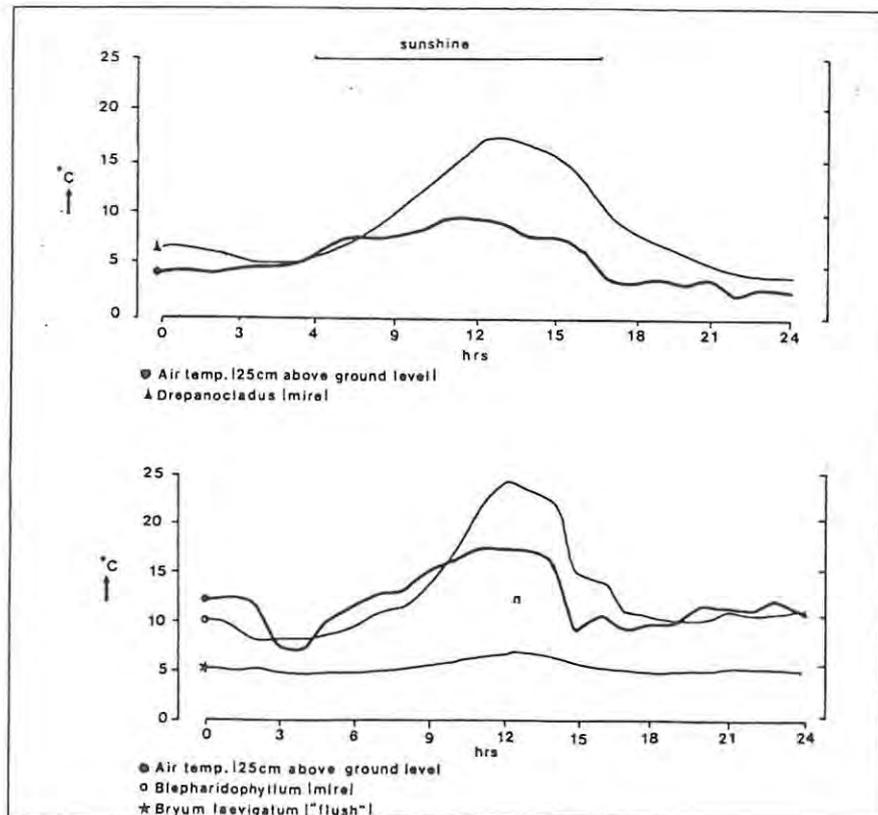


Figure 2.9 Diurnal temperature ranges in *Drepanocladus uncinatus* and *Blepharidophyllum densifolium* (mires), and *Bryum laevigatum* ("flush") (Huntley, 1971).

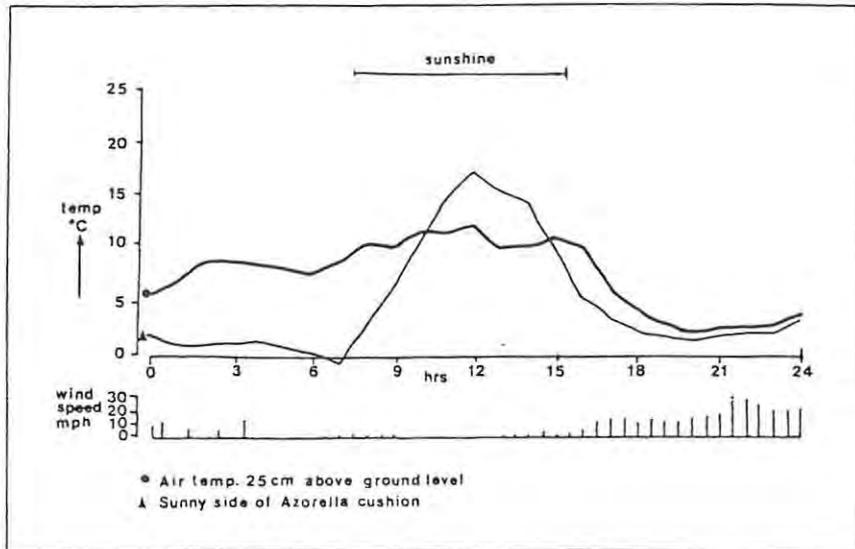


Figure 2.10 Diurnal temperature range in *Azorella* (fellfield)(Huntley, 1971).

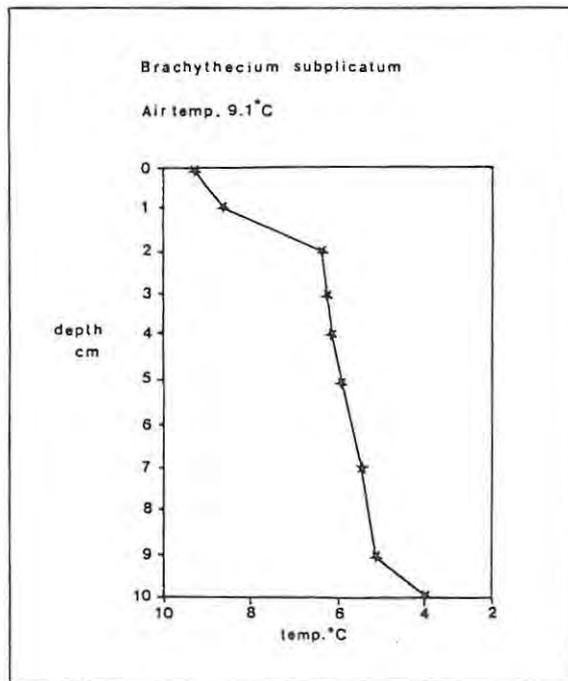


Figure 2.11 Curve of temperature with depth in a tall turf of *Brachythecium subplicatum* (drainage line)(V Smith, 1985).

Acaena magellanica. This compared with a 15°C variation in air temperature during the same 24 hour period.

A very constant temperature in relation to air values, was also maintained by waterlogged Bryum laevigatum which was subject to continuous flushing with cold water at a spring site. Exposed cushions of Azorella (an umbelliferous flowering plant that is co-dominant in the fellfield habitat with the large cushion-forming moss Ditrichum stictum) showed a large diurnal temperature range of 20°C in response to heating by the sun. This compared with a 10°C air temperature range during the same 24 hour period.

Radiative heating to above air temperature and a fairly broad diurnal range, was shown by Drepanocladus uncinatus and Blepharidophyllum densifolium from two mire sites. At only 2cm depth however, the thermistors were probably placed above the saturated zone in which the bulk of bryophyte tissue occurs in this habitat.

When studying Brachythecium subplicatum in drainage lines at Marion Island, V Smith (1987) found that temperature decreased rapidly in the first 2cm of the moss layer (down to the water table) and then decreased only slowly down through the remainder of the waterlogged layer (Figure 2.). The author has also taken incidental measurements of temperature in a turf of the same species during the two week, midsummer study of nitrogen fixation referred to earlier. It was found that moss temperature at approximately 3cm depth remained constant between 4-10°C (max. 12°C) during daylight hours, even

during periods When air temperatures could rose as high as 22°C.

In general therefore, microclimate temperature conditions at even shallow depths in hydric moss turves at Marion Island probably remain relatively constant and always above the 0°C threshold. However, significant temperature variation might be expected in exposed habitats and where the effect of the sun's heating interacts with varied microsite hydrology at the surface of bryophyte colonies that show an irregular microtopography.

2.7 Summary

Marion Island shows the overall climatic characters of the sub-Antarctic zone viz: strong winds due to the island's unobstructed oceanic fetch, almost continuous cloud cover and high humidity with very high levels of precipitation. Low average temperatures with small diurnal and seasonal variations occur, but with the mean monthly value remaining above °C throughout the year. Implications of these macroclimatic parameters for vegetation development at Marion Island are discussed in the next chapter.

CHAPTER THREE

BIOTIC ENVIRONMENT**3.1 Climatic influences and ecological zonation of the Antarctic region:**

The southern sub-polar regions have been zoned according to various criteria e.g. oceanographic (Deacon, 1960); climatic (Holdgate, 1964); zoological (Gressitt, 1970) and botanical (Wace, 1965). Holdgate (1964) differentiated the sub-Antarctic from his temperate zone on the basis of the latter having mean annual temperatures lower than 8.5°C, i.e. the threshold above which woody vegetation could be expected to develop. Wace (1960) also arranged the islands of the southern ocean according to a temperature gradient, but stressed aspects of the island's vegetation physiognomy in his zonal scheme.

The vegetation of Marion Island was poorly known at that stage and Wace initially included the Prince Edward group in his southern temperate zone (although the group's vegetational characteristics fitted his own definition of the sub-Antarctic zone). Greene & Greene (1963) corrected this (without explanation) in their paper on the vascular flora of the Antarctic regions, and Wace confirmed this improved scheme in his 1965 publication which also dealt with the vascular plants.

Refined systems which have re-emphasized climatic criteria in addition to the vegetation structural aspects, followed the early schemes e.g. Holdgate (1970,1977); R Smith (1984). The latter scheme is most appropriate for Antarctic studies (Table 3.1), while the

Table 3.1 Geobotanical regions of the sub-Antarctic and Antarctic (from R Smith, 1984).

Region	Province	Climatic features	Biotic features	Localities
Sub-Antarctic	South Atlantic Ocean South Pacific Ocean South Indian Ocean	Cool oceanic climate, small annual air temperature range, annual mean above 0°C; mean monthly temperature above freezing for at least 6 months, coldest month rarely below -2°C; precipitation over 90 cm per annum.	Tundra-like vegetation from the southern limit of arborescent vegetation southwards to the southern limit of extensive closed phanerogamic communities; vascular plants dominate vegetation near sea level; high proportion of pteridophytes. Abundant sea bird and marine mammal fauna; some land birds and many higher insects, also spiders, molluscs and earthworms.	South Georgia (South Atlantic province); Macquarie Island (South Pacific province); Marion and Prince Edward Islands, Heard and McDonald Islands, Îles Crozet, Îles Kerguelen (South Indian Ocean province).
Maritime Antarctic	Northern	Cold moist maritime climate, mean monthly temperatures exceed 0°C for 3-4 months in summer, but rarely fall below -10°C in winter; precipitation 35-50 cm per annum with much falling as rain in summer.	Semi-desert dominated by cryptogams but including small closed stands of the only two phanerogams in the Antarctic, locally diverse vegetation near coast; mosses form closed stands in wetter habitats locally accumulating peat, lichens predominate in exposed situations and inland; liverworts frequent. Snow algae and macrofungi frequent in summer. Abundant marine bird and mammal fauna; substantial invertebrate fauna dominated by mites and springtails and including the only higher insects (Diptera) in the Antarctic.	South Sandwich, South Orkney, South Shetland Islands, west coast of Antarctic Peninsula and offshore islands to c. 66°S; also Bouvetøya.
	Southern	Cold dry maritime climate, mean monthly temperatures exceed 0°C for 1-2 months in summer but rarely fall below -15°C in winter; precipitation 35 cm or less water equivalent; occasional rain.	As for Northern Province but cryptogamic diversity less and closed stands restricted in area; two phanerogams not infrequent to 68°S; liverworts, macrofungi and Diptera rare; no accumulation of moss peat.	West coast of Antarctic Peninsula and offshore islands from c. 66-70°S; also north-east coast of Peninsula to c. 63°S.
Continental Antarctic	Coastal	Cold arid climate, mean monthly temperatures exceed 0°C for 0-1 month in summer; winter means from -5 to -25°C, but some maritime influence narrowing temperature range; precipitation above 10-15 cm water equivalent. Rain very rare.	Semi-desert with moss and alga vegetation present on ahumic soil but restricted in species and extent; lichens numerous and locally form extensive stands; snow algae occasional in some localities. Invertebrates locally abundant and diverse. Seabird colonies frequent and large; marine mammals abundant (mainly offshore).	Coastal fringe of Greater Antarctica, and Lesser Antarctica south of 70°S, and on east coast of Antarctic Peninsula south of c. 63°S; includes ablation areas (dry valleys and oases); also Peter I Øy, Balleny and Scott Islands.
	Slope	Cold and more continental climate, all mean monthly temperatures below -5°C, low winter temperatures; precipitation c. 10 cm water equivalent, no rain.	Desert with mainly open very discontinuous lichen vegetation; occasional moss patches near rare snow and Antarctic petrel colonies and other favourable oases. Some mites, springtails and other invertebrates.	Mountain and glacier zone inland from coast encircling the central ice plateau; includes isolated nunataks in plateau.
	Ice Plateau	Extreme continental conditions, all mean monthly temperatures below -15°C, falling well below -30°C in winter; slight precipitation.	No life besides occasional microorganisms and stray birds.	Interior of the continent, generally above 2000 m altitude.

recent compilation of Longton (1988) successfully integrates some basic characteristics of northern and southern zones into a single scheme (Table 3.2).

The sub-Antarctic has thus been defined as the region beyond the southern limit of woody vegetation and extending to the limit of extensive closed communities of flowering plants cease to occur. These communities include herbfield in which large leaved perennials are common, and tussock grass communities. Fellfield vegetation with cushion forming vascular plants is also characteristic and mires dominated by bryophytes and rushes occur, rather than the Sphagnum cushion bogs more typical of islands in the temperate zone to the north.

Marion Island classifies in the sub-Antarctic zone of most authors based on vegetation criteria such as those stated above. However, its northerly geographic position and distance from the Antarctic convergence give it temperatures (e.g. a mean of 8°C in midsummer) which align the island with several vegetationally temperate localities. Godley (1960) intimated that similar temperatures experienced by parts of the related Magellanic Moorland of southern South America, would not be limiting for tree growth.

The simplified scheme of Longton (1988) referred to above, substantially improves upon the efforts of previous northern hemisphere-based authors in relating polar ecological zones in both hemispheres (e.g. Aleksandrova, 1980; Bliss, 1981). Longton's scheme is founded on broad features of vegetation physiognomy with temperature criteria also considered. Marion Island occupies a somewhat ambiguous position according to the

Table 3.2 Vegetation zones in polar regions (from Longton, 1988).

<i>Vegetation zones in polar regions</i>				
Zone	Approximately corresponding zones of previous authors		Highest mean monthly air temperature (°C)	Characteristics of the vegetation
	Arctic	Antarctic		
Mild-polar	Low-Arctic (B, P). Part of the mid-Arctic (P). Sub-Arctic tundra subregion (A)	Those parts of the southern temperate region lacking arboreal vegetation (G, W)	6-10 (to 12)	Extension grass heath, dwarf shrub heath, mire and other closed phanerogamic vegetation. <i>Sphagnum</i> abundant in many mires, though local in the mild-Antarctic. Fellfields on the drier uplands.
Cool-polar	Most of the high-Arctic (B, P). Part of the mid-Arctic (P). Arctic tundra subregion (A)	Sub-Antarctic zone (G)	3-7	Open fellfields and barrens predominant but mire, dry meadow and other closed angiosperm-dominated communities locally extensive in favourable habitats. Dwarf shrub heaths of restricted occurrence or absent. <i>Sphagnum</i> seldom a major component of mires.
Cold-polar	Parts of the high-Arctic (B, P). Arctic polar desert region (A)	Maritime Antarctic (H). Low-Antarctic (W)	0-2	Closed stands of bryophytes, lichens or algae extensive where wet or mesic conditions occur, with open cryptogamic vegetation on drier ground. Herbaceous phanerogams subordinate to cryptogams or absent. Liverworts frequent. Vegetation largely restricted to scattered colonies of mosses, lichens or algae, and to endolithic microorganisms. Phanerogams absent. Liverworts very rare.
Frigid-polar	—	Continental Antarctic (H)	<0	

A = Aleksandrova (1980)
 B = Bliss (1979)
 G = Greene (1964)
 H = Holdgate (1964b)
 P = Polunin (1951)
 W = Wace (1965)

secondary temperature criterion of this scheme, being classed as mild Antarctic (equivalent to the "southern temperate zone" of earlier authors). However, Longton recognises the problem of the "warmer" yet treeless southern sites such as Marion Island, the Magellanic Moorland and the Falkland Islands.

The oceanic influence may preclude the occurrence of mean subzero temperatures and thus long periods of snow cover and frozen ground at Marion Island; but the proximity of the Antarctic convergence ensures a uniformly low, year round temperature by southern South American standards. Coupled with the little studied, but probably severe effects of wind chill, this factor contributes to the lack of tree growth, and prevalence of fellfield habitats that denote the island's more Antarctic aspect and thus sub-Antarctic classification.

3.2 Floristics

The depauperate nature of Marion Island's flora has been noted since the time of the earliest visitors to Marion Island. In December 1776, Captain James Cook sailed between Marion and Prince Edward Islands while on his third voyage of exploration, in the ships "Resolution" and "Discovery". Notes from his journal and that of his first mate Lieutenant Anderson, include the following observations: "On the 12th, at noon, we saw land extending from SE. by S to SE by E. Upon a nearer approach, we found it to be two islands... We passed through [a] channel at equal distance from both islands, and could not discover, with the assistance of our best glasses either tree or shrub on either of them.

They seemed to have a rocky and bold shore, and excepting the south east parts, where the land is rather low and flat, a surface composed of barren mountains, which rise to a considerable height, and whose summits and sides were covered with snow, which in many places seemed to be of considerable depth. The ground, where it was not hid by the snow, from the various shades it exhibited, may be supposed to be covered with moss, or, perhaps such a coarse grass as is found in some parts of Falkland's Islands" (Beaglehole, 1967).

Notwithstanding the frequency of sealing visits to Marion Island in the nineteenth century, there is only one record of a scientific visit to the island before 1939. Members of Sir James Clarke Ross's "Erebus" and "Terror" expedition (including the botanist J.D. Hooker) had failed in their attempts to land in 1840; and so H.M. Moseley, naturalist with the "Challenger" expedition of 1873 became the first scientist to make botanical collections at Marion Island.

Plants were again collected during the visit by members of the "Bougainville" expedition in 1939, and in greater quantities following the establishment of the meteorological station at the island in 1948. R.W. Rand made a fairly extensive plant collection during a mainly zoological survey in 1951-52 and Professor E.M. van Zinderen Bakker made a small botanical collection during a short visit in 1963, in preparation for the 1965-66 Biological Geological expedition to Marion Island (van Zinderen Bakker et al, 1971). This expedition saw the first fully detailed investigation of the island's flora and fauna (Huntley, 1971).

With the development of the Marion Island bioenergetics and mineral cycling programme during the 1970s, a phytosociological study of the island's vegetation was carried out by Gremmen (1981), which represents one of the most detailed studies of polar vegetation ever undertaken.

3.2.1 Vascular plants

Smith and French (1988) note that oceanicity and geographical isolation lead to species poverty, and the overwhelming importance of bryophytes in the vegetation of sub-Antarctic islands. It has been suggested by Pisano (1983) that oceanically influenced climatic and edaphic factors alone may be sufficient to account for the abundance of bryophyte rich habitats in such "sub-Antarctic" environment e.g. the Magellanic Moorland of southern Chile, where isolation could be assumed to play a less important role.

However, the simple successional relationships, and success of invaders in the vegetation at Marion Island (evidence for "unfilled niches"?), coupled with restricted diversity in the indigenous vascular flora, support geographical isolation as a major factor controlling colonization at the Prince Edward Islands. Recent geological origins and glaciation are also likely to have influenced the small size of the vascular flora at Marion Island, which comprises 24 indigenous species and 15 aliens (Table 3.3).

The species have their strongest biogeographical affinities with other island's of the "Kerguelen Province" (the Crozet group and Kerguelen Island) e.g. Poa cookii

Table 3.3 List of indigenous and alien vascular plant species recorded from the Prince Edward Islands (from Heymann et al, 1987).

INDIGENOUS VASCULAR SPECIES	ALIENS
Lycopodiaceae	<u>Restricted naturalised aliens</u>
<i>Lycopodium magellanicum</i> Sw	
<i>L. saururus</i> Lam	<i>Rumex acetosella</i>
Hymenophyllaceae	<i>Alopecurus australis</i>
<i>Hymenophyllum peltatum</i> (Poir) Desv	<i>Elytrigia repens</i>
Polypodiaceae	<i>Festuca rubra</i>
<i>Blechnum penna-marina</i> (Poir) Kuhn	<u>Transient aliens</u>
<i>Polystichum marionense</i> Alston & Schelpe	<i>Avena sativa</i>
<i>Grammitis kerguelensis</i> Tard	<i>Holcus lanatus</i>
<i>Elaphoglossum randii</i> Alston & Schelpe	<i>Hypocheiris radicata</i>
Potamogetonaceae	<i>Plantago lanceolata</i>
<i>Potamogeton</i> sp.	
Poaceae	<u>Widespread naturalised aliens</u>
<i>Agrostis magellanica</i> Lam	
<i>Poa cookii</i> Hook f	<i>Cerastium fontanum</i>
Cyperaceae	<i>Poa annua</i>
<i>Uncinia compacta</i> R Br	<i>Stellaria media</i>
Juncaceae	<i>Sagina apetala</i>
<i>Juncus scheuchzerioides</i> Gaud	<i>Agrostis stolonifera</i>
<i>Jeffusus</i> L	<i>Poa pratensis</i>
Portulacaceae	unidentified thistle
<i>Montia fontana</i> L	
Caryophyllaceae	
<i>Colobanthus kerguelensis</i> Hook f	
Brassicaceae	
<i>Pringlea antiscorbutica</i> R Br	
Crassulaceae	
<i>Crassula moschata</i> Forst f	
Rosaceae	
<i>Ac aena magellanica</i> Lam	
Callitrichaceae	
<i>Callitriche antarctica</i> Engelm	
Apiaceae	
<i>Azorella selago</i> Hook f	
Scrophulariaceae	
<i>Limosella australis</i> R Br	
Asteraceae	
<i>Cotula plumosa</i> Hook f	

(Skottsberg, 1960). They also show relationships with the flora of the southern tip of South America, and Gough Island (Gremmen, 1981). Several Marion Island species are found in Australia and New Zealand, but links with the southern African flora are almost non-existent. This emphasises the dominating influence of the circum-Antarctic westerly winds and ocean currents in controlling dispersal patterns in the sub-Antarctic flora.

3.2.2 Bryophytes

Plant collections made in 1873 by H.N. Moseley of the "Challenger" expedition included 30 species of bryophytes according to Mitten (1855a;1855b;1876;1877). Collections at BM and PRE, including some bryophytes, evidence the incidental collecting activities of members of the early meteorological teams after the weather station was set up at Marion Island in 1948. R.W. Rand's 1951-2 collections included Hepatics treated by Arnell (1953), and mosses which were studied by A.M. Norkett at the British Museum of Natural History (Van Zanten, 1971).

Van Zanten (1971) and Grolle (1971) reported on mosses and liverworts respectively, from the 1965-66 Biological/Geological expedition (collected mainly by E.M. van Zinderen Bakker and B. Huntley). During his (mid 70s) phytosociological study of approximately 500 relevees at Marion Island, Gremmen (1981) made a large collection of bryophytes, many of which were sent to Grolle and Van Zanten for determination.

The present author collected approximately 500 numbers, during the bryophyte production study in 1981-2. Most of these await critical study and are located in the

Table 3.4 List of mosses recorded from the Prince Edward Islands.

- Acrocladum auriculatum* (Mont.) Mitt.
Andreaea acuminata Mitt.
Andreaea acutifolia Hook. f. & Wils.
Andreaea gainii Card.
Andreaea regularis C. Muell.
Anisothecium hookeri (C. Muell.) Broth.
Bartramia patens Brid.
 var. *papillata* (Hook. f. & Wils.) Zant.
Blincha magellanica Schimp.
Brachythecium austro-salchrasum (C. Muell.) Par.
Brachythecium paradoxum (Hook. f. & Wils.) Jaeg.
Brachythecium rutabulum (Hedw.) B.S.G.
Brachythecium subplicatum (Hamp.) Jaeg.
Bretzia integrifolia (Tayl.) Jaeg.
Bretzia pendula (Sm.) Mitt.
Bryum amblyolepis Card.
Bryum argenteum Hedw.
Bryum dichotomum Hedw.
Bryum eatonii Mitt.
Bryum kerguelense Mitt.
Bryum larvigatum Hook. f. & Wils.
Campylopus arcticola Card. & Dix. = *purpureocaulis*
Campylopus cavifolius Mitt.
Campylopus clavatus (R. Brown) Wils.
Campylopus introflexus (Hedw.) Brid.
Campylopus polystichoides De Not.
Campylopus subnuens Kaal.
Catagonium politum (Hook. f. & Wils.) Broth.
Ceratodon cf. purpureus (Hedw.) Brid.
Cheilothea chilensis (Mont.) Broth.
 cf. *Cratoneuron filicinum* (Hedw.) Spruc.
Dicranoloma hillardieri (Brid.) Par.
Duranoweisia brevipes (C. Muell.) Card.
Duranoweisia breviseta Card.
Distichum capillaceum (Hedw.) B.S.G.
Distichophyllum fasciculatum Mitt.
Distichophyllum imbricatum Mitt.
Ditrichum conicum (Mont.) Mitt.
Ditrichum immersum Zant.
Ditrichum strictum (Hook. f. & Wils.) Mitt.
Drepanocladus aduncus (Hedw.) Warnst.
Drepanocladus uncinatus (Hedw.) Warnst.
Fripius apiculatus (Hook. f. & Wils.) Mitt.
Eustichia longirostris (Brid.) Brid.
Lunaria lava (Hook. f. & Wils.) Broth.
Grimmia kerguelensis Card.
Holodontium pumilum (Mitt.) Broth.

Hygroamblystegium filum (C. Muell.) Reim.
Hypnum cupressiforme Hedw.
Isopterygium pulchellum (Hedw.) Jaeg.
 var. *antarcticum* (Mitt.) Zant.
Leptodontium proliferum Herz.
Mielichhoferia campylocarpa (Hook. & Arnott) Mitt.
 var. *australis* (Hamp.) Zant.
Orithodontium lineare Schwaegr.
Orithricum crassifolium Hook. f. & Wils.
Philonotis cf. augustifolia Kaal.
Philonotis scabrifolia (Hook. f. & Wils.) Broth.
Philonotis tenuis (Tayl.) Jaeg.
Plagiothecium platyphyllum Moenk.
Pohlia albicans (Wahlenb.) Lindb.
Pohlia nutans (Hedw.) Lindb.
Polytrichum juniperinum Hedw.
Polytrichum piliferum Hedw.
Psilopilum cf. tristaniense Dix.
Ptychomnion ringianum Broth. & Kaal. = *densifolium*
Racomitrium crispulum (Hook. f. & Wils.) Hook. f. & Wils.
Racomitrium lanuginosum (Hedw.) Brid.
Schistidium falcatum (Hook. f. & Wils.) Zant.
Schistidium stylostegium (C. Muell.) Zant.
Tortula cf. gehebiaeopsis (C. Muell.) Broth.
Tortula cf. rubra Mitt.
Trematodon flexipes Mitt.
Willia austro-leucophaea (Besch.) Broth.
Verrucidens microcarpus (Mitt.) Zant.

author's personal herbarium. Other principal repositories for Marion Island bryophytes are:

The New York Botanical Garden ("Challenger" collections in Herb. Mitten); Stockholm (Arnell); the Bolus Herbarium, University of Cape Town (Arnell duplicates); the British Museum of Natural History (London); the Botanical Research Institute, Pretoria; and the University of the Orange Free State, Bloemfontein.

Gremmen (1981) lists 72 mosses and 36 hepatics for Marion Island, but predicts that more species will be discovered following intensive collecting. The present author has noted several genera, previously unrecorded at the island e.g. Fissidens and Thuidium, and a recent visit by Prof R.M. Schuster (University of Massachusetts, Amherst) has resulted in several new hepatic records.

A future comprehensive inventory will probably approach 150 species of bryophytes, compared to 24 indigenous vascular plants. This represents a relatively rich bryoflora when considering the small area, geographical isolation, geological youthfulness and ostensibly harsh environmental conditions of the habitat (more than 80% of the island's area is fellfield). A nomenclaturally updated species list, based largely on information in Gremmen (1981) is given in Table 3.4.

Phytogeographical information concerning Marion Island's bryoflora is difficult to collate due to problems of synonymy associated with piecemeal and uncoordinated studies of the bryofloras of the sub-Antarctic islands. In general however, the bryoflora

shows similar biogeographical affinities to those of the vascular flora. Ranges are predominantly circum-Antarctic, with strong representation in the Kerguelen Province and southern South America, but also with records from Australasia and to some extent from South Africa (Grolle, 1971; Van Zanten, 1971; Schuster, 1985).

The flora of the southern islands has fascinated biogeographers since the time of Darwin and Hooker, even though these investigators tended to have knowledge only of the depauperate vascular floras. The bryofloras of the southern islands on the other hand are relatively abundant and diverse, and offer greater scope for biogeographical analysis and investigation of dispersal patterns between the southern continents. There is a great need therefore, for exchange of specimens between the different research groups working at the sub-Antarctic islands, and the apportioning of critical taxa to specialists for study. This would accelerate the appearance of a more complete synthesis of phytogeographical information for the sub-Antarctic, that has been awaited by biogeographers for more than a century.

3.2.3 Lichens

Lichens are abundant at Marion Island, especially crustose forms, and approximately 50 species were recorded by Lindsay (1976a,b). Several papers on Marion Island lichen floristics have appeared more recently as a result of the 1982 collecting expedition by Prof A Henssen (Marburg) and Dr H Hertel (Staatsmuseum, Munchen). Examples are Henssen (1985a,b, 1986); Henssen & Budel (1984) and Henssen & Lumbsch (1985).

3.3 Vegetation

Strong relief and uneven topography interact with climatic factors to provide a wide range of habitats at Marion Island, ranging from exposed, barren fellfields, to well vegetated slopes protected from exposure to strong winds. Salt spray and biotic (animal) influences affect coastal sites and hydrological gradients lead to the development of complex spatial patterning and mosaic formation in the vegetation, especially at the extensive mire areas.

This pattern has been studied by Gremmen (1981) using the techniques of the "Zurich-Montpellier" school of vegetation scientists. Gremmen distinguished 42 plant communities at the level of association and sub-association, including several variants at the sociation and facies level. Due to the paucity of higher plants and their often wide ecological amplitude, diagnostic vascular species are few, and the communities thus described for Marion Island may be characterised by as few as a single species.

In large parts of the lowlands, mosses and liverworts play an important role and in the mires especially, communities are discerned on the basis of species composition in the bryophyte layer (Gremmen, 1983). The importance of bryophytes in the vegetation can be gauged by the nomenclature employed in Gremmen's system (Table 3.5).

The earlier scheme of Huntley (1971) is shown in Table 3.6. Both schemes recognise five major habitat vegetation "complexes" viz: Fellfield, slopes ("fernbrake"), mires,

Table 3.5 List of plant communities recognised at Marion Island (from Gremmen, 1982).

1. *Crassula moschata* complex
 - 1.1. *Cotula plumosae* - *Crassuletum moschatae*
 - i.1. a. *Crassula* - variant
 - b. intermediate variant
 - c. *Cotula* - variant
 - 1.2. *Crassulo moschatae* - *Clasmatocoleetum vermicularis*
 - 1.3. *Crassulo moschatae* - *Azorelletum selaginis*
(*Crassula* - *Racomitrium crispulum* mosaic)
2. *Callitriche antarctica* - *Poa cookii* complex
 - 2.1. *Montio fontanae* - *Callitrichetum antarcticae*
 - 2.1.1. *agrostietosum magellanicae*
 - 2.1.2. *typicum*
 - 2.1.2.a. *Montia fontana* variant
 - b. intermediate variant
 - c. *Callitriche antarctica* variant
 - 2.2. *Callitriche antarcticae* - *Poetum annuae*
 - 2.3. *Poa cookii* - *Cotuletum plumosae*
 - 2.4. *Montio fontanae* - *Clasmatocoleetum vermicularis*
 - 2.5. *Leptodontio proliferi* - *Poetum cookii*
 - 2.5.1. *inops*
 - 2.5.2. *brachythecietum rutabuli*
(*Poa cookii* - *Callitriche antarctica* mosaic)
3. *Acaena magellanica* - *Brachythecietum* complex
 - 3.1. *Brachythecietum subplicati*
 - 3.1.1. *philonotidetosum*
 - 3.1.2. *inops*
 - 3.1.3. *breutelietosum integrifoliae*
 - 3.2. *Acaeno magellanicae* - *Drepanocladetum wiciniati*
 - 3.2.1. *breutelietosum integrifoliae*
 - 3.2.2. *brachythecietosum rutabuli*
 - 3.3. *Acaeno magellanicae* - *Brachythecietum rutabuli*
 - 3.4. *Acaeno magellanicae* - *Agrostietum stoloniferae*
4. *Juncus scheuchzerioides* - *Blepharidophyllum densifolium* complex
 - 4.1. Community of *Juncus scheuchzerioides*
 - 4.1. a. *Campylopus clavatus* variant
 - b. *Ranunculus biternatus* variant
 - 4.2. *Juncus scheuchzerioides* - *Drepanocladetum wiciniati*
 - 4.2.1. *juncetosum scheuchzerioidis*
 - 4.2.2. *montietosum fontanae*
 - 4.2.3. *clasmatocoleetosum humilis*
 - 4.3. *Disticlophylletum fasciculati*
 - 4.4. *Blepharidophyllum densifolii* - *Clasmatocoleetum humilis*
 - 4.4.1. *ranunculetosum biternati*
 - 4.4.2. *clasmatocoleetosum humilis*
 - 4.4.3. *blechnetosum penna-marinae*
 - 4.5. *Uncinio compactae* - *Ptychomnietum ringicani*
 - 4.6. *Lycopodium magellanicum* - *Jamesonielletum coloratae*
 - 4.6.1. *ranunculetosum biternati*
 - 4.6.2. *catagonietosum politi*
(degradation stages of *Lycopodium* - *Jamesonielletum* and other mire communities)
 - 4.7. *Jamesonielletum grandiflorae*
 - 4.8. *Bryo laevigati* - *Breutelietum integrifoliae*
 - 4.8.1. *uncinietosum compactae*
 - 4.8.1.a. *Breutelia* - variant
 - b. *Riccardia* - variant
 - 4.8.2. *acaenetosum magellanicae*
5. *Blechnum penna-marina* complex
 - 5.1. *Isopterygio pulchelli* - *Blechnetum penna-marinae*
 - 5.1.1. *wicinietosum compactae*
 - 5.1.2. *brachythecietosum rutabuli*
 - 5.1.3. *typicum*
6. *Andreaea* - *Racomitrium crispulum* complex
 - 6.1. *Jungmannio coniflorae* - *Racomitrietum crispuli*
 - 6.2. *Andreaea acutifoliae* - *Racomitrietum crispuli*
 - 6.2.1. *hymenophylletosum*
 - 6.2.2. *hypnetosum cupressiformis*
7. other communities
 - 7.1. *sociation of Limosella australis*
 - 7.2. *sociation of Potamogeton spec.*
 - 7.3. *sociation of Azorella selago*
 - 7.4. *community of Azorella selago and Acaena magellanica*

Table 3.6 List of plant communities recognised at Marion Island (from Huntley, 1971).

Salt Spray Complex

1. *Tillaea moschata* halophytic herbfield.
2. *Cotula plumosa* herbfield.

Biotic Complex

3. *Poa cookii* tussock grassland.

Swamp Complex

4. *Blepharidophyllum densifolium* bog.
5. *Agrostis magellanica* mire.
6. *Acaena* – *Pringlea* spring.
7. *Bryum* – *Breutelia* flush.

Slope Complex

8. *Acaena adscendens* herbfield.
9. *Blechnum penna-marina* fernbrake.
10. *Azorella selago* herbfield.
11. *Azorella*-*Poa montane* herbfield.

Wind Desert Complex

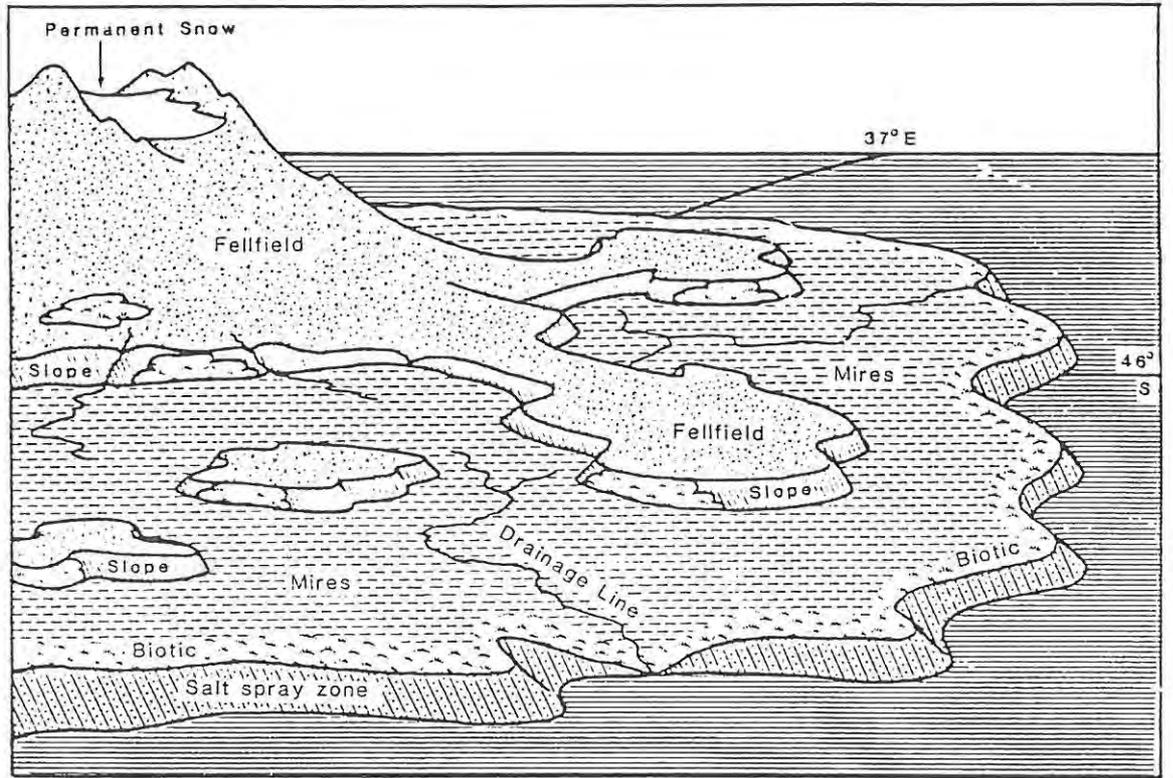
12. *Azorella selago* fjaeldmark.
13. *Ditrichum* – *Bartramia* montane desert.

biotic and salt spray zones, with a sixth (drainage lines) recognised at the complex level by Gremmen. A generalized diagram showing the relationship of these vegetation complexes to physiography at Marion Island is given in Figure 3.1.

Aerial mapping of these major vegetation complexes over the entire island's surface has not been possible to date, due to constraints of weather and logistics. Cloud cover has hampered satellite remote sensing and conventional aerial photography, but smaller scale studies have been carried out particularly on the eastern coastal plain. Data on community distribution in this area, gathered by V Smith (1976; 1977) from a transect survey, and from a portion of the eastern coastal zone (Burger pers. comm.) are shown in Table 3.7.

A detailed survey of the eastern coastal plain vegetation to the south of the meteorological station was undertaken at the time of the investigation into the proposal to site an emergency aircraft landing facility in this area (Heymann et al, 1987). The complexity of the vegetation mosaic in that locality is revealed by maps in the latter publication, even though communities were only mapped at a relatively coarse scale during that study.

Gremmen (1981) concluded that gradients of soil moisture (and related minerotrophy) most strongly controlled expression of pattern within the Marion Island vegetation complexes, and his major communities are shown arranged according to these parameters in Table 3.8. The fine scale at which this pattern occurs, is exemplified by



Key to shading of Vegetation Types

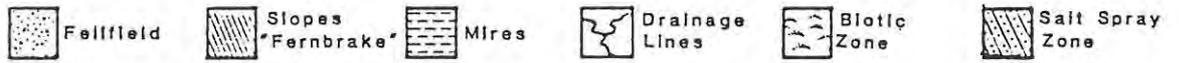


Figure 3.1 Habitat diagram of Marion Island, showing spatial relationships of the main plant community complexes.

Table 3.7

Percentage area of the Eastern Coastal Plain of Marion Island occupied by the major plant communities.
Data for 200m coastal strip from Burger (pers. comm.).
Data in lower right block from V Smith (1976, 1977c).

habitat complex	community	area of 200m coastal strip occupied (%)	complex	community	area of 200m coastal strip occupied (%)				
	Juncus bog	4		Callitriche/Poa	3				
	Drepanocladus/Agrostis mire	4	Biotic	Poa tussock	9				
	Blepharidophyllum/Agrostis mire	5		Clasmatocolea vermicularis/ Marchantia berteriana mire	3				
	Clasmatocolea humilis/ Agrostis mire	6		Cotula/Crassula	9				
mire	Jamesoniella colorata/ Agrostis mire	3	lowland fjaeldmark	Azorella/Andreaea	1				
	Mixed species mire	17							
	Agrostis/Ranunculus degenerated bog	2					Black lava area (%)	Grey lava area (%)	Eastern coastal plain
	Uncinia/Ptychomnium mire	11		fernbrake		18	0.04	13.15	
	Blechnum fernbrake	7	slope	open scrub		21.6	1.1	16.07	
slope	Acaena herbfield	6		Acaena drainage line		0.3	0	0.22	
	Agrostis bergiana grass.	2	biotic	Poa cookii/Azorella		1	0.43	1.5	
	Crassula flats	1		Poa tussock		0.6			
salt spray zone	Cotula/Crassula	2	mire	Agrostis mire		37.4	59	43.23	
	Mixed spray community with Azorella	5	fellfield	Azorella fellfield		20.9	39.3	25.9	

Table 3.8 Marion Island plant communities arranged according to their soil moisture characteristics. [from Gremmen, 1982]

Soil water content (%)	Communities of sites with no pronounced lateral water flow	Communities of sites with a pronounced lateral water flow
Open water	Comm. of <i>Juncus scheuchzerioides</i> (<i>Ranunculus</i> -variant)	Brachythecietum subplicati philonotidetosum
3000	Junco-Drepanocladetum juncetosum Junco-Drepanocladetum montietosum Junco-Drepanocladetum clasmatoceletosum	Brachythecietum subplicati inops Brachythecietum subplicati breutelietosum
2000	Distichophylletum fasciculati	Acaeno-Drepanocladetum breutelietosum
	Blepharidophyllo-Clasmatoceletum ranunculetosum	(Bryo-Breutelietum uncinietosum) (Bryo-Breutelietum acaenetosum)
	Blepharidophyllo-Clasmatoceletum clasmatoceletosum	
1000	Blepharidophyllo-Clasmatoceletum blechnetosum	Acaeno-Drepanocladetum brachythecietosum
	Lycopodio-Jamesonielletum ranunculetosum	
	Lycopodio-Jamesonielletum catagonietosum	
	Isopterygio-Blechnetum uncinietosum	Acaeno-Brachythecietum rutabuli
500	Isopterygio-Blechnetum brachythecietosum	Acaeno-Agrostietum stoloniferae
	Isopterygio-Blechnetum typicum	
	Community of <i>Azorella</i> and <i>Acaena</i> Sociation of <i>Azorella selago</i>	
	Jungermannio-Racomitrietum crispuli	
100	Andreaeo-Racomitrietum crispuli	

the vegetation zonation visible at mire margins, noted by Huntley (1971, Figure 20) and Gremmen (1981). Plate 3 and Figure 3.2 show an example of this occurring at one of the present author's study sites.

Cryptogams also play a large role in fellfield communities, especially at higher altitude where small liverworts and lichens may be the only vegetation able to survive in crevices and under stones on exposed hilltops. At lower altitude vascular plants such as the fern Blechnum penna-marina, become increasingly more important in fellfield, and the latter species combines with Acaena magellanica to form a well developed vascular vegetation cover on protected slopes. Bryophytes continue to form a large component of this vegetation however, with Brachythecium rutabulum for example, often forming a dense "understory" beneath the vascular stratum. There is also some evidence for invertebrate grazing of bryophytes in this most protected of Marion Island microhabitats.

At the coast, the influence of wind blown sea spray maintains a generally bryophyte-poor vegetation of salt tolerant plants e.g. Crassula moschata and Cotula plumosa. The Grimmiaceous moss Muelleriella crassifolia is however recorded growing on rocks just above the tidal zone as it does elsewhere in the sub-Antarctic; while the leafy liverwort Clasmatocolea vermicularis also occurs on salt spray-influenced cliff tops. This species also shows surprisingly high cover values at coastal sites that are strongly influenced by animal activity.

In general however, the salt spray and biotic complexes have only a small number of



Plate 3 Bryophyte zonation bordering a pool near to the meteorological station at Marion Island.

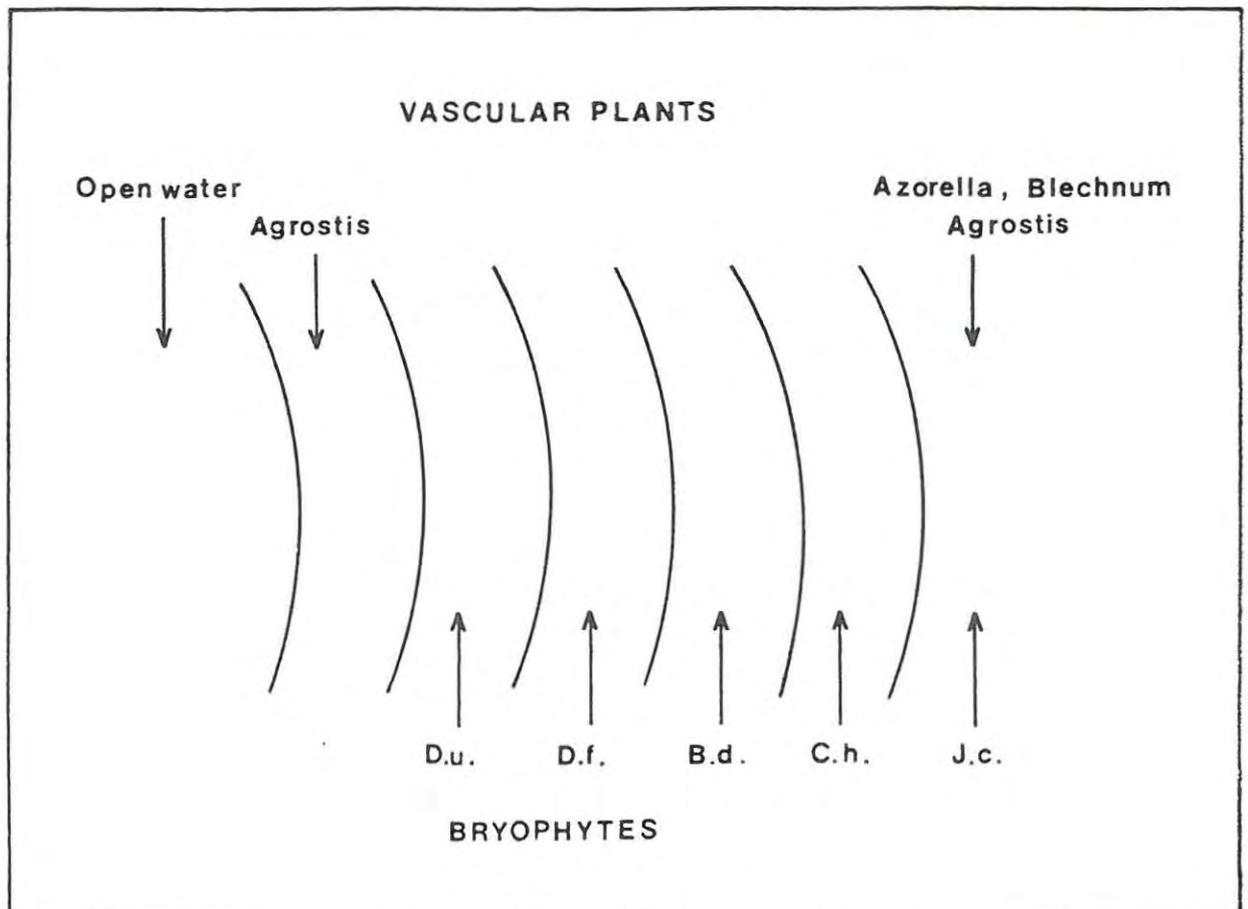


Figure 3.2

Diagram of bryophyte zonation shown in Plate 3.
Bryophyte sp. name abbreviations as in Table 4.1.

bryophytes and vascular plants that can withstand the manuring and trampling effects of the rich marine animal life that crowds ashore along the island's coastline (Elephant and Fur seals, Penguins and many other oceanic bird species).

During the first two months of the author's initial visit to Marion Island, much time was spent in reconnaissance of the vegetation, and in gaining knowledge of the pattern of distribution of natural communities over the island's surface. This was a necessary prelude to species and site selection during the ensuing bryophyte production study.

CHAPTER FOUR

BIOMASS AND PRODUCTION**4.1 Introduction**

At the primary producer level, biomass and growth (production) are acknowledged as fundamental characteristics of ecosystems which allow comparison between diverse sites, and are related to factors of importance to man, such as yield and carrying capacity.

The subject of the International Biological Programme of the late 1960s and early 1970s was defined as "The Biological Basis of Productivity and Human Welfare". Biomass and net production were therefore the primary factors studied by researchers at many tens of sites around the world during the IBP years.

One of the world's five major habitat types studied during the IBP, was the Tundra Biome. Representing approximately 6% of the earth's land surface, the tundra is the last and largest of the world's least explored and exploited ecosystems. Human pressure on this ecosystem is increasing however (Sugden, 1982), and therefore in relation to the IBP's objective as stated above, the Tundra Biome Project had as its first aim the measurement of net primary production in the main terrestrial ecosystems of the Arctic and Antarctic (Bliss 1981). For the purposes of the IBP studies, the concept of "tundra" included a range of high latitude and high altitude sites, "beyond the climatic limit of tree

growth" in both the northern and southern hemispheres (see Chapter 1).

