THE ECOLOGY OF AN ATLANTIC LIVERWORT COMMUNITY

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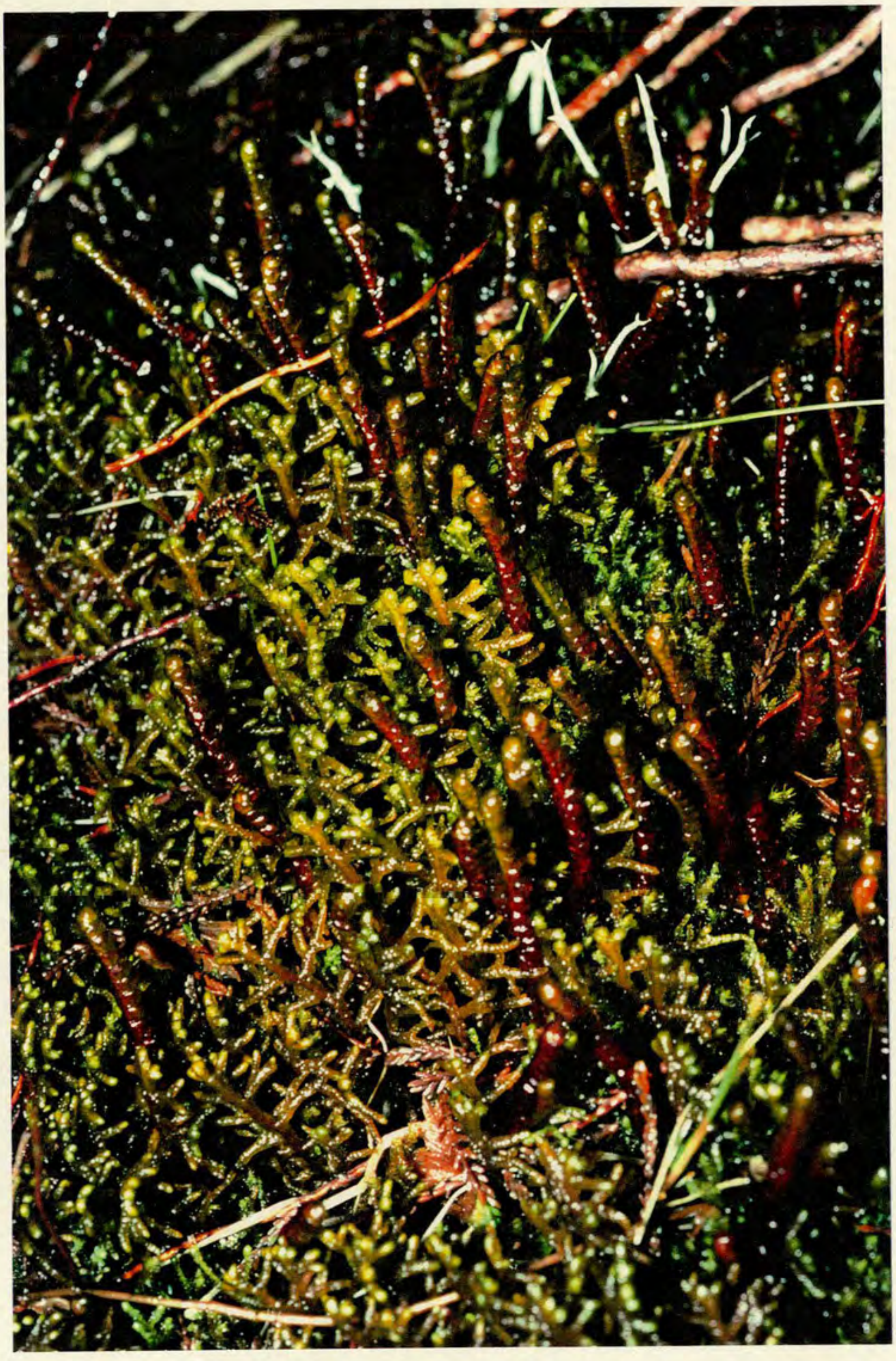

The Atlantic hepatic mat on Liathach, Wester Ross, showing *Pleurozia purpurea*, *Mastigophora woodsii* and *Herbertus aduncus*. Photographed by Colin Legg in April 1990.

ABSTRACT

The Atlantic hepatic mat is an assemblage of large leafy liverworts. The component species are *Herbertus aduncus* (ssp. *hutchinsiae*), *Pleurozia purpurea*, *Mastigophora woodsii*, *Bazzania tricrenata*, *B.pearsonii*, *Anastrepta orcadensis*, *Mylia taylorii*, *Scapania gracilis*, *S.ornithopodioides*, *S.nimbosa*, *Plagiochila carringtonii*, *P.spinulosa*, *Lepidozia pearsonii*, *Anastrophyllum donnianum*, *A.joergensenii* and *Adelanthus lindenbergianus*. Up to 15 of these species can grow together in mixed mats.

These species need a climate with heavy and frequent rainfall and equable temperatures. They grow mainly in north-west Europe, north-west America and the Himalayas. The hepatic mat community was once thought to be confined to western Scotland and western Ireland but this study has shown that it also occurs in the Lake District and North Wales. Hepatic mats similar to the British ones, but with fewer species, occur on the Faroe Islands and in western Norway. The community is most extensive and species-rich in the mountains of western Scotland. It occurs on a variety of substrates from quartzites to mica-schists and basalt. Members of the community occasionally grow close to strict calcicoles, showing that they can tolerate basic substrates. The community is usually on steep, well-drained slopes in the British Isles, but there are good patches on level, peaty ground on Beinn Eighe in West Ross and in blanket-bog in

Sutherland. The community is especially luxuriant on shaded slopes facing between north-west and east, but can develop in favourable spots on slopes facing all ways but south-west. Hepatic mats occur in a range of vegetation including woodlands, dwarf-shrub heaths, montane heaths and grasslands, snow-beds and cliff-ledge communities.

The diversity of species within individual stands of the community can be very great, with as many as 10 species occurring together in a 5cm x 5cm quadrat in the north-west Highlands. The typical mountain-side habitat is not particularly stable over time and the community is probably a dynamic one with a high turnover of individuals.

Some members of the community can tolerate temperatures up to 50°C and most can withstand periods of drought for much longer than they are likely to experience in the field. The distribution of the species is probably limited by the rate of evaporation of water from the surface of the cushion or mat.

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NOMENCLATURE AND ABBREVIATIONS

Nomenclature for British species follows Smith (1980) for mosses, Smith (1990) for liverworts, Clapham, Tutin & Moore (1987) for vascular plants and Hawksworth, James & Coppins (1980) for lichens. Author citations are given for foreign taxa.

Abbreviations

ASL: Altitude (in metres) above sea-level.

m.y.a. Million years ago

NVC: National Vegetation Classification (Rodwell 1991a, 1991b, 1992)

RBG: Data obtained from packet notes in the herbarium of the Royal Botanic Garden, Edinburgh.

SSSI: Site of Special Scientific Interest

UVS: Upland Vegetation Survey (run by the Nature Conservancy Council 1981-88).

CONTENTS

CHAPTER ONE

INTRODUCTION

Atlantic or oceanic bryophytes (Ratcliffe 1968) are plants which are strongly associated with the humid, equable climate of the Atlantic coast of Europe and the adjacent islands. The group is better represented in the British Isles than anywhere else in Europe (Ratcliffe 1968, Hodgetts 1992).

Macvicar (1910) first described the Atlantic element of the British liverwort flora. Ratcliffe (1968) sub-divided these Atlantic species into those confined to the Atlantic coastal regions and those which are more widespread but still markedly western, either in the British Isles or in the whole of Europe. He divided the species occurring in the strictly Atlantic region into three groups: Northern Atlantic, Southern Atlantic and Widespread Atlantic, according to their latitudinal distribution in the British Isles. The Northern Atlantic species generally occur from north Wales northwards with most records from the north-west Highlands of Scotland. The Southern Atlantic species occur from south-west Scotland southwards: their main centre of distribution is south-west Ireland. The Widespread Atlantic species are widely distributed in the west of the British Isles from south-west Ireland to north-west Scotland. The remaining species fall into the Sub-Atlantic, Mediterranean-Atlantic and Western British groups. The Sub-Atlantic species are fairly widespread in Europe as far east as the Black Sea, but are most abundant in the west between Macaronesia and the Faroes. Mediterranean - Atlantic species have their headquarters around the Mediterranean coast but extend northwards up the western seaboards of Portugal, Spain and France as far as the south of Britain and Ireland. Western British species are widely distributed throughout the Holarctic but are northern and western in Britain, possibly because they need an upland habitat as much as an oceanic climate.

Some Atlantic bryophytes tend to grow together in distinct and easily recognised communities (Ratcliffe 1968). One such assemblage is what Ratcliffe (1968) called the mixed northern hepatic mat. It consists of members of a set of 16 species of leafy liverworts which grow together as an understorey to *Calluna vulgaris* and *Vaccinium myrtillus* heaths, in woodlands and grasslands and on cliffs in the mountains of the most oceanic climatic regions of the British Isles (McVean & Ratcliffe 1962, Ratcliffe 1968, Birks 1973, Corley 1983, Rodwell 1991b, Averis 1992). The community includes 11 Northern Atlantic species (*Adelanthus lindenbergianus*, *Anastrophyllum donnianum*, *A.joergensenii*, *Bazzania pearsonii*, *Herbertus aduncus* (ssp *hutchinsiae*), *Lepidozia pearsonii*, *Mastigophora woodsii*, *Plagiochila carringtonii*, *Pleurozia purpurea*, *Scapania nimbosa* and *S.ornithopodioides*), three sub-Atlantic species (*Anastrepta orcadensis*, *Plagiochila spinulosa* and *Scapania gracilis*) and two Western British species (*Bazzania tricrenata* and *Mylia taylorii*).

Individual examples of the community may not include all the species, because some of them are commoner than others and their distributions differ, but up to 15 of them can grow together in an area 4m x 4m (Ratcliffe 1968).

Modern distribution maps suggest that *Plagiochila spinulosa* would be better placed in the Widespread Atlantic group (Averis 1991). Otherwise none of the species in Ratcliffe's Southern Atlantic, Widespread Atlantic or Mediterranean Atlantic groups are regular members of the hepatic community, although the Widespread Atlantic *Saccogyna viticulosa* has been recorded in hepatic mats on Skye (Birks 1973) and in woods (Averis 1991). The Widespread Atlantic species *Colura calyptrifolia, Frullania teneriffae* and *Harpalejeunea ovata* are occasionally recorded as epiphytes on *Calluna vulgaris* and *Erica cinerea* in hepatic-rich heaths (Birks 1973). The Atlantic mosses *Dicranodontium uncinatum, Campylopus setifolius* and *C.atrovirens* are frequently mentioned in published accounts of hepatic-rich heaths and there is usually a small contribution from the common mosses *Rhytidiadelphus loreus, Hylocomium splendens, Hypnum cupressiforme, H.jutlandicum, Pleurozium schreberi, Dicranum scoparium*, *Sphagnum capillifolium* and *Racomitrium lanuginosum* and from the liverwort *Diplophyllum albicans* (McVean & Ratcliffe 1962, Ratcliffe 1968, Birks 1973, Corley 1983).

Mat formation is a common property of bryophytes. Many mosses and most leafy liverworts grow by forming lateral branches which become detached from the parent and make more branches in turn. Large clumps and patches gradually build up (Lye 1966, Schuster 1983). Mixed mats of different species with similar ecological requirements are also common. For instance, in Scottish woodlands over 20 assemblages of species can be found repeatedly, each characteristic of a particular habitat (Averis 1991). Lye (1966, 1967) has recorded communities of oceanic bryophytes in woods in western Norway, and mixed communities of several species of *Sphagnum* are common in bogs (Slack 1990, Rodwell 1991b).

Northern hepatic mats seem to have been first described by Macvicar (1910). The community was first quantified by McVean and Ratcliffe (1962), who sampled it on 10 hills in north-west Scotland. Ratcliffe (1962) found the community in western Ireland and (1968) discussed its species composition and relationships with the environment. Birks (1973) described hepatic-rich *Calluna* heaths on Skye and Corley (1983) listed the species found in hepatic mats in the Inner Hebrides, but did not describe the communities in detail. In the National Vegetation Classification (NVC), Rodwell (1991b) summarised what was already known about hepatic mats in plant communities in the British uplands. He presents floristic tables for the *Mastigophora woodsii - Herbertus aduncus* ssp *hutchinsiae* sub-community of *Calluna vulgaris - Vaccinium myrtillus - Sphagnum capillifolium* heath (NVC type H21b) and for the *Bazzania tricrenata - Mylia taylorii* sub-community of *Vaccinium myrtillus - Racomitrium lanuginosum* heath (H20c).

These heaths with the hepatic mat are almost confined to the parts of the British Isles where there are more than 220 wet days, or days with more than 1mm of rain, a year (Ratcliffe 1968). Within this climatic region they show a marked bias towards the most humid and sheltered habitats: steep, rocky slopes facing north or east, damp cliffs and boulder-fields (Macvicar 1910, McVean & Ratcliffe 1962, Ratcliffe 1968, Birks 1973, Hobbs 1988, Rodwell 1991b). This suggests that the hepatic mats depend on high atmospheric humidity, equable temperatures, shade and shelter from the prevailing wind.

The hepatic mat species have been admired and collected in the British Isles since they were first discovered from the late 18th century onwards (Hooker 1816, Carrington 1874-5, Macvicar 1910, RBG). Most were first found in the eastern Highlands by early explorers such as Greville and Don in the 1830s (Macvicar 1910, RBG) or in the west of Ireland and their abundance in the west Highlands was not recognised until the mid-eighteenth century (Macvicar 1910). Since then there has been an increasing amount of information on their British and world distributions, as well as some speculation on their origins and ecology (Richards 1957; Ratcliffe 1968; Schofield 1968, 1984, 1988a, 1988b). However, no-one has yet made a detailed study of the community and the relationships between the component species and the environment. As Rodwell (1991b) says in his discussion of damp *Calluna* heaths:

"we are not really any closer now to understanding which {climatic} factors are important to which members of this distinctive assemblage {of liverworts}."

The aim of this study is to work towards such an understanding of the ecology of the hepatic mats and the component species and to explain their modern distribution. I hope that the results will be used to promote the conservation of these species and their habitats.

This thesis is a study of the ecology and distribution of the hepatic mat species at five different scales from the whole world down to individual plants. Chapter 2 is a summary of the species and their habitats throughout the world, together with a possible explanation for their modern patterns of distribution. Chapter 3 is a study of hepatic mats in the British Isles, looking at variation in the habitat and species composition in the mountains of western Ireland, north Wales, the Lake District and western Scotland. Chapter 4 is an investigation of the occurrence of hepatic mat species on one mountain - Beinn Eighe in West Ross. Chapter 5 is a study of the community at a small scale, looking at association between species in one stand and at the differences in microclimate between places with and without hepatic mats. Chapter 6 is an experimental study of the physiological tolerance of some of the hepatic mat liverworts, to find out whether there is a relationship between their distribution and their response to temperature and humidity.

CHAPTER TWO

PHYTOGEOGRAPHY OF THE HEPATIC MAT SPECIES: THEIR ORIGINS AND CURRENT WORLD DISTRIBUTION

2.1. Introduction

Some Atlantic bryophytes are not only rare in Europe but have markedly disjunct world distributions (Crundwell 1970, Corley & Wallace 1974, Smith 1990, Hill, Preston & Smith 1991). This group consists of the mosses *Campylopus schwarzii*, *Dicranodontium subporodictyon* and *Leptodontium recurvifolium* and the liverworts *Adelanthus lindenbergianus*, *Anastrepta orcadensis*, *Plagiochila carringtonii*, *Pleurozia purpurea*, *Scapania nimbosa*, *S.ornithopodioides*, *Mastigophora woodsii*, *Herbertus aduncus*, *H.stramineus*, *H.borealis*, *Anastrophyllum donnianum*, *A.joergensenii* and *Bazzania pearsonii*. In the British Isles most of these bryophytes are plants of well-drained substrates on steep rocky slopes, usually facing between north-west and east and sheltered by cliffs or dwarf shrubs (Macvicar 1910, McVean & Ratcliffe 1962, Ratcliffe 1968, Crundwell 1970, Corley & Wallace 1974, Hill, Preston & Smith 1991). Wherever these species grow in the world they are recognised as members of a distinct phytosociological group (Macvicar 1910; Greig-Smith 1950; Richards 1957; Proctor 1967; Ratcliffe 1968; Crundwell 1970; Birks 1973; Schofield 1968, 1984, 1988a, 1988b; Long & Grolle 1990). All the liverworts apart from *Herbertus stramineus* and *H.borealis* are typical members of the hepatic mat community.

The ecology of these plants in the British Isles is easier to understand if it is seen in the context of the whole world. Their habitats and associated climates in other countries can show whether their habitats in the British Isles are typical or unique. Their world distribution can suggest where they evolved and why they are now in the places they are. A study of their methods of reproduction and dispersal can show how easily they can colonise new areas and maintain populations.

This chapter collates the available information on the world distribution of the hepatic mat liverworts, their habitats and the climates they experience. Their potential for reproduction and spread and their possible origins and current patterns of distribution are discussed. Their tendency to grow together in mixed mats was investigated in the Faroe Islands and in Norway during the study.

2.2 World Distribution

Ten of the 11 hepatic mat species with disjunct distributions (see above) are disjunct between the same three regions: (1) the British Isles, Faroe Islands and western Norway, (2) north-west North America and (3) the Himalayas and western China (Nicholson 1930, Greig-Smith 1950, Richards 1957, Ratcliffe 1968, Schofield 1984). There are a few records of these species elsewhere, notably Japan and Taiwan (table

2.1). *Adelanthus lindenbergianus*, the other disjunct species, grows in eastern and southern Africa, central and south America and Antarctica. *Mylia taylorii* and *Bazzania tricrenata* are widespread in the Holarctic (temperate and arctic parts of the northern hemisphere). *Lepidozia pearsonii*, *Plagiochila spinulosa* and *Scapania gracilis* are almost confined to western Europe and the adjacent islands (Hill, Preston & Smith 1991).

The world distributions of the 16 hepatic mat species are reasonably well-known, although there is still much work to be done especially in tropical montane forests where most of the genera are best-represented (Smith 1990, Hill, Preston & Smith 1991).

2.3 Environment and Climate

2.3.1 Habitats of the hepatic mat species

The only known habitat for *Adelanthus lindenbergianus* in Ireland and Scotland is damp mountain slopes and cliff-ledges with *Calluna vulgaris* heath, mostly between 450 and 800m above sea-level (Ratcliffe 1962, Hill, Preston & Smith 1991, Long 1991). It is known from Cape Horn and the Cape of Good Hope (Douin 1904). In Malawi it grows on the slopes of Mount Mulanje at 3000m or more (M.J.Wigginton pers. comm.). It grows in montane rain-forests and sub-alpine *Erica arborea* L. forests in Tanzania and Zaire, and also in sub-alpine heath

Table 2.1. World distributions of the hepatic mat liverworts.

SPECIES	B	N	F	WE	CE	JM	NA	GR	A	G	HW	SA	H	J	T	CA	P	SCA	NAF	ANT
Adelanthus lindenbergianus	1											1						1		1
Anastrepta orcadensis	1	1	1	1			1				1		1		1					
Anastrophyllum donnianum	1	1	1				1						1							
Anastrophyllum joergensenii	1	1											1							
Bazzania pearsonii	1						1						1							
Bazzania tricrenata	1	1	1	1	1		1		1				1							
Herbertus aduncus	1	1					1		1						1					
Lepidozia pearsonii	1	1																1		
Mastigophora woodsii	1		1				1						1			1				
Mylia taylorii	1	1	1	1	1		1	1	1				1	1						
Plagiochila carringtonii	1		1										1							
Plagiochila spinulosa	1	1	1	1								1	1							
Pleurozia purpurea	1	1	1			1	1			1			1						1	
Scapania gracilis	1	1	1	1	1							1								
Scapania nimbosa	1	1											1							
Scapania ornithopodioides	1	1	1	1			1				1		1	1	1		1			
TOTAL	16	12	10	6	3	1	9	1	3	1	2	3	12	2	3	1	1	1	1	1

B: British Isles, N: Western Norway, F: Faroe Islands, WE: Elsewhere in western Europe. CE: Central Europe, JM: Jan Mayen, NA: North-west Canada and Alaska, GR: Greenland, A: Appalachians, G: Guadeloupe, HW: Hawaii, SA: South America, H: southern slopes of the Himalayas including parts of Tibet, Sikkim, Bhutan, Nepal and Yunnan, J: Japan, T: Taiwan, CA: Central Asia, P: Phillipines, SCA: Central and southern Africa, NAF: North Africa, ANT: Antarctica.

Herbertus aduncus *is represented by ssp.* hutchinsiae *in Europe, by ssp.* aduncus *in Pacific north America and Taiwan and by ssp.* tenuis *(Evans) Miller & Scott in the Appalachians of eastern America (Smith 1990). There is some evidence that* Plagiochila carringtonii *ssp.* lobuchensis *Grolle, recorded from Bhutan, is a different species from* P.carringtonii *ssp* carringtonii *recorded in the British Isles and the Faroes (D Chamberlain, pers. comm.).*

Sources: Hill, Preston & Smith 1991, Schofield 1988a, Herbarium of the Royal Botanic Garden, Edinburgh.

with *Podocarpus latifolius* (Thunb.) R.Br ex Mirb, *Hagenia abyssinica* Bruce and *Erica arborea*. It has been recorded on rotting logs as well as on the ground. All east African records are above 1800m and most are above 2500m (RBG).

Anastrepta orcadensis is predominantly a woodland plant in the British Isles, but is also common on shaded rocky mountain slopes with *Calluna vulgaris*. It grows from sea-level to over 1100m (Hill, Preston & Smith 1991). In Norway it is plentiful on boulders and mossy banks in *Betula* and *Pinus* woodland and in wet *Calluna vulgaris* and *Erica tetralix* heaths, close to sea-level (RBG, Averis & Averis 1992). It grows on mossy ledges on mountains above 1000m in Norway and in Germany (RBG). It has been recorded in boulder-fields at 450m in the Faroe Islands (Hobbs & Averis 1991a). In British Columbia it has been recorded in wet hollows in fens and on tundra slopes (Schofield 1968). *A.orcadensis* has been recorded in Bhutan in forests of *Abies densa* Griff. - *Tsuga dumosa* (D.Don) Eichler, *Betula utilis* D.Don - *Tsuga*, *Abies* - *Rhododendron* L. and *Abies-Juniperus* L. and in *Juniperus-Rhododendron* scrub. It is often epiphytic on trees as well as occurring on rotting logs and boulders (Long & Grolle 1990, RBG).

Anastrophyllum donnianum grows on shaded mountain slopes and in places where snow lies late on the higher hills of the Scottish Highlands. It has been recorded from 280m (personal observation) to over 1000m (Hill, Preston & Smith 1991). It grows under *Calluna* in Norwegian woods from 100m up to 600m (RBG), usually on slopes facing north or west (Joergensen 1934). It grows in snow-beds and among boulders in the Faroes (H.J.B. Birks pers. comm.). It grows on flushed slopes in fens in Alaska at about 300m (RBG) and in fens and on tundra slopes in British Columbia (Schofield 1968). In Bhutan it is a plant of high-altitude forests and has been recorded on mossy banks in *Abies densa-Rhododendron* forest between 3200m and 4000m (Long & Grolle 1990, RBG).

Anastrophyllum joergensenii has been recorded in Scotland, Norway and the Himalayas. Most of the Scottish records are from shaded rocky slopes and snow-beds from 325m to 950m. It has occasionally been found in high-altitude blanket bog (Ratcliffe 1977; Hill, Preston & Smith 1991; personal observation). It has been recorded between 350m and 450m in western Norway (Joergensen 1934). In Bhutan it grows on rotting logs in forests of *Tsuga dumosa - Rhododendron*, *Tsuga-Abies densa* and *Abies-Rhododendron* and in scree in open *Juniperus-Rhododendron* scrub (Long & Grolle 1990, RBG).

Bazzania pearsonii grows on steep, shaded mountain slopes among dwarf shrubs and boulders in Scotland and western Ireland. It occurs in snow-beds in the eastern Highlands. The records are from 125m to 1000m (Hill, Preston & Smith 1991). It is epiphytic on coniferous and deciduous trees in *Tsuga heterophylla* (Raf.) Sarg. forest and also grows on rotten logs, damp cliffs and tundra slopes in British Columbia

(Schofield 1968). It grows on logs in *Abies - Rhododendron* forests in Nepal and Bhutan (Long & Grolle 1990, RBG).

Bazzania tricrenata is frequent in the north-west of the British Isles in woodland, on shaded mountain slopes and on cliffs from sea-level to over 1100m (Hill, Preston & Smith 1991). In Norway it is common in woodland and damp *Calluna-Erica* heath on rocky slopes down to sea-level (Averis & Averis 1992, RBG). It has been recorded from cliff-ledges at 1040m in northern Norway and from granite rocks at 2000m in Turkey (RBG). In the Faroes it occurs on cliffs and in boulder-fields from 325m to over 450m (Hobbs & Averis 1991a). It has been recorded on rotting logs and moist ground in north-west America, mostly at low altitudes but extending to 600m in *Thuja plicata* D.Don - *Tsuga* forest (RBG). It grows in the Appalachian mountains on shaded ledges with acidic soil and occasionally on trees (Schuster 1966). In Bhutan it grows on damp rocks, logs or tree-bases in *Abies densa-Tsuga dumosa, Betula-Tsuga, Abies-Rhododendron* and *Abies-Juniperus* forest, mostly above 2400m. Several Himalayan records are from wooded ravines (Long & Grolle 1990, RBG).

Herbertus aduncus occurs as three rather weakly-defined sub-species (Schuster 1966). The European ssp *hutchinsiae* is most common in the British Isles, on shaded mountain slopes, cliffs and boulder-fields, in upland woods and in ravines from sea-level to around 750m (Hill, Preston & Smith 1991). It is rare in Norway, but has been recorded from wet rocks by waterfalls in woods (Joergensen 1934, Lye 1966). Ssp *aduncus* grows in woods in north-western North America. It has been recorded as an epiphyte on tree-roots and on the ground in boggy pine woodland. It grows in *Tsuga* and *Thuja* forests where it has been recorded from about 250m to 600m ASL. It is also common on cliffs and boulders and in bogs (Schofield 1968, RBG). In Taiwan it has been recorded from bark in mossy forest (RBG). Ssp *tenuis* grows on shaded cliffs and on the bark of trees (particularly *Abies fraseri* (Pursch.) Poir in the Appalachian mountains (Schuster 1966).

Lepidozia pearsonii is common in woods and on shaded slopes from sea-level to 800m in the west of the British Isles (Hill, Preston & Smith 1991). It grows in Norway in woods of *Betula* and *Juniperus* or *Pinus* and *Betula* up to about 700m, typically creeping among other bryophytes on mossy banks or boulders (Joergensen 1934, Averis & Averis 1992, RBG). It has recently been recorded in Malawi, East Africa (O'Shea 1993).

Mastigophora woodsii grows on shaded mountain slopes and occasionally in upland woods in Scotland and Ireland. It has been recorded once on deep ombrogenous peat in the Highlands (A. M. Averis unpublished). Records are from below 100m to 1000m or more (Hill, Preston & Smith 1991). In the Faroes it grows on ravine-sides close to sea-level, on cliff-ledges, in damp *Calluna vulgaris* heaths and in soligenous mires and flushes in blanket-bogs up to 500m (Hobbs & Averis 1991a). It grows epiphytically on coniferous and deciduous trees in

Tsuga forests in British Columbia as well as on banks and wet cliffs (Schofield 1968). It has been recorded from *Tsuga dumosa-Abies densa*, *Abies-Rhododendron* and *Tsuga-Rhododendron* forest in Bhutan, usually growing epiphytically on trees or on rotting wood. Most records are from above 3000m (Long & Grolle 1990, RBG). *M.woodsii* has also been recorded from rocky mountainsides in the Darjeeling region of India (RBG).

Mylia taylorii is common in the British Isles in western woods, on shaded mountain slopes, in bogs and wet heaths and in late snow-beds from sea-level to over 1200m (Hill, Preston & Smith 1991). It grows in woods in continental Europe. In western Norway it is common in low-altitude *Betula -Juniperus* and *Pinus-Betula* woods and *Calluna-Erica* damp heaths (Averis & Averis 1992) but has also been recorded from wet cliff-ledges in a limestone valley at 950m (RBG). It has been found at 1500-1600m in Hungarian pine-woods and at 800m in Germany (RBG). It is common in damp *Calluna vulgaris* heaths and in ravines at low altitudes in the Faroe Islands (Hobbs & Averis 1991a). In north-western America it grows down to sea-level on granite cliffs, in bogs and in woods (RBG). It occurs on acidic mountain rocks in the Appalachians (Schuster 1966). In Bhutan it grows on moist peaty banks in *Abies-Rhododendron* forests between 2900m and 4100m (RBG).

Plagiochila carringtonii grows on shaded mountain slopes and among boulders in Scotland and western Ireland from 15m to over 900m. There are a few records from upland woods and from snow-beds (Hill, Preston & Smith 1991, Averis 1991). It is rare in the Faroe Islands and has been recorded on cliffs and in boulder-fields between 300m and 450m (Hobbs & Averis 1991a). It has been recorded in scree in rocky *Juniperus - Rhododendron* scrub in Bhutan (Long & Grolle 1990).

Plagiochila spinulosa is common in rocky woodland in the west of the British Isles. It also grows on sheltered mountain slopes. Its altitudinal range is from sea-level to over 600m (Hill, Preston & Smith 1991). It is rare on the European mainland and grows mostly in woods. It has been collected in northern France in low-altitude deciduous woodland (N.G. Hodgetts pers. comm.). In the Canary Islands it has been recorded from shaded rock-faces in gorges and in *Laurus azorica* Franco - *Erica* forests between 400 and 950m (RBG).

Pleurozia purpurea grows in Scotland and Ireland in blanket-bogs, on shaded mountain slopes and occasionally in snow-beds from sea-level to over 900m. It grows down to sea-level in damp *Pinus sylvestris* and *Betula* woodland and in *Calluna-Erica* damp heath in western Norway (Lye 1966, Averis & Averis 1992). It grows in blanket-bogs, montane grasslands and damp *Calluna vulgaris* heaths on the Faroe Islands (Hobbs & Averis 1991a). It has been recorded in bogs on the Queen Charlotte Islands in British Columbia (RBG); it also grows there on rotten logs and on damp cliffs (Schofield 1968). In Bhutan it has been recorded at over 3500m on damp logs in *Abies-Rhododendron* forest (Long & Grolle 1990). It has been found on rocky mountainsides in Darjeeling, India (RBG).

Scapania gracilis grows in the west of the British Isles in rocky woodlands, on mountain slopes and on cliffs from sea-level to over 700m (Hill, Preston & Smith 1991). It is common in western Norway, occurring down to sea-level in *Betula* and *Pinus* woodland and in *Calluna-Erica* damp heath (Averis & Averis 1992). In the Canary Islands it has been recorded under *Erica arborea* and *Laurus* at 600m and at 950m; in one locality on a dry dusty path (RBG). In the Faroe Islands it is common from sea-level up to about 450m in damp *Calluna vulgaris* heath and blanket-bog, on cliff-ledges, in ravines and in boulder-fields (Hobbs & Averis 1991a).

Scapania nimbosa is a plant of steep shaded mountain slopes, cliff-ledges and snow-beds in Scotland and western Ireland, from 350m to almost 1000m. There is an old record in North Wales. It is rare in western Norway and has been recorded from 220m to 320m (Joergensen 1934). It has also been recorded from the Himalayas (Hill, Preston & Smith 1991).

Scapania ornithopodioides grows in the west of the British Isles on shaded rocky mountain slopes and, less commonly, in upland woods and in snow-beds from 230m to over 950m (Hill, Preston & Smith 1991). It has been seen once on deep ombrogenous peat (A. M. Averis unpublished). In south-west Norway it occurs rarely up to 600m in *Pinus* and *Betula* woodland and on wet rocks by waterfalls (Joergensen 1934, Lye

1966, Averis & Averis 1992, RBG). In British Columbia it grows on wet peaty slopes from sea-level to the sub-alpine regions (W. B. Schofield pers. comm., RBG). In Bhutan it has been recorded on mossy logs, in stream-side turf and on damp rocks in *Abies-Juniperus, Tsuga-Rhododendron, Quercus - Pinus - Picea* L., *Quercus* L.- *Rhododendron*, *Abies-Rhododendron* and *Betula-Tsuga* forests above 2400m. Several sites are in deep ravines (Long & Grolle 1990, RBG). It has been found at 700m and 1000m on moist rocks in the mountains of Japan, and at over 2000m on trees and on humus in Taiwan.

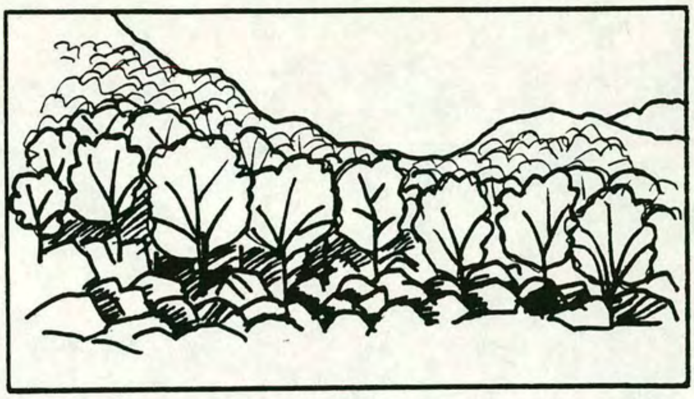
2.3.2 Habitats and climates in north-western Europe.

In the British Isles and Faroe Islands the hepatic mat species occur most often on well-drained rocky mountain slopes. Some of them are also common woodland plants in the British Isles. One or two of the species grow in wet heaths and bogs. There is no natural woodland on the Faroe Islands and the vegetation is predominantly sheep-grazed grassland, *Calluna* heathland and blanket-bog, with moss heaths, snowbeds and fell-fields on the montane ground (Ostenfeld 1908, Bocher 1940, Hobbs & Averis 1991a). The hepatic mat species are most often encountered in damp *Calluna* heaths, in boulder-fields and on cliff-ledges. In Norway the main habitats for the hepatic mat species are rocky banks and among boulders in woods dominated by *Betula pubescens* with *Juniperus communis* and *Sorbus aucuparia* or by *Pinus sylvestris* with occasional *Betula* (Lye 1966, 1967; Ratcliffe 1968; Averis & Averis

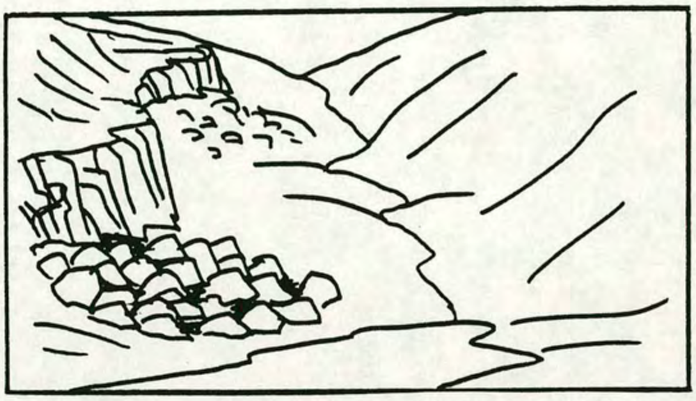
1992). The woods look like those in eastern Scotland, but the bryophyte floras have similarities to those of both eastern and western Scotland (Averis & Averis 1992). The rocks are usually hard, acidic gneiss or granite (Lye 1966). Several of the species also grow in damp heaths dominated by *Calluna vulgaris, Erica tetralix, Molinia caerulea, Scirpus cespitosus, Narthecium ossifragum* and *Racomitrium lanuginosum* (fig.2.1). Records of hepatic mat species further east in Europe tend to be in woodlands at high altitudes.

The British Isles, the Faroes and western Norway have a cool temperate marine climate (Monkhouse 1975), characterised by cool summers, mild winters, heavy and frequent rainfall, strong winds and a high incidence of cloudy skies. Winter temperatures are ameliorated by the Northern Atlantic Drift. The hepatic mat species grow mostly where mean daily temperatures are below 19°C in July and above 0°C in February (Meteorological Office 1975, Averis 1991, Lysgaard 1969). Parts of all three places have over 250 rain days (0.1mm) a year and an average annual rainfall exceeding 1200mm (Climatological Atlas 1952, Meteorological Office 1977, Averis 1991, Lysgaard 1969). Average windspeeds exceed 5.6 m s^{-1} in the western British Isles (Climatological Atlas 1952) and 5.1 m s^{-1} in the Faroes (Lysgaard 1969). These regions (and Iceland) have the lowest annual average potential water deficit in Europe (Green 1964). Western Scotland, the Lake District and North Wales have some of the highest annual precipitation figures in Europe (Monkhouse 1975). The British

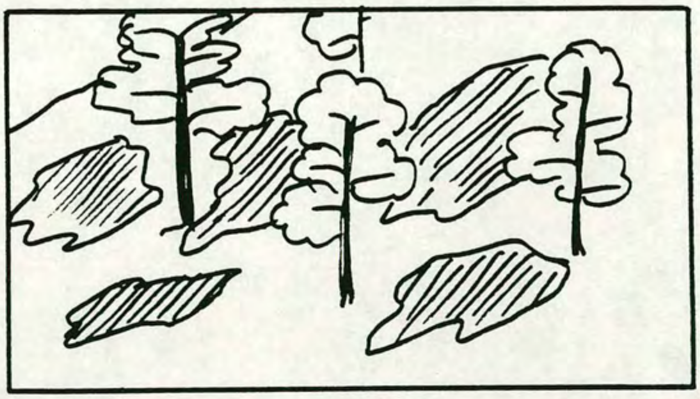
Figure 2.1 Typical habitats of hepatic mat communities in north-west Europe



Rocky woods: British Isles and western Norway



Rocky mountainsides, boulders and cliffs: British Isles and Faroes



Wet heaths on rocky slopes: western Norway

Bogs and ravine sides: Faroes and (rarely) British Isles

Isles, the Norwegian coast and British Columbia are the cloudiest places in the northern hemisphere (Monkhouse 1975).

2.3.3 Habitats and climate in north-west North America

Nine of the hepatic mat species grow in British Columbia and Alaska in coastal Western Hemlock forests between Vancouver Island and south-east Alaska, including the Queen Charlotte Islands and the Coast Mountains (Hill, Preston & Smith 1991; Schofield 1968, pers. comm.). This temperate forest is dominated by *Tsuga heterophylla*, *Chamaecyparis nootkatensis* (D.Don) Spach, *Alnus rubra* Bong., *Pinus contorta* Dougl. and *Acer macrophyllum* Pursh. (Schofield 1968). There are extensive bogs with a *Sphagnum*-rich ground flora and a thin cover of trees such as *Pinus contorta*, *Thuja plicata* and *Chamaecyparis nootkatensis* (Hong *et al.* 1991). The coasts of British Columbia and southern Alaska are kept warm in winter by the North Pacific Drift (Monkhouse 1975). The mean minimum monthly temperature in January is -4°C and the mean monthly maximum in July is 17.7°C. Annual average precipitation ranges from 1778mm to 6654mm and snow is common in winter (Krajina 1965). In the Queen Charlotte islands the average January temperature is 4°C and the average August temperature 17°C. Rainfall averages 1400mm a year but exceeds 5500mm on the western coasts (Hong *et al.* 1991). Average windspeeds are evidently less than in the British Isles because trees grow 60m tall on the coast and even in the far west the tree-line is between 2000m and 3000m ASL (B. Taylor pers. comm.).

2.3.4 Habitats and climate in the Himalayas and western China

Ten hepatic mat species grow in western Tibet, Nepal, Sikkim, Bhutan and Yunnan (Hill, Preston & Smith 1991). Nepal, Sikkim and Bhutan have an extraordinarily rich bryophyte flora (Long & Grolle 1990) and Yunnan has the richest liverwort flora of all the provinces of China (Piippo 1991). The main habitat of the hepatic mat liverworts (at least in Bhutan and Nepal) is *Tsuga dumosa* and *Abies densa* forest which extends from 2800 to 3300m, and woodland dominated by *Abies densa* with *Rhododendron* species between 3100m and 3800m. A few hepatic mat species grow in *Juniperus* and *Rhododendron* scrub between 3700 and 4200m (Long & Grolle 1990). The southern slopes of the Himalayas, including Nepal, Bhutan and Sikkim and the mountains of Yunnan have a monsoon climate, characterised by a distinct rainy season associated with south-westerly winds and a dry, cold but short winter (Monkhouse 1975). There are few weather-stations in the remote forests of these regions and so the local climates are not well-documented. However the available evidence suggests that south-east Nepal, Bhutan and Sikkim are particularly wet. Some upland valleys in the Himalayan foothills of south-east Nepal have about 6000mm of rain a year (Joshi 1986) and parts of Bhutan have over 4000mm (Ohsawa 1987). This extreme wetness is partly caused by orographic effects - moist air from the south is funnelled up narrow valleys surrounded by high mountains. The air is forced to rise over the mountains and its load of water condenses and falls (Joshi 1986). The dry season is short (November to February) and precipitation exceeds evapotranspiration by over 2000mm a year (Ohsawa 1987). The region has equable temperatures because of the sub-tropical latitude, with an annual range of about 10°C. Temperature decreases with altitude so that mean monthly temperatures are 17°C at 2000m and 10°C at 3000m (Barry 1981). The *Tsuga* and *Abies* forests have a cold temperate climate and the *Juniper-Rhododendron* scrub has a cold temperate to alpine climate (Ohsawa 1987).

2.4 Communities of hepatic mat species

A notable characteristic of the hepatic mat species in the British Isles is their tendency to grow together in intimate mixtures. Similar hepatic communities were discovered and sampled by 25cm x 25cm quadrats on the Faroe Islands in July 1990 (fig.2.2) and in western Norway in June 1992 (fig.2.3).

2.4.1 The Faroe Islands

On the Faroe Islands there are assemblages of species which are similar to British hepatic mats, but contain fewer of the characteristic species. The associated vascular plants and bryophytes are generally those which occur with the hepatic mat species in the British Isles (Hobbs & Averis 1991a). *Herbertus aduncus* does not occur in the Faroes, although its calcicole relative *H.stramineus* does, and most of the mats

Figure 2.2. A map of the Faroe Islands showing sites where a hepatic mat community was sampled in July 1990.