The amount of bryophyte growth in a habitat can influence diverse ecological processes e.g. precipitation throughfall and mineral cycling. This is especially true where these plants form a significant component of the total biomass e.g. the forest floor stratum in northern coniferous "Taiga" woodland and the epiphyte synusium in montane, tropical forests. Knowledge of bryophyte production may also be of direct importance to man where mosses are harvested e.g. peat for energy and horticultural purposes.

Bryophytes attain their maximum relative importance in terms of biomass in the vegetation of the tundra biome, and they have come under pressure from harvesting in related habitats (e.g. oceanic moorland in NE Maine, USA and Ireland). Dahl & Gore (1968) and Heal (1971) therefore emphasized the need for measurement of bryophyte biomass and production during the IBP tundra studies.

High bryophyte biomass and production figures were also predicted in the sub-Antarctic zone, where two islands were studied during the IBP. Holdgate (1967) noted that there was at that time "negligible" information on rates of productivity of Antarctic bryophytes" and he stated that direct measurements of bryophyte production were therefore urgently needed in this zone.

However, notwithstanding the importance of bryophytes at tundra sites as revealed by

biomass studies, bryophyte production values were obtained from only approximately half of the IBP study sites. Unsuccessful attempts to extend some of the concepts of vascular plant production ecology to the bryophyte component of the vegetation, resulted in a range of incompatible and sometimes crude methods being used to measure bryophyte growth throughout the biome. Much of the information remained unpublished or distributed in reports with limited circulation.

In the overall project synthesis, Wielgolaski et al (1981) concluded that insufficient data and a lack of conformity in techniques, restricted the interpretation and comparison of results from the IBP bryophyte production investigations. They emphasised the need for improved methodology in future studies of bryophyte biomass and growth.

Following Holdgate's (1967) suggestions, several productivity studies were made in Antarctic bryophyte communities, especially in relation to the unique "moss banks" of the Antarctic peninsula and South Orkney Islands (Longton 1970; Baker 1972; Collins 1973, 1976, 1977; Collins & Callaghan 1980). As late as 1982 however, R Smith noted that there was "remarkably little information available [on bryophyte productivity] for the sub-Antarctic islands."

At the end of the 1970s the ecosystem programme at Marion Island had also reached the stage of requiring quantitative inputs concerning the contribution of bryophyte vegetation to biomass and primary production at the island. Gremmen et al (1975) had suggested

methods for measuring bryophyte growth at Marion Island, and V Smith had made a preliminary study of this aspect in the late 1970s. However, the sampling technique used in this study allowed only approximate estimates of bryophyte production for a few intermixed species (Smith 1985). The present author was therefore recruited to carry out an intensive investigation of bryophyte growth during the 1980-81 and 1981-82 expeditions to Marion Island.

The background to this study has been related in the introduction to the thesis, along with the rationale behind the bryophyte production investigation. The following chapter deals with the methodology and results of the bryophyte production study and is followed by separate chapters on the intrinsic and extrinsic factors hypothesized to correlate with growth. A short conclusion is therefore included in the present chapter, but with a fuller synthesis and conclusion being reserved until after the presentation of data from the ancillary investigations.

4.2 Methods

4.2.1 Selection of study species

For the purpose of this study, bryophytes were chosen that were likely to contribute the most significant quantities to vegetation biomass and production, and might therefore be of greatest importance to ecosystem functioning at Marion Island. Species were also chosen that would be representative of the broad range of vegetation types at the island.

i.e. from all six major vegetation complexes. Within the largest, and most bryophyte rich complex (mires), species were selected from the wet-dry gradient in order to further investigate Gremmen's (1981) proposal of soil moisture as the principal factor controlling vegetation pattern in this habitat. The bryophyte species studied here, listed by community (sub-association sensu Gremmen, 1981) and arranged according to a wet-dry gradient based on mean soil moisture contents, are given in Table 4.1.

Because of the wider questions of bryophyte ecophysiology that this study also hoped to address (Chapter 1), it was intended that a range of taxonomic types should be represented among the study species i.e. liverworts, and acrocarpous and pleurocarpous mosses; and that several different growth forms e.g. cushions, turfs, mats, wefts and carpets, would be included in the survey.

Little previous work had been done to indicate biomass values for specific bryophytes at Marion Island. Huntley (1972) and V Smith (1978) obtained biomass values of bulk bryophyte material (not sorted into species) for a limited number of sites on the Eastern Coastal Plain. During his extensive phytosociological study at Marion Island, Gremmen (1981) included the collection of cover/abundance, sociability and presence data for individual bryophyte species from nearly 500 relevées. This provided a useful basis for determining the relative importances of species for the production study.

Gremmen's phytosociological tables include approximately 60 bryophytes which act as

Table 4.1

List of bryophyte study species with the communities in which they occur, arranged on a soil moisture gradient. Species numbers and name abbreviations (left columns) apply throughout the thesis.

No	Species abbreviation	Species	Sub-Association	Soil water content (%)	Habitat
1	Bs	<i>Brachythecium subplicatum</i>	Brachythecietum subplicatum inops	2896	Drainage Line
2	Df	<i>Distichophyllum fasciculatum</i>	Distichophylletum fasciculati	2333	Mire Wet
3	Du	<i>Drepanocladus uncinatus</i>	Junco-Drepanocladetum clasmatocoleetosum	1882	Mire
4	Cp	<i>Campylopus purpureocaulis</i>	Blepharidophyllum-C'asmatocoleetosum Campylopus facies	1832	Mire
5	Bi	<i>Breutelia integrifolia</i>	Bry-Breutelietum uncinietosum Breutelia variant	1652	Mire
6	Pd	<i>Ptychomnium densifolium</i>	Uncinio-Ptychomnietum	1650	Mire
7	Ch	<i>C'asmatocolea humilis</i>	Blepharidophyllo-C'asmatocoleetosum clasmatocoleetosum	1633	Mire
8	Bd	<i>Blepharidophyllum densifolium</i>	Blepharidophyllo-C'asmatocoleetosum blechnetosum	1160	Mire
9	Jc	<i>Jamesoniella colorata</i>	Lycopodio-Jamesonielletum ranunculetosum	1041	Mire
10	Cg	<i>Cryptochila grandiflora</i>	Cryptochiletum grandiflorae	779	Mire
11	Rl	<i>Racomitrium lanuginosum</i>	Lycopodio-Jamesonielletum catagonietosum	770	Mire Dry
12	Br	<i>Brachythecium rutabulum</i>	Ispterygio-Blechnetum brachythecietosum	588	Slope
13	Ds	<i>Ditrichum strictum</i>	Andreaeo-Racomitrietum crispuli	85	Fellfield
14	Aa	<i>Andreaea acutifolia</i>	Andreaeo-Racomitrietum crispuli	85	Fellfield
15	Cv	<i>C'asmatocolea vermicularis</i>	Montio-C'asmatocoleetosum vermicularis	1081	Biotic/Salt Spray



Plate 4 *Brachytheticium subplicatum*. Tall turf-forming drainage line species showing one year's shoot extension growth.



Plate 5 Waterlogged mire habitat of *Distichophyllum fasciculatum*.

character species for his designated communities. Many of these show low cover values however. Taking all Gremmen's character bryophytes with a cover of greater than 25% provides a more manageable list of species, several of which are however of restricted occurrence and only attain high cover values locally. Further restricting the list to include only those character species with maximum cover on the Braun-Blanquet scale (>75%) and maximum presence (81-100% frequency of occurrence across all relevées) i.e. an index of "V5" in Gremmen's tables, gives a total of 14 potentially ecologically important species.

From this list, Riccardia multifida was omitted for reasons of its relatively restricted occurrence. Its thallose growth form and habit of occurring intricately intermixed with other species would also cause difficulties for growth measurement studies. Two other species were added to the list viz. the two dominant cushion-forming mosses of fellfield habitats which, although they rarely show high absolute cover values, still form the bulk of the vegetation cover at most fellfield sites on Marion Island.

The fifteen bryophyte species on which the main production study was based, are listed in Table 4.1. The list includes the two dominant mosses from fellfield habitats; the main species (Brachythecium rutabulum) that forms the bryophyte understory stratum in the slope complex; the single species (B. subplicatum) that consistently reaches high levels of cover in the drainage line habitat; ten species representing the range of soil moisture conditions in the mires complex including Breutelia integrifolia of minerotrophic flushes; and Clasmatocolea vermicularis, which frequently occurs with high levels of cover in both the salt spray and biotic zones.



Plate 6 The carpet forming moss - *Drepanocladus uncinatus*.

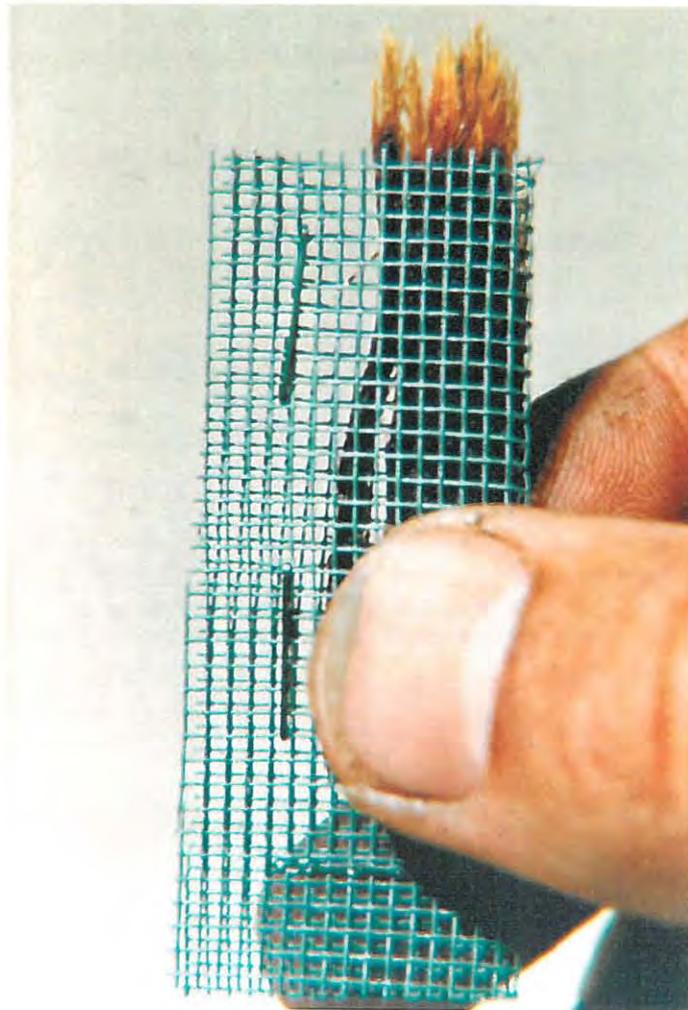


Plate 7 *Campylopus purpureocaulis* showing how stems are inserted into a nylon mesh bag for growth measurement purposes.

It was calculated that 15 study species would be a manageable number, given the logistic constraints of monthly growth measurements using a range of techniques. The spread of species included five Hepatics, five acrocarpous mosses and five pleurocarpous mosses.

Brief descriptions of the growth forms of the species identified according to the criteria of Gimingham & Birse (1957) and Gimingham & Smith (1971) are given below. Measures of average stem lengths for the study species, are given in the results (biomass) section (4.3). Photographs of some of these species and/or their habitats are reproduced in Plates 4-17.

Brachythecium subplicatum -

Bright yellow-green pleurocarpous moss of drainage line habitat, stems 2mm in diameter to 100mm long or more, condensed weft-like growth form at base, but with densely spaced erect shoots and fine vertical side branches giving tall turf appearance in the upper part of the colony i.e. the typical sub-Antarctic "carpet" growth form of Gimingham & Smith (1971).

Distichophyllum fasciculatum -

Pale yellow- or greyish-green pleurocarpous moss, weak and soft stems to 50mm long, 1-2mm diam.. short (2-3mm) spreading side branches, dense vertical stem spacing giving tall turf growth form in waterlogged mires.

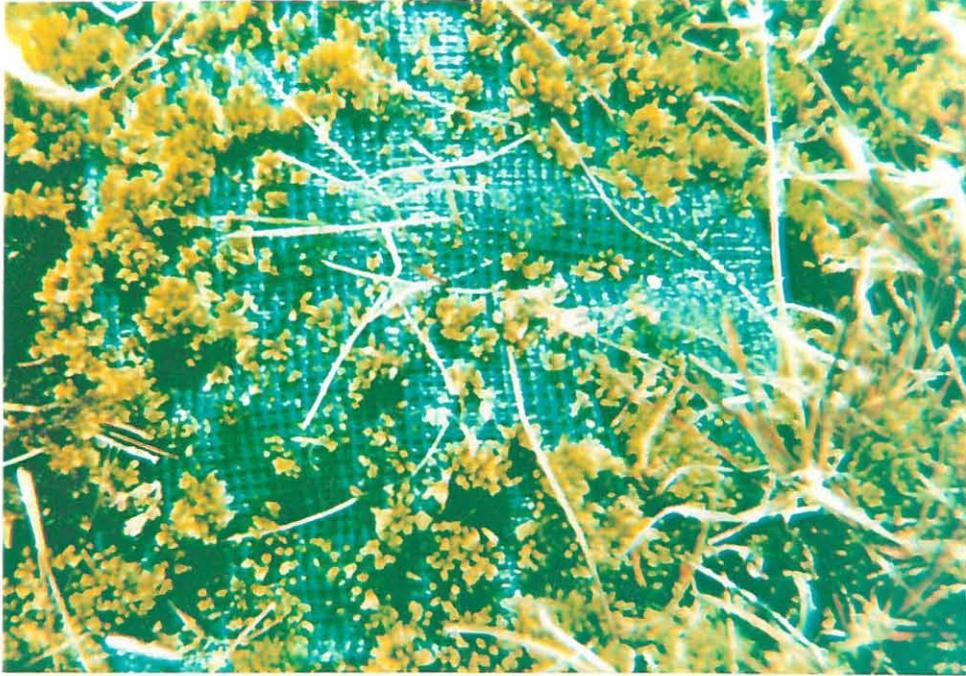


Plate 8 *Breutelia integrifolia* after several months growth through a net.



Plate 9 Clump of stems from a colony of *Ptychomnium densifolium* showing robust growth form.

Drepanocladus uncinatus -

Golden yellow to bright green (when wet) pleurocarpous moss, stems to 70mm, 1-2mm diam., characteristic falcato-secund leaves, spreading side branches, weakly straggling weft-like growth form in drier hummocks, but condensation of stems with some vertical "carpet" growth in wet pools.

Campylopus purpureocaulis -

Yellowish green acrocarpous moss, rusty coloured below due to felt-like rhizoid tomentum, main stems stiff and fairly robust, to 100mm long, 3mm diam., dense vertical growth with many finer erect growing side branches to form tall turf. Seasonal variation in leaf length gives obscure segmented appearance to shoots.

Breutelia integrifolia -

Dark olive-green acrocarpous moss with rusty coloured rhizoid investiture below, robust stems to 100mm, 3mm diam., erect growth to form tall turf form, regular seasonal branching from a single point to give bunched appearance of (at first) finer side branches, which may continue vertical growth to overtop the main stems.

Ptychomnion densifolium -

Pale yellow pleurocarpous moss, very robust stems to 50mm long and 4mm diam., large squarrose leaves, irregular branching but predominantly erect growth to form lax tall turf in non-waterlogged mires.



Plate 10

Blepharidophyllum densifolium.

Plate 11

Jamesoniella colorata, showing closely appressed and imbricate leaf arrangement.

Clasmatocolea humilis -

Bright green leafy Hepatic, stems 20-30mm long and 1mm diam., irregularly branched vertical growth from mat-like basal system to form short to tall turf.

Blepharidophyllum densifolium -

Reddish brown leafy Hepatic, fairly robust stems to 50mm by 2mm diam., characteristic conduplicate and reflexed leaves, stems frequently and irregularly branched with dense vertical growth to form tall turf, but mat-like when poorly developed.

Jamesoniella colorata -

Orange/reddish brown leafy Hepatic, fine vermiform stems to 50mm, 0.5-1mm diam., mat-like at first but with irregular vertical branching to form short to tall turf.

Cryptochila grandiflora -

Blackish brown leafy hepatic, stems as for Jamesoniella but to 30mm by 0.5-1mm. Short to tall turf.

Racomitrium lanuginosum -

Hoary grey to dark green when wet, "pseudo-pleurocarpous" moss, robust stems to 100mm by 4mm diam., frequently and regularly branched, branches of limited growth, forming large cushions in drier areas but with vertical growth from a weft-like basal system to form a lax carpet in wet habitats. In places the colony may be deep (> 20cm) and preserve many years of growth due to low decomposition (Plate 18).



Plate 12 Turf of *Cryptochila grandiflora* after coring.



Plate 13 Growth plot of *Racomitrium lanuginosum* (dry mire).



Plate 14 Growth plot of *Brachythecium rutabulum* (slope complex).



Plate 15 Growth plot of *Andreaea acutifolia* and *Ditrichum strictum* (lowland fellfield).

Ditrichum strictum -

Dark olive green above to reddish brown below (rhizoids), acrocarpous moss, stems to 50mm by 1-2mm diam. when dry, densely packed vertical stem growth including fairly frequent vertical branches, to form large cushions. Faint seasonal leaf size variation to give annual "banding" in cushion sections.

Andreaea acutifolia -

Brown-black acrocarpous moss, stems fine, 5-10mm long by <0.5mm diam. when dry. Sparingly branched to give compact vertical growth in small to large cushions.

Clasmatocolea vermicularis -

Pale (often whitish) green leafy hepatic, fine weak stems to 20mm by <0.5mm. Sparingly branched from mat-like basal system to give vertical growth in short or occasionally tall turf form. It is difficult to identify C. vermicularis in the field, and to distinguish it from its close relative C. humilis in hand specimen (both species often occur together on the Eastern Coastal Plain at Marion Island). At the end of the first year's growth measurement study it was found on close examination that the growth plot set out in a stand of vegetation dominated by C. vermicularis had a considerable admixture of C. humilis. A new plot was therefore set up for C. vermicularis during the second year's growth measurements 1981-82, and no data are therefore included for this species in the tables of results for the summer 1980-81 six month growth study.

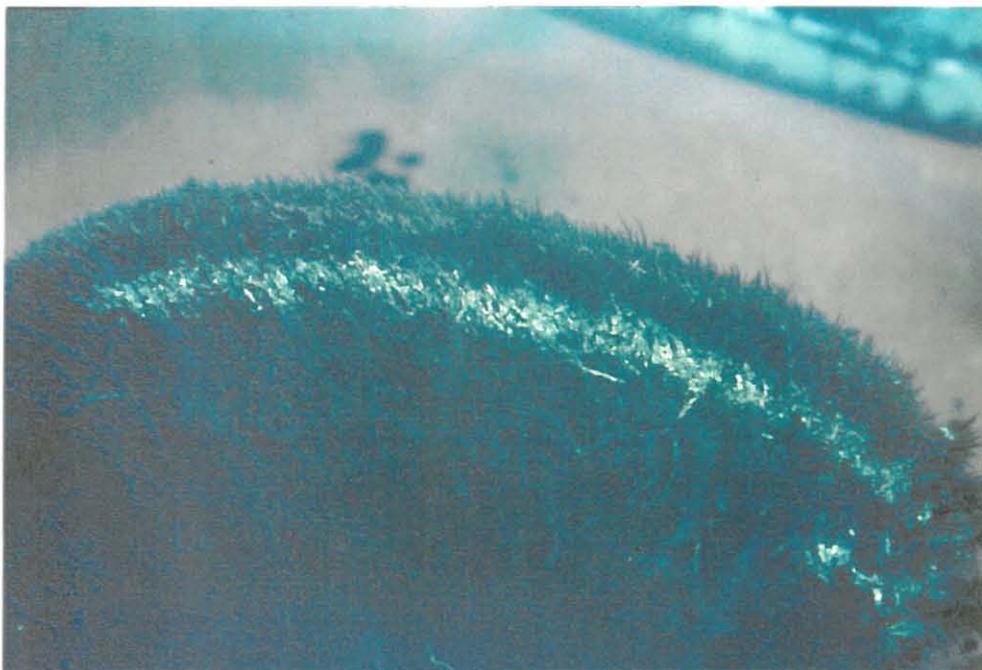


Plate 16

Cross section of *Ditrichum strictum* cushion photographed under ultra-violet light to show year old band of staining by the fluorescent compound "Blancophor".



Plate 17

Clasmatocolea vermicularis of the biotic/salt spray zone.



Plate 18

Cross section of deep and well preserved turf of *Racomitrium lanuginosum*, showing many previous year's stem and branch growth.

4.2.2 Selection of study sites

Representative sites for the situation of growth plots for the 15 study species were sought during the first two months reconnaissance programme in 1980. Study sites were selected to satisfy the requirement of high levels of bryophyte cover (>75%), but which were typical of the naturally occurring communities recognised by Gremmen (1981). It was also necessary that small areas of the study species should occur within the plot at 100% cover, to satisfy the requirements of some of the sampling procedures. The sites were also chosen as far as possible, to have a typical representation of associated bryophyte and vascular plant species for the community concerned.

In practice the sites often included virtually monospecific stands of the species under study, that extended for many square metres. By comparison with representative stands of bryophyte communities in other temperate and tropical localities, the existence of such "pure" stands is unusual. At Marion Island however, as at other southern sub-polar sites, such stands are typical (R. Smith 1982). The combination of a varied microenvironment and depauperate flora has resulted in a broad range of communities but with relatively few component species. The same species may therefore occur repeatedly, in differing relative and characteristic combinations in the different communities, or as in the mire complex, a single species may come to dominate large areas of the ground surface on its own.

The sampling design suffers from the same constraints as the phytosociological approach on which species selection was based i.e. that only "homogeneous" stands of vegetation

were selected for the growth studies. This is of less concern for the reasons just stated. The approach does however tend to make the results of lesser significance for areas of intermediate or transitional vegetation, although this drawback is also offset by the fact that Gremmen defined communities at a very fine level (e.g. sociations and facies), and these communities regularly occur as a mosaic rather than in extensive areas of clinal vegetation at Marion Island.

An additional criterion applied during site selection was that the stand should be extensive enough at a single site (several square metres) to allow convenient application of all the growth measurement methods in a single subdivided plot with buffer zones between each treatment. Also, the sites were selected as far as possible within easy reach of the base station to allow regular visits to all 15 plots. This would facilitate measurement of monthly stem increments while allowing time for additional ecophysiological experiments that were being conducted during the same period.

After arrival at Marion Island in September 1980, study plots were located and marked out at the end of October, thereby allowing for an initial six month summer growth trial to test methodology in preparation for the 1981-2, full year's measurement period. Location of the study plots is indicated in Figure 4.1. Plots varied in size from 12 to 90m² in extent according to the scale and pattern of the vegetation being studied. The area was roped off and smaller growth study plots were marked out within this area for each measurement technique that was to be applied. The size of the small plots also varied according to the measurement method being used.

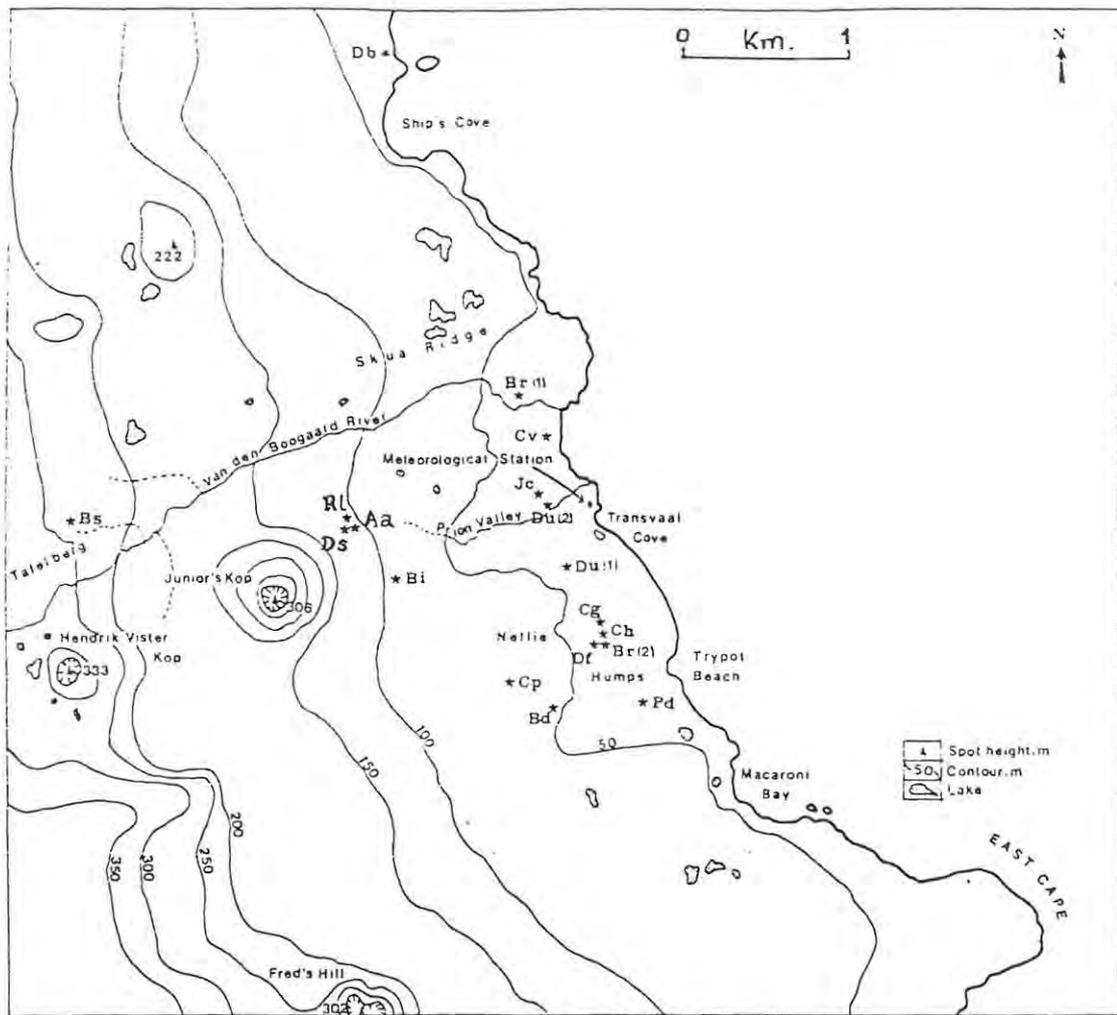


Figure 4.1

Map showing location of bryophyte growth plots on the Eastern Coastal Plain of Marion Island.

* = Growth plot. Species name abbreviations as for Table 4.1.

A survey was undertaken at each site to collect basic ecological data e.g. altitude, aspect, slope, depth of water table below the vegetation surface, soil water content, pH and temperature at time of sampling, and height and cover of vascular and bryophyte vegetation. Cover/abundance according to the Braun-Blanquet scale (Table 4.2) was also scored for all species in the plot in order to determine the community classification for the site according to Gremmen (1981). Other species occurring at or near to the plot were also recorded for the same reason. The site descriptions including ecological data for each plot, are set out in Appendix 1.

Most sites were situated in the mosaic of slope and mire communities on the Eastern coastal plain below 100m asl and within approximately 1.5km of the base station. Exceptions were the drainage line study site (Brachythecium subplicatum) which was in a protected valley 4km from the base and situated at 210m asl; and the fellfield study site which was 2km inland from the meteorological station and at a little over 100m asl. Growth plots for Ditrichum strictum, Andreaea acutifolia and Racomitrium lanuginosum were laid out at the fellfield site. Floristic data from the first two of these sites (see Appendices A12 & A13) show them to be more typical of the higher altitude fellfields represented in the island's interior (Gremmen, 1981) than the lowland fellfields of the coastal plain. On a phytosociological basis, the Racomitrium lanuginosum plot turned out to be more closely related to the "dry end" of the series of communities in the mire complex as defined by Gremmen (1981).

The Brachythecium rutabulum plot was situated at the base of a protected slope in the

Table 4.2 The Braun-Blanquet cover-abundance scale.

r	one or a few individuals, covering less than 5% of total plot area
+	occasional and covering less than 5% of total plot area
1	abundant and covering less than 5% of total plot area
2m	very abundant, covering less than 5% of total plot area
2a	covering 5-12% of total plot area, irrespective of number of individuals
2b	covering 12.5-25% of total plot area, irrespective of number of individuals
3	covering 25-50% of total plot area, irrespective of number of individuals
4	covering 50-75% of total plot area, irrespective of number of individuals
5	covering 75-100% of total plot area, irrespective of number of individuals

Nellie Humps area (Figure 4.1) and was selected to be representative of the slope ("fernbrake") complex. This plot appeared intermediate in some respects, showing some characteristics of the biotic complex (e.g. proximity to the sea and high presence of the tussock grass Poa cookii), yet having a percentage cover of Brachythecium rutabulum that was more typical of the Acaena-Brachythecium drainage line complex. However, several other features, including the presence of character species such as Plagiothecium platyphyllum, justified the retention of the community as a representative of the slope complex.

At the end of the six month study in the Drepanocladus uncinatus growth plot, areas of the bryophyte carpet had altered their position with respect to the water table as measured at the beginning of the study. Most of the bryophyte shoots for this species were measured at positions intermediate between depressed and saturated green portions of the carpet, and drier, yellowing crests of hummocks on the colony surface. At the end of the six month period, almost the entire surface of the area being studied had dried out, and stem length increments decreased radically. This situation was atypical compared with other Drepanocladus uncinatus stands on the Eastern Coastal Plain at Marion Island which maintained larger areas of well hydrated carpet. As further surface area of normal carpet was not available at the same site therefore, another growth plot was selected for this species for the second year's study.

4.2.3 Theory behind growth measurement methodology

Methods for the measurement of bryophyte growth can be classified into two major categories:

1. Biomass or "Harvest" Techniques
2. Gas exchange techniques

Gas exchange techniques allow "instantaneous" measures of photosynthesis and respiration which can be related to dry matter production in the short term, using accepted conversion factors (Sestak et al, 1971). Measurement of gas exchange can give a precise indication of plant photosynthetic response to a range of environmental factors and, through the quantification of the respiratory component, allows the determination of gross production also. Following the recent availability of lightweight portable equipment that is relatively easy to operate in the field, there is likely to be an expansion in the use of this methodology.

However, the extrapolation of gas exchange measurements of productivity to the prediction of long term dry matter accumulation can be unreliable due to the unknown interactions of microclimatic variables, nutrient levels etc., with plant physiological processes that vary seasonally (Whittaker & Marks, 1975) . Extrapolation of gas exchange measurements may therefore only be feasible where good long term microclimatic data are available (an expensive and seldom met criterion in such research). Some success has been achieved using simulation techniques however

(Collins, 1977; Oechel & Sveinbjornsson, 1978; Collins & Callaghan, 1980; Davis & Harrison, 1981; Davis, 1983).

Preliminary investigations of photosynthetic gas exchange in five Marion Island bryophyte species were undertaken by the author and Prof. G.C. Bate (University of Port Elizabeth) in 1982. The results of this study indicated that Marion Island bryophytes show rates of photosynthesis closely equivalent to those recorded at other sites in the tundra biome (Arctic). In the absence of comprehensive microclimate data however, the results of the photosynthetic study were not comprehensive enough to allow prediction of annual production quantities. The results of the study did confirm however, that there is nothing unusual about the responses of these sub-Antarctic plants to environmental conditions (as suggested by Wielgolaski et al (1981) when accounting for the "exceptionally high" plant production in this region). The same authors went on to suggest that the longer growing season in the sub-Antarctic was a more feasible explanation for this phenomenon, and the same conclusion was reached by V Smith (1985) after detailed production/bioenergetics studies of Marion Island compared with other sub-Antarctic islands and tundra sites in general.

Biomass techniques usually involve harvesting over extended periods of time, and allow integration of the effects of environmental and physiological variables on a seasonal or annual basis. Also, certain biomass techniques may more readily take account of changes over large areas of vegetation, compared with the few individual plants that are usually studied using gas exchange cuvette techniques.

Growth can be expressed as:

$$P_n = \Delta B + L + G$$

where P_n = net primary production between times t_1 and t_2
 ΔB = change in quantity of plant (living biomass) from t_1 to t_2
 L = losses by death and shedding (includes decomposition, leaching and exudates) from t_1 to t_2
 G = losses by grazing/herbivory (primary consumption) from t_1 to t_2
 (Milner & Hughes 1968, Newbould, 1967)

The change in biomass (ΔB) can be measured by the "direct" method of harvesting the entire biomass from a sample area for comparison with a similar (often adjacent) sample at a later date. The difference in dry weights of the samples will represent net production for the experimental period (or decomposition in the case of a negative value). Variability between samples can be great however and many samples of large areas of vegetation may be needed to ensure statistical confidence in the results. This is especially true where the difference between biomass values at the beginning and end of an experiment is slight due to the balancing of production by decomposition, as occurs in some stable vegetation formations that approach a "steady state".

Harvesting enough replicates of representatively large areas of the total bryophyte biomass may therefore be time consuming and problematical due to contamination with soil and other plant material for example. It can also be unjustifiably destructive to natural communities. "Indirect" methods are therefore often used, e.g. measuring the increase in stem length over a period of time, and converting this to a corresponding increase in

total biomass (expressed in g dry weight per m² of ground area). The spatial biomass increment for a given amount of shoot extension growth is found by subsampling the bryophyte colony to determine areal stem densities and shoot length:weight ratios. The latter measurement will also involve some "clipping" of plant material and both direct and indirect biomass measurement techniques have therefore been grouped under the heading "harvest" methods (Richards, 1959).

Problems with applying the above formula in studies of bryophyte growth centre on the concept of biomass in bryophytes, and methods for determining the contribution of L (principally decomposition) and G (consumption of plant production by herbivores). Many authors have defined biomass strictly as living plant tissue only (the term "necromass" is reserved for standing dead tissue, Cresswell, 1979).

Early workers partitioned bryophyte tissue into live and dead, based on the colour difference between "green" and "brown" tissue. In many bryophytes however, the green apical zone of active growth grades imperceptibly into the lower brown region, which frequently contains a preponderance of living, although inactive cells. Active translocation of photosynthate back into the brown, region of bryophyte stems has also been recorded (Collins & Oechel, 1974). This process would result in a decrease in apparent biomass production values in the current year's growth as measured by stem length increment methods.

Acropetal translocation of storage products from this "brown" region of the plant towards

the apex may also occur (Eschrich & Steiner, 1967). However, movement of such materials may occur in significant quantities only in mosses with an effective endohydric conducting system (Collins 1977).

Several studies have shown that protonemal or bud growth can occur from viable cells throughout a bryophyte colony profile. This can even occur in partially decomposed and humifying parts of a bryophyte turf (Longton, 1972). Pickard (1979) has therefore suggested the use of "vital" microscopic stains to differentiate live from dead tissue in bryophytes. Two such stains: "Evan's Blue" and Tetrazolium salts (Gaff & Okong'ogola, 1971) were tested at Marion Island. Results were ambiguous however, due to resistance of the bryophyte cell walls to infiltration by these stains in several cases. Thicker, pigmented cell walls also interfered with the microscopic visibility of cytoplasmic colouration when it occurred. It was confirmed however, that in the cases where staining did occur (indicating living cells) the colouration could be seen extending deep within the moss colony profile to just above the decomposition zone.

If facilities are available it may be possible to determine the extent of active tissue and the importance of acro- or basipetal translocation by C_{14} labelling (Skre & Oechel, 1979; Wielgolaski, 1975). Although time consuming and difficult to apply in the field and with the degree of replication necessary in large scale production studies, this may be the only viable technique for critically determining the biomass/necromass partition in most bryophytes. Using this technique, Wielgolaski (1975) found that only approximately 4-5% of the standing crop of bryophytes at a Norwegian site was completely dead, which

equates with the findings of the vital stain studies mentioned above.

The pragmatic solution to the biomass problem in bryophytes has been to regard all living and dead tissue above the decomposition zone as "biomass" i.e. above the point where intact plant tissue becomes indistinguishable from humified material. With this usage, biomass becomes synonymous with the terms phytomass or standing crop, and was accepted in this sense by workers during the IBP. The term "bryomass" has also been used to identify this component (V Smith, 1985).

Other problems with the above formulation of the net production equation centre on the methodology for measuring 'L'. Several methods have been used to measure decomposition in tundra e.g. litter bags, cotton strips, peat bulk density measurements, respiratory O₂ uptake etc. Litter bag techniques can be applied to bryophytes with diffuse growth forms, while measurement of bulk density changes with depth may be possible in species with deep and close-growing colony forms which show little vertical compaction (Davis, 1980). Relative advantages and disadvantages of these methods are discussed in Rosswall (1974) and R. Smith (1985).

The relative importance of bacterial decay, leaching and exudation processes, litterfall and export abrasion of plant tissue by wind/snow/sand etc., are very seldom studied aspects of moss production and decomposition, and may be more or less important in particular habitats. As explained above, direct decomposition measurements could not be carried out during the course of this investigation. However, production:biomass

turnover ratios and initial annual loss based on mass differences between shoot production and residual biomass, have been calculated in Section 4. .

There has been some work carried out on the "G" component of the above equation. Grazing of bryophytes by herbivores is often insignificant, and has been assumed to be zero by many authors (Kilbertus, 1968; Clymo, 1970; Pakarinen & Vitt, 1973; Whittaker & Marks, 1975; Smith & Forrest, 1978; Pickard, 1979). The low palatability of bryophytes may be due to their low energy values, high wall to protoplast volume ratios, and the presence of repellent phenolics and mineral substances (Longton, 1988). Walton (1985) has also noted that bryophytes have higher carbon to nitrogen ratios and larger amounts of holocellulose and crude fibre that make them a less attractive food resource for herbivores. However, there is evidence that in certain situations, significant quantities of bryophytes may be consumed by herbivores (Longton, 1988). This factor should therefore be taken into account where field observations indicate that a fraction of bryophyte production is being lost to consumption.

Barbour et al (1980) noted that 2-3% of bryophyte production may be lost to grazing by Lemmings and Caribou in Arctic tundra. Only low rates of consumption have been measured in the Antarctic however, e.g. 0.04% per year in moss turfs at Signy Island (Block, 1984). Early observations had suggested that an insignificant amount of plant production was consumed by invertebrates at Marion Island (Van Zinderen Bakker, 1971), and that invertebrates may feed more extensively on the epiphytic micro flora fauna of the moss turfs and carpets (Heatwole pers. com.). However, recent studies

(V Smith pers. comm.) have shown invertebrate grazing to be important at Marion Island and there have been several accounts of high numbers of invertebrates in bryophyte vegetation at the Island. Time did not allow detailed studies of this component of "G" to be measured during the present study; the calculations of biomass and production must therefore be regarded as underestimates, as potential loss to "G" has not been factored into the results.

As absolute measurement of net production taking into account all of the above factors is usually not possible, the term Annual Shoot Production (ASP) has been coined to describe the values for production obtained from simple yearly measurements of stem length/mass increments in bryophytes (Clarke et al. 1971). The degree of equivalence of ASP with net production depends however, on the degree of rigour applied in obtaining an understanding of the influence of L and G on production. Longton (1972) formalised the relationship between the two quantities thus:

$$P_n = ASP + (P_{2+} - R_{2+}) + (T_d - T_u) + S$$

Where P_{2+} & R_{2+} = Photosynthesis and respiration in the older parts of the colony respectively

T_d & T_u = translocation away from and towards the apex respectively

S = production of sporophytes

Sporophyte production is generally low in tundra bryophytes and was ignored by workers during the IBP. It may be possible to do the same for bryophytes that show predominantly vegetative growth. However there is a need for data on the contribution of sporophyte production to overall net production in a wider range of species in both

polar and Extra-polar zones. This is especially necessary in microsites where bryophytes produce large numbers of capsules.

Clarke et al (1971) & Collins (1977) working in the tundra , provided evidence that the difference between ASP and net production due to translocation and growth in older parts of the stem, may be minimal in many bryophytes due to their lack of conducting tissues. The distinction may also be insignificant where the active zone encompasses little more than a year's growth. However, these factors may assume importance in species with endohydric water relations and a more perennial habit e.g. Polytrichaceae (Longton, 1972).

It is possible (theoretically at least) to take into account growth in the older parts of the shoot, by dividing the shoot up into equal annual segments based on extension growth measurements, and measuring the biomass of the largest age class thus defined (Skre & Oechel, 1979). This will represent mean net production irrespective of differences in the partitioning of production with age of the shoot.

Problems with this approach centre firstly on the extrapolation of mean annual stem length increments over seasons of extant biomass for which growth measurements were not taken (growth during an abnormally warm season could influence the calculations for example). The problem is lessened where only a few years of growth are represented in the biomass and or where several yearly increment measurements are taken. A fortuitous solution is provided in cases where the plant itself has "innate" markers that

define annual growth.

The maximum age class approach assumes a steady state i.e. production in equilibrium with decomposition, which may not be far from the truth in many stable "climax" communities. There is support for this assumption from classical growth studies in vascular plants, and empirical findings in several investigations of bryophyte production. Most species follow a sigmoid growth curve (Longton, 1979) with growth being proportional to the amount of biomass present and occurring rapidly at first ("logistic" phase). Productivity then falls as stem density increases, until an equilibrium state is approached when dry matter accumulation balances death and litterfall.

This may have appeared intuitively to be the case in the superficially "stable" tundra, and led to the assumption of a steady state by many workers studying productivity in this ecosystem. Bryophytes however, occur as pioneers in many habitats, and their productivity may be high in relation to decomposition during the early stages of succession. Alternatively, where higher plants assume dominance or microorganisms increase in numbers (e.g. in eutrophic situations) bryophyte communities may become moribund, with decomposition assuming the dominant role.

Climatic changes since the glacial period have probably kept relative production decomposition rates dynamic rather than stable for long periods at many tundra sites. In stable communities in the short term however, the maximum age class method is appealing due to its simplicity, especially where innate annual markers of

growth are present. Plants can be divided into age classes based on increment measurements, and bulked to determine biomass over a given area for each class.

This procedure also allows a historical profile of biomass accumulation and loss to be built up for each species, which is of greater value than simply collecting data on current production quantities. The sequential biomass information can be compared with data on energy content, chlorophyll content, inorganic mineral content etc. from subsamples of the same material, and allows further conclusions to be drawn concerning temporal/ecophysiological relations of the plants under study.

In a short term study however, and where innate markers are not present (as at Marion Island), it is difficult to apply the maximum age class method without making unwarranted assumptions concerning the constancy of annual production. Due to these constraints, the rationale at Marion Island was to measure 1-2 year's growth accurately, thus allowing qualitative prediction of growth over longer periods by reference to climatic information.

Most of the above procedures for estimating bryophyte production, rely on a method of measuring the amount of shoot extension growth taking place over a given time period (usually one year or a growing season). It is these specific techniques which will be treated in the following section.

4.2.4 Practical application of growth measurement techniques

Due to microhabitat diversity, a wide range of growth forms is demonstrated by Marion Island's bryophytes (Table 4.3). A preliminary study by Gremmen et al (1975) showed that growth patterns in Marion Island bryophytes were highly variable, and it was decided therefore to use several different techniques for measuring shoot increments (Figure 4.2). This is preferred methodology as, according to Clymo (1970), there is no absolute and independent yardstick for measuring the accuracy of these results and therefore: "the more diverse the methods, the better their mutual support".

Because of the requirement to survey as wide a range of habitats and species as possible within the given time limits, the overall sampling strategy was thus designed to be extensive rather than intensive. It was beyond the scope of the study to address certain of the theoretical problems that had emerged during the IBP, such as the definition of "biomass" in bryophytes; or to investigate physiological aspects such as translocation of photosynthate. Measurements of Annual Shoot Production would however be compatible with results from previous studies and would enable comparison with other tundra sites. To improve on IBP methodology, a broad spectrum of growth measurement methods were applied, to achieve precision through mutual corroboration and by satisfying basic statistical criteria.

Calculations of total biomass ("standing crop") were carried out at each study site by coring areas of 100% cover of each bryophyte colony down to the "humification" zone in May 1982. This follows the practice of other workers in the tundra i.e. to differentiate

Table 4.3 Growth form of study species

Habitat Complex*	Species	Predominant growth form in study plot	Mean shoot density cm ² ±SD	
Drainage Line	<i>Brachythecium subplicatum</i>	Carpet	23.2±9.04	
Mires	wet	<i>Distichophyllum fasciculatum</i>	Tall turf, branches erect	49.7±5.64
		<i>Drepanocladus uncinatus</i>	Carpet	15.8±8.77
		<i>Campylopus purpureocaulis</i>	Tall turf with dense felt of rhizoids	26.3±11.80
		<i>Breutelia integrifolia</i>	Tall turf with dense felt of rhizoids	16.0±10.20
		<i>Ptychomnium densifolium</i>	Tall turf, branches erect	4.3±12.66
		<i>Clasmatocolea humilis</i>	Short - tall turf	100.0±11.18
		<i>Blepharidophyllum densifolium</i>	Tall turf, branches erect	42.0±4.96
		<i>Jamesoniella colorata</i>	Mat, thread-like form - tall turf	47.7±14.36
		<i>Cryptochila grandiflora</i>	Mat, thread-like form - tall turf	40.2±13.66
		dry	<i>Racomitrium lanuginosum</i>	Carpet
Slope	<i>Brachythecium rutabulum</i>	Weft	11.0±19.63	
Fellfield	<i>Ditrichum strictum</i>	Large cushions	23.7±7.75	
	<i>Andreaea acutifolia</i>	Small - large cushions	280.0±9.53	
Biotic/Salt spray	<i>Clasmatocolea vermicularis</i>	Mat, thread-like form - tall turf	106.5±7.83	

* From Gremmen (1982)

** Terminology after Gimingham & Birse (1957) and Gimingham and Smith (1971).

*** Standard error less than 10% of the mean

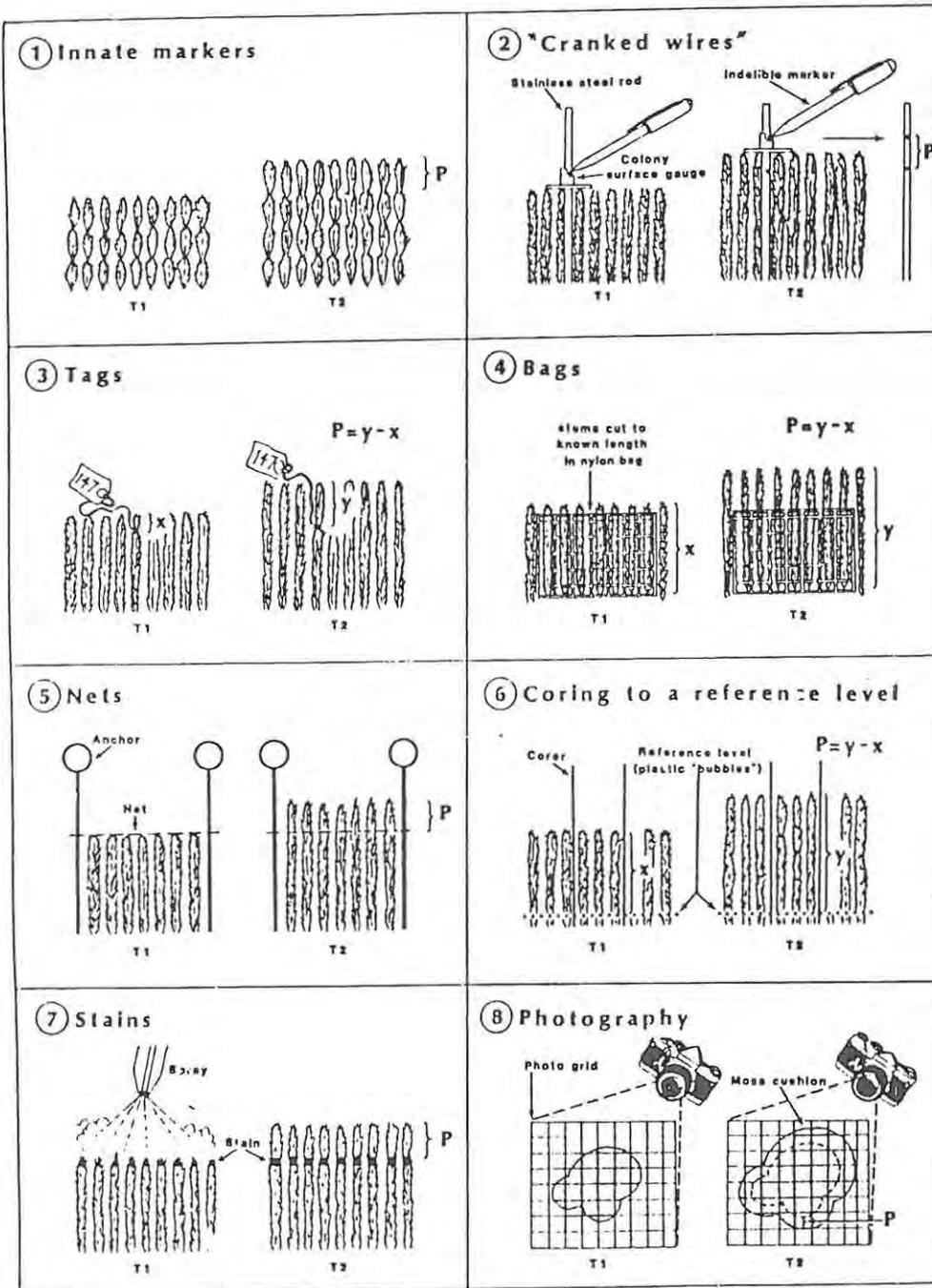


Figure 4.2

Diagrammatic representation of the methods used to measure bryophyte growth at Marion Island.

T1 = beginning of expt. T2 = end of expt. (see text).

The boundary with the lower zone of amorphous peat was occasionally quite diffuse and difficult to delineate accurately. However in many instances, groups of stems could be detached from the substrate at a fairly constant "break point" where the stems lost their structural integrity associated with a browning and softening of the tissue. This usually meant however, that a certain amount of partially decomposed plant material was not included in the biomass cores, and this should be borne in mind when comparing the results with other biomass measurements based on either "total organic matter" or "living tissue only."

20 cores were taken for each species (corers of 44.5mm diameter were used for the larger species and 26mm diam. for the smaller species). It was intended that mean spatial stem density would be calculated by counting stems in only as few of the cores as necessary, to achieve a standard error of approximately 10% of the mean. However, due to high and/or variable numbers of stems in several cases, this was not possible within the manageable limit of 20 cores per species, and higher variability is therefore accepted in the instances where this occurs.

The lengths of the blocks of stems in each core were measured and the plant material was then oven dried to constant weight at 80°C, to give an estimate of total biomass. Results were reduced to a community cover basis by reference to the areal cover figures obtained for each species at its growth plot (Appendix 1). These cover values were estimated to the nearest 5% by sight, except in the case of Ditrichum strictum which has

a more precise cover value derived from a point quadrat survey.

For estimation of annual shoot production, stem length increments were measured by the various techniques shown in Figure 4.2. A survey of 30 papers dealing with measurement of growth in bryophytes revealed that 14 authors had used the "innate marker" method, and seven had used variations of Clymo's "cranked wire" technique. Six researchers had tagged their plants, while two had used stems cut to known lengths in bags and a further three had measured growth through nets. One author had used photography to assess the growth of saxicolous bryophytes (a technique widely applied in lichenometric studies) and another had used coring to a reference level in a pilot study. The staining technique had been proposed but not implemented.

It was not known in advance which of these techniques would prove successful in providing statistically acceptable measures of stem length increment. Therefore all methods were tested in various combinations and modifications, depending on their adaptability to the growth form of the particular species under study, during the six month summer season November 1980-April 1981. The most effective methods were then selected for use in the following year's study, as assessed by field observations and low variability of results. Sampling intensity was then increased for the second year's growth measurement period May 1981-May 1982.

The distribution and intensity of sampling methods applied in the Marion Island bryophyte production study, are outlined in Table 4.4 and information on the individual

Table 4.4 Chart showing the distribution and intensity of sampling during the bryophyte growth study. x = method applied to relevant species. 6m = six monthly study and yr = year growth study.

Species	Monthly measurements	Innate Markers	Crank markers		Tags		Bags		Nets		Cores		Stains		Photos	
			6m	yr	6m	yr	6m	yr	6m	yr	6m	yr	6m	yr	6m	yr
<i>Brachythecium subplicatum</i>	X		X	X	X				X				X	X		
<i>Distichophyllum fasciculatum</i>	X		X	X			X		X				X	X		
<i>Drepanocladus uncinatus</i>	X		X	X	X				X	X			X	X		
<i>Campylopus purpureocaulis</i>		X	X				X		X				X			
<i>Breutelia integrifolia</i>	X	X	X	X	X	X	X	X	X	X			X	X		
<i>Ptychomnium densifolium</i>	X		X		X	X	X		X		X		X	X		
<i>Clasmatocolea humilis</i>	X		X				X		X	X	XX		X			
<i>Blepharidophyllum densifolium</i>	X		X	X			X	X	X	X	X		X	X		
<i>Jamesoniella colorata</i>	X		X	X			X		X	X	X		X	X		
<i>Cryptochila grandiflora</i>	X		X				X		X		X		X			
<i>Racomitrium lanuginosum</i>	X	X	X	X	X				X				X	X		
<i>Brachythecium rutabulum</i>	X		X	X	X				X				X	X		
<i>Ditrichum strictum</i>		X	X	X					X	X			X	X	X	X
<i>Andreaea acutifolia</i>			X						X	X			X	X	X	X
<i>Clasmatocolea vermicularis</i>			X		X					X			X			

techniques is given in the following section. Comment on the efficacy of the different techniques is to be made here as each is described, rather than repeating the information in the results or discussion section.

4.2.4.1 "INNATE MARKERS": Many species of bryophytes show visible annual growth segments resulting from seasonal differences in leaf size and spacing, branch zonation, production of sporophytes etc. Such "innate" markers may be well defined in mosses of highly seasonal climates and are often present in bryophytes with dense, vertical growth forms (cushions, turfs) e.g. Andreaea, Campylopus, Dicranoloma, Ditrichum, Meesia, Philonotis, Pohlia, Polytrichum, Tortula (Hagerup & Peterson, 1960; Bellamy & Rieley, 1967; Clarke et al, 1971; Gremmen et al, 1975; Vitt & Pakarinen, 1977; Longton 1979). Close scrutiny may also reveal evidence of rhythmic growth patterns in species with less compact growth form, from more equable regions e.g. Acrocladium, Hylocomium, Pleurozium, Ptilium, Racomitrium, Sphagnum, Thuidium (Lackner, 1939; Tamm, 1953; Tallis, 1959; Streeter, 1965; Clymo, 1970; Busby et al, 1978). Such zonation may be preserved for many years in species of bryophytes with slow decomposition rates e.g. Polytrichum, Racomitrium. This may allow correlation of production rates with climatic data for past years of growth.

Adverse environmental conditions may however, prevent the expression of annual segments e.g. by suppressing branching or sporophyte production in a particular year. For example, Racomitrium lanuginosum showed apparently seasonal production of capsules in localised colonies at Marion Island. However, tagging showed these zones to correlate

only approximately with one year's growth and measurements from these increments gave consistently larger values (i.e. more than one year's growth represented by each "segment") than those provided by other methods. This particular instance probably reflects the harsh conditions experienced at the dry mire/fellfield Racomitrium growth plot. Segments should therefore be checked for their relationship to a true year's growth before the assumption of annual periodicity can be made.

At Marion Island, the isothermal climatic conditions may partly account for the fact that innate markers are rare among the bryophyte species, compared to elsewhere in the tundra biome. Upon closer examination, seasonal differences in some of the above characters were noted in Dicranoloma billardieri, Breutelia integrifolia, Ditrichum strictum, Racomitrium lanuginosum, Campylopus purpureocaulis and Clasmatocolea vermicularis. However, this zonation was not consistent enough to allow reliable measurements over significant areas of the bryophyte colony in the latter two species without using unmanageably large statistical samples. Therefore, study of innate markers was undertaken only in the first four species. As mentioned in the introduction, Dicranoloma billardieri is not an important species in terms of biomass at Marion Island and its growth will therefore be reported on elsewhere (Russell in prep.).

Much reliance was placed on innate markers for defining annual growth during studies elsewhere in the tundra biome. On Marion Island however, as such markers were more commonly cryptic or lacking, indirect methods had to be relied upon in most cases, in order to provide a datum on or near the plant from which extension growth

measurements could be made.

4.2.4.2 "CRANKED WIRES": Stakes or wires may be inserted into a bryophyte turf, with a bent (cranked) or otherwise marked section at the level of the colony surface, to define a starting point for growth measurements. Variations of this technique have been used successfully by many authors (Leisman, 1957; Clymo, 1970; Baker, 1972; Kallio & Heinonen, 1975; Pitkin, 1975; Busby et al, 1978; Rieley et al, 1979; Sonesson 1980). Clymo (1970) suggested the use of a small perforated disc which could be slid down the wire to help define the average level of the moss surface. Using a modified "disc gauge" (Russell 1984) marks can be made on the wire before and after periods of growth, using an indelible pen (Figure 4.2b). Wires may then be withdrawn from the turf and growth increments measured from the marks on the wire. This can be done in the laboratory if weather conditions make extended periods of field measurement difficult.

Wires may also be colour coded with spots of enamel paint to facilitate monitoring of growth at individual microsites (Glime pers. com.). Dull colours may have to be used where the risk of disturbance from foraging birds or animals is high, as proved to be the case at Signy Island (Baker, 1972) and Marion Island (Russell 1984).

Cranked wires are useful where growth form of the bryophyte is predominantly vertical. Problems arise however, where compaction of the bryophyte colony takes place, for example due to deep snow overlying the surface, and where there is a dominant creeping or horizontal growth component as in many pleurocarpous types. Snow compaction and frost heave are less significant problems at Marion Island however, due to the relatively

mild climate. This method was therefore applied to all species in the study.

200mm long stainless steel rods were used for large species, and fine wire cranks for the smaller species. 30 "cranks" per species were used during the six month study, 50 per species for the year's study. The method proved most consistently successful among all the techniques, although least appropriate in the case of weft and small cushion growth forms.

4.2.4.3 TAGS: Many workers have attempted to measure growth in bryophytes with a diffuse or creeping habit, (pleurocarpous mats and wefts) by tying pieces of cotton around the stems (Fig. 4.2c). Distance from this point to the stem apex may be measured to define shoot extension growth (Overbech & Happach, 1956; Tallis, 1959; Chapman, 1965; Longton & Greene 1979). Numbered labels can be attached to the tags to facilitate relocation, although the above provisos concerning visibility to foraging animals also apply.

In some species at Marion Island, e.g. Brachythecium subplicatum and Breutelia integrifolia, rapid growth enveloped the tags and made them difficult to find and use as a measuring datum without unduly disturbing the colony. Tightly tied tags sometimes interfered with external conduction of water along the stems of the more ectohydric species e.g. Brachythecium rutabulum. The use of small strips of Velcro pressed around the stem in place of a cotton knot, has been suggested to lessen this problem (Raeymaekers & Glime, 1986; Glime 1987).

A large number of tags was necessary to encompass microsite-related variation in stem growth rates in the wet and loose turf forming species. Application of the technique was therefore tedious and time consuming, especially when bad weather conditions prevailed and when stems were small and fragile. The results were reliable however and consistent with those obtained using other techniques.

Plastic tags attached to fine stranded nylon string, were knotted loosely around bryophyte stems in the Marion Island study (50 plants in the six month study, 150 plants per species in the year's study).

4.2.4.4 CUT STEMS (BAGS): Several authors have cut bryophyte stems to a standard length and reinserted them into the moss turf in bags made of various materials (celluloid, cotton gauze, nylon cloth etc.) in order to measure growth. Stems may be removed at a later date for re-measurement and calculation of shoot extension. The method is useful for species with compact, parallel, vertical shoot growth with little lateral branching (e.g. tall turfs) (Fig. 4.2d). The technique also allows measurements to be made in the comfort of the laboratory where adverse weather conditions prevent long periods being spent in the field (R Smith, 1981).

Stems must be cut well below the zone of active growth in case excision is likely to effect growth potential. The researcher's subjective judgement regarding the extent of the active region, can be assisted by C_{14} tracer experiments where time and facilities allow (Skre & Oechel, 1979).

18 bags per species (12 shoots per bag) were used in the six month study at Marion Island, thus allowing for three bags to be withdrawn every month, for growth measurements. 30 bags were used per species in the year study. The results obtained using the bag technique tended to give lower values for stem elongation than the other methods which may have been an indication of hydrological disturbance to the bryophyte colony at the time of bag placement. This may also have been exacerbated by the small size of many of the species studied by this technique at Marion Island, in comparison with the more robust species that have been studied successfully using this method elsewhere (Overbech & Happach, 1956; R Smith, 1982).

4.2.4.5 NETS: Several workers have placed nets over the surface of moss colonies and measured growth beyond the level thus defined (Kallio & Heinonen, 1975; Rieley et al, 1979; Skre & Oechel, 1979). The method is also more applicable to bryophytes with vertical growth forms where little lateral growth beneath the surface of the net is expected (Fig. 4.2e). Mesh size will need to be adapted to the size of the moss, and the gauge of the netting material should be fine enough to preclude significant shading effects on the plants beneath.

Squares of plastic netting were used at Marion Island, from 20mm square in Andreaea acutifolia for example, to 250mm square in Brachythecium subplicatum. Mesh size also varied according to species, from 3 to 15mm. Green coloured netting used in the six month study proved attractive to Skua Gulls, so black netting was used during the year's study. Results using the net technique tended to be somewhat inconsistent except in the

case of the cushion forming mosses with their dense and smooth colony surface. Here, fine and carefully positioned nets provide one of the very few techniques that could be successfully applied to this otherwise difficult growth form.

4.2.4.6 CORING TO A REFERENCE LEVEL: Gremmen et al (1975) cut horizontally through the soil beneath a bryophyte carpet using a sheet of glass, and spread small pieces of pvc to define a reference level on the exposed soil surface (Fig. 4.2f). After replacing the moss turf, cores of bryophyte material were made down to the reference level, and their depths and biomass measured for comparison with similar cores taken at a later date. The method is thus useful for direct measurements (change in total biomass) or for shoot extension growth measurements.

In this study, polystyrene pellets were spread at the reference level. It was intended that ten cores per month would be withdrawn during the 1980-81 season, and eighteen at the end of the second, year's study. Increase in length of the cores was difficult to measure however, owing to compression and distortion during the coring process. Similarly, dry weights of the cores were excessively variable due to the soil fraction far outweighing the plant material present. This method was applied to six species during the six month study, but gave poor results and was therefore omitted from the range of techniques used in the one year measurements.

With good replication however, it is felt that the method could be applied to bryophytes which show a well defined plant-soil boundary, especially where the soil texture is

susceptible to "undercutting" of the bryophyte colony so as to cause minimal disturbance to the plant cover.

4.2.4.7 STAINS: The spraying of stains on the plant has been suggested as a method for providing a stem marker in bryophyte growth studies (Pickard, 1980). Coloured dyes (vegetable colouring, Fast Green microscopic stain and Fluorescein) were used during the six month study, but were found to have washed out of the bryophyte tissue after several months of rain.

Fluorescent brighteners such as Calcafluor (American Cyanamid), Calcafluor (Polysciences) and Blancophor (Bayer), are potentially useful stains for growth studies. These substances are relatively inert and should not interfere with growth. They are transparent i.e. unlikely to block photosynthetically active radiation, and they are cellulose specific, binding to the cell wall and thus reducing the possibility of being leached out over long periods of measurement. The fluorescence of these dyes can be viewed under ultra-violet light using a portable lamp in the field, or a mains operated unit in the laboratory.

A supply of these chemicals was obtained in time for the one year study, and the brightest fluorescing compound ("Blancophor BBU 200%") was used in an aqueous solution of 5% concentration, for application to 100mm square areas of bryophyte turf. This concentration was found to be sufficient to "fix" a permanent fluorescent layer on the plant's surface in most cases. This "bright" zone could then be traced at a later date

in colony cross sections (for example in small cushions) or on single stems. It was found that spraying of the stain should be carried out during dry conditions to prevent leaching by rain before it had fixed on the cell walls. Microscopic examination with a fluorescent light source will confirm successful application of the dye.

Trials with a limited selection of brighteners have been carried out by the author. Controls showed no interference with plant growth due to the chemicals, although there is the possibility that these substances may chelate Calcium (Hartmann pers. com.). Some species show a resistance to fixing of the stain in the cell wall in sufficient quantity to be visible macroscopically (Russell, 1984). The method has proven successful in the case of small cushion species whose growth was difficult to measure by other methods. The simplicity of the technique is appealing and further studies are recommended to test additional fluorescent compounds on a wider range of bryophyte species.

4.2.4.8 PHOTOGRAPHY: Proctor (1979) evaluated the use of serial close-up photography to measure growth in saxicolous bryophytes (Fig. 4.2h). Critically scaled photographs are required, and are of most use where growth takes place as radial extension of an appressed colony, or constant "hemispherical" expansion of a cushion. Shoot extension measurements can be made accurate to within fractions of a millimetre where careful photographic technique is employed.

This method was appropriate to Ditrichum strictum and Andreaea acutifolia in the Marion Island study, and six areas of stone pavement with abundant cushions of these

species were therefore staked out with markers to enable accurate vertical photographs to be taken at the end of each growth measurement period. Final prints were traced using a reducing/enlarging "plan-variograph" to compensate for small scale-errors, and measurements of cushion surface extension were made using fine point dividers.

The mean value of 0.8mm obtained for stem extension during the six month study is near the limit of accuracy (0.5mm) of the technique as applied in this study. Both this and the full year's growth value (1.3mm) lack variability however, and compare reasonably well with estimates made using other techniques. As mentioned above, conversion of increment lengths to production values by coring of the surface of the cushion assumes constant shoot expansion over the whole surface of the colony. Such "hemispheric" expansion was confirmed by the regularity of stem emergence over the whole area of the cushion as observed using the "net" method. It should be remembered that in cushion species, areal "community" production values will still be influenced by the degree of rigour applied in measuring percentage cover, especially where there is a high degree of rugosity or convolution in cushion surfaces.

A comparison of results from different measurement techniques is indicated in Figure 4.3 for three of the study species. A good general correspondence between values is apparent for the methods used except in the case of coring to a reference level. The poor precision (large standard error) of this measure shows that in this study the technique was inappropriate for the two species concerned.

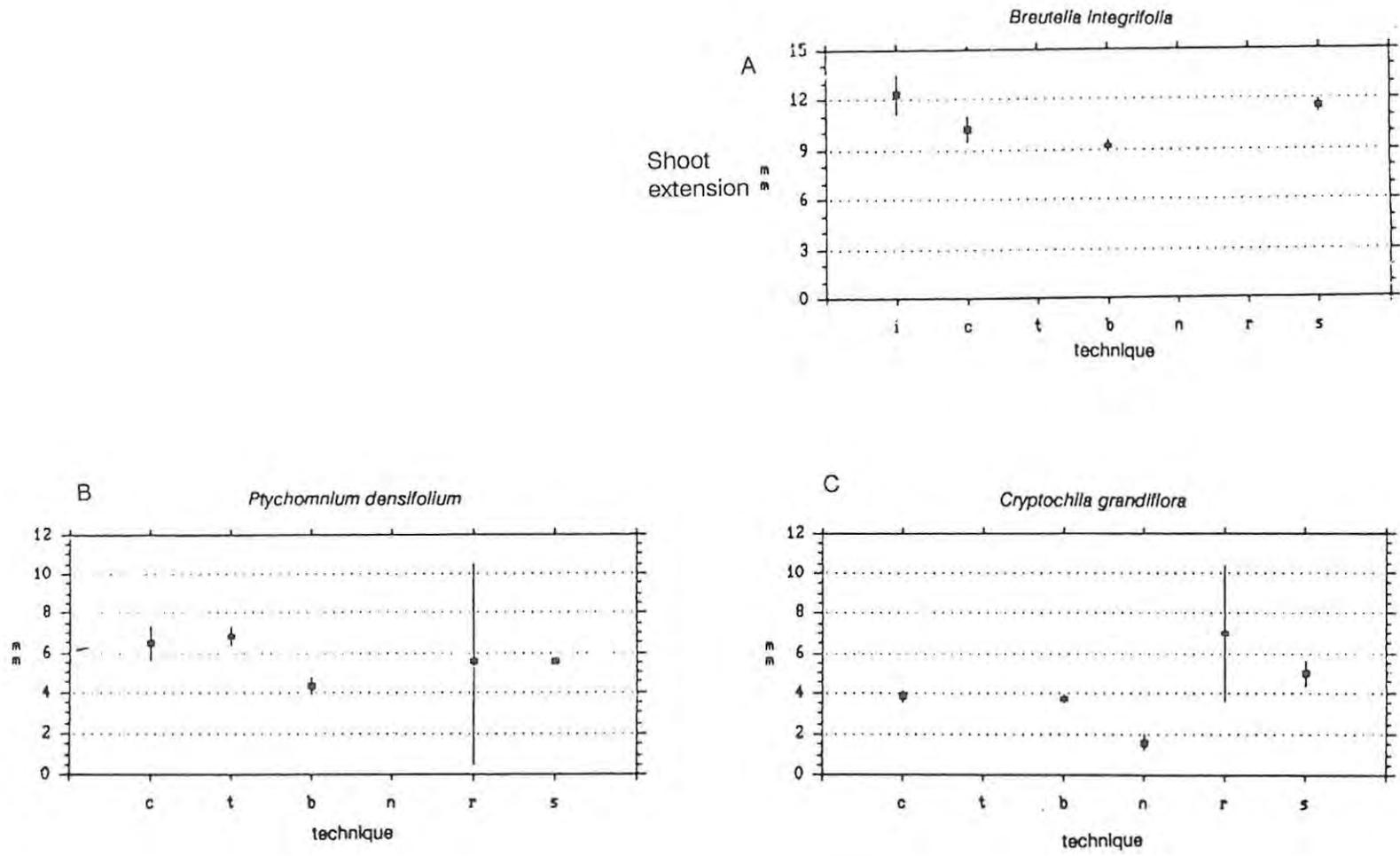


Figure 4.3

Comparison between results of various techniques used to measure stem extension growth in three species of Marion Island bryophytes. A-C Average shoot extension growth (1981-1982) in three bryophyte species from Marion Island as recorded by various growth measurement techniques. i = innate markers; c = cranked wires; t = tags; b = bags; n = nets; r = coring to a reference level; s = stains. Vertical bars indicate standard error of mean.

Three of the above methods were used during monthly measurements of growth during the six month study viz: tags, bags and cores. At the end of the full year's study in May 1982, mean annual shoot extension was calculated by pooling the data from all methods that showed mean values with low statistical variability. To calculate shoot production on a g m^{-2} basis, 20 cores of each species were removed above the decomposition layer at each plot in May 1982, in the same manner as the cores taken for biomass determination. The base of the stems were excised from the substrate at a depth equal to the stem lengths for the total biomass, as determined in the separate biomass study. The upper parts of the stems in each core were then excised, to a depth equalling the mean annual stem increment as calculated during the 1981-82 year's growth period. Both sections were then oven dried to provide weights for the shoot production calculations. By pooling the weights of both sections, an additional biomass figure could be obtained for comparison with the results of the first total biomass coring exercise.

As explained in Chapter 1, detailed decomposition studies were scheduled for completion later in the overall ecosystem programme and were not carried out during the author's visit to Marion Island. However, in the absence of a significant grazer component, approximate decomposition rates can be indirectly assessed from the production to biomass turnover ratio, calculation of which is therefore also included in the results section.

4.3 Results

Several researchers have noted the importance of hydrological gradients in bryophyte communities at polar sites (Vitt & Pakarinen, 1977; Gimingham & Smith, 1971). Gremmen (1981) also concluded that soil moisture was the principal environmental factor controlling the expression of spatial pattern in bryophyte communities at Marion Island. As stated during the introductory Chapter, one of the hypotheses addressed during the course of investigations for this thesis, was the degree of correlation with soil moisture of the factors studied i.e. biomass, production, plant energy, chlorophyll, water, mineral contents etc. When presenting data from the various studies therefore, the species are arranged in the left hand column of the tables, in a descending order based on predicted mean soil water content for the community in which each species occurs.

The mean soil water content has been calculated from information on the relevant communities in the tables of ecological data in Gremmen (1981) (based on 500 relevées dispersed around the island). Soil water contents actually measured at the bryophyte growth plots (Appendix 1) were remarkably similar to the community means calculated from Gremmen's data ($r= 0.8179$ $P< 0.0001$). However, the relevée-based data is used to order the species in the ensuing tables, because of the more extensive nature of the soil moisture sampling for the phytosociological study and thus wider applicability to the island's vegetation ecology.

The first fourteen species representing communities of the drainage line, mire, slope, and

Table 4.5 Stem spacing density and cover percentage of the study species.

Species	no. of cores	Mean shoot density stems per cm ²	Standard Deviation	areal cover in growth plot (%)
<i>Brachythecium subplicatum</i>	10	23.20	9.04	90
<i>Distichophyllum fasciculatum</i>	5	49.70	5.64	95
<i>Drepanocladus uncinatus</i>	20	15.80	8.77	85
<i>Campylopus purpureocaulis</i>	10	26.30	11.80	75
<i>Breutelia integrifolia</i>	20	16.00	10.20	80
<i>Ptychomnium densifolium</i>	20	4.30	12.66	75
<i>Clasmatocolea humilis</i>	5	100.00	11.18	70
<i>Blepharidophyllum densifolium</i>	5	41.90	4.96	95
<i>Jamesoniella colorata</i>	10	47.70	14.36	75
<i>Cryptochila grandiflora</i>	10	40.40	13.66	70
<i>Racomitrium lanuginosum</i>	20	4.50	11.49	60
<i>Brachythecium rutabulum</i>	20	11.00	19.63	65
<i>Ditrichum strictum</i>	10	23.70	7.75	5
<i>Andreaea acutifolia</i>	5	280.00	9.53	13
<i>Clasmatocolea vermicularis</i>	5	106.50	7.83	80

fellfield complexes are arranged in the manner outlined above. The fifteenth species (*Clasmatocolea vermicularis*) is placed separately at the end of the table, as the biotic and salt spray communities that it represents are not included in the soil moisture gradient referred to above, as they have differing primary ecological controls (Gremmen, 1981).

Results of stem counts for the given number of cores for each species are shown in Table 4.5., along with the areal cover estimates for each species at its growth plot. These latter values were taken from Appendix 1, and were used as multipliers in the calculation of the phytomass and production figures shown in the ensuing tables of this section.

Results of the first biomass measurements are given in Table 4.6. Stem lengths to the decomposition zone were often difficult to estimate due to the diffuse nature of this boundary in most cases. This accounts for the high degree of variability shown by these figures. Stem mass per unit stem length is also shown, as this gives an indication of tissue density and to some extent "robustness" of the stems of the individual species.

The total biomass or standing crop of bryophyte material above the decomposition zone is also listed on a 100% cover basis, which will correspond to the amount of plant material at sites locally dominated by a single species. The biomass for the species as it might be expected to occur in its wider "type" community context, is given in the column of figures corrected for % cover.

Table 4.6 Biomass of Marion Island bryophytes.

Species	stem length mm	±SD	single stem weight mg	±SD	single stem mass per mm	Phytomass @ 100% cover (g m ⁻²)	Cover corrected phytomass (g m ⁻²)
<i>Brachythecium subplicatum</i>	99.30	±38.2	7.90	±1.81	0.08	1,832.80	1,649.50
<i>Distichophyllum fasciculatum</i>	44.40	±15.1	1.96	±0.33	0.04	974.10	925.40
<i>Drepanocladus uncinatus</i>	60.50	±25.7	5.76	±3.26	0.10	910.10	773.60
<i>Campylopus purpureocaulis</i>	76.80	±16.7	10.24	±2.46	0.13	2,693.10	2,019.80
<i>Breutelia integrifolia</i>	106.20	±38.0	6.08	±2.79	0.06	972.80	778.20
<i>Ptychomnium densifolium</i>	53.80	±16.6	18.48	±5.01	0.34	794.60	596.00
<i>Clasmatocolea humilis</i>	27.40	±9.3	1.98	±0.29	0.07	1,980.00	1,386.00
<i>Blepharidophyllum densifolium</i>	50.30	±17.0	5.25	±0.98	0.10	2,199.80	2,089.10
<i>Jamesoniella colorata</i>	54.70	±19.1	3.12	±1.93	0.06	1,488.20	1,116.20
<i>Cryptochila grandiflora</i>	32.90	±12.9	1.94	±1.05	0.06	783.80	548.70
<i>Racomitrium lanuginosum</i>	74.10	±49.8	36.45	±15.77	0.49	1,640.30	984.20
<i>Brachythecium rutabulum</i>	38.60	±20.0	3.68	±1.28	0.10	404.80	263.10
<i>Ditrichum strictum</i>	49.20	±8.2	13.98	±4.72	0.34	3,313.30	165.70
<i>Andreaea acutifolia</i>	7.60	±1.1	0.80	±0.01	0.11	2,240.00	291.20
<i>Clasmatocolea vermicularis</i>	23.00	±14.2	0.66	±0.02	0.03	702.90	562.30

An ancillary set of biomass figures is shown in Table 4.7 for comparative purposes. These were obtained from cores taken during the chlorophyll analysis experiment. They also reveal a wide variability, but the order of magnitude of this variation and the general trend of biomass distribution in the main habitat types is similar to that seen in the biomass measurements resulting from the main survey.

Table 4.7 Ancillary set of bryophyte biomass figures obtained from cores taken during the chlorophyll analysis.

Study plot	bryomass g m ⁻²	cover corrected bryomass g m ⁻²
<i>Brachythecium subplicatum</i>	2462	2339
<i>Distichophyllum fasciculatum</i>	1388	1319
<i>Drepanocladus uncinatus</i>	3766	3390
<i>Campylopus purpureocaulis</i>	4887	3665
<i>Breutelia integrifolia</i>	3657	2925
<i>Ptychomnium densifolium</i>	1178	884
<i>Clasmatocolea humilis</i>	1279	959
<i>Blepharidophyllum densifolium</i>	2642	2514
<i>Jamesoniella colorata</i>	2690	2017
<i>Cryptochila grandiflora</i>	1835	1285
<i>Racomitrium lanuginosum</i>	3919	2351
<i>Brachythecium rutabulum</i>	930	605
<i>Ditrichum strictum</i>	9100	455
<i>Andreaea acutifolia</i>	2640	343
<i>Clasmatocolea vermicularis</i>	1597	1277

Mean shoot extension figures for the various growth measurement methods applied during the six month summer season of 1980-81 are given in Table 4.8. Average extension growth figures were pooled from the means from all the methods applied (last column) except where the method proved inappropriate for the species in question. For example, very variable results were obtained using the "coring to a reference level" method. This was due to unavoidable distortion of the columns of plant material during the coring process, especially in waterlogged turfs, and the high and variable quantity of non-plant material included with the cores. The monthly withdrawal of cores was therefore abandoned early on, and the method omitted during the ensuing full year's study.

The first year's use of stains also gave variable results, due to dilution and washing out of the colouring agents by heavy rainfall. This made the green marker zone difficult to see in all but the naturally pale yellow- coloured moss species. New fluorescent stains were therefore applied during the second year's study, but subject to the constraint that these chemicals had not been pretested in a "field trial" during 1980-81.

Several methods failed altogether for certain species. For example, nets were pulled up by birds in several cases, rainwashings from the coated metal wire used for fine "cranks" in the case of *Andreaea acutifolia* proved toxic to the plant, and all stems died in several bag treatments which reduced the value of the monthly measurements made using this technique.

Table 1.8. Six month trials for bryophyte spore extension recorded during summer 1981. **XXX** = method failed. () = \pm as percentage of mean. *Species not studied during six month programme.

	lunate spherules	cranks	tags	bags	nets	coring	stains	photography	n	mean success of all methods, and standard deviation
<i>Leptodermis subulniformis</i>	13.9 \pm 2.7 (9.1)	28.3 \pm 1.7 (5.9)							2	29.1 (1.15)
<i>Dicranella heterophylla</i>	4.8 \pm 1.3 (26.5)			2.4 \pm 1.2 (49.3)	3.9 \pm 0.5 (11.6)				3	3.7 (1.21)
<i>Leptodermis subulniformis</i>	9.2 \pm 0.8 (8.5)		7.3 \pm 0.7 (9.1)	6.8 \pm 0.4 (6.3)	6.3 \pm 1.7 (27.7)				3	7.6 (1.47)
<i>Leptodermis subulniformis</i>	6.8 \pm 0.3 (4.1)			13.8 \pm 7.8 (57.7)	15.6 \pm 1.6 (10.2)		XXX		3	6.4 (0.58)
<i>Leptodermis subulniformis</i>	13.7 \pm 1.9 (13.8)		10.5 \pm 0.8 (7.8)	4.3 \pm 0.4 (9.0)	2.3 \pm 0.2 (7.8)	5.5 \pm 5.0 (10.5)	5.8 \pm 1.9 (33.7)		6	12.1 (1.04)
<i>Leptodermis subulniformis</i>	6.5 \pm 0.9 (13.7)		6.8 \pm 0.5 (7.0)	3.8 \pm 0.4 (10.2)		13.4 \pm 1.2 (22.7)*	7.0 \pm 2.5 (35.8)		5	1.7 (0.94)
<i>Leptodermis subulniformis</i>	3.4 \pm 0.4 (7.1)			4.8 \pm 0.5 (11.2)		4.5 \pm 2.9 (64.0)	5.5 \pm 0.1 (1.8)		3	3.8 (1.55)
<i>Leptodermis subulniformis</i>	5.3 \pm 0.6 (11.1)			2.2 \pm 1.2 (7.8)		7.0 \pm 3.4 (48.3)*	4.1 \pm 0.38 (9.3)*		2	5.3 (0.55)
<i>Leptodermis subulniformis</i>	6.6 \pm 0.7 (11.7)			3.7 \pm 0.2 (6.5)	1.6 \pm 0.4 (22.4)		5.0 \pm 0.6 (12.1)		3	4.4 (2.25)
<i>Leptodermis subulniformis</i>	3.8 \pm 0.3 (9.0)		6.1 \pm 0.3 (5.6)						4	3.5 (1.41)
<i>Leptodermis subulniformis</i>	5.9 \pm 0.9 (16.0)								3	6.7 (1.18)
<i>Leptodermis subulniformis</i>	10.3 \pm 2.9 (28.3)		9.3 \pm 0.6 (6.9)		6.5 \pm 0.8 (12.3)		15.7 \pm 0.8 (5.4)		4	10.5 (1.85)
<i>Leptodermis subulniformis</i>	1.5 \pm 0.1 (7.2)				3.0 \pm 0.5 (15.3)	XXX			3	3.2 (1.81)
<i>Leptodermis subulniformis</i>	XXX				1.6 \pm 1.1 (6.2)			0.8 \pm 0.03 (3.5)	2	1.2 (0.57)

*Species not studied during six month programme.

Tagging of stems proved the most difficult and time consuming of methods to apply, although it gave reliable results, especially in the monthly study. To increase the sampling intensity at the beginning of the second year's study using this method, would have required too much time to be spent in the field at the expense of the effort necessary to set out the other treatments in May 1981. Therefore, only three species were tagged (150 tags per species) for the 1981-82 study.

Other method/species combinations that were discarded for the second year's study can be seen by comparing Tables 4.8 and 4.9. A minimum of two of the most successful methods were applied to each species during the 1981-2 study. The only exception to this was Brachythecium subplicatum which showed a very high growth rate which caused nets and tags to become deeply buried in the carpet and therefore difficult to find and measure. The crank technique had proved particularly appropriate for the growth form of B. subplicatum during the six month study, and this was therefore the only technique applied to this species during the second year's growth period.

The results for stem length increment during the first year's monthly study as measured by the tagging technique are shown in Figure 4.4. Five out of the six species showed a peak in stem extension growth during the month of February, with the sixth (Brachythecium rutabulum) peaking in March. Of the six climatic variables measured at the weather station for the same period (Figure 4.8) this growth peak correlates most closely with ground level ("grass minimum") temperature which was also highest in the months of February and March. The rainfall peak in the preceding month of January may

Table 1.9 Annual shoot extension recorded during 1981-82 (in mm S.D.), () = SE as Percentage of mean.

Species	inmate markers	cranks	lags	buys	nets	coring	stains	photography	n	mean increments (standard deviation)
<i>Baccharis sp.</i>		42.0 ±1.4 (3.3)							1	42.0 ()
<i>Diapenthyon fasciculatum</i>		6.2 ±1.2 (18.7)							2	6.0 (0.28)
<i>Diapenthyon fasciculatum</i>		18.2 ±1.9 (7.6)	28.2 ±2.5 (8.7)		5.8 ±0.4 (6.2)		44.0 ±1.2 (2.8)*		2	23.2 (7.07)
<i>Camphorosma ripariense</i>		8.2 ±0.5 (5.7)		11.2 ±0.6 (5.1)					2	9.7 (2.12)
<i>Baccharis sp.</i>	12.3 ±1.2 (9.9)	10.2 ±0.8 (7.5)		9.2 ±0.4 (4.5)			11.5 ±0.4 (3.8)		4	10.8 (1.37)
<i>Phacelia nitens</i>		8.1 ±0.8 (9.9)		6.1 ±0.3 (5.2)			16.9 ±1.3 (7.4)*		2	7.1 (1.41)
<i>Chamaecrista humilis</i>		4.2 ±0.3 (6.3)			13.1 ±0.3 (2.4)				2	8.7 (6.29)
<i>Blennosiphium densiflorum</i>		7.0 ±0.3 (4.7)		8.7 ±0.1 (1.5)			8.8 ±0.3 (3.2)		3	8.2 (1.01)
<i>Chamaecrista colorata</i>		8.7 ±0.9 (10.6)		5.6 ±0.2 (3.8)			16.2 ±0.4 (2.3)*		2	7.15 (2.19)
<i>Cryptantha grandiflora</i>		6.2 ±0.5 (7.4)			13.3 ±0.3 (2.3)				2	9.8 (5.07)
<i>Baccharis lanuginosa</i>	8.2 ±0.8 (9.4)	3.0 ±0.3 (8.8)	4.9 ±0.2 (4.1)				19.6 ±1.9 (2.9)*		3	5.16 (2.64)
<i>Baccharis sp.</i>			19.0 ±1.3 (7.0)		12.3 ±1.4 (11.1)				2	15.7 (4.74)
<i>Chamaecrista sp.</i>									3	4.3 (1.30)
<i>Archaea acutifolia</i>	5.0 ±0.1 (2.6)	2.8 ±0.2 (5.8)			5.1 ±0.6 (11.2)		8.5 ±0.6 (7.6)*		3	2.0 (0.70)
<i>Chamaecrista vermicularis</i>					2.0 ±0.1 (4.3)		2.7 ±0.2 (8.2)	1.3 ±0.03 (2.3)	3	2.0 (0.70)
<i>Chamaecrista vermicularis</i>		15.2 ±1.6 (10.3)					10.0 ±0.8 (8.4)		2	12.6 (3.68)

show that greater stem weights are being achieved later in the growing season. This supports the findings of other studies, where main stem extension growth in bryophytes was found to occur in the early season, with stem weight increment becoming more important in the later season as structural and storage materials are consolidated by the plants. These trends are confirmed when length and weight increments for all species are combined, as presented in Figure 4.7.

Shoot length increment results for all methods from the 1981-82 full year's growth period are given in Table 4.9, with the pooled mean for each species calculated as in Table 4.8. In most cases, low variability of means confirmed the efficacy of the method for the species in question. Exceptions occurred in the case of the stain technique which as mentioned earlier, had not been pre-tested using the same chemicals during the six month study. Microscopical examination of each plant under ultra violet light revealed that the stain had not adsorbed successfully to the surface of five of the species, but had formed a precipitate on the surface which had "washed down" the stem to become trapped at leaf bases in a layer deeper in the turf. Thus, although the variability of the distance from the stem apex of this layer was low, the standard error statistic is misleading in this instance. The shoot increment means obtained with this method can be seen to be very high in relation to the results of other methods applied to the same species. These values were therefore omitted from the calculation of the overall mean for shoot extension in these cases.

There are two other anomalous figures worthy of comment viz. the values obtained by

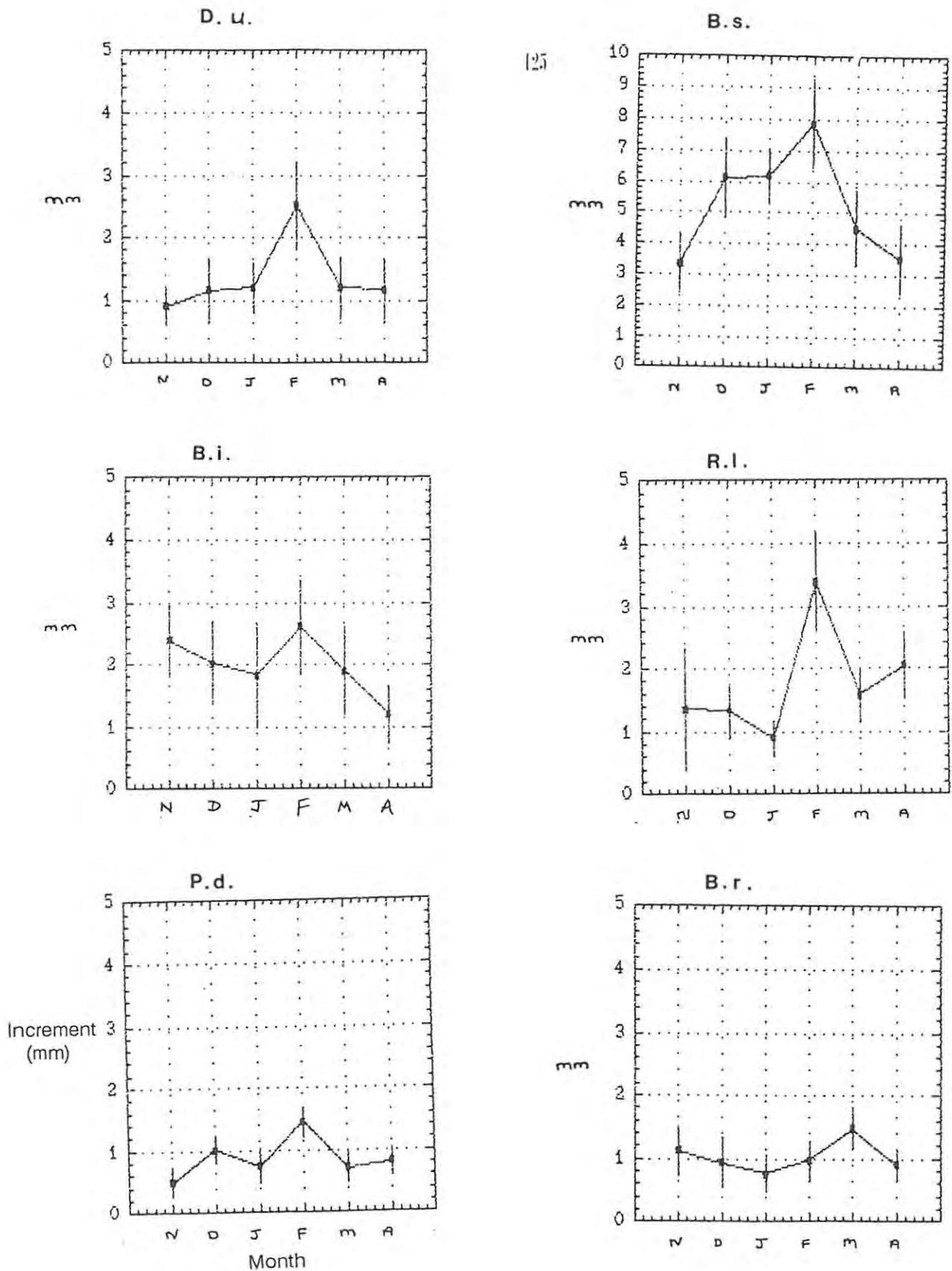


Figure 4.4

Mean monthly shoot length increment in six species of Marion Island bryophytes during summer 1980-81, as measured by tags. Species abbreviations as in Table 4.1.

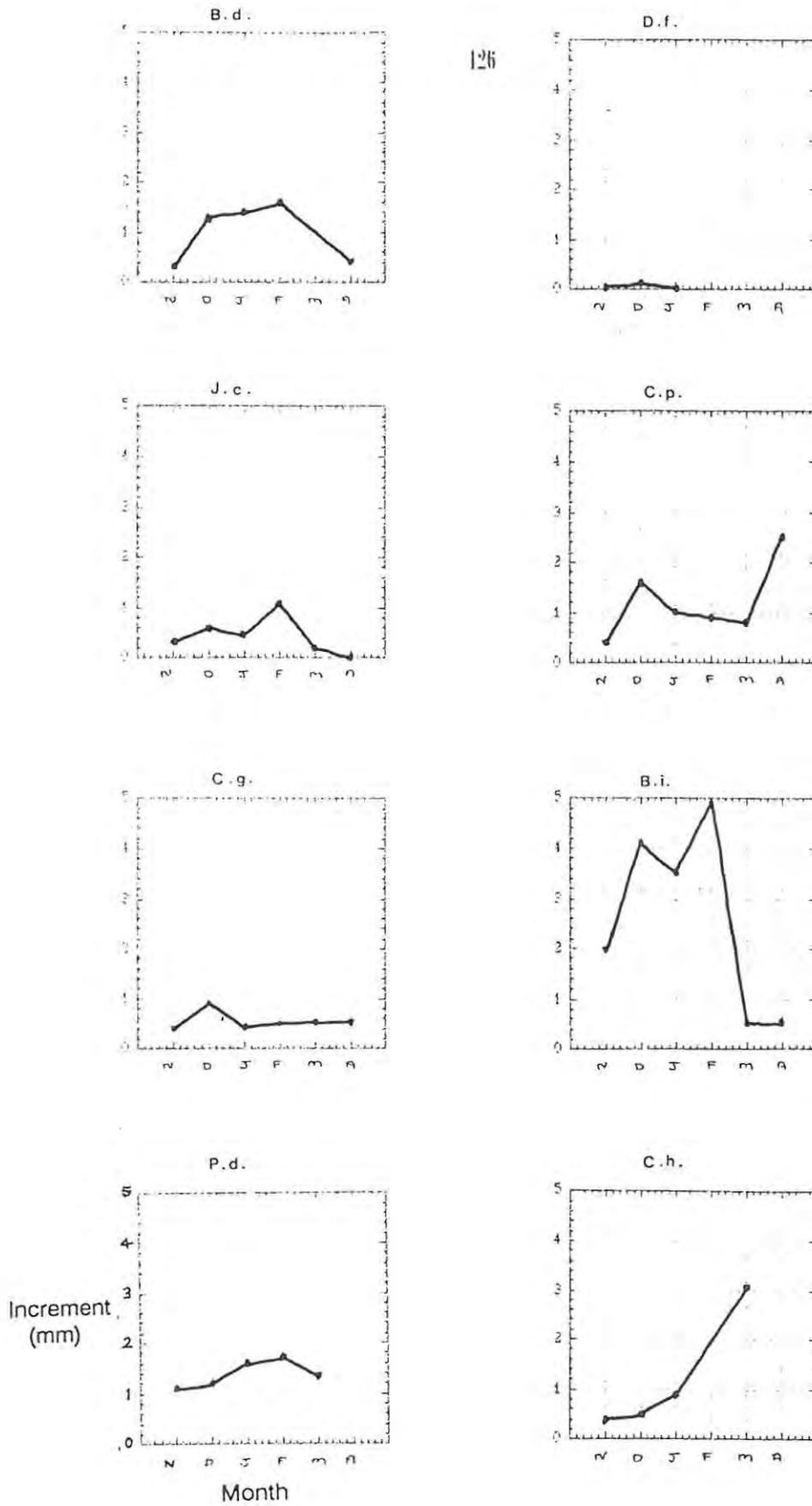


Figure 4.5

Mean monthly shoot length increment in eight species of Marion Island bryophytes during summer 1980-81, as measured by the bag technique. Species abbreviations as in Table 4.1.

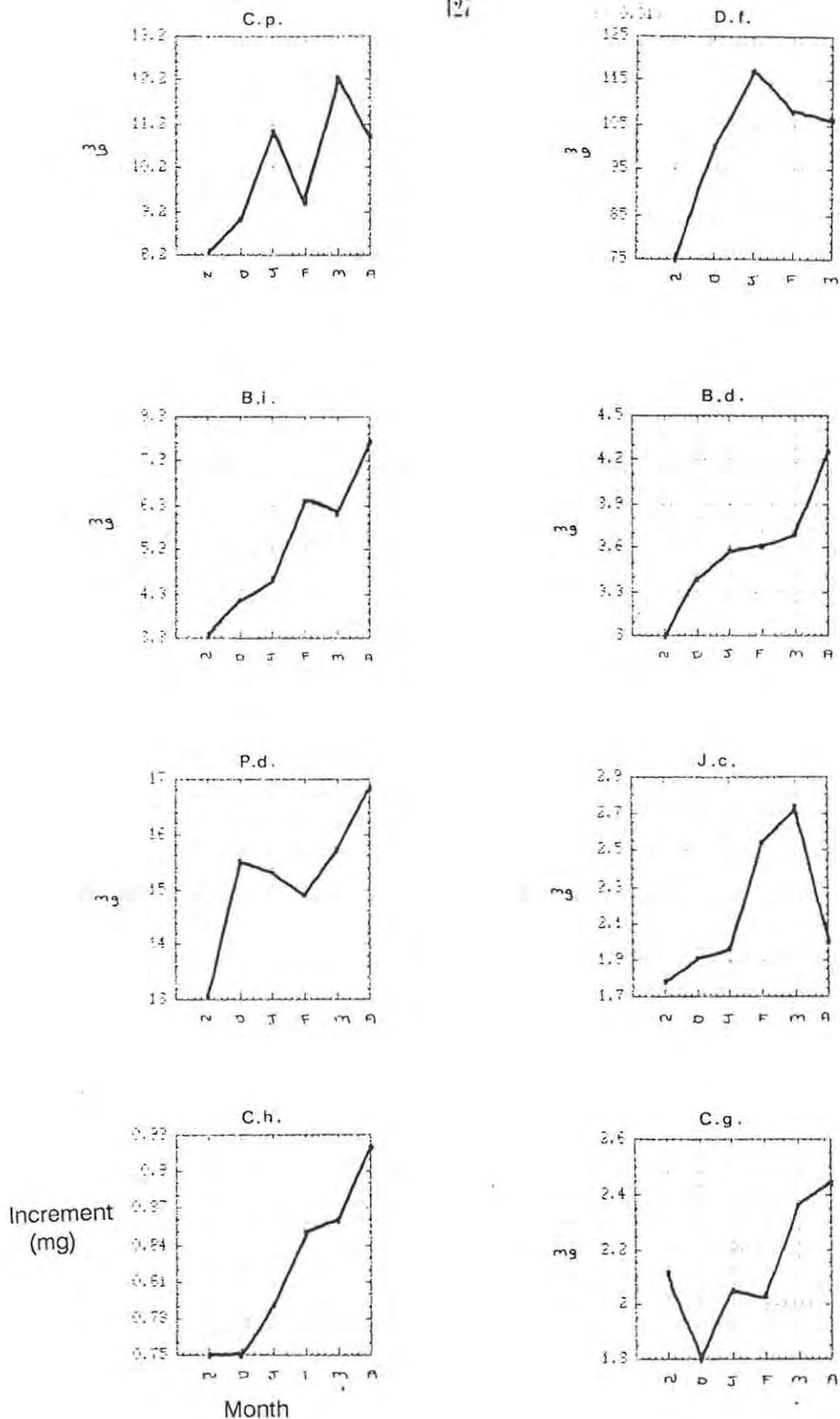


Figure 4.6 Mean monthly shoot weight increment in eight species of Marion Island bryophytes, as measured by the bag technique. Species abbreviations as in Table 4.1.