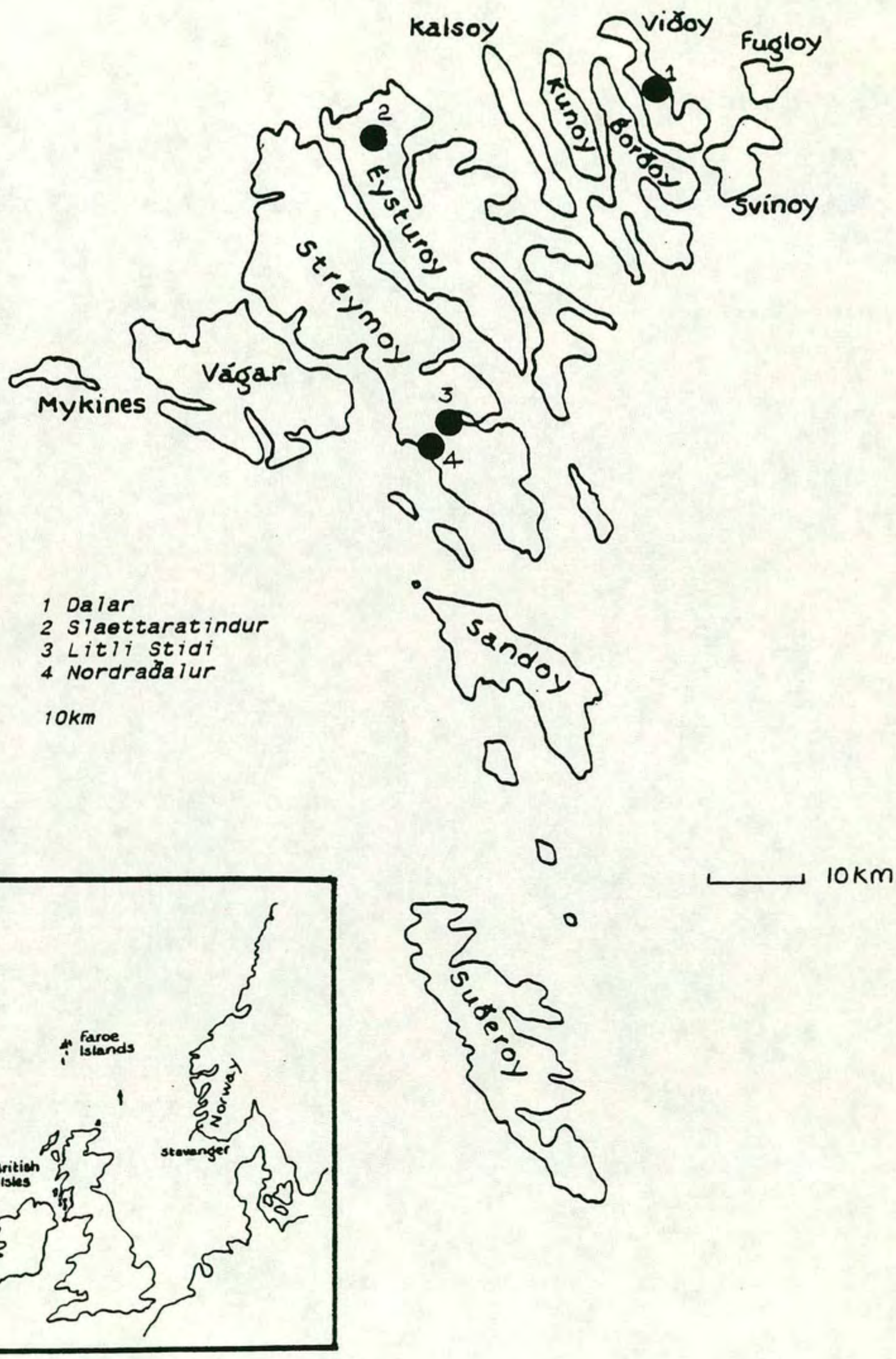
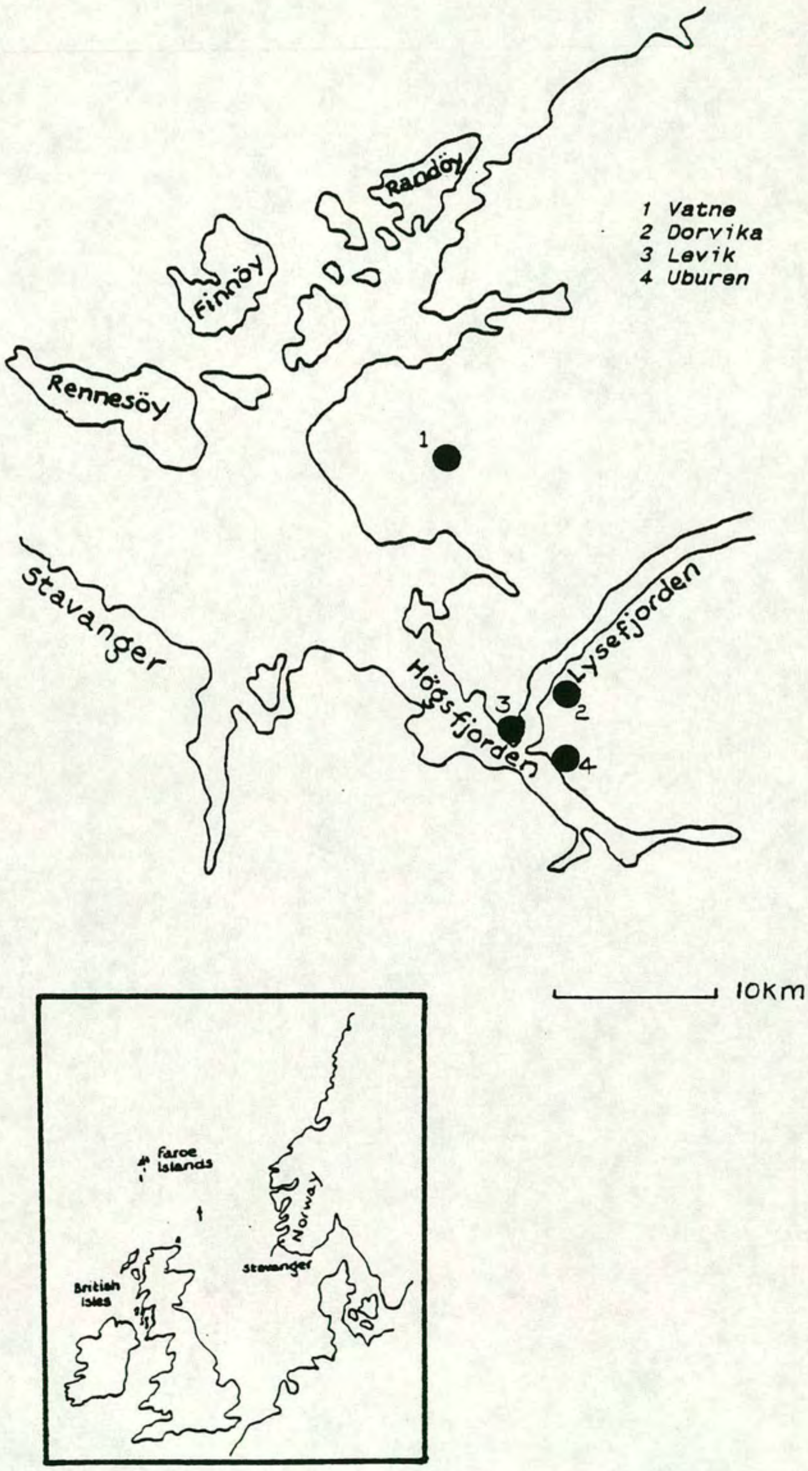


Figure 2.3. A map of south-western Norway showing the sites where liverwort communities were sampled in June 1992



are dominated by *Mastigophora woodsii*. My hepatic mat samples from damp heaths (table.2.2) showed that although four of the hepatic mat species grow in this type of vegetation, it is rare for all of them to grow in the same close proximity that they do in the British communities. Assemblages of hepatic mat species are also common on cliff-ledges, ravine sides and in boulder-fields in the Faroes (table 2.3), but again the mats consist of fewer species than one would expect in similar habitats in the British Isles. *Mastigophora woodsii*, *Scapania gracilis* and *Pleurozia purpurea* grow in mixed mats in blanket-bogs, damp grassland and soligenous mires on the Faroes, often associated with the oceanic mosses *Breutelia chrysocoma* and *Campylopus atrovirens*. In the British Isles it is common to find *Pleurozia*, *Scapania*, *Breutelia* and *Campylopus* growing together in bogs (McVean & Ratcliffe 1962, Rodwell 1991b), but not in soligenous mires or grasslands.

2.4.2 Western Norway

In Norwegian *Pinus-Betula* woodlands *Anastrepta orcadensis*, *Bazzania tricrenata*, *Lepidozia pearsonii*, *Mylia taylorii* and *Scapania gracilis* grow mixed together (table 2.4) with *Pleurozia purpurea* and *S.ornithopodioides* in some stands. They grow on rocks, tree-bases and steep slopes by streams. The oceanic liverwort *Bazzania trilobata* was also recorded in this community.

Pleurozia purpurea occurs in Norwegian hepatic mats in two

Table 2.2. Hepatic mats in damp Calluna *heath at Dalar, Viðoy, Faroe Islands. Figures show % cover of each species in ten 25cm x 25cm quadrats. 100m ASL, NW-facing. July 1990.*

Species	1	2	3	4	5	6	7	8	9	10
Mastigophora woodsii	25	25	5		30	75	75	50	50	15
Scapania gracilis			5	15	5		7		10	5
Pleurozia purpurea		20	10	20			7			
Mylia taylorii	30									1
Calluna vulgaris	10	35	5	5	10	5	15	10	10	10
Scirpus cespitosus	20	20	20	15	40		10	10		
Potentilla erecta				5	3			5	1	2
Molinia caerulea	2		15			6	1		5	
Juncus squarrosus			5	10		3	10			
Eriophorum angustifolium				7					2	5
Narthecium ossifragum	5			2						1
Hypericum pulchrum					1		1	1		
Erica cinerea	5							1		
Racomitrium lanuginosum	10	15	7	15	7	5	3	3		
Rhytidiadelphus loreus				2		2		3	1	2
Diplophyllum albicans		7		5			5	10	5	
Isothecium myosuroides					10	3				50
Hypnum jutlandicum								10	5	2
Thuidium tamariscinum						3			5	

Table 2.3. Examples of hepatic mat communities from the Faroe Islands showing % cover of species in 25cm x 25cm quadrats.

Hepatic mat communities	LS	S	S	S	N	N
Altitude ASL (m)	325	470	470	470	5	5
Aspect	NNE	E	E	E	NW	NW
Anastrepta orcadensis		50	70	10		
Bazzania tricrenata	3		20	75		
Mastigophora woodsii	2				25	50
Scapania gracilis	3	5				5
Plagiochila carringtonii	5			10		
Herbertus stramineus					25	
Saccogyna viticulosa						1
Deschampsia flexuosa		6	5	5		15
Agrostis canina		3	5			
Angelica sylvestris					2	1
Galium saxatile			2	15		
Hieracium sp					3	5
Hymenophyllum wilsonii					2	3
Luzula sylvatica	5				2	
Sedum rosea	2					1
Thalictrum alpinum	5	40				
Racomitrium lanuginosum	65	30	10	10	5	3
Polytrichum alpinum	2	6	2	5		5
Dicranum scoparium	2	1	1	1		
Diplophyllum albicans	18	10		2	2	
Hylocomium splendens		3	5	1	2	
Hypnum cupressiforme		10		1	5	2
Tritomaria quinquedentata	1		2		2	1
Rhytidiadelphus loreus		2	2		1	
Isothecium myosuroides					10	5
Rhizomnium punctatum			2	1		
Peltigera membranacea					2	1

Sites were cliff-ledges at Litli Stidi, Streymoy (LS), a boulder-field on Slaettaratindur, Eysturoy (S) and ravine sides at Nordraðalur, Streymoy (N). July 1990.

Table 2.4. A sample of ten 25cm x 25cm quadrats recorded in a community of large liverworts on rocks in rocky NNW-facing Betula/Pinus sylvestris *woodland. Vatne, W.end of Tysdalsvatnet, Norway. June 1992.*

	1	2	3	4	5	6	7	8	9	10
Scapania gracilis	*	*	*	*	*	*	*	*	*	*
Bazzania tricrenata	*	*		*	*	*	*		*	*
Anastrepta orcadensis		*	*				*	*	*	*
Lepidozia pearsonii				*	*	*				*
Mylia taylorii						*		*	*	*
Deschampsia flexuosa			*				*			
Racomitrium lanuginosum	*	*	*	*	*	*	*	*	*	
Bazzania trilobata	*	*		*	*	*	*	*		*
Dicranodontium denudatum			*	*	*	*	*	*	*	
Hypnum cupressiforme	*	*	*	*	*	*				
Plagiothecium undulatum	*						*	*		
Polytrichum formosum				*	*					*
Hylocomium splendens								*		*

Table 2.5. A sample of 10 25cm x 25cm quadrats on and among shaded rocks in N-facing rocky Betula *wood. 150m. Uburen, Forsand, Norway. June 1992.*

	1	2	3	4	5	6	7	8	9	10
Lepidozia pearsonii		*	*	*				*	*	
Anastrepta orcadensis		*	*	*		*			*	
Bazzania tricrenata		*	*	*			*		*	
Scapania gracilis		*					*	*	*	
Mylia taylorii	*			*						
Pleurozia purpurea										*
Hymenophyllum wilsonii	*	*	*	*	*	*	*	*	*	*
Vaccinium myrtillus		*		*			*			
Vaccinium vitis-idaea							*	*	*	
Diplophyllum albicans	*	*						*	*	*
Dicranum majus		*		*	*	*			*	
Sphagnum quinquefarium		*	*	*		*	*			
Rhytidiadelphus loreus		*	*		*				*	
Bazzania trilobata		*	*							
Dicranum scoparium			*					*		*
Plagiothecium undulatum			*		*	*	*		*	
Racomitrium lanuginosum			*	*						*
Thuidium tamariscinum					*		*		*	
Hylocomium splendens						*		*		
Ptilium cristacastrensis						*	*			

distinct habitats. One is damp, open woods of *Pinus sylvestris* and occasional *Betula pubescens* (table 2.5). Locally this woodland has a ground-layer of deep cushions of *Sphagnum capillifolium* with *Calluna vulgaris*, *Vaccinium myrtillus*, *V.vitis-idaea*, *Empetrum nigrum*, *Blechnum spicant* and *Deschampsia flexuosa*, forming vegetation much like the hepatic-rich *Calluna* heaths of the British Isles with the addition of trees (table 2.6). The other habitat for hepatic mats with *Pleurozia purpurea* is a damp heath disposed among large, smooth slabs of bare rock on steep slopes near sea-level (table 2.7). The hepatic mat liverworts usually grow together in a fringe along the lower edges of the patches of heath, presumably because there is a steady supply of water from the mat of roots and humus (Averis & Averis 1992).

Scapania ornithopodioides is a rare member of these bryophyte communities and was only found once, growing with *Pleurozia purpurea* in birch woodland (table 2.8).

The oceanic bryophyte communities of south-west Norway were sampled by Lye (1966) using 25 x 25 cm quadrats. One quadrat contained *Anastrepta orcadensis*, *Bazzania tricrenata*, *Lepidozia pearsonii*, *Mylia taylorii*, *Scapania gracilis* and the oceanic fern *Hymenophyllum wilsonii*; another had *Bazzania tricrenata*, *Mylia taylorii*, *Pleurozia purpurea* and *Scapania ornithopodioides*. The communities sampled in his study were almost all on steep, boulder-strewn slopes facing between north-west and east and the community with *Pleurozia purpurea*

Table 2.6. A sample of ten 25cm x 25cm quadrats in damp heath on WNW-facing banks on slopes above waterfall, beneath fairly open canopy of Betula *and* Pinus sylvestris. *100m. Dorvika, Lysefjorden, Norway. June 1992.*

	1	2	3	4	5	6	7	8	9	10
Pleurozia purpurea	*	*	*	*	*	*	*	*	*	*
Mylia taylorii	*									*
Scapania gracilis							*			
Bazzania tricrenata									*	
Vaccinium myrtillus	*	*	*				*		*	
Vaccinium vitis-idaea		*	*	*		*		*		*
Vaccinium uliginosum	*							*		
Calluna vulgaris				*	*			*		
Molinia caerulea						*	*			
Trientalis europaea							*			*
Erica tetralix									*	*
Sphagnum capillifolium	*		*	*	*					
Kurzia trichoclados	*	*	*	*	*			*		*
Racomitrium lanuginosum	*		*							*
Dicranum scoparium		*	*		*		*			
Hypnum jutlandicum					*	*	*	*	*	*
Bazzania trilobata					*				*	
Cladonia arbuscula	*		*		*	*	*		*	*

Table 2.7. A sample of ten 25cm x 25cm quadrats in between large, smooth rock slabs facing east. 40m. Levik, N.of Oanes, Norway. June 1992.

	1	2	3	4	5	6	7	8	9	10
Pleurozia purpurea	*	*	*	*	*	*	*	*	*	*
Scapania gracilis				*			*			
Mylia taylorii		*								
Calluna vulgaris	*	*	*		*	*	*	*	*	*
Molinia caerulea	*		*		*	*	*	*	*	*
Scirpus cespitosus	*	*		*	*		*	*	*	*
Erica tetralix	*	*	*	*			*			
Succisa pratensis	*	*	*	*						
Juniperus communis				*		*		*	*	
Potentilla erecta	*	*	*							
Carex panicea			*		*		*			
Pedicularis sylvatica	*		*							
Narthecium ossifragum				*						
Racomitrium lanuginosum	*		*	*	*	*	*	*	*	*
Hypnum jutlandicum		*				*	*	*		
Diplophyllum albicans								*		*
Cladonia arbuscula	*	*				*			*	

Table 2.8. A sample of four 25cm x 25cm quadrats on steep, moist banks near small stream in N-facing Betula *wood. 200m. Uburen, Forsand, Norway. June 1992.*

	1	2	3	4
Scapania ornithopodioides	*	*	*	*
Pleurozia purpurea	*	*	*	
Narthecium ossifragum	*	*	*	*
Calluna vulgaris		*	*	*
Sphagnum auriculatum	*	*	*	*
Racomitrium lanuginosum	*	*	*	*
Scapania nemorosa		*	*	
Calliergon sarmentosum	*		*	

was in the sites with the lowest density of trees.

Several other hepatic mat liverworts occur rarely in Norway. *Herbertus aduncus* has been recorded with *Pleurozia purpurea* and *Scapania ornithopodioides* (Joergensen 1934, Lye 1966). *Anastrophyllum donnianum* has been recorded with *Scapania ornithopodioides*, *Anastrepta orcadensis* and *Lepidozia pearsonii* (Joergensen 1934), and *Scapania nimbosa* has been recorded with *S. ornithopodioides* (Joergensen 1934).

2.4.3. British Columbia, Canada

Anastrepta orcadensis, *Anastrophyllum donnianum*, *Bazzania pearsonii*, *Bazzania tricrenata*, *Herbertus aduncus*, *Mastigophora woodsii*, *Mylia taylorii*, *Pleurozia purpurea* and *Scapania ornithopodioides* have been recorded in British Columbia, where they appear to be members of a rich bryophyte flora. It is unclear whether they grow together as mixed mats, but *Scapania ornithopodioides*, *Pleurozia purpurea*, *Herbertus* spp. and Sphagna have been collected together on wet peaty slopes (RBG).

2.4.4 Southern Himalayas and Yunnan

The hepatic mat species grow mixed with other bryophytes in a rich flora of mosses and liverworts. Some of the hepatic mat species grow close together. *Scapania ornithopodioides* has been collected mixed with *Anastrepta orcadensis* (RBG).

Anastrophyllum joergensenii and *Plagiochila carringtonii* grow together under *Juniperus* scrub in mats which look like some British hepatic communities (D.G.Long, pers. comm.).

2.4.5 Hepatic mat communities elsewhere in the world.

Communities resembling the British and Irish hepatic mats have been seen in Japan at 1800m in the Tanigawa mountain range (Ikegami 1957). A community on a rock included species of *Anastrophyllum, Herbertus, Plagiochila, Saccogyna* and several Lejeuneaceae. *Pleurozia purpurea, Anastrepta orcadensis* and *Scapania ornithopodioides* often occur together in Japan (Ikegami 1957). At about 3000m on the upper slopes of Mount Mulanje in Malawi there is hepatic mat vegetation with *Herbertus* spp. and *Adelanthus lindenbergianus* (M. J. Wigginton pers. comm.). *Mastigophora woodsii* and *Pleurozia purpurea* have been found mixed together on rocky hillsides in Darjeeling Region, India (RBG). In the Appalachian mountains of North America, *Herbertus aduncus* ssp *tenuis, Bazzania tricrenata* and *Mylia taylorii* grow together in mixed mats, often with the British oceanic liverworts *Plagiochila exigua* and *Leptoscyphus cuneifolius* (Schuster 1966).

2.5. Reproduction and Dispersal

2.5.1. Spore production

Only five of the hepatic mat liverworts have been known to reproduce sexually in the British Isles. *Scapania gracilis* produces capsules frequently; *Mylia taylorii* and *Lepidozia pearsonii* occasionally do so (Hill 1988, Smith 1990, Hill, Preston & Smith 1991). *Anastrophyllum donnianum* has been recorded once with sporophytes in Britain - in the Cairngorms in 1922 (RBG). Hooker (1816) had never seen fertile material of *Herbertus aduncus* in Britain, but had been given specimens by Dickson, collected in the late 18th or early 19th century in the Scottish Highlands. Hooker's book includes high quality hand-coloured drawings of British leafy liverworts. Fertile material of *H.aduncus* is illustrated. There is little doubt that the plant shown is indeed this species. The illustration shows that the capsule on its fully-extended seta projects only 1-2mm above the shoot apex; such structures could easily be overlooked in the field.

Bazzania tricrenata and *Anastrepta orcadensis* have been recorded with antheridia and archegonia but not with capsules in Britain (Hill, Preston & Smith 1991). *A.orcadensis*, *Anastrophyllum donnianum* and *Pleurozia purpurea* have been recorded with antheridia and archegonia in Norway (Joergensen 1934). *Herbertus aduncus* (ssp. *aduncus*) is fertile when growing on trees in British Columbia (Schofield 1968). *Anastrophyllum joergensenii*, *Mastigophora woodsii* and *Scapania nimbosa* have never been seen with reproductive structures (Hill, Preston & Smith 1991).

Apart from *Pleurozia purpurea*, all 16 species are dioecious.

(The species which have never been seen with sexual structures are presumed to be dioecious because all other species in the genus or sub-genus are (Smith 1990).) Many populations appear to be unisexual. All the British and Irish plants of *Adelanthus lindenbergianus, Bazzania pearsonii, Herbertus aduncus, Plagiochila spinulosa* and *Scapania ornithopodioides* are apparently female, and all our *Plagiochila carringtonii* plants are apparently male (they are all female in the Himalayas) (Hill, Preston & Smith 1991). Most bryophytes which do not produce sporophytes are dioecious (Longton 1990). Dioecious species are usually long-lived perennials occupying stable habitats. Failure to produce sporophytes is also associated with disjunct distributions and lack of sub-species or variants over the world, and liverworts which do not reproduce sexually are especially common in regions affected by Pleistocene glaciations (Douin 1904, Nicholson 1930, Longton 1990).

2.5.2. Vegetative spread

Asexual spread in liverworts is almost always by specialised structures such as gemmae, deciduous leaves or branches and very rarely by fragmentation of the gametophyte (Schuster 1983). *Anastrepta orcadensis, Mylia taylorii* and *Scapania gracilis* frequently have gemmae and *Scapania ornithopodioides* occasionally has them. The gemmae of *A.orcadensis*, *M. taylorii*, *S.gracilis* and *S.ornithopodioides* are 1-2-celled structures less than 30um long. Those of *M.taylorii* are up to

70um long (Smith 1990). It is possible that gemmae of this size could disperse over long distances. The leaves of *Plagiochila spinulosa* fall off easily and may grow into new plants (Smith 1990; Hill, Preston & Smith 1991). The two *Bazzania* species have deciduous flagelliform branches which probably function as vegetative propagules (Smith 1990). None of the other hepatic mat species have specialised structures for vegetative propagation. Mosses commonly regenerate from shoot-tips with leaves, but liverworts only occasionally do so (Miller & Ambrose 1976).

2.5.3. Sexual populations

Even when bryophytes do produce spores or gemmae, long-distance migration is difficult. New sexual populations can only become established when the parent population is bisexual and plants of different sexes are close enough (within about 30cm) for fertilisation to occur. Spatial separation of the sexes has been shown to cause failure to produce sporophytes (Longton 1990). Spores must be transported to a suitable climatic region and fall in an unoccupied niche. Spores of different sexes must land in the same area, otherwise the plants will be able to spread only by clonal growth. This may be why so many British populations are apparently of just one sex. These populations could represent clonal growth continuing over thousands of years. Such growth could maintain populations indefinitely, providing that the environment never exceeded critical limits of temperature and humidity (Schuster 1983). If plants of both sexes become established, environmental conditions must allow both male and female plants to grow and produce gametes and, again, plants of different sexes must grow close enough to fertilise each other. It is possible that some populations in the British Isles are single-sex because one sex has become extinct. In America there is some evidence that the Pleistocene glaciations depleted the populations of some species so much that present populations derive from surviving female individuals (Longton 1992).

It is quite likely that environmental factors affect the expression of sexuality. It is well-known that plants have a temperature range in which they can survive, a narrower one in which they can grow and a still narrower one in which they reproduce (Begon, Harper & Townsend 1986). The current climate may be unfavourable for the development of gametes of either or both sexes of the hepatic mat species. It has been shown in some bryophytes that archegonia will develop at lower temperatures than antheridia (Longton 1990). Longton (1990) has shown that the colder the climate the smaller the proportion of the bryophyte flora that produces sporophytes. Sporophyte production also declines towards the edge of a species' geographical range. In some species, such as the moss *Polytrichum alpestre*, antheridia are produced only in exceptionally warm conditions. Even when fertilisation occurs the developing sporophytes are commonly killed by frost in some sensitive species (Longton 1990). There is some evidence that day-length affects gametophyte production but this has not been tested on the hepatic mat plants (Longton 1992). However it is possible that modern British conditions are not suitable for sporophyte production in these species. Observations of hepatic mat species suggest that environmental variation influences sexual reproduction. In British Columbia *Herbertus aduncus*, which is sterile in Europe, grows on cliffs, among boulders, in bogs and fens and as an epiphyte on trees, but is fertile only on trees (Schofield 1968, Schuster 1983). The single instance of *Anastrophyllum donnianum* producing capsules in Britain was in the eastern Highlands (RBG), where the summers are warmer and the winters cooler than they are in the west (Climatological Atlas 1952, Meteorological Office 1975). The observation was made in the 1920s, when the climate was somewhat warmer than it is today (Sharrock 1976). *Mylia taylorii* rarely produces capsules (see above), but material collected in the field and cultivated indoors (where temperatures varied between 5°C and 33°C) did so (Hobbs 1990).

There is always the possibility that fertile plants have been overlooked. Archegonia and antheridia are small and only obvious when the plants are examined closely. The plants may reproduce at times of the year when bryologists do not often go out collecting. The oceanic moss *Campylopus setifolius* has only once been reliably recorded with capsules. They were seen on Christmas Day 1989 on the northern slopes of Cader Idris in Wales. The capsules were buried in the moss cushion and were only discovered when the specimen was closely examined (A. B. G. Averis, pers.comm). Gemmae are said to be rare in *Scapania ornithopodioides* (Smith 1990), yet plants collected for my experimental work in February were producing them abundantly. There is evidence that bryophytes have two peaks of growth during the year: in spring and autumn (Slack 1990) when the shade from vascular plants is reduced. Bryophytes can photosynthesise at low temperatures and low light intensities (Russell 1990), which is why they dominate late snow-bed vegetation. My experience is that most of the hepatic mat species are more obviously growing, with fresh green shoots, in spring and autumn than they are in summer. If the plants are most active at these times of year, it is possible that sporophytes are produced then.

2.5.4. Recent spread

Occurrence on temporary or recently-formed substrates can give some idea of the species' potential for spread. In the British Isles, *Bazzania tricrenata*, *Herbertus aduncus*, *Lepidozia pearsonii*, *Mastigophora woodsii*, *Mylia taylorii*, *Scapania gracilis*, *S. ornithopodioides* and *Plagiochila spinulosa* have been recorded growing in large clumps on the lower parts of the trunks and on fallen branches of *Betula pubescens* and *Quercus petraea*. All the hepatic mat species regularly grow on the lower stems of *Calluna vulgaris*, and *Pleurozia purpurea* grows on *Juniperus communis* in Norway (personal observation). This may be growth from cushions on the ground rather than direct establishment on the trees, but it shows that the liverworts do spread vegetatively within the lifespans of these woody species. *Anastrepta orcadensis*, *Anastrophyllum joergensenii*, *Scapania ornithopodioides*, *Bazzania pearsonii*, *B.tricrenata*, *Mastigophora woodsii* and *Pleurozia purpurea* grow on logs in Bhutan (Long & Grolle 1990) and *B.pearsonii* and *P.purpurea* grow on logs in British Columbia (Schofield 1968). Logs are not a permanent habitat, which suggests that the plants must be able to colonise new sites fairly readily, even if they do not reproduce sexually.

Anastrepta orcadensis (which produces gemmae) and *Bazzania tricrenata* have been seen colonising disturbed ground on roadsides (D. G. Long pers. comm.) and *Herbertus aduncus* has been recorded on a stone wall in Inverness-shire (A. B. G. Averis, pers. comm.), showing that dispersal over short distances is possible even with species which do not produce spores or gemmae. In these instances, however, it is possible (though unlikely) that the plants were already growing on the rocks which were used to build the wall or roadside verge.

2.6. Origin and history of the hepatic mat species

2.6.1. Origins of the species

Most of the hepatic mat species belong to genera which are best represented in the Tropics. This suggests that wherever the genera originated, it was in a tropical climate that they diversified most (Cox & Moore 1985). Some species have migrated to other parts of the world (e.g. Nicholson 1930, Greig-Smith 1950, Schofield 1988b) (table 2.9).

Some bryophytes which are disjunct in Pacific North America (for example *Scapania ornithopodioides* and *Pleurozia purpurea*) have also been found in parts of eastern Asia such as Japan, Taiwan and the Phillipines. The sub-species of *Herbertus aduncus* in Taiwan is the same as that in north-west north America. The Aleutian Islands are a possible migration route between the two continents (Sharp 1972). *Anastrepta orcadensis* grows on the islands and in north-west America, Japan and Taiwan (Hill, Preston & Smith 1991).

Nicholson (1930) and Schofield (1988b) suggested that the hepatic mat species are of ancient origin because in general they lack sporophytes, are confined to undisturbed habitats and grow in a wide range of habitats. It is not clear why these characteristics indicate great age. Species which do not reproduce sexually are likely to succeed only in relatively stable environments (because they lack the potential for rapid change in response to a changing environment), but the lack of evidence for reproduction this century does not imply that the plants have never been able to do so. Dioecism is, however, regarded as a primitive feature in bryophytes (Schuster 1981). Not all species of stable habitats are ancient. One of the most rapidly-evolving families of liverworts, the Lejeuneaceae, are mostly species

Table 2.9. Number of species and world distributions (excluding British Isles, Atlantic Europe, Faroes, British Columbia, Alaska and the Himalayas) of the hepatic mat genera.

Genus	known number of species	Distribution
Anastrophyllum	25-30	Tropical montane rainforests
Pleurozia	15	Tropical montane rainforests, mainly southern hemisphere
Herbertus	100	Montane tropical islands and unglaciated parts of continents Mainly southern hemisphere
Bazzania	250	Montane tropics & southern hemisphere
Lepidozia	150	Tropics, sub-tropics, antipodes
Adelanthus	?	Montane tropics in southern hemisphere
Mastigophora	10	Montane tropics, mainly antipodes
Scapania	60	Northern hemisphere extending into tropics
Plagiochila	1200-1300	Cosmopolitan, many montane - tropical & southern hemisphere
Anastrepta	1	Eurasia
Mylia	4	Eurasia

Sources: Hill, Preston & Smith (1991), Smith (1990), Greig-Smith (1950), *Crundwell (1970).*

of tropical forests (Smith 1990): one of the most stable environments on the earth (although some of the species grow on the leaves of forest trees). Neither does occurrence in many types of habitat indicate great age: it depends on how similar the micro-habitats are. The hepatic mat species (and other oceanic bryophytes) certainly exist in a variety of habitats from cloud forests in the tropics to boulder-fields near the summits of mountains in temperate regions. All these habitats have in common freedom from drought and from large fluctuations in temperature. At the scale perceived by the plants themselves the differences observed by us may not be very great. It has been shown, for instance, that the radiation climate of steep, north-facing rocky slopes is remarkably similar to that of woodland (Proctor 1980b). A *Calluna vulgaris* heath on a Scottish hillside may produce the same microclimate through ameliorating the general climate of the region as a *Tsuga heterophylla* forest in British Columbia, and a blanket of snow may provide similar conditions in the corries of the Cairngorm mountains.

The tropical affinities of the hepatic mat species are the best indicator of an ancient origin, suggesting that they evolved long ago when all the continents were closer to the equator and the climate was hotter. It also seems that the modern populations have been genetically isolated for a long time. Plants in widely - separated populations are morphologically distinct; so much so that *Herbertus aduncus* and *Plagiochila carringtonii* have each evolved into two or more sub-species (Hill, Preston & Smith 1991). This suggests that they have been capable of sexual reproduction since the original populations became fragmented, although they have been separated long enough for somatic mutations also to occur. As far as I know the genetic differences between the sub-species have not been quantified.

2.6.2. History of current distribution

Disjunct distributions have interested biologists since the early 19th century, as knowledge of the world and its biota increased. In the early days there were arguments about whether disjunct populations were the result of separate creations, or of migration by individuals of a single population (Vincent 1990). There has been much modern speculation (e.g. Greig-Smith 1950, Richards 1957, Ratcliffe 1968, Schofield 1984; 1988a; 1988b; 1989) which has resolved into two possible explanations for the current distribution of the species - long-distance dispersal between areas with a suitable environment or survival since a time when their distribution was continuous between their current localities.

Direct migration depends on having spores or propagules such as gemmae and a method of dispersal. Of the hepatic mat species with disjunct distributions, only *Herbertus aduncus* and *Anastrophyllum donnianum* are known to produce spores anywhere in the world and only *Anastrepta orcadensis* and *Scapania ornithopodioides* have gemmae. Direct migration between north-west America, north-west Europe and south-east Asia is hard to imagine, but cannot be ruled out. The spores or propagules could be carried by winds or by birds (Watson 1971). Moss spores have been known to travel 1000km. Species of *Tortula* and *Funaria* colonised a new volcanic crater in Antarctica within nine months of the eruption (Vincent 1990). However, liverwort spores are notoriously short-lived and probably could not survive the freezing, desiccating, brightly-lit conditions of air currents in the upper atmosphere (Watson 1971). If such long-distance dispersal was easy and regular, the distinctive floras of parts of the world might not have developed so markedly (Sharp 1972). The coincidence of so many species with similar disjunct world distributions makes chance dispersal between these areas unlikely, particularly over such vast distances (Watson 1971, Schuster 1983, Schofield 1988b).

The hepatic mat species belong to a larger group of species with similar disjunct distributions. About 7% of the hepatic flora of Pacific North America is disjunct between there and Atlantic Europe; most of these species are confined to the hyperoceanic climate of the western seaboard (Schofield 1984). About 14% of the hepatic flora of Bhutan has a disjunct distribution (Long & Grolle 1990). The disjunct species in Pacific North America do not often produce gemmae and more are dioecious than might be expected, suggesting that they do not often spread by long-distance dispersal (Schofield 1984) and that they evolved along with the forest vegetation with which they are associated (Schuster 1981).

If long-distance dispersal is an unlikely reason for the current distribution of these species, the plants must once have been much more widespread, even if discontinuously distributed, in the temperate and sub-tropical parts of the northern hemisphere. There are no fossil records of the hepatic mat liverworts, but genera of mosses with similar disjunct modern distributions have been found in Pliocene (late Tertiary) deposits in the western Caucasus, where they no longer occur (Dickson 1973). The earliest fossils of leafy liverworts are from Upper Jurassic and Lower Cretaceous deposits (Schuster 1981). There is good fossil evidence that genera of the Jungermanniales, identical to modern ones, existed in the Tertiary period (Schofield 1988b).

The former distribution of the hepatic mat species and their movements before and during the Pleistocene Epoch can be tentatively inferred from what is known about the climate and vascular flora in those days. Table 2.10 shows the relevant geological sequences and their approximate duration.

At the beginning of the Tertiary Period, 65 million years ago, there were two large continents in the Northern Hemisphere. One corresponded to Europe and eastern north America, the other to Asia and western North America. The two continents were separated by shallow seas and the flora of the entire area was apparently continuous (Schofield 1988b,

Table 2.10. Diagram to show the chronology of the Tertiary and Quaternary Periods.

Period	Age (m.y.a.)	Epoch		Comments
QUATERNARY	0.01	HOLOCENE		Post-glacial stage
	0.10	UPPER PLEISTOCENE		
	0.30	MIDDLE PLEISTOCENE		Oceanic flora in inter-glacial stage in Ireland
	1.80	LOWER PLEISTOCENE		
TERTIARY	5.00	PLIOCENE)	Neogene	Oceanic climate in NW Europe and NW America
	22.50	MIOCENE)		
	37.50	OLIGOCENE)	Palaeogene	Warm temperate climate in N hemisphere
	55.00	EOCENE)		
	65.00	PALAOCENE)		Humid tropical climate in N hemisphere

Time not drawn to scale. Source: Vincent (1990).

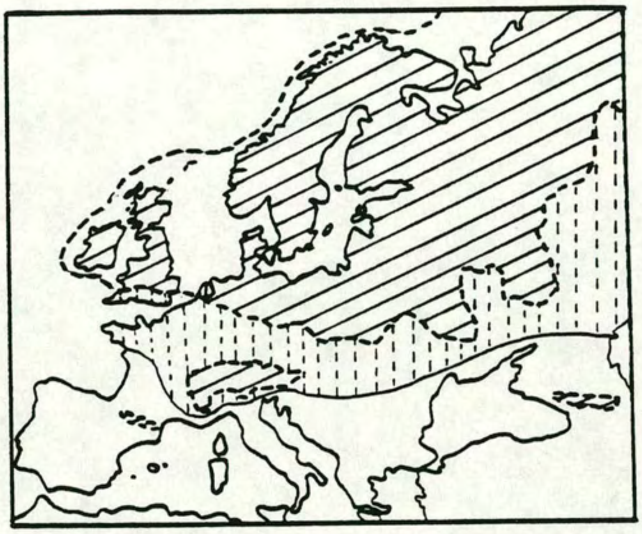
Vincent 1990), particularly in the north where the water barriers were narrow (Schuster 1983). In the early Tertiary period the Atlantic ocean began to form, although there were land bridges between America and Europe via Greenland until about 50 million years ago. At the beginning of the Tertiary period the southern parts of the British Isles were about 40°N and had a warm, wet climate (Vincent 1990).

It is unlikely that the climate was stable during the 60 million years of the Tertiary Period. There were probably fluctuations much as there have been since the end of the Pleistocene. It is possible (though still disputed) that the cooling of the world started after the collision of the Indian and Asian continental plates 50 million years ago. The theory is that the uplift of the Tibetan plateau caused changes in air circulation which led to the establishment of monsoon rainfall and a lowering of the temperature in the north of the northern hemisphere (Paterson 1993). It is thought that by the end of the Tertiary period, 5 million years ago, the continents of the northern hemisphere had moved about 10° further north and that there was an oceanic climate in north-west Europe (Vincent 1990). This probably extended all around the Pole at high latitudes, adjacent to the Arctic Ocean (Schuster 1983). Atlantic weather patterns would have been established and temperatures would have been similar to today, although rainfall would have been higher (Vincent 1990). Temperate forests would probably have extended to at least 60° or 70° north (Schuster 1983) and there was certainly an oceanic vascular flora in south-east Ireland at this time, with species of *Erica*, *Rhododendron*, *Betula*, *Ilex* and *Tsuga* (Vincent 1990). This suggests that conditions would have been suitable for hepatic mat species.

It is possible that the hepatic mat liverworts and other oceanic bryophytes have grown continuously in their modern locations in British Columbia and the Himalayan foothills since Tertiary times. These areas were never completely covered by ice during the Pleistocene glaciations (Horton 1982; Schofield 1984, 1988a, 1989; Gansser 1983). The hepatic mat species and other oceanic bryophytes in these places are associated with a vascular flora similar to that which was apparently widespread in the northern hemisphere in late Tertiary times: mixed coniferous and deciduous forests dominated by *Tsuga* species. (*Tsuga* died out in Europe in the Pastonian (Middle Pleistocene) glacial stage about 0.3 million years ago (Vincent 1990).)

It seems likely that the hepatic mat species were widespread in the northern hemisphere before the climatic fluctuations of the Pleistocene and survived in their original locations in unglaciated areas. But what happened to the populations in north-west Europe? There is no doubt that most if not all of the present upland habitats of the hepatic mat species in the British Isles, western Norway and the Faroes were completely covered by ice at some time during the Pleistocene glacial stages (Richards 1957, Ratcliffe 1968, Crundwell 1970). Some coastal mountains in western Norway were apparently free of ice during the last glacial advance and there may have been similar but very narrow unglaciated zones in the extreme west of Scotland and Ireland (Vincent 1990). There was also possibly some ice-free land west of the British Isles and Faroe Islands. The absence of foreign erratics and the radial patterns of glacial striae suggest that the Faroe Islands had their own ice-cap during the last glaciation (Johansen 1985). They may not have been completely covered with ice and some animals evidently survived close to their current localities as they have no means of reaching an island otherwise (Bocher 1940). However the paucity of the vascular flora and the fauna of Ireland compared with Great Britain, and of Great Britain compared with mainland Europe, suggests that post-glacial migration was from the south and east rather than the west. The hepatic mat species probably migrated into Ireland, Britain, the Faroes and Norway from a refuge in the south during the last 10,000 years. Richards (1957) considered that this refuge was the Mediterranean zone between Macaronesia and the Caucasus (fig.2.4), as Central Europe was probably underlain by continuous permafrost at the maximum of the last glaciation and the climate would have been cold and continental (Karte 1987). In Southern Europe a few small areas in Spain, Portugal, Italy and North Africa have a locally high rainfall and populations of oceanic bryophytes (Richards 1957, Ratcliffe 1968). These populations could be relicts from a time when the general climate of the region was suitable for oceanic species (Richards 1957).

Figure 2.4. Southern refugia for the hepatic mat species during the glacial stages of the Pleistocene.



---- Maximum extent of ice in Europe
///// Covered by ice
|||||| Permafrost tundra and forest
Milder regions where oceanic species might have survived.

Redrawn from maps in West (1968).

The colder, drier stages and successive advances of ice during the Pleistocene would have fragmented the ranges of the hepatic mat and other oceanic species. However they would probably have moved north again whenever there was an interglacial period with a temperate oceanic climate. Fossils of *Rhododendron ponticum, Erica ciliaris, E.mackaiana, Daboecia cantabrica* and *Hymenophyllum* species, together with the oceanic moss *Hyocomium armoricum*, have been discovered at Gort in County Galway, western Ireland (Dickson 1973, Vincent 1990), suggesting that there was an oceanic flora there during the second to last interglacial stage, about 150,000 years ago. The presence today of hepatic mats in places which were completely covered by ice until about 10,000 years ago shows that the species are capable of recolonising during inter-glacial stages.

Could any hepatic mat species have survived the last glaciation in the British Isles? Many of them grow today in snow-beds in the Cairngorms, in conditions similar to those at the edge of permanent ice. It is possible that the species could have survived the ice age in such habitats in the unglaciated south of England (Ratcliffe 1968). *Scapania gracilis* and *Plagiochila spinulosa* occur in Kent and Sussex, in south-east England, and may have been there continuously since before the last glacial advance. However Greig-Smith (1950) thought that this was unlikely and that climatic fluctuations since the Pleistocene were sufficient to have limited the modern ranges of the plants.

The most likely periods for an expansion of range since the last glaciation are those when the climate was more oceanic with an increase in precipitation: about 7300, 6200-5800, 4200-3900 and 3300 years ago (Birks 1988). Flandrian deposits from Fort William, Scotland, from between 6500 and 9000 years ago (Dickson 1973, Vincent 1990), include the oceanic mosses *Dicranum scottianum* and *Hyocomium armoricum*. These periods of recolonisation would have been interspersed with less favourable times, when the species would have died out in dry areas with extremes of temperature (such as the Mediterranean region and eastern Europe), leaving isolated populations in places where the climate was still locally suitable (Richards 1957). Even within the British Isles, the populations of hepatic mat species in snowbeds in the Cairngorm mountains show that suitable conditions still obtain on a small scale where the general climate of an area is unfavourable (Ratcliffe 1968). Likewise the small populations in the mountains of north-west England and north Wales are probably relicts from a time when the species were more widespread at these latitudes. Bryophytes have the advantage that they are small plants which can survive in small areas of suitable habitat (Richards 1957, Schofield 1989).

The species must have had some means of long-distance dispersal during the last 10,000 years. The Faroe islands have a rich flora of oceanic bryophytes, including six of the hepatic mat species, but have not been connected to the mainland of Europe since the last glaciation (Johansen 1985).

The periods with an oceanic climate in which the hepatic mat and other oceanic species are supposed to have expanded their ranges all occurred after the British Isles were separated from Europe by the English Channel about 8,300 years ago. This means either that the species were capable of dispersing by spores or by vegetative propagules from continental refugia or that they were already in Britain by this time. Gemmae and fragments of gametophyte would probably have been effective for dispersal over short distances and may have been sufficient to maintain populations that were already large and extensive.

During the latest (Flandrian) interglacial stage the hepatic mat species have reached the north of the British Isles, Norway and the Faroe Islands. The peculiar absence of some of the species from apparently suitable sites is probably a result of patchy and incomplete re-establishment (Ratcliffe 1968, Crundwell 1970) as well as of local extinction. Although the species grow together and presumably have similar ecological requirements, they may have different methods of establishment and may need different conditions for sexual reproduction. Their distribution in the British Isles is studied in Chapter 3.

CHAPTER THREE

DISTRIBUTION AND VARIATION IN SPECIES COMPOSITION OF THE HEPATIC MAT IN THE BRITISH ISLES.

3.1 Introduction

Macvicar (1910), McVean and Ratcliffe (1962), Ratcliffe (1968) and Hobbs (1988) suggested that the hepatic mat community is confined to mountains in the most oceanic parts of the British Isles, where the temperature range is low and rainfall is high and evenly distributed. In the British Isles such habitats are restricted to Scotland, the English Lake District, North Wales and the west of Ireland.

Ratcliffe (1968) mapped 55 locations of the hepatic mat (by 10km square) in Scotland and 33 in Ireland. The Nature Conservancy Council's Upland Vegetation Survey (UVS) mapped the distribution of hepatic-rich *Calluna vulgaris* heaths on the set of upland areas (most of which are Sites of Special Scientific Interest (SSSI)) surveyed since 1981 (Hobbs 1988, Hobbs & Sydes 1988). Although the hepatic mat community seems to be most common in damp *Calluna vulgaris* heaths above the tree-line (Ratcliffe 1968, Hobbs 1988, Rodwell 1991b), McVean & Ratcliffe (1962) and Birks (1973) also found hepatic mats with some of the same species in *Pinus sylvestris* woodland, *Juniperus communis* ssp *nana* scrub, *Racomitrium* - rich dwarf *Calluna* heath and *Vaccinium* - *Empetrum* heath.

Proctor (1967) analysed the distribution of British liverworts based on the Census Catalogues of mosses and liverworts in Britain, which preceded the Atlas edited by Hill, Preston & Smith (1991). Ratcliffe (1968) included a study of the hepatic mat in his paper on the ecology of Atlantic bryophytes in the British Isles. However since the late 1960s there have been many new records of the hepatic mat species, and patterns of distribution are now better known (Hill, Preston & Smith 1991, Averis 1991).

The purpose of this chapter was to relate the distribution and variation of the hepatic mat community to the environment over its range in the British Isles. This was done in two ways. The first was a study of the potential distribution of the hepatic mat community based on the relationships between climate and topography and the number of the constituent species. The second was an study of variation in the habitats and species composition of known examples of the community.

3.2 Methods

3.2.1 The potential distribution of the community

The number of recorded hepatic mat species was summarised for each of 488 upland 10km squares in the Scottish Highlands, Galloway, the Lake District, North Wales and western Ireland using Hill, Preston & Smith (1991) and Averis (1991) supplemented by my own records. Upland squares are those containing mountains or moorland and associated semi-natural vegetation. Regions with few or no records of hepatic mat species (such as south-west England and the North York Moors) were excluded.

The number of species in each square was compared with values of climatic elements likely to be important for bryophyte distribution on a national scale. The annual number of wet days (days with >1mm of rain) (Ratcliffe 1968), highest and lowest annual rainfall (mm) (Meteorological Office 1977) and mean monthly temperatures (°C) in February and July (Meteorological Office 1975) were determined for each 10km square. Sea-level temperatures were adjusted for altitude by calculating the lapse-rate for the mid-altitude of each 10km square (formulae in Meteorological Office 1975). Temperature range and rainfall range (highest minus lowest values) were calculated from the data. The 10km grid was superimposed on maps of temperature, wet-days and rainfall and the values for each square were estimated. This can be done reasonably accurately because climatic gradients are steep in the west of the country and the isotherms and isohyets are close together.

The highest and lowest altitude (metres ASL), area of dry land (% of square) and number and area (km^2) of north-facing slopes were recorded from the Ordnance Survey 1:50 000 maps.

The relationship between the number of species and the environmental values in each square was analysed by stepwise multiple regression using the SPSS-X statistical package (SPSS Inc, 1988). The number of species was log-transformed (log(n+1)) for the analysis because the large number of squares with no records distorted the distribution of the residuals.

3.2.2 Hepatic mats found by the Upland Vegetation Survey

The boundaries of stands of heath with hepatic mats recorded by the UVS (1981-89) were transferred from aerial photographs onto Ordnance Survey maps at the same scale (1:25 000). The area (ha), altitudinal range (m), aspect (degrees East of North) and slope (degrees from horizontal) of each stand were measured. Maximum summer and minimum winter temperatures were calculated for each stand using the data and lapse rates in Meteorological Office (1975).

3.2.3 Sampling the hepatic mat community

A range of sites was selected to study variation in species composition of the hepatic mat community. Sites were chosen to cover the British range of the community from western Ireland to north-west Scotland. Some were included because they were remote and under-recorded (e.g. Ladhar Bheinn in Knoydart and Ben Breen in Connemara), others where there seemed to be gaps in the known distribution of the community (e.g. Islay and Stob Gabhar). The sites in England and Wales were chosen in areas with high rainfall and rugged topography.

The northern and eastern slopes of these sites were visited and searched for one day. All vascular plants, bryophytes and lichens (except saxicolous and corticolous species) were recorded. Clumps of the hepatic mat community were sampled by 25cm x 25cm quadrat to ensure a thorough search of the vegetation and to give an estimate of the relative abundance of the species in the richer patches of the community. As the community forms discontinuous patches rather than unbroken sheets the quadrats were taken selectively rather than randomly. All species growing in each quadrat were recorded. The surrounding vegetation was classified into one of the sub-communities of the National Vegetation Classification (NVC) (Rodwell 1991a, 1991b, 1992). Altitude, aspect and geology were recorded at each site. Details such as the presence of boulders, open water, signs of management and use by herbivores were also noted. Data for temperature and rainfall were taken from Meteorological Office (1975, 1977) and for wet days from Ratcliffe (1968). Values for temperature were corrected for the altitude of the stand (see above).

3.3 Results.

3.3.1 The potential distribution of the community

The 488 10km squares encompassed the entire range of all the

Northern Atlantic members of the hepatic mat in the British Isles except for *Pleurozia purpurea* and *Lepidozia pearsonii* together with a large proportion of the ranges of the more widespread oceanic species, most of which also occur in woodlands and lowland habitats (table 3.1)

The distribution map (fig.3.1) of all 16 hepatic mat species combined shows a scatter of squares, largely because of the wide ranges of those species whose distribution is not strictly Atlantic. The map of the Northern Atlantic members of the community (fig.3.2) shows a more restricted distribution. 36 of the richest squares for the Northern Atlantic species (8-10 spp.) are in Scotland; there are three in Ireland. There are 14 squares in Ireland and one in Wales in the second richest category (5-7 spp.), but none in Galloway or the Lake District.

The stepwise multiple regression analysis of the relationship between the number of hepatic mat species and their environment suggested that the highest numbers of species tend to be in squares with high rainfall, low temperature range and a large number of north-facing slopes (table 3.2).

The distribution of the 11 Northern Atlantic members of the hepatic mat fits better with the known distribution of the community (fig.3.3). A similar stepwise multiple regression of these species and the environment in the British Isles gave slightly different results (Table 3.3), showing that the

Table 3.1. Proportion of the range of hepatic mat liverworts included in the 10km squares of the Ordnance Survey National Grid selected for analysis.

Region	No.of squares with hepatic mat species recorded	No.of squares sampled	% of range sampled
HIGHLANDS	436	344	78.9
GALLOWAY	15	11	73.3
LAKE DISTRICT	37	26	70.3
NORTH WALES	41	33	80.5
IRELAND	271	75	27.7
Total	800	488	61.0

Source: Hill, Preston & Smith 1991.

Table 3.2 Stepwise multiple regression analysis of the relationship between the number of hepatic mat liverworts in a 10km square and their climate and topography.

	regression coefficient	t	p
Intercept	0.923		
highest rainfall (mm)	0.030	9.6	<0.00001
temperature range (°C)	-0.057	-6.1	<0.00001
no. of N-facing slopes	0.011	2.7	<0.0066

R^2 = 0.340, n = 488. Dependent variable log-transformed (log(n+1)).

Sources of data:

Highest *annual rainfall* (mm) - *Meteorological Office 1977*
Temperature range (°C) - *mean monthly temperature in July minus mean monthly temperature in February (Meteorological Office 1975). Sea-level temperatures adjusted for altitude by calculating lapse-rate for mid-altitude of each 10km square (formulae in Meteorological Office 1975).*
Number of north-facing slopes - Ordnance Survey 1:50 000 sheets.

Figure 3.1 Total number of hepatic mat species in 10km squares in the uplands of Britain and Ireland.

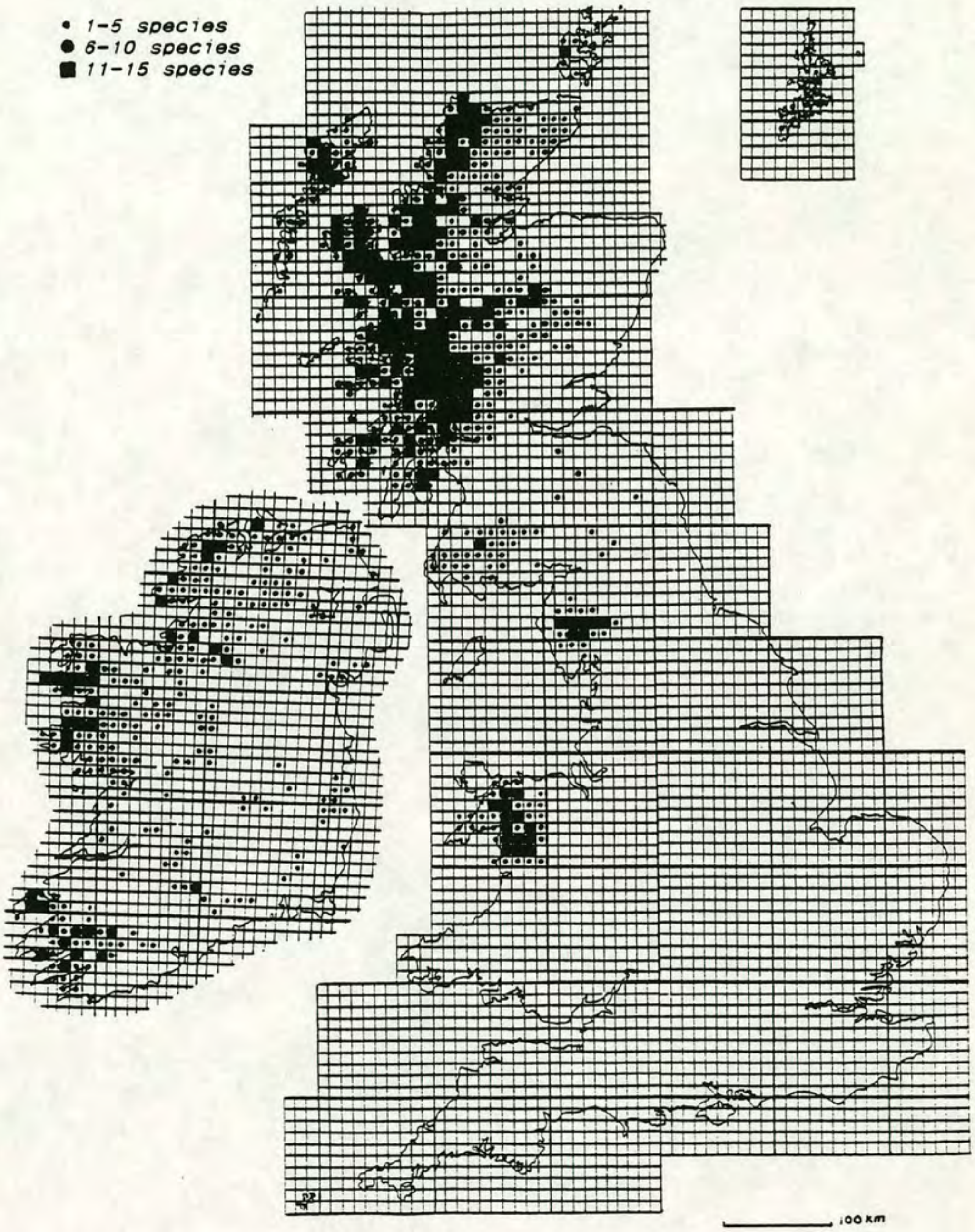


Figure 3.2 Total number of hepatic mat species with a Northern Atlantic distribution in 10km squares in the uplands of Britain and Ireland

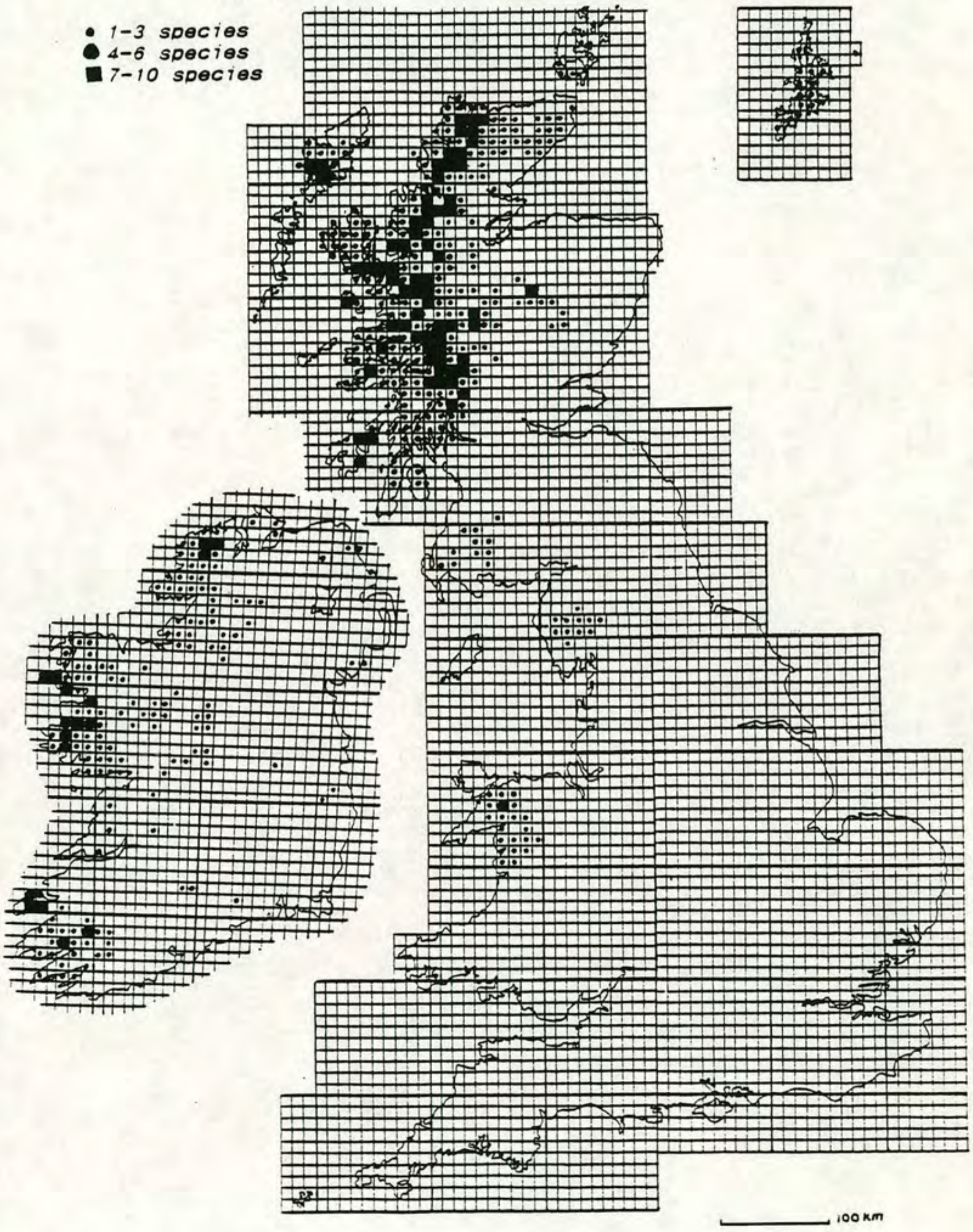
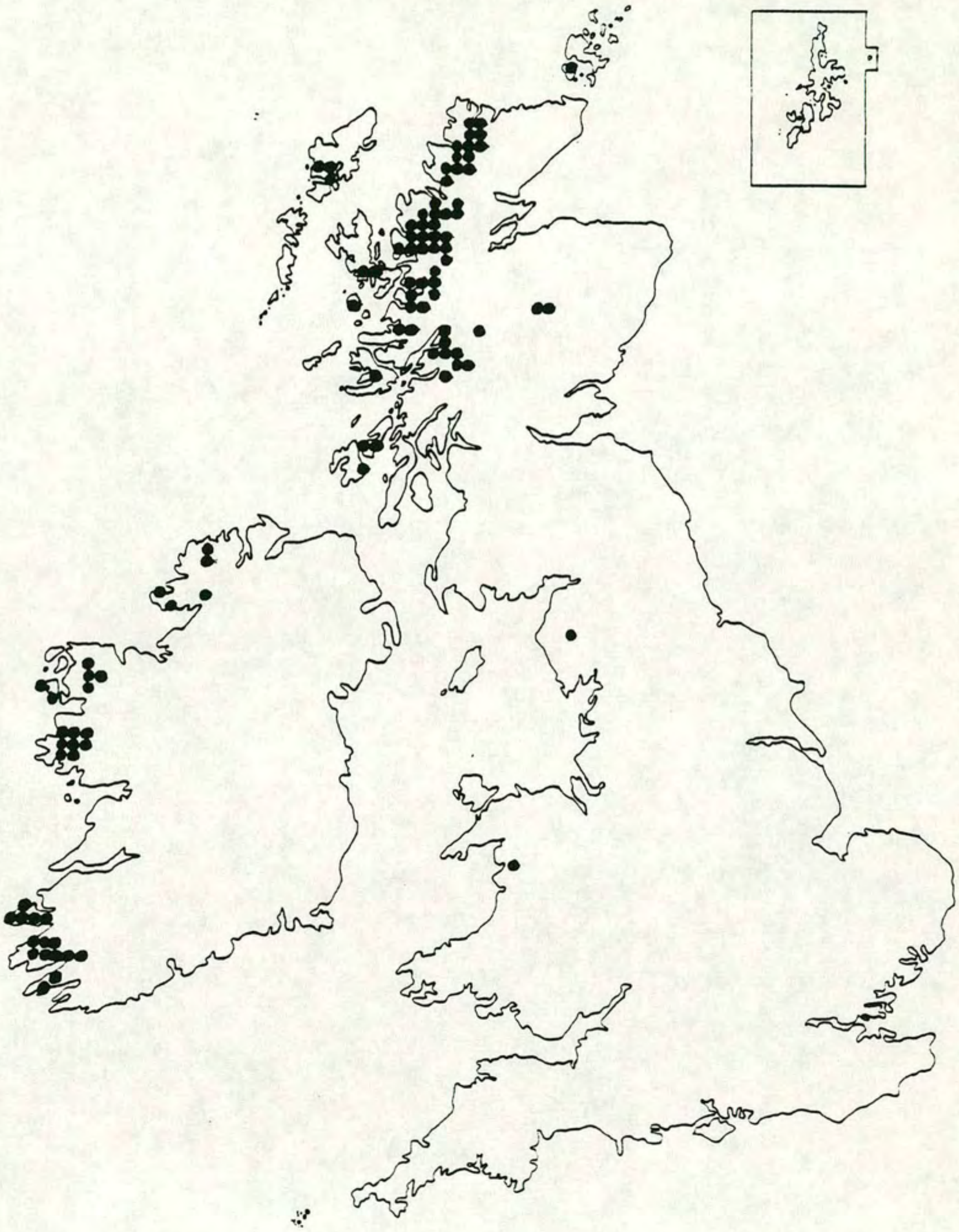


Figure 3.3 Known distribution by 10km square of the Atlantic hepatic mat community in Britain and Ireland



Sources: Ratcliffe (1968), Upland Vegetation Survey (NCC) 1981-1989, A. M. & A. B. G. Averis 1989 - 1993.

Table 3.3 Stepwise multiple regression analysis of the relationship between the number of Northern Atlantic liverworts of the hepatic mat community in a 10km square and climate and topography.

	regression coefficient	t	p
Intercept	0.004		
Highest annual rainfall (mm)	0.013	4.706	<0.00001
Temperature range (°C)	-0.525	-5.178	<0.00001
Number of N-facing slopes	0.016	4.749	<0.00001
Number of wet days a year	0.0036	4.736	<0.00001

R^2 = 0.447. n = 488. Data log-transformed (log(n+1)).

Highest annual rainfall **(mm)** - *Meteorological Office 1977*
Temperature range (°C) - *mean monthly temperature in July minus mean monthly temperature in February (Meteorological Office 1975). Sea-level temperatures adjusted for altitude by calculating lapse-rate for mid-altitude of each 10km square (formulae in Meteorological Office 1975).*
Number of wet days (>1mm) (Ratcliffe 1968)
Number of north-facing slopes - Ordnance Survey 1:50 000 sheets.

Table 3.4 The area (in hectares) of Calluna vulgaris *heath with the hepatic mat community on 17 sites in the west Highlands of Scotland.*

SITE	No of stands	Total area (ha)	Mean area of stand (ha) (standard error)
North Hoy	1	10.0	10.0
North Harris	17	84.4	5.0 (1.2)
Foinaven	7	108.8	15.5 (9.7)
Ben More Assynt	1	6.3	6.3
An Teallach	3	25.1	8.4 (4.3)
Fannich Hills	2	3.2	1.6
Letterewe/Fisherfield	4	14.5	3.6 (1.9)
Beinn Eighe/Liathach	9	184.4	20.5 (11.6
Beinn Dearg (Flowerdale)	4	33.1	8.3 (0.9)
Beinn Alligin	4	63.7	15.9 (7.1)
Monar Forest	1	1.9	1.9
Beinn Bhan	3	15.6	5.2 (2.7)
Glas Cnoc	1	0.6	0.6
Cuillin	2	6.3	3.1 (0.6)
Mam na Gualainn	1	0.6	0.6
Ben Nevis	1	0.6	0.6
Beinn an Oir (Jura)	1	50.0	50.0

Total mapped area of hepatic-rich heath 609.1ha
Mean number of stands on site 3.65 (SE=*1.00*)
Mean area of hepatic-rich heath on site 35.83ha (SE=*12.15*)

Source: NCC Upland Vegetation Survey unpublished maps.

number of wet days a year was also a predictor of high numbers of these species.

3.3.2 Hepatic mats found by the Upland Vegetation Survey

The Upland Vegetation Survey (UVS) found the hepatic mat community in damp *Calluna vulgaris* heaths on 17 (14.2%) out of 120 upland SSSI and other mountain areas surveyed between 1981 and 1989 in Scotland (Fig.3.4). The 17 sites were all in the north and west of Scotland. Sixty-two individual stands were mapped.

The number of separate stands on a site ranged from 1 to 17, with an average of 3.65 (table 3.4). The total measured area of heathland with the hepatic mat community on the 17 sites was 609.1 ha, with an average of 35.8 ha on a site. The community tended to occur as small patches rather than large expanses. Most stands were smaller than 10ha, and almost all covered 50ha or less. Only one stand, on Liathach in West Ross, was over 100ha.

The altitudinal range of the hepatic mat community in *Calluna* heaths mapped by the UVS was from a few metres above sea-level on North Harris to 762m on An Teallach. The most frequent lowest altitude was between 300 and 400m and the most frequent highest altitude was between 500 and 600m (fig. 3.5). In common with other types of vegetation and many plant species, there was a marked altitudinal descent towards

Figure 3.4 Upland areas surveyed by the Upland Vegetation Survey 1981 - 1989 (a) and those where the hepatic mat community was recorded (b).

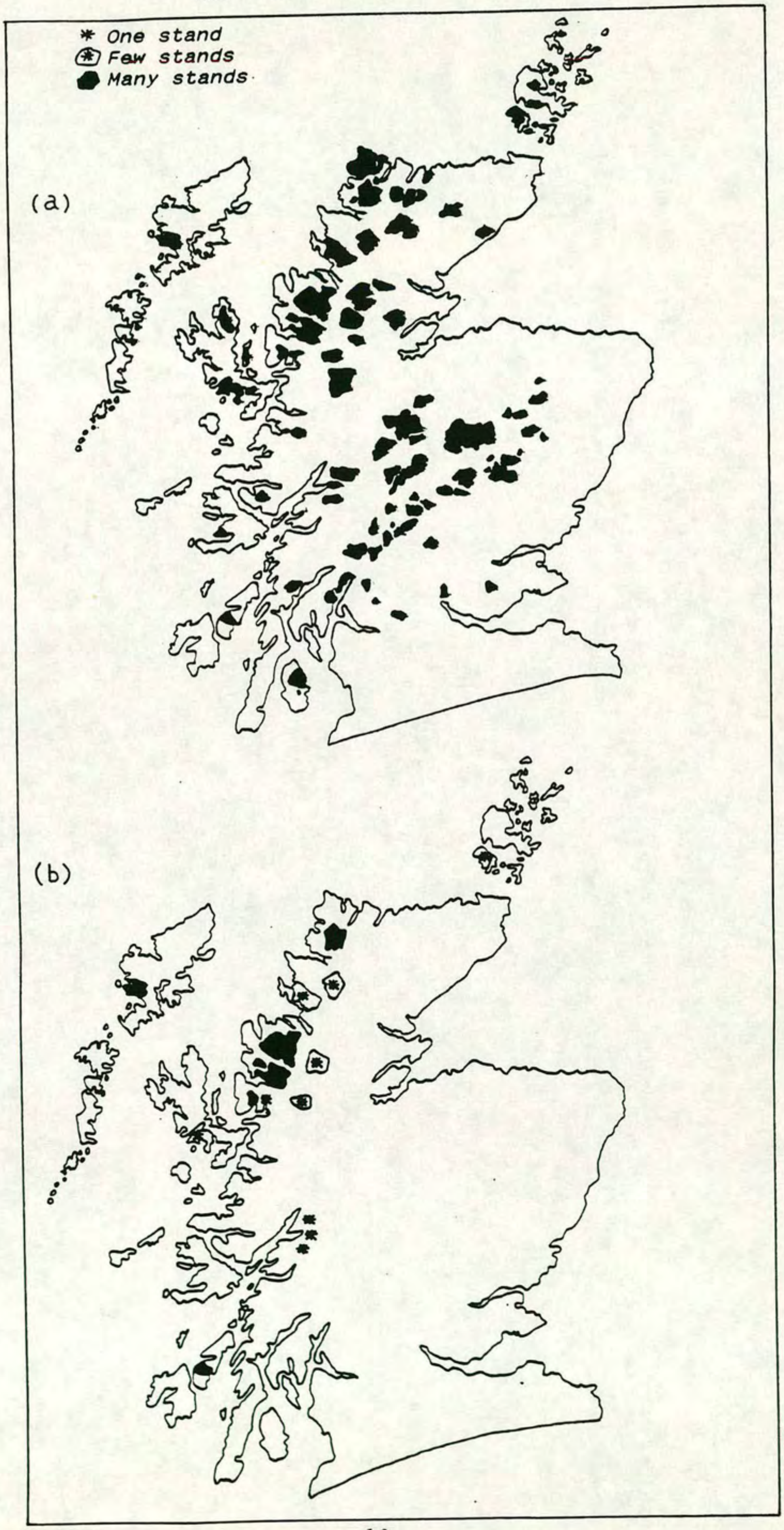
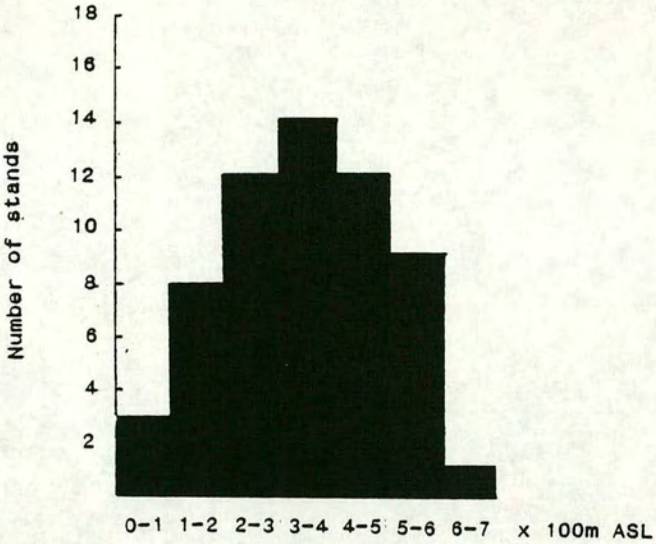
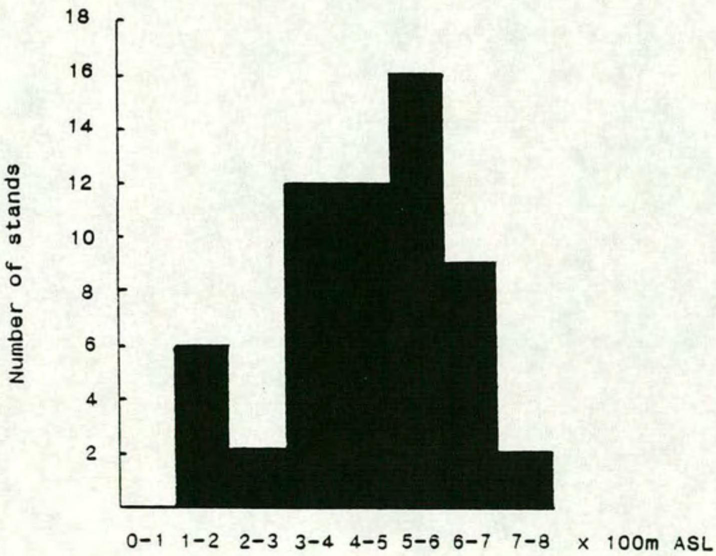


Figure 3.5 Frequency distribution of lowest (a) and highest (b) altitude of 62 stands of the hepatic mat community on 17 upland areas in the west Highlands.





the north and west of the Scottish Highlands (Fig.3.6).

Most examples were on slopes between 20° and 40° from horizontal (fig.3.7).

All the mapped stands faced somewhere between 310° and 130° East from North, but most were between 10° and 60° and, particularly, between 20° and 30° East of North (fig.3.8).

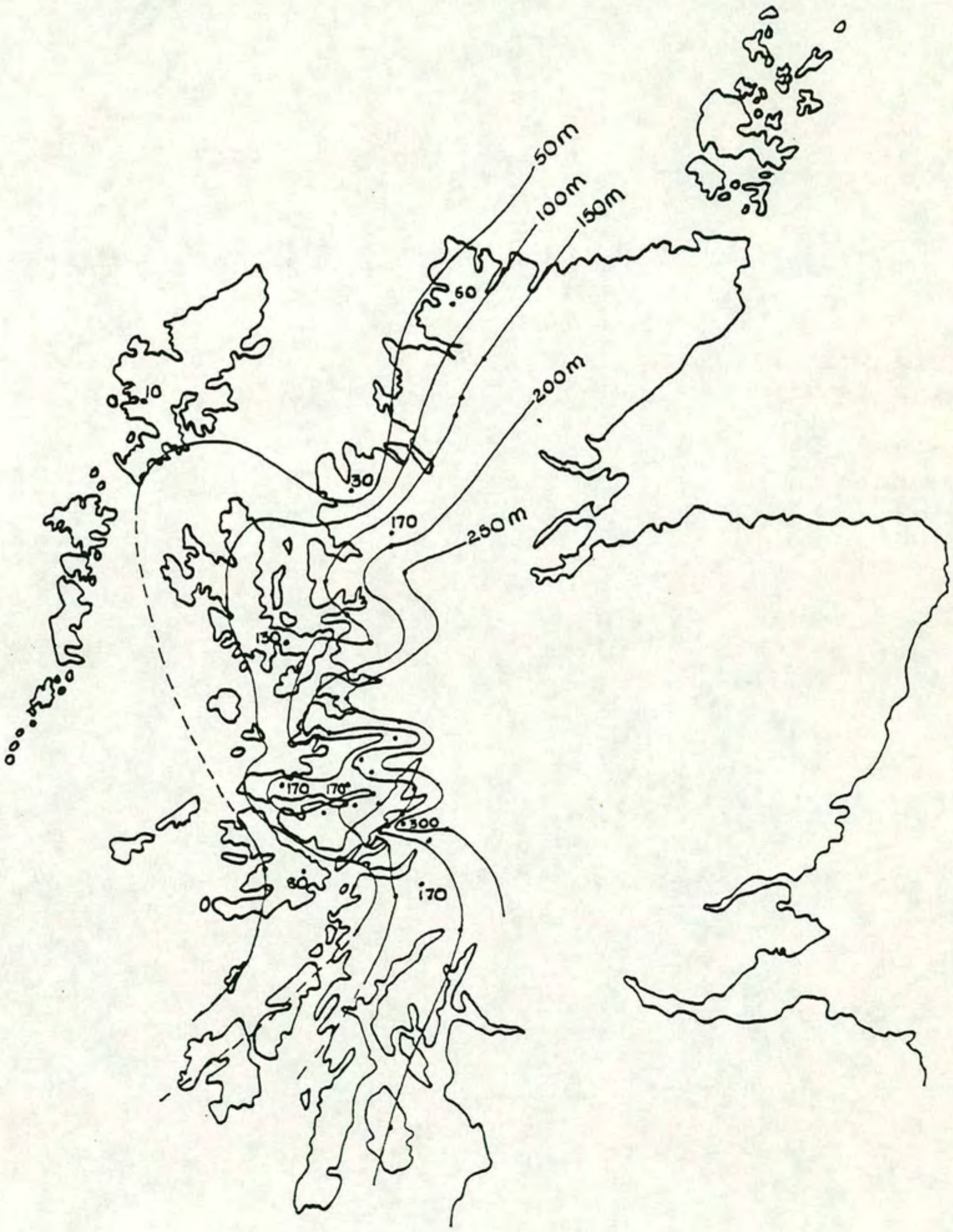
The estimated mean monthly temperatures experienced by the community (at the scale of the 10km square in which they occur) varied from -3.7°C in winter on the Fannich Hills and Monar Forest to 16.0°C in summer on Glas Cnoc (table 3.5).

The steep mountain slopes where these hepatic-rich heaths occurred were often broken by cliffs, screes and boulder-fields. This irregular and rocky topography seemed to provide many suitable habitats for the hepatic mat (table 3.6). The community was most often on rocky slopes or in boulder-fields. It was usually better-developed in these habitats than on open slopes, especially on sites where there was evidence of intensive burning or grazing.

3.3.3 The range of variation in hepatic mats

Nineteen sites with hepatic mats were sampled between Ben Breen in western Ireland and Beinn Stack in Sutherland, including North Wales and the English Lake District

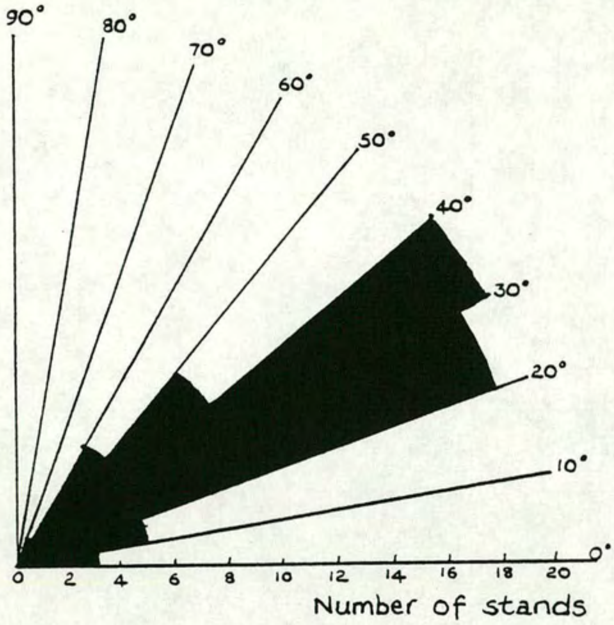
Figure 3.6 Altitudinal descent of the hepatic mat community towards the north and west of its range.



Lines join sites of the same altitude. Spot-heights are given for some points which lie between contours.

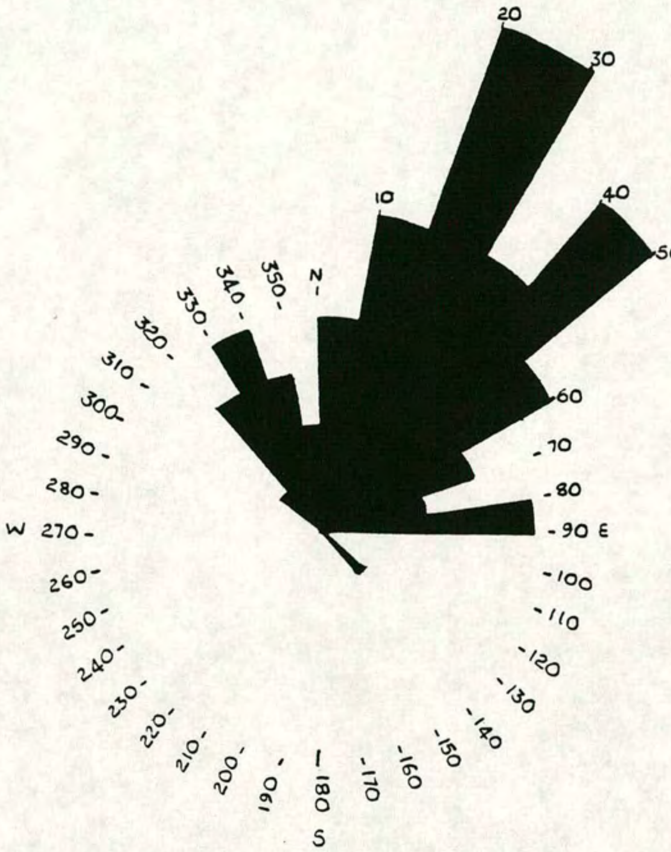
Sources: Upland Vegetation Survey 1981 - 1989, Averis 1991, A. M. & A. B. G. Averis 1989 - 1993.

Figure 3.7 The distribution of 62 stands of the hepatic mat community in the west Highlands in relation to angle of slope in degrees from horizontal.



Sectors are shaded according to the number of stands in each class of 10 degrees.

Figure 3.8 The distribution of 62 stands of the hepatic mat community in the west Highlands in relation to aspect of slope in degrees east of north.



Sectors are shaded according to the number of stands in each class of 10 degrees. The lengths of the bars represent the number of stands. ▬ *1 stand*

Table 3.5 Lowest and highest mean monthly temperatures experienced by the hepatic mat in Calluna vulgaris *heaths on 17 sites in the west Highlands of Scotland.*

SITE	Lowest temp(°C) in February	Highest temp(°C) in July
North Hoy	-1.60	12.60
North Harris	-0.05	15.50
Foinaven	-1.80	14.05
Ben More Assynt	-2.20	14.50
An Teallach	-3.50	12.00
Fannich Hills	-3.70	12.40
Letterewe/Fisherfield	-2.40	13.50
Beinn Eighe/Liathach	-2.50	13.40
Beinn Dearg (Flowerdale)	-2.20	13.30
Beinn Alligin	-1.60	13.70
Monar Forest	-3.70	12.90
Beinn Bhan	-1.20	14.60
Glas Cnoc	-0.20	16.00
Cuillin	0.80	15.10
Mam na Gualainn	-1.30	15.05
Ben Nevis	-1.00	15.50
Beinn an Oir	-1.30	14.80

Lowest temperature is the mean February temperature at sea-level corrected for the highest altitude at which the community was recorded, and the highest temperature is the mean July temperature at sea-level corrected for the lowest altitude at which the community was recorded. Source: Meteorological Office (1975).

Table 3.6 The habitats of the hepatic mat community in the west Highlands of Scotland.

HABITAT	Number of occurrences as % of surveyed sites
Rocky slopes with dwarf shrubs	30.20
Boulder-fields	16.70
Heathy slopes without rocks	10.30
Slopes in rocky woodland	8.00
Cliffs	4.80
Ravine sides	1.60

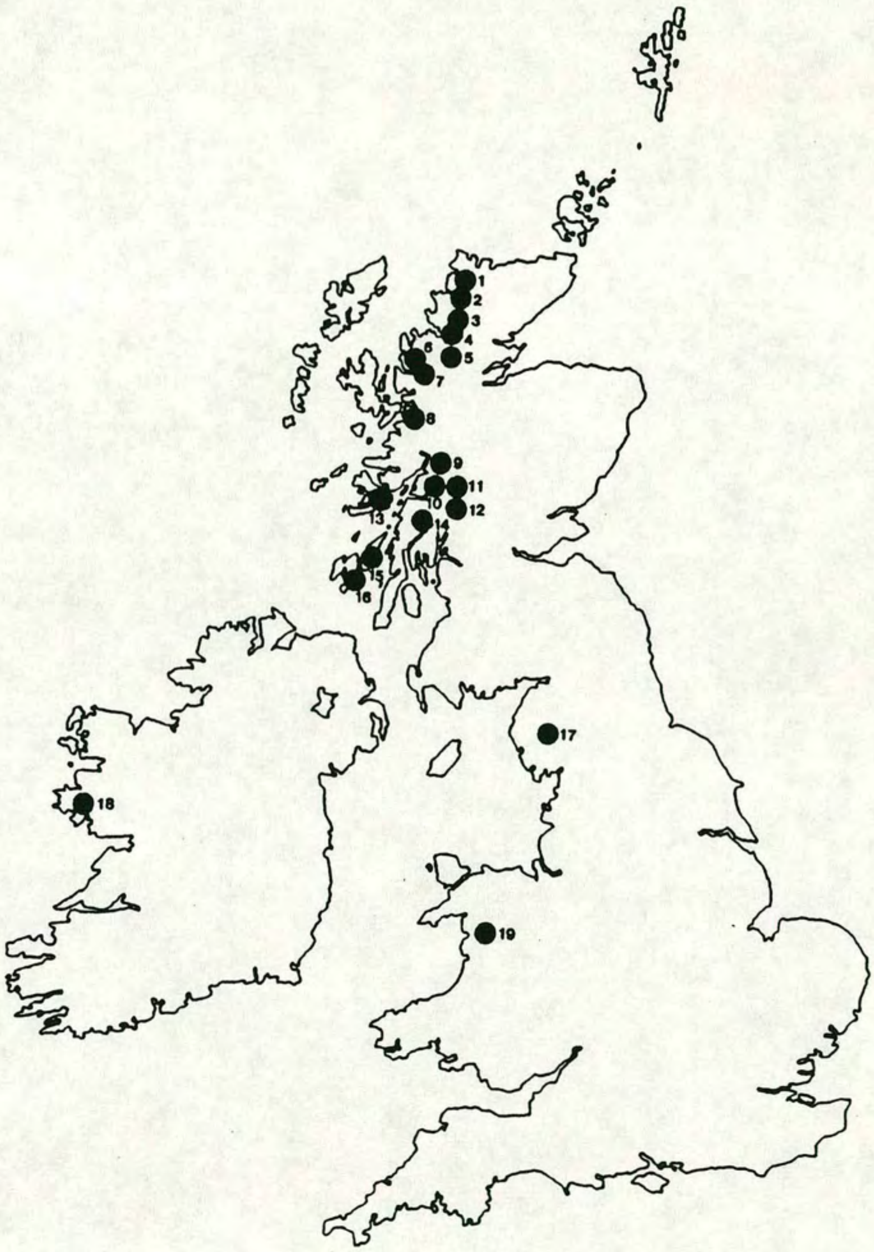
Sources: NCC Upland Vegetation Survey unpublished maps, A. M. Averis unpublished, Averis (1991). For woodlands n=448, for other habitats n=126.

(fig.3.9). Each species mentioned in published accounts of the community (Macvicar 1910, McVean & Ratcliffe 1962, Birks 1973, Rodwell 1991b, Chapter 1) was recorded on at least one of the sites (Appendix 1). In May 1990 I discovered *Adelanthus lindenbergianus* new to Scotland, growing as a member of the hepatic mat community just as it does in Ireland (Ratcliffe 1962, Perry 1983, Horsfield *et al.* 1991). During this work A.B.G. Averis and I recorded every species in at least one 10km square where it was previously unknown. We made 50 new records: an addition of 1.4% to the existing 3612 records for the 16 species. The record of *A. lindenbergianus* added 16.7% to the known distribution, and our 4 records for *Bazzania pearsonii* raised the total by 7.3%. Other species for which our records increased the number of records by more than 1% were *Anastrophyllum joergensenii* (6.3%), *Scapania ornithopodioides* (5.0%), *Plagiochila carringtonii* (4.8%), *Anastrophyllum donnianum* (3.8%), *Scapania nimbosa* (3.3%) and *Mastigophora woodsii* (2.7%).

The only other oceanic liverwort recorded in the community was the Widespread Atlantic *Saccogyna viticulosa*: on Honister Crag, Cader Idris and Bidean nam Bian. The oceanic mosses *Dicranodontium uncinatum*, *Campylopus setifolius*, *C.atrovirens* and *Breutelia chrysocoma* and the oceanic fern *Hymenophyllum wilsonii* were recorded occasionally (Appendix 1).

The number of hepatic mat species on a site varied from 6 to

Figure 3.9 The 19 sites in Britain and Ireland where the hepatic mat community was sampled.



1 *Ben Stack*
2 *Quinag*
3 *Cul Mor*
4 *Ben Mor Coigach*
5 *Fannich Hills*
6 *Baosbheinn*
7 *Liathach*
8 *Ladhar Bheinn*
9 *Glen Nevis*
10 *Bidean nam Bian*
11 *Buachaille Etive Mor*
12 *Stob Gabhar*
13 *Beinn Fhada*
14 *Ben Cruachan*
15 *Beinn an Oir*
16 *South-east Islay*
17 *Honister Crag*
18 *Ben Breen*
19 *Cader Idris*

14 (the maximum possible is 15 because the ranges of *Adelanthus lindenbergianus* and the *Anastrophyllum* species do not overlap). Table 3.7 shows the number of species in each of Ratcliffe's groups (Ratcliffe 1968) on these sites.

There was a lot of variation in the species composition of the hepatic mats (table 3.8, Appendix 1). On the sites sampled in England and Wales the community consisted of *Anastrepta orcadensis, Bazzania tricrenata, Herbertus aduncus, Mylia taylorii, Plagiochila spinulosa* and *Scapania gracilis*. These species were recorded in the community on almost every site from western Ireland to northern Scotland, although *A.orcadensis* was not recorded at the Irish site and *P.spinulosa* was only sparsely recorded in Scotland.

Pleurozia purpurea, Lepidozia pearsonii and *Scapania ornithopodioides* were common in the community in Scotland and were recorded in Ireland but not in England or Wales. *Plagiochila carringtonii* was on most sites from Jura northwards. *Mastigophora woodsii* was recorded from Bidean nam Bian northwards, *Bazzania pearsonii* on Ben Breen and from Ladhar Bheinn northwards, and *Anastrophyllum donnianum* and *Scapania nimbosa* from Liathach northwards. Most of these species do grow further south than this, but were not recorded in mixtures with the more widespread hepatic mat species. For example *Anastrophyllum donnianum* grows on Ladhar Bheinn, but in pure cushions at high altitude and not with other members of the hepatic community.

Table 3.7 The total number of oceanic species and numbers of Northern Atlantic, Sub-Atlantic and Western British hepatic mat species on 19 sites in Britain and Ireland.

SITE	Total no. of hepatic mat species	Northern Atlantic	Sub-Atlantic	Western British
Ben Stack	12	7	3	2
Quinag	12	8	2	2
Cul Mor	14	9	3	2
Ben More Coigach	12	8	2	2
Fannich Hills	12	8	2	2
Baosbheinn	13	8	3	2
Liathach	14	9	3	2
Ladhar Bheinn	11	7	2	2
Glen Nevis	9	5	2	2
Bidean nam Bian	10	5	3	2
Buachaille Etive Mor	6	2	2	2
Stob Gabhar	7	3	2	2
Beinn Fhada	7	3	2	2
Ben Cruachan	7	2	3	2
Paps of Jura	11	6	3	2
SE Islay	9	4	3	2
Honister Crag	6	1	3	2
Ben Breen	11	7	2	2
Cader Idris	6	1	3	2

Northern Atlantic: confined to British Isles, Faroes, W Norway. Sub-Atlantic: western in Europe from Macaronesia to Scandinavia. Western British: Widespread in Europe but western in the British Isles.

Groups from Ratcliffe (1968). Sites are north-facing slopes on the listed hills. See fig 3.9. Sites are arranged in sequence from north (top) to south.

Table 3.8 Number of records for each of the hepatic mat species on 19 sites in Britain and Ireland.