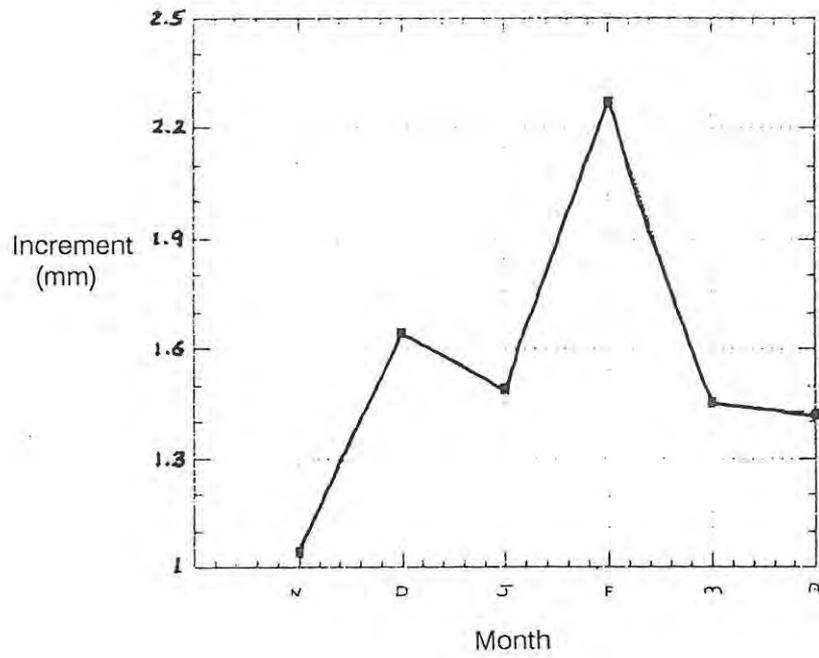
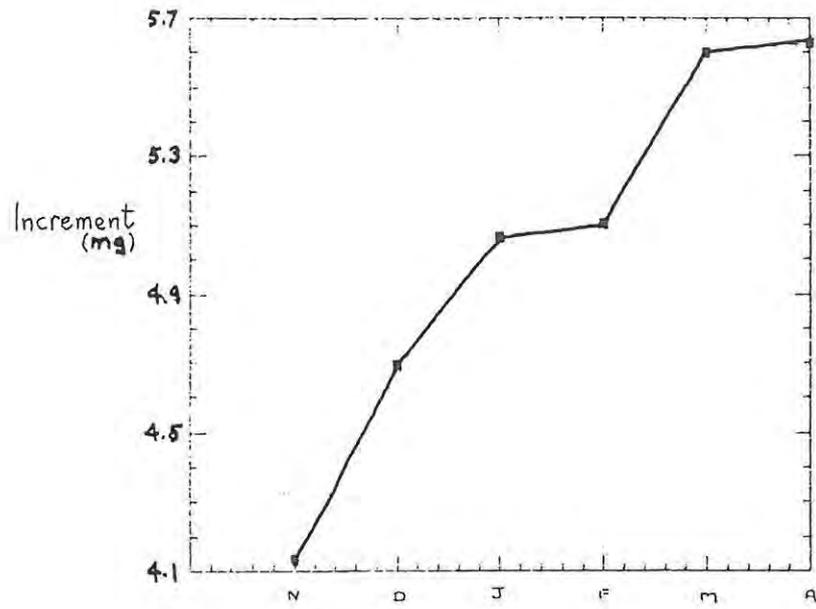


Figure 4.7

Combined mean monthly shoot increments for all Marion Island bryophyte species studied during summer 1980-81.

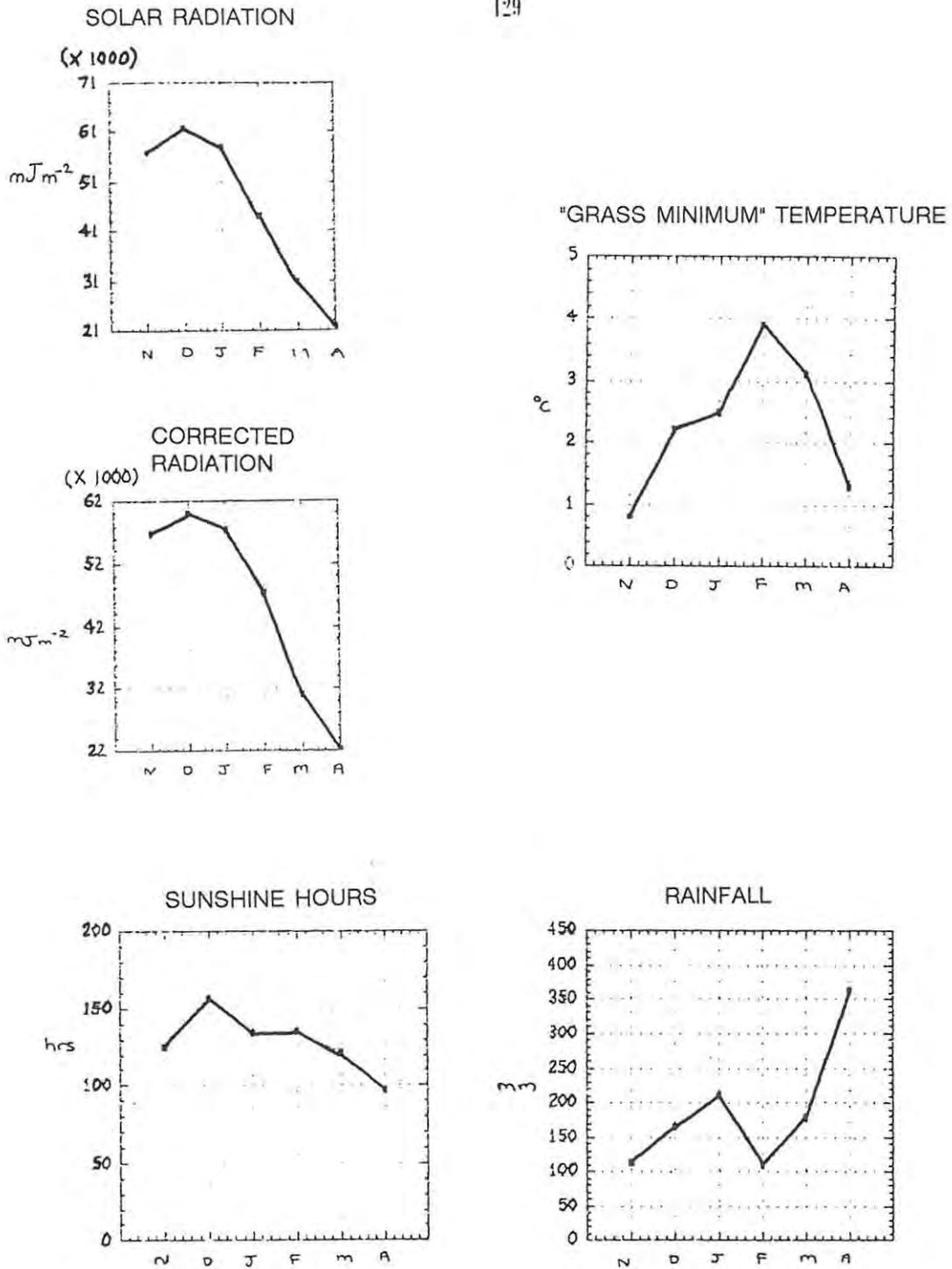


Figure 4.8 Climatic variables measured during the course of the monthly shoot increment study in summer 1980-81.

measurement of growth through a net in the cases of two of the leafy liverworts: Clasmatocolea humilis and Cryptochila grandiflora. These figures appear to be somewhat high compared with the values obtained by use of the crank technique (unfortunately the only other method applied during the full year's study of these species). However, no obvious reason could be found to account for this, and it is therefore accepted as natural microsite variation in growth plot production. The values from the net study are therefore retained in the calculation of the pooled shoot extension mean for these species.

Results of the core measurements which provided weights of stems cut to the mean 1981-82 increment length, are given in Table 4.10. Stem mass per unit length, shoot production on a 100% cover basis, and shoot production corrected to growth plot cover, are calculated in the same manner as the biomass figures of Table 4.6.

4.4 Discussion

4.4.1 Spatial shoot density

Shoot density (Table 4.5) ranged from a high of 280 cm⁻² in the tightly packed small cushion growth form of Andreaea acutifolia in the fellfield habitat, to circa 4 cm⁻² in the mire species Racomitrium lanuginosum and Ptychomnium densifolium, with their robust stems and more lax growth form.

Table 4.10 Annual shoot production of Marion Island bryophytes.

Species	stem length (mm)	single stem weight (mg)	±SD	Production 100% cover (g m ²)	Cover corrected production (g m ²)
<i>Brachythecium subplicatum</i>	42.00	3.61	±1.01	837.50	753.80
<i>Distichophyllum fasciculatum</i>	6.00	0.51	±1.27	253.50	240.80
<i>Drepanocladus uncinatus</i>	23.20	2.14	±0.56	338.10	287.40
<i>Campylopus purpureocaulis</i>	9.70	1.98	±0.48	520.70	390.50
<i>Breutelia integrifolia</i>	10.80	2.16	±1.33	345.60	276.50
<i>Ptychomnium densifolium</i>	7.10	7.79	±2.09	335.00	251.30
<i>Clasmatocolea humilis</i>	8.70	0.36	±0.04	360.00	252.00
<i>Blepharidophyllum densifolium</i>	8.20	0.82	±0.21	343.60	326.40
<i>Jamesoniella colorata</i>	7.20	1.09	±0.67	519.90	389.90
<i>Cryptochila grandiflora</i>	9.80	0.98	±0.42	395.90	277.10
<i>Racomitrium lanuginosum</i>	5.40	2.29	±1.02	103.10	61.70
<i>Brachythecium rutabulum</i>	15.70	1.59	±0.3	174.90	113.70
<i>Ditrichum strictum</i>	4.30	2.30	±0.76	545.10	27.30
<i>Andreaea acutifolia</i>	2.00	0.16	±0.01	448.00	58.30
<i>Clasmatocolea vermicularis</i>	12.60	0.48	±0.06	511.20	408.90

4.4.2 Biomass

Biomasses (Table 4.6) of individual species increase by an order of magnitude from fellfield (Ditrichum strictum: 165.7 g m⁻²) to the drainage line habitat (Brachythecium subplicatum: 1649.5 g m⁻²). A similarly wide span of biomass values is also found among species within the mire habitat. This is influenced by the larger number of species present at each site in the mires and the corresponding differences in cover values of each species. There is no obvious soil moisture correlation among these species, and it is probable that other factors such as mineral and fibre content are more important in controlling standing biomass levels through their influence on decomposer activity in this environment (Heal et al. 1981).

This may also account for the highest biomass levels on a 100% basis being recorded in the fellfield habitat. The more extreme climatic conditions might be expected to inhibit decomposer activity in this environment, and the dense cushion growth forms of the characteristic mosses, with their low energy values and poor bacterial degradability, could also contribute to the high biomass figures.

This thesis provides biomass data for the dominant individual bryophyte species of Marion Island, which are of value for future ecological studies whenever these same species are present. Biomasses of other e.g. vascular plants were not assessed in this study, and as measurements were not made of the aerial cover of the larger scale communities in which the bryophytes occur, it is therefore not possible to present accurate "whole vegetation" biomass figures for comparison with those from other tundra

sites. However, a crude estimate of whole vegetation biomass at each bryophyte study plot can be obtained by multiplying the cover values for each species at the plot (see Appendices) with biomass values for those same species at Marion Island, where this data is available.

Rough approximations of community biomass are thus presented in Table 4.1 with data drawn from this thesis for bryophytes, and V Smith (1985) for vascular plants. Multiplying these figures by the percentage aerial distribution of related habitat types as assessed by V Smith (1976, 1977c) (see also Table 3.7) gives a further crude approximation of the biomass of bryophyte dominated communities on the Eastern Coastal Plain of Marion Island. The value of 1280 g m^{-2} can in no way be considered accurate for the reasons given above, and because the communities assessed by Smith (1976, 1977c) do not correspond closely with those studied here. However, it supports the intuitive prediction of high biomass for the well-vegetated Eastern Coastal Plain of Marion Island, and compares logically with the mean value of 118 g m^{-2} for all IBP sites (predominated by much more open and sparse vegetation particularly in the Arctic) and with the $1000\text{-}2000 \text{ g m}^{-2}$ figures for similar mire dominated sites elsewhere in the sub-Antarctic (see below).

4.4.2.1 Review of bryophyte biomass data from other tundra sites.

The individual bryophyte species biomass figures, and the derived "pseudo-community" figures for Marion Island can be compared with the broad range of biomass data from

Table 4.11 Community Biomass at study plots g m^{-2} . t.v. = total vegetation, bryos = bryophytes only. * from V Smith 1977c.

Study plot	t.v.	bryos
<i>Brachythecium subplicatum</i>	2600	1650
<i>Distichophyllum fasciculatum</i>	1003	925
<i>Drepanocladus uncinatus</i>	891	818
<i>Campylopus purpureocaulis</i>	2321	2192
<i>Breutelia integrifolia</i>	1280	820
<i>Ptychomnium densifolium</i>	1255	765
<i>Clasmatocolea humilis</i>	2195	1822
<i>Blepharidophyllum densifolium</i>	2360	2209
<i>Jamesoniella colorata</i>	2264	1363
<i>Cryptochila grandiflora</i>	1502	641
<i>Racomitrium lanuginosum</i>	1582	1208
<i>Brachythecium rutabulum</i>	1394*	695
<i>Ditrichum strictum</i>	784	320
<i>Andreaea acutifolia</i>	821	373
<i>Clasmatocolea vermicularis</i>	2188	1650

Table 4.12 Mean bryophyte biomass (g m^{-2}) for each habitat complex, and as represented on the Eastern Coastal Plain (ECP) of Marion Island

	t.v	bryos	habitat complex cover on ECP %	habitat complex biomass on ECP (g m^{-2})
Drainage Line	2600	1650	0.5	1300
Mires	1665	1276	43	71595
Slope	1394	695	13	18122
Fellfield	2188	347	42	33705
Biotic/Salt spray	2188	1386	1.5	3282

mean 1280 g m^{-2}

other sub-polar/tundra sites. These have been tabulated in Longton (1980), Wielgolaski et al (1981), V Smith (1976, 1985) and R Smith (1984). Values from the IBP tundra sites (Wielgolaski et al, 1981), ranged from less than 1 g m^{-2} in polar desert "barrens", to over 1000 g m^{-2} at some Antarctic sites, with an overall mean of 118 g m^{-2} .

As at Marion Island, biomass correlated with soil water regime at most of the IBP tundra sites. At Point Barrow in Alaska, bryophyte biomass was less than 20 g m^{-2} in dry heaths and meadows dominated by vascular plants. It ranged from $149\text{-}290 \text{ g m}^{-2}$ in polygon tundra, $37\text{-}244 \text{ g m}^{-2}$ in sedge meadows, $60\text{-}500 \text{ g m}^{-2}$ in mesic to moist sedge-moss meadows and $142\text{-}499 \text{ g m}^{-2}$ in wet meadows (Wein & Bliss, 1974; Webber, 1978; Miller et al, 1980).

At more southerly Alaskan stations figures tended to be somewhat higher in the relatively dry habitats for which data is available e.g. 89 g m^{-2} in grass heath, $300\text{-}400 \text{ g m}^{-2}$ in sedge heath and dwarf shrub tundra. A very high biomass figure of 4753 g m^{-2} was obtained in wet meadow at Dempster, Alaska, where a 10cm deep accumulation of biomass occurred due to low decomposition (Wein & Bliss, 1974).

Similar results were obtained from the Canadian IBP site at Truelove Lowland on Devon Island e.g. 2.4 g m^{-2} in barrens, $75\text{-}166 \text{ g m}^{-2}$ in raised beach cushion plant-lichen and dwarf shrub communities, and up to 623 g m^{-2} in a cushion plant-moss community (Bliss, 1975, 1977; Svoboda, 1977; Bliss et al, 1984). Values from wet habitats were more equivalent to those at Marion Island, for example Vitt & Pakarinen (1977) recorded

a biomass range of 752-1100 g m⁻² in bryophytes from wet sedge moss sites.

As with the biomass accumulation noted at Dempster in Alaska, high values were obtained in the Canadian study for two bryophyte species occurring in relatively dry and protected niches on rock outcrops where decomposition was slow viz. Hylocomium splendens - 2218 g m⁻², Racomitrium lanuginosum - 4928 g m⁻². The latter species also occurs at Marion Island, where it had a biomass of 1640 g m⁻² on a 100% cover basis in its wet (relative to the Canadian site) growth plot. In certain areas at Marion Island however e.g. at the edge of mires above the water table, Racomitrium lanuginosum forms poorly decomposed turves of 200-300mm depth (Plate 18). Measurements on a restricted number of cores from these sites indicated biomass values (including the brown, inactive portion of the turf) of 4000-5000 g m⁻², closely equivalent to those obtained at Arctic sites for the same species.

High biomass figures have been recorded elsewhere in Arctic Canada e.g. 2128 g m⁻² in grass heath at Elef Ringnes Island and 2136 g m⁻² in moss-grass meadow at King Christian Island. In general however, bryophyte biomass decreases southwards as climatic conditions improve and vascular plants increase in cover (Table 4.13).

In the Scandinavian Arctic, bryophyte biomass ranged from 9 g m⁻² in lichen heath to 68 g m⁻² in dwarf shrub tundra. Bryophytes attained far higher levels of biomass in the protected understory of "woodland" tundra e.g. 611 g m⁻² in Birch thicket and 3072 g m⁻² in Willow thicket at Hardangervidda in Norway (Kallio & Karenlampi, 1975; Wielgolski, 1975). A similar trend was noted at Kevo in Finland, from 72 g m⁻² in low alpine heath

to 332 g m⁻² in Birch woodland. During the Fennoscandian IBP studies, mire habitats were only studied at Stordalen in Sweden, where bryophyte biomass ranged from 299-312 g m⁻² (Roswall et al. 1975; Sonesson & Bergman, 1980).

Table 4.13 Bryophyte biomass at decreasing latitudes in Arctic Canada (Svoboda, 1977).

Site	Latitude	Bryophyte biomass
Mellville Island	75° N	716g m ⁻²
Banks Island	73° N	567g m ⁻²
Victoria Island	71° N	139g m ⁻²

High bryophyte biomass also occurs in the "forest tundra" zone of the USSR e.g. 319-1345 g m⁻² in shrub tundra at Vorkuta and 3178 g m⁻² in Birch scrub at Koni. A narrow span of values of between 200-400 g m⁻² is reported for a wide range of tundra communities across many sites in the Russian Arctic, although some wetter areas have higher levels of bryophyte biomass e.g. >800 g m⁻² in polygon troughs, even in the far north.

In the more extreme fellfield habitats of the northern tundras however, levels are usually less than 200 g m⁻² e.g. Franz Josef Land: 98 g m⁻²; polar desert: 40 g m⁻² (Rodin & Bazilevich, 1967; Alexandrova, 1970; Gorchakovsky & Andreyashkina, 1972; Pospelova, 1972; Bliss et al. 1975; Vassilevskaya, 1975).

In continental Antarctica, some similarities with the extreme conditions of the High Arctic are reflected in generally low biomass figures for bryophytes. Bryum argenteum and Bryum antarcticum had biomasses of less than 20 g m^{-2} in Victoria Land and at Ross Island respectively (Longton, 1974), although Kappen (1984) recorded a figure of 177 g m^{-2} for B. algens in northern Victoria Land. Within individual colonies (i.e. on a 100% cover basis) accumulation may be locally high however, especially in areas of snow melt at coastal sites. Longton recorded 602 g m^{-2} and 1108 g m^{-2} for B. argenteum and B. antarcticum on this basis, and Seppelt & Ashton (1978) recorded 1097 g m^{-2} for B. algens at Mawson Rock.

Very low decomposition and long term accumulation leads to the formation of massive, partially compacted deposits of bryophyte biomass in the unique moss turves of the Antarctic Peninsula and South Orkney islands. 28400 g m^{-2} of bryophyte biomass was recorded in 240mm deep turves of Polytrichum alpestre on the Antarctic peninsula, and 43600 g m^{-2} was measured in 330mm deep turves at Signy Island (Longton, 1970). One metre deep banks of Chorisodontium aciphyllum at Signy Island, contained 46000 g m^{-2} , the upper limit for bryophyte biomass at any site (estimates have ranged from $10000\text{-}24300 \text{ g m}^{-2}$ for biomass in the "live" upper layer of about 200mm depth in this species)(Longton, 1970; Baker, 1972; Collins, 1973; Edwards, 1973; Fenton, 1980).

Vegetation types at Signy Island that more closely approximate those at Marion Island, show similar biomass figures e.g. $140\text{-}254 \text{ g m}^{-2}$ in grass turfs and 2100 g m^{-2} in wet moss carpets (Collins, 1973; 1976).

Limited bryophyte biomass data are available from two other sub-Antarctic islands (South Georgia and Macquarie). At South Georgia, Festuca grassland had a bryophyte biomass of 140-240 g m⁻², grass heath: 500 g m⁻² and Acaena herbfield: 130-500 g m⁻² (Callaghan, 1973; Greene & Walton, 1975; Smith & Stephenson, 1975).

Macquarie Island showed figures ranging from 6 g m⁻² in Poa grassland, to 20-400 g m⁻² in Pleurophyllum herbfield. A cover corrected figure of 150 g m⁻² for Ditrichum strictum is similar to the value of 166 g m⁻² obtained for this species at Marion Island (but see later discussion concerning production of this species). Unfortunately, it has not been possible to trace biomass data from wet, bryophyte dominated habitats at any of the sub-Antarctic islands, to compare with those obtained at Marion Island.

V Smith (1976, 1985) reported data for bulked bryophyte biomass from his study of vascular plant dominated communities at Marion Island. These figures are tabulated alongside those for habitats from the present study in Table 4.14. The differences between the data are explained by the differences in habitat type between the two studies, and also the disparity in cover value of bryophytes at the sites chosen by the two authors (trace presence in many of Smith's sites, dominant presence at Russell's sites). Results are very similar however, if the data are compared on an equivalent cover basis between the two studies, and also where similar microsites were chosen e.g. the Brachythecium understory.

Table 4.14 Data for bulked bryophyte biomass from previous studies at Marion Island (V Smith, 1976; 1985).

Habitat	Bryophyte biomass
<i>Acaena</i> drainage line with <i>Brachythecium rutabulum</i> understory	224 - 482 g m ⁻²
Mire grassland	147 - 219 g m ⁻²
Mire grassland (peak biomass)	321 - 400 g m ⁻²
Fellfield	1 - 15 g m ⁻²
<i>Poa cookii</i> tussock grassland (biotic)	70 - 230 g m ⁻²

At temperate and tropical sites, bryophyte biomass only becomes significant at higher altitude sites where vascular plants become less frequent, and in some wet communities such as mires and higher altitude tropical forest. Some figures are given in Table 4.15 for comparison with the tundra values.

In general therefore, it can be seen that Marion Island shows high bryophyte biomass figures compared with the rest of the world. Even within the tundra biome there are few sites to compare, as the Arctic for example has more extreme conditions of temperature and physiological drought that will tend to depress bryophyte production and hence biomass accumulation, notwithstanding the slowed decomposition rates. Equivalent biomass levels to those found at Marion Island are only approached in comparable habitats such as wet mires elsewhere in the world, with higher accumulations occurring locally in unusual instances such as in the case of *Racomitrium lanuginosum* noted above, and in the unique "moss banks" of the Maritime Antarctic.

Table 4.15 Sample data for bryophyte biomass at temperate and tropical stations

Locality	Habitat	Biomass g m ⁻²
Mt Washington, NH, USA	Alpine zone	170 - 238
	"Krummholz"	47
	Coniferous	51 - 61
	Northern Hardwood	3
	Oak	2
U.K.	Welsh Oakwood	158
	Montane grassland (Snowdonia)	80
	Wet Sedge Mire (Moor House)	146
Ireland (Glenamoy)	Woodland understory	32
	Open bog	569
	Grass/Heath Mire	569
Poland	Woods	1 - 48
	Meadows	224 - 446
Hungary	Woodland epiphytes	4.3
South Western USA	Desert	0 - 2
South Africa	"Thornveld"	17 - 53
Tanzania	Forest epiphytes	1365
India	Ephemeral pans	2 - 11
	Pools	23 - 95

4.4.3 Production

4.4.3.1 **Six month growth study 1980-81:**

As stated above, the objective of the six month summer growth study was primarily to assess the effectiveness of the different growth techniques in advance of the full year's study, and to carry out monthly measurements to note any seasonal trends in bryophyte growth rate at Marion Island. The techniques aspect has been discussed in the results section, and the relationship of the complete six month growth increment (1981) with the full year's figures (1982) will be treated at the end of the discussion of the 1982 data.

With respect to the summer seasonal growth pattern, the tagging technique proved most consistent in measuring monthly growth increments during the 1980-81 study. Results of these measurements for six species are given in Figure 4.4. Results were less consistent using the bag technique due to many missing values caused by shoot death. However, these results are included for comparative purposes in Figure 4.5, with the missing values indicated on the curves. Climatic variables recorded at the weather station during the same period are also graphed for comparison with the shoot increment curves (Figure 4.8).

Most species showed a curve of increasing stem extension growth during the summer months with a peak in February. The only exceptions were four of the bagged species

which had stunted growth due to disturbance of the colony caused by the technique. Of the tagged species only Racomitrium lanuginosum showed a peak later than February (by one month) which may have been related to its higher altitude and proximity to fellfield conditions. The greater distance of the Racomitrium growth plot from the weather station, also makes the climatic data less reliable in relation to the likely microclimate conditions pertaining at the study site.

In most cases, shoot length increment was two or three times greater in midsummer (February) than at the beginning or end of the summer period (November or May). This would seem to conflict with the idea of very constant climatic conditions causing continuous and little varying growth rates at Marion Island. There is evidence in bryophyte growth phenology however, for rapid shoot elongation in early summer to provide a greater volume of new photosynthetic tissue to take advantage of optimum conditions later in the growth season (Longton, 1988). This is followed by a period of reduced extension growth but increased mass accumulation later in the season, associated with the need to provide a reserve of materials for the oncoming period of reduced net photosynthesis (winter).

Only the bag technique was amenable to monthly weight increment measurement and as explained above, this method gave incomplete results due to shoot death in the smaller species. However, Longton (1988) has stated that there is little data on vegetative phenology in polar bryophytes, and the small amount of mass accumulation data obtained in the Marion Island study is therefore worthy of note. The weight increment curves are

therefore included for comparison in Figure 4.6, and several of them show a slowing of weight increase in mid season which supports the above observations concerning bryophyte phenology.

The dip in the mass accumulation curve often correlates with the February peak in length increment and this becomes clearer if the pooled means for all species are compared with respect to both parameters (Figure 4.7). Midsummer depression of biomass increment has been noted in other studies of tundra bryophyte production, where it is associated with shading effects due to overclosure of the vascular plant canopy (Hicklenton & Oechel, 1976; V Smith, 1985). However, as this factor was not relevant to the species of this study, an effect such as midsummer radiation/desiccation stress might have been more important at the microsite level, as noted for bryophytes in the U.K. by Proctor (1981). The February growth peak also coincided with the time of maximum mean monthly temperature, and the pooled mean monthly length increments for all species (both methods) showed a positive correlation ($r = 0.8444$ $P < 0.001$) with "grass minimum" temperature as recorded at the weather station during the experimental period.

The curves for sunshine hours and radiation show little or no correlation with growth, which is surprising considering the significant relationship between these variables recorded during the IBP studies (Wielgolaski et al, 1981). The low levels of solar radiation or differences in spectral composition under the cloudy skies could possibly be of relevance here.

It is interesting to note that a significant correlation exists (-0.4941 $P < 0.05$ for the pooled species means, both methods) between rainfall and shoot growth. The correlation was negative in all cases except for some of the inconclusive bagged samples. This is of interest in relation to the suggestions of Pisano (1983) concerning the relationship of climatic conditions with vegetation in the western Magellanic Moorland of southern Chile and Tierra del Fuego. Pisano inferred that the climate of this region could be "too wet" for the growth of Sphagnum and he hypothesised that the species of Sphagnum occurring in central southern Patagonia require at least brief periods of relatively dry conditions when the moss turf is not totally inundated, for optimum growth and success against other species. He cites this as a reason for the dominance instead, of leafy liverworts e.g. Blepharidophyllum, Jamesoniella etc., in the mires of western Patagonia.

There is plenty of experimental evidence for the depression of photosynthesis and slowing of growth of bryophytes subject to levels of tissue water content that are the norm at Marion Island (heavy external water loads are thought to slow diffusion of environmental CO₂ to the photosynthetic sites (Proctor, 1982). The bryophyte rich mire vegetation of Marion Island is structurally and floristically more closely related to that of south western Patagonia than anywhere else (excepting the other islands of the Kerguelen Province). Pisano's ideas could therefore apply to Marion Island also, as the extreme rainfall conditions are equivalent, and Sphagnum is missing from the island's flora, notwithstanding its common occurrence in upwind spore source areas such as Gough Island and Central Patagonia for example.

4.4.3.2 Annual Shoot Production 1981-82:

Mean shoot length increments (Table 4.9) of Marion Island bryophytes during the 1981-2 season ranged from 2mm in Andreaea acutifolia (fellfield) to 42mm in Brachythecium subplicatum (drainage lines). This falls within the range noted by Longton (1988) for polar/tundra sites viz: from <1mm for Bryum inconnexum at Syowa Station on the Antarctic coast (Matsuda, 1968) to 170mm for Sphagnum riparium forming tall turfs in a Swedish mire (Sonesson & Johansson, 1973). Increments in the Antarctic region range from less than 1mm per year (this study) to an extreme of 89mm for Pohlia wahlenbergii in a wet flush at South Georgia (R Smith, 1982).

In the same habitat, Brachythecium subplicatum showed a mean increment of 48mm (max. 58mm) according to R Smith (1982). This compares with a mean figure of 42mm (max 60mm using the crank method) for the same species at Marion Island. The plants at South Georgia occur in snow patch flushes and have a looser growth form with lower colony density but more robust stems than their Marion Island counterparts.

The results of the production measures for the 1981-2 full-year's study are given in Table 4.10. As the final figures are themselves products of several other averaged components that contain differing and uncorrelated levels of variation, no fiducial limits can be given.

The mean ASP values (cover corrected basis) ranged from 27.3 g m⁻² yr⁻¹ in Ditrichum strictum (fellfield) to 753.8 g m⁻² yr⁻¹ in Brachythecium subplicatum (drainage line). As

with the biomass figures, production on a 100% cover basis in Andreaea acutifolia and Ditrichum strictum was equivalent to many of the species from the more mesic habitats, which emphasises the efficiency of the cushion growth form in the fellfield environment.

Unlike the variable levels of biomass found among the mire species, production appears remarkably constant in the range $240.8 \text{ g m}^{-2} \text{ yr}^{-1}$ to $390.5 \text{ g m}^{-2} \text{ yr}^{-1}$ for the species in the mire habitat. The only exception was Racomitrium lanuginosum ($61.7 \text{ g m}^{-2} \text{ yr}^{-1}$) which as already explained, occurred in a dry mire habitat that verged on fellfield conditions. This species has been noted for its low productivity at several other stations (Tallis, 1959). The low bulk density of tissue on an areal basis in Racomitrium lanuginosum, is equivalent to that of the pleurocarpous species with lax growth forms, and contributes to its minimal production on a 100% cover basis (see also energy calculations Chapter 5).

Clasmatocolea vermicularis, showed a higher cover corrected production figure than any of the other species excepting Brachythecium subplicatum from the drainage line, which may indicate the nutrient status advantage pertaining in the biotic habitat.

A comparison of total stem length increments recorded during the six month measurement period and the following full year's study, showed that summer shoot length increase amounted to 68% of the full year's value. The figure is influenced by three anomalous values. Drepanocladus uncinatus, which was studied in a different growth plot during the second year's study, showed significantly less growth at its first site compared to the second. This was caused by slowing of growth in shoots which were

measured in elevating portions of the colony, where drying out occurred as the water table receded during the first year. The results suggest that there may have been a degree of sub-conscious overcompensation for this during the laying out of the growth plot in the second year. The wetter, green parts of the carpet may therefore have received more attention during 1981-2 when much higher increments were recorded. By the end of the second year's study, many of these green areas had also elevated into yellowing, dried out mounds and it had become clear that the carpet was acting as a small scale cyclical "hummock-hollow" complex, similar to the *Sphagnum* bogs of oceanic moorland in other regions of the world (Clymo, 1982).

In addition there were two species that showed greater average shoot increments during the six month summer period in 1980-81 than during the entire year's growth in 1981-2 (*Racomitrium lanuginosum* and *Breutelia integrifolia*). This could be partly a result of the high variability in these particular figures, but could also be a true reflection of differing microenvironmental conditions at the growth plots of these species in ensuing years. Unfortunately both species were relatively distant from the weather station (Figure 4.1), and climatic figures recorded at the base station may not have been as relevant to them, as to the other species studied.

If the three anomalous values are omitted therefore, an average figure of 62% (SD \pm 12.8%) is calculated for the summer season's growth as a proportion of the full year's shoot extension. By comparison, the full year period received 22.5% more "degree months" (based on mean monthly grass minimum temperature), 50.1% more sunshine

hours and 79.4% more rainfall than the six month summer season, according to the weather station figures for the respective periods.

For most of the species therefore, these figures suggest that a mean figure of about 40% of stem extension growth may take place during the six month winter period. By reference to the climatic data presented in chapter two, and by taking into account empirical evidence concerning bryophyte light/temperature/moisture photosynthetic response envelopes (Oechel & Sveibjornsson, 1979; Longton, 1980; Proctor, 1982), climatic conditions can be calculated to be theoretically favourable for net photosynthesis and growth of bryophytes the whole year round at Marion Island as predicted by V Smith, 1985. The above figures for extension growth therefore support the finding (V Smith, 1987b) that a significant amount of annual production takes place during the winter period.

4.4.3.3 Comparison of Marion Island bryophyte production with other regions:

The following values for community production from elsewhere in the world, are presented for comparative purposes with the Marion Island species data. Where the Marion Island values refer to species with cover approaching 100% and no well developed overstory, the figures will approximate to community values. However, it should be remembered that the Marion Island data refer to single species and not whole communities, and are therefore only strictly compatible when compared with values for other named species.

Bryophyte shoot production values recorded at the U.S. IBP site at Point Barrow in Alaska, ranged from $<20 \text{ g m}^{-2} \text{ yr}^{-1}$ in dry heaths to $27\text{-}162 \text{ g m}^{-2} \text{ yr}^{-1}$ in wet meadows (Rastorfer, 1978; Miller et al. 1980). Wein & Bliss (1974) measured values of between 25 and $127 \text{ g m}^{-2} \text{ yr}^{-1}$ at various sites (Dempster, Eagle Creek, Elliot) in Eriophorum/dwarf shrub tundra further South in Alaska. At the Canadian IBP site on Devon island, values ranged from $<0.1 \text{ g m}^{-2} \text{ yr}^{-1}$ in polar desert "barrens" (Bliss, Svoboda & Bliss, 1984), through $0.5\text{-}20 \text{ g m}^{-2} \text{ yr}^{-1}$ in cushion plant-lichen and moss fellfield, and dwarf shrub tundra (Bliss, 1975), $8\text{-}105 \text{ g m}^{-2} \text{ yr}^{-1}$ in sedge moss meadows (Bliss, 1975, 1977; Muc, 1977), and $60\text{-}350 \text{ g m}^{-2} \text{ yr}^{-1}$ in moss dominated carpets (mean = $293 \text{ g m}^{-2} \text{ yr}^{-1}$ for the latter habitat, Vitt & Pakarinen, 1977). Measurements at eight other sites in Arctic Canada spanned the range $1\text{-}32 \text{ g m}^{-2} \text{ yr}^{-1}$ for grass heaths and herb or grass-moss meadows, rising to a maximum of $70 \text{ g m}^{-2} \text{ yr}^{-1}$ in a wet sedge moss meadow on Banks Island (Bliss & Svoboda, 1980; 1984).

Callaghan (1981) reported a production figure of $350 \text{ g m}^{-2} \text{ yr}^{-1}$ for Pohlia wahlenbergii at a sheltered site on Disko Island in Greenland, with an extreme figure of $1400 \text{ g m}^{-2} \text{ yr}^{-1}$ for localised areas of the carpet. At Scandinavian IBP sites, bryophyte production values ranged from $2\text{-}7 \text{ g m}^{-2} \text{ yr}^{-1}$ in "forest tundra" through $50\text{-}67 \text{ g m}^{-2} \text{ yr}^{-1}$ in alpine heath and Birch tundra at Kevo in Finland (Kallio, 1975); with a Sphagnum mire site at Stordalen in Sweden giving $(43\text{-}) 70 \text{ (-}150) \text{ g m}^{-2} \text{ yr}^{-1}$ (Roswall et al. 1975; Wielgolaski et al. 1981). At Hardangervidda in Norway, figures spanned the range $10 \text{ g m}^{-2} \text{ yr}^{-1}$ in dwarf shrub tundra, $48\text{-}88 \text{ g m}^{-2} \text{ yr}^{-1}$ in dry meadow and heath, $210 \text{ g m}^{-2} \text{ yr}^{-1}$ in Salix shrub tundra and $70\text{-}173 \text{ g m}^{-2} \text{ yr}^{-1}$ in wet sedge-moss meadows. Wet habitats dominated by bryophytes e.g.

Dicranum elongatum, produced 148-270 g m⁻² yr⁻¹ (Wielgolaski & Kjølsvik, 1973; O'stbye, 1975; Kallio & Heinonen, 1975) with 800-900 g m⁻² yr⁻¹ predicted in "creeks" (equivalent to drainage lines at Marion Island).

In contrast to the large amount of biomass data reported for the USSR, very little bryophyte production data exists for the Soviet Arctic. A range of 0.9-15 g m⁻² yr⁻¹ was quoted by Tikhomirov et al (1981) for the major habitats of the Eastern European forest and Arctic tundra, but these figures are based on the uncritical methods of Andreev (1966) who assumed production to be 10% of biomass in all cases. Pyavchenko, incompletely cited in Sukachev & Dylis (1964) gives a bryophyte production value in "swamp herbage" in Russia of 96 g m⁻² yr⁻¹.

The average bryophyte production value for all IBP sites was 91 g m⁻² yr⁻¹ but this figure is inflated by high values from the sub-Antarctic sites. A mean production figure for typical northern tundra would approximate to half this value, which equates more closely with the 20-50% range for bryophyte production in relation to vascular plant production quoted by Wielgolaski et al (1981). Due to more amenable conditions in the Arctic, vascular plants tend to predominate in the vegetation, which accounts for their higher production figures. More extreme conditions in the Antarctic lead to a predominance of cryptogamic plants, and oceanic conditions in the sub-Antarctic favour bryophyte growth which leads to relatively higher production figures for these plants in southern latitudes.

Notwithstanding the large amount of work carried out on bryophytes in the Antarctic

region, there are no published values based on harvest techniques for bryophyte production in continental Antarctica (Longton, 1988). Seppelt & Ashton (1978) noted cover corrected "green biomasses" of 116.5 and 80.9 g m⁻² for Bryum algens and Grimmia lawiana at Mawson Station and Longton (1974) estimated 5 g m⁻² yr⁻¹ for community production of Bryum argenteum at Ross Island (approx 100 g m⁻² yr⁻¹ on a 100% cover basis).

The production in turves of Polytrichum alpestre on the Antarctic Peninsula ranged from 390-420 g m⁻² yr⁻¹ with higher values pertaining elsewhere in the Maritime Antarctic e.g. at Signy island (430-660 g m⁻² yr⁻¹) (Longton, 1979; Collins, 1976 a,b; Collins & Callaghan, 1980; Fenton, 1980). Production in banks of Chorisodontium aciphyllum at Signy Island spanned the range 223-477 g m⁻² yr⁻¹ (Baker, 1972; Collins, 1973; Collins et al, 1975). A low bryophyte production value of 85 g m⁻² yr⁻¹ was recorded in Deschampsia (grass) sward at Signy Island (Collins et al, 1975), but with higher values being recorded in wet moss carpets at that locality: 223-893 g m⁻² yr⁻¹ (Calliergidium austro-stramineum, Calliergon sarmentosum and Brachythecium austro-salebrosum).

A mean 100% cover production range of 630-710 g m⁻² yr⁻¹ is cited for Drepanocladus uncinatus in two communities at Signy Island according to Collins (1973). These figures were obtained in plant material from a wet hollow and are approximately double the 100% cover value for the same species at Marion Island. As explained in the results section however, the Marion Island figures for this species also included some values from drier hummocks. Nevertheless, the mean Marion Island shoot length increment was

23mm as compared with only 16mm in Drepanocladus uncinatus at Signy Island, which emphasizes the difference in growth form and habitat between the two localities.

At Marion Island, Drepanocladus uncinatus forms loose carpets in oligotrophic mires and along the edges of standing water pools, and has a lax, almost weft-like form in drier parts of the carpet. At Signy Island the species has a much denser growth form, covering rocky areas in a shallow carpet and in hollows between cushion and turf forming mosses along the margins of melt water channels (see photos in Collins, 1976).

Turning to the sub-Antarctic, a range of 120-1055 g m⁻² yr⁻¹ was quoted for production in bryophyte communities at South Georgia (Clarke et al. 1971; R Smith, 1984). 250 g m⁻² yr⁻¹ was recorded in dry Festuca grassland, and 120-400 g m⁻² yr⁻¹ for a Tortula robusta understory in Acaena ("low shrub") herbfield (similar to the niche of Brachythecium rutabulum at Marion Island). 450-510 g m⁻² yr⁻¹ was measured in Polytrichum moss banks, and the highest figures were obtained in wet flush and stream bank habitats (e.g. 1028 g m⁻² yr⁻¹ for Pohlia wahlenbergii and Tortula robusta (Clarke et al. 1971). Once again it should be emphasized that these figures are indicative, but are not strictly comparable where whole communities have been measured, as the Marion Island data refer to single species only.

R Smith (1982) conducted a production study using the bag technique, on eleven species of bryophytes at South Georgia, partly during the same period over which the Marion Island study was taking place. The results of this investigation are shown in Table 4.16.

Table 4.16 Shoot production data (120 days growth) for bryophytes at South Georgia (from R Smith, 1982).

Equivalent Marion Island habitat complex	South Georgia habitat and species	Shoot production g m^{-2}	Habitat mean
Drainage Line	Pohlia wahlenbergii stream bank	711	766
	Pohlia wahlenbergii stream margin	782	
	Brachythecium subplicatum flush	1017	
	Brachythecium austro-salebrosum	554	
Mire	Calliergidium austro-stramineum bog	642	483.5
	Tortula robusta bog	325	
	Tortula serrata bog	251	
	Sphagnum fimbriatum bog	716	
Slope	Tortula robusta slope	111	157.5
	Tortula serrata slope	93	
Fellfield?	Andreaea rock face	104	104
Biotic zone?	Polytrichum alpinum	957	957

The range of colony production values at South Georgia (93-1017 g m⁻² yr⁻¹) is similar to that obtained from the fifteen species at Marion Island (103-838 g m⁻² yr⁻¹). At both localities, Brachythecium subplicatum showed the highest production figures. For the purposes of comparison in Table 4.16, the South Georgia species have been classified into broad ecological habitat groupings corresponding as nearly as possible with those defined at Marion Island. Omitting the moss bank species (a growth form absent from Marion Island) the mean production levels from these habitat groupings at South Georgia correspond very closely with those obtained at Marion Island, and follow the same moisture gradient.

At Macquarie Island, bryophyte production in Poa grassland was measured at 21 g m⁻² yr⁻¹, and at 146 g m⁻² yr⁻¹ in Pleurophyllum herbfield (the latter figure is similar to the value for Brachythecium rutabulum in Blechnum/Acaena "herbfield" at Marion Island). Seppelt & Ashton (1978) quote a figure of 145 g m⁻² yr⁻¹ for "green biomass" of Ditrichum strictum moss field (fellfield) at Macquarie Island and they cite the suggestion of J.F. Jenkin that annual production could be about double this i.e. 290 g m⁻² yr⁻¹ (plants with 22% areal cover).

Based on measured figures for the same species at Marion Island, Ditrichum strictum could be expected to have 120 g m⁻² yr⁻¹ production at the same level of cover, i.e. less than half the Macquarie Island value. This might be explained by the less precise method of estimating production in the Macquarie plants, but could also be a result of the somewhat different growth forms of the study material. In the lowland fellfield growth

plot at Marion Island. Ditrichum strictum formed fairly large and isolated, smooth-surfaced cushions. In the study site at Macquarie Island (see photo p. 385 in Seppelt & Ashton, 1978) the same species formed a larger surface area of very convoluted and coalescing cushions. The greater surface area of moss colony per plane unit area of moss-covered ground at Macquarie Island could thereby account for the discrepancy noted above.

In an independent study, V Smith (1985) gave a mean production estimate of $280 \text{ g m}^{-2} \text{ yr}^{-1}$ for bulked (several species) bryophyte samples from two mires at Marion Island, which compares closely with the average value of $275.4 \text{ g m}^{-2} \text{ yr}^{-1}$ obtained for the same habitat in this study.

This thesis provides production data for the dominant individual bryophyte species of Marion Island, which are of value for future ecological studies whenever these same species are present. Production values of other e.g. vascular plants were not assessed in this study, and as measurements were not made of the aerial cover of the larger scale communities in which the bryophytes occur, it is therefore not possible to present accurate "whole vegetation" production figures for comparison with those from other tundra sites. However, a crude estimate of whole vegetation production at each bryophyte study plot can be obtained by multiplying the cover values for each species at the plot (see Appendices) with production values for those same species at Marion Island, where this data is available.

Table 4.17 Total vegetation community production figures ($\text{g m}^{-2} \text{yr}^{-1}$) at bryophyte study plots, corrected for cover percentage of each species present.

Study plot principal species	total vegetation
<i>Brachythecium subplicatum</i>	1528
<i>Distichophyllum fasciculatum</i>	303
<i>Drepanocladus uncinatus</i>	337
<i>Campylopus purpureocaulis</i>	504
<i>Breutelia integrifolia</i>	642
<i>Ptychomnium densifolium</i>	446
<i>Clasmatocolea humilis</i>	603
<i>Blepharidophyllum densifolium</i>	437
<i>Jamesoniella colorata</i>	612
<i>Cryptochila grandiflora</i>	784
<i>Racomitrium lanuginosum</i>	340
<i>Brachythecium rutabulum</i>	497
<i>Ditrichum strictum</i>	243
<i>Andreaea acutifolia</i>	254
<i>Clasmatocolea vermicularis</i>	987

Table 4.18 Mean community production values for the major habitat complexes on the Eastern Coastal Plain at Marion Island.

	Community production value ($\text{g m}^{-2} \text{yr}^{-1}$)
Drainage Line	1528
Mires	501
Slope	497
Fellfield	249
Biotic/Salt spray	987

Rough approximations of community production are thus presented in Table 4.17, with data drawn from this thesis for bryophytes, and V Smith (1985) for vascular plants.

Overall, Marion Island shows high production figures due to its preponderance of wet sites. Values within the various island habitat groupings tend also to be significantly higher than in similar habitats in Arctic tundra, although not strikingly so as is the case with biomass figures. Values in the 200-600 g m⁻² yr⁻¹ range are commonly met with in wet (e.g. mire) habitats elsewhere in the world, although only a few unusually productive sites equal the rates commonly recorded for "flush" and drainage line species in the sub-Antarctic. Several of these very high production figures (> 1000g m⁻²yr⁻¹) were reported for sub-Antarctic bryophytes during the IBP (e.g. Collins, Baker & Tilbrook, 1975). The present study has confirmed that these so called "anomalous" levels of production, are frequently met with in the sub-Antarctic, especially where minerotrophic conditions or biotic enrichment occurs.

In general, high productivity in the sub-Antarctic can be stated as being primarily due to the long growing season, constantly wet conditions and lack of competition from vascular plants in this region (R. Smith, 1982, V. Smith, 1987b). These factors will be discussed further in the conclusion (Chapter 10).

4.5 Grazing and decomposition of Marion Island bryophytes

Although bryophyte decomposition at Marion Island was not measured directly during this study, production:biomass turnover rates and initial annual loss rate based on mass differences between the most recent year's production segment and the residual biomass can be calculated from the data already presented. These parameters provide an approximation to maximum expected decomposition and allow a relative comparison between species of this study, and with similar data from other investigations.

Data for residual biomass (biomass/standing crop minus production) are given in Table 9.2. These values are combined with the production values from Table 4.10, to give a second biomass estimate to compare with that of the independently measured first biomass calculation. Close agreement ($r=0.9127$ $P<0.0001$) exists between the two sets of figures.