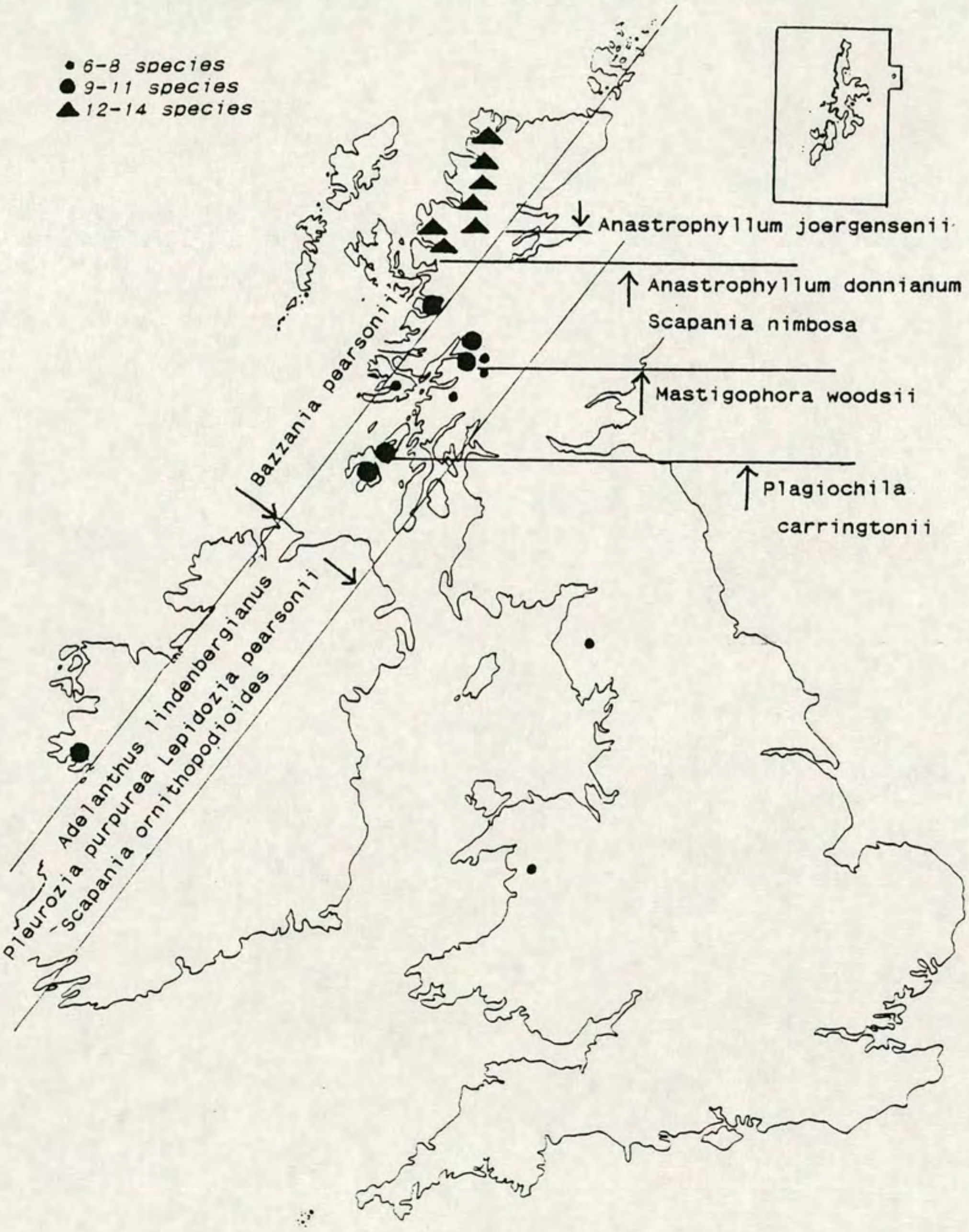
Species	number of sites	% of sites
Northern Atlantic		
Adelanthus lindenbergianus	2	10.5
Anastrophyllum donnianum	6	31.6
A.joergensenii	1	5.3
Bazzania pearsonii	11	57.9
Herbertus aduncus	17	89.5
Lepidozia pearsonii	14	73.7
Mastigophora woodsii	7	36.8
Plagiochila carringtonii	11	57.9
Pleurozia purpurea	15	78.9
Scapania nimbosa	4	21.1
S.ornithopodioides	13	68.4
Sub-Atlantic		
Anastrepta orcadensis	18	94.7
Plagiochila spinulosa	11	57.9
Scapania gracilis	19	100.0
Western British		
Bazzania tricrenata	19	100.0
Mylia taylorii	19	100.0

Northern Atlantic: confined to British Isles, Faroes, W Norway. Sub-Atlantic: western in Europe from Macaronesia to Scandinavia. Western British: Widespread in Europe but western in the British Isles. Groups from Ratcliffe (1968).

The total species-richness increased with distance west as well as distance north as a result of the increasing representation of Northern Atlantic species (fig.3.10). A regression analysis showed that the number of species in a stand had a significant negative relationship with summer temperature (table 3.9).

Comparing the distribution of the individual species with environment at the sites (table 3.10) showed that *Adelanthus lindenbergianus, Anastrophyllum donnianum, A.joergensenii* and *Scapania nimbosa* were not recorded below 450m ASL, while *Bazzania pearsonii* and *Mastigophora woodsii* were always above 350m. *Adelanthus lindenbergianus, Herbertus aduncus, Plagiochila spinulosa* and *Pleurozia purpurea* were not recorded above 550m. *Herbertus aduncus, Mastigophora woodsii, Pleurozia purpurea* and *Plagiochila spinulosa* were not recorded on the site with the coldest winters, and *Adelanthus lindenbergianus* was recorded only on sites where the lowest temperature was above -0.25°C. *Adelanthus lindenbergianus, Anastrophyllum donnianum, A.joergensenii, Bazzania pearsonii, Mastigophora woodsii* and *Scapania nimbosa* were on the sites with the lowest maximum summer temperatures. All but *Adelanthus lindenbergianus* and *Anastrophyllum joergensenii* were in places with a maximum of over 3600mm of rain a year. *Anastrophyllum donnianum, A.joergensenii, Bazzania pearsonii, Mastigophora woodsii* and *Scapania nimbosa* were in places with more wet days a year than the other species.

Figure 3.10 Changes in the species composition of the hepatic mat community with distance north and west.



Lines show southern or south-eastern limits of species as members of the hepatic mat community. Herbertus aduncus, Bazzania tricrenata, Scapania gracilis, Mylia taylorii *and* Plagiochila spinulosa *are present throughout the range of the community.*

Table 3.9. Analysis of variance of the relationship between summer temperature and number of hepatic mat species on 19 sites in Britain and Ireland

Source	ss	df	F	p
Summer temperature	44.86	1	8.3	0.01
error	90.92	17		

The regression line is $y = -1.28\,x + 27.26$ where x is temperature in °C and y is number of species. $r^2 = 0.29$.

Table 3.10 The environmental limits of the hepatic mat species sampled on 19 sites in Britain and Ireland.

Spp	n	%	LSUMT	HSUMT	LWINT	HWINT	LA	HA	LR	HR	LWD	HWD
Alin	2	10.5	13.05	13.20	-0.25	0.25	450	550	12	24	200	220
Aorc	18	94.7	10.75	15.75	-4.50	0.00	250	750	12	40	200	235
Adon	6	31.6	10.75	13.00	-4.50	-1.25	450	750	14	36	210	235
Ajoe	1	5.3	10.75	10.75	-4.50	-4.50	750	750	18	28	235	235
Bpea	11	57.9	10.75	14.00	-4.50	0.25	350	750	14	36	210	235
Btri	19	100.0	10.75	15.75	-4.50	0.25	250	750	12	40	200	235
Hadu	17	89.5	11.95	15.75	-2.50	0.25	250	550	12	40	200	235
Lpea	14	73.7	10.75	15.75	-4.50	0.25	250	750	12	36	200	235
Mwoo	7	36.8	11.95	14.00	-2.50	-1.25	350	500	14	36	210	230
Mtay	19	100.0	10.75	15.75	-4.50	0.25	250	750	12	40	200	235
Pcar	11	57.9	10.75	15.75	-4.50	-0.75	250	750	14	36	200	235
Pspi	11	57.9	11.95	15.75	-2.50	0.25	250	550	12	40	200	225
Ppur	15	78.9	11.95	15.75	-2.50	0.25	250	550	12	36	200	230
Sgra	19	100.0	10.75	15.75	-4.50	0.25	250	750	12	40	200	235
Snim	4	21.1	10.75	13.00	-4.50	-1.25	450	750	14	36	215	235
Sorn	13	68.4	10.75	15.75	-4.50	0.25	250	750	14	36	200	235

For full names of species see table 3.8. n = number and % = percentage of sites with each species. LSUMT, HSUMT, LWINT, HWINT = lowest and highest summer and winter temperatures (° C) (July and February mean monthly temperatures corrected to altitude of stand). LA, HA = lowest and highest altitude (metres ASL). LR, HR = lowest and highest average annual rainfall recorded on site (dm). LWD, HWD = lowest and highest number of wet days a year. From Meteorological Office (1975, 1977) and Ratcliffe (1968).

The 25cm x 25cm quadrat samples taken at 15 of the sites (table 3.11) showed that, in the richer patches of the community, *Anastrepta orcadensis* was more frequent on the woodland sites of Glen Nevis and Bidean nam Bian than elsewhere. *Anastrophyllum donnianum* was more frequent on the high-altitude site in the Fannich hills than elsewhere, and this was the only site for *A.joergensenii*. *Bazzania tricrenata, Herbertus aduncus* and *Scapania gracilis* were common on nearly all their sites, while *Scapania nimbosa* and *Plagiochila spinulosa* were always infrequent as well as being on few sites. *Mylia taylorii* was recorded on all the sites but was more frequent on the southern and eastern ones. Up to 10 hepatic mat species were recorded in a single 25cm x 25cm quadrat (table 3.12) - most if not all of the species recorded at a site.

The hepatic community was recorded in 14 different plant communities on the sites sampled (fig.3.11). 59% of the records were in *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* damp heath (H21), 12.6% were in *Nardus stricta-Galium saxatile* grassland (U5) and 13% in *Quercus petraea-Betula pubescens-Dicranum scoparium* woodland (W17). The remainder were in montane *Vaccinium myrtillus-Racomitrium lanuginosum* heaths (H20), *Nardus stricta-Carex bigelowii* (U7) and *Deschampsia cespitosa - Galium saxatile* (U13) grasslands, *Athyrium alpestre - Cryptogramma crispa* snow-beds (U18) and *Luzula sylvatica-Geum rivale* tall-herb communities (U17).

Table 3.11 Number of occurrences of hepatic mat species in ten 25cm x 25 cm quadrats placed selectively to represent the richer patches on 15 hills in Great Britain.*

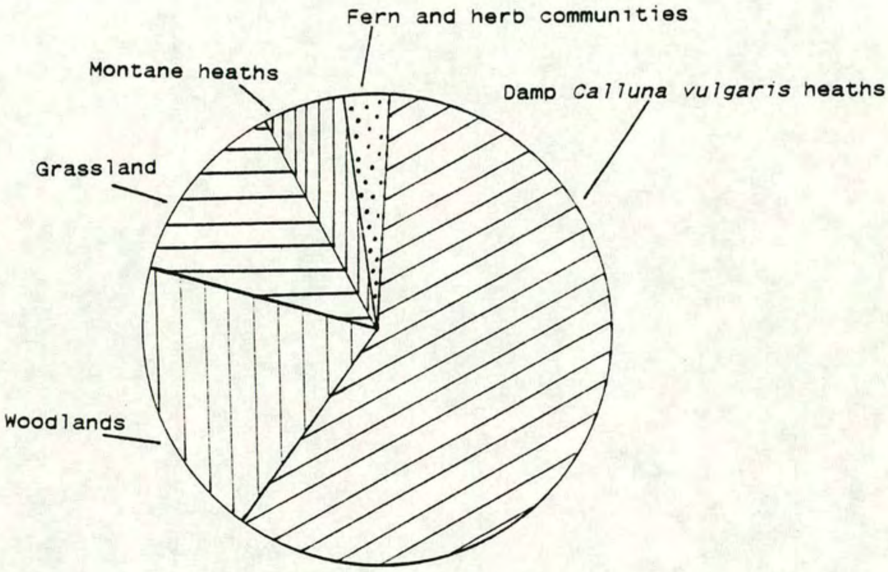
Species	Site														
	BS	Q	CM	BMC	F	L	LB	GN	BB	BEM	SG	BF	BC	HC	CI
Aorc	5	2	5	7	4	3	4	10	8	3	6	2	6	2	4
Adon		2	1	1	8	1									
Ajoe					4										
Bpea	1	5	2	4	2	1	2								
Btri	10	9	10	10	9	10	5	9	9	3	10	5	10	10	5
Hadu	7	8	7	9		10	8	10	10	5		9	4	7	10
Lpea		2	1	2	1	3	2	4	1		4	1			
Mwoo	3	6		6		3	4								
Mtay	3	4	4	2	3	4	3	4	4	1	7	3	8	7	8
Pcar	8	8	7	6	4	10	4	1	6						
Pspi	1								1				2	1	2
Ppur	7	9	7	7		10	7	9	8	4		7	2		
Sgra	10	10	10	9	3	6	6	9	2	2	1	9	8	3	9
Snim	1		1		2	2									
Sorn	3	5	3	4	4	5	7	2	5		2				

*BS Ben Stack, Q Quinag, CM Cul Mor, BMC Ben Mor Coigach, F Fannich Hills, L Liathach, LB Ladhar Bheinn, GN Glen Nevis, BB Bidean nam Bian, BEM Buachaille Etive Mor, SG Stob Gabhar, BF Beinn Fhada, BC Ben Cruachan, HC Honister Crag, CI Cader Idris. For full names of species see table 3.8. * Only 5 quadrats were recorded on Buachaille Etive Mor*

Table 3.12 Maximum number of hepatic mat species occurring together in a 25 x 25cm quadrat on 15 hills in Great Britain.

Site	Max. no of species in one quadrat	% of total number at that site
Ben Stack	8	66.7
Quinag	10	83.3
Cul Mor	8	57.1
Ben Mor Coigach	10	83.3
Liathach	10	71.4
Fannich Hills	6	50.0
Ladhar Bheinn	8	72.7
Glen Nevis	8	88.9
Bidean nam Bian	8	80.0
Buachaille Etive Mor	5	83.3
Stob Gabhar	4	57.1
Beinn Fhada	5	71.4
Ben Cruachan	5	71.4
Honister Crag	4	66.7
Cader Idris	6	100.0

Figure 3.11. Vegetation types with the hepatic mat community on 19 sites in Britain and Ireland.



The figure shows the distribution of 125 samples of the hepatic mat community among five broad classes of vegetation in Britain and Ireland.

The community occurred on several types of rock (table 3.13) ranging from quartzite and Torridonian sandstone to Moine schist and volcanic andesite and rhyolite (British Geological Survey 1979). The hepatic mats on Quinag, Ben More Coigach and Cader Idris were in deep corries and were close to lochs.

The slopes studied on Ben Mor Coigach and the Fannich Hills and some of the patches of hepatic mat recorded by the UVS on Foinaven and Ben More Assynt had been burnt in the last few years. On Ben Mor Coigach, Beinn Dearg (Flowerdale), Buachaille Etive Mor, Stob Gabhar, Ben Cruachan, Honister Crag, Cader Idris and Ben Breen there were extensive *Nardus stricta* grasslands (NVC U5) and, often, dead and dying bushes of *Calluna*. This was presumed to be caused by recent intensification of grazing and by uncontrolled moor-burning.

3.4 Discussion

The maps of the hepatic mat species appear to be reasonably complete. The species are characteristic of the west of the country, where there has been plenty of recording (Hill, Preston & Smith 1991). They are all large, conspicuous and distinctive plants. Most can be determined in the field without using a hand-lens. Although few people have studied the ecology of these plants, many bryologists are interested in seeing and recording them in new places.

It is misleading to conclude anything about the limits to

Table 3.13. Types of rock on which the hepatic mat community was developed on 19 sites in Britain and Ireland

Rock type	number of sites	Characteristics
Torridonian Sandstone	6	Hard, mostly acidic, weathers to produce block-scree and free-draining soils
Cambrian & Dalradian Quartzite	4	Hard, acidic, produces soil with almost no organic matter. Forms cliffs and scree
Moine Schist	3	Varying base-status; mostly hard and weathering to coarse scree
Dalradian Schist	4	Locally base-rich. Forms block-scree on some sites
Andesite/rhyolite	1	Fairly base-rich but weathers to give free-draining soils and block-scree
Rhyolite and basalt	1	Locally base-rich, weathers to give free-draining soils and block-scree

distribution from maps which show only recorded presence, since the absence of a record does not necessarily imply either actual absence or unsuitable conditions. Combined distribution maps are more useful than individual ones because they give a better picture of where conditions are favourable for several of the species.

The stepwise multiple regression analyses were done to explore the patterns in the data and to suggest which environmental factors were most strongly associated with the distribution of the species. The regression analyses were re-run several times following the discovery of more species in some squares, without affecting the results, although the regression coefficients did alter slightly. It is unlikely that new records in the future will change the distribution patterns so much that re-doing the analysis would give a different set of variables in the regression equation. The analyses were not used to test specific hypotheses, mainly because the conditions of randomness, normal distribution and independence of the variables were not satisfied by these data. Similar work by Hedderson and Brassard (1990) looked at the microhabitat relationships of five mosses using multiple regression. This technique successfully separated the different habitats of the five species and showed which environmental variables were best-correlated with the distribution of the species.

The squares with large numbers of hepatic mat species tended to be those where the average annual rainfall is high. Maximum rainfall was the variable which contributed most to the regression function, both for the hepatic mat species as a whole and for the Northern Atlantic members of the group. Bryophytes have a wide range of tolerance to drought (see, for example, Dilks & Proctor (1974)) but the distributions of the oceanic species suggest that they have a low tolerance and need to be wet for most of the time (Ratcliffe 1968, Chapter 2).

The abundance of the Northern Atlantic members of the community was related to the number of wet days a year. Ratcliffe (1968) found a relationship between the distribution of the hepatic mat community and number of wet days a year. The community does occur on hills which experience as few as 200 wet days, but several of the Northern Atlantic species are rare outside the areas with 220 wet days (see below). The hepatic mat species are confined to the parts of the British Isles where the annual potential water deficit is less than 1cm; another measure of high rainfall and low temperatures (Green 1964).

A low temperature range was also associated with a large number of hepatic mat species in a square. They grow in places where summers are cool and winters mild. There may be physiological reasons for this, because metabolic processes only operate between certain temperatures (Begon, Harper & Townsend 1986). Alternatively, if the requirement for wetness is overriding, low summer temperatures may be important in slowing down the rate of evaporation and prolonging the period of moistness after rain, while mild winters reduce the chances of prolonged desiccating frosts. Most of these species are able to grow high on mountains where much of the winter precipitation falls as snow, and several grow in the Cairngorm corries. In such situations the plants are protected from extreme cold because temperatures rarely fall below 0°C under a thick layer of snow (McVean & Ratcliffe 1962).

The presence of mountains seems to be important for these species, presumably because of the effects of altitude on the climate. With increasing altitude rainfall is heavier and more frequent, mist is common (Monkhouse 1975, Meteorological Office 1977) and temperatures are lower (Meteorological Office 1975). The amount of solar radiation is reduced by the frequency of cloud (Harding 1979).

Climatic factors and topography are not independent of each other. As stated above, steep mountainous terrain modifies the local climate. Temperature and humidity are interdependent. The cloudy skies associated with frequent rainfall ameliorate the temperature so that the days are cooler and the nights warmer than they would be if the skies were clear. At low temperatures the rate of evaporation is reduced and soils and vegetation stay wet for longer.

The results suggest that climate and topography interact such that a low number of wet-days may be compensated for by a low temperature range (as on the Hebridean island of Islay), and that the hepatic mat community can grow in places with a high annual temperature range where the rainfall is high and there are 230 wet-days or more a year, such as the Fannich hills and Monar Forest in Wester Ross. This was also found in a study of oceanic species in woodlands (Averis 1991).

Although these analyses give a general idea of the environmental limits of the hepatic mat species, it is obvious that the scale of the community is different from that of the environmental factors affecting an entire 10km square. There was no relationship between species-richness and area, either of land or of north-facing slopes. An isolated mountain with one suitable slope can hold as many of these species as a 10km square full of mountains. Meteorological data may give misleading information about comparative distributions where the plants being studied live in regions with steep ecological gradients (Dilks & Proctor 1975). The figures for temperature, rainfall and wet days are estimates. They are based on maps drawn from data collected at a few, widely-scattered weather-stations, most of which are on low ground close to sea-level. The map of rainfall (Meteorological Office 1977) is corrected for altitude, but obviously makes no allowance for local rain-shadows and the effects of eddying on sheltered slopes. Ballantyne (1983) concluded that the actual average annual precipitation on the Wester Ross hills might be as much as 40% higher than the published maps suggest. Temperature figures were adjusted for altitude, but again temperatures are modified by local topography and this cannot be allowed for. Solar radiation, which has profound effects on temperature and evaporation (Dilks & Proctor 1975, Proctor 1980b), was not considered at all in this analysis.

The Upland Vegetation Survey was done by people who were familiar with the work of McVean & Ratcliffe (1962) and Birks (1973). They expected to find liverwort mats only in damp *Calluna* heaths on north-facing slopes and in boulder-fields. It is likely that they found the community on north-facing slopes because they looked for it there, although the connexion had already been noted by researchers who went out without expectations (e.g. Macvicar 1910). Nevertheless most sites with hepatic mats were surveyed by experienced people who would have noticed large stands of the hepatic community on slopes facing other ways than north, if they had been there. There are heaths with hepatic mats on west-facing slopes on the Twelve Bens of Connemara (Horsfield *et al.* 1991) but this has not been seen in Scotland. The results of the Upland Vegetation Survey are a useful way to show the conditions the community can tolerate, even though they do not show precise geographical limits or relationships with aspect.

The classification used by the UVS (H. J. B. Birks & D. A. Ratcliffe, unpublished) recognised only the hepatic-rich

Calluna heaths. The hepatic mat community was noted by the UVS in montane *Vaccinium myrtillus* heaths (NVC H20) on Beinn Bhan, the Fannich Hills, Ben Hope, the Affric-Cannich hills, Beinn Eighe and Baosbheinn. Again, these stands were on rocky slopes facing north or east, but since they were not delimited from the surrounding vegetation they could not be included in these analyses.

The results suggest that most stands of the community face between north and east, and are especially likely to be on slopes which face between 20° and 30° east from north. However one stand faced south-east - 130° east from north. This was in a boulder-field in the corrie of Toll a' Mhadaidh Mor on Beinn Alligin in the Torridon Forest, West Ross. The boulders are enormous: the biggest ones are the size of caravans, and there are plenty of shaded sheltered places for the liverworts among them (Stacey 1984). It is possible that the hepatic mat liverworts could grow in boulder-fields on any aspect. However boulder-fields tend to develop on the northern sides of hills where glacial ice persisted longest and where there was frost-shattering of steep slopes. This is worth further investigation.

The variation in number and mean area of the stands on a site can usually be related to the topography of that site. For instance there are a great many small rocky hills on North Harris, and a great many small stands of the hepatic mat community. Conversely there is only one high north-facing slope on North Hoy, and this has one stand of the community. Small patches are more common than large ones, probably because it is rare to find large expanses of suitable habitat which have not been disturbed or damaged. One of the few is on Liathach, part of the Torridon Forest SSSI. The hill is owned by the National Trust for Scotland and the vegetation is never deliberately burnt (the late L. MacNally pers. comm.). Another site with a large stand is part of the Gualin National Nature Reserve on the lower slopes of Foinaven, where there has been no deliberate burning since 1975 (D. B. A. Thompson pers. comm.).

Variation in altitudinal range is most likely related to environmental variation which runs parallel with altitude. On the wet hills of Harris with their cool summers the community can grow near sea-level, while in the more easterly sites such as An Teallach, the Fannich Hills and Monar Forest rainfall and temperature fall within acceptable limits only at high altitudes. Again this shows the shifting balance between climatic elements suggested by the distribution of the hepatic mat species (see above) and also shown by Averis (1991). The coldest sites. the Fannich Hills and Monar Forest, are in the east of the range of the community, where winter temperatures are not ameliorated by the sea as they are further west, and the warmest site, Glas Cnoc, is only 137m ASL.

The community is almost always associated with rocky habitats. This is partly because most north-facing slopes in the west Highlands are rocky. It could indicate a need for shade and shelter. This is probably true in the boulder - field on Beinn Alligin where outside the boulders the ground slopes gently to the south-east, is exposed to the sun and has a short open vegetation of *Scirpus-Erica* wet heath (NVC M15) on shallow peat. This vegetation usually dries out in hot weather in early summer and the only Atlantic liverwort recorded in it is *Pleurozia purpurea* (personal observation).

The results of the UVS and this study support the observations of Macvicar (1910), McVean and Ratcliffe (1962) and Ratcliffe (1968) that the hepatic mat community is less common and less widespread to the east of the west Highland watershed. Even the hills which form the watershed, from Ben More Assynt in Sutherland down to Ben Lui, have not got such rich hepatic mats as the hills to the west such as Quinag, the Torridon hills and Beinn Bhan. The islands of Mull, Islay and Jura have better hepatic mats than the hills on the adjacent mainland. This is most likely to be because of the steep gradients of temperature and rainfall from west to east (Ratcliffe 1968). Ballantyne (1983) found an unexpectedly steep gradient in precipitation between Badachro on the west coast and Loch na h-Oidhche to the east of An Teallach; the gradients across this part of Wester Ross were steeper than those measured anywhere else in upland Britain. Temperature gradients eastward from the Inner Hebrides are steep in winter (Meteorological Office 1975), because of the warming influence of the sea.

The detailed study of 19 stands of the hepatic mat community suggests that there is a basic assemblage of the more widespread species *Herbertus aduncus*, *Bazzania tricrenata*, *Scapania gracilis*, *Mylia taylorii* and *Anastrepta orcadensis* to which other species are added with increasing distance west and north. Ratcliffe (1968) defined the mixed hepatic community as an assemblage of at least 6 of 12 montane species - although he only mentions 11 species and not all of these are montane plants. My results and those of Averis (1991) suggest that of all the hepatic mat species only *Anastrophyllum donnianum*, *A.joergensenii*, *Adelanthus lindenbergianus*, *Bazzania pearsonii* and *Scapania nimbosa* are truly montane in the British Isles - absent or rare below the altitudinal limit of closed woodland. The other species all occur in woods and some grow at surprisingly low altitudes (Averis 1991).

With increasing distance north and west, summer temperatures are cooler at low altitudes and this is probably the reason for the altitudinal descent of the montane species. In the more southerly areas the high-altitude and low-altitude species are spatially separated and do not coexist in the same stand. For instance *Scapania ornithopodioides* is rare in England and North Wales where it grows in boulder-fields and on cliffs (D.A. Ratcliffe pers. comm.). In several places in southern Scotland - for instance on Mull - it grows on the same hills as the rest of the hepatic mat community but at higher altitudes among boulders and not mixed with the other species. Further north than the latitude of the Kyle of Lochalsh the climate is evidently suitable for the more montane species to grow at the same altitude as the other members of the community. The montane plants are presumably intolerant of warm summers, probably because of the increase in evaporation rate with temperature. Their association with cold winters may be because of the balance between photosynthesis and respiration. In the northern Highlands the winter temperatures at low altitudes are quite high (Meteorological Office 1975). In such places it might be possible for the plants to be sufficiently warm and wet to respire but to have insufficient light to photosynthesise. This has been demonstrated as a limit to growth in pine trees (Bannister 1976 in Vincent 1990). Growing in places with cold winters may ensure that this does not happen and could explain why the montane *Anastrophyllum joergensenii* seems to be restricted to the parts of the west Highlands where winters are coldest.

The variation in species composition over the British Isles suggests that each species has different ecological limits as well as different efficiency of distribution (see for example Ratcliffe 1968, Crundwell 1970).

The richest stands of the hepatic mat are in western Scotland and western Ireland, again fitting the pattern described by

Ratcliffe (1968). There are fragmentary and species-poor stands in the high rainfall areas of England and Wales (as noted by Birks (1973)) and in Galloway. There are few of the characteristic species in the drier Mourne Mountains in Northern Ireland, despite the abundance of suitable topography and a reasonably oceanic climate (Hobbs & Averis 1991b). England and Wales have a notably poor representation of these species considering that locally there are places with very high rainfall and 200 wet days or more. However summer temperatures are higher, which may be unfavourable for the less thermophilous species.

Herbertus aduncus, Pleurozia purpurea and *Plagiochila spinulosa* were rare in or absent from the stands at higher altitudes, which suggests that they might be the more thermophilous members of the group.

According to Ratcliffe (1968), *Scapania nimbosa, Mastigophora woodsii, Bazzania pearsonii* and *Herbertus aduncus* are the least tolerant of drought. My results concur with this for all but *Herbertus aduncus,* which was recorded in places with fewer wet-days a year and a lower minimum annual rainfall than the other three species. All the species except *Adelanthus lindenbergianus* and *Anastrophyllum joergensenii* were on sites where the maximum annual rainfall was 3600mm or more, supporting the idea that they need a wet climate. *A. lindenbergianus* grows on sites where the summers are cool: this may reduce the rates of evaporation such that the low annual rainfall is not so critical as it would be in places with warmer summers. At the other extreme, *A.joergensenii* tends to grow at high altitudes and in places which are irrigated for much of the year by water from melting snow. At the altitude at which the hepatic mat plants often grow the annual rainfall may be 4000mm a year or more (Ballantyne 1983), at least in the far west of Scotland. All the species were in places with at least 200 wet days a year, but *Anastrophyllum donnianum, A.joergensenii, Bazzania pearsonii, Mastigophora woodsii* and *Scapania nimbosa* were more demanding than the others. None of these five species occurred on sites with fewer than 210 wet days a year.

This set of 19 sites is a small sample and the results cannot be extrapolated too far beyond them. For example, in this study *Plagiochila carringtonii* was not a component of hepatic mats further south than Jura. However it grows in hepatic mat vegetation at its Irish sites (Ratcliffe 1962). *P. carringtonii* has also been recorded growing with *Herbertus aduncus, Anastrepta orcadensis* and *Mylia taylorii* on Arran (Kenneth 1976) and this would be worth investigating.

The hepatic mat community occurs in a wider range of vegetation than previously thought (McVean & Ratcliffe 1962, Ratcliffe 1968, Rodwell 1991b). The present distribution of hepatic mats suggests that if British vegetation had not been changed by human activities the community would probably have occurred from woodland near sea-level, through the natural dwarf-shrub heaths above the tree-line and on into montane heaths and grasslands at high altitudes. The community would probably have been best-developed and most species-rich at around the altitudinal limit of woodland, as it still is today. Whether there would have been more of it on slopes not facing north than there is now is not easy to tell.

It is also possible that because the suitable areas in England and Wales are small there has been more lost by extinction with a changing climate than in Scotland and Ireland, where there are more refugia at high altitudes and where the climate is more consistently wet and cool. The examples of the community in England and Wales tend to be on cliffs and among boulders, so it is possible that more intensive grazing and burning on the English and Welsh hills has contributed to the scarcity of the community.

Six of the 19 stands which were studied were on Torridonian sandstone, four were on quartzite and seven were on Moine and Dalradian schists. All these rocks (except the quartzite) are locally base-rich, although most stands of the community were on acidic rocks. The rocks are all hard and resistant to chemical weathering. The effects of glaciation have been to produce cliffs, corries, steep slopes and boulder-fields. This has given a range of shaded habitats for the plants to grow in. The soils which have developed on these mountain slopes are mostly thin peaty rankers overlying scree and so free-draining (McVean & Ratcliffe 1962). They are leached and acidic. The hepatic mats on Honister Crag were on andesite and rhyolite of the Borrowdale Volcanic Group and those on Cader Idris were on rhyolite and basalt. These are rather base-rich. This fits with the observations of Ratcliffe (1968) that some of the species apparently need a richer substrate in England and Wales. The reasons for this are not obvious, although there is a similar trend in vascular plants. Species such as *Silene acaulis, Minuartia sedoides* and *Armeria maritima* are calcicoles in the south and east of their ranges, but become less so with distance north-west (McVean & Ratcliffe 1962).

Although the hepatic mat community seems to have a narrow geographical range there is a great deal of variation in its habitat, in the size and number of stands in a given area and in the species composition. In general the distribution of the community fits with the observations of Macvicar (1910), McVean & Ratcliffe (1962), Ratcliffe (1968) and Birks (1973) and shows that the results of the analyses of distribution and environment are reasonably accurate. This study has confirmed that the community occurs in England and Wales as well as in the Inner Hebrides. What it has not shown is whether the community is confined to steep, north-facing rocky slopes. This will be studied in Chapter 4.

CHAPTER FOUR

THE DISTRIBUTION OF THE HEPATIC MAT SPECIES ON BEINN EIGHE, WEST ROSS

4.1 Introduction

Most authors who have described the Atlantic Hepatic Mat suggest that it occurs only on slopes facing between north-west and east (e.g. Macvicar 1910, McVean & Ratcliffe 1962, Ratcliffe 1968, Hobbs 1988). There have been no studies of the distribution of the individual species in relation to aspect in their mountain habitats, although some of them have been studied in woods (Averis 1991). Their relationships with altitude have been noted: *Anastrophyllum donnianum*, *A. joergensenii*, *Scapania nimbosa* and *Bazzania pearsonii* are reported to be montane species which rarely grow below 300m, while *Plagiochila spinulosa* tends to be more common at low altitudes and is rare in more elevated stands of the community (Ratcliffe 1968; Hill, Preston & Smith 1991; Chapter 3). The hepatic mat community is said to be adversely affected by grazing and burning of the heathlands in which it occurs (McVean & Ratcliffe 1962, Ratcliffe 1968, Chapter 3).

The validity of these observations was tested by a detailed study of the distribution of the hepatic mat species on Beinn Eighe in Wester Ross, where all of the species except *Adelanthus lindenbergianus* and *Anastrophyllum joergensenii* were known to occur (Hill, Preston & Smith 1991). The aims of the study were to find out whether the hepatic mat species really are confined to north-facing slopes and to compare their distributions with aspect, altitude, steepness and rockiness of slope, the structure of the vegetation and intensity of use by red deer (*Cervus elaphus* L.).

Beinn Eighe (NG 985625) rises on the north side of Glen Torridon, close to the sea and surrounded by other high hills. It has some of the best-developed hepatic mat communities in Britain (Ratcliffe 1977). The altitudinal range of the hill is from 100m ASL in Glen Torridon to 1010m at the summit of Ruadh-stac Mor. The area of ground is about 3540 ha. The topography is characteristic of the western Highlands, with steep rocky slopes rising to narrow ridges and sharp summits. The southern slopes are smooth except for the high hollow of Coire an Laoigh (NG 967594), but the northern side is broken by the long, north-running ridges of Ruadh-stac Mor, Ruadh-stac Beag and Creag Dubh and the corries between them. These corries have spectacular cliffs, screes and boulder-fields. There is one large loch (L. Coire Mhic Fhearchair) and several small lochans.

The rock is Pre-Cambrian Torridonian sandstone overlaid by Cambrian quartzite. The quartzite runs diagonally across the site so thet it outcrops lower down at the east end than at the west. Bands of fucoid beds and serpulite grits run transversely across the north face of Ruadh-stac Beag (British Geological Survey 1979). These base-rich sediments have a marked effect on the vegetation (Upland Vegetation Survey 1990).

Most of the hill is a National Nature Reserve owned by Scottish Natural Heritage. Management is principally for nature conservation and several areas have been fenced against livestock to allow regeneration of the Scots pine and birch woodland. Some trees have been planted within these exclosures and there are a few small plantations of alien conifers on the low ground to the south and east. The rest of the site is grazed by red deer (T. Clifford pers. comm.).

The semi-natural upland vegetation has been mapped and classified by the Nature Conservancy Council's Upland Vegetation Survey (UVS) (1990), using H. J. B. Birks' and D. A. Ratcliffe's unpublished classification and the National Vegetation Classification (Rodwell 1991a, 1991b, 1992). The most extensive type of vegetation on the hill is damp heath with *Calluna vulgaris, Scirpus cespitosus* and *Molinia caerulea* with sedges and bryophytes (NVC M15) growing on shallow peat. There is not much blanket bog because the slopes are steep and the valleys narrow: the largest expanses are in Glen Torridon. Most of the bog is the western *Scirpus cespitosus - Eriophorum vaginatum* blanket-mire (M17) with abundant *Myrica gale.* Dry heaths are uncommon - as might be expected in this wet region - and include more of the western community dominated by *Calluna vulgaris* and *Erica cinerea* (H10) than the eastern type with *C.vulgaris* and

Vaccinium myrtillus (H12). Most is on well-drained, podsolised mineral soils. Damp heaths on thin peaty rankers are typically dominated by *C.vulgaris*, *Vaccinium myrtillus* and *Sphagnum capillifolium* (H21). There are pine and birch woodlands on the slopes above Loch Maree. Above the theoretical tree-line (here at about 300m ASL) there are montane heaths dominated by *Calluna vulgaris* and *Cladonia arbuscula* (H13), by *C.vulgaris* and *Racomitrium lanuginosum* (H14) or by *Vaccinium myrtillus* and *R.lanuginosum* (H20). There is a distinctive assemblage of *Calluna vulgaris* and *Juniperus communis* ssp *nana* (H15) on quartzite debris; this community is the main locus for the liverwort *Herbertus borealis*, for which Beinn Eighe is the only known locality in the British Isles. The predominant vegetation of the corries is *Nardus stricta - Carex bigelowii* snowbed grassland (U7). *Deschampsia cespitosa-Galium saxatile* grasslands (U13) occupy flushed slopes below cliffs and where melt-water runs from late-lying snow. The vegetation of the high exposed ground is *Carex bigelowii-Racomitrium lanuginosum* moss heath (U10).

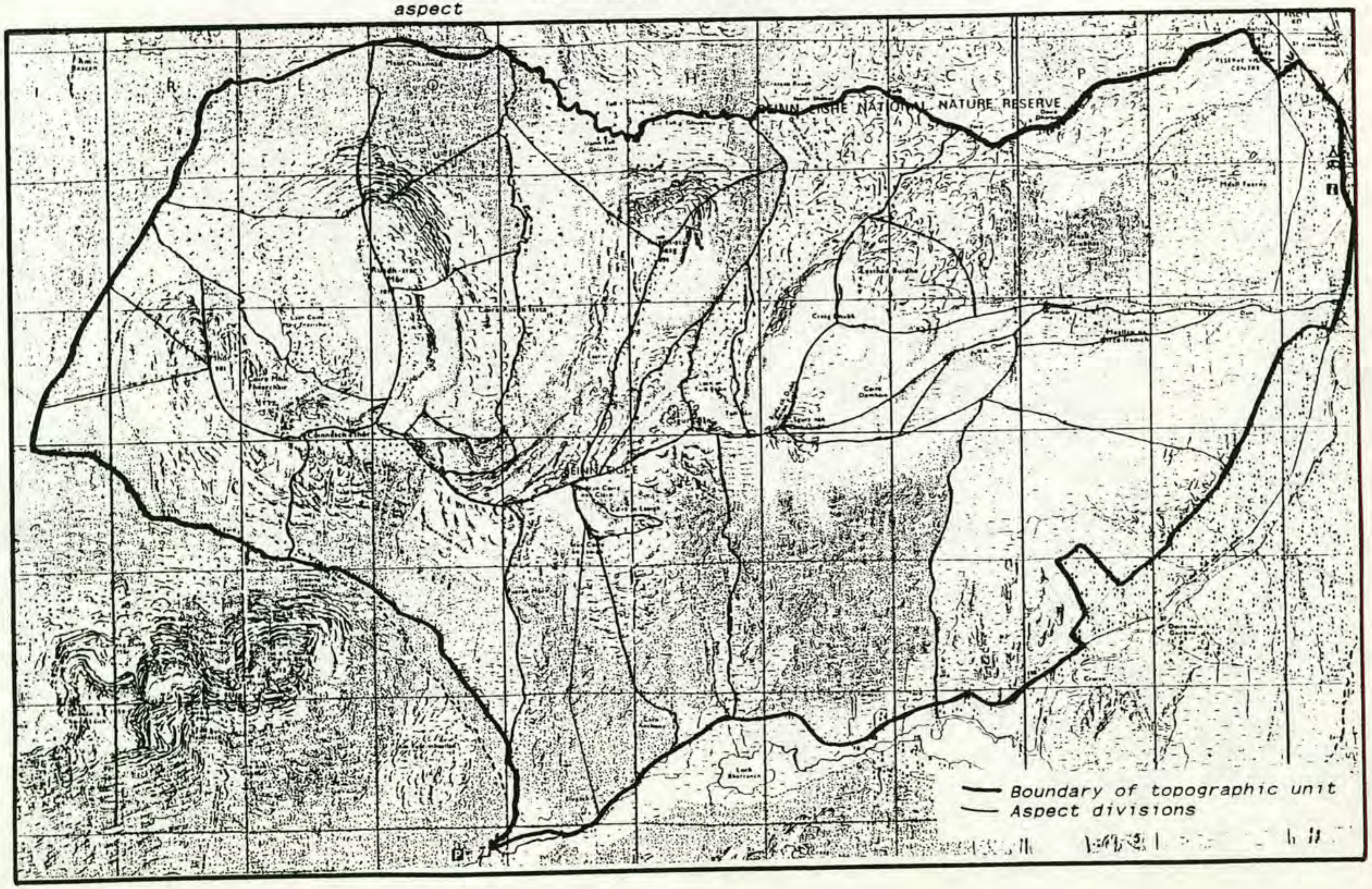
Hepatic mats have been recorded by the UVS in the damp *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* (H21) heaths on the north faces of Ruadh-stac Mor and Ruadh - stac Beag and are also known from the *Vaccinium myrtillus - Racomitrium lanuginosum* (H20) heaths in Coire Mhic Fhearchair (McVean & Ratcliffe 1962). The distributions of the individual species have not been systematically recorded, although *Pleurozia purpurea* is widespread in the bogs and wet heaths (McVean & Ratcliffe 1962).

4.2 Methods

Completely random sampling was impracticable on this wild, rocky terrain so the hill ground was stratified by aspect and altitude. The sampled area was the entire topographic unit of Beinn Eighe excluding cliffs, scree, open water, roads, paths and any man-made constructions. (A topographic unit includes the hillsides on each aspect from top to bottom and is delimited by rivers or the middle of dry glens or valleys.)

The area was divided into sections each of which sloped more-or-less towards one of eight compass points (north, north-east, east, south-east, south, south-west, west and north-west), based on the 1:25,000 Ordnance Survey map of the site (fig.4.1). Small areas within each section which sloped in different directions from the main slope (such as streamsides) were ignored. Two sections were chosen from each aspect class, ensuring the widest practicable spatial separation. Each selected slope was sampled at the 100m contours. Three 1m x 5m quadrats were taken at each 100m with the long axis of the quadrat parallel to the contours. The quadrats were evenly distributed over the slope without prejudice to the distribution of the hepatic mat. This objective survey could then be contrasted with the results of Chapters 3 and 5 where quadrats were chosen subjectively to represent communities recognised in the field.

Figure 4.1 The study site of Beinn Eighe showing the divisions into sections of more or less uniform aspect



All plant species in each quadrat were recorded, except for crustose lichens growing on the rocks or shrubs. Aspect (° east of north) was measured by compass and slope (° from horizontal) by clinometer at the centre of each quadrat. The percentage cover of rock, shrubs, herbs and lower plants was estimated by eye. Evidence of red deer was assessed on a scale of 1 to 5: (1) Deer excluded by fence (occasional marauding individuals), (2) Present but no signs of trampling or browsing, (3) Droppings present within the quadrat, (4) Hoofprints and grazed shoots in quadrat and (5) Flattened patches of vegetation, shrubs killed. Other signs of management such as burning and tree-planting were noted.

The quadrat data were ordinated using detrended correspondence analysis (DECORANA) (Hill & Gauch 1980) and classified using two-way indicator species analysis (TWINSPAN) (Hill 1979). Rare species were not down-weighted. The TWINSPAN end-groups had to have at least 6 species in them. Relationships between species and environmental variables were investigated using analysis of variance.

In addition to the quadrat survey, stands of vegetation with a hepatic mat community - defined as cushions of at least 5 of the constituent species growing in intimate mixtures - were mapped at a scale of 1:25,000

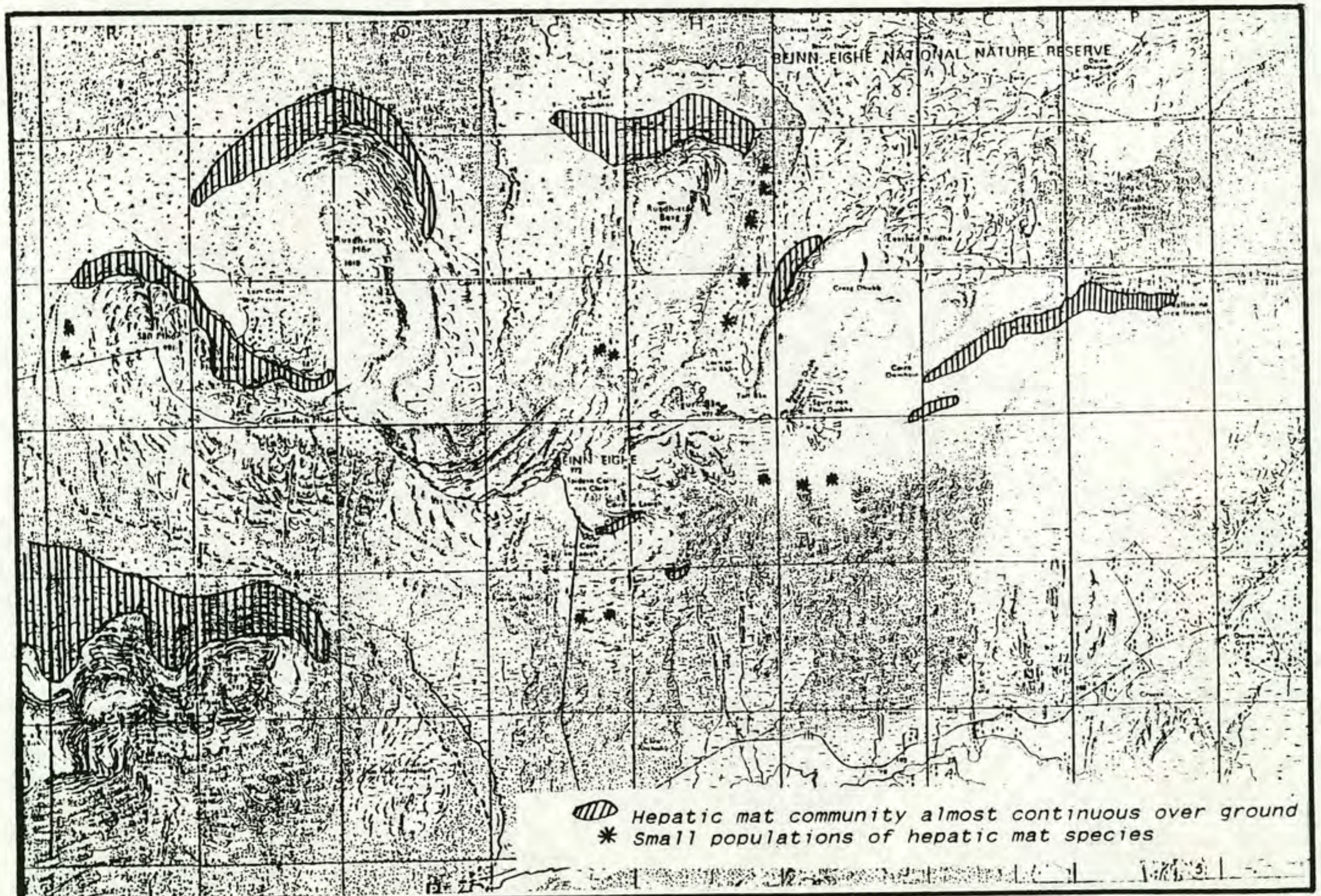
4.3. The hepatic mat community on Beinn Eighe

The hepatic mat community was extensive on the north-facing slopes of Ruadh-stac Mor, Ruadh-stac Beag and Sail Mhor and in Coires Domhain and Mhic Fhearchair (fig.4.2). Most of the stands were in damp *Calluna-Vaccinium-Sphagnum* heath. In Coire Mhic Fhearchair the community was in *Vaccinium-Empetrum* heath. The hepatic mats on the west-facing slope of Creag Dubh were in *Nardus stricta* grassland in hollows among quartzite moraine where snow lies late. The two small stands in Coire an Laoigh were where there was a ridge or knoll with a slope facing north. Here there was an abrupt change in the vegetation from wet heaths with no hepatic mat liverworts other than *Pleurozia purpurea* to damp *Calluna* heath with a luxuriant carpet of liverworts, coinciding with the change in exposure from south to north-east. There were scattered examples of the community on the west-facing side of Sail Mhor (with *Anastrepta orcadensis*, *Bazzania tricrenata*, *Herbertus aduncus*, *Lepidozia pearsonii*, *Plagiochila carringtonii* and *Scapania gracilis*), on the slopes below Stuc Coire an Laoigh (with *Anastrepta orcadensis*, *Herbertus aduncus*, *Plagiochila spinulosa* and *Scapania gracilis*) and in prostrate *Calluna vulgaris* - *Racomitrium lanuginosum* heath on the south-facing slope below Sgurr nan Fhir Dhuibhe (with *Anastrepta orcadensis*, *Bazzania tricrenata*, *Mylia taylorii*, *Plagiochila carringtonii*, *Pleurozia purpurea*, *Scapania gracilis*, *S. ornithopodioides* and *S. nimbosa*).