The ratio between the figures for shoot production weights and the first biomass measurements are given in Table 9.2 to provide an estimate of "turnover" (Heal et al, 1981). "Annual loss rate" based on production and residual biomass is also given in Table 9.2. Both sets of figures show the same trends. The turnover ratio varies between 0.06:1 (Racomitrium lanuginosum) and 0.73:1 (Clasmatocolea vermicularis) with an equivalent range for loss rate (6.3-59%, in the same species respectively).

"Decomposition" measured in this way appears lowest in the species of relatively xeric (fellfield and dry mires) sites, and highest at the moist sites (e.g. the drainage line). High

variability between species values indicates that other factors may be at least as important in influencing these results however. The highest loss rate is predicted for the nutrient rich, biotic habitat where most of a year's production of Clasmatocolea vermicularis may be lost in less than two years. High environmental and plant nutrient levels are normal at this site and in drainage lines (see Chapter 8), and such levels correlate with enhanced decomposer activity in tundra ecosystems generally (Heal et al, 1981).

In addition, resistant cell walls and the presence of phenolic/antibiotic compounds can also slow the microbial degradation of bryophytes so that an accumulating peat profile may come to consist largely of bryophyte remains. Heal, Flanagan, French & Maclean (1981) and M. Smith (1982) concluded that microbiological substrate quality and water availability were the most important controls on decomposition in tundra, and that latitude related temperature effects on microbial activity were of lesser significance.

Tissue Carbon to Nitrogen ratios were not measured in the bryophytes of the present study. However, those species with qualitatively "tough" stems, thick cell walls and large amounts of hyaline tissue (e.g. Campylopus purpureocaulis and Racomitrium lanuginosum etc.) do show the lowest decomposition rates according to the turnover figures.

The loss rate figure of nearly 30% for Andreaea acutifolia appears anomalous in this

regard. This could be partly due to the difficulty experienced in delimiting the zone of "clearly recognisable shoots" and separating this from "peat" within the Andreaea cushions. There is evidence however for ameliorated microclimate, moisture retention and presence of invertebrates inside these cushions at Marion Island (Huntley, 1971), which might account for the unexpectedly high "decomposition" rate predicted for this species. Alternatively the production component may have been overestimated due to wind abrasion and litter loss, as this species occurs in the most windswept habitats on Marion Island, and often forms "moss balls" where cryo-nival perturbation phenomena are prevalent.

On average, more than 10% of annual production is lost to decomposition by bryophytes at most tundra sites according to IBP figures (Heal et al, 1981). However, lower rates pertained at wet sites, particularly in the Antarctic. Baker (1972) for example obtained values of 1.3-2.4% in mires on Signy Island. Moss turfs at Signy Island showed an annual loss rates of 0.7-3% and similar results were obtained at South Georgia (R Smith, 1984). Wet moss carpets (Calliergon and Drepanocladus) on the other hand, lost 14-25% per year, and Brachythecium austro-salebrosum from a minerotrophic flush lost 40-50% (Collins, 1973). These latter data compare closely with the results for bryophyte species in the mire and drainage line habitats at Marion Island.

The following general picture of bryophyte decomposition in relation to peat

accumulation in tundra emerged as a result of IBP studies. In exposed fellfield habitats, production is generally low and decay rates are also low, leading to only shallow peat accumulation. In mesic to wet sites and especially where nutrients are not limiting, production may be high but so too may be decomposition, which again limits peat accumulation. In very wet sites, although surface decay may be high, decomposition at depth will be severely retarded by waterlogging, and where nutrients are low, by high tissue C:N ratios. Considerable accumulation is therefore likely to occur at these sites.

In respect of decomposition rates this picture is supported by the Marion Island results. It would be preferable however, to conduct direct measures of decomposition at the island, and to compare peat depths beneath the different bryophyte communities to confirm the above observations. It is well known already, that maximum peat depths measured at Marion Island all occur beneath the most bryophyte-rich mire communities (Schalke & van Zinderen Bakker, 1971).

4.6 Conclusion

4.6.1 Suggestions regarding methodology

This study has confirmed that techniques for the measurement of shoot extension growth in bryophytes should firstly be appropriate to the growth form of the species under study. Secondly they should be applied in combination to allow mutual corroboration of findings as there is no absolute means of determining the accuracy of results using the methods cited (Clymo, 1970).

A high degree of variability of bryophyte growth is commonplace in relation to spatial heterogeneity of the microhabitat, and large numbers of samples may be required to ensure statistically valid results. Many replicates may also be required to guard against unforeseen factors that may negate long periods of work (e.g. removal of markers by animals, or effects on growth caused by the marking method itself). Studies in the tundra biome have proved that the amount of time that it is possible to spend in the field is also a critical factor where adverse weather conditions may hinder the marking out of the large numbers of replicates necessary.

Coring to a reference level proved ineffective in this study. Tags were difficult to apply and could interfere with growth, but may be the only method suitable for species with diffuse growth forms e.g. wefts and loose turfs. Staining with fluorescent dyes offers an attractive method, particularly if a consistently adsorbent compound can be found. Nets also provide a convenient method if little lateral growth is expected, while bags

overcome this latter constraint but require careful use if stem excision is likely to affect growth potential.

Innate markers are useful where present and may allow integration of past growth for many years. The segments should be checked for their relationship to a true year's growth however, before assumption of annual periodicity can be made. The variation of the "cranked wire" technique used in this study proved the most successful method, and applicable to the widest range of growth forms at Marion Island.

Biomass or harvesting methods in general are cheap and usually simple in execution, although as stated above some techniques may prove tedious to apply to difficult growth forms where large numbers of replicates are required. There is a need for controlled studies on the effects of experimental techniques currently used, on the growth of bryophytes. Further testing of methods that show promise for future use is also required e.g. fluorescent staining.

4.6.2 Biomass and Production data

Mean bryophyte biomass in the different habitat complexes at Marion Island parallels the soil moisture gradient noted by Gremmen (1981)(lowest in fellfield, highest in the drainage line. There is a wider variability among species of the mire complex however, which is probably due to differing nutrient relationships and plant tissue degradability. The monthly shoot production data point to year round growth, with a mid summer season temperature (and probably radiation) related peak. There is also some evidence

for depression of growth due to superabundant moisture at certain times.

Annual bryophyte production (cover corrected) is also clearly related to the moisture gradient, although colony production (on a 100% cover basis) in the fellfield species may be equivalent to that of mire species, confirming the efficiency of the cushion growth form in the more extreme habitat. Very constant production figures were measured across the range of conditions in the mire habitat in contrast to the variable biomass data. This points to decomposition being a stronger control than production on net biomass accumulation in this habitat complex. This in turn correlates with findings from other mire habitats around the world, and validates the increased effort put into decomposition and microbiological studies at Marion Island during the mid and late 1980s.

The data support a scenario of fairly slow decomposition in fellfield due to poor decomposer substrate quality and relatively xeric conditions, coupled with little production due to the adverse climatic conditions. This leads to low overall levels of biomass accumulation in the fellfield habitat. In contrast, high production occurs in the wet and more nutrient rich habitats (biotic zone and drainage line). High decomposition rates will pertain here also however, so that low amounts of biomass occur in relation to production (although absolute levels of biomass may still be appreciable). In wet but more nutrient-poor habitats such as most of the mire sites, intermediate to high production occurs but decomposer activity may be slowed by poor substrate quality and waterlogging, thus allowing often heavy biomass accumulation.

Conclusions regarding the relationship of biomass and production at Marion Island with intrinsic and extrinsic variables affecting growth, will be reserved until after these factors have been treated in the following chapters.

CHAPTER FIVE

ENERGY CONTENT**5.1 Introduction**

Ultimately, all substances are simply patterns of energy, and the amount of energy present in a substance can therefore be regarded as the most fundamental measurable characteristic when comparing natural materials. Following the seminal studies of Arthur Tansley and Charles Elton in the 1920s, and the pioneering work of Raymond Lindeman (1942) on energy in ecosystems, Howard Odum (1957) introduced the concept of modelling trophic dynamics which has since strongly influenced the methodology of ecosystem studies worldwide (e.g. the International Biological Programme (Cousins, 1975), the South African Savanna Ecosystem Project (Huntley & Morris 1978).

Criticisms have been raised against this methodology in respect of energy transfer at the consumer levels (Cousins, 1985). However, the measurement of energy levels at the primary producer level remains an important component of ecosystem studies for purposes of the calculation of photosynthetic efficiencies, defining agricultural potential and comparing natural ecosystems on a worldwide basis.

Forman (1968) cited energy measurement as the most accurate method for comparing bryophyte standing crop in various ecosystems. He also commented on the paucity of

published data on bryophyte energy values at that time. More data became available however, during the IBP investigations into productivity of the tundra biome. Bryophytes reach their greatest relative importance in terms of biomass in this biome, when compared with other ecosystems (Richardson 1981).

During the tundra biome project, the highest values of production, and efficiency of solar energy conversion were found in vegetation at sub-Antarctic sites (Wielgolaski et al 1981). However, energy values for only four species of bryophytes were measured in this zone i.e. at South Georgia (Smith & Walton, 1973).

The objectives of the present investigation of energy contents were:

- 1) to contribute to the calculation of energy values at the primary production level for the modelling of trophic dynamics in the Marion Island ecosystem
- 2) to allow calculation of radiant energy conversion efficiency for the bryophyte component of this ecosystem
- 3) to determine whether energy values are correlated with production in Marion Island bryophytes
- 4) to test the suggestion of Forman (1968) that caloric values may be related to phylogenetic groupings within the Bryophyta.

5.2 Materials and methods

Clumps of stems of 15 bryophyte species were collected from the study plots on the Eastern Coastal Plain of Marion Island during May (late summer/early winter) 1981. This material was frozen in polythene bags and returned to the mainland for determination of energy value during 1982. The bunches of shoots included the entire standing crop (green and brown portions of the stem) down to soil level or to the point where decomposition rendered extrication of intact stems impossible.

Samples were washed in distilled water and visible foreign particles removed by forceps. Samples were then oven dried at 70°C for 24 hours and milled in a tissue grinder to give a uniform powder. Three tablets of about 1g each were prepared for each species from the powdered samples by use of a pill press.

Pre-weighed tablets were ignited with platinum fuse wire in a Gallenkamp adiabatic bomb calorimeter equipped with a microprocessor unit for temperature control. The energy content of the sample was calculated from the hydrothermal equivalent of the equipment (measured with reference to material of known energy content - Benzoic Acid: 26.473 kJ g⁻¹) multiplied by the temperature rise of the ignited sample, minus small corrections for fuse wire oxidation and acid production (Lieth, 1975).

The mean energy content of two ignitions was recorded for each species. The third tablet

was bombed if variation between the first two exceeded 0.209 kJ (50 calories). In common with all other studies of bryophyte energy contents known to the author, it proved impossible to obtain a precision of 0.105 kJ (25 cal) between replicates (the maximum deviation stipulated by Lieth, 1975). As it is preferable to compare energy values on the basis of organic dry matter, this component was determined by ashing subsamples of each species. Ashing was carried out in a muffle furnace at 550°C for two hours, followed by cooling of the sample crucibles from 200°C to room temperature in a desiccator before weighing.

5.3 Results and discussion

The replicate and mean energy values for Marion Island bryophytes are given in Table 5.1, expressed on a dry weight and ash-free dry weight basis. Percentage ash contents are given in the final column of the table. For ease of interpretation, energy values are given in both kilojoules and calories in the table. The data represent single tissue samples which will show trends between species, but not intra-species variation. The standard deviations show variation between bomb samples due to experimental error.

5.3.1 Energy values

The replicate and mean energy values for bryophytes at Marion Island ranged from 14.09kJ g⁻¹ (14.79 ash free) in Breutelia integrifolia of water tracks in mires, to 16.55kJ g⁻¹ (17.21) for Jamesoniella colorata typical of the drier mire soils. In common with the

Table 5.1 Energy values and ash content of Marion Island bryophytes.

Species	Energy kJ/g dry weight \pm standard deviation.	Calories	Energy kJ/g ash free	Calories ash free	Ash content (%)
<i>Brachythecium subplicatum</i>	14.75 \pm .131	3523	15.52	3708	5.3
<i>Distichophyllum fasciculatum</i>	15.72 \pm .075	3755	16.37	3910	4.1
<i>Drepanocladus uncinatus</i>	15.47 \pm .446	3695	15.83	3781	2.3
<i>Campylopus purpureocaulis</i>	15.81 \pm .060	3776	16.07	3838	1.7
<i>Breutelia integrifolia</i>	14.09 \pm .306	3366	14.79	3533	5.0
<i>Ptychomnium densifolium</i>	14.67 \pm .035	3505	15.52	3707	5.8
<i>Clasmatocolea humilis</i>	16.55 \pm .065	3952	16.84	4029	1.8
<i>Blepharidophyllum densifolium</i>	15.62 \pm .110	3730	16.23	3877	4.0
<i>Jamesoniella colorata</i>	16.55 \pm .065	3952	17.21	4110	2.0
<i>Cryptochila grandiflora</i>	15.84 \pm .099	3783	16.68	3983	3.3
<i>Racomitrium lanuginosum</i>	16.46 \pm .236	3932	16.56	3956	0.6
<i>Brachythecium rutabulum</i>	16.04 \pm .180	3830	16.48	3935	2.7
<i>Ditrichum strictum</i>	16.29 \pm .095	3890	16.37	3910	0.5
<i>Andreaea acutifolia</i>	16.04 \pm .090	3830	16.10	3846	0.4
<i>Clasmatocolea vermicularis</i>	15.71 \pm .020	3753	15.91	3401	1.3
\bar{X}	15.71 \pm 0.695	3755	16.17	3864	2.714

findings of Pakarinen & Vitt (1977), mean energy values for individual species thus show a weak trend from lower values at hydric sites (drainage lines and mires) to higher values at the more xeric sites (slopes and fellfield) when expressed on a dry weight basis. Clasmatocolea vermicularis of the biotic/salt spray zone is intermediate in this regard, with an energy value similar to the mean for the group of mire species. The correlation coefficients for regression of energy content on soil water and plant water are -0.4446 ($P < 0.01$) and -0.3836 ($P < 0.05$) respectively.

However, as found by Pakarinen & Vitt, the variability at hydric sites is high. In the case of the Marion Island species, the range of values shown by bryophytes of the mire sites exceeds the range for the species from the other habitat types (Figure 5.1), and this contributes to the limited significance of the overall hydric-xeric trend in the dry-weight energy values.

A weak negative correlation also exists between energy content on a dry weight basis and production ($r = -0.4304$ $P < 0.05$) (Figure 5.2). The data for energy content in Figures 5.1 and 5.2 are expressed on a dry weight basis, representing energy content as related to entire plant biomass, including inorganic mineral content. This is a valid basis for comparing total standing crops of plant material, but is inappropriate when considering the accumulation of purely organic matter through photosynthetic energy fixation. In this case results must be expressed on an ash free basis.

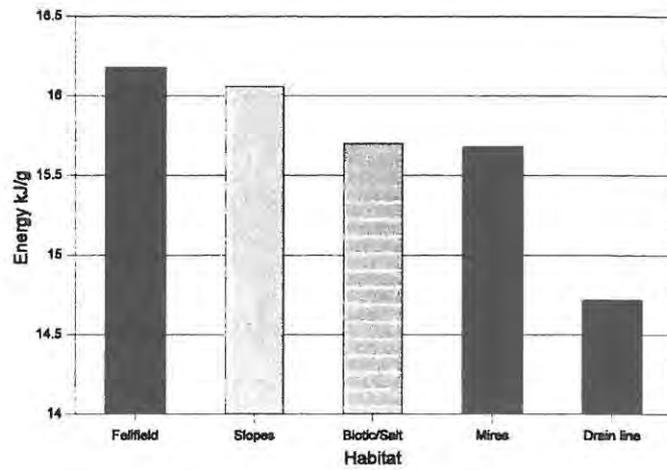


Figure 5.1 Mean bryophyte energy levels in the major habitat complexes at Marion Island

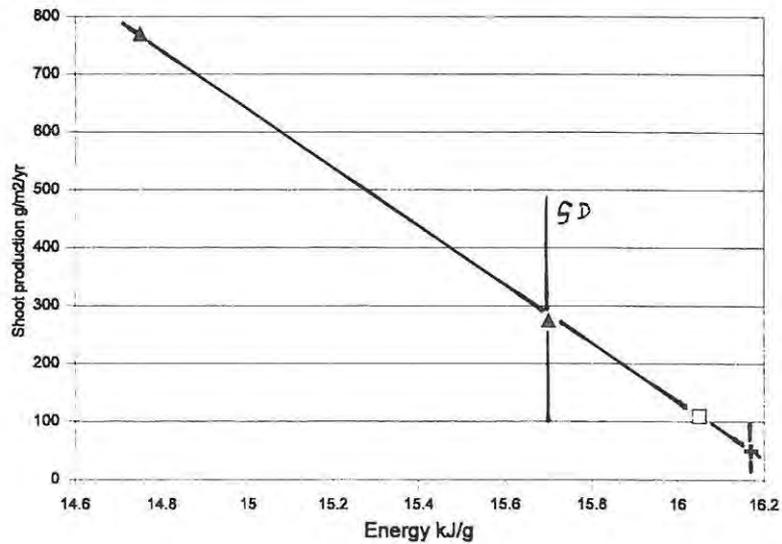


Figure 5.2 Regression of mean habitat production on mean habitat energy levels for bryophytes on the soil moisture gradient at Marion Island.

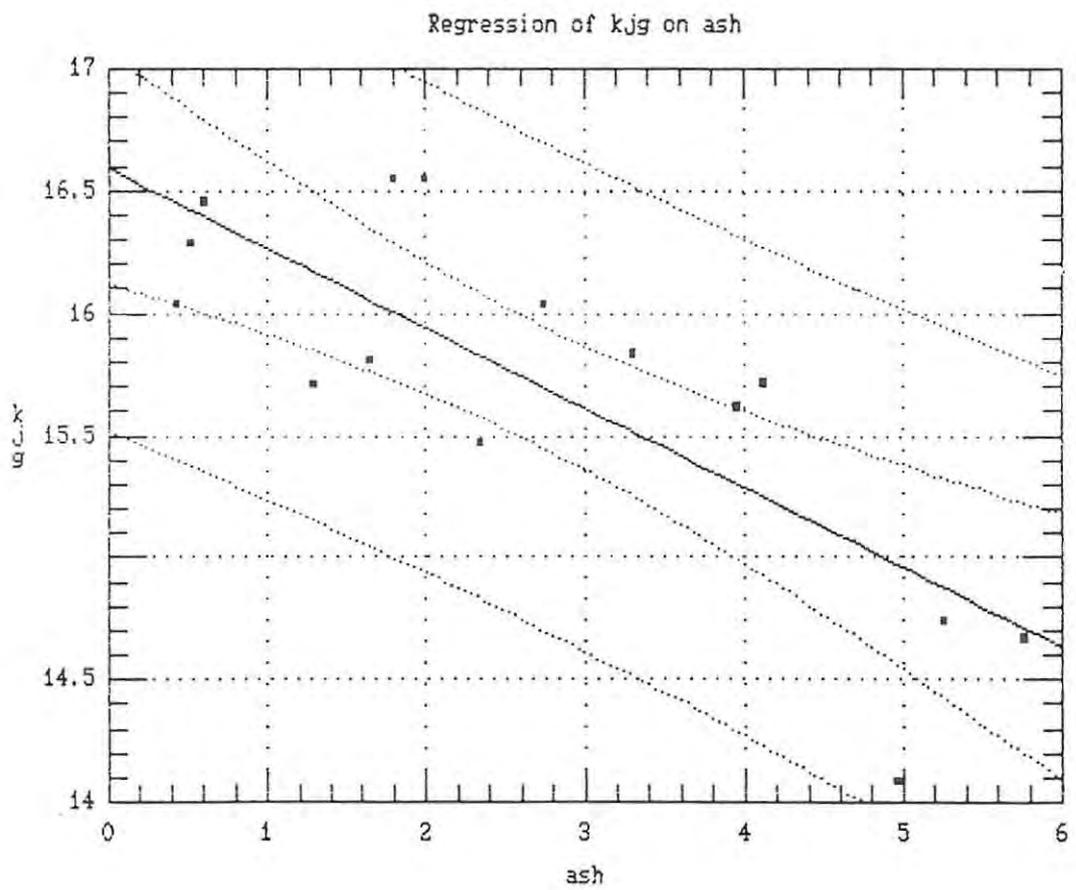


Figure 5.3

Regression of bryophyte energy content on ash content.

Ash content is negatively correlated with energy content (-0.8007 $P < 0.001$) in the bryophytes of this study, and similar results were obtained by Pakarinen & Vitt (1977) i.e. the less productive species of more xeric habitats show slightly higher energy contents and low ash contents, with the converse true of hydric species (Figure 5.3). The correlation coefficients for regression of ash content on soil water and plant water are 0.5995 ($P < 0.001$) and 0.624 ($P < 0.001$) respectively (see also Chapter 9).

However, the inverse relationship between energy and ash content results in a fairly constant range of energy values for all bryophyte species at Marion Island when compared on an ash free basis. No significant differences were therefore found when habitat/species groups were compared with respect to the energy content of their organic tissue only.

The range of energy contents between species (approx. 2 kJ) is similar to that found by workers at other tundra sites (Smith & Walton, 1973; Wielgolaski & Kjølvik 1975; Vitt & Pakarinen, 1977). The mean energy values for bryophytes from the drier, more exposed fellfield and slope habitats on Marion Island (16.15 - 16.26 kJ g^{-1}) compare well with the value of 16.14 kJ g^{-1} found by Forman (1968) for *Polytricha* from alpine tundra at Mt. Washington in New Hampshire. Forman's method of analysing the entire standing crop (green and brown portions of the stems) was also applied in the Marion Island study.

This methodology however, explains the discrepancy between the values obtained in the present study compared with results from elsewhere in the tundra biome. Other workers have analysed the upper green part of the stem only ("active" zone/current years growth), which accounts for the higher energy values reported in their studies. This method can be expected to show up differences between species more clearly, but will provide less accurate energy estimates for standing crop.

Several researchers have analysed green and brown parts of the bryophyte stem separately, but no other study has compared the energy contents of the green portion with the green plus brown portion of the plant. This prevents **direct** comparison of the results of the present study with other tundra data.

However, Forman's (1968) data for whole stems were supplementary to those of Bliss (1962, 1968) for seven bryophyte species from the same habitat and locality, which were analysed for current year's growth only. As Forman did not include ash free values it is only possible to directly compare dry weight figures between their respective studies. Bliss's mean value of 18.18 kJ g^{-1} for the green portion of alpine tundra bryophytes is 12.4% higher than Forman's 16.20 kJ g^{-1} for green plus brown tissue of the same or related species from the same site.

Wielgolaski and Kjelvik (1975) found energy differences of up to only 5% between green and brown portions of bryophyte stems at Fennoscandian sites. This could be

explained by less discrete partitioning of the active/non-active parts of the stem in growth forms at these more mesic sites. Unfortunately it is not possible to calculate green plus brown values from the Fennoscandian data as relative proportions of these tissues are not given. Using the only available mean figure of 12.4% (Mt. Washington data) for difference between green, and green plus brown biomass, the Marion Island energy values can be revised as shown in Table 5.2 to allow approximate comparison with values from other tundra sites.

Because it is based on alpine *Polytricha* only, the conversion factor probably overestimates the difference between green, and green plus brown tissue by a few percent, compared with the figure to be expected over a broader range of bryophytes from more mesic habitats. The revised mean ash-free energy figure of 18.18 kJ g⁻¹ for Marion Island bryophytes is, however, similar to the mean figure of 18.38 kJ g⁻¹ for bryophytes at all tundra sites studied during the IBP (Wielgolaski et al, 1981).

5.3.2 Correlation of energy content with latitude

The range of data collated in Table 5.2 is necessarily limited by the paucity of work in this field. However, the figures seem to indicate a trend of increasing energy values in bryophytes with increasing latitude (Figure 5.4). Wielgolaski & Kjølsvik (1975) noted a similar trend in vascular plants and lichens compared between southern and northern Fennoscandian tundra sites. The same authors cite a tendency for increase in the levels of energy rich compounds in plants in response to low temperature stress, that may

Table 5.2 Corrected energy values for Marion Island bryophytes compared with other tundra sites.

Locality	latitude	no. of spp. studied	kJ g ash free		Authors
Devon Island, Canada	76 N	17	(18.84-)	19.54 (-20.81)	Vitt & Pakarinen, 1977
Pt. Barrow, Alaska	71 N	3	(18.84-)	19.05 (-19.18)	Rastorfer, 1976
Hardangervidda, Norway	60 N	?	(17.54-)	18.42 (-18.92)	Wielgolaski & Kjølsvik, 1975
Mt Washington, USA	44 N	7	(17.63-)	18.47 (-20.01)	Bliss, 1962
Marion Island	46 N	15	(16.50-)	18.18 (-19.34)	this study
South Georgia	55 N	4	(18.25-)	19.47 (20.47)	Smith & Walton, 1973

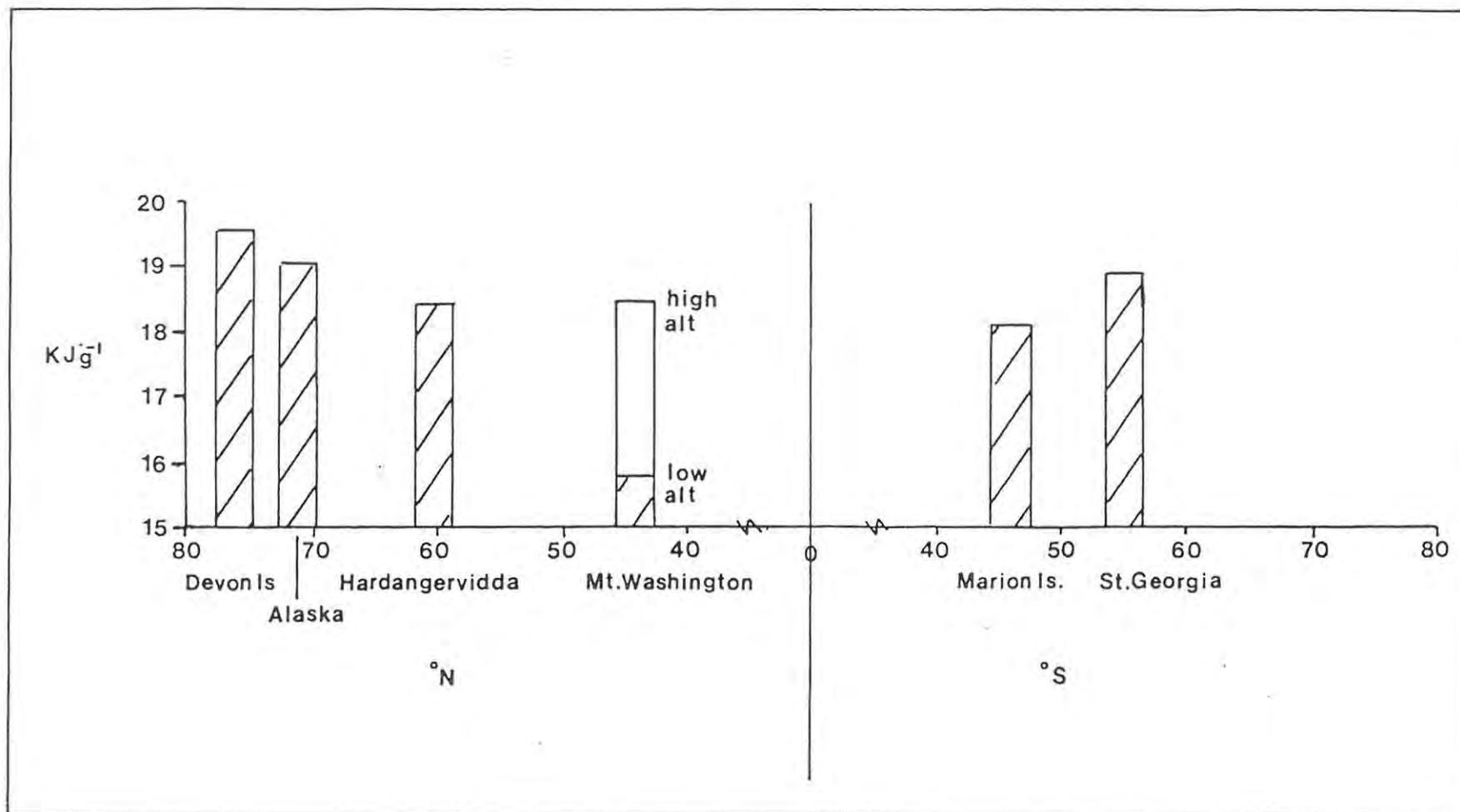


Figure 5.4

Energy contents of bryophyte tissue from a range of sites at different latitudes in the northern and southern hemispheres. For references see Table 5.2.

account for this latitudinal and altitudinal correlation.

The small difference between energy values found at the Norwegian and New Hampshire sites despite their latitudinal difference, may be accounted for by the large altitudinal differences between these sites. Also, the exposed alpine tundra of Mt. Washington has a more severe climate than the lower altitude environment at Hardangervidda which is able to support the growth of woody perennials.

The only other bryophyte energy data from a southern "tundra" site are those from South Georgia, which is at a higher latitude and has a more extreme temperature range than Marion Island. The South Georgia data show a range of higher energy values than those at Marion Island, which parallels the trend of energy values with latitude and site exposure in the northern hemisphere. However, the existing data are extremely limited in scope and serve only to indicate an interesting field for further study.

5.3.3 Radiant energy conversion efficiency

Relating energy fixation in a plant as measured by calorimetry, to the measured receipt of photosynthetically active radiation allows calculation of radiation utilization efficiency (otherwise known as photosynthetic or production efficiency). Energy efficiencies for the individual bryophytes of this study are presented in Table 5.3 . The values were calculated thus: stem density per cm^2 X annual production per stem X energy content of the produced stem material \div incoming energy per cm^2 . The value of 1.272 kJ

Table 5.3 Species and growth plot community energy efficiency

Study plot	Species energy efficiency	Community energy efficiency
<i>Brachythecium subplicatum</i>	0.50	1.09
<i>Distichophyllum fasciculatum</i>	0.14	0.29
<i>Drepanocladus uncinatus</i>	0.19	0.30
<i>Campylopus purpureocaulis</i>	0.29	0.50
<i>Breutelia integrifolia</i>	0.22	0.55
<i>Ptychomnium densifolium</i>	0.20	0.51
<i>Clasmatocolea humilis</i>	0.21	0.69
<i>Blepharidophyllum densifolium</i>	0.18	0.44
<i>Jamesoniella colorata</i>	0.28	1.59
<i>Cryptochila grandiflora</i>	0.22	0.93
<i>Racomitrium lanuginosum</i>	0.06	0.45
<i>Brachythecium rutabulum</i>	0.10	1.27
<i>Ditrichum strictum</i>	0.29	0.20
<i>Andreaea acutifolia</i>	0.24	0.21
<i>Clasmatocolea vermicularis</i>	0.29	0.87

$\text{cm}^{-2} \text{ day}^{-1}$ total incoming radiation (from Schulze 1971 was multiplied by a factor of 0.50 to approximate the photosynthetically active radiation component (Anderson 1971) over a full 365 day growing season.

Photosynthetic efficiencies range from 0.06% in the slow growing Racomitrium lanuginosum of a dry mire, to 0.50% in the fast growing Brachythecium subplicatum of a eutrophic drainage line. These figures are low by comparison with production efficiency percentages for the vascular component of vegetation at sub-Antarctic sites, which are renowned for their high production values (Wielgolaski et al 1981). This is probably because of low chlorophyll contents which give bryophytes a poor overall production efficiency compared with vascular plants (Rastorfer, 1976).

Summing the relevant bryophyte production figures with vascular plant values from Smith (1985) calculated on the same community cover basis as in Table 5.3, and then dividing by incoming energy per m^2 , allows an estimation of community efficiency (the IBP tundra average value of 18.38kJ g^{-1} is used for the plant material in this calculation, as energy values were not available for vascular plants from Marion Island).

Community efficiency values range between 0.2% (fellfield) to 1.59% (drainage line), and are similar to the range 0.75 - 1.9% calculated by Smith (1985) for related habitats at Marion Island.

Energy utilization efficiency values are regarded as a useful basis for comparing primary productivity, but should be viewed with reservation due to the difficulty of defining the growing season in different environments (Caldwell, 1975).

5.3.4 Phylogenetic significance of energy content in bryophytes

Forman (1968) detected a tendency for liverworts to have higher energy than mosses. A similar trend was noted by Rampedi (1984). When compared on an ash free or dry weight basis, the liverworts of Marion Island also show a higher mean energy level than the mosses (Figure 5.5) although the ranges overlap considerably. Forman and Rampedi also noted a tentative trend for mosses with a pleurocarpous growth form to have higher energy levels than acrocarpous types.

Vitt (1984) has reaffirmed the artificiality of the acrocarp/pleurocarp distinction as a primary phylogenetic divisor in moss classification. Pleurocarpy is seen as a derived condition that has evolved independently in several moss lineages in response to specific environmental pressures and niche opportunities. On Marion island, no significant difference in energy content were found between pleurocarpous and acrocarpous mosses, possibly due to the fact that the two growth form types are more evenly mixed in each habitat than in the studies previously referred to. An interpretation of the Marion Island results might therefore be that environmental factors outweigh "phylogeny" where allocation of energetic resources during moss production is concerned.

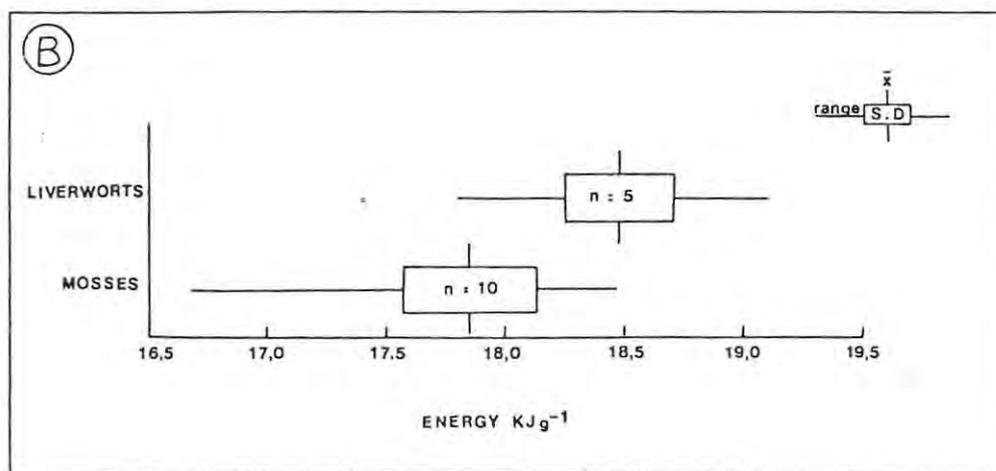
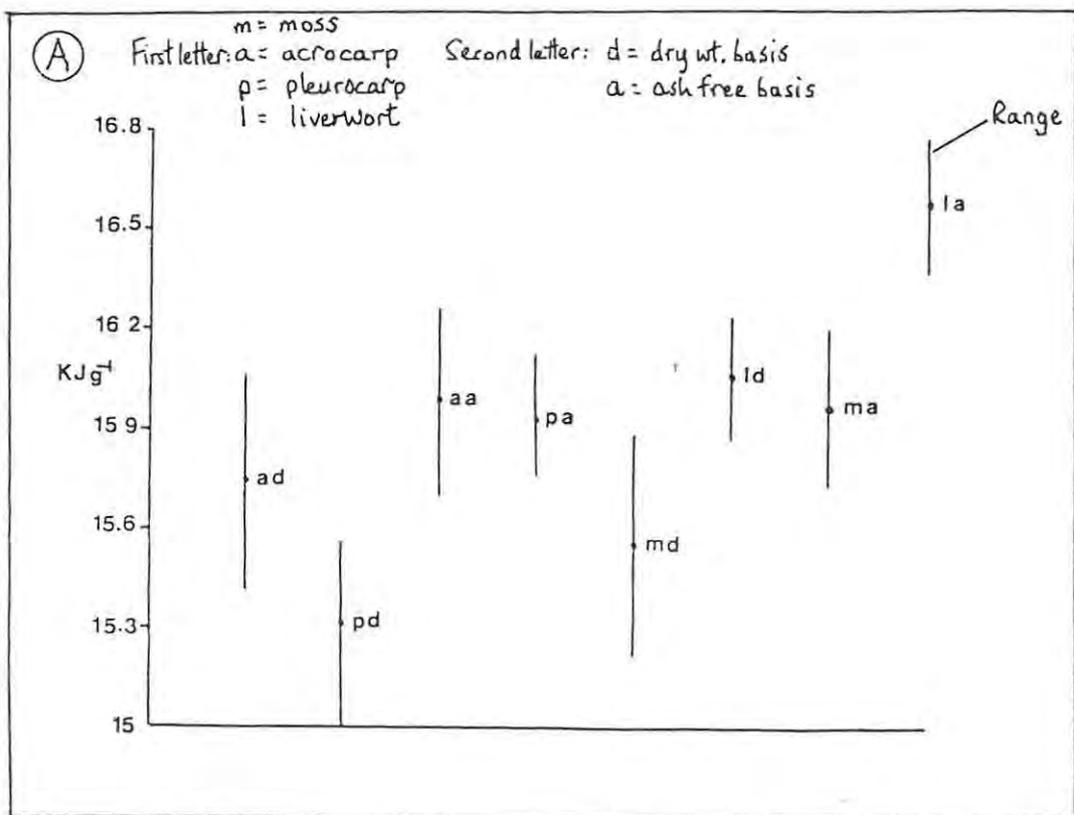


Figure 5.5

A) Mean energy levels on a dry weight and ash free basis, of bryophytes at Marion Island separated into their major taxonomic groupings. B) Ranges and variability of mean energy levels of Marion Island mosses and liverworts compared.

However the proposal that energy content might constitute a factor influencing bryophyte evolution deserves further consideration. Lieth (1975) stated that: "The ability to construct tissue with less energy expenditure per unit weight has conferred an adaptive advantage on the Angiosperms compared with Gymnosperms". If differences between mosses and liverworts prove similarly consistent then Lieth's idea could also be applied to the bryophytes and the following inference derived: the lower energy content per unit weight of the Musci may have placed them at an energetic advantage during their evolution, compared to the less widespread Hepaticae.

Liverworts have higher protoplast:cell wall ratios and oil bodies in the cytoplasm that may account for their higher energy values. Similarly, mosses of the principal pleurocarpous families have larger cells with thinner walls than most acrocarpous types. The putative energetic advantage attending the trend towards smaller cells with thicker walls, might therefore be viewed as complimentary to the suite of xeromorphic characters that has adapted many acrocarpous mosses to a broader range of environments than could be colonized by either their less specialized progenitors or the mesophytic pleurocarpous forms.

Such interpretations must however remain speculative until inherent mechanisms influencing potential ecological amplitude within the Bryophyta are more fully understood. Further studies of bryophyte energetics across a wider range of latitudes and altitudes are therefore needed to throw further light on this question.

5.4 Conclusion

No strong trends were found in the relationship of bryophyte energy content to biomass or production at Marion Island, and only weak relationships with other variables such as water and mineral nutrient levels were discovered (see Chapter 9). Small but consistent differences were found between the energy content of liverworts and mosses, and this aspect deserves further study. Additional information on energy correlation with latitude is also needed, especially from the extremes of plant ranges e.g. in the tropics and Antarctica.

CHAPTER SIX

CHLOROPHYLL CONTENTS**6.1 Introduction**

The photosynthetic capacity of a plant is related to its chlorophyll content and the measurement of this component has therefore often been used as an alternative to growth studies in estimating production (Whittaker & Marks, 1975; Brower & Zar, 1977). Chlorophyll content is used regularly as an index of production in algal studies, where leaf areas and dry weights are inappropriate or less easily measured. Methods for the analysis of chlorophyll content in plant tissues are commonly given in texts that also deal with the measurement of photosynthetic production (Sestak, Catsky & Jarvis, 1971; Coombs, Hind, Leegood, Tieszen & Vonshak 1985).

The relationship between chlorophyll content and photosynthesis may be expected to vary with light intensity, nutrient levels, age and density of individual plants in a stand (Brower & Zar, 1977). Lieth (1975) found photosynthetic efficiency to vary widely in different communities, and he noted only a loose correlation between chlorophyll content and production in different biomes. This has led some authors to the generalization that there is little correlation between chlorophyll content and photosynthetic production, particularly in vascular plants (Salisbury & Ross, 1985). Stronger correlations have been recorded however, within single species and communities (Whittaker & Marks, 1975).

At the beginning of the International Biological Programme's investigations into the productivity of the biosphere, many researchers conceded that the relationships between chlorophyll content, photosynthesis and production were poorly understood (Tieszen & Johnson, 1968; Rastorfer, 1972). It was accepted that the relationship was unlikely to be a simple one, and that it would require further investigation before the use of chlorophyll content as an index of production could be applied universally. It was therefore suggested that the various IBP programmes would provide an ideal opportunity for establishing these relationships and that chlorophyll content should be measured in as many IBP investigations as possible (Newbould, 1967).

Additional motivation for the analysis of chlorophyll concentration in the study of bryophyte production at Marion Island, was provided by the evidence for a correlation between chlorophyll content and habitat moisture levels found in earlier studies elsewhere (Rastorfer, 1972; Berg, 1975; Vitt & Pakarinen 1977; Tallwin, 1977). Community variation in relation to habitat moisture levels had been demonstrated by Gremmen (1982) at Marion Island and it was therefore hypothesized that chlorophyll content - as a potential index of production - might be similarly correlated with environmental moisture gradients.

6.2 Methods

Various methods have been used for the extraction of chlorophyll from plant tissues. The method used in this study was the standard technique prescribed for many years since the

early work of MacKinney (1941) and Arnon (1949), and adopted by most IBP investigators (Rastorfer, 1970, 1972; Berg, 1975; Muc, 1977; Vitt & Pakarinen 1977; Svoboda, 1977). One modification was introduced to the procedure i.e. centrifugation rather than filtration of the chlorophyll solution in order to speed up and enhance separation of the supernatant from the plant tissue residue.

During March (late summer) of 1981, 21mm diameter cores of plant material were cut from colonies of the 15 experimental bryophyte species in the production study plots (12 cores per species). Cores were cut to the base of visible green material so as to include at least the current year's growth. The plant material was collected in plastic bags and returned to the laboratory on Marion Island for immediate analysis. 6 Cores were then centrifuged at 1000 rpm for one minute to remove surface water. Each core was ground in a pestle and mortar to which had been added a small amount of washed grinding sand and a pinch of magnesium carbonate to neutralize acidity in the extract. 80% acetone was used as a solvent and all reagents and containers were refrigerated and kept under low light conditions during the course of the analysis.

5ml aliquots of the solvent were added to the mortar until the grinding process yielded a fine, homogeneous slurry which was then transferred to a centrifuge tube. The slurry was centrifuged at 3500rpm for 3 minutes and the supernatant collected in a measuring cylinder. Additional 5ml aliquots of acetone were used to wash the mortar and redilute the slurry which was then centrifuged 5-7 more times until a clear yellowish solvent and colourless residue were obtained.

5ml of extract was drawn off from the solution, stored in the measuring cylinder and diluted by a known amount to bring the absorbance of the solution within the scale range of the spectrophotometer. Absorbance was measured at wavelengths of 663 and 645 Angstroms. Values were multiplied by Arnon's (1949) factor ($8.02A_{663} + 20.2A_{645}$) to give chlorophyll concentration in mg l^{-1} (C). These values were converted to mg g^{-1} by calculating VC/DW where V = the total solvent in which each tissue extract was dissolved and DW = dry weight of the tissue sample. The six additional moss cores were oven dried to provide an estimate of the average dry weight per core for green tissue (standard errors of all average weights less than 10% of the mean).

In the Marion Island study, a Beckman DB-GT spectrophotometer was used as its narrow bandwidth (2nm) offers an advantage over the Spectronic 20 (20nm). Problems were however experienced with maintaining calibration of the DB-GT due to an intermittent light source and a second set of readings was therefore made on the refrigerated chlorophyll solutions after two days storage, using a Spectronic 20 spectrophotometer.

The two sets of readings showed close agreement however ($r=0.9908$ $p<0.0001$), with a small discrepancy at the upper limit of absorbance where responses between machines differed slightly. It was decided to use the readings from the Spectronic 20 in the results tables in order to facilitate comparison with values from other tundra studies that used the same instrument.

6.3 Results

Means and standard deviations for chlorophyll contents of the 15 Marion Island bryophyte species are given in Table 6.1 (six replicates per species). Results are expressed on a dry weight basis due to the difficulty of measuring leaf area in the material under study.

An estimate of chlorophyll content of green bryophyte tissue on an areal basis is given in the second data column of Table 6.1. This was calculated by multiplying the chlorophyll content from column one of Table 6.1, with the cover corrected annual production values from Table 4.10. This will not give an exact value for chlorophyll in the annual tissue production, as more or less than a year's growth may be represented in the green tissue sampled for chlorophyll. However, it will allow a crude comparison with data from other sites where total "green tissue" was also sampled for chlorophyll content.

6.4 Discussion

Summer chlorophyll contents of Marion Island mosses range from 0.143mg g⁻¹ (dry weight) in Ditrichum strictum, a cushion moss of the fellfield habitat, to 2.534 mg g⁻¹ in Brachythecium subplicatum of the drainage line habitat (Table 6.1). Corresponding values expressed on an areal basis as explained above, span the range 3.9 - 1916.9g m⁻². The high value for B. subplicatum may be influenced by the heavy infestations of epiphytic cyanobacteria that occur at the drainage-line site (Smith & Russell, 1982).

Table 6. | Chlorophyll contents of Marion Island bryophytes.

Species	mg g ⁻¹ ± SD	mg m ⁻² in cover-corrected production
<i>Brachythecium subplicatum</i>	2.543 ± .326	1916.9
<i>Distichophyllum fasciculatum</i>	2.127 ± .05	512.2
<i>Drepanocladus uncinatus</i>	0.44 ± .024	126.5
<i>Campylopus purpureocaulis</i>	0.367 ± .024	143.3
<i>Breutelia integrifolia</i>	2.296 ± .355	633.7
<i>Ptychomnium densifolium</i>	1.252 ± .197	314.6
<i>Clasmatocolea humilis</i>	2.099 ± .073	528.9
<i>Blepharidophyllum densifolium</i>	0.868 ± .074	283.3
<i>Jamesoniella colorata</i>	0.814 ± .013	317.4
<i>Cryptochila grandiflora</i>	1.031 ± .029	285.7
<i>Racomitrium lanuginosum</i>	0.313 ± .023	19.3
<i>Brachythecium rutabulum</i>	1.375 ± .314	156.3
<i>Ditrichum strictum</i>	0.143 ± .004	3.9
<i>Andreaea acutifolia</i>	0.236 ± .016	13.6
<i>Clasmatocolea vermicularis</i>	1.116 ± .28	456.3

Chlorophyll levels tended to be lowest in the drier and more exposed habitats e.g. fellfield and the Racomitrium mire, and higher at the more sheltered and eutrophic sites (Brachythecium rutabulum slope, Breutelia integrifolia flush, Brachythecium subplicatum drainage line). However, a broad range of otherwise inconsistent values occurred within the mire habitat, and this reduced the significance of the correlations for chlorophyll content:soil water content, and chlorophyll:cover-corrected production (0.513 $P < 0.05$; 0.489 $P < 0.06$ respectively). These correlations were in any case strongly influenced by the outlier result for Brachythecium subplicatum so that no overall correlation can be inferred for the relationship between these variables.

Notwithstanding the admonition to collect information on chlorophyll contents from as many sites as possible during the IBP, comparative bryophyte chlorophyll data were collected at only two localities during these investigations (Wielgolaski, Bliss, Svoboda & Doyle, 1981). These data are tabulated for comparison with Marion Island values in Table 6.2, along with bryophyte and vascular plant data from selected localities at other latitudes.

Chlorophyll values in mosses from xeric and hydric habitats found by Pakarinen and Vitt at Devon Island in Canada, are closely paralleled by the figures for bryophytes from Marion Island (Table 6.2). The results also agree with the findings Berg (1975) and Tallwin (1977). Somewhat higher values were noted by Rastorfer (1972) in his study of Antarctic Peninsula mosses. In that study, results were expressed on a fresh weight

Table 6.2 Comparison of Marion Island bryophyte chlorophyll values with data from tundra and temperate sites.

Locality	Chlorophyll content (mg g ⁻¹)	Authors
BRYOPHYTES		
Marion Island	0.143 - 2.534	This study
West Antarctica	1.130 - 3.860	Rastorfer, 1972
Truelove Lowland, Devon Island, Canada	0.250 - 2.640	Vitt & Pakarinen, 1977
Hardangervidda, Norway	1.50 - 2.90	Berg, 1975
Turku, Finland	1.04 - 7.17	Kallio & Valanne, 1975
UK (Brachythecium rutabulum)	1.71 - 11.1	Kershaw & Webber, 1986
Indiana	2.16	
New Hampshire Polytricha	1.78	Rastorfer, 1962
Tennessee	0.65	
Japan (epiphytes)	0.035 - 0.070	Miyata & Hosokawa, 1961
Checkoslovakia woodland	7.73 - 11.68	Masarovicova & Elias, 1985
VASCULAR PLANTS		
Marion Island (grasses)	6.094	Pammenter et al, 1986
Maquarie Island	1.10 - 7.05	Jenkin, 1975
South Georgia	2.0 - 6.7	R Smith, 1984
Devon Island, Canada	1.0 - 12.0	Muc, 1977; Svoboda, 1977
Hardangervidda, Norway	2.0 - 6.0	Berg, 1975

basis. The dry weight values indicated for Rastorfer's data in Table 6.2 have been calculated using water content figures for the same species, but from another experiment quoted in Rastorfer's paper. Nevertheless, assuming validity of the conversion from fresh weight, Rastorfer's figures still appear unusually high by comparison with bryophytes from other habitats in polar regions.