4.4 Results of the quadrat survey

One hundred and sixty-five quadrats were taken in the 16

Figure 4.2 The distribution of the hepatic mat community on Beinn Eighe



sections. Between 6 and 18 quadrats were taken in a section, depending on the length of the slope. The altitudinal range sampled was from 100m in Glen Torridon to 700m in Coires Mhic Fhearchair and Domhain and on the north-west-facing slope of Sail Mhor.

4.4.1. Plants recorded in the quadrats

One hundred and eighty-six species were recorded: 15 hepatic mat liverworts and 84 other bryophyte species, 75 vascular plants, 11 lichens and one alga (Appendix 2). Some of the hepatic mat species were among the most frequently-recorded plants on the hill (table 4.1). The most frequent species in this study was *Calluna vulgaris*, followed by *Racomitrium lanuginosum*. Other common mosses were *Hylocomium splendens*, *Hypnum jutlandicum*, *Sphagnum capillifolium*, *Rhytidiadelphus loreus* and *Dicranum scoparium*. *Diplophyllum albicans* was the only common liverwort other than the hepatic mat species and lichens were infrequent apart from *Cladonia arbuscula* and *C.uncialis*. *Pleurozia purpurea* was the most frequent hepatic mat species, followed by *Scapania gracilis* and *Anastrepta orcadensis*. *Lepidozia pearsonii*, *Scapania nimbosa* and *Mastigophora woodsii* were scarce. *Plagiochila spinulosa* and *Anastrophyllum joergensenii* were rare. *Anastrophyllum joergensenii* was discovered new to the site. It was recorded in quadrats on Ruadh-stac Beag and in Coire Mhic Fhearchair.

Hepatic mat species were recorded in all but 30 of the

Table 4.1. Numbers of hepatic mat species compared with the number of vascular plants, other bryophytes and lichens present in at least 50 of 165 1m x 5m quadrats on Beinn Eighe

Hepatic mat species	Number
Pleurozia purpurea	112
Scapania gracilis	83
Anastrepta orcadensis	62
Bazzania tricrenata	50
Mylia taylorii	50
Plagiochila carringtonii	39
Herbertus aduncus	36
Scapania ornithopodioides	33
Anastrophyllum donnianum	32
Bazzania pearsonii	31
Lepidozia pearsonii	23
Scapania nimbosa	20
Mastigophora woodsii	15
Plagiochila spinulosa	6
Anastrophyllum joergensenii	2

Lichens	
Cladonia arbuscula	133
Cladonia uncialis	132

Vascular plants	Number
Calluna vulgaris	156
Potentilla erecta	134
Scirpus cespitosus	129
Vaccinium myrtillus	100
Molinia caerulea	96
Deschampsia flexuosa	79
Erica cinerea	68
Empetrum nigrum	62
Narthecium ossifragum	50
Succisa pratensis	50

Other bryophytes	Number
Racomitrium lanuginosum	146
Diplophyllum albicans	115
Hypnum jutlandicum	110
Hylocomium splendens	93
Sphagnum capillifolium	89
Rhytidiadelphus loreus	79
Dicranum scoparium	72
Pleurozium schreberi	53

quadrats, although 45 quadrats had only one of the species (fig.4.3). Most of these were records of *Pleurozia purpurea*, although infrequently there was *Scapania gracilis* and rarely *Anastrepta orcadensis* or *Mylia taylorii*. Several quadrats had large numbers of hepatic mat liverworts: 14 quadrats had 10 and two had 13 out of a possible 15 species.

4.4.2 Distribution of the hepatic mat species in relation to aspect, altitude and slope

The highest numbers of species were recorded on slopes facing north, north-east and north-west (table 4.2). Moderate numbers of species were seen on slopes facing east, west, south-east and south but these tended to be in localised patches and the mean number of species in a quadrat was small. Slopes facing south-west had a poor flora and a low mean number of species in a quadrat.

A one-way analysis of variance of the mean number of species in a quadrat at 500m ASL (the only altitude sampled on every aspect) showed that the differences between slopes on different aspects were significant (table 4.3).

Some of the hepatic mat species were recorded on a wider range of aspect than others (fig.4.4), although all of them were most abundant on the northern slopes and least abundant or absent on the slopes facing south-west. Only *Pleurozia purpurea*, *Scapania gracilis*, *Anastrepta orcadensis* and *Mylia*

Figure 4.3 The frequency distribution of number of hepatic mat species in 165 5m x 1m quadrats on Beinn Eighe.

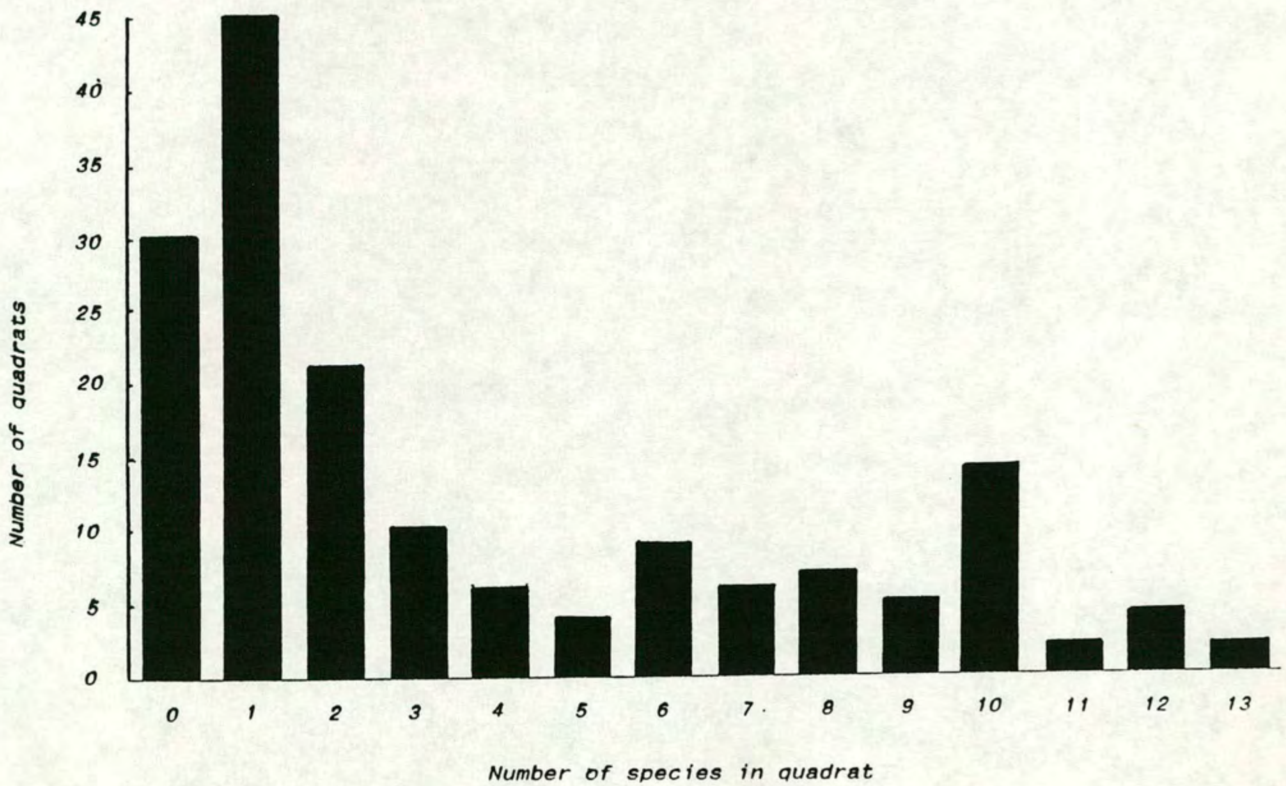


Table 4.2. Mean number of hepatic mat species recorded in a quadrat on each sample of two slopes facing each of eight aspects.

Aspect	number of quadrats	max. no. of species in quadrat	mean no. of species in quadrat	standard error
North	21	13	7.48	0.78
North-east	12	11	8.92	0.60
East	27	7	2.04	0.40
South-east	27	4	1.56	0.22
South	30	7	1.57	0.31
South-west	15	3	0.60	0.24
West	18	8	2.78	0.65
North-west	15	13	8.47	0.91

Table 4.3 One-way analysis of variance of the number of hepatic mat species in a quadrat at 500m on slopes of eight different aspects on Beinn Eighe.

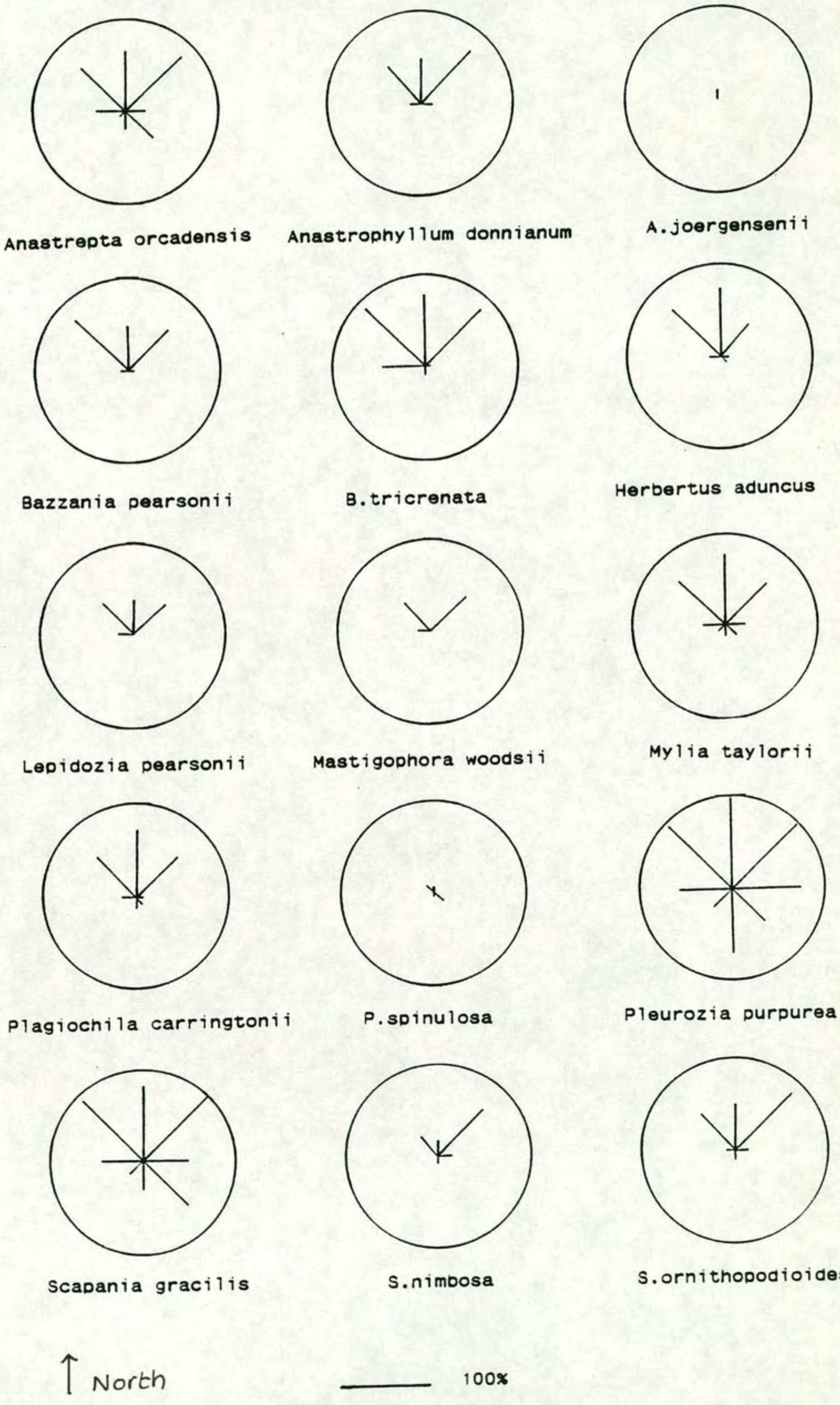
Source	df	SS	F	P
Aspect	7	136.6	4.1	0.042
Error	7	33.4		

The eight aspects were north, north-east, east, south-east, south, south-west, west and north-west.

Table 4.4. Mean number of hepatic mat species recorded at each altitude above sea-level in 165 quadrats on Beinn Eighe.

Altitude (m)	number of quadrats	mean number of species	standard error
100	3	1.33	0.88
200	18	1.06	0.17
300	24	1.92	0.46
400	36	3.25	0.56
500	45	4.33	0.59
600	30	6.03	0.79
700	9	3.56	1.43

Figure 4.4 The distribution of the hepatic mat species as percentage occurrence in quadrats on Beinn Eighe in relation to aspect.

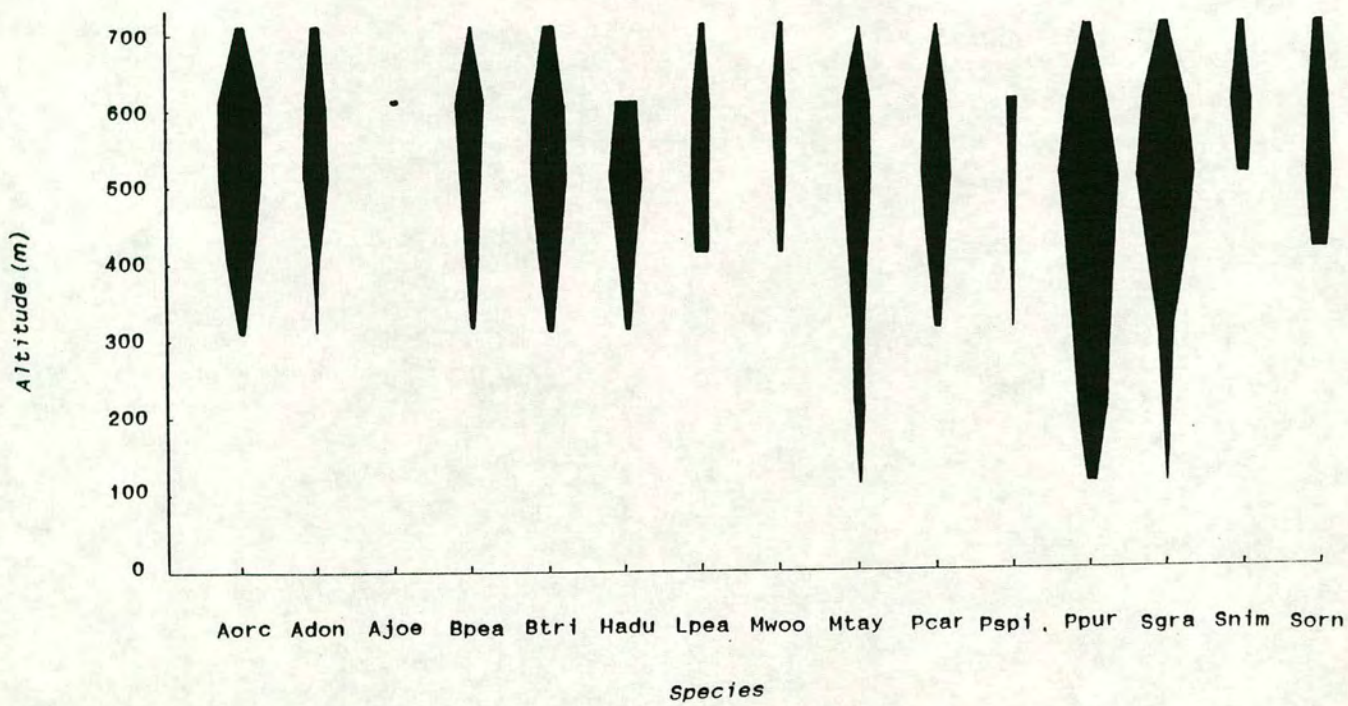


taylorii were recorded on all aspects. *Anastrophyllum joergensenii* had the narrowest range: both samples were on north-facing slopes. The species does occur on slopes facing north-west, north-east and east elsewhere on the hill but is not common anywhere (personal observation). *Mastigophora woodsii* and *Scapania nimbosa* were most frequent on slopes facing north-east and north-west but were curiously rare on the north-facing slopes. *Anastrophyllum donnianum, Bazzania pearsonii* and *Lepidozia pearsonii* were all on the northern slopes of the hill, with records from due west round to north-east or east. *Herbertus aduncus*, *Plagiochila carringtonii* and *Scapania ornithopodioides* were most frequent on aspects between north-west and north-east, although all three were occasional on slopes facing east and west.

Every sampled altitude from 100 to 700m ASL had a record of at least one of the hepatic mat species (fig.4.5). Few of the records were below 300m; most of these were records of *Pleurozia purpurea* with occasional *Scapania gracilis* or *Mylia taylorii*. *Herbertus aduncus* and *Plagiochila spinulosa* were absent from the highest altitude, while *Anastrophyllum joergensenii* and *Scapania nimbosa* were confined to the quadrats at high altitudes. The highest numbers of hepatic mat species were recorded in quadrats at 600m and the lowest numbers at 300m (table 4.4).

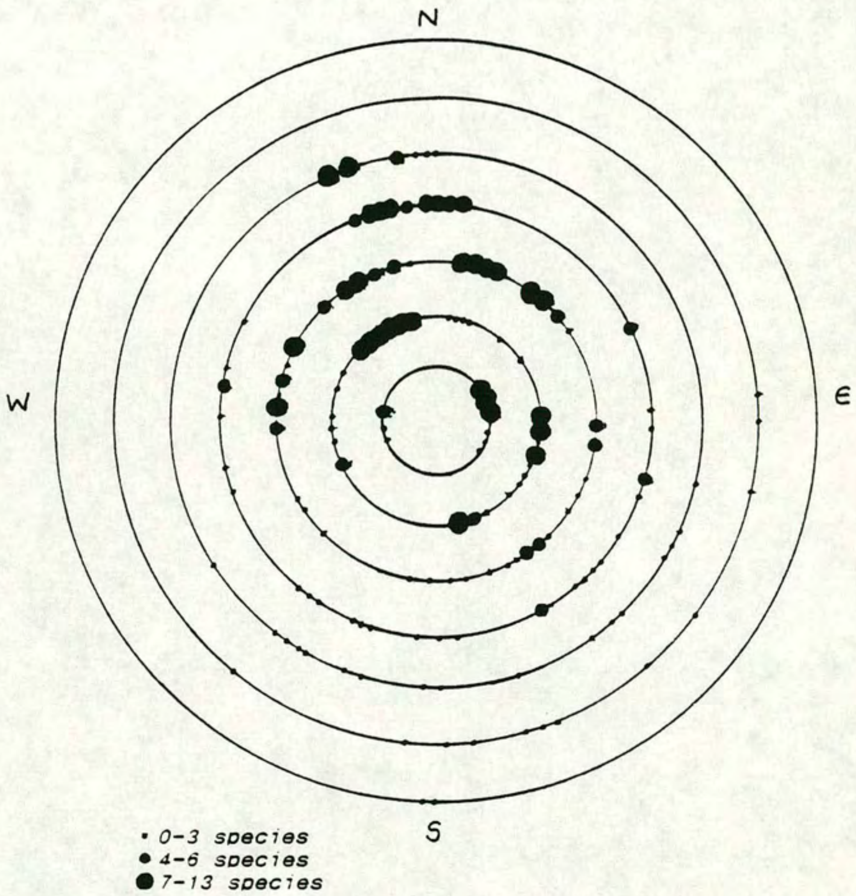
The distribution of species-richness in relation to altitude was affected by aspect (fig.4.6). The north slope was most different from the south; similarly the north-east slope

Figure 4.5 The frequency over the recorded altitudinal range of each of the hepatic mat species on Beinn Eighe



See fig.4.4 for full names of species. ■ *10 records*

Figure 4.6 Number of hepatic mat species in quadrats on Beinn Eighe in relation to aspect and altitude



Circles are at 100m intervals from 100m (outer circle) to 700m (inner circle).

differed from the south-west and the north-west from the south-east. There were always more of the species on the northerly aspects and they were more evenly distributed in relation to altitude. Four or more species were occasionally recorded in quadrats sloping towards the south-east or south, but only at altitudes of 600m or more. Note that even on the northern slopes there were several quadrats with few hepatic mat species, showing their discontinuous distribution.

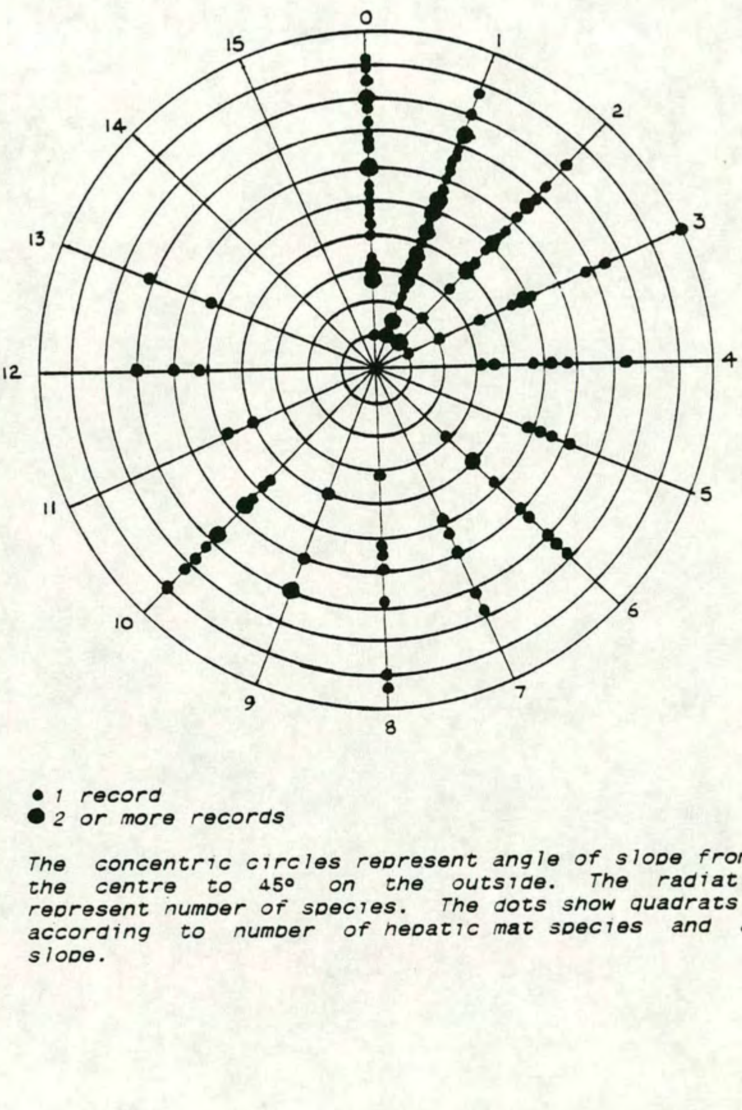
The relationship between number of species and steepness of slope (fig.4.7) showed that the highest numbers of species were on moderately steep slopes between 20° and 35° from horizontal, although quadrats with 10 or more species were recorded on slopes ranging from 15° to 40°. Shallow slopes below 10° from horizontal had few species (Slopes steeper than 45° were considered to be inaccessible and were not sampled in this survey.)

4.4.3. The relationships between vegetation and the hepatic mat species

a. Vegetation with hepatic mat species

Most of the quadrats with large numbers of hepatic mat species were on slopes with damp *Calluna-Vaccinium-Sphagnum* heaths (NVC H21). There were also rich assemblages at higher altitudes in *Vaccinium myrtillus - Racomitrium lanuginosum* heath (H20), *Deschampsia cespitosa-Galium saxatile* grassland

Figure 4.7 The relationship between angle of slope and number of hepatic mat species in a quadrat on Beinn Eighe



The concentric circles represent angle of slope from 0° in the centre to 45° on the outside. The radiating bars represent number of species. The dots show quadrats plotted according to number of hepatic mat species and angle of slope.

(U13) and *Calluna vulgaris-Racomitrium lanuginosum* heath (H14). *Pleurozia purpurea* was common in blanket-bogs and wet heaths; *Mylia taylorii* and *Scapania gracilis* were also occasionally recorded in bogs. The hepatic mat community was most often associated with *Calluna vulgaris, Deschampsia flexuosa, Empetrum nigrum, Potentilla erecta, Scirpus cespitosus, Vaccinium myrtillus, Dicranum scoparium, Diplophyllum albicans, Hylocomium splendens, Hypnum jutlandicum, Racomitrium lanuginosum, Rhytidiadelphus loreus, Sphagnum capillifolium, Cladonia arbuscula* and *C.uncialis.*

b. Structure of the vegetation

There was no clear relationship between the percentage cover of shrubs and herbs and the number of hepatic mat species in this survey, although the quadrats with few shrubs and few herbs were those in which bryophytes - usually *Racomitrium lanuginosum* - were dominant. There was a weak negative relationship between the percentage cover of rocks in a quadrat and the number of hepatic mat species (sum-of-squares 96.6 for rock with one degree of freedom, 15.7 for error with 79 degrees of freedom. $F = 6.13$, $p = 0.05$. The regression equation was $y = 0.11x + 2.65$. r^2 was 0.06).

4.4.4. Management

The relationship between intensity of use by red deer and number of hepatic mat species was impossible to elucidate at the scale of the quadrats, because although the deer range over most of the hill above 300m they tend to use set paths and their effects are local. The areas from which deer are excluded by fences are all below 300m - lower than any of the slopes with large numbers of hepatic mat species. This makes it look as though high numbers of species are associated with high numbers of deer when this is not necessarily true.

There were no signs of recent burning on the hill.

Pine and birch trees are colonising some of the formerly treeless slopes within the area which is fenced against deer. Pine, birch, juniper and alder saplings have been planted in various places (T.Clifford, pers.comm.)

4.4.5 Ordination and classification of the quadrats.

The ordination of the quadrat samples by detrended correspondence analysis produced a pattern in which quadrats with many hepatic mat species had a low score on axes one and two, while those with few or none of these species had high scores on both axes (fig.4.8). The quadrats with low scores on Axis 1 (with large numbers of hepatic mat species) were generally on slopes facing north-east, north or north-west, while those with high scores and few hepatic mat species tended to be on slopes facing south, south-west or south-east (fig.4.9). Similarly most of the quadrats with low scores on Axis 1 were at high altitudes, while those with high scores

Figure 4.8 The number of hepatic mat species in a quadrat plotted on the first two ordination axes of a detrended corespondence analysis (DECORANA) of 165 quadrats on Beinn Eighe

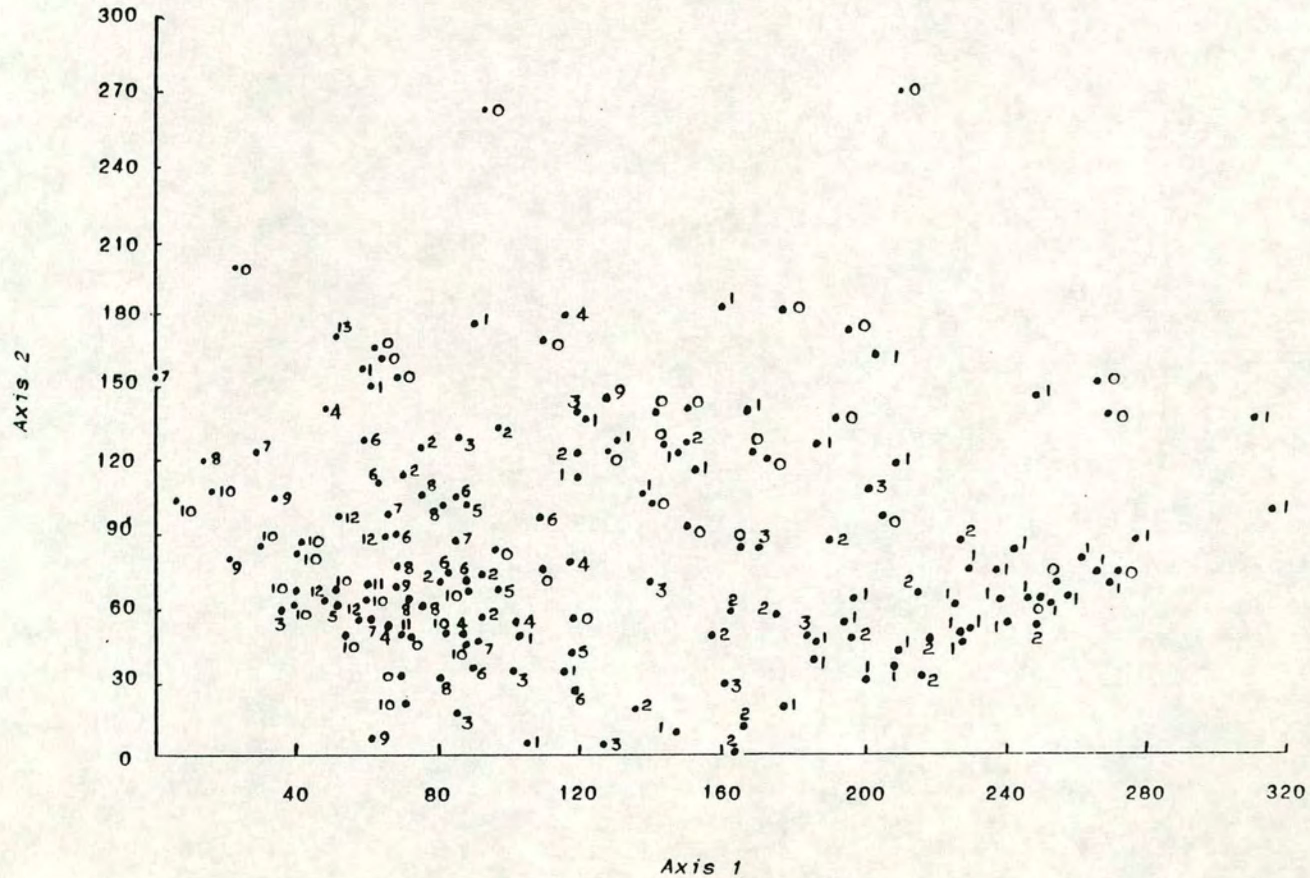
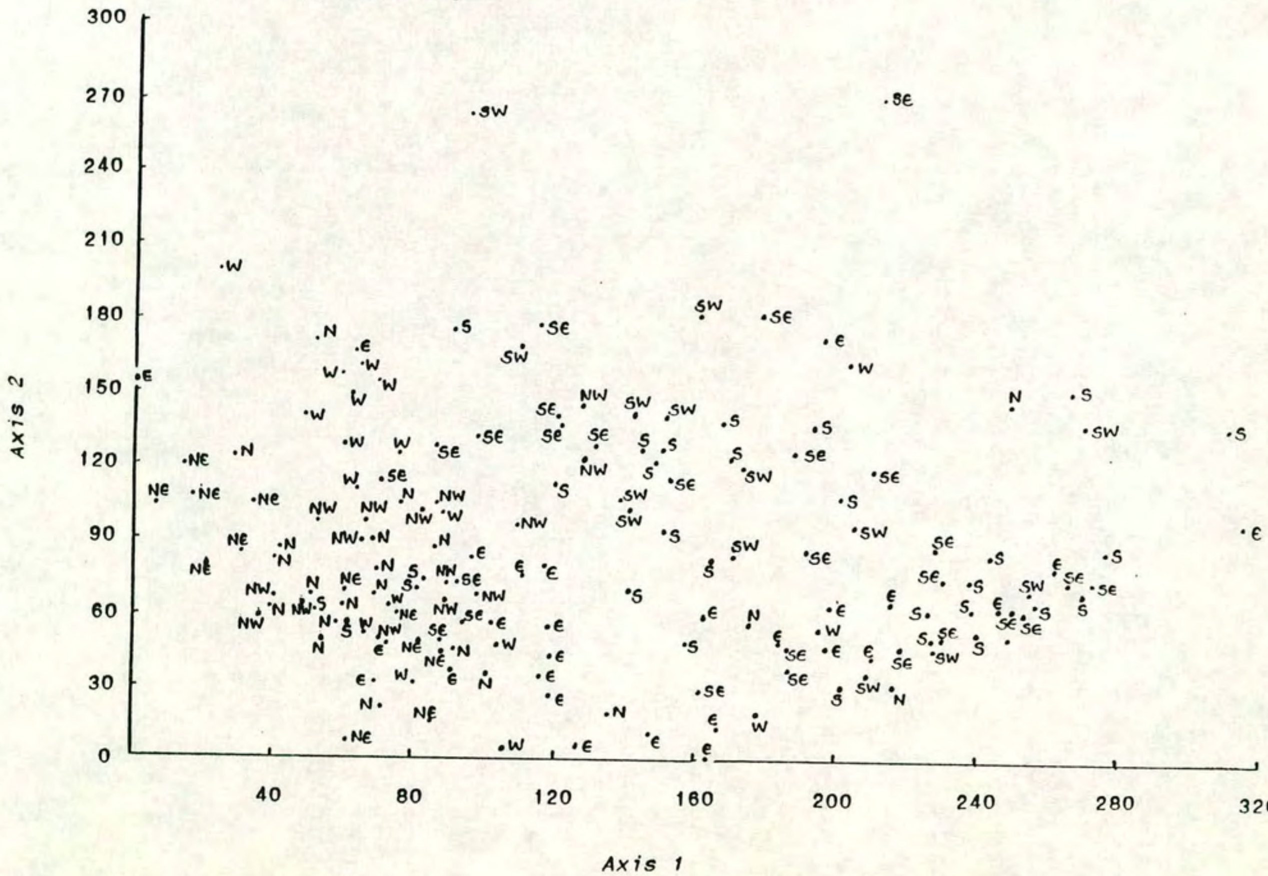


Figure 4.9 Aspect of slope superimposed on a plot of the first two ordination axes of a detrended corespondence analysis (DECORANA) of 165 quadrats on Beinn Eighe.



were at low altitudes (fig.4.10). There was also a significant negative relationship between axis 1 score and steepness of slope (1 and 156 degrees of freedom for model and for error respectively, $F = 39$, $p = 0.05$). Axis 1 (eigenvalue 0.350) seems to be related to northerly aspect and high altitude (and to a lesser extent steep slopes) with the quadrats on steep north-facing slopes at one end and those on the low south-facing boggy ground at the other. This is borne out by the ordination of the species (fig.4.11). The hepatic mat liverworts had low scores on Axis 1, while species of flat, low ground and blanket bogs such as *Myrica gale*, *Sphagnum papillosum*, *Drosera intermedia* and *D. rotundifolia* had high scores. Axis 2 (eigenvalue 0.297) seemed to be related to wetness of the ground. The ordination of species showed that plants with a low score on this axis were montane calcifuges typical of the dry quartzite scree at the eastern end of the site: *Juncus trifidus*, *Herbertus borealis*, *Juniperus communis* ssp *nana*, *Arctostaphylos alpinus*, *A. uva-ursi* and *Antennaria dioica*. The species with high scores were mostly plants of springs and flushes including *Montia fontana*, *Juncus bulbosus*, *J. effusus*, *Chrysosplenium oppositifolium*, *Epilobium anagallidifolium*, *Bryum pseudotriquetrum*, *Dicranella palustris* and *Philonotis fontana*.

The two-way indicator species analysis of the samples produced 13 end-groups (fig.4.12) which tended to consist of clusters of adjacent quadrats on the site and to make

Figure 4.10 The relationship between axis 1 score and altitude of the quadrat from a detrended correspondence analysis (DECORANA) of 165 quadrats on Beinn Eighe.

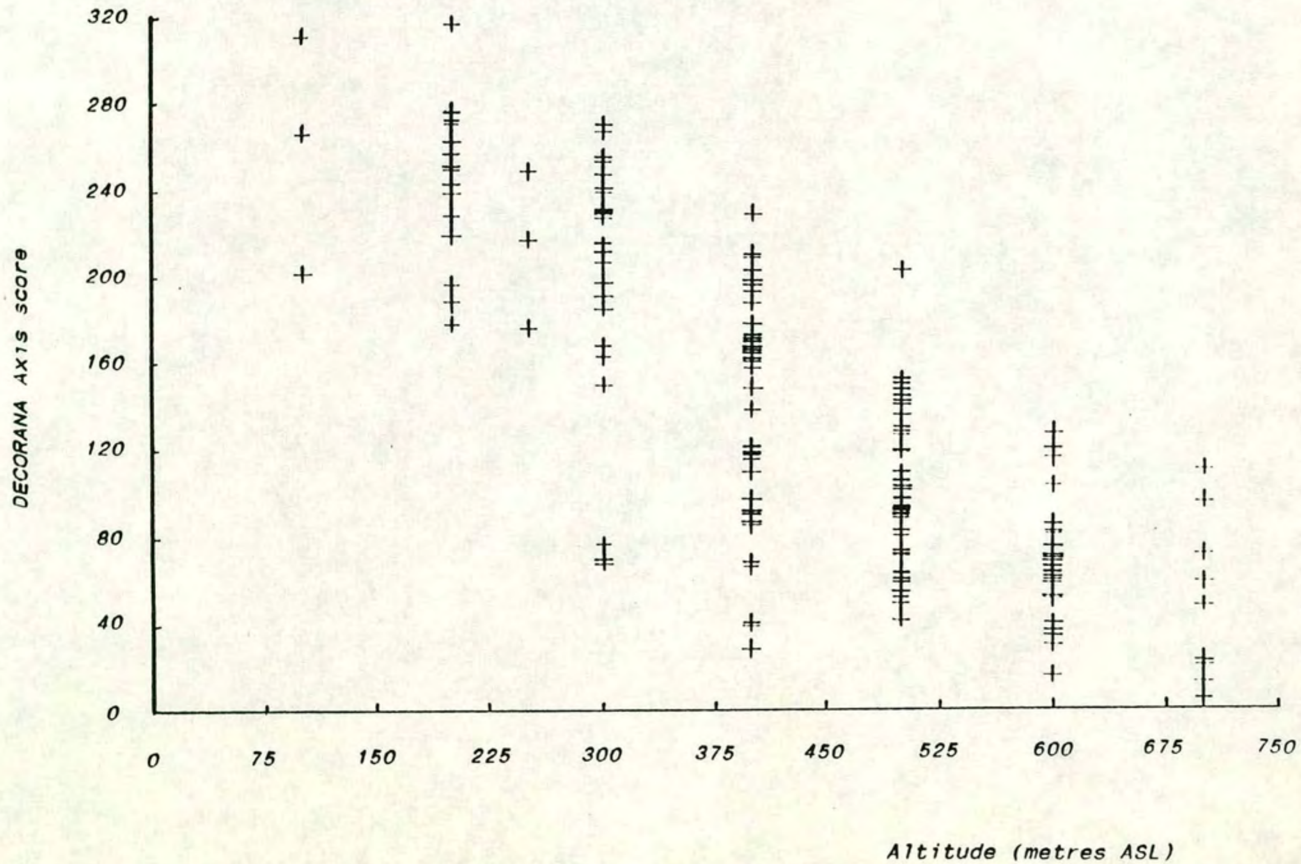


Figure 4.11 The groups of species which fall at either end of the first two ordination axes of a detrended corespondence analysis (DECORANA) of 165 quadrats on Beinn Eighe.

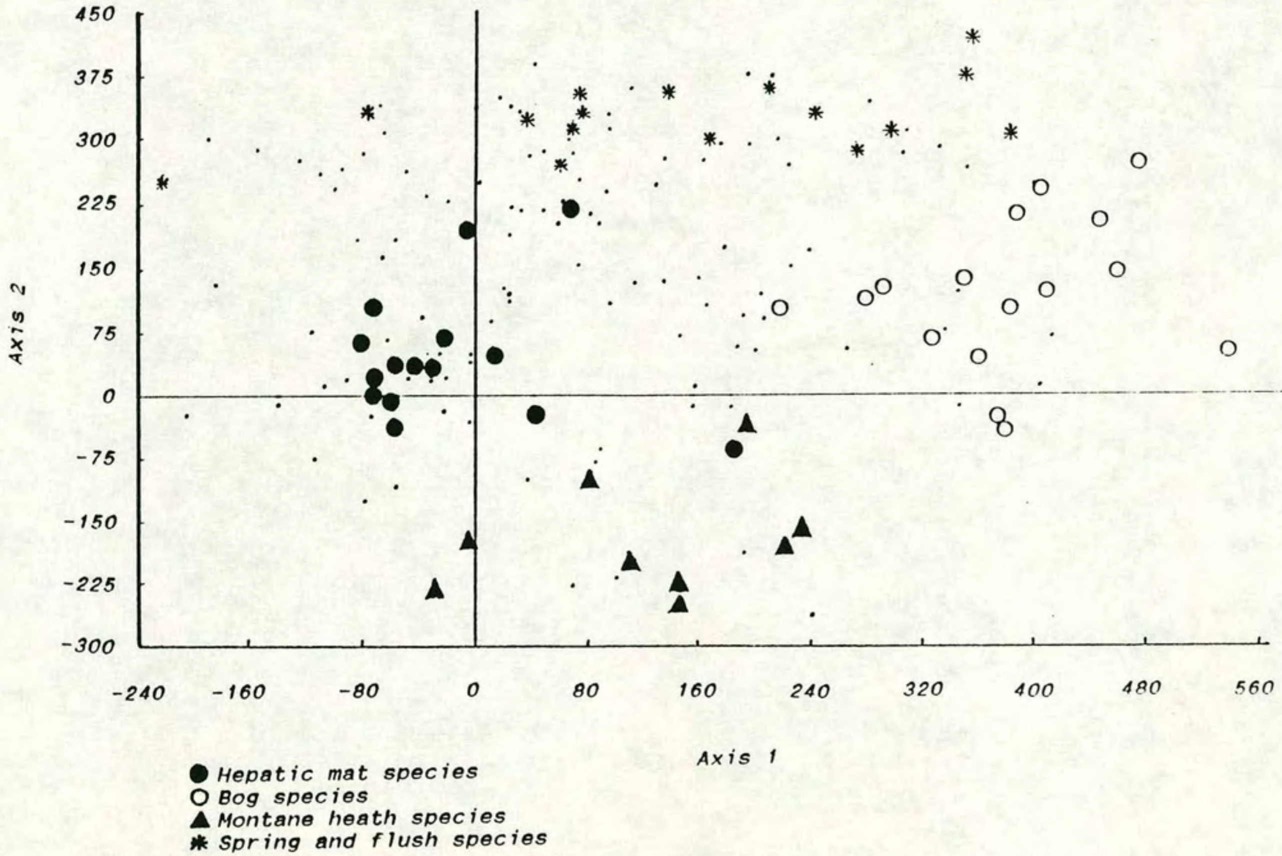
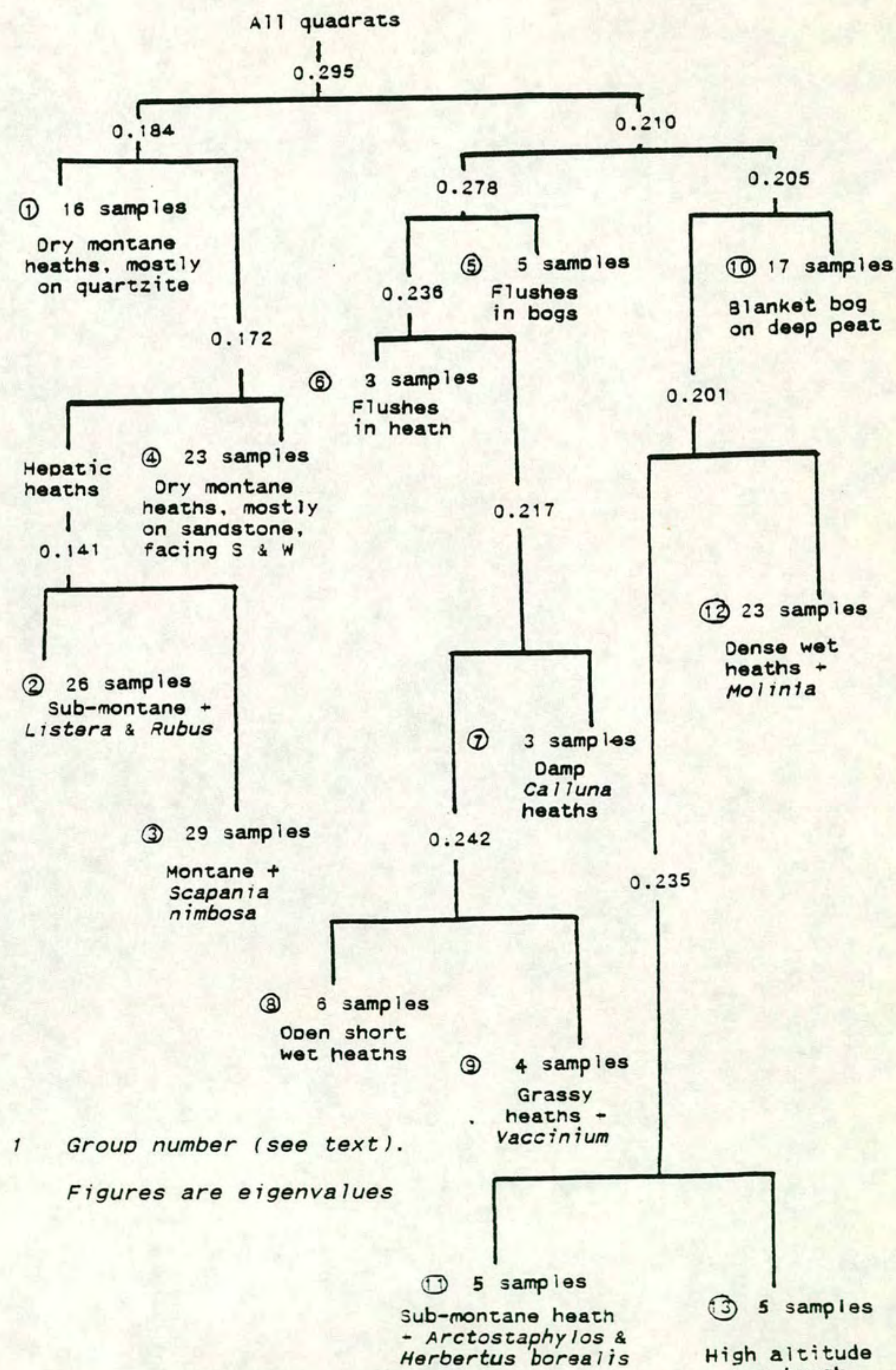


Figure 4.12. A dendrogram to show the end-groups of a two-way indicator species analysis (TWINSPAN) of 165 quadrats on Beinn Eighe.