Polytricha from the USA showed a similar range of chlorophyll contents (Rastorfer 1962) to those found on Marion Island (values converted from fresh weight on the same basis as above), whereas figures for epiphytic bryophytes in Japan were somewhat lower (Miyata & Hosokawa 1961).

In Britain, Kershaw and Webber (1986) found a post-winter chlorophyll concentration of 1.71 mg g^{-1} in Brachythecium rutabulum, which compares with the summer level of 1.375 mg g^{-1} for this species at Marion Island. Racomitrium lanuginosum had levels of $0.357 - 2.10 \text{ mg g}^{-1}$ in Southern Finland (Kallio & Heinonen, 1975; Kallio & Valanne, 1975) and 0.313 mg g^{-1} on Marion Island. This species is notoriously variable in its physiology and the higher chlorophyll contents recorded at the Finnish site may be an indication of the relatively mesic conditions found there, and the low light intensities under which the mosses were maintained before analysis in the Finnish studies.

Another very variable species is Drepanocladus uncinatus, for which Rastorfer (1972) measured a high chlorophyll content of 3.86 mg g^{-1} at the Antarctic Peninsula. The collection of D. uncinatus from the drier, yellowing crests of hummocks in the mire

habitat on Marion Island may account for the low values obtained in the present study.

Reference has been made to the lack of correlation between chlorophyll content and production noted by earlier researchers working outside the tundra biome. As a result of investigations at the IBP tundra sites however, Wielgolaski et al (1981) noted a strong correlation between these variables ($r=0.9090$ $P < 0.01$) based principally on vascular plant data. Kallio and Valanne (1975) went so far as to suggest that a closely positive correlation might be the general rule in this biome type.

The values for the tundra biome are however based on closely related communities at relatively few sites. The greater range of habitat types studied at Marion Island may have led to the high degree of variability between species with regard to chlorophyll content and the lack of correlation between chlorophyll content and production noted in this study. Similar results were obtained in bryophyte dominated communities at Devon Island in Canada (Vitt & Pakarinen, 1977).

The above observations may be related to differences in photosynthetic mechanisms between bryophytes and vascular plants at the subcellular level. Most vascular plants are known to have a surplus of light gathering molecules (chlorophyll b) at each chloroplast synthetic site, and this molecular redundancy is thought to be an adaptation to cope with fluctuations in environmental light intensity especially in the short term (Bonner, 1962). (In the longer term, vascular plants and bryophytes may compensate by the production of more chlorophyll (Sluka, 1982. Masarovicova & Elias, 1985. Kershaw & Webber,

1986)). There can therefore be large differences in the chlorophyll content but, as it is the number of synthetic sites that is limiting to photosynthesis, little correlation will be expected between chlorophyll content and production in vascular plants of well lit environments.

Under low light conditions however, the light gathering capacity of the "surplus" molecules will become fully utilised and the amount of chlorophyll will become limiting to photosynthesis, leading to a closer link (correlation) between the levels of photosynthetic production and chlorophyll content. Low radiation receipts due to high latitudes and often cloudy conditions may therefore account for the higher correlations between chlorophyll content and production in vascular plants of such environments.

With regard to bryophytes however, recent ultrastructural evidence supports the view that these plants are evolutionary sciophytes i.e. they exhibit adaptations for survival in shady, low-light environments (Valanne, 1984). Although bryophytes typically have chlorophyll contents lower by a factor of about 2 or 3 compared to vascular plants (Table 6.2), they also have lower chlorophyll a:b ratios i.e. proportionately higher levels of the light harvesting chlorophyll b molecule (Rastorfer, 1970, 1972; Berg, 1975).

This surplus of light harvesting molecules in sciophytic bryophytes could therefore be regarded as analagous to the condition in vascular plants of well lit environments, where molecular redundancy leads to a poor correlation between chlorophyll content and photosynthetic production. This could account for the lower correlations noted in

bryophyte production studies at higher latitudes, when compared with the results for vascular plant studies at tundra sites as quoted by Wielgolaski et al (1981).

The evidence from previous studies that chlorophyll levels are lower in bryophytes by about 2-3 times compared with vascular plants is confirmed by the Marion Island results. However, only one set of fresh weight figures exists for Marion Island vascular plants i.e. two grass species (Pammenter, Drennan & Smith, 1986). Conversion to a dry weight basis using the fresh weight:dry weight ratios supplied in the above paper, indicates vascular plant chlorophyll levels approximately three times higher than those for bryophytes at Marion Island.

One reference has been made to differences in chlorophyll content between major taxonomic groupings within the bryophytes. Rastorfer (1972) noted chlorophyll contents two times greater in pleurocarpous mosses compared to acrocarpous forms. No such difference was noted during the study of Marion Island bryophytes. Mean chlorophyll content values of the acrocarpous and pleurocarpous mosses differ insignificantly, and Marion Island hepatics are also indistinguishable from mosses on the basis of chlorophyll content.

6.5 Conclusion

Chlorophyll contents of Marion Island bryophytes are similar to those found at tundra sites in the northern hemisphere. In common with the findings of several previous

studies, chlorophyll contents are not strongly correlated with production in Marion Island bryophytes, although species from hydric and eutrophic sites tend to show higher chlorophyll contents than species from more xeric fellfield situations and dry mires. The poor correlation of chlorophyll content with habitat moisture levels also leads to the conclusion that the hypothesis advanced at the end of the introduction to this chapter, is not supported by the results available from the Marion Island study.

CHAPTER SEVEN

WATER RELATIONS

7.1 Introduction

It is often stated that environmental moisture is the single most important factor controlling bryophyte growth, and that this is especially true in polar environments where water may only be available for short periods due to freezing conditions (Gimingham & Smith, 1971; R Smith, 1972; Pakarinen & Vitt, 1977; Ando, 1979). Marion Island has very low solar radiation receipts, a high degree of cloud cover and constantly high humidity (relative humidity annual mean 83%, mean diurnal range 4%)(Schulze, 1971). It also has probably the highest rainfall of any "polar" station (Loewe, 1957; Longton, 1982) with a mean of 2454mm spread over 308 precipitation days per year.

These statistics would tend to suggest an environment where water is a constant rather than variable and limiting factor. However clear differences are apparent between bryophytes of shallow soils and rock surfaces in exposed habitats and plants of deep peat soils in protected valleys and depressions. Plants of the former habitats show classic xeromorphic adaptations such as compact cushion growth form, appressed leaves with hair points and incrassate areolation, papillose surfaces etc., and bryophytes in the latter situations often show open growth forms and spreading leaves with lax areolation.

This is a common phenomenon at polar sites and has been commented on by several previous authors (Gimingham, 1967; Longton, 1967; Lindsay, 1971; Pakarinen & Vitt 1977; Flock, 1978; Ando, 1979). R Smith (1972) has demonstrated the importance of soil moisture as influenced by soil texture and microtopography, in controlling plant community distribution at Signy Island. Gremmen (1982) has also related plant community patterns at Marion Island with soil moisture gradients.

Broad correlations between habitat moisture and plant production have been found at several other polar sites (see Pakarinen & Vitt, 1977, and the review of Wielgolaski et al, 1981). However, no intensive work had been carried out to more closely specify species water economies in relation to production. The precise degree to which the distinct, soil-moisture related community spatial pattern was related to plant water contents and plant production was also unknown at Marion Island. The author therefore undertook to complete a study of plant water contents in the principle bryophyte species at the production study sites.

Several authors have proposed that the capability for "desiccation resistance" of many bryophytes (i.e. tolerance to the reduction of tissue water contents below full turgor and therefore suspension of metabolic processes such as photosynthesis) resides principally in the physiological properties of the cytoplasm (Bewley & Pacey, 1978; Busby & Whitfield, 1978). This would infer that morphological differences are therefore of lesser importance (Lee & Stewart, 1971), especially in plants of xeric environments.

However, after long and careful experimentation, Dilks & Proctor (1976) concluded that, at least in plants of mesic and hydric environments, physiological resistance to desiccation shows little variability between species. Differences in performance of these plants are therefore likely to be related less to their cytoplasmic drought tolerance than to the length of time they can retain high enough water contents for continued metabolic activity. This in turn is closely related to the growth form and capillary structure of stem and branch arrangement and fine surface morphology (Proctor, 1981).

As various authors had confirmed the importance of growth form in influencing water uptake and retention in bryophytes, it was decided to study this aspect also at Marion Island. As shown in Chapter 4, a wide range of growth forms are displayed by bryophyte species at Marion Island, even within a single community complex. This offered the opportunity to test further the theories of growth form adaptation to gross habitat factors, advanced by proponents of life form classifications for bryophytes (Gimingham & Robertson, 1950; Omura, 1950; Horikawa & Ando, 1952; Horikawa & Nakanishi, 1954; Gimingham & Birse, 1957, Iwatsuki, 1960, Vorster, 1970; Magdefrau, 1982).

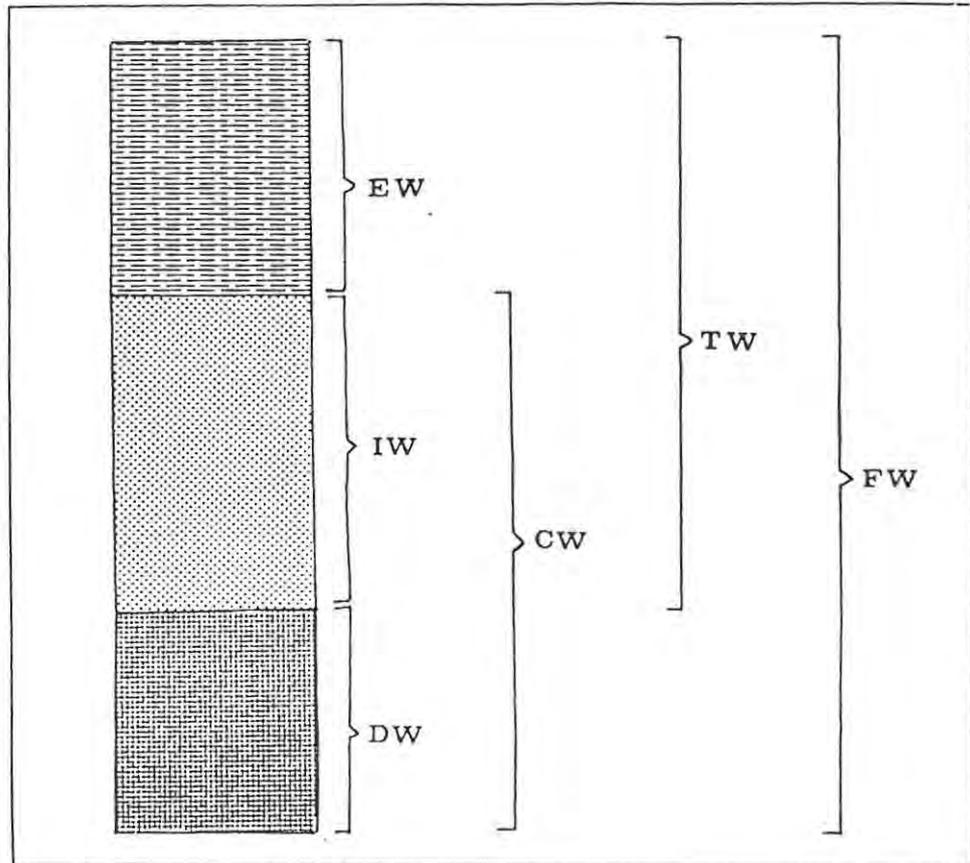
7.2 Methods

Soil core samples were collected in January 1981 from the growth plots of the 15 bryophyte species being analysed for production (Chapter 4). Samples had to be oven dried at 80°C for up to 36 hours to attain constant weight, due to their high water contents.

Gremmen (1982) noted rainfall-related fluctuations of water table varying between 3 and 14 cm below what would correspond to the active growth zone of bryophytes in mires and slopes respectively. Frequency of rainfall will therefore be important in maintaining a water level within external conducting distance of the bryophyte shoot apex, in order to maintain hydration of the growing point (Anderson & Bordeau, 1955). Gimingham & Smith (1971) have also commented on the necessity for several readings of plant water contents to be spaced over a representative period.

The measurements were therefore made at the production plots on three occasions during February - April 1981, to allow for rainfall/water table fluctuations. These readings were related to the daily record of rainfall kept at the nearby meteorological station. Three separate weighings were made of the eight cores per species that were collected on each sampling date i.e. fresh weight, weight after centrifugation and oven dry weight (80°C 24h). Centrifugation was carried out at 1500 r.p.m. (approx 377g) for a period of one minute, after the method of Gimingham & Smith (1971). This procedure was designed to remove the bulk of externally held water, and allow comparison with the data on bryophyte capillary water from Signy Island. Higher levels of relative centrifugal force may be necessary for complete removal of water from the capillary system of many, especially xeromorphic species e.g. 3600 r.p.m. (1200g) for 10 mins (Dilks & Proctor, 1979). Figure 7.1 shows some of the parameters of bryophyte water content that can be calculated from the above measurements.

Complex relationships of fine structure, stem and leaf architecture and colony growth



FW = Fresh weight

CW = Centrifuged weight ("Initial" weight of Gimingham & Smith, 1971)

EW = (FW-CW) External water content

DW = Dry weight

TW = (FW-DW) Total water content

IW = (CW-DW) Internal water content

TW% = (TW/(DW/100)) Total water as a % of dry weight

EW% = (EW/(DW/100)) External water as a % of dry weight

IW% = (IW/(DW/100)) Internal water as a % of dry weight

ETW% = (EW/(TW/100)) External water as a % of total water content

Figure 7.1 Diagram explaining terminology of water relations variables in bryophyte tissues.

form influence moisture retention capacity of bryophytes. A detailed investigation of these aspects was beyond the scope of this investigation. However a crude assessment of the resistance of growth form to water loss can be obtained by weighing fresh material before and after a period of air drying. Freshly collected samples of the 15 bryophyte species were therefore exposed to an atmosphere of 35% relative humidity and 20°C for a period of 13 hours in a constant temperature room at the meteorological station on Marion Island. Gimingham and Smith (1971) found little difference in the pattern of water loss at differing experimental humidities. The value of 35% used here is similar to the figure at which the above authors obtained their clearest results and is similar to the levels experienced on Marion Island during rare occurrences of Föhn wind conditions (Huntley, 1971; Schulze, 1971).

In order to compare the results with those of Gimingham & Smith (1971), bryophyte samples were first saturated with distilled water then centrifuged as above. The experiment will therefore give an indication of the effect of colony growth form on prevention of water loss from initially hydrated stems, but without a surrounding layer of external capillary water i.e. at the point where further dehydration will begin to effect physiological processes. The procedure will not however, allow comparison of the manner in which growth form delays the loss of externally held water, which is usually present in large quantities on the mosses of mesic and hydric habitats at Marion Island. This capillary water acts as an effective buffer against dehydration under most conditions. Therefore a simple additional test was made of external water loss, by weighing freshly collected 10cm diameter clumps of each species, before and after 24

hours exposure to the same temperature and humidity conditions described above. The bunches of stems were held upright in narrow beakers with the colony "evaporating surface" level with the top of a beaker.

7.3 Results and discussion

Water contents of plant material and soil cores collected from the bryophyte study plots are shown in Tables 7.1a & b. The Marion Island growth plot values agree closely ($r=0.9131$ $P < 0.0001$) with soil moisture means calculated from the relevee tables of Gremmen (1982) for communities corresponding to those in which the growth plots were situated.

Average total water content for eight cores of bryophyte material per species are graphed in Figure 7.2a for each of the sampling dates. Total water comprises internal (apoplast and symplast) water plus external capillary water (Dilks & Proctor, 1979). External water was measured on the last two dates only, and is graphed in Fig 7.2b. Fluctuations in the high level of rainfall are known to affect ground water levels at Marion Island within 30cm of the surface, with a lag phase of one or more days (Huntley, 1971; Gremmen, 1982). Such short term fluctuations may have little effect on bryophyte tissue water contents as external water contents of the species under study remained fairly constant, with an average variation between species of only 4.9% between February and March 1981. Cumulative effects may be important however as suggested by the increased level of total plant water content measured in February, which may correlate with the higher

Table 7.1a Total field water content (% dry weight) measured on three dates and external water (% total water) measured on two dates in 1981, for Marion Island bryophytes. Rainfall figures for the *prev.* months also shown.

Species	Feb	SD	Mar	SD	Apr	SD	ETW% 3/81	SD	EW%	ETW% 4/81	SD	EW%
<i>Brachythecium subplicatum</i>	3143	304	2200	347	1056	348	54.90	14.40	1208	54.60	15.60	577
<i>Distichophyllum fasciculatum</i>	3358	516	2466	108	2811	198	53.30	3.80	1314	57.60	3.60	1619
<i>Drepanocladus uncinatus</i>	1109	130	1106	108	960	90	48.30	6.90	534	43.90	11.90	421
<i>Campylopus purpureocaulis</i>	967	111	633	36	730	168	41.00	4.30	260	43.00	7.10	314
<i>Breutelia integrifolia</i>	1609	90	1180	179	1228	115	63.40	6.70	748	64.90	3.20	797
<i>Ptychomnium densifolium</i>	915	169	741	106	868	276	36.50	10.90	270	42.20	14.20	366
<i>Clasmatocolea humilis</i>	1696	122	1205	87	1446	77	40.20	4.00	484	50.40	3.50	729
<i>Blepharidophyllum densifolium</i>	1503	553	1378	18	1359	49	53.00	3.80	730	51.90	2.10	705
<i>Jamesoniella colorata</i>	769	106	737	290	517	62	28.50	15.60	210	24.00	4.20	124
<i>Cryptochila grandiflora</i>	840	46	453	73	630	58	17.60	7.50	80	29.80	3.40	188
<i>Racomitrium lanuginosum</i>	417	33	150	54	227	24	4.90	1.30	74	5.20	2.40	118
<i>Brachythecium rutabulum</i>	1170	119	689	182	483	106	32.90	14.90	227	32.70	5.10	158
<i>Ditrichum strictum</i>	192	40	228	19	189	18	20.20	4.10	46	10.30	2.40	19
<i>Andreaea acutifolia</i>	197	9	151	45	126	21	16.80	10.00	25	17.40	3.20	22
<i>Clasmatocolea vermicularis</i>	1033	9	952	282	979	84	47.50	18.30	452	31.10	5.90	304

101c

Table 7.1b Soil moisture at bryophyte growth plots.

Species	Soil water 10 cores (SD)
<i>Brachythecium subplicatum</i>	2787 (784.2)
<i>Distichophyllum fasciculatum</i>	2396 (662.6)
<i>Drepanocladus uncinatus</i>	1808 (52.3)
<i>Campylopus purpureocaulis</i>	2469 (451.8)
<i>Breutelia integrifolia</i>	1599 (198.7)
<i>Ptychomnium densifolium</i>	1480 (212.1)
<i>Clasmatocolea humilis</i>	1417 (111.0)
<i>Blepharidophyllum densifolium</i>	2216 (746.7)
<i>Jamesoniella colorata</i>	1299 (24.0)
<i>Cryptochila grandiflora</i>	746 (183.1)
<i>Racomitrium lanuginosum</i>	895 (88.4)
<i>Brachythecium rutabulum</i>	649 (43.1)
<i>Ditrichum strictum</i>	260 (123.7)
<i>Andreaea acutifolia</i>	184 (35.0)
<i>Clasmatocolea vermicularis</i>	895 (131.5)

Figure 7.2a Total field water content (% dry weight) measured on three dates for Marion Island bryophytes. Rainfall figures for the prev. month are also shown.

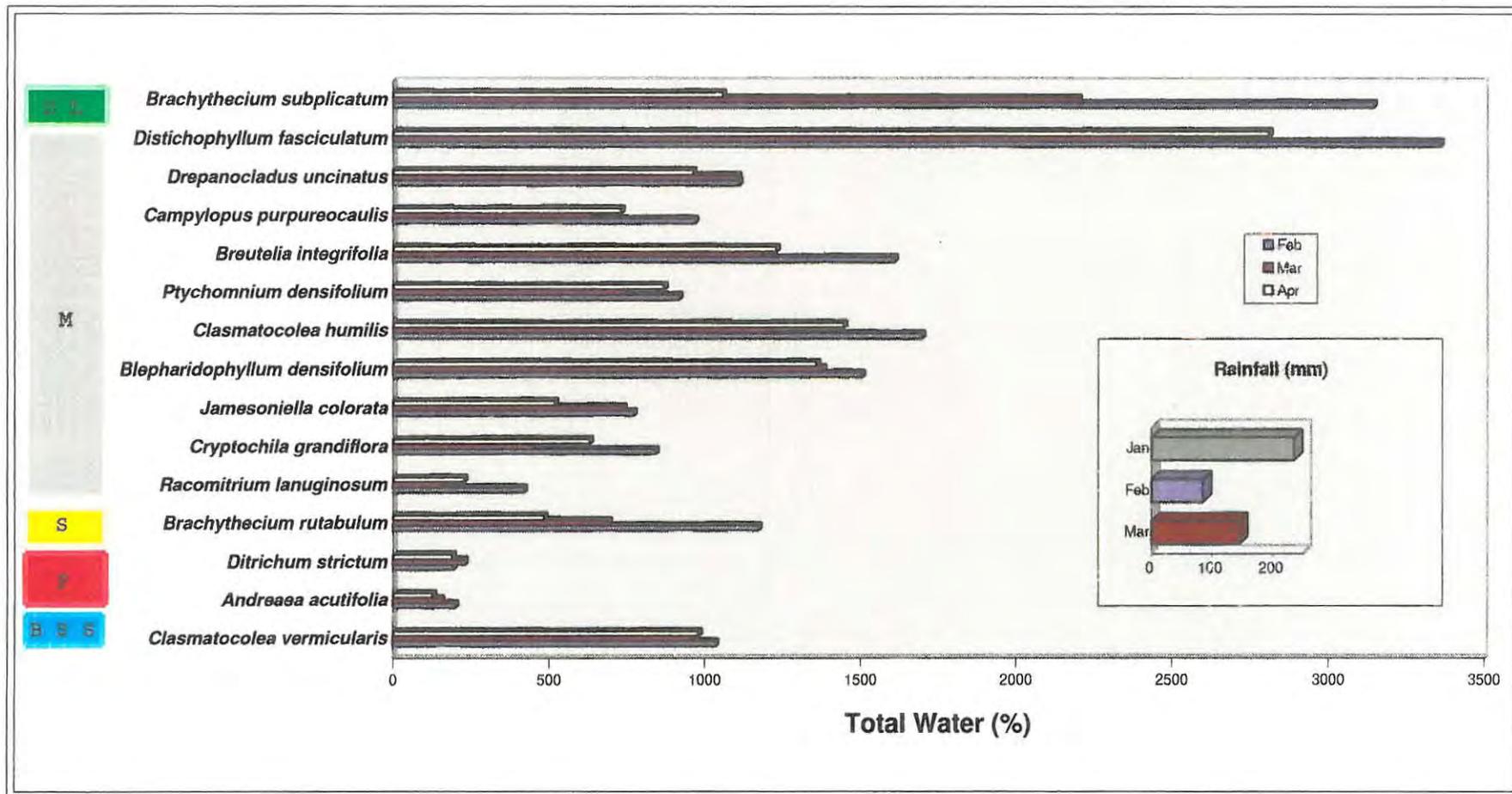
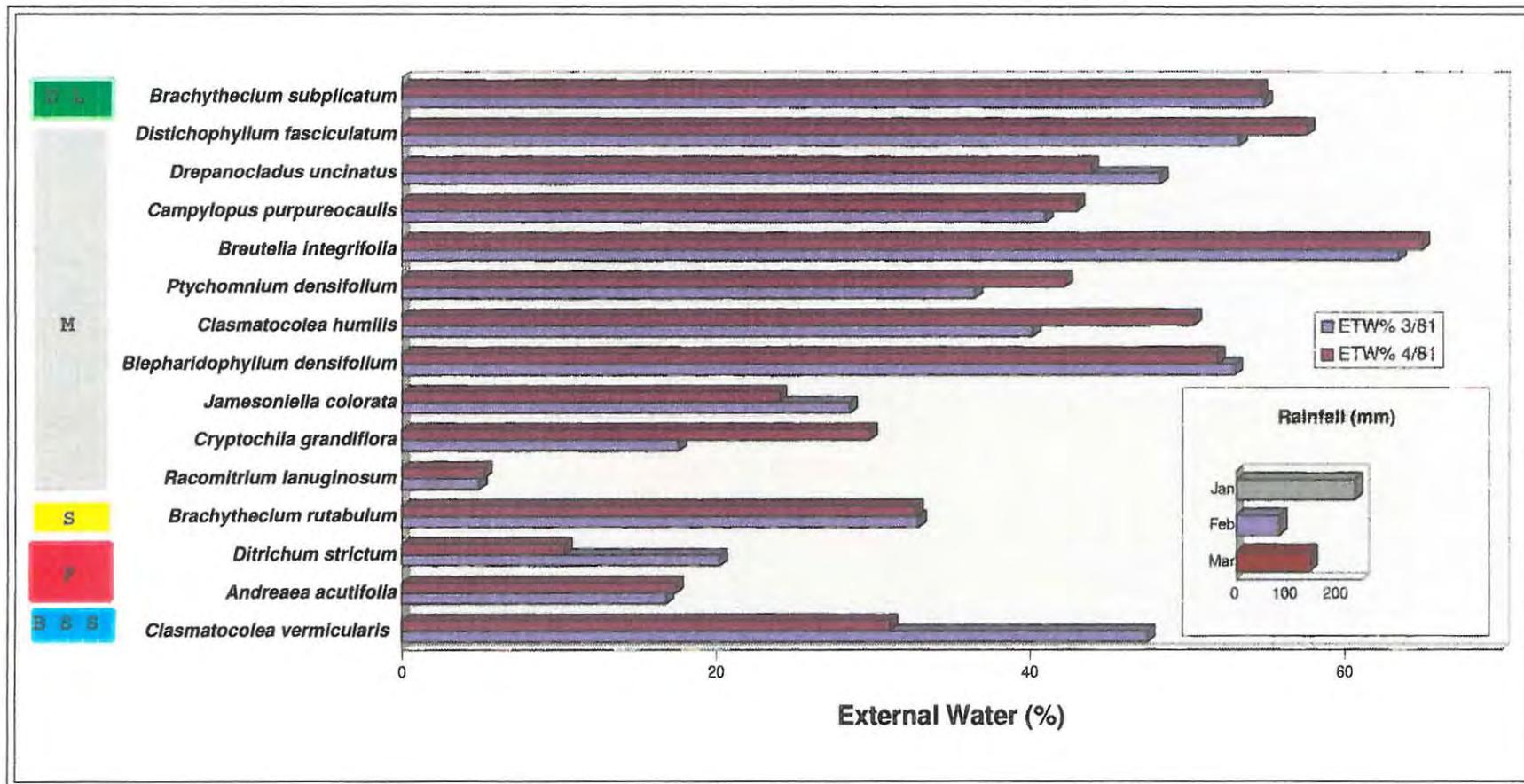


Figure 7.2b External water (% total water) measured on two dates in 1981, for Marion Island bryophytes. Rainfall figures for the *prev.* months also shown.



level of rainfall recorded in the preceding month. Comparison of the data presented in Figure 7.2 shows that lower water contents are found in species of the fellfield habitat, and high values in the drainage line species, with an intermediate water content for the slope species.

Reference to Figure 7.2 reveals that the range of water contents found in the mire species, exceeds that found between the fellfield and drainage line species. This reflects the heterogeneous nature of the mire complex, while the trend of plant moisture values in this habitat further confirms the broad xeric-hydric moisture gradient postulated for the mires by Gremmen (1982).

Correlation between soil water content and plant water content is positive (TW% $r=0.7640$; EW% $r=0.7645$ $P < 0.001$). The degree of statistical significance of this relationship is high, given the lack of an absorptive root system and previously noted susceptibility to rainfall fluctuations in Marion Island bryophytes.

The results of the thirteen hour desiccation test are indicated in Table 7.2. Resistance to water loss from fully hydrated stems appears to be closely linked to growth form of the species concerned. Growth form and stem spacing data are included in Table 7.2, and comparison of the information allows the following generalisations.

Those species with less robust growth forms and higher areal stem densities ($>20\text{ cm}^{-2}$)

Table 7.2 Growth form, stem spacing density and water content after 13 hours desiccation for Marion Island Bryophytes. Water content after desiccation expressed as a % of internal water content at the start of the experiment.

Species	Growth form	Mean shoot density per cm ²	Retained water (%)
<i>Clasmatocolea vermicularis</i>	Mat, thread-like form - tall turf	106.5	53.5
<i>Blepharidophyllum densifolium</i>	Tall turf, branches erect	42.0	51.7
<i>Clasmatocolea humilis</i>	Short - tall turf	100.0	50.8
<i>Campylopus purpureocaulis</i>	Tall turf with dense rhizoid felt	26.3	49.0
<i>Ditrichum strictum</i>	Large cushions	23.7	48.9
<i>Cryptochila grandiflora</i>	Mat, thread-like form - tall turf	40.2	47.6
<i>Distichophyllum fasciculatum</i>	Tall turf, branches erect	49.7	37.9
<i>Andreaea acutifolia</i>	Small - large cushions	280.0	35.2
<i>Drepanocladus uncinatus</i>	Carpet	15.8	31.7
<i>Jamesoniella colorata</i>	Mat, thread-like form - tall turf	47.7	28.1
<i>Ptychomnium densifolium</i>	Tall turf, branches erect	4.3	11.9
<i>Racomitrium lanuginosum</i>	Carpet	4.5	6.9
<i>Breutelia integrifolia</i>	Tall turf with dense rhizoid felt	16.0	4.7
<i>Brachythecium subplicatum</i>	Carpet	23.2	3.6
<i>Brachythecium rutabulum</i>	Weft	11.0	3.1

tend to be most resistant to water loss i.e. the cushion and mat growth forms, all of which retained more than 25% of their initial water content. Those species with more robust growth forms and lower stem densities ($<25 \text{ cm}^{-2}$) were less resistant to drying out, i.e. the carpet and weft types, which all retained less than 35% of their initial fully hydrated water content.

The tall turf growth form gave variable results, but openness of growth habit appeared to counteract factors such as erect, parallel stem arrangement or dense rhizoid felts where resistance to water loss was concerned. Turfs with stem densities of less than 20 cm^{-2} retained less than 40% of their initial water, with the converse was true of colonies with greater than 20 cm^{-2} stem spacing.

Results of the 24 hour external water desiccation test (not shown) broadly confirmed the above findings but were considerably less conclusive due to the small percentage of water lost compared to the total external water present in fresh material of most species. Longer periods of desiccation are rarely if ever experienced at Marion Island and it is therefore probable that species of the mire and drainage line habitats at least, are always fully hydrated in the field.

Similar conclusions were reached by Miller & Oechel (1978) working in the tundra at Barrow, Alaska. Only isolated, raised growing points of such species may be subject to more frequent desiccation e.g. in the raised hummocks of Drepanocladus uncinatus carpets for example at Marion Island. This may have a bearing on the highly variable

production values obtained for the latter species (Chapter 4).

Inundation of the active region of the stem will also have adverse effects on growth due to the restriction of CO₂ exchange at high water contents (Busby & Whitfield, 1978; Dilks & Proctor, 1979). This phenomenon probably accounted for the poor productivity of Distichophyllum fasciculatum at Marion Island. This species had the highest water contents recorded during the study, due to the stems being totally submerged for most of the growing season.

Percentages of water remaining after the 13 hour drying period have been graphed against the initial water content in Figure 7.3b to allow comparison with the data of Gimingham and Smith (1971) from Signy Island (Figure 7.3a). Plants of permanently wet habitats and water tracks on Signy Island and Marion Island e.g. Brachythecium species, occupy similar positions in the centre left of the scatters in both diagrams (group 1). Species of drier, mire margin habitats occur towards the lower left of the scatter (group 2), and species of the exposed, fellfield habitats also correspond in position on the lower right of both graphs (group 3). The species of the central groups 4 and 5 on Signy Island (wet rocks and flushes, peat bank *Polytricha* etc.) do not have taxonomic/ecological counterparts among the species studied on Marion Island, and this area of the graph is correspondingly unoccupied in Figure 7.3b.

Liverwort mats and turfs of the mire habitat are however, more important on Marion Island, as evidenced by the group of species to the upper right of the scatter in Figure

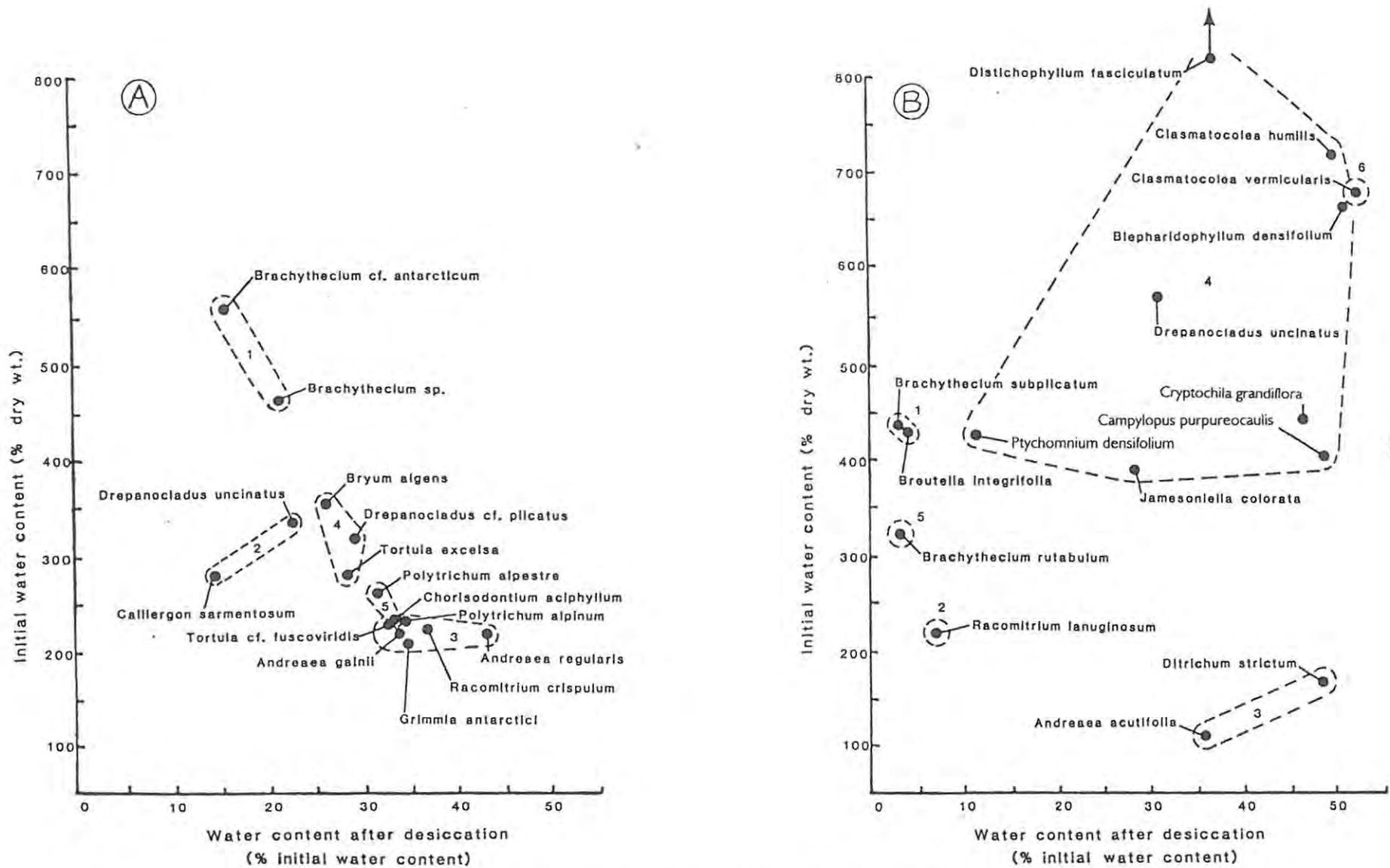


Figure 7.3 Relationship between initial water content, water content after a period of desiccation, and habitat occupied in bryophyte species from A) Signy Island and B) Marion Island. For explanation see text.

7.3b (group 4). Drepanocladus uncinatus also occurs in group 4 on Marion Island as a species of the wettest mire habitat. On Signy Island however, the same species occurs only on temporarily wet ground at swamp margins (group 2) according to Gimingham & Smith (1972), which further confirms the versatility of this widespread species.

As stated earlier, the 13 hour desiccation experiment tests only for short term water loss from fully turgid plants, but does not test for survival thereafter. Dilks & Proctor (1976) found that a 24 hour wetting period would allow most xeric bryophytes to recover completely from periods of desiccation of up to several weeks duration. Studies of photosynthesis and regrowth are necessary to determine survival potential at low water contents, and it must be restated that results of the simple drying test carried out here may not necessarily relate to the physiological "desiccation resistance" of the species concerned.

Racomitrium lanuginosum for example, is another species capable of surviving in a wide range of habitats and is notoriously resistant to long periods of desiccation (Tallis, 1959; Dilks & Proctor, 1974). In the mire habitat at Marion Island however this species has an open growth form and very low resistance to loss of water from its tissues.

An interesting result of this investigation, is the high resistance to short term drought shown by Clasmatocolea vermicularis. This species has a poorly resistant mat growth form, and is also the only bryophyte that reaches high cover values in the biotic/salt spray zone at Marion Island. This environment has a high osmotic stress e.g. from the

influence of salt spray and high nutrient levels at bird colonies. Further investigations into the drought resistance and osmotic tolerance of C. vermicularis would therefore be of interest from an ecological and physiological viewpoint.

On a community basis, shoot production figures (from Table 4.) regressed against either the monthly plant water content data or soil water data, show only a limited correlation (0.4219 $P < 0.2$). This suggests that although moisture regime strongly affects species distribution and community pattern, overall production processes are not limited by this factor due to the high and constant rainfall at Marion Island.

7.4 Conclusion

The results of this study indicate that field water content and resistance to short term water loss follow a trend in Marion Island bryophytes, correlated with soil moisture and growth form. Species with compact growth forms, low field water contents and high resistance to water loss occupy the exposed fellfield habitats e.g. Andreaea acutifolia, Ditrichum strictum, while species with more open growth forms, high water contents and low resistance to drying out, occupy drainage line and wet mire habitats e.g. Brachythecium subplicatum, Breutelia integrifolia.

A large group of mire species with high cover values can also be sequenced on the soil moisture gradient, and represent an ecological group that is important on the wetter and more northerly islands of the Antarctic region, but is less prominent in the maritime

Antarctic. These species, mainly of the liverwort genera Blepharidophyllum, Clasmatocolea, Cryptochila and Jamesoniella, have high field water contents but also relatively high resistance to water loss in the short term, due to their closely packed mat or turf growth forms. This growth habit may adapt such species to short periods of desiccation associated with fluctuating water tables or frequent gale force winds at the sub-Antarctic islands. However, the term "desiccation" is used in a relative sense here, as these plants are probably never subjected to drying out of anything more than a portion of the externally held water.

CHAPTER EIGHT

MINERAL NUTRIENT STATUS

8.1 Introduction

The sensitivity of bryophytes to certain trace elements, particular types of substrate mineralization, heavy metal and radioactive fall out, SO₂ pollution etc., is well known and has resulted in the use of bryophytes as bioindicators in pollution studies worldwide (Barkman, 1968; Gilbert, 1970; Brooks, 1971; Winner & Bewley, 1978). The absorptive and adsorptive properties of bryophytes may influence nutrient cycling in ecosystems to a far greater degree than their biomass might suggest (Tamm, 1953; Pyavchenko, 1960; Skre & Oechel, 1979; Pocs, 1982) and the mechanisms of these influences are only recently beginning to be understood (Brown, 1982, 1984).

Bryophytes perform an important role in the rapid turnover, closed nutrient cycles of forest ecosystems (Rieley, Richards & Bebbington, 1979) and Pakarinen & Vitt (1977) concluded that the bryophyte layer could be exerting a dominant effect on nutrient dispersal and availability in Arctic meadow habitats. It has also been suggested that certain minerals e.g. Phosphate, may have an important role in limiting bryophyte growth in many environments (Babb & Whitfield, 1977; Pakarinen & Vitt, 1977; Brown, 1982).

As confirmed by R Smith (1984) and Laws (1985), the most extensive studies on soil-plant relationships and terrestrial nutrient cycling in the Antarctic zone, have been carried out on Marion Island (V Smith, 1976, 1977, 1977, 1978, 1985). However, notwithstanding the importance of the bryophyte component at Marion Island, the few nutrient determinations that had been carried out on this group used "bulk" collections of mixed species. Neither had it been possible to relate gross mineral nutrient budgets to production processes in bryophytes, as critical work on community structure and plant productivity had yet to be completed (Gremmen, 1975).

There was therefore an urgent need for bryophyte mineral content data for the ecosystem model being prepared by researchers at Marion Island during the early 1980s viz: "what are the patterns and rates of nutrient utilization, transformation, translocation and accumulation, and what are the inputs to a nutrient sub-model?" (SASCAR, 1981).

In addition, the broad range of soil nutrient types represented across the pattern of bryophyte communities at Marion Island suggested that mineral nutrient status might also be a factor influencing production in at least some of these sites e.g. "oligotrophic" mires and the nutrient rich coastal zone (Gremmen, 1975; R Smith, 1984).

Nutrient determinations of Marion Island bryophytes were therefore carried out primarily as an adjunct to the production studies, and more generally as a contribution to the limited knowledge of nutrient relations in bryophyte ecology.

8.2 Methods

For the plant chemical analyses, five replicate core samples of the 15 bryophyte study species, were collected from the growth plots after the period of peak biomass, during May 1982. Samples were partitioned for separate analysis into the green, current year's growth or "active" portion of the stems, and the brown tissue below this according to length criteria determined during the production study (see Chapter 4).

200mg subsamples of dried, ground, plant material were digested in $\text{HNO}_3\text{-H}_2\text{SO}_4\text{-HClO}_4$ mixture. Phosphorous concentrations in dilutions of the digest were determined using a phosphomolybdate-blue procedure (Murphy & Riley 1962). The hydrogen ion concentration of the colour developing reagent was adjusted to compensate for the acidity of the digest.

Calcium, Magnesium, Sodium and Potassium concentrations were determined on suitable dilutions of the digest by atomic absorption spectrometry. Lanthanum (in HCl) suppressant was added to the aliquots for Ca determination. Kjeldahl Nitrogen was measured by a modified Solorzano colorimetric procedure (V Smith, 1985), after digesting subsamples of the dried, ground plant material in $\text{H}_2\text{SO}_4\text{-K}_2\text{SO}_4\text{-CuSO}_4$ mixture.

8.3 Results

The mean results of the mineral element determinations on current season's growth are given in Table 8.1. Overall means of each element for all bryophyte species are given in the bottom row, and totals of all elements for each species in the last column of the table. The species are arranged in their habitat groupings on the xeric-hydric soil moisture gradient. Mean nutrient element values for each habitat are graphed in Fig 8.1.

Values are expressed on a dry weight basis in order to allow easy comparison with the results of other workers in the tundra biome. However, the provisos of Brown (1982) should be noted concerning the potential influence of differing cation exchange capacities and acropetal nutrient translocation at different sites when making comparisons on this basis.

An indication of standing stocks of minerals in bryophytes at the growth plots is given in Table 8.2. These values have been derived from the macronutrient concentration data from the separated green and brown portions of the stem, multiplied by the calculated biomass data for the production segment (green) and remaining standing crop (brown). The values are corrected for percentage cover of the species at each growth plot.

8.4 Discussion

8.4.1 Plant mineral nutrient status

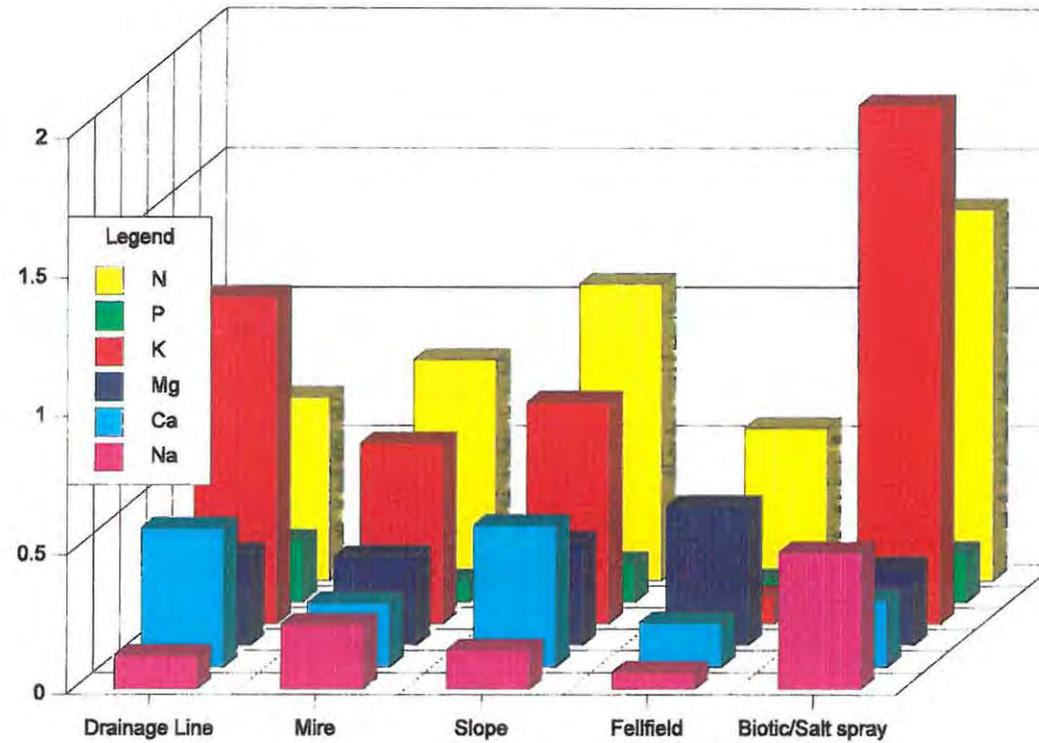
Plant mineral nutrient levels (N, P, K and Ca) are highest in species of the drainage line,

Table 8.1 Mineral content of Marion Island bryophytes.

Mineral content (% dry weight, mean \pm standard deviation).

Species	N	P	K	Mg	Ca	Na	Total Minerals
<i>Brachythecium subplicatum</i>	0.656 \pm 0.033	0.220 \pm 0.013	1.184 \pm 0.052	0.326 \pm 0.016	0.501 \pm 0.030	0.118 \pm 0.009	3.010
<i>Distichophyllum fasciculatum</i>	1.279 \pm 0.067	0.147 \pm 0.013	1.184 \pm 0.086	0.668 \pm 0.019	0.325 \pm 0.025	0.855 \pm 0.087	4.460
<i>Drepanocladus uncinatus</i>	0.995 \pm 0.107	0.124 \pm 0.062	0.653 \pm 0.070	0.280 \pm 0.006	0.175 \pm 0.009	0.116 \pm 0.012	2.343
<i>Campylopus purpureocaulis</i>	0.596 \pm 0.033	0.064 \pm 0.003	0.235 \pm 0.011	0.173 \pm 0.012	0.101 \pm 0.021	0.193 \pm 0.024	1.362
<i>Breutelia integrifolia</i>	0.909 \pm 0.125	0.090 \pm 0.037	0.536 \pm 0.201	0.463 \pm 0.020	0.483 \pm 0.025	0.143 \pm 0.013	2.624
<i>Ptychomnium densifolium</i>	0.831 \pm 0.102	0.068 \pm 0.003	0.247 \pm 0.013	0.218 \pm 0.010	0.197 \pm 0.005	0.006 \pm 0.007	1.621
<i>Clasmatocolea humilis</i>	0.789 \pm 0.054	0.081 \pm 0.041	1.680 \pm 0.106	0.207 \pm 0.009	0.161 \pm 0.010	0.355 \pm 0.063	3.273
<i>Blepharidophyllum densifolium</i>	0.577 \pm 0.041	0.056 \pm 0.028	1.185 \pm 0.067	0.425 \pm 0.013	0.255 \pm 0.012	0.013 \pm 0.014	2.845
<i>Jamesoniella colorata</i>	0.560 \pm 0.054	0.054 \pm 0.027	0.349 \pm 0.008	0.291 \pm 0.007	0.215 \pm 0.012	0.121 \pm 0.005	1.590
<i>Cryptochila grandiflora</i>	0.774 \pm 0.038	0.043 \pm 0.022	0.341 \pm 0.032	0.294 \pm 0.008	0.276 \pm 0.007	0.101 \pm 0.016	1.829
<i>Racomitrium lanuginosum</i>	0.645 \pm 0.000	0.048 \pm 0.000	0.107 \pm 0.000	0.171 \pm 0.000	0.120 \pm 0.000	0.001 \pm 0.002	1.132
<i>Brachythecium rutabulum</i>	1.069 \pm 0.108	0.141 \pm 0.010	0.796 \pm 0.025	0.373 \pm 0.009	0.506 \pm 0.115	0.138 \pm 0.019	3.023
<i>Ditrichum strictum</i>	0.412 \pm 0.004	0.068 \pm 0.034	0.099 \pm 0.009	0.465 \pm 0.041	0.128 \pm 0.033	0.021 \pm 0.017	1.193
<i>Andreaea acutifolia</i>	0.682 \pm 0.710	0.093 \pm 0.002	0.107 \pm 0.042	0.524 \pm 0.075	0.188 \pm 0.007	0.100 \pm 0.025	1.694
<i>Clasmatocolea vermicularis</i>	1.338 \pm 0.032	0.183 \pm 0.012	1.871 \pm 0.125	0.280 \pm 0.014	0.235 \pm 0.023	0.489 \pm 0.066	4.396
X	0.887 \pm 0.134	0.099 \pm 0.027	0.705 \pm 0.293	0.338 \pm 0.075	0.264 \pm 0.066	0.212 \pm 0.111	

Figure 8.1 Mean macronutrient levels (% dry weight) in Marion Island bryophytes grouped according to habitat.