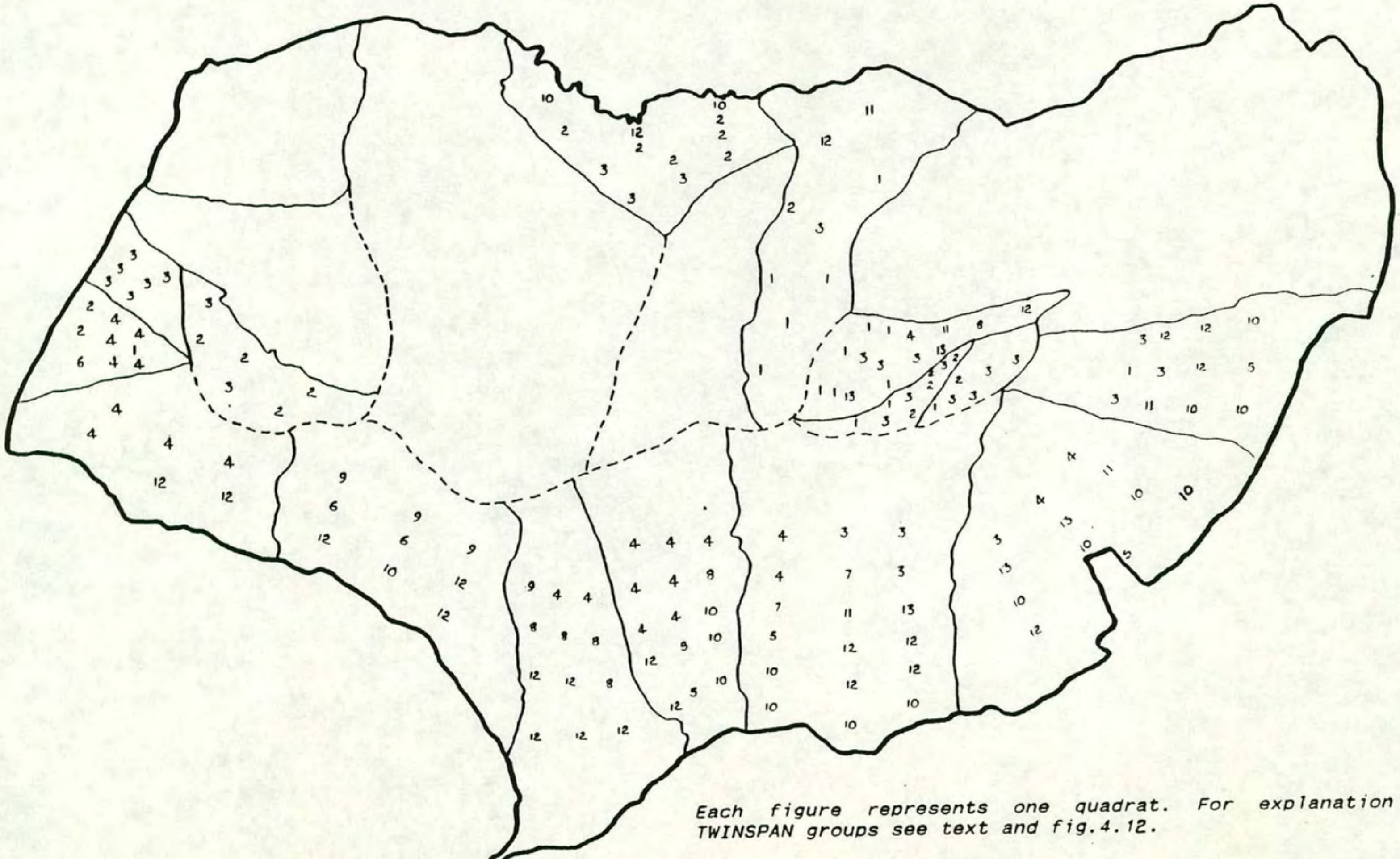


ecological sense (fig.4.13). The quadrats with a hepatic mat community came out as a distinct group which divided weakly (eigenvalue 0.141) into two sub-groups: sub-montane heaths with *Calluna* and *Sphagnum* and abundant *Listera cordata* and *Rubus chamaemorus* (group 2) and a more montane set of samples with abundant *Scapania nimbosa* and *Cetraria islandica* (group 3). Eleven of the 15 hepatic mat species were preferential for these two groups, as were the northern Atlantic moss *Dicranodontium uncinatum* and the orchid *Listera cordata.* These quadrats were almost all on the northern slopes facing between west and east; note the three quadrats in group 3 where small cushions of the hepatic mat community were recorded high on the south-facing slope.

Group 1 was a distinctive set of quadrats from dry montane heathland, almost exclusively on quartzite scree at the eastern end of the site. The preferential species included *Herbertus borealis, Juniperus communis* ssp *nana, Vaccinium uliginosum* and *Carex bigelowii.*

The samples in group 4 were from high-altitude dry heaths with prostrate *Calluna vulgaris* growing with *Racomitrium lanuginosum* and lichens. They were all on slopes facing between west and east. *Carex bigelowii, C.binervis, Erica cinerea* and *Frullania tamarisci* were preferential species.
Groups 5 and 6 were quadrats where wet heaths or blanket-bogs were flushed with water and where the flora was augmented by species such as *Juncus bulbosus, J.effusus, Scapania*

Figure 4.13 An outline of Beinn Eighe showing the TWINSPAN end-groups of each of 165 quadrats.



Each figure represents one quadrat. For explanation of TWINSPAN groups see text and fig.4.12.

— Sampled section
--- Ridge

undulata, *Philonotis fontana*, *Saxifraga stellaris* and *Viola palustris*. The quadrats in group 5 were from flushed bogs and also contained species of ombrogenous conditions including *Sphagnum papillosum* and *Eriophorum vaginatum*. They were all low on the south or south-east slopes. The quadrats in group 6 were from wet heaths facing south-west or west which were interrupted by bryophyte-dominated springs.

Group 7 was a set of three quadrats taken in damp heathland dominated by *Calluna vulgaris* but lacking the hepatic mat species. There were stands on the south-facing slope where peat has built up on a narrow shelf of ground, and on the north-facing slope of Ruadh-stac Mhor where the hepatic mat species were locally absent.

Group 8 was a set of quadrats on stony ground on the south-facing slope, with thin peat and a sparse flora of wet heath species such as *Narthecium ossifragum*, *Dactylorhiza maculata*, *Calluna vulgaris* and *Scirpus cespitosus*. The hepatic mat species *Pleurozia purpurea* and *Scapania gracilis* were preferential for this group.

Group 9 comprised quadrats taken at high altitude on the south and south-west slopes where *Calluna* heath was giving way to a montane *Vaccinium myrtillus* heath with *Empetrum nigrum* and *Nardus stricta*.

Group 10 consisted of quadrats from ombrogenous blanket-mire on deep peat. Quadrats in this group were concentrated on low ground in Glen Torridon. The group was also represented in bogs at 400m ASL in Toll a' Ghiubhais below Ruadh-stac Beag.

The samples in group 11 were all at the eastern end of the site and, like those in group 1, were distinguished by the presence of *Herbertus borealis.* However the vegetation in this case was a closed heath with *Calluna* and *Arctostaphylos uva-ursi.* It was on steeper slopes than the *Juniperus* - dominated vegetation represented by group 1. *Anastrepta orcadensis* and *Scapania gracilis* were preferential for the group and one quadrat included *Plagiochila carringtonii.*

The vegetation in group 12 was a wet heath dominated by *Molinia caerulea* with sparse *Calluna vulgaris.* Most stands were on shallow peat and gentle slopes on the south side of the hill, although one quadrat was on flushed peat in Toll a'Ghiubhais. The preferential species were *Carex nigra, Sphagnum auriculatum* and *S.papillosum.*

Finally, group 13 represented high-altitude wet heath at the transition between sub-montane and montane vegetation. It was distinguished by the presence of the montane sedge *Carex bigelowii* as well as the typical wet heath species *Erica tetralix, Calluna* and *Dactylorhiza maculata.* The quadrats in this group were all on the south and east slopes of the hill.

In both classification and ordination the quadrats with a hepatic mat community appeared as a distinct group of associated species.

4.5 Discussion

The results support the observations that the hepatic mat species and the community they form are most abundant on steep, shaded slopes facing between north-west and east and at around 600m ASL (Macvicar 1910, McVean & Ratcliffe 1962, Ratcliffe 1968, Hobbs 1988, Averis 1991). They also show that most of the species grow on a wide range of aspects and that stands of the community occur where earlier workers might not have expected them.

The most surprising discovery in the study was of nine of the liverworts including *Plagiochila carringtonii, Scapania ornithopodioides* and *S.nimbosa* forming a hepatic mat in prostrate *Calluna vulgaris - Racomitrium lanuginosum* heath on a south-facing slope, albeit at high altitude. This shows the importance of microclimate and that small areas of suitable habitat, even on exposed aspects, can sustain populations of these species. There may be many more stands of the hepatic mat community awaiting discovery on south-facing slopes which have not yet attracted bryologists to explore them.

The results suggest that aspect is the most important of the measured environmental variables as a determinant of the number and abundance of the hepatic mat species. Some of the species are obviously more tolerant of exposure to direct sun and wind than others. The south-facing slopes have more species than those facing south-west: this may be related to the direction of the prevailing wind and to diurnal variation in temperature. On Beinn Eighe, as in all of Britain, south-westerly winds prevail. South-west-facing slopes are the ones most affected by direct sunlight. The air, soil and vegetation are driest in the afternoon, when the sun is high in the sky and they are fully exposed to it. In the northern hemisphere, slopes facing south-west have the highest surface temperatures (Geiger 1971). Slopes facing north and east probably have more species because the oceanic climate is enhanced here: they are the coolest, shadiest and most sheltered places (Geiger 1971, Clausen 1952). Analysis of hemispherical photographs taken vertically have shown that steep north-facing slopes with a similar bryophyte flora in southern Ireland and north-west Scotland do not experience direct sunlight between August and April and have less than half the total daily irradiance received by level ground at the same latitude (Proctor 1980b). However steep north-facing slopes do experience direct sunlight in mid-summer (Proctor 1980b, Chapter 5) and the surfaces of the liverwort cushions dry out for several days at a time (personal observation). McVean and Ratcliffe (1962) suggest that the confinement to north-facing slopes may be as much to do with lack of disturbance as with microclimate, because these damp, rocky slopes are difficult to burn. On the northern slopes of Ruadh-stac Beag there are places where the hepatic mat species grow on shelves of flat ground surrounded by scree and cliffs, often on fairly deep peat (personal observation). Ratcliffe (pers. comm.) described an unburnt island in Loch an Eoin, Beinn Damph forest, which has a hepatic mat on level ground. On Beinn Alligin, just west of Beinn Eighe, there is a boulder-field which slopes gently to the south-east and has a superb, well-developed hepatic community among and on the rocks (Chapter 3). In this case, however, the rocks must provide local shade and shelter and reduce the windspeed, thereby reducing the rate of evaporation.

Pleurozia purpurea, Scapania gracilis, Mylia taylorii and *Anastrepta orcadensis* were the most widely-distributed hepatic mat species on Beinn Eighe and also are the commonest nationally. This suggests that they are ecologically less exacting than the rarer species.

The vegetation sampled by the 165 quadrats was mostly dwarf shrub heath, ranging from wet heaths with *Molinia caerulea, Scirpus cespitosus* and *Sphagnum capillifolium* to dry ones with *Calluna vulgaris* and *Potentilla erecta. Racomitrium lanuginosum* heaths and other montane communities were under-represented in this sample. Many of them are inaccessible from below (slopes were worked from the bottom upwards) because of cliffs and scree running across the slope. It was not surprising to find no correlations between the structure of the vegetation or the amount of rock. Most of the slopes on the site are rocky and dwarf-shrubs dominate on all but the highest ground.

While the results suggest that the hepatic mat species may not be strictly confined to north-facing slopes after all, one must be cautious in extrapolating from these results to other hills. Beinn Eighe is in a region with an extremely oceanic climate and this alone may make conditions suitable for the species over a wider range of aspect than they can tolerate elsewhere in the country. Even on Beinn Eighe it is difficult to compare different slopes. The south-facing slopes are longer and smoother than the northern ones. There are few north-east-facing slopes and they are all at high altitude. The south-west-facing slopes are all at the western end of the hill. There is more quartzite in the east and more sandstone in the west. Nevertheless this study has shown that on this hill at least the hepatic mat species are relatively widely distributed plants which are able to grow together as a community wherever conditions are suitable. Suitable conditions obtain most often on the steep north-facing slopes which the community has always been thought to prefer, but smaller stands develop even on southern slopes.

The results suggest that the species avoid exposure to direct afternoon sunlight, strong winds and exposed situations. This, together with their known intolerance of drought (Ratcliffe 1968) implies that their distribution is most limited by the degree to which water is lost from their habitats. This will be discussed further in Chapters 5 and 6.

CHAPTER FIVE

THE FINE STRUCTURE AND MICROHABITAT OF THE LIVERWORT COMMUNITY

5.1 Introduction

What is the liverwort community really like? Is there any evidence that the species depend on each other, or do they just share a habitat which is favourable for them all? Which are the common members of the assemblage, and which are rare? How closely are they mixed: is the community an intimate mosaic of shoots or a patchwork of single-species cushions?

Small-scale patterning within the hepatic mat community was investigated on the north-facing slopes of Stuc a' Choire Dhuibh Bhig (NG9458, the eastern summit of Liathach in Wester Ross) to find the number of hepatic mat species on the hillside, the vascular plants, bryophytes and lichens associated with the liverworts, the distribution of species within individual patches of the hepatic mat and whether there were associations between species.

There is a hepatic mat on the north-facing slope of Liathach, but not on the south-facing slope of Beinn Eighe at the other side of Coire Dubh Mor. Measurements were made to compare the environmental conditions experienced by bryophytes on either side of the corrie.

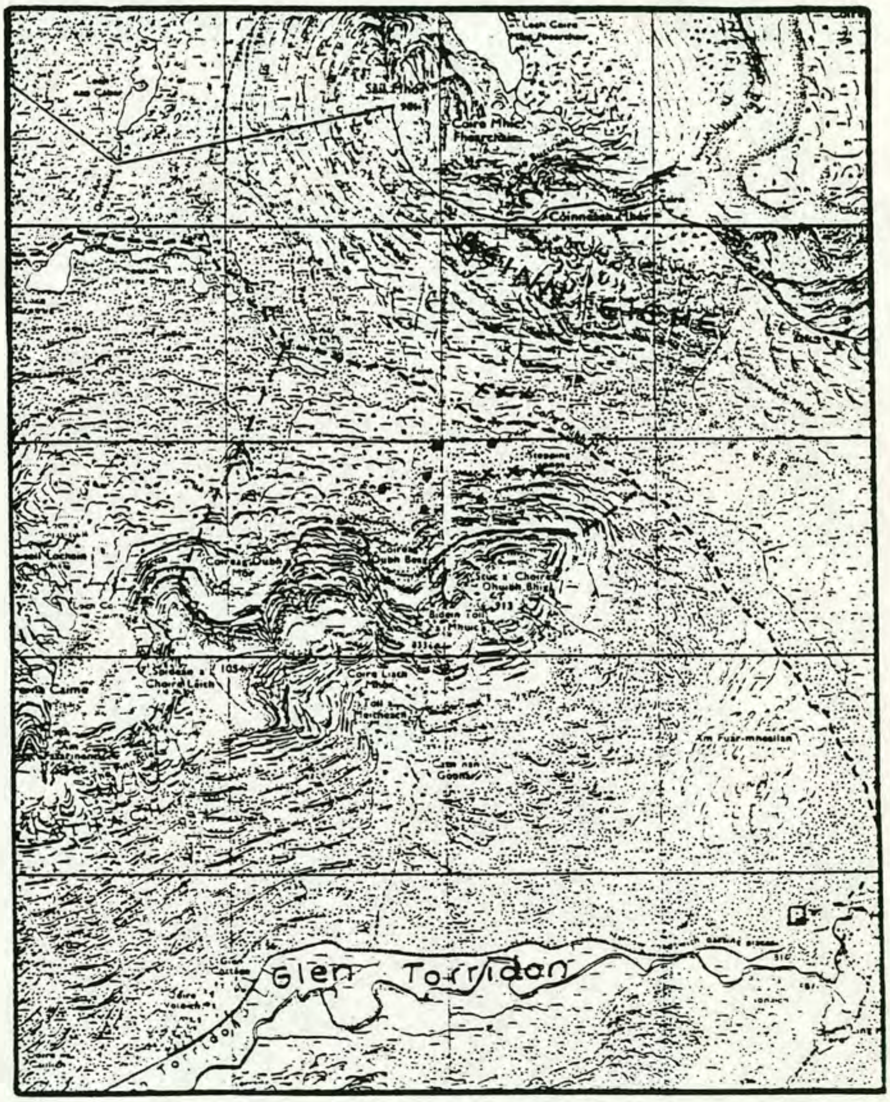
Site description

The area of study covered about 2km^2 of the north-facing slope of Stuc a' Choire Dhuibh Bhig between the valley floor at about 360m and the cliffs at around 650m (fig. 5.1). The slope is broken with rock outcrops and scattered with boulders. Tiers of cliffs rise above the slope from 650m to over 900m. The rock is Torridonian sandstone. Shallow peat on the lower slope gives way to humic rankers and coarse sandy soil on the steeper ground higher up. Several small streams run down the slope to join the Allt a' Choire Dhuibh Mhoir.

The vegetation is a mosaic of damp *Calluna vulgaris* heath with *Sphagnum capillifolium, Vaccinium myrtillus, Deschampsia flexuosa* and *Empetrum nigrum* (NVC H21) and wet heath with *Calluna vulgaris, Scirpus cespitosus, Molinia caerulea* and *Erica tetralix* (M15). With increasing altitude the *Calluna*-dominated heaths are replaced by a montane community of *Vaccinium myrtillus, Empetrum nigrum* and *Racomitrium lanuginosum* (H20). There are small *Nardus stricta* snow-beds (U7) and montane *Deschampsia cespitosa* grasslands (U13) in sheltered places below the cliffs and in gullies.

The hepatic mat community occurred in discontinuous mats and patches from below 400m to over 650m. On the lower slopes the community tended to form broad mats partly lying on the ground and partly supported by stems of *Calluna*. The larger

Figure 5.1 The study site on Liathach, Wester Ross



● 2m x 2m plot
X Sites for microhabitat measurements

mats were disintegrating at their lower (down-slope) edges. These mats tended to be dominated by *Herbertus aduncus* or *Mastigophora woodsii* with the other species occurring as scattered shoots. The liverwort stems were often very long - up to 15cm - yet only the top 1-2cm appeared to be alive and growing. The surfaces of the mats were being colonised by lichens, particularly *Cladonia uncialis* and *C.portentosa*. The annual incremental growth of *Calluna* produces shoots made up of distinct sections; the number of these suggested that the bushes were about 20 years old. At least half of the length of these stems was within the hepatic mat, implying that the liverwort community was at least 10 years old. Above the upper limit of *Calluna* (at about 600m) the hepatic community formed mats and also discrete tussocks up to about 50cm in diameter. In these the shoots of the liverworts tended to be shorter than in those on the lower slopes and a greater length of the shoots seemed to be alive. They were frequently growing on mineral soils rather than on peat.

5.2 The physics of evaporation

The rate of evaporation of water from bryophyte clumps is determined by the difference in the concentration of water vapour at the bryophyte surface and in the ambient air, and by the diffusion resistance to the movement of water in the boundary layer over the bryophyte surface. The boundary layer is a layer of relatively still air adjacent to a surface. There is little turbulence within this layer (it is laminar (Proctor 1982)) and its effect is to slow down the rate of molecular diffusion of water vapour from the vegetation to the surrounding air. If the boundary layer is thin, resistance to molecular diffusion is small and there is close coupling between the surface and the atmosphere. Conversely a thick boundary layer has more resistance and insulates the surface from the atmosphere (Grace & Unsworth 1988). Evaporation from bryophyte clumps is probably greatest when the canopy is moved and the boundary layer disturbed by gusts of wind. In such conditions, water vapour will move from the bryophyte surface by turbulent mixing rather than by the slow process of molecular diffusion (Longton 1988).

The latent heat of evaporation, which is the energy required for evaporation to take place, is supplied by a combination of solar radiation, radiation from the surroundings, heat exchange with the ambient air and conduction from the substratum (Proctor 1990).

Since bryophytes have no stomatal resistance (Proctor 1990), the rate of evaporation from a moist liverwort surface can be predicted by the Penman equation:

$$LE = \frac{s(R_n - G) + \rho c_p (\chi_s - \chi)/r_H}{\gamma^* + s}$$

where L is the latent heat of evaporation, E is the rate of evaporation, s is the slope of the saturation vapour density curve, R_n is the net radiation balance, G is the heat stored by the bryophyte or its substrate, ρ is the density of air, c_p is the specific heat of air, $(\chi_s - \chi)$ is the saturation deficit of the ambient air, r_H is the sensible heat transfer resistance and γ^* is the apparent psychrometer constant. These variables are discussed more fully by Monteith (1973), Campbell (1977) and Proctor (1982, 1990).

ρ, c_p, s and γ^* are temperature-dependent properties of air and can be obtained from tables (eg in Campbell 1977). R_n, G, $(\chi_s - \chi)$ and r_H are (in principle) measurable (Proctor 1990).

$s(R_n - G)$ describes the heat supplied by net incoming radiation and $\rho c_p(X_s - X)/r_H$ the heat supplied by convection from the air. In shady places the income from radiation is small and evaporation will be determined mostly by the saturation deficit of the air and the diffusion resistance of the boundary layer. In humid and sheltered but sunlit places the rate of evaporation will be determined mainly by the net incoming radiation.

It is generally true that when the sky is clear, solar radiation increases with altitude (because the air mass through which the radiation passes is less) and in the northern hemisphere is greater on south-facing slopes than on north-facing slopes. However the increasing incidence of cloud and rain with altitude in the British uplands means that most solar energy is received as diffuse rather than direct radiation. So incoming radiation declines with altitude and the energy supply to slopes of different aspects may not be so different as in less cloudy parts of the world (Grace & Unsworth 1988). In the British Isles, net radiation will be low in cool and cloudy climatic regions, at high altitudes, on north-facing slopes and under trees.

The saturation deficit is the difference between the saturation and actual water vapour content of the air. It varies with temperature and pressure. It decreases with altitude (because of decreasing temperature and pressure) and is lowest in places with a cool, wet climate, near the coast and by streams or waterfalls (Monteith 1973, Monkhouse 1975, Proctor 1990).

The boundary layer resistance depends on the roughness of the vegetation surface, on windspeed and on the nature of the surrounding terrain. In the uplands, boundary layer resistances tend to be low because windspeeds are high and the vegetation aerodynamically rough (Grace & Unsworth 1988). The resistance will be highest in places such as sheltered slopes, gullies, under taller vegetation (such as *Calluna vulgaris*) and in the lee of boulders where windspeeds are low (Proctor 1990). Clumps or cushions of bryophytes have a higher resistance than individual shoots (Longton 1988, Proctor 1990).

Evaporation from the surface of a liverwort is therefore likely to be least in regions with an oceanic climate, on steep sheltered slopes at high altitudes, and where there is shelter from a canopy of tall shrubs or trees.

5.3. Methods

5.3.1 Recording the species on the site

The northern slope of the hill was searched over four days in May 1990. The hepatic mat community was sampled by placing a 25cm x 25cm flexible wire quadrat over bryophyte cushions. These cushions were not randomly selected because the community is discontinuous. Cushions were chosen from a distance of about 10m, to avoid the temptation to put the quadrats on the ones with the most species. All of the bryophytes, vascular plants and lichens (except lichens on rocks or shrubs) in each quadrat were recorded. The cover of each species was estimated to the nearest 5%.

5.3.2 Sampling the hepatic mat community

The hepatic mat community was sampled in six plots on the north-facing slopes of Liathach in June 1992. Two stands of hepatic mat were selected at 400m, at 500m and at 600m ASL. The stands were sampled by 2m x 2m plots, placed where the community was more or less continuous. Each plot was divided into 100 20cm x 20cm squares. One 5cm x 5cm quadrat was placed at random in each 20cm x 20cm square. All hepatic mat species in each quadrat were recorded.

5.3.3. Measuring temperature and humidity

Temperature and humidity were measured in three different habitats on each side of the Coire Dubh Mhor on 24 and 25 June 1992 and on 4 September 1993. The habitats were an open slope with damp *Calluna* heath and scattered rocks, a boulder-field (rocks 50cm or more in diameter) and the bottom of a cliff. Similar habitats were selected on either side of the glen. Soil temperatures were measured by mercury thermometer with the bulb inserted 10cm into the peat. Ten samples were taken in each of the three habitats and the thermometer was always inserted into peat beneath a bryophyte carpet. This consisted of leafy liverworts on the north-facing side (mostly *Herbertus aduncus*) and *Racomitrium lanuginosum, Hypnum cupressiforme* and *Campylopus atrovirens* on the south-facing side.

Temperature and relative humidity of the bryophyte surfaces were measured in each habitat on each slope in June 1992. A Casella aspirated psychrometer was used to measure dry-bulb and wet-bulb temperatures with the ends of the thermometers close to the bryophytes. Relative humidity was calculated from the difference between the two readings. Measurements of relative humidity were made in the morning and in the evening so that changes over the day could be assessed.

Surface and internal temperatures of bryophyte cushions were measured by mercury thermometer in the three habitats on either side of the glen on 4 September 1993. Internal temperature was measured 5cm below the surface.

5.3.4 The chemistry of the environment

The chemistry of the environment of the hepatic mat species was studied in samples of water, peat and liverwort cushions collected in September 1993 from the north-facing slopes of Liathach and from the north slope of Ruadh-stac Beag, Beinn Eighe. Water samples were collected directly into $50cm^3$ screw-top plastic tubes. Peat and plant material were packed loosely into $50cm^3$ plastic tubes. Distilled water was added to fill the tube and the contents were left overnight. The liquid was vacuum-filtered. The pH of each sample was measured by glass electrode. The concentrations in ppm of calcium, potassium and sodium were found by atomic absorption spectrophotometry using a Unicam 919 spectrophotometer. Ammonium concentration in each sample was determined by a gas diffusion technique using a Perstorp Fiastar Flow-Injection Analyser. The method is described in the manufacturer's Application Note number ASN 50/-03/84.

5.4 Analyses

5.4.1 Records of species on the site

The data from the 25cm x 25cm quadrats were not collected randomly, which precludes most statistical analyses. The results were summarised to show the frequency and abundance of the vascular plants, bryophytes and lichens recorded on the slope and the types of vegetation with hepatic mats.

5.4.2 Patterns in the hepatic mat community

The data from the 5cm x 5cm quadrats were analysed by χ^2 tests of the null hypothesis of no association - either positive or negative - between pairs of species. In all the plots there were some quadrats with no hepatic mat species in them. There was a risk of concluding that there were more positive associations between species than there really were because some of the quadrats with no species in them fell in unsuitable habitats such as the tops of boulders. If the quadrats with no species were excluded from the analysis there was a chance of concluding that there were more mutually exclusive relationships than there really were, because some of the quadrats with no species were suitable for the plants to grow. The analysis was done once with the complete set of data and once excluding the quadrats with no records. The first was to give a conservative estimate of the negative relationships, the second was to give a conservative estimate of the positive relationships.

The frequency distributions of species within the plots were also analysed by χ^2 to see how they differed from randomness.

5.4.3 The microhabitat of the hepatic mat community

Differences in soil temperature, surface and internal temperature and relative humidity between sites (and between morning and evening for humidity measurements) were assessed by analysis of variance using the MINITAB statistical package (Ryan, Joiner & Ryan 1992).

5.5 Results

5.5.1 Species recorded on the site

Fourteen of the characteristic species were recorded on the slope: all but *Adelanthus lindenbergianus* and *Anastrophyllum joergensenii*. There were 24 other bryophytes, 32 vascular plants and six lichens (Appendix 3). Other oceanic species found were the mosses *Dicranodontium uncinatum* and *Campylopus setifolius* and the fern *Hymenophyllum wilsonii*. The hepatic mat species collectively were the most abundant bryophytes (table 5.1). *Racomitrium lanuginosum*, *Hypnum cupressiforme*, *Rhytidiadelphus loreus* and *Sphagnum capillifolium* were also common.

The number of species in a quadrat ranged from 6 to 22 (fig. 5.2). There was a tendency towards large numbers and the modal number of species was 13. There were between 2 and 12 hepatic mat species in each quadrat (fig. 5.3). Here the tendency was for smaller numbers and the modal number of species was 5. The percentage cover of the 14 species in the quadrats also varied a lot (table 5.2). *Herbertus aduncus* was the most abundant species, followed by *Pleurozia purpurea* and *Plagiochila carringtonii*. *Anastrepta orcadensis*, *Lepidozia pearsonii*, *Anastrophyllum donnianum* and *Plagiochila spinulosa* almost always occurred in small amounts.

Herbertus aduncus and *Pleurozia purpurea* were the most frequent species (fig. 5.4). *Scapania gracilis*, *Plagiochila carringtonii* and *Bazzania tricrenata* were also common. *Anastrophyllum donnianum* and *Plagiochila spinulosa* were rare.

The hepatic mat community was recorded in five types of

Table 5.1. Species with at least 50 records in 160 25cm x 25cm quadrats on Liathach, Wester Ross.

Hepatic mat species	no	Other bryophytes	no
Herbertus aduncus	*157*	*Racomitrium lanuginosum*	*129*
Pleurozia purpurea	*147*	*Hypnum cupressiforme*	*87*
Scapania gracilis	*125*	*Rhytidiadelphus loreus*	*70*
Plagiochila carringtonii	*121*	*Sphagnum capillifolium*	*50*
Bazzania tricrenata	*107*		
Scapania ornithopodioides	*64*	Vascular plants	
Mylia taylorii	*60*		
		Vaccinium myrtillus	*136*
Lichens		*Deschampsia flexuosa*	*92*
		Calluna vulgaris	*62*
Cladonia uncialis	*75*		

Each species is followed by the number of records.

Table 5.2 Mean percentage cover (+- standard error) of 14 hepatic mat species in 160 25cm x 25cm quadrats on Liathach, Wester Ross.

	mean	se
Herbertus aduncus	77.4	1.80
Pleurozia purpurea	16.5	0.94
Plagiochila carringtonii	4.5	0.85
Mastigophora woodsii	3.1	1.81
Scapania gracilis	2.9	0.31
Mylia taylorii	2.5	0.71
Bazzania tricrenata	2.1	0.29
Scapania ornithopodioides	1.3	0.31
Bazzania pearsonii	1.0	1.08
Scapania nimbosa	0.8	0.54
Anastrepta orcadensis	0.3	0.09
Lepidozia pearsonii	0.3	0.13
Anastrophyllum donnianum	0.1	0.11
Plagiochila spinulosa	0.1	0.16

Figure 5.2 Frequency distribution of the total number of species in 160 25cm x 25cm quadrats on Liathach, Wester Ross

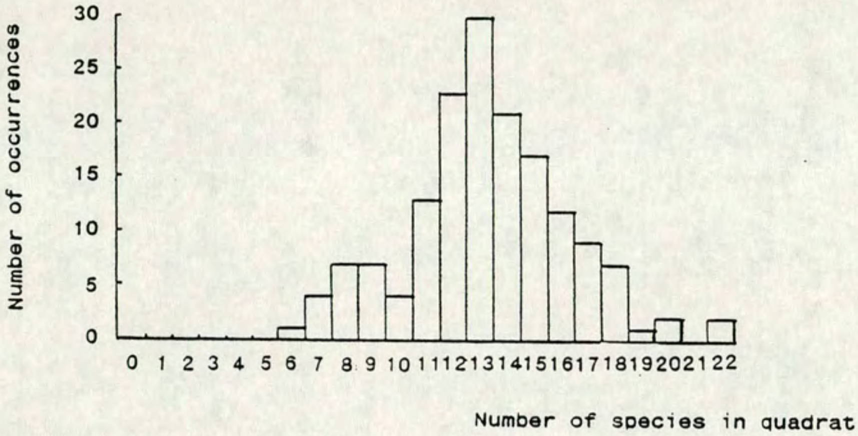


Figure 5.3 Frequency distribution of hepatic mat species in 160 25cm x 25cm quadrats on Liathach, Wester Ross

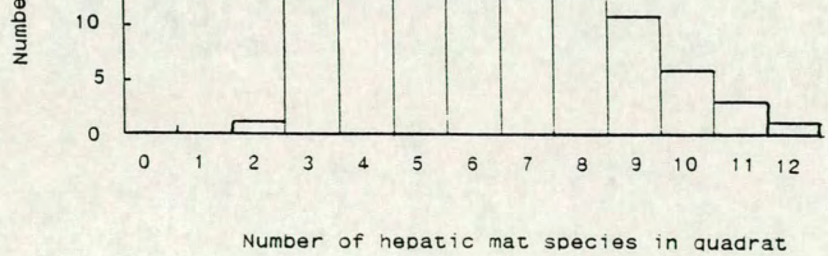
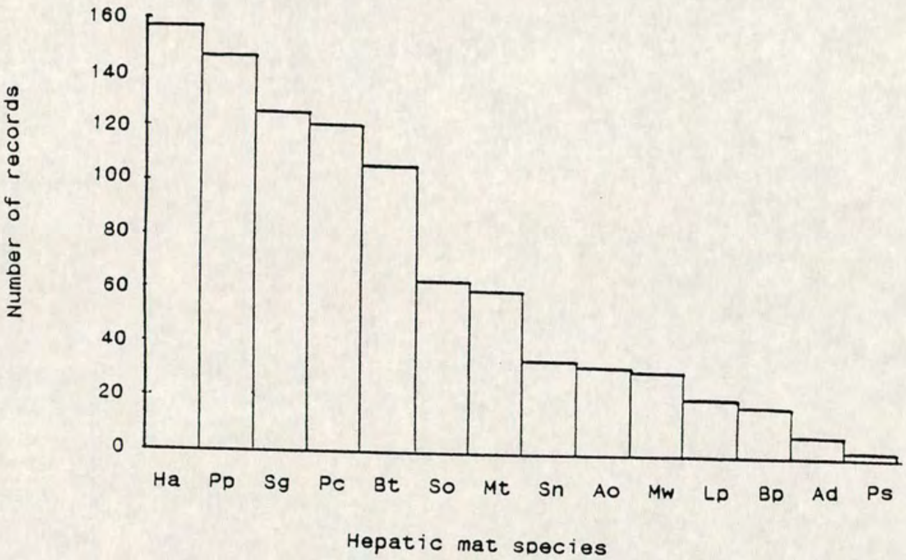


Figure 5.4. The fourteen hepatic mat species recorded on Liathach, West Ross, ranked in order of number of records in 160 25cm x 25cm quadrats.



Ha	Herbertus aduncus	Sn	Scapania nimbosa
Pp	Pleurozia purpurea	Ao	Anastrepta orcadensis
Sg	Scapania gracilis	Mw	Mastigophora woodsii
Pc	Plagiochila carringtonii	Lp	Lepidozia pearsonii
Bt	Bazzania tricrenata	Bp	Bazzania pearsonii
So	Scapania ornithopodioides	Ad	Anastrophyllum donnianum
Mt	Mylia taylorii	Ps	Plagiochila spinulosa

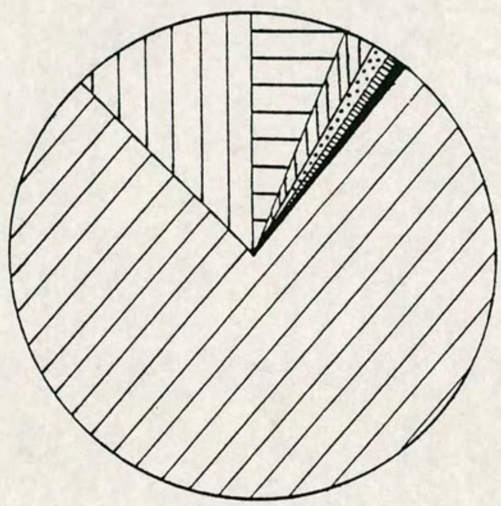
vegetation, on cliff-ledges and among boulders (fig. 5.5). Most records were in damp *Calluna* heath (H21). The *Calluna -Scirpus* wet heath (M15) was a poor habitat; the *Vaccinium* heath (H20) and montane grasslands (U7, U13) rather better.

5.5.2 Sampled populations of the hepatic mat community

The six 2m x 2m samples at 400m, 500m and 600m on Liathach included all the hepatic mat species previously recorded on the hillside (see above) except for *Plagiochila spinulosa*. The frequency of the species varied quite widely (table 5.3). Eleven hepatic mat species were common to all six plots. *Scapania nimbosa* was absent from one plot at 400m. *Anastrophyllum donnianum* was absent from two plots at 400m and one at 600m. A χ^2 test for homogeneity showed that the differences in frequency of species between the plots were significant at $p<0.001$ (χ^2 = 368.59; 60 degrees of freedom).

The most frequent species in all the plots were *Herbertus aduncus, Bazzania tricrenata, Pleurozia purpurea, Scapania gracilis* and *Anastrepta orcadensis. Anastrophyllum donnianum* was rare throughout. Although two replicates at each altitude were insufficient for statistical analysis, the results suggest that the distribution of some of the species varies according to altitude. *Anastrophyllum donnianum, Bazzania pearsonii, Lepidozia pearsonii* and *Scapania ornithopodioides* were least abundant at 400m, while *Herbertus aduncus* and *Scapania gracilis* were least abundant at 600m.

Figure 5.5 The plant communities and other habitats with which 160 sampled clumps of hepatic mat were associated on Liathach, Wester Ross



/// *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* damp heath (NVC H21)

||| *Vaccinium myrtillus-Racomitrium lanuginosum* heath (H20)

☰ *Nardus stricta-Carex bigelowii* grass heath (U7)

|||||| *Deschampsia cespitosa-Galium saxatile* grassland (U13)

:·:· *Scirpus cespitosus-Erica tetralix* wet heath (M15)

\\\\\\ Rock ledge   Boulder field

Table 5.3. Distribution of hepatic mat species in six 2m x 2m plots on the north face of Liathach, Torridon.

	number of records					
Altitude *(m)* >>>	400		500		600	
Plot >>>	1	2	3	4	5	6
SPECIES						
Anastrepta orcadensis	27	31	34	21	33	35
Anastrophyllum donnianum	0	0	2	1	7	0
Bazzania pearsonii	1	2	12	7	20	3
Bazzania tricrenata	42	38	42	61	38	44
Herbertus aduncus	47	50	56	79	35	17
Lepidozia pearsonii	11	12	49	18	20	42
Mastigophora woodsii	1	19	23	14	24	18
Mylia taylorii	9	16	25	25	12	4
Plagiochila carringtonii	5	45	45	51	22	31
Pleurozia purpurea	26	60	40	82	26	8
Scapania gracilis	31	47	36	42	25	13
Scapania nimbosa	0	10	14	17	20	6
Scapania ornithopodioides	10	9	26	17	33	51

The table shows the number of records for each species in 100 samples in a 2m x 2m plot stratified into 20cm x 20cm squares.

Table 5.4. Positive and negative associations between pairs of hepatic mat species in 100 random 5cm x 5cm quadrats in 6 plots on Liathach, Wester Ross.

	Species 2												
Species 1	Ao	Ad	Bp	Bt	Ha	Lp	Mw	Mt	Pc	Pp	Sg	Sn	So
Ana orc													
Ana don													
Baz pea		-1											
Baz tri			*1										
Her adu				+1									
Lep pea		-1	-1										
Mas woo		-1	+1	+1	-1	-1							
Myl tay	-1		*1			-1	-1						
Pla car		-1	-1	+1	+3		*1	+1					
Ple pur		+1	+1		+6	-2			+2				
Sca gra		+1			+2		+1		+1				
Sca nim		+1	+1	+1	+1		+1	+1	+2	+2	+2		
Sca orn			+1		+1				+1	+1	+1	+1	

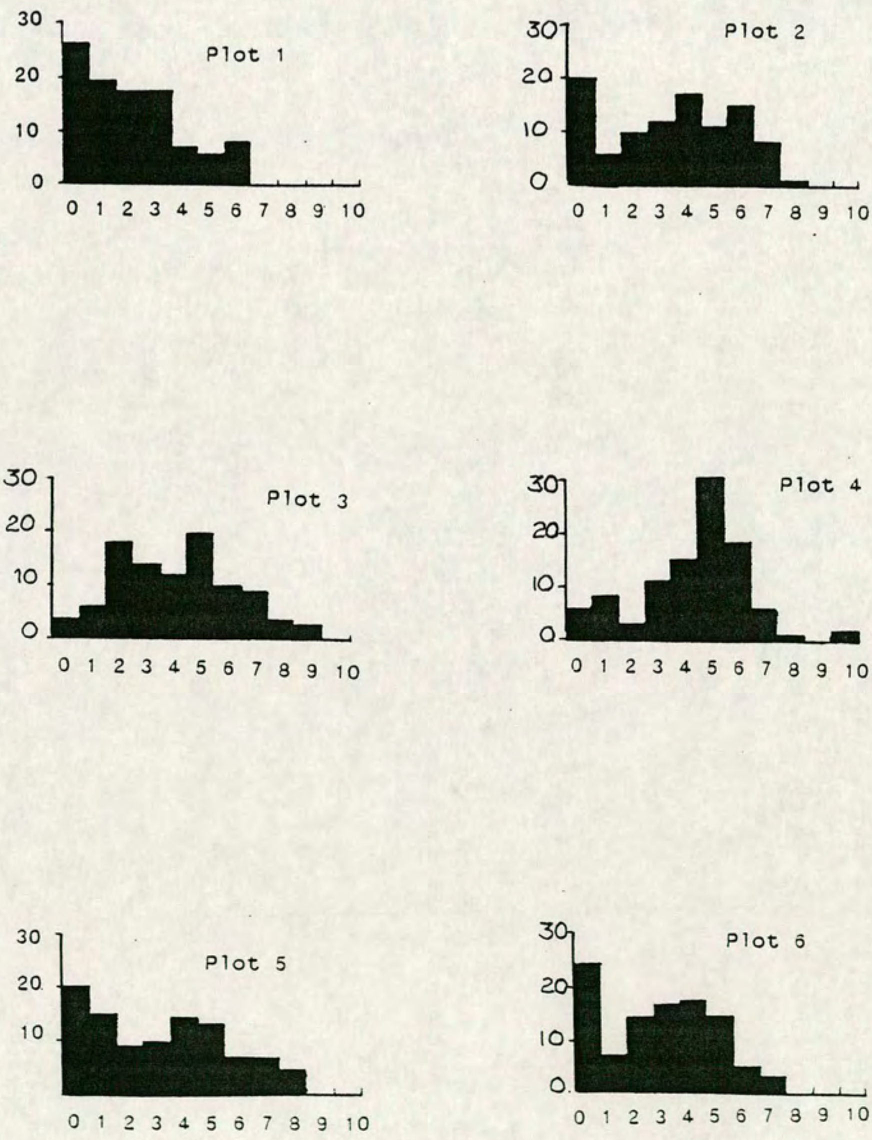
*Figures show the number of plots with large (χ^2 > 3.84) positive (+) and negative (-) associations recorded for each pair of species, measured by $\chi 2$. 1 degree of freedom for each pairwise test. * signifies both positive and negative relations (in different plots).*

Up to 10 hepatic mat species were recorded in some 5cm x 5cm quadrats, although most quadrats had fewer than this (fig.5.6) and in plots 1, 2, 5 and 6 at least 20% of the quadrats had no hepatic mat species in them at all.

Associations were tested between 78 pairs of species in each of the six plots. The analysis of the full set of data suggested that 15 pairs of species were mutually exclusive in at least one plot while the analysis excluding quadrats with no records suggested that 32 pairs occurred together more often than expected in at least one plot (table 5.4). Some of the species associate more than others. *Anastrepta orcadensis* and *Lepidozia pearsonii* were never in positive relationships, whereas *Herbertus aduncus* was in 14 positive relationships, *Pleurozia purpurea* and *Scapania nimbosa* in 13 and *Plagiochila carringtonii* in 12. Most associations between species, whether positive or negative, occurred only once. Some however were common to more than one plot. *Herbertus aduncus* and *Pleurozia purpurea* were together more than would be expected in all six plots and *Herbertus aduncus* and *Plagiochila carringtonii* were together more than expected in three. Five pairs of species were positively associated in two plots. *Lepidozia pearsonii* and *Pleurozia purpurea* were negatively associated in two plots.

Several of these associations occur because the expected values in the 2x2 χ^2 table were small. When the pairs with values below 5 in the contingency tables were removed from

Figure 5.6. Histograms to show frequency distribution of the number of hepatic mat species in 100 5cm x 5cm quadrats in six 2m x 2m plots on Liathach, Wester Ross.



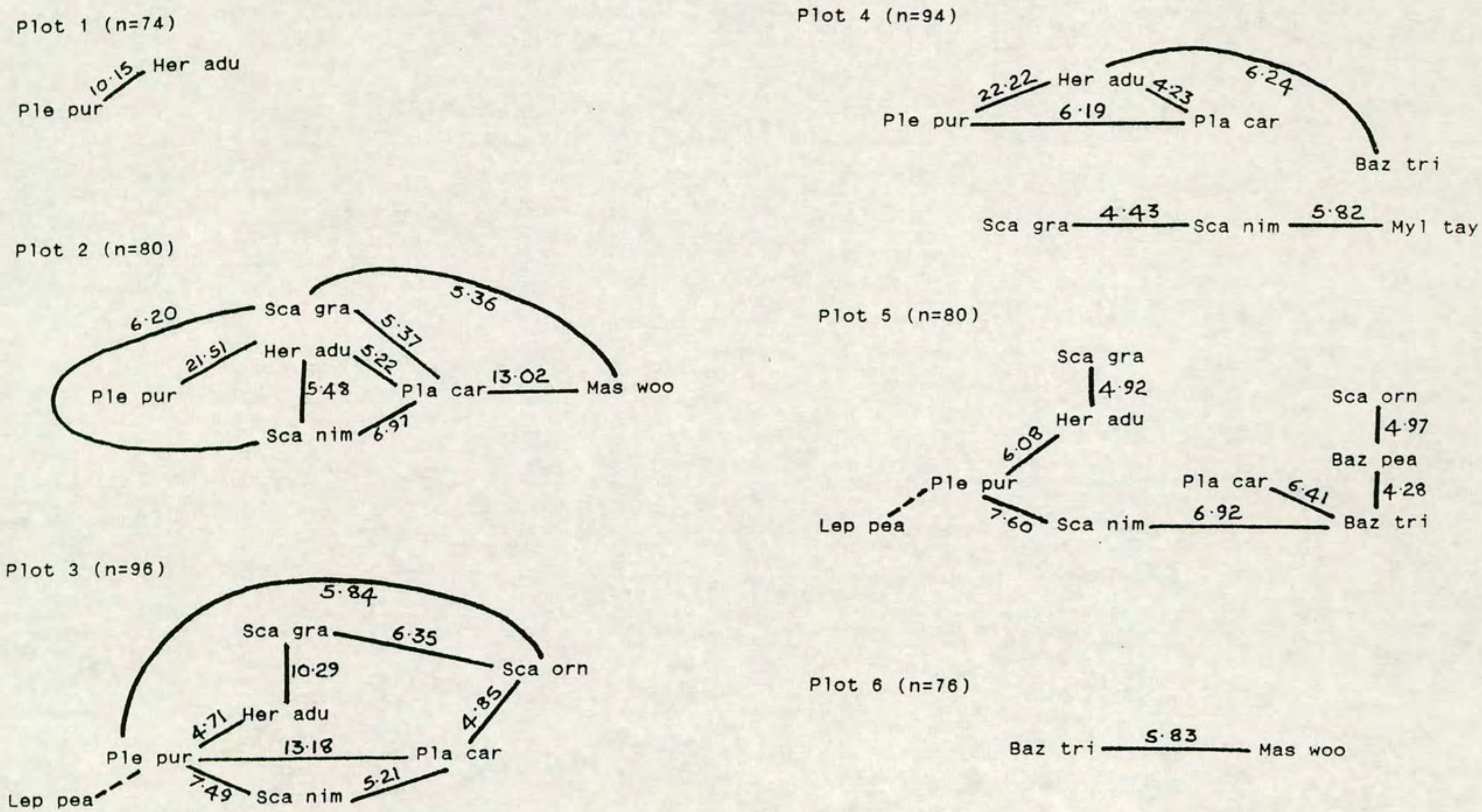
the results there was one pair of species negatively associated more often than expected and 22 pairs of species positively associated more often than expected (fig. 5.7). Since the set of data was so large - 468 pairwise comparisons in each of the two analyses - some apparently 'significant' results were likely to occur by chance (Type 1 errors). Therefore probabilities were not attached to these results.

In plots 2, 3, 4 and 5 there was a network of associations between species. The patterns in these four plots varied in complexity and detail but were similar. There was a consistent assemblage of *Herbertus aduncus, Pleurozia purpurea, Plagiochila carringtonii*, *Scapania gracilis* and *S.nimbosa*. *Bazzania tricrenata* was in three associations in plot 5 and *Scapania ornithopodioides* was in three associations in plot 3. *Lepidozia pearsonii* and *Pleurozia purpurea* were mutually exclusive in plots 2 and 3.

5.5.3 The microhabitat of the hepatic mat community

Temperature and relative humidity were measured on dry days with bright sunshine and scattered cumulus cloud. In June the trajectory of the sun was well to the north and both slopes were exposed to sunlight for most of the day. In September the north-facing slope was in deep shade all day and the differences in macroclimate between the two slopes were noticeable. Temperature differences were enough to necessitate an extra two layers of clothing while working on

Figure 5.7 Links between species in six 2m x 2m plots each sampled by 100 5cm x 5cm quadrats on Liathach, Wester Ross



Numbers are χ^2 values (where greater than 3.84) from pairwise tests of association between species

—— positive association (values of n shown in parentheses)

- - - negative association (n = 100)

the north-facing slope. Air temperatures in the shade and out of the wind 2m above the ground were 11°C on the north-facing slope and 19°C on the south-facing slope. There were many midges on the north slope but none on the south side.

Relative humidity

The morning measurements of relative humidity at the bryophyte surface were similar on both slopes in June, but the south-facing slope dried out more than the north-facing slope during the day (table 5.5). An analysis of variance showed that time of day and the interaction between aspect and time were significantly different (table 5.6).

Temperature

In June the surface temperatures of the bryophytes were much the same on both slopes (table 5.7). Bryophytes at the base of cliffs on the south-facing slope were slightly warmer than on the north-facing slope. In September the temperatures of the bryophyte surface on the south-facing slope were much higher than those on the north. Again the base of cliffs was the warmest habitat. The two aspects were significantly different from each other, and aspect combined with time was also significant (table 5.8).

There were steep gradients of temperature between the surface of the bryophyte cushions and 5cm inside the cushions,

Table 5.5. Average values for relative humidity on two opposing slopes at two times of day in three habitats in Coire Dubh Mor, Ross.

	North-facing		South-facing	
	am	pm	am	pm
slope	88.0+-1.3	85.2+-1.6	87.1+-2.5	79.7+-1.1
boulder-field	85.7+-1.7	88.9+-2.3	93.9+-1.1	77.8+-0.7
under cliff	89.9+-0.6	87.5+-1.7	92.1+-1.7	81.2+-0.4

Altitudes: slope: 400-500m, boulder-field: 400m, under cliff: 400m. Measurements made under vascular plant canopy at bryophyte surface. Figures show means +- standard errors. n=10.

Table 5.6. The results of an analysis of variance of the differences in relative humidity between north-facing and south-facing slopes in the morning and in the evening in Coire Dubh Mor, Ross, in June 1992.

Source	DF	MS	F	P
aspect	1	15	2.8	0.148
time	1	109	20.6	0.004
aspect x time	1	89	16.7	0.006
habitat	2	7	1.3	0.335
error	6	5		

Table 5.7. Average values for temperatures at the bryophyte surface on two opposing slopes, in three habitats, in June and September in Coire Dubh Mor, Ross.

	North-facing		South-facing	
	June	Sept	June	Sept
slope	14.5+-0.3	8.3+-0.2	14.8+-0.4	23.6+-0.9
boulder-field	12.9+-0.3	7.9+-0.2	12.7+-0.4	17.2+-0.8
under cliff	10.9+-0.2	8.8+-0.5	13.7+-0.7	25.8+-0.7

Altitudes: slope: 400-500m, boulder-field: 400m, under cliff: 400m. Measurements made under vascular plant canopy at bryophyte surface. Figures show means +- standard error. n=10.

Table 5.8. The results of an analysis of variance of the differences in surface temperature between north-facing and south-facing slopes in June and September in Coire Dubh Mor, Ross.

Source	DF	MS	F	P
aspect	1	65	29.6	0.002
time	1	12	2.2	0.190
aspect x time	1	125	22.4	0.003
habitat	2	8	1.4	0.319
error	6	6		

especially on the south-facing slope (table 5.9).

The average soil temperatures 10cm below the surface (table 5.10) on the south-facing slopes were significantly warmer than those on the north-facing slopes, but the three habitats were not significantly different from each other (table 5.11).

Five cushions of *Pleurozia purpurea* in wet heath on a slope facing south-east on a sunny day in September had a mean surface temperature of 23.5°C (+-1.5°C) and a mean temperature 5cm below the surface of 20.8°C (+-0.4°C). Single measurements taken in a sun-exposed patch of the hepatic mat community gave *Anastrophyllum donnianum* a surface temperature of 13.5°C and an internal temperature of 11.0°C, while *Herbertus aduncus* growing close beside it had a surface temperature and internal temperature of 10.0°C.

5.5.4 The chemistry of the environment

Chemical analyses of the samples from Beinn Eighe (table 5.12) showed that the hepatic mat clumps and their immediate environment had a fairly high pH but a low concentration of calcium. The liverwort clumps had more calcium, sodium and potassium than the peat or the stream-water. There was much less potassium in the stream-water than in the peat or the liverwort clumps. Some individual values for potassium were especially high: 17.0 ppm in one peat sample and 10.1, 12.1

Table 5.9. Average differences between temperatures at bryophyte surface and temperatures 5cm below the surface of the cushion on two opposing slopes in three habitats in Coire Dubh Mor, Ross.

	North-facing	South-facing
slope	0.2+-0.2	7.0+-1.1
boulder-field	0.2+-0.2	2.1+-1.0
under cliff	0.2+-0.6	4.8+-0.6

Altitudes: slope: 400-500m, boulder-field: 400m, under cliff: 400m. Figures show means +- standard error. n=5

Table 5.10 Average values for soil temperatures 10cm below the surface on two opposing slopes in three habitats in Coire Dubh Mor, Ross.

	North-facing	South-facing
slope	10.29+-0.07	10.79+-0.09
boulder-field	10.31+-0.03	10.68+-0.05
under cliff	10.07+-0.07	10.81+-0.06

Altitudes: slope: 400-500m, boulder-field: 400m, under cliff: 400m. Figures show means +- standard error. n=10.

Table 5.11. The results of an analysis of variance of the differences in soil temperature (10cm below the surface) between north-facing and south-facing slopes in June 1992 in Coire Dubh Mor, Ross.

Source	DF	MS	F	P
aspect	1	0.5	72.3	0.014
habitat	2	0.006	1.0	0.500
error	2	0.006		

Table 5.12. Analyses of samples of stream water, peat and clumps of hepatic mat liverworts for pH and concentrations in ppm of calcium (Ca), sodium (Na), potassium (K) and ammonium (NH_4).

sample	pH	Ca	Na	K	N-NH4	
Stream	*5.55*	*3.10*	*6.57*	*1.60*	*0.19*	mean
water	*0.21*	*0.21*	*0.19*	*0.71*	*0.01*	se
Peat	*5.62*	*1.36*	*6.96*	*7.44*	*0.47*	
	0.13	*0.34*	*1.02*	*2.41*	*0.07*	
Liverwort	*5.11*	*5.86*	*8.56*	*9.86*	*0.57*	
clumps	*0.14*	*0.47*	*0.61*	*1.18*	*0.04*	

Figures show means of 4 water samples, 5 peat samples and 6 liverwort samples with their standard errors.

and 14.2 ppm in three of the liverwort samples.

5.6 Discussion

The results suggest that *Herbertus aduncus* and *Pleurozia purpurea* were the most abundant species on this site as well as the two most often associated. This was shown in the 25cm x 25cm quadrats and in the 2m x 2m plots. *Bazzania tricrenata, Scapania gracilis* and *Plagiochila carringtonii* were also common. *Anastrepta orcadensis* was frequently recorded in the 2m x 2m plots; less so in the 25cm x 25cm quadrats. There was bias in the sampling because the 25cm x 25cm quadrats were taken subjectively, and *Herbertus aduncus* is the most conspicuous member of the community. McVean & Ratcliffe (1962) found that the most frequent and abundant species in hepatic-rich *Calluna* heath were *Mastigophora woodsii, Herbertus aduncus* and *Pleurozia purpurea*. Birks (1973) had *Herbertus* as the most abundant and frequent species in six 2m x 2m quadrats. Ratcliffe (1968) and Rodwell (1991b) described *Herbertus* as 'often the most abundant liverwort' in the hepatic mat and general observation of the community over its British range attests to the abundance of *Herbertus* when it is present. Nevertheless some stands are dominated by *Mastigophora woodsii* (McVean & Ratcliffe 1962, Rodwell 1991b, D. Chamberlain pers. comm.), and *Herbertus* is rare at higher altitudes (Chapter 4, Ratcliffe 1968).

There is a vast literature on the coexistence of species and the possible reasons why plant communities are structured the way they are. This has recently been reviewed by Zobel (1992) who concluded that most communities are less rich in species than they could potentially be. This is partly for historical reasons (migration has not occurred), but interspecific competition usually limits the number of coexisting species.

Competition between plants is not so straightforward as between animals. The classic theories of competition are based on differences in size, shape and niche breadth in different species and on niche differentiation (Begon, Harper & Townsend 1986). One problem with plant communities is that each individual will be surrounded by (and influenced by) a different set of other species. Individual shoots of hepatic mat liverworts are just as likely to be surrounded by shoots of the same species as by those of another species. Because of their cushion-forming habit the neighbouring shoots are likely to be parts of the same individual. Each individual can be in a totally different environment, which makes it impossible to discover how competition acts in the whole community. Another problem is that competition tends to act at the stages of establishment or early growth (Crawley 1986). These stages in the life-cycle have not been seen in the hepatic mat species. The community is fine-grained, with up to 10 hepatic mat species growing in an area 5cm x 5cm. It has been shown that in fine-grained bryophyte communities, mortality tends to be density-independent and related to variation in the microenvironment. Competition is not hierarchical and species are rarely excluded from the community (During & van Tooren 1987).

Hepatic mats can include several closely-related species growing together in a 2m x 2m plot (McVean & Ratcliffe 1962, Chapter 4): two species of *Anastrophyllum*, two of *Bazzania*, two of *Plagiochila* and three of *Scapania*. Even within their genus the two *Anastrophyllum* species are closely-related, as are *Scapania nimbosa* and *S.ornithopodioides*. Similar close association of congeneric bryophytes has been noted in mires where several species of *Sphagnum* often occur together (Slack 1990, Rodwell 1991b). Mires dominated by Sphagna are among the few studied bryophyte communities which are believed to be sufficiently stable and long-lived for competition to operate on the component species, although there is evidence of niche differentiation in such habitats (Slack 1990). This may also be the case in woodlands where characteristic sets of bryophytes are associated with habitats such as tree bark, rotting logs, rock-faces and stream-sides (Averis 1991).

Although the niches of the hepatic mat species must overlap, their different ecological limits must affect the balance between them over the range of their occurrence. Without controlled experiments it is hard to tell which species are strong competitors and to what extent the species compete with each other. Field observations suggest that the hepatic mat species as a group can out-compete other bryophytes such as *Hylocomium splendens*, *Hypnum cupressiforme*, *H.jutlandicum*, *Racomitrium lanuginosum*, *Rhytidiadelphus loreus* and *Sphagnum capillifolium* in undisturbed damp heaths and woods in the west of Scotland and Ireland, but that these common mosses oust the hepatic mat species from drier sites or where the microenvironment has been changed by burning and grazing of the vegetation.

In some 2m x 2m plots there was a whole network of species associated more often than one might expect. In others there were few associations. The associations between pairs of species might suggest that some of the species consistently need the presence of others (such as *Herbertus* or *Mastigophora*) to create a microclimate that is slightly warmer, damper and more sheltered than that of the surrounding open ground. Perhaps the dominant species in the mats are those which can tolerate the most adverse environments, and the other species are limited by their need for a preexisting hepatic mat - facilitation (Egler 1954 in Crawley 1986). However none of the rare species were consistently associated with the common ones, and there are plenty of places in the west Highlands where any of these species can be found alone. In any case facilitation between species is rare (Crawley 1986). The differences in abundance between the species are most likely the results of different rates of growth, ability to colonise new habitats and ability to survive the occasional catastrophe such as a landslip, trampling by deer or prolonged drought.

Bryophyte cushions have a higher boundary-layer resistance to the evaporation of water than do individual shoots (Proctor 1990). Cushions can also obtain more water by capillary uptake from the substrate. As a result the internal water content of a bryophyte shoot in a cushion or mat is likely to be higher than that of a shoot growing alone (Longton 1988). This could be why the hepatic mat species tend to occur in mixed colonies rather than as individual shoots.

The measurements of temperature and humidity show that north-facing and south-facing slopes have significantly different microclimates, especially on sunny days in Autumn. This is because both sides of the corrie are exposed to direct sun in June, while in September the south-facing slope is fully-exposed to the sun and the north-facing one is in shade all day. Sunny days such as this are comparatively rare at Beinn Eighe and for most of the year both slopes will have a similar income of energy from diffuse radiation (Geiger 1971, Grace & Unsworth 1988). However bryophytes are more likely to be limited by extreme than by mean conditions (Grace & Unsworth 1988), so it may be that the few sunny days each year are important in controlling their distribution. There was much less variation in temperature inside the bryophyte cushions than on the surface, and one would expect greater diurnal fluctuations on the surface than within the cushion (Lewis Smith 1988). Presumably the insides of cushions remain cool and damp for a long time even in dry weather, and there is probably a gradient in water potential which allows water to move up through the cushion so that the plant can photosynthesise and grow (Proctor 1990). There may also be lateral movement of water through the bryophyte clumps in the capillary spaces; this has apparently not been investigated (M. C. F. Proctor, personal communication).

On both slopes the bryophytes were growing below *Calluna*, which reduces the effects of insolation. The microclimate will be cooler, more equable and more humid than it is above the canopy of the heath (Delaney 1953, Barclay-Estrup 1971). The high temperatures measured at the base of south-facing cliffs in September were probably a result of radiation reflected from the rock surface added to the solar radiation.

The south-facing slope was more humid than the north-facing one in the morning in June. This is possibly because the south-facing slope was measured first and had not dried out in the sun to the same extent as the north-facing one by the time this was reached. It is also possible that more water had fallen on the south-facing slope during the previous two days' rain. The wind was from the south-west and was driving the rain against the south-facing slope, while the north-facing slope was comparatively sheltered. Less rain falls on sheltered slopes than on exposed ones because of atmospheric turbulence in the lee of high hills (Geiger 1971). However there was a smaller change in relative humidity over the day on the sheltered slope, probably because of a slower rate of evaporation. It is likely that differences in relative humidity are even greater at the times of the year when the north-facing slope is in shade.

It is possible to predict rates of evaporation from field measurements using the Penman equation (see section 5.2 above). The necessary measurements would have been the net radiation balance, the saturation deficit of the ambient air and the sensible heat transfer resistance (Proctor 1990). However I was reluctant to produce figures for evaporation rates because the variation in microtopography in stands of hepatic mat is so great that measurements made at one point would not have been generally applicable.

Solar radiation was not measured in this study. The original plan was to compare the radiation climates of slopes of different aspects (and of different habitats) using fish-eye photographs. This was not possible because my access to the equipment was limited, and when a camera was available the weather was poor - either too sunny or too wet. In bright sunlight the rays of the sun are concentrated by the lens and can damage the film and shutter, and if the cloud-base is low the tops of the hills are not photographed. However, work by Proctor (1980b) on the nearby Beinn Bhan suggests that north-facing slopes below steep cliffs do not experience direct sunlight between August and April.

Hepatic-rich *Calluna-Vaccinium* heaths have always been thought to be communities of oligotrophic or acidic environments (McVean & Ratcliffe 1962, Rodwell 1991b). The chemical analyses of peat, stream water and liverwort clumps, though based on few samples, suggest that the habitat is mesotrophic rather than oligotrophic and that there are high levels of sodium and potassium in the peat and the vegetation. Sodium and potassium are probably deposited by salt-laden winds from the sea (McVean & Ratcliffe 1962). Levels of ammonium are comparatively low, as might be expected in acid soils in this unpolluted part of the country. McVean & Ratcliffe (1962) obtained similar results from a sample of liverwort-rich *Calluna-Vaccinium* heath on Beinn Eighe in 1956, except that their sample had a lower pH (3.6) and a higher concentration of calcium (10.2 ppm). They also found that the soils under the *Juniperus communis nana* heath growing on the acidic quartzites of Beinn Eighe, not far from Ruadh-Stac Beag, had a fairly high pH (in one case 6.1). The authors attribute this to the build-up of nutrient-rich humus under the plants. The *Juniperus communis nana* heath has much in common floristically with the hepatic mat community and shares some of the liverworts (McVean & Ratcliffe 1962, Averis 1993), so it could be humus that contributes to the high pH of these samples.

The behaviour of the hepatic mat species in the field is so similar that controlled experiments are necessary to find out how the plants respond to different environmental conditions. This is studied in Chapter 6.

CHAPTER SIX

THE EFFECTS OF HEAT AND DROUGHT ON SOME MEMBERS OF THE ATLANTIC HEPATIC MAT

6.1 Introduction

It is impossible to deduce a cause-and-effect relationship between the distribution of plant species and climatic variables from inspection of maps or from descriptive field studies (Dilks & Proctor 1975). Distributions of plant species can be understood or predicted only when their ecological limits are known (Forman 1964). There have been few experimental studies on the physiology of bryophytes. Most have been done on mosses and almost all have looked at the effects of drought on survival or growth (e.g. Clausen 1964; Forman 1964; Lee & Stewart 1971; Hinshiri & Proctor 1971; Proctor 1972, 1980a; Dilks & Proctor 1974, 1976, 1979; Krochko, Bewley & Pacey 1978; Bewley 1979; DiNola, Mayer & Heyn 1983) or at the effects of temperature (e.g. Clausen 1964, Dilks & Proctor 1975, Hearnshaw & Proctor 1982).

Previous work including studies on some of the hepatic mat species (summarized by Proctor (1982)) suggests that many bryophytes can tolerate longer periods of drought than they are likely to experience in their natural habitats. Bryophytes have been shown to survive longer at low temperatures when dry than when wet (Dilks & Proctor 1974). Clausen (1964) studied the effects of drought and temperature on *Mylia taylorii*, *Scapania gracilis*, *Bazzania tricrenata*, *Plagiochila carringtonii*, *Mastigophora woodsii* and *Pleurozia purpurea*. She suggested that temperature affected response to drought: unfortunately she did not give details of her experiments or present analyses of the results, so the study is inconclusive. There has been no other work on the effects of combined heat and drought on the hepatic mat liverworts.

A pilot study was done to look at the effects of drought on some members of the hepatic mat community and to find out whether survival could be measured by infra-red gas analysis. An experiment was designed to test the effects of repeated exposure to high temperature and low water content on members of the hepatic mat. Several species were subjected to the same conditions at the same time, so that their responses could be compared. The aim of the work was to see whether there were differences in tolerance that might explain the differences in the distributions of the species.

Water contents of hepatic mat liverworts collected in the field were measured to compare with those experienced by the experimental plants.

6.2 Methods

6.2.1 Collecting species for the experiments.

a. Pilot experiment to assess the effects of drought

Herbertus aduncus, *Pleurozia purpurea*, *Bazzania tricrenata*, *Scapania gracilis*, *Plagiochila carringtonii* and *Mastigophora woodsii* were collected from a rocky slope at about 450 m ASL on Liathach, Torridon, in heavy rain on 14 October 1989.

b. A study of the cumulative effects of heat and drought

Scapania ornithopodioides and *Herbertus aduncus* were collected from cliff-ledges facing north at 210 m ASL in Glen Coe, Lochaber on 3 February 1993. The plants had not experienced drought or high temperatures for some weeks. *Scapania gracilis*, *Mastigophora woodsii*, *Pleurozia purpurea* and *Plagiochila carringtonii* were collected from a wooded boulder-field at 350 m in Glen Coe on 5 August 1993. These plants were still wet from recent rain. All samples were kept for a week in sealed polythene bags at 15 °C to acclimatise them to the control temperature for the experiments.

6.2.2 Preparation of experimental material

a. Pilot study of the effects of drought

Each collection of liverworts was divided into clumps to fit plastic pots 2 cm deep by 1.5 cm wide. The shoots were trimmed to 5 cm lengths (to reduce the effects of microbial respiration in the dead tissue at the base of the shoots (Bewley 1979)), soaked in water, blotted dry, placed in the pots and weighed. The samples were kept moist for 5 days, then placed in desiccators. Relative humidity was kept between 60% and 70% using calcium nitrate $Ca(NO3)_2.4H_2O$ in equilibrium with its saturated solution (Dilks & Proctor 1974). This is equivalent to a saturation deficit between 0.935 and 0.701 KPa (Monteith 1973). The desiccators were kept on a laboratory bench at about 23°C and close to a window, so the plants received natural light as well as fluorescent laboratory lighting.

b. A study of the cumulative effects of heat and drought.

The liverwort material was washed to remove soil and debris. Any stems of other bryophyte species were removed. The collections of *Scapania ornithopodioides* and *Herbertus aduncus* were each divided into 18 samples. The collections of *Scapania gracilis, Plagiochila carringtonii, Mastigophora woodsii* and *Pleurozia purpurea* were each divided into 30 samples. Each sample was trimmed to 5 cm in length, sprayed with distilled water, blotted dry and placed in a clean, dry tea-bag. The samples were divided into six groups. Each group contained three replicate samples of *Herbertus aduncus,* three replicates of *Scapania ornithopodioides* and five replicates of each of the other species. Care was taken to ensure that parts of the same initial clump were not in the same group - to avoid pseudoreplication - as they might have been parts of the same individual (Hurlbert 1984). Each group was allocated at random to one of six treatments:

Treatment 1: 15°C, 100% water content

Treatment 2: 50°C, 100% water content

Treatment 3: 15°C, 50% water content

Treatment 4: 50°C, 50% water content

Treatment 5: 15°C, 25% water content

Treatment 6: 50°C, 25% water content

Samples in treatments 3, 4, 5 and 6 were dried to approximately 50% or 25% of original water content in front of an electric fan at 25°C. To calculate drying times, five samples of each species were wetted, blotted dry and weighed. They were hung in front of the fan and reweighed periodically until they lost no more weight. The samples were oven-dried overnight at 80°C and weighed again to determine their oven-dry weights. Mean water content as a percentage of oven-dry weight was plotted against time. Drying times for water loss to 50% and 25% of original water content were read off the graph. This method was used because the samples were re-wetted before the gas analysis and had to be dried quickly before undergoing heat treatment the next day. It can take several hours for bryophyte clumps to dry out in a desiccator (Proctor 1972).

After weighing (and drying if appropriate), each sample of *Herbertus aduncus* and *Scapania ornithopodioides* in its tea-bag was fitted into a clear plastic pot so that it could be moved and re-wetted without touching the plant itself. (This can cause an increase in the rate of respiration (Hinshiri & Proctor 1971).) The samples were sealed in clear polythene boxes - one box for each treatment. The boxes were left for several hours for the water potentials of the samples to equilibrate in each one before the heat treatments began. Samples in treatments 1, 3 and 5 were kept in a growth-room maintained at 15°C. Samples in treatments 2, 4 and 6 were kept in a water-bath (inside the growth-room) timed to give a period of 10 hours in each 24 at 50°C. The plants were given a photoperiod of 5 hours dark and 19 hours light in each 24. Plants undergoing the heat treatment did so in the light. After each treatment the plants were returned to 15°C for at least an hour before having anything else done to them. The plants were illuminated at 104 μmol $m^{-2}s^{-1}$ PAR (photosynthetically active radiation) using a combination of mercury and tungsten bulbs.

6.2.3 Measuring the effects of the treatments

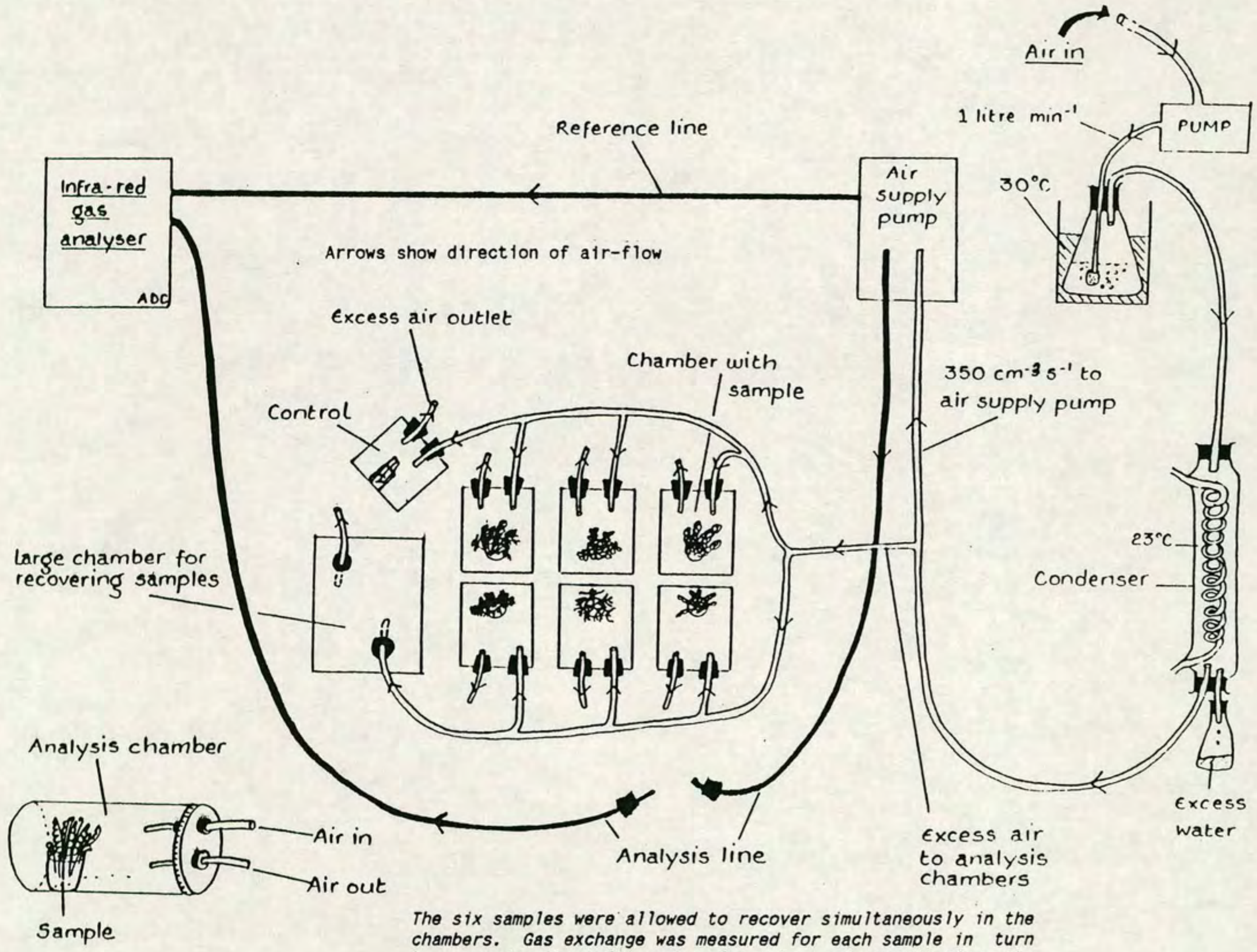
a. Pilot study of the effects of drought

After 1, 2, 3, 5, 7, 9, 13 and 21 days a sample of each species was removed from the desiccator and remoistened. Recovery was followed by measuring carbon dioxide exchange with an ADC portable infra-red gas analyser (LCA2, ADC Ltd., Hoddesdon, U.K.; Russell & Botha 1988). All six samples were allowed to recover simultaneously in 75cm^3 plastic chambers (fig. 6.1). The illumination was 110 μmol m^{-2}s^{-1} PAR from a tungsten bulb suspended above the chambers with a heat-shield of 8 cm of water in a glass tank. Relative humidity inside the analysis chambers was 85% and the temperature 23°C. Air was pumped into the gas analyser at 150 cm^{3}min.$^{-1}$ The gas analyser was calibrated daily using gas of 350 vpm CO_2.

b. Study of the cumulative effects of heat and drought.

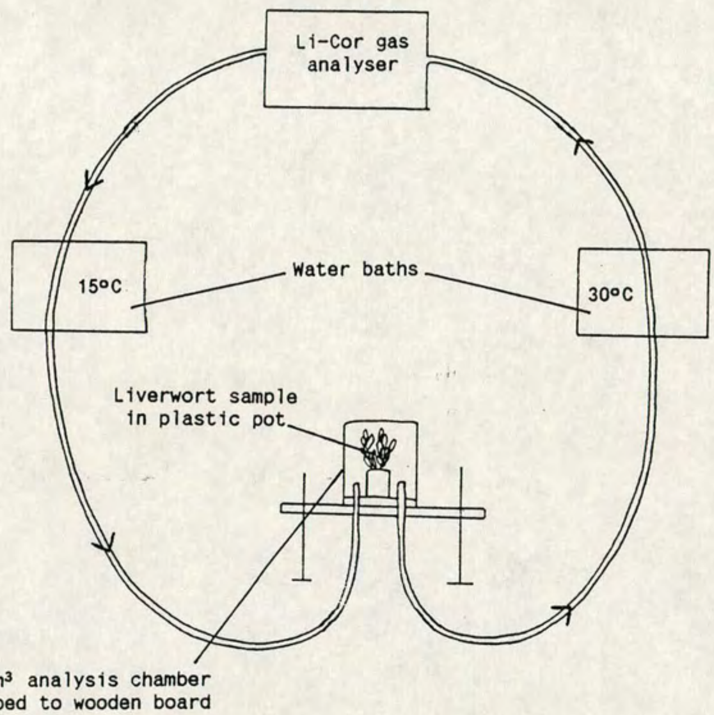
Survival and recovery of *Herbertus aduncus* and *Scapania ornithopodioides* was assessed by measuring carbon dioxide exchange using an LI-6250 infra-red gas analyser as a closed system (Li-Cor Inc., Lincoln, Nebraska, U.S.A.). A special 75 cm^3 chamber was constructed because the liverwort samples were so small. The circulating air-stream was cooled before passing over the sample and warmed before returning to the gas analyser, to avoid condensation in the tubing (fig. 6.2). The gas analysis was done inside the growth-room. An electric

Figure 6.1 Apparatus designed for a pilot experiment to determine the effects of increasing drought on six Atlantic liverwort species as measured by carbon dioxide exchange.



The six samples were allowed to recover simultaneously in the chambers. Gas exchange was measured for each sample in turn by removing the inlet and outlet tubes and substituting the two ends of the analysis line.

Figure 6.2 Apparatus designed to test the effects of combinations of temperature and humidity on Atlantic liverworts by measuring gas exchange.



The diagram shows a Li-Cor Li-6250 gas analyser used as a closed system. Air is pumped from the analyser in a tube passing through a water-bath at 15°C to the analysis chamber. The tube carrying air from the analysis chamber to the gas analyser passes through a water-bath at 30°C. This is to prevent condensation in the tubing (the liverwort samples have to be wet to photosynthesise).

fan was used to circulate the air inside the growth-room and prevent the level of carbon dioxide rising too far above ambient levels. In practice CO_2 concentration in the growth-room while the analyses were being done varied between 600 and 800 vpm. Relative humidity in the growth-room was set at 80%. The mean temperature inside the analysis chamber was 23.5 +- 1.5 °C. The gas analyser was calibrated daily using gas of 350 vpm CO_2 and the desiccant (magnesium perchlorate) changed when necessary.

One sample from treatment 1 was removed at random and re-wetted by spraying with distilled water. The sample was sealed in the analysis chamber and left for 30 seconds for the CO_2 concentration in the system to stabilise. The change in concentration of CO_2 (in vpm) was measured over 30 seconds. Then a sample was taken from treatment 2 and the process repeated. This was continued until a sample from every treatment had been measured. A second sample was then taken from treatment 2 and measured, followed by samples from treatments 3, 4, 5, 6 and 1 (fig. 6.3). The work continued until all samples had been rewetted. Each sample was reanalysed in turn until the change in concentration of CO_2 was negative - or until the end of the day if the sample did not recover. At the end of the day all samples were sprayed with water, blotted dry, dried in front of the fan if appropriate and returned to the polythene boxes. The treatments were applied to the plants for eight days and survival was measured after one, two, four and eight days.

Figure 6.3 The design for the experiments to test the effects of combinations of heat and drought on Atlantic liverworts

1 1	2 2	3 3	4 4	5 5	6 6
7 2	8 3	9 4	10 5	11 6	12 1
13 3	14 4	15 5	16 6	17 1	18 2
19 4	20 5	21 6	22 1	23 2	24 3
25 5	26 6	27 1	28 2	29 3	30 4
31 6	32 1	33 2	34 3	35 4	36 5

Top row of figures = sequence of analysis
Bottom row of figures = treatment

Treatments
1. 15°C, 100% water content
2. 50°C, 100% water content
3. 15°C, 50% water content
4. 50°C, 50% water content
5. 15°C, 25% water content
6. 50°C, 25% water content

Plants which had not recovered by the end of the eighth day were remeasured on the ninth without being subjected to further treatment.

The physical effects of the treatments were assessed by microscopic inspection of the liverworts. *Herbertus aduncus* and *Scapania ornithopodioides* were investigated at the end of the experiment. One leaf was taken from each of 12 shoots of *Scapania* and 18 shoots of *Herbertus* in each treatment. Shoots were selected at random from the three samples. The leaves were examined at 375X magnification under a light microscope. The percentage of living cells in each leaf was estimated. (Dead cells are either clear and empty or have severely disrupted contents which do not recover on wetting.) Survival of *Mastigophora woodsii, Pleurozia purpurea, Scapania gracilis* and *Plagiochila carringtonii* was assessed by this method alone after one, two, four and eight days of treatment. One leaf was taken at random from each of five shoots in each of the five replicates in each treatment. The percentage of living cells in each leaf was estimated. The differences between treatments and species were analysed by factorial analysis of variance (SYSTAT 1992).

6.2.4 Water contents of plants collected in the field

Five samples each of *Herbertus aduncus, Pleurozia purpurea, Mastigophora woodsii* and *Plagiochila carringtonii* were collected on Beinn Eighe in West Ross on 6 and 7 September

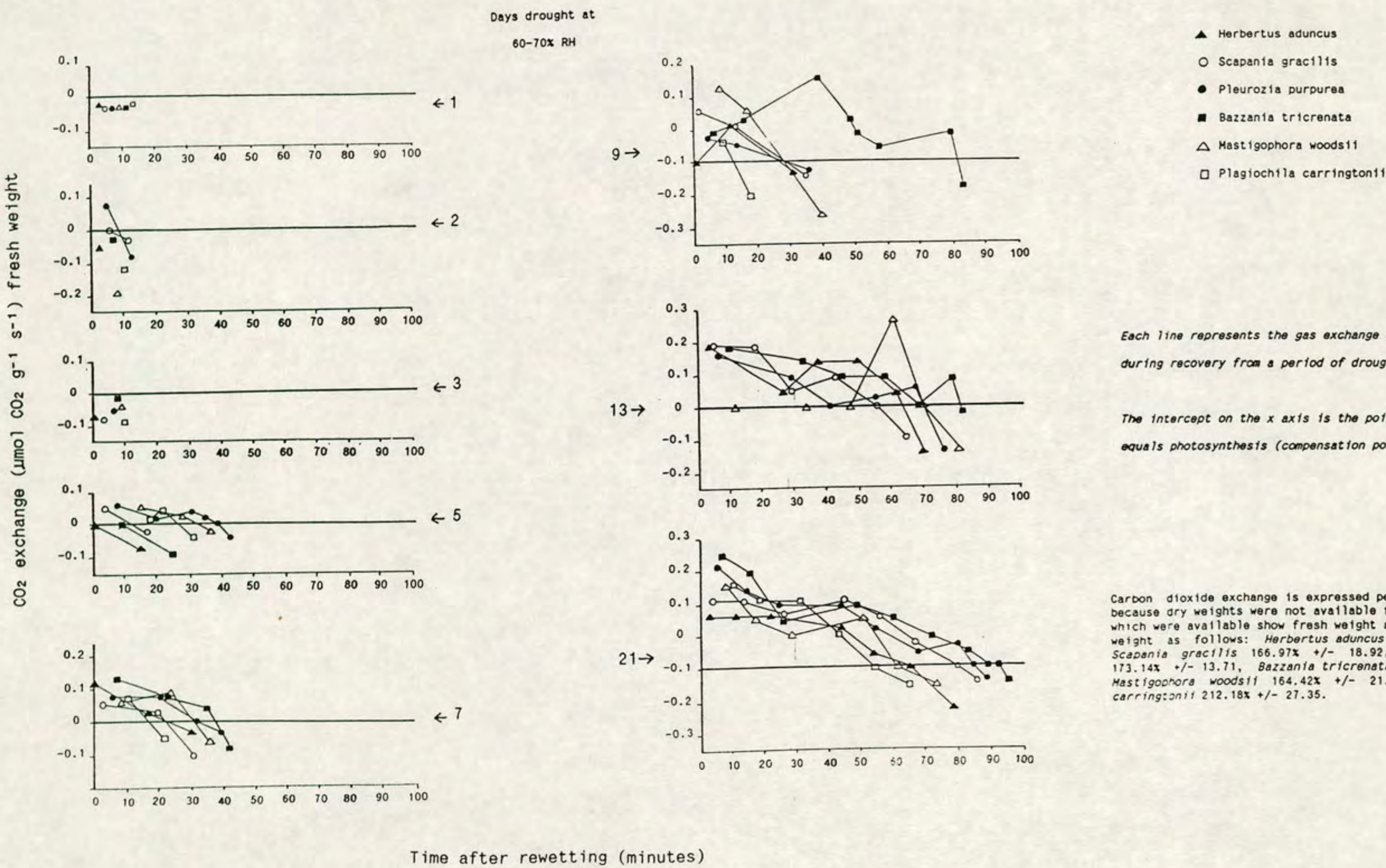
1993 after several days without rain. Tufts of the plants were cut with scissors at the base of the shoots and placed in plastic pots which were sealed immediately. The pots were weighed, then opened and oven-dried for a week at 80°C. They were re-weighed and the water content of each sample calculated.

6.3 Results

6.3.1 The pilot study to investigate the effects of drought on the hepatic mat species

The six species tested in the pilot study all survived 21 days at a saturation deficit between 0.935 and 0.701 KPa (60 to 70% relative humidity at 20°C) (Monteith 1973). The longer the period of drought before rewetting, the longer it took for the plant to recover (fig. 6.4). For *Bazzania tricrenata*, this period was less than 6 minutes after 3 days of drought and 89 minutes after 21 days. Some samples had a peak in respiration shortly after remoistening (*Bazzania tricrenata* on the ninth day of drought, *Plagiochila carringtonii* on the fifth day and *Mastigophora woodsii* on the seventh and thirteenth days). From 5 days of drought onwards the samples had increasingly higher rates of respiration when first measured. Recovery was much the same in all six samples. The exception was *Bazzania tricrenata*, which took far longer than the others to recover from 9 days of drought.

Figure 6.4 Recovery of six Atlantic liverworts from increasing lengths of drought



Each line represents the gas exchange of one individual during recovery from a period of drought.

The intercept on the x axis is the point at which respiration equals photosynthesis (compensation point).

Carbon dioxide exchange is expressed per gram fresh weight because dry weights were not available for all samples. Data which were available show fresh weight as a percentage of dry weight as follows: *Herbertus aduncus* 208.60% +/- 52.35, *Scapania gracilis* 166.97% +/- 18.92, *Pleurozia purpurea* 173.14% +/- 13.71, *Bazzania tricrenata* 126.13% +/- 16.67, *Mastigophora woodsii* 164.42% +/- 21.13 and *Plagiochila carringtonii* 212.18% +/- 27.35.

6.3.2 The cumulative effects of drought and heat.

a. Infra-red gas analysis as a measure of recovery

The response of *Scapania ornithopodioides* and *Herbertus aduncus* to the cumulative treatment of drought and heat varied from no interruption of photosynthesis to failure to recover even after 24 hours. The cost to the sample in carbon used for respiration varied from 0 to over 5.94 µg per gram dry weight (table 6.1). The figures for the samples which did not recover by the end of the day show the carbon used during the period of time over which measurements were made.

Plants exposed to 50°C for 10 hours each day were slower to recover when rewetted than those maintained at 15°C. The combination of 15°C and 100% water content - the control treatment - had little effect and in most cases the plants were already photosynthesising at the start of each analysis. The plants kept at 15°C fared better at high water contents, while those subjected to 50°C survived longer if the water content was low. Only one sample - of *Herbertus aduncus* - recovered from the combination of 50°C and 100% water content, and only after one day of this treatment. *Herbertus aduncus* was more tolerant of low water content than *Scapania ornithopodioides*, both at 15°C and at 50°C. In general the more times the treatments were repeated, the higher the cost to the plants as they recovered.