Mean % nutrients in production	N	P	K	Mg	Ca	Na
Drainage Line	0.660	0.220	1.180	0.330	0.500	0.120
Mire	0.796	0.078	0.652	0.319	0.231	0.233
Slope	1.070	0.141	0.800	0.370	0.510	0.140
Fellfield	0.550	0.080	0.100	0.500	0.160	0.060
Biotic/Salt-spray	1.340	0.180	1.870	0.280	0.240	0.490
\bar{X}	0.883	0.114	0.920	0.360	0.328	0.209

Table 8.2 Nutrient standing stocks in bryophyte production and residual biomass components.

Species	% in production	% in residual biomass	Mins. in production g m ²	Mins. in residual biomass g m ²	Mins. in total biomass g m ²	Prodn. mins. as % of mins. in standing crop
<i>Brachythecium subplicatum</i>	3.01	3.36	22.70	30.10	52.80	43.00
<i>Distichophyllum fasciculatum</i>	4.46	4.01	10.70	27.50	38.20	28.00
<i>Drepanocladus uncinatus</i>	2.34	1.61	6.70	7.80	14.50	46.20
<i>Campylopus purpureocaulis</i>	1.36	0.89	5.30	14.50	19.80	26.80
<i>Breutelia integrifolia</i>	2.62	2.08	7.30	10.40	17.70	41.20
<i>Ptychomnium densifolium</i>	1.62	1.76	4.10	6.10	10.20	40.20
<i>Clasmatocolea humilis</i>	3.27	1.84	8.20	20.90	29.20	28.20
<i>Blepharidophyllum densifolium</i>	2.85	1.89	9.30	33.30	42.60	21.80
<i>Jamesoniella colorata</i>	1.59	1.48	6.20	10.80	17.00	36.50
<i>Cryptochila grandiflora</i>	1.83	2.76	5.10	7.50	12.60	40.50
<i>Racomitrium lanuginosum</i>	1.13	1.10	0.70	10.20	10.90	6.40
<i>Brachythecium rutabulum</i>	3.02	2.99	3.40	4.50	7.90	0.43
<i>Ditrichum strictum</i>	1.19	1.40	3.40	1.90	2.20	13.60
<i>Andreaea acutifolia</i>	1.67	1.75	0.30	4.10	5.10	19.60
<i>Clasmatocolea vermicularis</i>	4.40	4.40	18.00	6.70	24.70	72.90

slope and biotic habitats at Marion Island. In common with the findings of Walton & Smith (1979) working at South Georgia, species of the fellfield habitat show the lowest values for most minerals with the exception of Mg.

Shacklette (1965) and R Smith (1985) state that plants of dry mineral soils may occasionally show high levels of minerals when concentrations in the substrate rocks are high. MgO is present in the alkali trachybasalts of Marion Island at high concentrations of up to 14% (Verwoerd, 1971) and may therefore account for this result. A contribution of Mg through marine influence may also be significant (R Smith, 1978; Smith & French, 1988). Salt spray is known to be blown in large quantities to high elevations by the strong wind at Marion Island (Huntley, 1971; V Smith, 1977).

Mean mineral nutrient values are generally low for the mire species but, in common with the findings of the water relations study, interspecific variability is great owing to the heterogeneity of the habitat. For example, the lowest values of P and Mg found in this study occurred in Cryptochila grandiflora and Racomitrium lanuginosum respectively, both of the driest mire habitats, whereas the highest levels of Mg and Na were found in Distichophyllum fasciculatum at the wet end of the mire soil moisture gradient.

Nutrient values for Jamesoniella colorata fall within the range quoted by V Smith (1985) for bulked bryophyte material from the Lycopodio magellanicum - Jamesonielletum coloratae community. The correlation between the absolute values of the present study

for Blepharidophyllum densifolium and V Smith's values for the Blepharidophyllo densifolii - Clasmatocoleetum humilis community do not correspond as closely, although the relative levels of individual nutrients agree. This is probably the result of annual and seasonal differences in nutrient levels which have been well documented in the sub-Antarctic by Walton & Smith (1979) and V Smith (1985). Values for the only individual species studied by V Smith (1976) i.e. Brachythecium rutabulum of the slope zone, are in very close agreement with the results for the same species observed in this study (see Table 8.3). The biotic/salt spray zone is particularly influenced by bird and seal manuring and salt spray from the nearby coast. Clasmatocolea vermicularis from this habitat, shows correspondingly high levels of N, K and especially Na.

P and Ca levels are highest in the drainage line moss Brachythecium subplicatum. This species occurs in a habitat with a near neutral soil pH, which therefore shares a more minerotrophic character with mire flushes dominated by Breutelia integrifolia. Both these habitats have pronounced lateral soil water flow (large throughput of dissolved minerals, Gremmen, 1982) and their bryophytes show high nutrient levels.

K is the most mobile macronutrient and is strikingly accumulated by mosses (Malmer & Nihlgaard, 1980; Proctor, 1981). Its mean level in Marion Island mosses (0.69%) is only surpassed by N concentration (0.81%). The high level of K in the biotic zone may also be due to uptake from marine sources as suggested by R Smith (1978) for islands elsewhere in the Antarctic.

Table 8.3 Mineral element data for bryophytes at Marion Island and from other tundra sites.

N	P	Macronutrients (%)			Na	Reference
		K	Mg	Ca		
0.412 - 1.338	0.043 - 0.220	0.099 - 1.871	0.171 - 0.668	0.101 - 0.506	0.021 - 0.855	This study
1.07	0.14	0.80	0.37	0.51	0.14	Brachythecium rutabulum (this study)
1.81	0.17	0.83	0.36	0.39	0.13	Brachythecium rutabulum (V smith, 1976)
0.60 - 0.85	0.03 - 0.05	1.0 - 1.7	0.22 - 0.30	0.35 - 0.40	0.10 - 0.13	Bulked species from Blepharidophyllum mire (V Smith, 1988)
0.40 - 1.50	0.02 - 0.10	0.10 - 1.00	0.20 - 0.40	0.20 - 0.40	0.05 - 0.20	Bulked species from Jamesoniella colorata mire (V Smith, 1988)
1.30	0.20 - 0.40	0.50 - 3.00	0.25	0.50 - 1.00	0.05 - 0.15	South Georgia (Walton & Smith, 1980)
0.09 - 0.15	0.08 - 0.20	0.25 - 0.56		0.26 - 0.65		Signy Island (Allen & Northover, 1967)
0.27 - 2.61	0.01 - 0.11	0.08 - 0.43		1.00 - 1.70		Devon Island (Pakarinen & Vitt, 1974)
	0.11 - 0.38	0.47 - 0.88	0.06 - 0.16	0.25 - 1.16		Ohio (Lawrey, 1978)
1.50 - 2.95	0.02 - 0.44	0.34 - 1.25	0.05 - 0.12	0.01 - 7.00	0.12 - 0.20	All mosses" (Huneck, 1984)

Tundra habitats are known to be relatively N rich (Rosswall & Granhall, 1980; Sikora & Keeny, 1983) especially where high concentrations of moss-epiphytic, nitrogen fixing blue-green algae occur e.g. in mires (Stewart, 1974; Broady, 1979). Such organisms are common and active at Marion Island (Lindeboom, 1979; Smith & Ashton, 1981; V Smith, 1984) and according to Smith & Russell (1982) are most abundant in association with Brachythecium subplicatum in the minerotrophic drainage line habitat.

The fact that bryophyte N levels are not outstandingly high in this habitat may therefore appear anomalous. However, loss of N from the system could occur through denitrification where waterlogging leads to anaerobiosis in the drainage line habitat, and leaching and fixation in the underlying peat will further deplete N levels in such environments (Sikora & Keeney, 1983). This situation has been confirmed by R. Smith (1985) on South Georgia, where hydrophytic mosses such as Brachythecium were also found to have high concentrations of all minerals except N.

In common with the findings of Vitt & Pakarinen (1977), N and P levels are closely correlated in Marion Island bryophytes ($r=0.8827$ $P < 0.001$ if Brachythecium subplicatum is omitted from the calculation)(Figure 8.2). B. subplicatum is known to store polyphosphates (V. Smith 1984) which may account for the relatively high level of P found for this species. The absolute bryophyte N levels recorded in this study are very similar to those found by other researchers working in tundra habitats (Northover & Allen, 1967; Vitt & Pakarinen, 1977; R Smith, 1978; Walton & Smith, 1979).

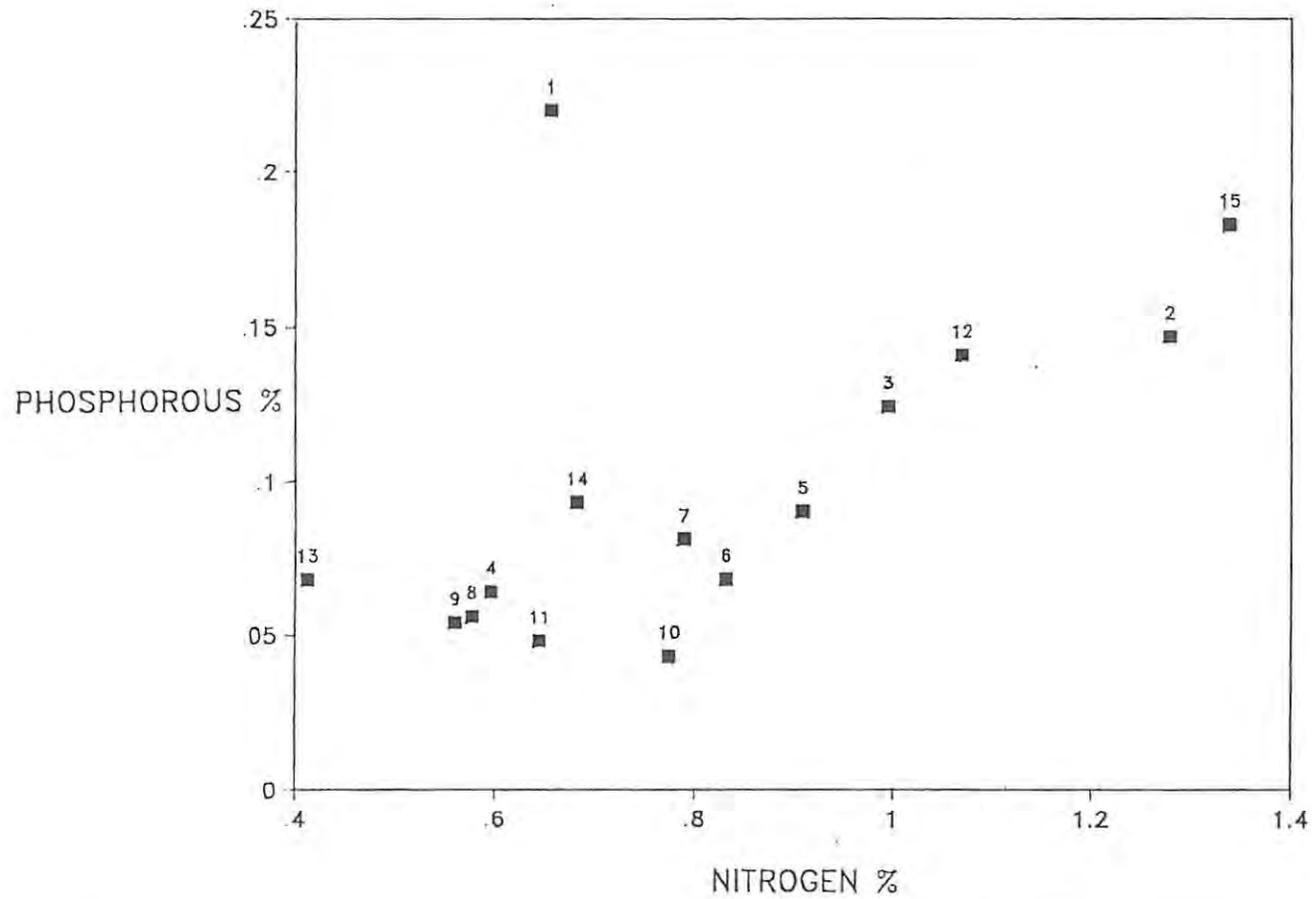


Figure 8.2

Regression of phosphorous against nitrogen content in Marion Island bryophytes. Species numbered according to sequence in Table 4.1.

Figure 8.3 Scatterplot of mineral content against water content for Marion Island bryophytes. Species name abbreviations as for Table 4.1, p. 67.

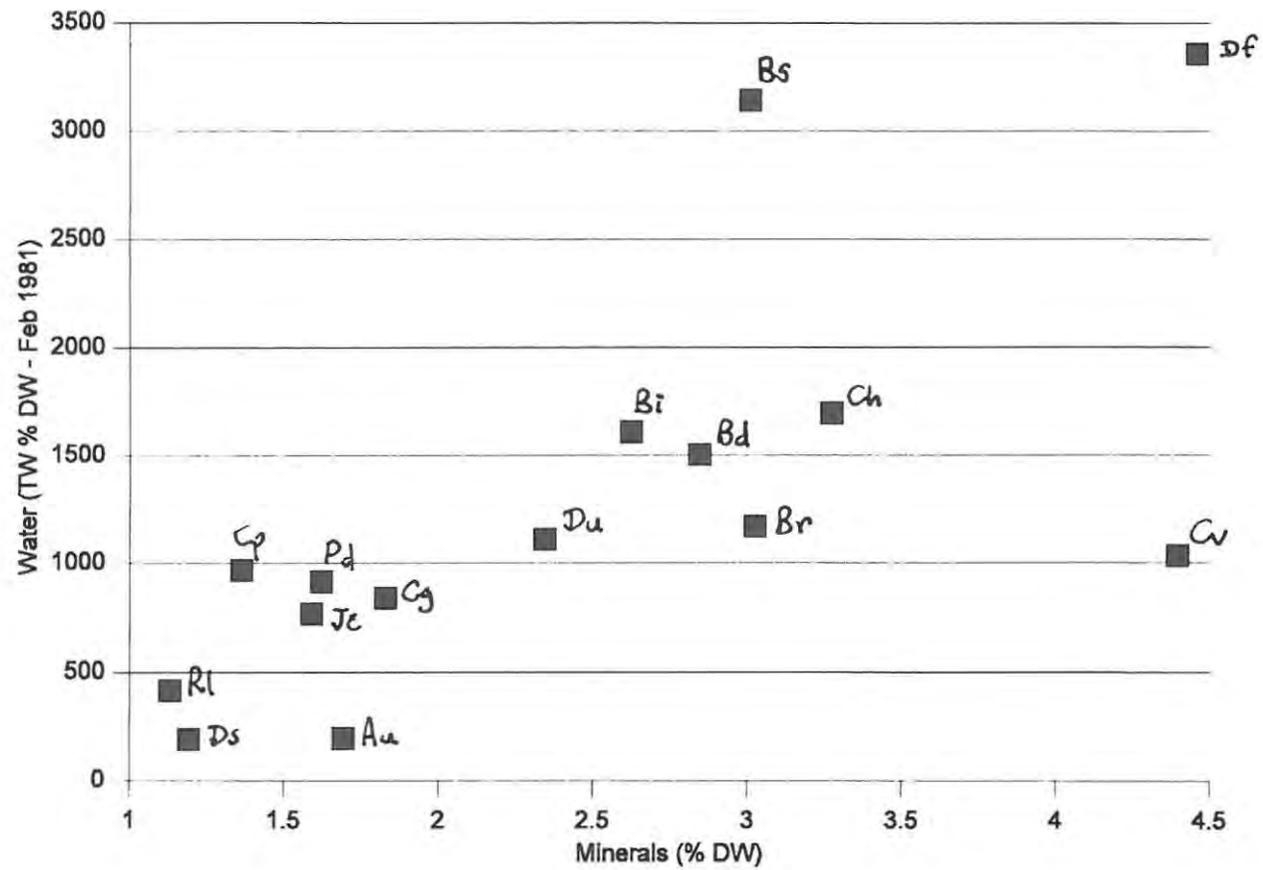
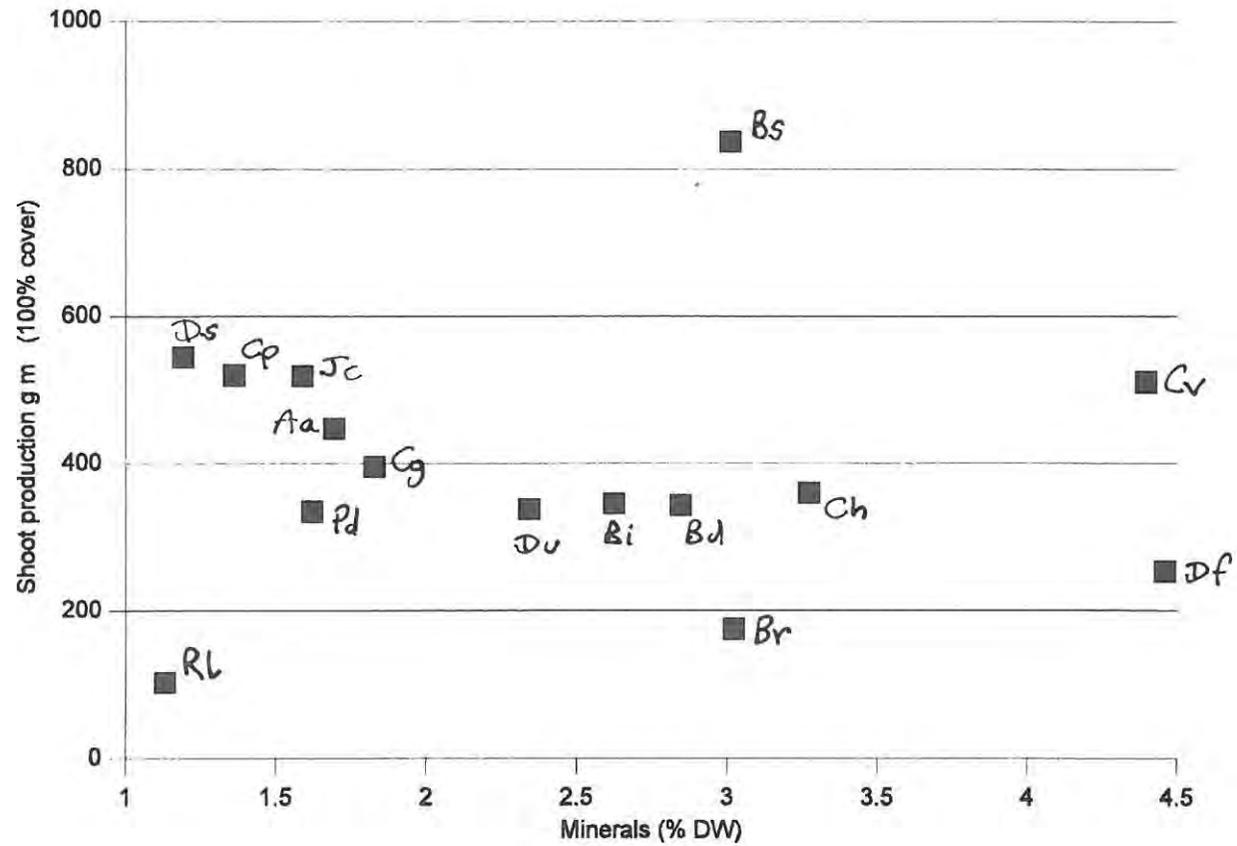


Figure 8.4 Scatterplot of mineral content against Annual Shoot Production for Marion Island bryophytes. Species name abbreviations as for Table 4.1, p. 67.



principal limiting nutrient where bryophyte growth is concerned (Babb & Whitfield, 1977; Pakarinen & Vitt, 1977; Brown, 1982).

Total mineral levels for the residual biomass (non-current year's production) of each species are given in the table of data on nutrient standing stocks (Table 8.2). Analysis of individual element concentrations in the residual biomass (author's unpublished data) showed that P, K and Na generally decreased in the older portions of the stem, while small increases were noted in some species in the cases of Mg and Ca. The latter cations are immobilized in the old cell walls (Dowding, 1981; Proctor, 1981). However, the greater cell wall to volume ratio in older stems will tend to exaggerate apparent values for these cations when expressed on a concentration per unit weight basis. Content of Ca and Mg on a length of stem basis may actually be declining in a similar fashion to the other elements (Bates, 1979).

Nitrogen was consistently present in higher concentrations in the older parts of the plant, which agrees with the findings of Allen (1967) and Grubb, Flint & Gregory (1969). Brown (1982) suggested that the increase of N with age may be due to microbial growth, which is known to be important in bryophyte communities on Marion Island (Smith & Russell, 1982).

8.4.2 Nutrient standing stocks

Nutrient standing stocks in Marion Island bryophytes (Table 8.2) show a trend from the lowest levels in the fellfield habitat, to the highest levels in the drainage line habitat.

Although the coastal species Clasmatocolea vermicularis has one of the highest macronutrient contents on a dry weight basis, standing stocks in this species are similar to the low mean level in the mire habitat. This is probably because of the low residual biomass of this species, due in turn to the high decomposition rate and rapid turnover in the biotic/salt spray zone.

As concentrations of minerals in green versus brown tissue are fairly equivalent, nutrient standing stocks in these separate components mirror the biomass partitioning closely on a cover corrected basis. Subject to the constraints on determining green ("active") and brown ("inactive") zones in bryophytes outlined in Chapter 4, it is possible to make the following observations. Bryophytes with thick cell walls (high cell wall to volume ratios) and/or a large proportion of the leaf composed of the costa, are exemplified by Racomitrium lanuginosum, Ptychomitrium ringianum and Ditrichum strictum. These species tend to retain most of their minerals in the greater biomass of "inactive" brown tissue which accumulates due to low decomposition in these species.

Species with thin cell walls (low cell wall to volume ratios) include "delicate" types such as the leafy liverworts and mosses of the hydric habitats e.g. Drepanocladus uncinatus, Distichophyllum fasciculatum and Brachythecium subplicatum. These species have a rapid turn over time and high decomposition rates and have most of their mineral nutrients concentrated in the relatively high biomass of the active portion of the stem.

In Andreaea acutifolia, only a short lived zone of standing crop survives beneath the active portion before decomposition to the soil-like interior of the moss cushion takes place. This accounts for the anomalous result in the case of this species. The low relative macronutrient level in the active zone of Jamesoniella colorata may be an artefact, due to underestimation of production in this species because of disturbance at the growth plot (see Chapter 4). An alternative explanation might be back-translocation of nutrients into the longer lived brown portion of the stem (Brown, 1982).

Overall nutrient element standing stocks as measured here at Marion Island, are significantly higher than those recorded at northern hemisphere tundra sites. This may be accounted for by biotic and salt spray influences, coupled with the well documented greater accumulation of standing crop at sub-Antarctic sites.

8.4.3 Plant substrate mineral relationships

Due to the ability of bryophytes to selectively accumulate mineral ions from very dilute solutions, several authors have noted the lack of complementarity between soil and mineral element concentrations (Walton & Smith, 1979; Longton, 1980; Proctor, 1981). A similar general conclusion can be drawn from the data of the present study.

The percentage inorganic component of soils from the main habitat complexes calculated from the loss on ignition data of Gremmen (1982), are given in Table 8.4, along with the soil mineral data of V Smith (1976, 1977b) for comparison. Attempting to correlate the values for total macronutrient concentration in Marion Island bryophytes

Table 8.4 Mineral element and loss on ignition data for Marion Island soils.

Species	% loss on ignition	% inorganic component	habitat complex	N %	P %	K	% saturation of CEC		
							Mg	Ca	Na
<i>Brachythecium subplicatum</i>	85.50	14.50	drainage line	2.5	0.66	2	32	26	4
<i>Distichophyllum fasciculatum</i>	95.20	4.80							
<i>Drepanocladus uncinatus</i>	89.80	10.20							
<i>Campylopus purpureocaulis</i>	91.50	8.50							
<i>Breutelia integrifolia</i>	73.20	26.80							
<i>Ptychomnium densifolium</i>	88.00	12.00	mire	2.34	0.6	3	13	5	5
<i>Clasmatocolea humilis</i>	94.40	5.60							
<i>Blepharidophyllum densifolium</i>	90.50	9.50							
<i>Jamesoniella colorata</i>	77.60	22.40							
<i>Cryptochila grandiflora</i>	56.70	43.30							
<i>Racomitrium lanuginosum</i>	68.60	31.40							
<i>Brachythecium rutabulum</i>	65.50	34.50	slope	2.18	0.74	7	40	21	4
<i>Ditrichum strictum</i>	16.20	83.80	fellfield	0.68	0.55	2	5	3	4
<i>Andreaea acutifolia</i>	16.20	83.80							
<i>Clasmatocolea vermicularis</i>	92.20	7.80	biotic	1.66	1.55	1	13	14	1

with the soil inorganic component, is likely to be an invalid exercise as total plant mineral levels may be strongly influenced by elements other than the conventional suite of nutrients studied here. As stated above, bryophytes may selectively accumulate nutrients from low concentrations of minerals in their environment, or take up excess amounts where substrate levels are high.

8.5 Conclusion

According to the results of this study, one of the highest mineral nutrient levels is shown in the species representative of the biotic and salt spray zones (Clasmatocolea vermicularis). This is probably related to the influence of animals and aerial deposition of minerals from the marine source in these habitats. In the other habitats, bryophyte nutrient levels tend to parallel the soil moisture gradient, although the relationship within the mire habitat is less clear. Highest values on this gradient are found in the wettest habitats (drainage lines and flushes) and lowest levels occur in fellfield (with the exception of Mg which may be more abundant in fellfield due to high levels in the substrate).

Results from the mire complex are heterogeneous, but overall levels confirm the relatively oligotrophic nature of this habitat. Standing stocks reflect biomass accumulation levels as minerals are immobilized in greater quantity in the more intractable tissues of bryophytes with low decomposition rates. It should be remembered however that on a unit weight basis, these plants have lower nutrient contents.

The results suggest that there is little correlation between between soil nutrients and individual or total plant macronutrients. The possibility of the influence of other minerals on bryophyte total (ash) mineral content remains to be investigated. A good correlation exists between plant P levels and production which tends to confirm that this element may be limiting to bryophyte growth in many habitats. In general, higher overall levels of the elements N, Mg and Na appear to occur at Marion Island than at most tundra sites, probably due to marine influence.

The above remarks must be regarded as speculative, based as they are on a relatively small scale survey. The influence of bryophyte mineral content on decomposition will be further discussed in the concluding chapter of the thesis.

CHAPTER NINE

SYNTHESIS

9.1 Introduction:

The primary aim of this study has been to measure growth and characterise some of the major factors influencing variability in growth patterns among Marion Island bryophytes. Correlations between biomass and production values and some of these factors have already been indicated during the relevant sections earlier in the thesis. Several of these correlations have appeared more clearly when species have been grouped for comparison on a habitat complex basis.

The aim of the following section is to investigate further using statistical techniques, the detailed relationships at the species level between production and biomass figures on the one hand, and some extrinsic and intrinsic factors hypothesized to correlate with growth on the other hand. The statistical analysis should also assist in the uncovering of less obvious or hidden relationships, identification of intervening variables and detection of spurious relationships.

9.2 Methods**9.2.1 Selection of variables for statistical analysis**

Extrinsic factors affecting plant growth include features of macroclimate such as solar radiation, temperature rainfall etc., and soil factors such as water content, mineral nutrient status and content of organic material (as measured by loss on ignition). Intrinsic factors that might be expected to correlate with production include plant water and mineral element content, energy levels and chlorophyll content. Data from studies on all the above aspects at Marion Island were included in the statistical analysis, excepting macroclimatic variables and soil mineral nutrient status values.

As mentioned in Chapter 4, the relationship of climatic factors with shoot production at Marion Island could not be fully investigated during this study. For the reasons given in Chapter 1, macroclimatic factors would be expected to vary little between the growth study sites and would also be inappropriate to include in the correlation matrix against one year's measure of annual production. A lack of correlation between soil nutrients and production in bryophytes has been reported by other workers (see Chapter 8) and soil nutrient data has therefore also been omitted from the analysis.

Production and biomass were included in the analysis on a cover corrected basis, with turnover ratio included also. The extrinsic and intrinsic factors were included in different forms also e.g. chlorophyll on dry weight and per unit area bases for comparative purposes. Soil organic content was extracted from the loss on ignition data of Gremmen (1982).

9.2.2 Statistical techniques:

The principal method used throughout the thesis for comparing variables has been simple linear regression. This procedure fits a model ($y=a+bx$) relating one variable to another, by minimizing the sum of squares of the residuals for the fitted line which can be plotted on an x/y graph. The degree of correlation between both variables is defined by the correlation coefficient (r) which varies between -1 (negatively correlated i.e. factors vary in inverse proportion) and +1 (factors vary in direct proportion).

Statistically independent variables have an expected correlation of zero. The correlation coefficient is preferred here to calculating the covariance of variable pairs, as it provides a normalized and scale free measure of the association between two variables (applicable to data types that are very different in scale such as the variables measured in the present study). The significance level of the correlation is based on the well known "Student's T" distribution (r^2).

All variables were regressed against each other to produce a correlation matrix. This matrix was then subjected to a more advanced multivariate statistical procedure viz: "Principal Components Analysis" (PCA). This technique reduces the number of variables in a data set by finding a small number of linear combinations of highly correlated variables that explain variations among the factors almost as effectively as the entire data set (Johnson & Wichern, 1982).

Analyses were carried out by the author using a statistical/graphical software package designed for use with a mainframe computer, but modified to operate on a personal computer ("Statgraphics" (STSC Inc.) and IBM AT).

9.3 Results:

An initial list of 44 variables was reduced to 36 for inclusion in the initial cross correlation. The variables comprised basic and transformed data measured for the fifteen species of this study and or the communities that they represented. This list was further reduced to 27 variables by omitting those that showed below a certain number of significant correlations with all other variables. This list has been further reduced for the purposes of clarity, by variables whose effects are duplicated by other closely related variables e.g. plant external water content was omitted in favour of plant total water content.

The final concentrated correlation matrix is shown in Table 9.1. The high number of significant correlations across the entire range of factors indicates that the variables chosen for study were pertinent to the questions being addressed in this thesis. The small number of highly significant correlations however, emphasizes the large degree of variability in the data that is attributed to microenvironmental heterogeneity. The dependent variables: biomass, production, turnover ratio and cover percentage will be discussed separately. The independent variables: energy, chlorophyll, water and minerals

Table 9.1 Correlation matrix for 19 variables associated with production and biomass in Marion island bryophytes.

	b/h	b/c	p/c	p/b	c/p	e/d	e/b	a/p	e/w	e/m	c/o	sum	t/w	n	f	k	ca	na	tm	lcl
b/h	1.0000 (.15)																			
b/c	.3289 (.15)	1.0000 (.15)																		
p/c	-.1250 (.15)	.5580*** (.15)	1.0000 (.15)																	
p/b	-.6708*** (.15)	-.3103 (.15)	.4677** (.15)	1.0000 (.15)																
e/p	-.5305*** (.15)	-.5776*** (.15)	.6581*** (.15)	.3250 (.15)	1.0000 (.15)															
e/w	.3317 (.15)	-.0651 (.15)	-.4304* (.15)	-.3822* (.15)	-.4037* (.15)	1.0000 (.15)														
a/p	-.4396** (.15)	.2359 (.15)	.5062** (.15)	.3159 (.15)	.6431** (.15)	-.8007*** (.15)	1.0000 (.15)													
e/w	-.3958* (.15)	.1511 (.15)	.5113** (.15)	.3183 (.15)	.5371*** (.15)	-.5072** (.15)	.7017*** (.15)	1.0000 (.15)												
e/m	.0343 (.15)	-.8799 (.15)	-.0012 (.15)	.1946 (.15)	.0002 (.15)	-.0013 (.15)	.0000 (.15)	.0000 (.15)	1.0000 (.15)											
c/o	-.0612 (.15)	.1677 (.15)	.2594 (.15)	.0627 (.15)	.2232 (.15)	-.1592 (.15)	.3337 (.15)	.7859*** (.15)	.0000 (.15)	1.0000 (.15)										
sum	1.0000 (.15)	.9505 (.15)	.5023 (.15)	1.0000 (.15)	.7213 (.15)	.9666 (.15)	.1438 (.15)	.0000 (.15)	.0000 (.15)	.0000 (.15)	.8667*** (.15)	1.0000 (.15)								
t/w	-.1476 (.15)	.4078* (.15)	.2912 (.15)	-.0247 (.15)	.5200*** (.15)	-.1160 (.15)	.3860* (.15)	.7694*** (.15)	.0000 (.15)	.0000 (.15)	.0000 (.15)	.0000 (.15)	1.0000 (.15)							
tm	.0046 (.15)	.8005*** (.15)	.7272*** (.15)	-.0423 (.15)	.7799*** (.15)	-.4146** (.15)	.5995*** (.15)	.1861** (.15)	.2045 (.15)	.4392** (.15)	1.0000 (.15)									
tw	-.2503 (.15)	.4114* (.15)	.5390*** (.15)	-.1354 (.15)	.7005*** (.15)	-.3836* (.15)	.6264*** (.15)	.7920*** (.15)	.5613*** (.15)	.7190*** (.15)	.7610*** (.15)	1.0000 (.15)								
n	-.7701*** (.15)	-.3074 (.15)	.0955 (.15)	.5925*** (.15)	.4372* (.15)	-.2256 (.15)	.2075 (.15)	.4985* (.15)	.1505 (.15)	.2362 (.15)	.0697 (.15)	.4627** (.15)	1.0000 (.15)							
f	-.3101 (.15)	-.0500 (.15)	.5234*** (.15)	.5564*** (.15)	.2838 (.15)	-.3343 (.15)	.2443 (.15)	.5247*** (.15)	.1818 (.15)	.1652 (.15)	.3051 (.15)	.5582*** (.15)	.5772*** (.15)	1.0000 (.15)						
k	.2268 (.15)	1.0000 (.15)	.0008 (.15)	.0002 (.15)	.3007 (.15)	.1420 (.15)	.5915 (.15)	.0007 (.15)	.9127 (.15)	.9556 (.15)	.2180 (.15)	.0002 (.15)	.0001 (.15)	.0000 (.15)	1.0000 (.15)					
l	-.2609 (.15)	.2835 (.15)	.4564*** (.15)	.3881 (.15)	.5330*** (.15)	-.0470 (.15)	.1847 (.15)	.5905*** (.15)	.5255*** (.15)	.6790*** (.15)	.3441 (.15)	.6376*** (.15)	.5657*** (.15)	.6065*** (.15)	1.0000 (.15)					
ca	-.4865 (.15)	-.3543 (.15)	.0065 (.15)	.0416 (.15)	.0006 (.15)	1.0000 (.15)	.9032 (.15)	.0001 (.15)	.0007 (.15)	.0000 (.15)	.1156 (.15)	.0000 (.15)	.0000 (.15)	.0000 (.15)	.0000 (.15)	1.0000 (.15)				
na	-.4651 (.15)	-.0089 (.15)	.4051 (.15)	.4354* (.15)	.3917 (.15)	-.5860*** (.15)	.6186*** (.15)	.7218*** (.15)	.4100 (.15)	.2898 (.15)	.2913 (.15)	.4928** (.15)	.3379 (.15)	.5653*** (.15)	.2629 (.15)	1.0000 (.15)				
tm	.0649 (.15)	1.0000 (.15)	.0270 (.15)	.0118 (.15)	.0381 (.15)	.0001 (.15)	.0000 (.15)	.0000 (.15)	.0237 (.15)	.3422 (.15)	.3195 (.15)	.0021 (.15)	.1316 (.15)	.0002 (.15)	.4746 (.15)	.0000 (.15)				
na	-.2453 (.15)	.2445 (.15)	.1579 (.15)	.1057 (.15)	.4795*** (.15)	.0431 (.15)	.1524 (.15)	.4271*** (.15)	.3851* (.15)	.5938*** (.15)	.3997 (.15)	.7470*** (.15)	.6441*** (.15)	.3681* (.15)	.6889*** (.15)	.1011 (.15)	1.0000 (.15)			
lcl	-.7658 (.15)	.7701 (.15)	.9685 (.15)	.9992 (.15)	.0032 (.15)	1.0000 (.15)	.9764 (.15)	.0147 (.15)	.0349 (.15)	.0001 (.15)	.0310 (.15)	.0000 (.15)	.0000 (.15)	.0676 (.15)	.0000 (.15)	.9995 (.15)	1.0000 (.15)			
tm	-.4802 (.15)	.0742 (.15)	.3381 (.15)	.4518 (.15)	.5355*** (.15)	-.1801 (.15)	.2850 (.15)	.6572 (.15)	.5088 (.15)	.6245 (.15)	.3372 (.15)	.7568*** (.15)	.7914*** (.15)	.7027*** (.15)	.9001*** (.15)	.8302*** (.15)	1.0000 (.15)			
lcl	-.0077 (.15)	1.0000 (.15)	.1312 (.15)	.0074 (.15)	.0005 (.15)	.9162 (.15)	.2648 (.15)	.0000 (.15)	.0013 (.15)	.0000 (.15)	.1638 (.15)	.0000 (.15)	.0000 (.15)	.0000 (.15)	.0000 (.15)	.0086 (.15)	1.0000 (.15)			
lcl	-.4093 (.15)	.6418*** (.15)	.5995*** (.15)	.2210 (.15)	.9381*** (.15)	-.2644 (.15)	.4799*** (.15)	.4823 (.15)	.1659 (.15)	.5376 (.15)	.7582*** (.15)	.6344*** (.15)	.4290 (.15)	.2626 (.15)	.5931*** (.15)	.8302*** (.15)	1.0000 (.15)			
lcl	-.0842 (.15)	.0000 (.15)	.0001 (.15)	.6145 (.15)	.0000 (.15)	.4650 (.15)	.0032 (.15)	.0029 (.15)	.9543 (.15)	.0005 (.15)	.0000 (.15)	.0000 (.15)	.0142 (.15)	.4762 (.15)	.0001 (.15)	.9520 (.15)	.0013 (.15)	.0009 (.15)	.0000 (.15)	

Key to variables

- b/h - colony biomass
- b/c - cover corrected biomass
- p/c - cover corrected production
- p/b - turnover ratio
- c/p - % cover
- e/w - energy (dry weight basis)
- a/p - ash %
- e/m - chlorophyll mg g⁻¹
- c/o - chlorophyll mg m⁻²
- cc - chlorophyll mg m⁻² cover corrected
- swm - soil water content (this study)
- tw - total plant water
- n - nitrogen
- p - phosphorous
- k - potassium
- ca - calcium
- na - sodium
- tm - total macronutrients
- lcl - soil loss on ignition

Key to data

- .5772 - r
- (.15) - number of samples
- * - p < 0.05
- ** - p < 0.01
- *** - p < 0.001

etc., will be discussed under one heading.

9.3.1 Correlation Analysis

9.3.1.1 DEPENDENT VARIABLES:

9.3.1.1.1 Biomass: Soil water and plant water contents are positively correlated with biomass on a cover-corrected basis, showing the greater accumulation of plant material in more moist habitats. Loss on ignition values (soil organic component) are also positively correlated with biomass and point to the stronger development of bryophytes on deeper and more nutrient-rich soils.

9.3.1.1.2 Production: The striking aspect of the production data was the total lack of significant correlations between growth expressed on a 100% cover basis, and any other variable except biomass (which accounts for the omission of colony production from the matrix in Table 9.1). Similar findings have been reported by other researchers analysing bryophyte data in the tundra biome (French, 1981; Wielgolaski et al, 1981).

This is likely to be the result of high microsite variability in production patterns, as many of the point measurement techniques used for growth analysis are applied to very small segments of bryophyte turf or even single stems.

Intercorrelation diagrams ("casement plots") for six of the most important variables are shown in Figure 9.1. These diagrams are included to show the spread of individual

species points, and directions of the correlations involved.

There was a weak correlation between colony production and colony biomass (second set of biomass readings) but a highly significant correlation between these factors only appeared when both were expressed on a cover corrected basis. If the weak correlation between production and biomass compared on a 100% cover basis is reflecting a true relationship, then this would again emphasize the higher significance of decomposition versus production in controlling biomass accumulation, at least in the bulk of mire species that dominate the correlations due to their higher numbers. There is a lack of correlation between production (100% basis) and areal cover (coefficient -0.0288 (P=0.9143) not shown in table), suggesting that species with low cover may still be efficiently adapted to achieve high levels of colony production in the more extreme habitats.

Most of the soil and plant water content variables are significantly correlated with production, which supports the main hypothesis of the thesis that growth in Marion Island bryophytes is largely dependent on the same soil moisture gradients noted by Gremmen (1982) in respect of community distribution. The provisos regarding depressed production in species of the wettest habitats should however be noted as modifying this overall conclusion (see Chapter 7).

Other factors that are related to the moisture gradient and thus also to production, are

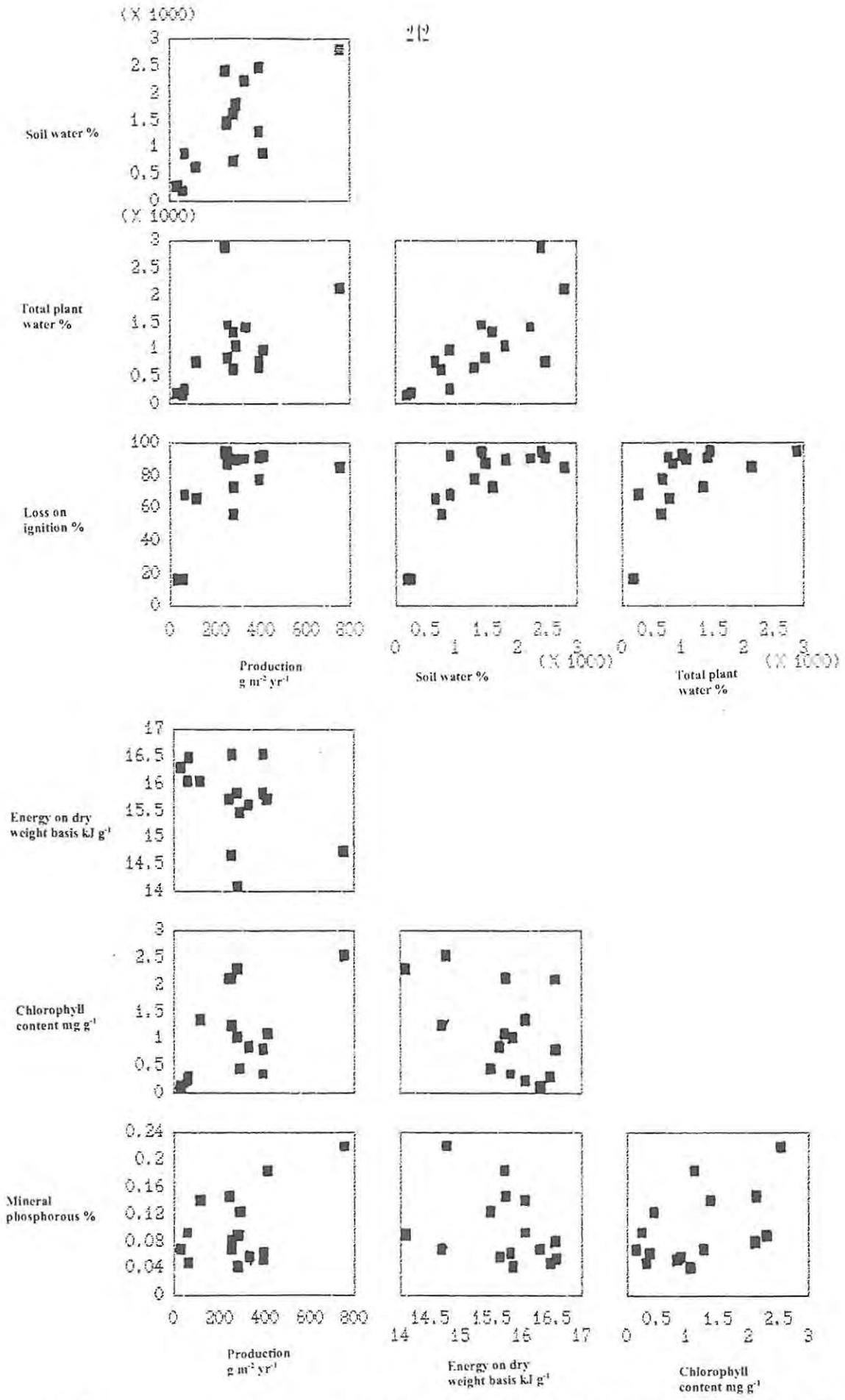


Figure 9.1 Intercorrelation diagrams for the six most highly correlated variables against production in Marion Island bryophytes.

chlorophyll content and mineral nutrient status. This trend is not shown by the totals for all macronutrients studied, but is seen in the relationship between ash content, and several individual nutrient elements and production (see Chapter 8).

9.3.1.1.3 Turnover: Energy levels are negatively correlated with production:biomass turnover ratios (Table 9.2) in the same way as they are to production. On a shoot per shoot basis, the bryophytes of physiologically drier and more exposed habitats (e.g. fellfield) are often better performers (on a 100% cover basis) than those of wetter habitats, and may be more efficient users of energy. The fellfield plants also show lower decomposition and greater biomass accumulation. There is also evidence to suggest (Lindeboom, 1979; Grobler et al, 1987) that bacterial activity is more dependent on the "energy quality" than on the nutrient quality of the substrate at Marion Island.

9.3.1.1.4 Cover: Energy also correlates negatively with plant cover, for example the fellfield mosses with their low cover values also show the highest energy levels as explained above. Conversely, there is a high number of strong positive correlations between cover percentage and all the principle factors that are associated with growth (water, nutrients, chlorophyll). This once again suggests a greater relevance of the factors measured here, to production on a community rather than colony basis.

One of the strongest correlations in the entire data set is shown between soil loss on ignition (organic content) and cover. This reflects the occurrence of the highest levels

Table 9.2 Production:biomass turnover ratios and initial annual loss rates for Marion Island bryophytes.

Species	Production:biomass turnover ratio (:1)	Initial annual Loss rate (%)
<i>Brachythecium subplicatum</i>	0.46	48.1
<i>Distichophyllum fasciculatum</i>	0.26	28.5
<i>Drepanocladus uncinatus</i>	0.37	39.1
<i>Campylopus purpureocaulis</i>	0.19	19.8
<i>Breutelia integrifolia</i>	0.36	31
<i>Ptychomnium densifolium</i>	0.42	34.1
<i>Clasmatocolea humilis</i>	0.18	25.9
<i>Blepharidophyllum densifolium</i>	0.16	19.8
<i>Jamesoniella colorata</i>	0.35	30.1
<i>Cryptochila grandiflora</i>	0.51	46.3
<i>Racomitrium lanuginosum</i>	0.06	6.3
<i>Brachythecium rutabulum</i>	0.43	40.3
<i>Ditrichum strictum</i>	0.16	13.1
<i>Andreaea acutifolia</i>	0.22	29.6
<i>Clasmatocolea vermicularis</i>	0.73	59

of bryophyte cover in the mire and drainage line areas. The thick, peaty deposits in the mires retain large amounts of water, thereby promoting often high production levels that lead in turn to the high cover percentages recorded in this habitat.

9.3.1.2 PREDICTOR VARIABLES: The intrinsic and extrinsic variables of energy, ash content, chlorophyll, soil and plant water content, mineral nutrient level and soil loss on ignition are intercorrelated to various degrees, and some of these relationships have already been discussed above and in the preceding chapters. The most important variables in terms of numbers of strong correlations are soil water and organic content. These are most significant in terms of their relationships with biomass and production through their effect on plant water content. This last factor shows the highest number of correlations (with 16 out of the 19 variables included in the final matrix) and confirms the overriding importance of moisture in the ecology of bryophyte vegetation at Marion Island.

The individual mineral nutrient elements show various correlations among themselves for example the relationship of N with P that has been referred to here and by others working in the tundra (Chapter 8).

9.3.2 Principal Components Analysis:

In order to test the statistical validity of the conclusions drawn by manual interpretation

of the correlations noted above, a principal components analysis was conducted on the 19x19 cross-correlation matrix shown in Table 9.1.

The procedure extracted seven components to account for 95% of the variance represented in the data (Table 9.3). This is a relatively high number and once again reflects the variability of the basic data. However, more than two thirds of this variance was accounted for by the first two components whose weights are plotted in Figure 9.3. The value of a variable on a component (i.e. the component weighting) is most important in describing the relationships of the data.

The first component (horizontal axis) appears to represent (fairly weakly) a gradient from high energy bryophytes to wet bryophytes with high chlorophyll contents and total nutrients, both on a dry weight basis and a high percentage cover. The second (vertical) component relates more obviously to biomass (defined at top and bottom of the graph by biomass and production:biomass turnover ratio respectively).

A plot of the actual components (Figure 9.4) shows a wide scatter along both axes which confirms the orthogonality of the production and biomass axes. Lines representing the original variables have been overlain on the PC plot in Figure 9.5. The length of each vector is proportional to its contribution to the principle components, and the angle between any two is inversely proportional to the correlation between them.

Table 9.3. Principal Components Analysis of the correlation matrix in Table 9.1.

Component Number	Percent of Variance	Cumulative Percentage
1	46.08413	46.08413
2	15.95501	62.03914
3	12.57590	74.61505
4	9.02948	83.64453
5	6.10729	89.75182
6	4.11662	93.86844
7	2.12279	95.99123
8	1.37281	97.36403
9	1.11834	98.48237
10	.80016	99.28253
11	.32306	99.60559
12	.23020	99.83580
13	.12624	99.96204
14	.03769	99.99973
15	.00019	99.99992
16	.00006	99.99998
17	.00001	99.99999
18	.00001	99.99999
19	.00001	100.00000

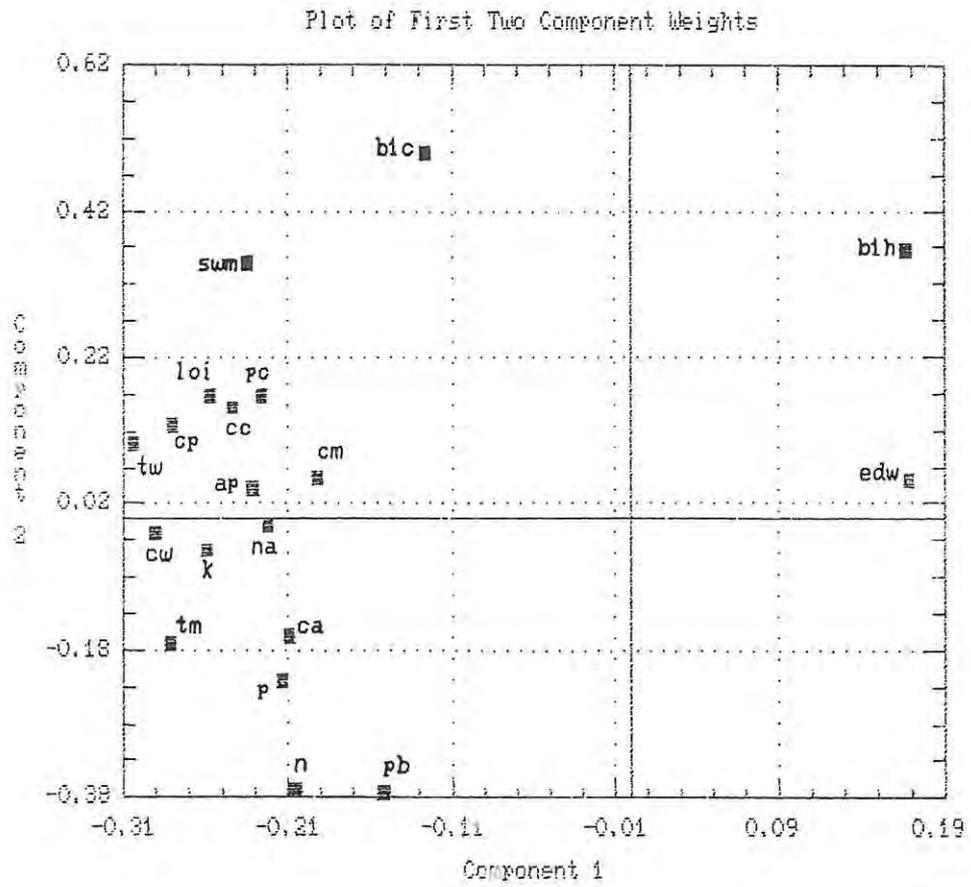


Figure 9.3

Plot of first two component weights in bryophyte principal component analysis. Variable names as for Table 9.1

Plot of First Two Principal Components

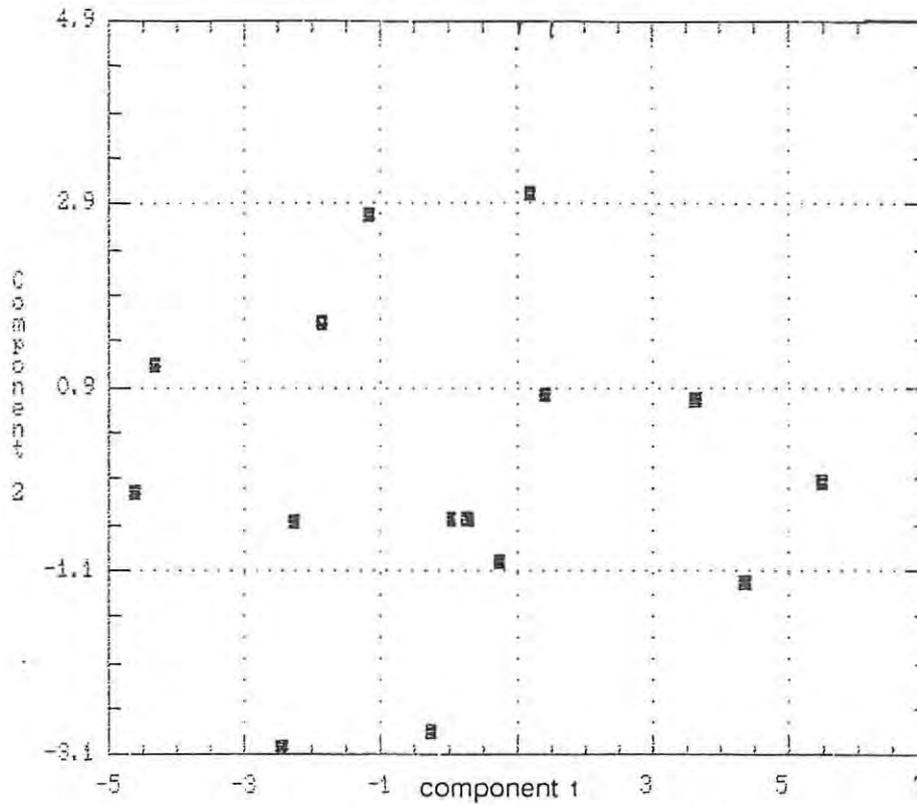


Figure 9.4 Plot of first two principal components in bryophyte PCA.

Biplot for First Two Principal Components

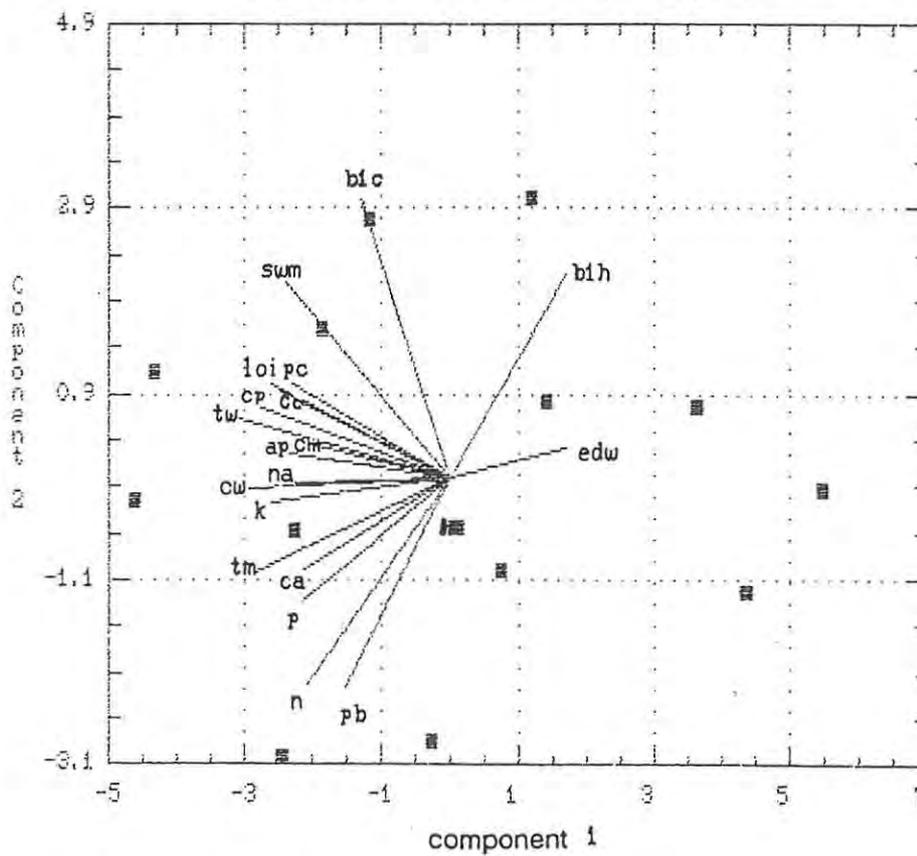


Figure 9.5 Biplot for first two principal components including starplot for individual variables.

This author is not qualified to comment further on the significance of the scatters in these diagrams, and they have therefore been included to permit interpretation by those better skilled in interpretation of PCA plots. Comparisons may be made with PCAs of site characteristics presented for Marion Island by Smith and Steyn (1982) and for South Georgia (M Smith and Walton, 1985).

Considerable potential for further investigation resides in the data presented in this thesis, for example through the application of further statistical techniques such as Analysis of Variance. Comparison of extrinsic and intrinsic growth factors with production expressed on a 100% cover basis would also be a more relevant measure of many of the relationships being explored here. It is hoped therefore, that much of the basic data presented will be of value to other researchers who will carry forward the investigations of sub-Antarctic ecology at Marion Island.

CHAPTER TEN

CONCLUSION

10.1 Conclusion

The findings presented in this thesis can be viewed firstly from the standpoint of their contribution to the ecology of tundra vegetation, and to that of Marion Island in particular; and secondly, the information can be assessed on the basis of its relevance to bryophyte physiology in general. Both these aspects have been addressed when discussing the results of the individual studies in previous chapters. In this concluding section therefore, the general findings will be related to the original aims of the investigation, as set out in the introductory chapter.

Aim 1: to provide a set of measured production values for representative bryophyte species, as necessary basic information for workers involved in the ecosystem bioenergetics and nutrient cycling studies at Marion Island.

The tabulated data on cover, biomass, seasonal and annual production, and turnover rates in Chapter 4, are based on a wide range of bryophyte species, selected to be most representative of the range of habitat types occurring on Marion Island. They also include the bryophyte species that are likely to contribute most to the overall biomass and

production quantities, and will therefore be of greatest significance in relation to other aspects of ecosystem functioning at the island. Information from this study has already been used in other studies, for example investigations into nutrient cycling at Marion Island (V Smith, 1985); and has been referred to in broader discussions of polar bryophyte ecology (R smith, 1984; Longton, 1988).

Although few other relevant studies in the tundra biome have continued for longer than the two growing seasons over which the present investigation was conducted, this time scale still limits the interpretation of results in respect of prediction of bryophyte performance at related stations in the long term. There is much evidence for climatic fluctuation in the sub-Antarctic e.g. the warming trend documented in Chapter 2; and significant departures from the values reported here for annual shoot production could therefore be expected during warmer or drier periods.

The information presented, should also be of benefit if future work on the ecology of vegetation at Marion Island follows the trend that is apparent in ecophysiological investigations elsewhere in the tundra biome i.e. the use of gas exchange experiments and microclimate monitoring to predict production patterns. Production measurements made by annual harvesting techniques are a useful adjunct to such studies and a necessary check on prediction accuracy.

Aim 2: to characterise certain extrinsic and intrinsic properties that are hypothesized to

correlate with growth at Marion Island, and may act as indices and/or limiting factors where bryophyte production is concerned. These factors include aspects of climate, soil moisture, plant energy, chlorophyll, water and mineral nutrient contents.

The summer series of monthly growth measurements made in relation to macroclimatic parameters during 1981-2 provided interesting information regarding bryophyte growth phenology. The midsummer peak in stem extension growth coincided with the temperature maximum rather than the solar radiation solstice, and mass increment slowed during this same period according to the limited data available on this latter aspect. This adds support to observations of assymmetric stem length/mass phenology in bryophytes from other stations.

The lack of correlation of production with solar radiation is noteworthy as this was the only climatic variable that correlated significantly with bryophyte growth at the IBP tundra sites. However, the almost continuously cloudy skies at many sub-Antarctic islands may partly explain this observation, and would lend support to the prediction of Smith & French (1988) that moisture is instead a more important factor in explaining differences in soils and vegetation in the sub-Antarctic zone. The possible connection between "overabundant" rainfall and reduced bryophyte growth suggested by the correlations in Chapter 4, could also be pertinent in this regard.

The most significant aspect of the energy data was the negative correlation with growth

and its positively associated variables. This has been noted elsewhere in the tundra biome and may be related to storage of energy rich compounds that are protective against freezing damage in species of the more extreme habitats. The low production efficiency of Marion Island bryophytes based on their energy contents (and related to low chlorophyll contents) also appears superficially anomalous in comparison to the high overall levels of production achieved. This directs attention towards other factors such as the long growing season and equable temperatures, rather than efficient energy capture to explain the latter phenomenon.

The energy differences between species on a dry weight basis may simply reflect differences in cell wall components or plant mineral nutrient levels because when reduced to an ash free basis (plant organic tissues only) the data showed that energy values varied insignificantly among the species under review. On this basis therefore, energy may be simply a correlate of tissue mineral content or C:N ratio. Ash free differences were significant between the taxonomic groups: hepatics and mosses however, and this may have phylogenetic implications. The data are also useful for inter-site comparison purposes and confirm a trend of increasing energy content in bryophytes of higher latitudes.

The information on chlorophyll contents of bryophytes at Marion Island contribute to the very small pool of such data available for mosses and liverworts from any station. They compare closely with the results of the Canadian IBP study (i.e. quantitatively and in

respect of the close correlation between chlorophyll content and soil/plant water levels). There is a positive correlation between chlorophyll content and cover corrected bryophyte production at Marion Island. However, this is insufficiently significant to lend strong support to the contention of Kallio & Valanne (1975) that the relationship between chlorophyll and production may be closely positive throughout the tundra. Further reasons for this are explained in Chapter 5.

Smith & French (1988) predict that extreme oceanicity will place emphasis on water relations rather than temperature as a primary controlling factor in vegetation development at the sub-Antarctic islands. This variable could be expected to be even more significant in terms of the bryophyte vegetation, as water has frequently been cited as the most important factor controlling bryophyte growth under a broad spectrum of environmental conditions.

Marion Island is the wettest of the sub-Antarctic islands in terms of rainfall quantity and frequency, and it represents the extreme among all tundra sites in this regard. Far from being a constant and non-limiting factor in vegetation ecology at Marion Island however, water levels in soil and plant tissue vary depending on topographic situation and nature of the substrate, and lead to a wide range of clearly differentiated plant communities that are consistently related to often small differences in soil moisture level.

Although temporal rainfall variations may cause fluctuations in soil and plant moisture

levels, the mean quantities remain remarkably constant in the different communities as shown by the close correlation between the results of soil moisture measurements made during this study, and those of Gremmen (1982). Results of the present investigation support evidence from other wet tundra sites that bryophytes, through their growth form adaptations, can retain high tissue water contents which in turn maintain optimum metabolic function and hence production at virtually all times.

After an extensive series of studies, Dilks & Proctor (1974; 1976; 1979) concluded that physiological resistance to desiccation appears broadly similar in all mosses. This led to the generalization that in bryophytes of most habitats, differences in productive performance will be related primarily to the length of time that adequate tissue hydration levels can be maintained, as influenced by growth form and capillary structure. This is likely to be true for species at Marion Island that are subject to periods of drying, for example in fellfield and slope habitats, but also in some mire species whose growth form raises the shoot growing point significantly above the water table.

However, the tentative relation between periods of high rainfall and depressed growth in some species noted during the six month summer production study, points to the possibility that, in the extreme rainfall conditions of Marion Island species in constantly wet habitats may have more of a problem with "over-hydration". In the full year's study also, certain species showed evidence of this. For example, Distichophyllum fasciculatum had the highest water content measured among the study species, yet

produced only a small amount of shoot growth. This particular species occurred at a site that had become constantly waterlogged, and growing points of the plant appeared to be immersed for most of the time.

There is plenty of experimental evidence to show that very high tissue water levels will cause depression of photosynthetic rates through effects on CO₂ diffusibility. It is therefore tempting to speculate that selection in the extremely wet conditions pertaining at Marion Island would favour firstly species that could behave as facultative aquatics in the wettest habitats (e.g. Drepanocladus uncinatus of mire margins and pools); or secondly those that show adaptations that would tend to maximise gas exchange during the frequent conditions of inundation associated with fluctuating water table levels in the mires themselves.

In this regard it is interesting to note that all the liverwort species that dominate the communities of the mire complex in the intermediate soil moisture range, have complex and/or often tightly conduplicate arrangements of leaves that can be seen to enclose many trapped air bubbles when viewed under a handlens in the field (Blepharidophyllum densifolium, Clasmatocolea humilis, Jamesoniella colorata, Cryptochila grandiflora, and Schistochila carnosa which supplants some of these species on Prince Edward Island). This could therefore represent the reverse of the moisture trapping function erroneously attributed to such leaf arrangements by early plant morphologists.

In any event, the above species contribute to the formation of a series of liverwort-dominated bog communities that are better developed at Marion Island than elsewhere in the sub-Antarctic. This equates with the high rainfall, and the only close parallel in terms of physiognomically equivalent vegetation is seen in the hepatic bogs of Fuegia, which occur in a region with similar conditions of extreme rainfall.

Mineral nutrient relations at Marion Island are dominated at coastal sites by high levels of marine derived elements e.g. Mg and Na, which can be regarded as "super-abundant" at many of the sub-Antarctic islands. Several macronutrients show little correlation with production as a result of this. Previous studies have shown that mineral elements may be low in some habitats however (for instance in oligotrophic ombrogenous bogs), but the high "scavenging" potential of bryophytes for nutrients in dilute solution seems to overcome this limitation in respect of production performance in the mire habitat. The low level of P recorded in Marion Island bryophytes is associated with a high correlation between production and this element, which supports the proposal of P as the limiting nutrient where bryophyte growth is concerned.

The soil loss on ignition data correlate with growth, presumably through the relationship of soil organic content with water holding capacity, rather than the reciprocal soil mineral content. Levels of soil nutrients measured during previous work in similar habitats on Marion Island, relate poorly to the bryophyte macronutrient concentrations and growth measured in the present study. This points instead to selective accumulation

of mineral elements by mosses and liverworts at Marion Island.

Percentage ash content also shows little relationship to the quantities of plant tissue macronutrients, which would indicate the importance of accumulation of elements other than those measured in tissues of bryophytes at Marion Island. Tissue nutrient levels show a closer (negative) relationship with biomass quantities, pointing to the role they might play in enhancing substrate quality for decomposer organisms. The extremes of the production:biomass turnover range are represented by Clasmatocolea vermicularis of the biotically influenced zone (high nutrients, high production, low biomass) and Racomitrium lanuginosum of dry mires and fellfield (low nutrients, low production, high biomass).

Most of the correlations with growth referred to above, were diagnosed when production was expressed on a cover corrected basis rather than a colony (100% cover) basis. Similar findings have been reported by others working on tundra bryophytes, and this may be due to a high degree of intra-site variability in growth patterns, and the kind of methodology used for measuring growth and its correlates (see Chapter 9).

The overall results support a general, although not linear influence on production of moisture related variables, overlain by nutrient factors especially in the more eutrophicated environments. Biomass accumulation seems to be controlled mainly by tissue degradability factors, and maximum peat accumulation results from high soil

organic content, waterlogging and lower mineral levels in the mires.

In addition to the environmental variables that have been discussed here, several other factors may have important consequences for bryophyte growth at Marion Island in the long term. For example, glacier retreat and the sequence of arrival of the plants themselves from spore source-areas was no doubt important in determining production patterns during the Quaternary.

Factors that are certainly important today as agents of sudden or catastrophic change in community and production patterns, include new volcanic lava flows and ash falls, and substrate mass movement on unstable slopes ("peat slips"). Freeze thaw cycles and wind abrasion may also have a large part to play in influencing bryophyte production at the micro scale, in fellfield habitats that dominate the interior of the island. However these factors are less pertinent to the short term aims of this project, or to the vegetation in which the bulk of the biomass is concentrated at Marion Island.

Aim 3: Comparison of bryophyte production with other polar/alpine habitats to help define the bioclimatic/ biogeographic relationships of Marion Island in the "tundra" context, and in relation to other sub-Antarctic islands.

Bryophyte biomass followed broadly the same soil moisture gradient at Marion Island as recorded at North American and Fennoscandian tundra sites, although absolute levels

of biomass tended to be higher at Marion Island due to the preponderance of wet habitats typical of the sub-Antarctic zone. Equivalent biomass levels are only attained in the wettest habitats in the Arctic, which occur rarely there compared to their ubiquity in the sub-Antarctic.

Biomass in the lowland fellfield at Marion Island was high compared with other tundra sites, although lower figures would be expected in the fellfield of the island's interior which would more closely resemble the polar desert habitats studied in the Arctic. On the other hand, the high colony biomass figures recorded in fellfield mosses at Marion Island are similar to those obtained in the Antarctic, and point to reduced decomposition and thus higher accumulation at these sites. Production is low however in these localities, resulting in low overall biomass figures on a cover corrected basis.

Racomitrium lanuginosum shows very low decomposition figures and produces deep cushions of well preserved stem material in certain localities at Marion Island. These resemble the acid moss turfs of the Maritime Antarctic, albeit on a far smaller scale.

Bryophyte production at most tundra sites follows a general xeric-hydric gradient as noted for Marion Island. As with the biomass data however, higher absolute figures pertain at Marion Island due to the wet conditions. The results confirm previous records of very high rates of plant growth at sub-Antarctic localities, and only a few sites show higher overall production figures (e.g. Pohlia flushes on South Georgia).

High production values at other localities tend to occur in habitats that are limited in extent (e.g. flushes), whereas the relatively high production levels of mire bryophytes at Marion Island are typical of a habitat which occupies extensive areas of terrain in the coastal lowlands.

The preponderance of wet conditions and the northerly position of Marion Island result in relatively warm conditions by sub-Antarctic standards, which promote high production:biomass turnover rates compared with other tundra sites. This is especially true of species with higher nutrient levels that are susceptible to rapid decomposition e.g. Clasmatocolea vermicularis of the biotic zone. Slow decomposition in nutrient-poor habitats such as mires however, may allow thick peat accumulations to occur; although there is no equivalent at Marion Island to the drier, deep acid turves of Signy Island and the Antarctic Peninsula.

In comparison with most Arctic and Alpine tundra sites, Marion Island shows higher and far more constant mean temperatures, and a higher precipitation to evaporation ratio than anywhere else except the "sub-Antarctic" region of Fuegia (sensu Skottsberg, 1905). Marion Island has the typical sub-Antarctic features of high cloudiness, low sunshine, constant cool temperatures, high rainfall and relative humidity, and strong winds. The zone is unique compared with most other tundra sites as its mean monthly temperature remains above 0°C throughout the year (observation supported by microclimate measurements in moss turves). This contributes to the long growing season of

approximately 300 days for vascular plants and 365 days for bryophytes at Marion Island according to V Smith (1985). The extreme wetness also combines with geological youth and geographical isolation and thus lack of competition from vascular plants, to explain the great importance of bryophytes at the sub-Antarctic islands in comparison with other tundra sites (R Smith, 1984).

The bryophytes occupy many niches that would otherwise be filled by cushion and mat dicotyledons, and lichens in northern hemisphere tundra. The bryophyte flora also comprises many different and individually adapted species, in contrast to the wide ecological amplitude shown by the few vascular plant species. In fact, as mentioned earlier, the southern sites exhibit almost the full range of vegetation types found in northern tundras despite the floristic poverty of the sub-Antarctic islands (Smith & French, 1988).

The same conditions of extreme wetness, lack of vascular plant competition, equable temperatures and the long growing season contribute to the high production figures recorded for Marion Island (and other sub-Antarctic) bryophytes, in comparison with other tundra sites. Marion Island is also distinct within the sub-Antarctic as it has the most ameliorated temperature conditions and the highest rainfall figures. There are many similarities with South Georgia and Macquarie Island, but the predominance of moss and especially liverwort dominated mires at Marion Island, sets it apart from all except the other islands of the Kerguelen Province. In several respects e.g. the widespread

occurrence of "fernbrake" vegetation on the island slopes (Smith & French, 1988), Marion Island shares characteristics with cool temperate islands such as Tristan da Cunha, Gough Island and the Falklands (as noted even from a distance, by Captain James Cook (see Chapter 1). However, these latter localities support communities of Sphagnum moss which does not occur at Marion Island (see Chapter 4).

Aim 4: Evaluation of a range of biomass harvest techniques for measurement of bryophyte growth, in the light of unsatisfactory comparability of results due to the diverse methods applied during IBP tundra biome studies.

A wide range of habitats is represented in a small area at Marion Island due to wind influenced exposure and nutrient gradients (Smith & French, 1988). The island thereby demonstrates some of the extremes of northern tundras i.e. "polar desert" fellfields and mesic, well-vegetated slopes and drainage lines. Coupled with the occurrence of a number of different bryophyte growth forms, this factor provided an ideal opportunity for testing a range of bryophyte growth measurement methods.

The results of these studies have been discussed in detail in Chapter 4, and recommendations concerning preferred methodology have also been given (loc. cit). It must be emphasized that the methods applied during this investigation, provide information that is comparable with that of previous studies in respect of "annual shoot production", but does not represent absolute annual net production in the sense of

vascular plant studies. This is due to the difficulty of defining the biomass/necromass partition in bryophytes in general. Rigorous studies of net production should take account of decomposition, grazing and litter losses, basipetal/acropetal metabolite translocation, exudates etc. Some of these factors may be insignificant or counteractive in their effects, but their potential influence on production should be appreciated nonetheless. Better understanding of these factors, and comparison of results from harvest experiments with climate-correlated gas exchange studies, should allow a more accurate determination of production in future studies, and help define precision limits for the traditional techniques.

It is hoped that the investigation reported in this thesis has gone some way towards addressing the plea of Wielgolaski et al (1981) for improved methodology and more data on tundra bryophyte production. It is hoped also that the study will contribute to a better understanding of the sub-Antarctic in particular, as the remoteness and peculiar characteristics of the region have led to inaccurate appraisals in the past. For example Korotkevich (1966) classified Marion Island as "Forest tundra", and Aleksandrova (1980) stated that "the role of bryophytes is insignificant in the sub-Antarctic."

Gaps in knowledge pinpointed by this study, that should be dealt with in future research include the following:

1. Characterization of bryophyte photosynthetic response surfaces (by gas exchange

experiments) in relation to environmental variables such as water content, temperature and light levels. This would allow an appreciation of the diurnal responses of bryophyte growth processes to the unique climatic conditions of the sub-Antarctic.

2. Long term microclimate recordings would also allow prediction of production over longer periods and under a broader range of climatic conditions than may currently be experienced (e.g. in relation to the current warming trend at Marion Island).

3. There is still a need for studies of bryophyte production in the more extreme but extensive upland fellfield habitats, especially as there is a paucity of this kind of data in southern polar regions (e.g. no measured production data for mosses of continental Antarctica).

4. In relation to the requirements of the Marion Island ecosystem project, decomposition of bryophyte vegetation and relationships with peat accumulation rates and mire formation are still a desideratum for further study.

5. The studies carried out for this thesis have highlighted particular areas of research in relation to general bryology, that might fruitfully be followed up e.g. the possible importance of liverwort leaf arrangement for continued gas exchange in "hyper-hydric" conditions; the relationship of bryophyte cell wall:protoplast volume ratios to energy and chlorophyll differences in the major phylogenetic groupings; and not least a critical

taxonomic revision of sub-Antarctic bryophytes and synthesis of biogeographic data on the group. This would allow a more thorough understanding of patterns of evolution and dispersal in the circum-Antarctic zone than has hitherto been possible when based solely on the depauperate vascular flora.

6. Finally, following on the successful use of bryophytes as pollution indicators in industrial nations, mosses and liverworts from remote and undisturbed tundra habitats such as Marion Island could offer useful experimental material for monitoring the environmental influence of human activities that have potential for repercussions on a global scale e.g. atmospheric CO₂ build up, greenhouse effect climatic warming, ozone layer destruction, acid deposition and the impacts of other marine and terrestrial pollutants.

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APPENDICES

A 1

SPECIES	Brachythecium subplicatum		DATE	13.03.1981
COMMUNITY	Acaena-Brachythecium complex Brachythecietum subplicati; subassoc. "inops". examples of S.A. philonotidetosum, breutelietosum and Montia facies occur nearby.			
HABITAT	750m N. of Hendrik Vister kop (peak) at foot of grey lava slope below Tafelberg, headwater tributary of Van den Boogard River			
LOCALITY	Quaking mire at foot of grey lava slope with continually flowing stream running through (landslide on W. edge of mire).			
BEARINGS				
ALTITUDE	210m	ASPECT	250°	
PLOT SIZE		SLOPE	10°	
PHOTOS PLOT	/	TAGS	/	
SPP.	/	BAGS	x	
METHODS	/	B.G. ALGAE	/	
WATER LEVEL	= surface	SOIL WATER	2787%	
TEMP.	12°	CHLOROPHYLL	/	
pH	(1) 6.82 (2) 7.05	AREA/DENSITY	/	
GROUND COVER	B.subplicatum = 90%	ANN SEGS.	x	
BRYO. COVER	95%	BRYO. HEIGHT	10cm max	
VASC. COVER	75%	VASC. HEIGHT	20cm max	
S P E C I E S	C/A	S	OTHER SPECIES	
Acaena magellanica	4	4	Other species found nearby include	
Brachythecium subplicatum	5	5	Philonotis angustifolia	
Poa cookii	+	1	Breutelia integrifolia	
Agrostis magellanica	+	1	Drepanocladus uncinatus	
Ranunculus biternatus	+	1	Pohlia cf. nutans	
Montia fontana	+	1	Azorella selago	
Hygroamblystegium filum	1	1	Fossombronia australis	
			Bryum laevigatum	
			Leptoscyphus expansus	
			Hygroamblystegium filum	
			Riccardia cf. subantarctica?	
			(too small for pinguis, thallus x not multifida).	
			Marchantia berteriana	
			Drepanocladus aduncus (in stream)	

SPECIES Drepanocladus uncinatus		DATE 19.03.1981	
COMMUNITY 4.3.3 Juncus-Blepharidophyllum complex Juncus scheuchzerioidis-Drepanocladetum uncinati Probably clasmatocoleetosum humilis sub association (because of Blepharido. presence)			
HABITAT La va depression, very wet Agrostis mire with central pool & standing water around, Drepanocladus border zone.			
LOCALITY 200m N.W. of Met. Station at foot of Blechnum slope.			
BEARINGS			
ALTITUDE 25m PLOT SIZE 10 x 1,5 = 15m ² PHOTOS PLOT / SPP. / METHODS x WATER LEVEL = surface TEMP. 7° (air 8°) pH (1) 4,60 (2) 5.14 GROUND COVER 5% (water) BRYO. COVER 90% D. uncinatus VASC. COVER 10% = 85%		ASPECT - SLOPE 0° TAGS / BAGS x B.G. ALGAE / SOIL WATER W.C. = 1808% CHLOROPHYLL / AREA/DENSITY / ANN SEGS. x BRYO. HEIGHT 20cm max above water VASC. HEIGHT Agrostis fls. 40cm above water level.	
S P E C I E S	C/A	S	OTHER SPECIES
Agrostis magellanica	1	2	
Juncus scheuchzerioides	+	2	
Blechnum penna-marina (margin)	r	2	
Ranunculus biternatus	r	1	
Acaena magellanica (margin)	r	1	
Drepanocladus uncinatus	5	5	
Blepharidophyllum densifolium	+	2	

SPECIES <i>Campylopus purpureocaulis</i>		DATE 30.03.81
COMMUNITY 4.5.1 <i>Blepharidophyllo densifolii</i> - <i>Clasmatocoleetum humilis</i> " <i>Campylopus purpureocaulis</i> facies (of S.A.) <i>ranunculetosum</i> ".		
HABITAT		
LOCALITY Approx. 2km s.w. of Met. Station in line with Tate's Hill on s.w. side of Nellies Humps before starting up the first black lava slopes towards Tate's.		
BEARINGS Freds 230° Jnrs 324°		
ALTITUDE 55m	ASPECT -	
PLOT SIZE 3,1 x 4,6 = 14,26m ²	SLOPE -	
PHOTOS PLOT x	TAGS x	
SPP. x	BAGS /	
METHODS x	B.G. ALGAE -	
WATER LEVEL 7cm below moss	SOIL WATER 2469%	
TEMP. 10 moss 13 air 12	CHLOROPHYLL -	
pH (1) 4,4 (2) 4,84	AREA/DENSITY -	
GROUND COVER -	ANN SEGS. /	
BRYO. COVER 90% <i>Campyl</i> = 75%	BRYO. HEIGHT 7cm above surface	
VASC. COVER 10%	VASC. HEIGHT <i>Agrostis</i> 30cm heads	
S P E C I E S	C/A	S
<i>Campylopus purpureocaulis</i>	5	5
<i>Juncus scheuchzerioides</i>	2m	3
<i>Agrostis mag.</i>	2a	2
<i>Blepharidophyllum densifolium</i>	1	3
<i>Distichophyllum fasciculatum</i>	2a	4
<i>Drepanocladus uncinatus</i>	+	2
<i>Leptoscyphus expansus</i>	r	2
<i>Blechnum pennamarina</i>	r	2
<i>Peltigera polydactyla</i>	r	1
OTHER SPECIES		

SPECIES <i>Breutelia integrifolia</i>		DATE 26.03.81
COMMUNITY 4.9.1 Bryolaevigatae-Breutelietum integrifoliae sub assoc: Uncinietosum compactae.		
HABITAT		
LOCALITY 1,6km wsw of Met Sta in direct line with and at foot of Jnr's Kop where <i>Agrostis mire</i> begins. Flush area where drainage water from scoria enters mire.		
BEARINGS 246° Freds in line with Jnr's and Base.		ASPECT 134° SLOPE 2° TAGS / BAGS / B.G. ALGAE / SOIL WATER Soil depth 40cm to CHLOROPHYLL gravel WC-276 (with gravel 1599% without AREA/DENSITY / ANN SEGS. / BRYO. HEIGHT max 20cm above water VASC. HEIGHT <i>Agrostis</i> fls 40cm
ALTITUDE 90m		
PLOT SIZE 11,8x2,6 = 30,68m ²		
PHOTOS PLOT /		
SPP. /		
METHODS /		
WATER LEVEL = surface		
TEMP. 8,5°C (air 7°C) Plot 2		
pH (1) 7.11 (2) 6.04 5.78		
GROUND COVER 1%		
BRYO. COVER 82% <i>Breut</i> 80%		
VASC. COVER 35%		
SPECIES	C/A	S
<i>Breutelia integrifolia</i>	5	4
<i>Agrostis mag.</i>	2b	3
<i>Azorella selago</i>	+	3
<i>Montia fontana</i> (SR3017)	+	3
<i>Blechnum penna-marina</i>	2a	3
<i>Acaena magellanica</i>	+	2
<i>Drepanocladus uncinatus</i>	1	3
<i>Uncinea compacta</i>	1	2
<i>Ranunculus biternatus</i>	r	2
<i>Brachythecium paradoxum</i> (SR 3018)	r	2
<i>Plagochila heterodonta</i> (SR 3019)	r	2
<i>Jamesoniella</i>	r	2
OTHER SPECIES		

SPECIES <i>Ptychomnion densifolium</i>		DATE 20.03.81
COMMUNITY 4.6 "Uncinia compactae-Ptychomnietum ringiani" intermediate between or including "Uncinia variant" and "Blechnum variant"?		
HABITAT		
LOCALITY 1,5km sse Met Sta between Nellie's Humps and "The Fault".		
BEARINGS Freds 258° Jnrs 320°		
ALTITUDE 25	ASPECT 164°	
PLOT SIZE 2,5x20,2 = 50,5m ²	SLOPE 2°	
PHOTOS PLOT /	TAGS /	
SPP. /	BAGS /	
METHODS x	B.G. ALGAE /	
WATER LEVEL -4cm (rain)	SOIL WATER W.C. 1480%	
35cm (in pipe)	CHLOROPHYLL -	
TEMP. 8.5°C (air 10°C)	AREA/DENSITY /	
pH (2) 4,29	ANN SEGS. x	
GROUND COVER -	BRYO. HEIGHT 20cm	
BRYO. COVER 80% Ptycho 75%	VASC. HEIGHT Agrostis 35cm	
VASC. COVER 35%		
SPECIES	C/A	S
OTHER SPECIES		
Racomitrium lanuginosum	1	3
Azorella selago	1	3
Blechnum penna-marina	2m	2
Agrostis magellanica	2a	3
Campylopus <i>purpureocaulis</i>	+	2
Ptychomnion <i>densifolium</i>	5	4
Uncinea compacta	2a	4
Blepharidophyllum densifolium	1	4
Leptodontium proliferum (SR 3008)	r	1
Liverworts 1		
2		
3		

SPECIES <i>Clasmatocolea humilis</i>		DATE 27.03.81
COMMUNITY 4.5.2 <i>Blepharidophyllo densifolii</i> - <i>Clasmatocoleetum humilis</i> s.a. <i>Clasmatocoleetosum humilis</i>		
HABITAT		
LOCALITY 790m sse of Met Sta. Shallow depression leading from Jamesoniella plot down to <i>Brachythecium</i> slope. Nellies Humps. Water collecting at level spot.		
BEARINGS Jnrs 310 Freds 249		
ALTITUDE 33m	ASPECT -	
PLOT SIZE 2x6,4 = 12,8m ²	SLOPE 0°	
PHOTOS PLOT /	TAGS x	
SPP. /	BAGS /	
METHODS /	B.G. ALGAE /	
WATER LEVEL 5cm below soil	SOIL WATER W.C. 1417%	
TEMP. 7 (air 8) surface	CHLOROPHYLL /	
pH (2) 4,58	AREA/DENSITY /	
GROUND COVER -	ANN SEGS. x	
BRYO. COVER 30% <i>Clasmat</i> 75%	BRYO. HEIGHT 5/8cm	
VASC. COVER 35%	VASC. HEIGHT <i>Agrostis</i> 40cm	
SPECIES	C/A	S
<i>Clasmatocolea humilis</i>	5	5
<i>Blepharidophyllum densifolium</i>	2b	4
<i>Agrostis mag.</i>	3	3
<i>Ranunculus biternatus</i>	+	2
<i>Marchantia berteroana</i>	r	2
<i>Azorella selago</i>	r	2
<i>Drepanocladus uncinatus</i>	+	2
		OTHER SPECIES

SPECIES <i>Blepharidophyllum densifolium</i>		DATE 30.03.81	
COMMUNITY 4.5.3 <i>Blepharidophyllum densifoli</i> - <i>Clasmatocolectum humilis</i> probably sub assoc. <i>blechnetosum pennamarinae</i>			
HABITAT			
LOCALITY approx 2km SSW of Met Sta in line with Fred's Hill, on the S. side of Nellie's Humps at foot of first large black lava slope before Fred's. Mire emptying into shallow hole below fjældmark area			
BEARINGS Freds 249 335 Jhrs			
ALTITUDE 55m PLOT SIZE 2.4X12.7 = 30.48 PHOTOS PLOT / SPP. / METHODS / WATER LEVEL 8cm below bryo TEMP. 7 (air 12) surface pH 4.4 (1) 4.82 (2) GROUND COVER 0.1% BRYO. COVER 96% Bleph 95% VASC. COVER 5%		ASPECT SLOPE TAGS X BAGS / B.G. ALGAE / SOIL WATER 2216% CHLOROPHYLL / AREA/DENSITY / ANN SEGS. X BRYO. HEIGHT surface VASC. HEIGHT <i>Agrostis</i> max 40cm	
S P E C I E S	C/A	S	OTHER SPECIES
<i>Blepharidophyllum densifolium</i>	5	5	
<i>Agrostis mag.</i>	2a	2	
<i>Blechnum penna-marina</i>	+	1	
<i>Campylopus</i>	1	2	
<i>Uncinia compacta</i>	+	2	
<i>Distichophyllum fasciculatum</i>	2m	3	

SPECIES <i>Cryptochila grandiflora</i>		DATE 27-3-81
COMMUNITY Jamesonielletum grandiflora s.a. probably peltigeretosum polydactyli		
HABITAT		
LOCALITY 780m sse met sta. along edge of convex slope below lowland fjaeldmark vegetation, Nellies Humps		
BEARINGS Jnrs 310° Freds 249° ALTITUDE 34m PLOT SIZE 1.4X12.2 = 17.08m PHOTOS PLOT / SPP. / METHODS / WATER LEVEL -30cm at rock surf TEMP. soil 6 air 7.5 moss 8° pH 5.23 GROUND COVER 2% BRYO. COVER 72% Crypt 70% VASC. COVER 60%		ASPECT - SLOPE 0° TAGS X BAGS / B.G. ALGAE / SOIL WATER 746% CHLOROPHYLL / AREA/DENSITY / ANN SEGS. X BRYO. HEIGHT 6cm VASC. HEIGHT 40cm <i>Agrostis</i>
S P E C I E S	C/A	S
Azorella selago	2a	3
<i>Cryptochila grandiflora</i>	4	4
<i>Agrostis</i>	3	4
<i>Ruanunculus biternatus</i>	r	1
<i>Juncus scheuchzerioides</i>	+	2
<i>Blepharidophyllum densifolium</i>	+	2
<i>Drepanocladus uncinatus</i>	+	2
<i>Acaena magellanica</i>	+	2
<i>Blechnum penna-marina</i>	1	2
<i>Uncinia compacta</i>	+	2
<i>Jamesoniella colorata</i>	+	2
<i>Montia</i>	r	2
<i>Acrobolbus ochrophyllus</i>	r	2
OTHER SPECIES		

SPECIES <i>Racomitrium lanuginosum</i>		DATE 26-3-81
COMMUNITY <i>Lycopodio magellanicae - Jamesonielletum coloratae</i> probably subassociation <i>catagonietosum politi</i>		
HABITAT		
LOCALITY Adjacent to sand filter on grey lava bench below "P" rock, ne foot of Juniors Kop		
BEARINGS Freds 221°		
ALTITUDE 109m PLOT SIZE 2.2X17.3 = 38.06m PHOTOS PLOT / SPP. / METHODS / WATER LEVEL - 5cm TEMP. 7° (air 5°) pH 5.8 GROUND COVER - BRYO. COVER 65% Raco 60% VASC. COVER 35 %		ASPECT 80° SLOPE 2° TAGS / BAGS X B.G. ALGAE / SOIL WATER 895% CHLOROPHYLL / AREA/DENSITY / ANN SEGS. / BRYO. HEIGHT max 15cm VASC. HEIGHT max 30cm
SPECIES	C/A	S
<i>Racomitrium lanuginosum</i>	4	4
<i>Jamesoniella colorata</i>	2a	3
<i>Agrostis mag.</i>	2b	3
<i>Blechnum penna-marina</i>	2m	3
<i>Uncinia compacta</i>	1	2
<i>Distichophyllum fasciculatum</i>	+	2
<i>Azorella selago</i>	+	3
<i>Blepharidophyllum densifolium</i>	+	2
<i>Campylopus purpureocaulis</i>	r	2
<i>Acrobolbus ochrophyllus</i>	+	2
<i>Cryptochila grandiflora</i>		
<i>Andrewsianthus</i>		
OTHER SPECIES		

SPECIES <i>Brachythecium rutabulum</i>		DATE 20-3-81	
COMMUNITY <i>Isopterygio pulchelli</i> - <i>Bléchnetum penna-marinae</i> sub association <i>brachythecietosum rutabuli</i>			
HABITAT 800m sse Met Sta on SE facing <i>Blechnum/Poa</i> slope forming deep and narrow depression in black lava of Nellies Humps			
LOCALITY			
BEARINGS Freds 248 Jnrs 304			
ALTITUDE 32m PLOT SIZE 2.2X7.0 = 15.4m ² PHOTOS PLOT / SPP. / METHODS X WATER LEVEL -60cm TEMP. 8°C (air 12.5°) pH 4.92 GROUND COVER - BRYO. COVER 70% Br 65% VASC. COVER 30%		ASPECT 175° SLOPE 27° TAGS / BAGS X B.G. ALGAE / SOIL WATER 649% CHLOROPHYLL / AREA/DENSITY / ANN SEGS. X BRYO. HEIGHT 30cm max VASC. HEIGHT <i>Poa</i> 50cm max	
S P E C I E S	C/A	S	OTHER SPECIES
<i>Brachythecium rutabulum</i>	4	4	
<i>Drepanocladus uncinatus</i>	2a	4	
<i>Lophocolea randii</i>	+	2	
<i>Blechnum penna-marina</i>	2a	3	
<i>Acaena magellanica</i>	2a	3	
<i>Poa cookii</i>	1	2	
<i>Agrostis magellanica</i>	+	2	
<i>Ranunculus biternatus</i>	+	2	
<i>Stellaria media</i>	+	2	
<i>Amblystegium</i> (SR 3009)	+	2	
<i>Plagiothecium platyphyllum</i>	+	2	
<i>Leptoscyphus</i>	r	2	

SPECIES <i>Ditrichum strictum</i>		DATE 1-4-81	
COMMUNITY <i>Andreaea acutifolia</i> - <i>Racomitrium crispulum</i> sub association <i>Hymenophyllum peltatum</i>			
HABITAT			
LOCALITY Grey lava bench adjacent to ravine running past sand filter on NE foot of Juniors Kop			
BEARINGS Freds 220 Jnrs 268			
ALTITUDE 110m PLOT SIZE 10.2X6.5 = 66.3m ² PHOTOS PLOT / SPP. / METHODS / WATER LEVEL -6cm TEMP. 9.5°C (air 9.5) pH (1) 4.6 (2) 5.41 GROUND COVER 85% BRYO. COVER 10% Ds 5% VASC. COVER 6%		ASPECT 343° SLOPE 4° TAGS X BAGS X B.G. ALGAE / SOIL WATER 260% CHLOROPHYLL / AREA/DENSITY / ANN SEGS. / BRYO. HEIGHT Ds cushions max 20cm VASC. HEIGHT <i>Agrostis</i> hds 30cm	
S P E C I E S	C/A	S	OTHER SPECIES
<i>Ditrichum strictum</i>	2a	3	
<i>Andreaea acutifolia</i>	2m	2	
<i>Agrostis mag.</i>	2m	2	
<i>Azorella selago</i>	2a	3	
<i>Schistochila carnosus</i>	+	2	
<i>Psilopilum cf. tristaniense</i>	+	2	
<i>Grimmia kerguelense</i>	+	2	
<i>Hymenophyllum peltatum</i>	r	2	
<i>Bryum laevigatum</i>	r	2	
<i>Catagonium politum</i>	r	1	
<i>Jensenia</i> (SR 3030)	+	2	
<i>Ranunculus biternatus</i>	r	1	
<i>Lycopodium saururus</i>	r	1	
<i>Racomitrium crispulum</i>	1	2	
<i>Jamesoniella colorata</i>	r	1	
<i>Herzogobryum</i> (SR 3034)			
<i>Funaria</i>			
<i>Philonotis</i> (SR 3032)			
<i>Plagiochila</i>			
<i>Lethocolea</i>			
gelatinous green alga	1	3	

SPECIES <i>Andreaea acutifolia</i>		DATE 1-4-81
COMMUNITY <i>Andreaea acutifolii</i> - <i>Racomitrium crispuli</i> s.a. <i>Hymenophylletosum peltati</i>		
HABITAT		
LOCALITY Grey lava bench adjacent to channel running past sand filter on NE foot of Junior's Kop		
BEARINGS Freds 220 Jnrs 268		
ALTITUDE 110m PLOT SIZE 1.2X5.7 = 6.84m ² PHOTOS PLOT / SPP. / METHODS / WATER LEVEL not evident TEMP. - pH 5.42 GROUND COVER 80% BRYO. COVER 15% Aa 13% VASC. COVER 5%		ASPECT 342° SLOPE 2° TAGS X BAGS X B.G. ALGAE / SOIL WATER 184% CHLOROPHYLL / AREA/DENSITY / ANN SEGS. X BRYO. HEIGHT max 2cm VASC. HEIGHT <i>Agrostis</i> hds 30cm
S P E C I E S	C/A	S
Azorella selago	2a	3
<i>Agrostis</i> mag.	1	2
<i>Andreaea acutifolia</i>	2b	2
<i>Racomitrium crispulum</i>	1	2
<i>Ranunculus biternatus</i>	r	1
<i>Grimmia kerguelense</i>	+	2
<i>Ditrichum strictum</i>	+	2
<i>Racomitrium lanuginosum</i>	r	2
<i>Montia fontana</i>	1	1
gelatinous green alga	1	2
OTHER SPECIES		

SPECIES <i>Clasmatocolea vermicularis</i>		DATE 29-3-81
COMMUNITY Montio fontanae - Clasmatocoleetum vermicularis		
HABITAT		
LOCALITY 600m NNW of Met Sta at level plateau 250m from coast in spray zone and biotically influenced (Petrels)		
BEARINGS		
ALTITUDE 20m PLOT SIZE 15.6X1.5 = 23.4m ² PHOTOS PLOT / SPP. X METHODS X WATER LEVEL -8cm below bryo TEMP. 7°C (air 7°) pH 5.06 GROUND COVER X BRYO. COVER 80 Cv 80% VASC. COVER 50%		ASPECT 0° SLOPE 0° TAGS X BAGS X B.G. ALGAE / SOIL WATER 895% CHLOROPHYLL / AREA/DENSITY / ANN SEGS. X BRYO. HEIGHT 10cm VASC. HEIGHT <i>Agrostis</i> hds 50
SPECIES	C/A	S
<i>Clasmatocolea vermicularis</i>	5	5
<i>Poa cookii</i>	2b	2
<i>Montia fontana</i>	1a	2
<i>Agrostis magellanica</i>	2b	1
<i>Acaena magellanica</i>	r	1
OTHER SPECIES		