Table 6.1 The cost in µg of carbon per g oven-dry weight for Herbertus aduncus *and* Scapania ornithopodioides *recovering from treatment with heat and drought.*

Average water content (% original water content)

	Day	100			50			25		
Herbertus 15°C										
	1	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	4	0	0	0.024	0.004	0.039	0	0	0	0.006
	8	0	0	0	0	0.004	0	0	0	0.016
Herbertus 50°C										
	1	>0.334	0.004	>0.070	0.136	0	0	0.012	0.004	0
	2	>1.759	>1.285	>1.114	>0.345	>0.225	>0.249	>0.282	>0.258	0.050
	4	>1.315	>0.938	>0.561	>0.165	0.014	0.099	>0.260	0.144	0.114
	8	>5.313	>2.999	>3.287	>1.001	>1.292	>0.835	>0.740	>0.992	>0.495
Scapania 15°C										
	1	0	0	0	0	0	0	0	0	0
	2	0.031	0	0	0	>0.273	0	>0.285	0.057	0.058
	4	0	0	0.009	0.220	>0.311	0.013	>0.478	0.035	0.267
	8	0	0	0	0.255	0	>3.510	>1.899	0.261	>0.597
Scapania 50°C										
	1	>0.291	>0.575	>1.323	0.074	0	0.051	0.295	0.074	>0.526
	2	>0.442	>1.496	>1.609	>0.600	>0.672	>0.417	>0.696	>0.839	>0.508
	4	>0.732	>1.154	>2.347	0.037	>0.396	>0.211	>0.240	>0.393	>0.389
	8	>2.844	>5.085	>5.940	>2.701	>3.664	>3.815	>1.497	>1.702	>2.128

Figures show µg of carbon per g oven-dry weight used in respiration before the compensation point was reached. > shows that sample did not reach the compensation point during the period of measuring (up to 24 hours from rewetting).

b. The physical effects of the treatments

The physical effects of the treatments confirmed the observations of gas exchange (table 6.2). All of the samples kept at 15°C had living cells at the end of the experiment. Of these samples, those at 100% water content had more living cells than those at 50% water content, which in turn had more than those at 25% water content. Few of the samples survived for long at 50°C. Those that did showed a pattern opposite to those kept at 15°C: the samples at 25% water content survived longer than those kept at 50% water content. The samples subject to 50°C and 100% water content had no living cells at all at the end of the experiment. As the experiment progressed the differences between water contents became greater in the samples kept at 15°C, so that after 8 days of treatment all the species were doing better at 100% water content than at 50% or 25% water content.

Herbertus aduncus was the only species to survive for 8 days at 50°C and 50% water content, although the apices of *Pleurozia purpurea* survived four days and some cells of *Plagiochila carringtonii* survived two days of this treatment. Some cells of *Scapania gracilis* and *Mastigophora woodsii* survived one day of it. The leaves of *Herbertus aduncus* and *Scapania ornithopodioides* were not examined until the end of the experiments. However the results of the gas analysis suggest that some samples of *Scapania ornithopodioides* survived one day at 50°C and 50% water content and one day at

Table 6.2 Mean number (+- standard error) of surviving cells in samples of six liverworts subjected to varying combinations of heat and drought.

		P.purpurea	S.gracilis	M.woodsii	P.carring.	H.aduncus	S.ornithop.
C100	1	93.9+-1.0	92.3+-1.2	98.2+-0.7	92.0+-1.9		
	2	96.0+-0.9	96.0+-0.7	93.0+-1.6	95.4+-1.1		
	4	96.0+-0.4	94.6+-0.8	93.0+-1.8	91.7+-1.0		
	8	97.7+-0.5	92.6+-1.2	94.1+-1.6	90.8+-0.9	90.0+-0.0	89.2+-0.6
C50	1	85.7+-2.8	89.0+-2.1	89.6+-4.0	87.0+-3.4		
	2	92.1+-2.6	86.4+-4.2	92.1+-0.3	88.2+-2.0		
	4	92.9+-1.0	92.0+-0.6	88.7+-4.5	83.6+-3.2		
	8	90.4+-1.7	91.4+-2.0	90.2+-1.2	73.4+-5.8	87.2+-1.1	75.4+-6.1
W50	1	1.4+-1.0	0.2+-0.2	1.0+-0.6	0.9+-0.2		
	2	0.0 0.0	0.0 0.0	0.0 0.0	3.2+-2.3		
	4	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0		
	8	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0	18.9+-9.7	0.0 0.0
C25	1	71.7+-11.9	67.2+-15.7	45.2+-17.6	76.7+-5.9		
	2	87.2+-6.5	70.2+-9.1	62.2+-13.1	85.0+-2.4		
	4	90.4+-2.3	74.0+-7.6	79.0+-5.7	80.0+-4.1		
	8	82.2+-3.2	80.6+-4.3	83.8+-3.6	82.0+-2.9	73.1+-6.3	65.0+-3.0
W25	1	2.8+-1.0	0.8+-0.8	3.2+-3.2	10.8+-3.9		
	2	0.0 0.0	0.0 0.0	1.4+-0.9	1.6+-0.6		
	4	0.0 0.0	0.0 0.0	0.8+-0.8	0.0 0.0		
	8	0.0 0.0	0.0 0.0	0.0 0.0	0.4+-0.4	42.2+-15.8	0.0 0.0

C - 15°C, W - 50°C. 25, 50, 100 - water contents as percentage of original
Figures are means of five replicates.

. The combination of 50 °C and 100% water content was fatal in all species except Herbertus aduncus, *one sample of which survived for 1 day.*

50°C and 25% water content. *Herbertus aduncus* and *Plagiochila carringtonii* had some surviving cells after 8 days at 50°C and 25% water content. *M.woodsii* survived 4 days of this treatment. In most species the young unexpanded leaves at the shoot-tips survived for longer than the older leaves and were fresh and green when all the fully-expanded leaves were dead. All of the samples kept at 50°C had a strong smell of decomposition about them by the end of the experiment. Over 20% of the sampled leaves from *Herbertus* kept at 50°C were contaminated with blue and purple fungal hyphae.

Of the samples kept at 100% water content, all those kept at 15°C lived and all those kept at 50°C were dead after two days of the treatment. This shows that in fully saturated plants, temperature has a significant effect on survival and there is no difference between species. An analysis of variance of the samples kept at 50% and 25% water contents showed that after 1, 2 and 4 days of the experiment both water content and temperature (and the interaction between them) had significant effects on the number of surviving cells but there was no significant difference between species. By 8 days water content was not significant, but temperature was, and now there were significant differences between species (table 6.3).

6.3.3 Water contents and rates of drying.

The six liverwort species used in the experiment to test the

Table 6.3. Results of analysis of variance to test the effects of two temperatures and two water contents on % cell survival of members of the hepatic mat.

Day	Source	MS	DF	F	P
1	Species	281	3	1.1	0.348
	Water content	1820	1	7.2	0.009
	Temperature	109106	1	434.5	0.000
	Water x Temp	3411	1	13.6	0.000
	Water x Species	388	3	1.5	0.211
	Species x Temp	167	3	0.7	0.578
	Water x Species x Temp	244	3	1.0	0.413
	Error	251	64		
2	Species	211	3	2.0	0.122
	Water content	923	1	8.8	0.004
	Temperature	134956	1	1279.5	0.000
	Water x Temp	913	1	8.7	0.005
	Water x Species	159	3	1.5	0.220
	Species x Temp	180	3	1.7	0.174
	Water x Species x Temp	226	3	2.1	0.103
	Error	105	64		
4	Species	97	3	2.1	0.103
	Water content	341	1	7.5	0.008
	Temperature	144398	1	3182.2	0.000
	Water x Temp	376	1	8.3	0.005
	Water x Species	63	3	1.4	0.256
	Species x Temp	101	3	2.2	0.094
	Water x Species x Temp	65	3	1.4	0.244
	Error	45	64		
8	Species	584	5	7.6	0.000
	Water Content	52	1	0.7	0.412
	Temperature	142083	1	1841.8	0.000
	Water x Temp	726	1	9.4	0.003
	Water x Species	92	5	1.2	0.323
	Species x Temp	736	5	9.5	0.000
	Water x Species x Temp	200	5	2.6	0.032
	Error	77	80		

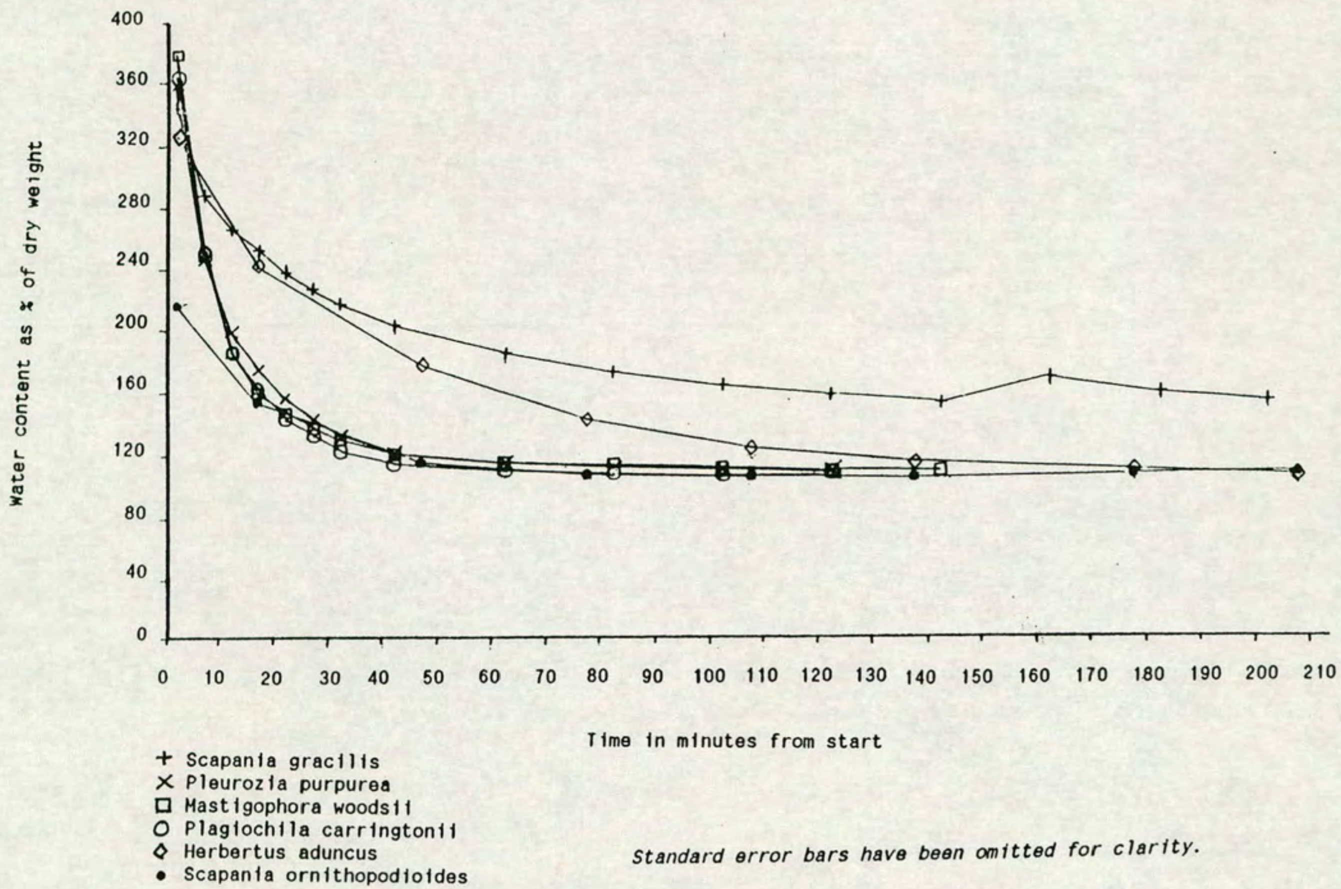
Species tested on days 1 to 4 were Mastigophora woodsii, Plagiochila carringtonii, Pleurozia purpurea *and* Scapania gracilis. *On Day 8* Herbertus aduncus *and* S.ornithopodioides *were included. The two water contents were 50% and 25% of original fresh weight and the temperatures 15 °C and 50 °C.*

cumulative effects of heat and drought dried out in front of an electric fan at similar rates (fig. 6.5, Appendix 4). After 2.5 hours there was no more measurable loss of water. *Scapania gracilis* and *Herbertus aduncus* dried more slowly than *Plagiochila carringtonii, Pleurozia purpurea*, *Scapania ornithopodioides* and *Mastigophora woodsii,* and *Scapania gracilis* did not lose as much water as the other species. The mean initial water content of most of the samples was about 350% of oven-dry weight (table 6.4). The exception was *Scapania ornithopodioides* which held an average of only 215.2% of its dry weight in water.

The mean water contents of the samples of *Herbertus aduncus* and *Scapania ornithopodioides* which were dried out for the experiments (table 6.5) showed that the samples of *Scapania* dried to 50% of original water content always had a higher actual average water content than those dried to 25%, while the samples of *Herbertus* dried to what should have been 25% of original water content actually had nearer 50%.

The plants collected to investigate field water contents held widely-varying amounts of water (table 6.6). *Herbertus aduncus* and *Pleurozia purpurea* had water contents between 140% and over 400% of dry weight. Water content in *Mastigophora woodsii* varied from 194% to 477% of dry weight. The samples of *Plagiochila carringtonii* had the greatest variation - from just over 100% to over 500% of dry weight. On average *Herbertus aduncus* and *Pleurozia purpurea* had

Figure 6.5 Drying curves for six Atlantic liverworts dried at 20°C in front of an electric fan



Standard error bars have been omitted for clarity.

Table 6.4. Oven-dry weight and water content of six Atlantic liverwort species.

	Oven-dry weight (g)	% water content
Herbertus aduncus	0.245 (0.02)	325.1 (18.9)
Mastigophora woodsii	0.201 (0.01)	376.8 (9.8)
Plagiochila carringtonii	0.186 (0.001)	362.8 (11.4)
Pleurozia purpurea	0.204 (0.01)	358.9 (10.6)
Scapania gracilis	0.386 (0.01)	342.2 (37.6)
Scapania ornithopodioides	0.210 (0.01)	215.2 (12.3)

Standard errors in parentheses. Figures are means of five replicates.

Table 6.5. Mean water contents of samples of Herbertus aduncus *and* Scapania ornithopodioides *dried to a theoretical 50% and 25% of original water content.*

Species	*Temp* °C	*Water* % *original*		Day of treatment 1	2	4	8
Herbertus	15	50	*mean*	54.6	58.5	43.2	36.7
			se	0.7	6.5	6.5	0.2
Scapania	15	50	*mean*	44.1	47.7	45.7	38.5
			se	1.6	0.9	4.0	12.4
Herbertus	50	50	*mean*	66.2	53.0	35.2	31.5
			se	3.9	15.0	8.2	5.4
Scapania	50	50	*mean*	52.5	39.1	40.4	49.4
			se	5.2	8.6	5.7	5.9
Herbertus	15	25	*mean*	53.3	51.9	55.8	21.8
			se	4.0	4.4	7.7	5.3
Scapania	15	25	*mean*	32.4	24.4	19.1	37.2
			se	4.0	3.3	3.0	2.7
Herbertus	50	25	*mean*	56.8	30.1	27.7	17.9
			se	4.8	7.1	4.2	2.8
Scapania	50	25	*mean*	38.4	29.6	18.0	37.8
			se	5.7	3.7	2.9	1.8

Temp - temperature at which samples were kept. Those at 50°C had 10 hours at this temperature in every 24.

Water - theoretical water content calculated from drying times of a sample of liverworts. $n = 3$ for each species.

Table 6.6 The water contents (as % of dry weight) of five samples each of four hepatic mat species collected on Beinn Eighe and Liathach, West Ross, on a dry day in September 1993.

Species	Herbertus aduncus	Pleurozia purpurea	Mastigophora woodsii	Plagiochila carringtonii
	139.4	192.4	228.4	116.8
	226.6	408.6	370.0	260.3
	242.1	210.1	477.6	167.3
	449.8	140.7	373.8	465.6
	165.9	288.3	194.6	530.0
Mean	244.8	248.0	328.9	308.0
St. dev	54.5	46.5	51.9	81.3

higher water contents than *Mastigophora woodsii* and *Plagiochila carringtonii*, but the differences were not significant.

6.4 Discussion.

The results of the pilot experiment confirm the observations of Clausen (1964) and Dilks & Proctor (1979) - members of the hepatic mat community can indeed tolerate drought for longer than they are likely to experience in the field. It was impossible to make useful comparisons between species since this experiment was done on one individual on each occasion without replication to assess differences within species.

The results of the experiment to test the cumulative effects of heat and drought suggest that the effects of water content and temperature are linked. At low temperatures the species survive better when they are wet; at high temperatures they survive better when they are dry. High temperature combined with high water content is fatal. This confirms the suggestions made by Clausen (1964). Proctor (personal communication) considers that fully-hydrated bryophytes will probably be killed by temperatures above 45°C.

The survival of shoot-tips in conditions which kill expanded leaves suggests that these species may retain the ability to sprout again even if many leaves die in times of drought. The results are surprising because one would expect the young leaves to be most sensitive, and some studies have found this to be so (e.g. Clausen 1964). Some liverworts can regenerate from detached shoots with a living apex (Miller & Ambrose 1976, Schuster 1983), and this would be worth field investigation.

The experimental temperature might seem to be unnecessarily severe. However surface temperatures of 50°C have been recorded on mountain slopes in the Alps on sunny days (Geiger 1971), and in the British Isles dry bryophytes in the sun can experience 65°C or more (Proctor 1982). *Herbertus aduncus*, *Scapania gracilis* and *Plagiochila spinulosa* have been shown to have optimal temperatures for photosynthesis of 18°C to 20°C (Proctor 1982). These are comparatively high temperatures in the usual habitats of these species. Many bryophytes are able to tolerate water contents of less than 10% of their oven-dry weights (Proctor 1990). The results suggest that many of the hepatic mat species may well be able to tolerate the temperatures and water contents they would experience on south-facing slopes (Chapter 5).

Several samples of *Scapania ornithopodioides* and *Herbertus aduncus* which apparently respired throughout the experiment had no living cells by the end of the treatment. This must have been microbial respiration from organisms attacking the dead plant material, especially since the amount of respiration increased with time. One would expect respiration to decline in a plant which was succumbing to unfavourable conditions. Microbial respiration is apparently insignificant in living bryophytes (Hinshiri & Proctor 1971), but is important when the plants are dead, presumably because large populations of bacteria and fungi build up on the leachates from the dead cells as well as on structural tissue (Bewley 1979). This is a disadvantage of gas analysis as a method for measuring survival. Although it can record photosynthesis in living bryophytes, it will not distinguish between a live, respiring plant and a dead, rotting one.

The necessity for bryophytes to be wet in order to photosynthesise can cause problems with gas analysis which do not arise with vascular plants. If a wet bryophyte sample is sealed in an analysis chamber there will soon be water vapour and condensation in the system. As well as damaging the analysis cell, water vapour dissolves carbon dioxide and can cause errors in the measurements of gas exchange. Water adsorption onto the walls of the chamber and tubing can also change the concentration of carbon dioxide in the circulating air (Field, Ball & Berry 1989). In my experiments the air in the system was cooled before entering the chamber and warmed after leaving it and all the air entering the gas analyser was passed through a desiccant. In practice there was no condensation in either the analysis chamber or the tubing.

The main shortcoming of the experiment to test the cumulative effects of heat and drought was that the water contents used - 100%, 50% and 25% of original water contents - are imprecise and cannot really be related to the water potentials of the plant cells. In fact there was quite a wide variation in the actual water contents of *Herbertus aduncus* and *Scapania ornithopodioides* after drying. (Dry weights of *Pleurozia purpurea*, *Scapania gracilis*, *Mastigophora woodsii* and *Plagiochila carringtonii* were not recorded because of destructive sampling to examine the leaves during the experiments.) The problem arose because of the limited time available for experimental work. The aim of the experiment was to repeat the heat and drought treatments on the same samples. The treatments had to be repeated daily. Therefore the plants had to be dried quickly each day so that they could undergo the treatment before the next day. A better system, had I had more time, would have been to keep the plants in desiccators in which water content was controlled by saturated salt solutions and to repeat the treatments weekly rather than daily. This method of maintaining plants at constant humidities has been used with success by Dilks & Proctor (1974, 1979). It might also have been possible to relate the water contents of the experimental plants to water potentials (Dilks & Proctor 1979). The method would have been to incubate samples of each species in desiccators in equilibrium with saturated salt solutions to give a range of water potentials. The actual water content (as % of dry weight) of these samples would be determined. Actual water content could be plotted against known water potential, and the water potentials in plants at 50% and 25% water content read off the graph. This more precise method may have shortcomings: tests done during my pilot experiments showed that the relative humidity in a desiccator containing samples of liverworts and calcium nitrate $Ca(NO_3)_2.4H_2O$ in equilibrium with its saturated solution was actually somewhere between 60% and 70% at 20°C even after two weeks, although the salt solution should have maintained it at 54.5% (Dilks & Proctor 1974). Another method is to measure the water content of the plant cells. Tissue water content in vascular plants can be defined fairly accurately as relative water content or RWC, because there is little external water even when the cells are fully turgid. However bryophytes can store a lot of water in their external capillary spaces and their thick cell walls, and the tissue water content at full turgor is not easy to measure accurately. Therefore RWC is not as useful in bryophytes as in vascular plants (Dilks & Proctor 1979).

Several authors (summarized by Proctor 1982) have recorded a rapid rise in respiration following rewetting and have linked recovery time to the time taken for photosynthesis to return to normal having been offset by this peak in respiration. There were signs of this in the pilot experiment, but not in the comparative experiments. This may be because maximum respiration happens very soon after remoistening and had already happened by the time the sample was first analysed. It is also possible that the plants were already respiring at the time that they were remoistened. This needs further work but if it is true (as suggested by Proctor 1982) it implies that the plants can respire when they are too dry to photosynthesise. In this case they would need to be wet for enough of the time to allow net photosynthesis to exceed net respiration, which would be one reason why they might need a wet climate.

The hepatic mat liverworts grow in places where they are cool and damp for most of the time. They are obliged to tolerate high temperatures only when they are exposed to bright hot sun in early summer (Chapters 4 and 5), and the cushions dry rapidly in these conditions. Tolerance of heat and drought seems to depend on a combination of ability to hold and retain water and the physiological limits of the cells. Water retention is probably closely-related to the structure and arrangement of the leaves and branches (Basile & Basile 1987, Proctor 1990). Species with small leaves and a complex structure probably hold more water than these wih large leaves and simple shoots (Landsberg & Thom 1971). The tightly-packed shoots of *Scapania gracilis* and the dense tufts of *Herbertus aduncus* seem to retain water better than the loose clumps or wefts of the other species. *Herbertus* is also apparently relatively physiologically tolerant of heat and drought. Species such as *Mastigophora woodsii*, *Pleurozia purpurea* and *Plagiochila carringtonii* lose water rapidly, but are able to hold a lot. These species are also relatively tolerant of heat and drought. Although it is a widespread species, *Scapania gracilis* appears relatively intolerant of heat and drought. It may overcome this by its slow rate of drying. *Scapania ornithopodioides* holds relatively little water, dries out rapidly and has little physiological tolerance. The behaviour of the plants correlates broadly with their distributions in the British Isles. *Herbertus aduncus*, *Scapania gracilis* and *Pleurozia purpurea* are widespread, although *P.purpurea* is absent from England and Wales (where summers are warmer than in western Scotland and western Ireland). *Herbertus* and *Scapania gracilis* are both frequent in wet, western areas with relatively warm summers: north-west England, north Wales and south-west Ireland. The other three species are rare outside the high-rainfall areas of the western Highlands.

CHAPTER SEVEN

GENERAL DISCUSSION

7.1 Distribution

The hepatic mat species are probably survivors of a widespread oceanic flora which developed in the northern hemisphere during the Tertiary period (Schofield 1988b). The Pleistocene glaciations fragmented this Tertiary vegetation in western Europe. Many species only survived by migrating far to the south, and many became extinct (Vincent 1990). This ancient flora probably persisted in the unglaciated refugia of coastal British Columbia and the Himalayan foothills (Schofield 1988b). Some of the hepatic mat species may have survived the Ice Age in refugia to the west of the British Isles, although this is unlikely (Greig-Smith 1950). The hepatic mat liverworts are unique among the flora of the British Isles (Crundwell 1970). They share disjunct world distributions and ecological requirements (Chapters 2-6). They frequently grow together as a discrete unit, apparently unchanged in its composition since the end of the Tertiary period.

In Europe the community is best-developed in the wettest parts of western Scotland and western Ireland (Chapter 3). However there are - admittedly species-poor - hepatic mats in the Faroe Islands and western Norway (Chapter 2) and on mountains in the high-rainfall areas of Wales and north-west

England (Chapter 3). Species lists made by the Nature Conservancy Council, now the Countryside Council for Wales (unpublished) suggest that there could be hepatic mats on the Rhinogs, the Aran mountains and the Glydeirau in North Wales as well as on Cader Idris. There are fragments of the community in Ennerdale in Cumbria (personal observation).

Chapters 3 and 5 show that the hepatic mat species are not equally abundant at all their sites in the British Isles. *Bazzania pearsonii* is especially frequent on Liathach (personal observation) and *Scapania ornithopodioides* is unusually abundant on the cliffs of Bidean nam Bian (Chapter 3). Other observers have found the same. For example, *Scapania nimbosa* is particularly common in the Letterewe Forest in Wester Ross (Ratcliffe 1977) and *Plagiochila spinulosa* is more abundant in hepatic mats on Skye than it is on the mainland (Birks 1973). Of the 16 hepatic mat species, *Adelanthus lindenbergianus* is markedly southern in its distribution and *Anastrophyllum joergensenii* is markedly northern. This suggests that although the community is an assemblage of liverworts which have similar ecological requirements, the relative abundance of each species at each locality is controlled by variation in the environment and by different rates of colonisation and growth.

The distribution of the hepatic mat species in the British Isles is strongly associated with a low annual temperature range and a wet climate. These results agree with the findings of Ratcliffe (1968). However hepatic mats can develop in places with fewer than 220 wet-days a year as long as there is a low annual temperature range, and there are hepatic mats on hills where summers are warm and winters cold, but where the climate is extremely wet (Chapter 3). This shows how climate elements interact to give favourable conditions (Averis 1991). The hepatic mat can develop on aspects other than north or east in parts of the north-west Highlands where temperatures are equable and rainfall heavy and frequent, such as the boulder-field on Beinn Alligin (which faces south-east) (Chapter 3) and on Beinn Eighe (Chapter 4). At least some members of the community occur on all aspects on Beinn Eighe but they are rare on slopes facing south-west and most common on aspects between north-west and east. *Pleurozia purpurea*, *Mylia taylorii* and *Scapania gracilis* often occur as scattered individuals or clumps in bogs and wet heaths, but the other species tend to grow mixed together in cushions, even on slopes facing south or west. There is a general impression that where conditions are suitable for these plants there will be a lot of them, rather than just one or two. *Herbertus aduncus* is usually the most abundant species on heathy slopes below about 600m, but tends to be sparse at higher altitudes, where *Scapania nimbosa* and *Anastrophyllum donnianum* are more common (Ratcliffe 1968, Rodwell 1991b, Chapters 3 & 4).

Generally the species become less confined to northerly aspects with increasing altitude, as has already been suggested by Proctor (1980b). This is perhaps because mean temperatures are lower because of the lapse rate with altitude (Meteorological Office 1975), rainfall is higher and there are many days a year when the high slopes are covered by cold drifting clouds. Mist can be an important source of water even on days with no measurable precipitation (Russell 1984). Where there is mist as well as rain, the actual precipitation may be more than double that recorded at low-altitude weather stations where there is heavy rainfall but less low cloud (Geiger 1971, Russell 1984b, Grace & Unsworth 1988). Although steep south-facing slopes do not hold late snow they are frequently covered by a thin layer of snow through much of the winter, which must protect the liverworts from desiccating frost.

The world distribution of hepatic mats (Chapter 2) is obviously considered from the point of view of the British Isles. An ecologist in British Columbia or the Himalayas might have a very different idea of what constitutes a hepatic mat and how the British and Irish communities fit into the pattern.

7.2 Habitat

The records for hepatic mat species throughout the world suggest that they grow in similar habitats in the same countries, even though they may not actually grow in intimate mixtures as they do in the British Isles. They show a clear preference for damp shaded habitats wherever they occur whether this is provided by woodland, ravines, steep rocky slopes or the permanently wet surface of bogs (Chapters 2, 3 & 4). They are able to grow at sea-level in western Europe and western North America with their mild oceanic climates, but in south-east Asia they are plants of montane forests. The climate here is mild and moist as a result of altitude rather than of proximity to a large ocean. Weather conditions at 3000m ASL in the Himalayas and western China are similar to those experienced at sea-level in western Scotland ((D. F. Chamberlain pers. comm.) It seems clear that it is the highly oceanic climate of the western parts of the British Isles, combined with the mountainous topography, that allows these species to grow here in such abundance (Chapters 2 & 3).

The hepatic mat species are woodland plants throughout most of their modern range, and most probably evolved in tropical or warm temperate woodlands, probably as epiphytes (Chapter 2, D. F. Chamberlain pers. comm.). They are common in open habitats only in north-west Great Britain, Ireland and the Faroe Islands. There is no natural woodland in the Faroes (Johansen 1985). The Scottish and Irish mountains are largely treeless as a result of cool summers and strong winds, as well as a long history of deforestation, burning and grazing (Birks 1988). The distribution of hepatic mats in the British Isles has probably been reduced by burning and grazing of dwarf-shrub heaths and bogs and felling of the natural woodland (Chapter 3). McVean & Ratcliffe (1962), Ratcliffe

(1968) and Birks (1973) noted that the hepatic mat community was absent from slopes where the vegetation had been repeatedly burnt. I found more evidence of this on several hills in the north-west Highlands. However it is not known why the liverworts are unable to recolonise burnt ground. Perhaps the open canopy lets in too much light and wind. Maybe the burnt peat surface is chemically unfavourable, or perhaps exposed peat simply gets too hot and dry. Other bryophytes, especially the large pleurocarpous mosses, may be better competitors on dry, exposed peat.

The hepatic mat and associated damp heaths are increasingly confined to relatively inaccessible ground in the south of Scotland and in England and Wales (Chapter 3). Sheep-grazing (in western Ireland, north Wales, the Lake District and the southern Highlands) seems to be more damaging than deer-grazing (in north-west Scotland), perhaps because the density of animals is greater. Red deer concentrate in valleys in winter where they cause local damage to dwarf-shrub heaths (Nicholson 1970). They also shelter in corries and damage heaths with hepatic mats (mainly by trampling), for example on Ben More Coigach, Ben More Assynt (D.A. Ratcliffe pers. comm.), Beinn Dearg Flowerdale (personal observation) and the Twelve Bens of Connemara (Horsfield *et al.* 1991). However they may use these places less in still summer weather because of the high numbers of midges which also frequent these sheltered slopes (Chapter 5).

The hepatic mat species are not such strict calcifuges as Ratcliffe (1968) and Smith (1990) suggest. *Mastigophora woodsii, Scapania ornithopodioides, S.gracilis, Plagiochila carringtonii, Anastrepta orcadensis, Bazzania tricrenata, Mylia taylorii* and *Anastrophyllum donnianum* grow on the basalt of the Faroe islands, often in close proximity to calcicoles such as *Juncus triglumis, Herbertus stramineus, Saxifraga oppositifolia* and *Selaginella selaginoides* (Chapter 2). In Scotland *Mastigophora woodsii* is abundant in species-rich grassland on the basalt hills of northern Skye, and on Beinn Eighe *M.woodsii* is rare on the quartzite slopes but fairly common on the sandstone (Chapter 4). On Beinn Eighe there are cushions of hepatic mat species mixed with the calcicoles *Herbertus stramineus* and *Leptodontium recurvifolium* on outcrops of the base-rich serpulite grits and fucoid beds on Ruadh-stac Beag (personal observation). I have also seen *Herbertus aduncus* growing on mica-schist on Ben Laoigh in Argyll. The preference of the hepatic mat species for base-enriched substrates in England and Wales has already been noted (Ratcliife 1968, Chapter 3).

Rocky mountain slopes look like stable habitats but are not necessarily so. When doing fieldwork all day on Liathach in an area of at most 1km^2 I used to hear a stone falling about every 20 minutes. Assuming that this goes on all year round, over 26,000 stones move each year. There are inevitably a lot of small-scale changes. Deer make tracks across the slopes, and cause local erosion of the soil. Boulders are dislodged by the actions of frost and soil-creep. Flooding streams deposit silt and peat over the vegetation. Amorphous solifluction at higher altitudes causes the soil surface to wrinkle and fold over. In such conditions the hepatic mat is likely to be a dynamic community with a high turnover of individuals, and not in equilibrium. If the community was in equilibrium one might expect the species to have specialised niches (Crawley 1986), especially regeneration niches at the time of establishment (Grubb 1977). It has been shown that many bryophyte communities, once thought to be long-lived and stable, are actually rapidly-changing systems (During 1979, Vitt 1990).

There are significant differences in temperature and humidity between north-facing and south-facing slopes, especially at the times of the year when the north-facing slopes receive no direct sunlight at all. However, even on the same slope on the same day, individual clumps of each species experience a fairly wide range of surface and internal temperature, relative humidity and water content. This gives some indication of the complexity of the relationships between these species and the environment. The pattern of species in the community is probably affected by biotic as well as abiotic factors, but nothing is known of this.

7.3 Species composition

The study of the community over its range in the British

Isles (Chapter 3) shows that *Bazzania tricrenata, Herbertus aduncus, Mylia taylorii, Anastrepta orcadensis, Plagiochila spinulosa* and *Scapania gracilis* are the most common members of the hepatic mat and probably have the widest ecological range. *Lepidozia pearsonii, Pleurozia purpurea, Plagiochila carringtonii* and *Scapania ornithopodioides* are slightly more demanding, perhaps being less tolerant of warm summers. *Bazzania pearsonii* and *Mastigophora woodsii* have still narrower limits. *Adelanthus lindenbergianus, Anastrophyllum donnianum, A.joergensenii* and *Scapania nimbosa* appear to be the most exacting of all. These results are borne out by the detailed studies of hepatic mats (Chapters 4 and 5) and supported by the data on physiological limits (Chapter 6).

The 5m x 1m quadrats on Beinn Eighe had a maximum of 13 hepatic mat species in them. Some of the 25cm x 25cm quadrats on Liathach had 12 species, while two of the 5cm x 5cm ones, also on Liathach, had 10. It makes one wonder how small a quadrat could be and still contain most of the species. This suggests that the needs of the different species must be similar. It is clear that all their niches overlap. They are not dependent on each other - they simply need the same conditions. All of them can occur as separate clumps and, as far as I know, none of the species always occur together wherever they grow.

Patches of the hepatic community vary in size and species-richness. Almost all of the species present at any site will occur together in some patches there, and the frequency of those species will differ in each patch. The distribution of species is not random and the species tend to be clumped, partly because some hillsides include unsuitable habitat such as the tops of boulders. The hepatic nat community as a whole often appears to be dominated by *Herbertus aduncus* (Chapters 1 and 3) but at the small scale of a 5cm x 5cm quadrat it is apparent that any of the species can be dominant or codominant (Chapter 5).

The hepatic carpet is always discontinuous. There are no known sites where the hepatic mat forms an unbroken sheet of more than a few square metres. There is always uncolonised space among stones and between the shrubs. It is most likely that at any site the 'community' is a mosaic of small-scale associations, all at different stages of development. The population dynamics of the hepatic mat on open slopes are probably closely coupled to the life-cycle of the dwarf shrubs (Watt 1947, Barclay-Estrup & Gimingham 1969), although Ratcliffe (1968) noted that the cushions of liverworts were larger and more luxuriant in rocky places, on cliff ledges and in the spaces between *Calluna* bushes than directly beneath the *Calluna*. Among boulders and on cliffs the community probably has a cyclical pattern of its own, with a build-up of cushions which eventually become unstable and collapse, exposing new ground for the process to start again, as shown in Norwegian woods by Lye (1966). Interspecific competition might act at some stage of the cycle. The changes which occur in the hepatic mat during this process have not been studied and would be worth researching.

One great problem in this study was how to sample this discontinuous community in a way that minimised bias and did not take too much time. This is always a problem in bryophyte-dominated vegetation, because the distribution of species is affected by microhabitat (Slack 1984). Any completely random method would have resulted in large numbers of quadrats with no hepatic mat species in them and would have been likely to miss important variation. It would also have been spurious because of the difficulty of navigating to randomly-chosen points on steep rocky hillsides covered with long heather and loose boulders, often in appalling weather. It was not easy or safe for a single person to carry heavy or awkward equipment onto some of the sampled sites. It took two hours to record the 100 small quadrats in each 2m x 2m plot on Liathach - a long time to lie in wet vegetation in bad weather. The best compromise was probably the method used on Beinn Eighe, where the ground to be sampled was stratified according to aspect and altitude and large quadrats were taken at regular spacing. Even this method was time-consuming - it took two weeks to record 165 quadrats. The 25cm x 25cm quadrats used on most sites were a useful way of comparing the richer patches of hepatic mat vegetation at a range of sites with the advantages of speed and ease of use. Nevertheless the conclusions from these samples apply only to these richer patches of vegetation and cannot be extrapolated to the whole community, because of the bias in the sampling.

7.4 Physiology and interaction with the environment

Members of the hepatic mat respond differently to experimental combinations of temperature and water content (Chapter 6). They hold different amounts of water and dry out at different rates. All the tested species were relatively intolerant of high temperatures but survived them better when dry than when wet. Within this pattern some species were better able to cope with heat and drought than others - some held more water and lost it more slowly, some seemed more physiologically tolerant of extreme conditions. In general the species which are most confined to the cool, high-rainfall parts of Scotland and Ireland are least tolerant of high temperature and low water content. In most cases the apices of the shoots survived longest, potentially ready to grow again when conditions improved. The problem is that the distribution of plants is governed not only by the tolerances of the adult, but by the conditions which can be endured by the propagules or young plants. Most of the classic models of community structure (for summaries see Begon, Harper & Townsend 1986, Crawley 1986) concern the establishment of a diversity of individuals which depends on the maintenance of sources of propagules of the less competitive species. It is not known how the hepatic mat species become established, nor what conditions are needed for this. Nevertheless the presence of hepatic mat species on some temporary or man-made habitats suggests that they can disperse and establish at new sites (Chapter 2).

Most of the hepatic mat species have never been seen with reproductive structures (Chapter 2). Most authors (e.g. Nicholson 1930, Crundwell 1970, Ratcliffe 1968) assume they have lost the capability to reproduce sexually. It is more likely that reproduction is controlled by environmental factors, rather than that the plants themselves have changed. As a result of this failure to reproduce, the British populations probably have little genetic variation. This is being tested (Ennos & Legg unpublished) on samples of *Herbertus aduncus, Pleurozia purpurea* and *Scapania gracilis* collected by me from Glen Coe and Beinn Eighe in 1993. However, it is also possible that fertile populations of the hepatic mat species have been overlooked, particularly as they may produce sporophytes in the winter.

It is not known whether the hepatic mat species interact with each other (Chapter 5). The resources they need are space, light, nutrients and water. Like most bryophytes they live entirely above ground so do not compete for anything in the soil. Bryophytes obtain water and nutrients from precipitation, from water running over them and directly from the surface of the substrate (Brown & Bates 1990).

All plants need water and light in order to photosynthesise and grow. Water is especially important to bryophytes because they can only grow when they are wet. As a result they can live only where they are wet for enough of the time to allow them to grow. In particular, daytime conditions must be such that they can photosynthesise enough to produce a positive carbon balance - the excess of photosynthesis over respiration. Bryophytes photosynthesise in exactly the same way as vascular plants (Proctor 1990), but differ from vascular plants in the way they organize the supply of water to their cells. The hepatic mat species are ectohydric, which means that water is taken in equally through all the tissues and lost equally from all of them. Bryophytes have no roots and access to water is intermittent for terrestrial species. Proctor (1990) has suggested that bryophytes behave as if they run on rechargeable batteries, compared with vascular plants which are connected to the mains supply.

Water can be transported in a bryophyte in several ways. Some mosses, notably members of the Polytrichaceae, have stems with a central strand of elongated, water-conducting cells. These plants have a transpiration stream in much the same way that vascular plants do. Water can also be conducted through the cell walls, from cell to cell across the walls and membranes and through the capillary spaces on the outside of the plant (Proctor 1982). Transport along central strands and through capillary spaces can be rapid and effective, but is unlikely to account for all water movement (Proctor 1982). Within the plant, transport in the cell walls is probably more important than transport between cells, because the resistance to water movement is much greater in cell membranes than in cell walls. The cell walls are probably the main route for water movement in bryophytes with small, thick-walled cells (Proctor 1982).

The rate of evaporation from the surface of the cushion is probably the most important limiting environmental factor for the hepatic mat liverworts. These species grow in sheltered habitats in cool, high-rainfall parts of the world, and even in the north-west Highlands they are absent from slopes facing the prevailing wind and subject to afternoon sunshine. Evaporation rates are low in these conditions because the net incoming radiation is low, the saturation deficit is low and the boundary layer resistance is high.

Elaborately folded, lobed and toothed leaves in leafy liverworts may have evolved because they increase water retention. When clumps of hepatic mat liverworts were artificially dried (Chapter 6), the dense tufts of *Scapania gracilis* and *Herbertus aduncus* held more water and dried out more slowly than the looser clumps of the other tested species. The larger and perhaps faster-growing species have the advantage at intercepting water and nutrients and the ability to store water in the lower parts of the cushion, but their growing tips are farther from the substrate and water has further to travel to the growing shoots (Proctor 1982).

Space is believed to be the main limiting factor in vegetation dominated by *Sphagnum* (Slack 1990). Some of the hepatic mat species, notably *Herbertus aduncus, Mastigophora woodsii, Pleurozia purpurea* and *Mylia taylorii*, tend to form bigger, more vigorous-looking mats and cushions than the other species and in competition for space it would not be hard to imagine these ones winning. However at higher altitudes, where these species are disadvantaged by cold, *Anastrophyllum donnianum, Scapania ornithopodioides* and *S. nimbosa* are more abundant and grow in larger cushions (as on the Fannich Hills, Affric-Cannich hills and Beinn Eighe). Competition for space includes competition for light. Species such as the hepatic mat liverworts which live in dark shaded places are able to photosynthesise at low light intensities (Russell 1990). The different colours of the species evidently affect surface temperature and possibly their response to light, but there are no data on how this might affect rates of growth. If different species really do experience different temperatures, (perhaps because darker plants absorb more radiation than paler ones and because the different structures of the clump affect their boundary layers) some might be able to photosynthesise and grow faster than others.

One of the mysteries about the hepatic mat species is their apparent immunity to predators and parasites. They live in cool, damp, still places - why are they not infected by fungi? They form large cushions with a lot of phytomass, but nothing seems to eat them. Part of the answer must be their secondary metabolic products. There has been much work on the chemical constituents of liverworts, summarized by Asakawa (1982). Most of the hepatic mat species have a strong aromatic smell, especially when wet. These smells are apparently from volatile organic compounds such as monoterpenes, sesquiterpenes, terpenoids and flavone derivatives, some of which have antibiotic and antifungal effects and most of which taste bitter (Huneck 1983, Zinsmeister & Mues 1988). Matsuo, Yuki & Nakayama (1986) found that an extract from *Herbertus aduncus* containing sesquiterpenes depressed the growth of some pathogenic fungi by 50%. Sesquiterpenes have also been isolated from *Anastrepta orcadensis*, *Bazzania tricrenata* and *Scapania ornithopodioides* (Andersen *et al.* 1977). Polyphenolic compounds in mosses are believed to protect the plants from herbivory by molluscs (Davidson, Harborne & Longton 1990).

7.5 Applying the results and further work

Conservation

The data on the distribution, habitats and species composition of hepatic mats can be used to help conserve them. Since the hepatic mat species are better-represented in the British Isles than anywhere else in Europe (Ratcliffe 1968, Hodgetts 1992), we have an international responsibility to protect them and their habitats. The results of Chapter 3 have made it easier to predict where more stands might be found. As the community is intolerant of burning and grazing, the presence of the Atlantic hepatic mat on a site is a good indication that there has not been a long history of mismanagement. Once a population is lost, the chances of re-establishment are small. Although existing populations seem to be self-maintaining and, indeed, flourishing, there is unlikely to be migration between widely-separated stands, because most of the species apparently do not produce spores or gemmae. Sympathetic management of existing exammples of the community is possible by using incentives such as the Environmentally Sensitive Area schemes: SSSI designation is not always the best answer especially if most of the vegetation on a hill with the hepatic mat is already represented elsewhere.

Management

Much of what is believed about the effects of burning and grazing on the hepatic mat liverworts is based on field observation and speculation rather than on scientific study, and this could be remedied. It would be instructive to find out more about the history of woodland cover and management at known sites of the community. There is some evidence (A. H. Kirkpatrick & A. J. McDonald pers. comm.) that damp *Calluna* heaths on north-facing slopes are self-perpetuating and do not need to be burnt. The *Calluna* rejuvenates itself by adventitious rooting (layering) into the bryophyte carpet. This is also the case in many blanket-bogs and probably little vegetation in the west Highlands actually needs burning to maintain it (McVean & Ratcliffe 1962). However it is still a popular practice and even when land managers are encouraged to let north-facing *Calluna* heaths alone, there are still accidental fires or deliberate ones which get out of control. It is difficult to protect slopes with the hepatic mat from being burnt. Sub-montane stands on open slopes (not protected by boulders) are most threatened. The tall, mature *Calluna* on these slopes is a fire-risk. Making fire-breaks between managed heaths and slopes with the hepatic community is a possible solution, as is desisting from burning on days with a south or west wind.

Monitoring environmental change

The effects of climatic change are uncertain. Even within the British Isles the hepatic mat species can tolerate a wide range of temperature and wetness (within the limits of a generally oceanic climate (Chapter 3)), but it is possible that populations outside the main area of distribution would suffer in a warmer and drier climate. The eastern populations in the Cairngorms and the southern ones in Ireland, Wales and northern England might find that summers were becoming too warm and dry. The northern and montane species such as *Anastrophyllum donnianum, A.joergensenii* and *Scapania nimbosa* might be unable to survive as far south or at such low altitudes as they do today. A series of monitoring sites across the range of the community would be valuable, to show the natural dynamics in the community as well as the effects of a changing environment.

The effects of acidic deposition on the hepatic mat species are unknown. The only clue is that the community is scarce in the southern Highlands (Ratcliffe 1968), which apparently have a suitable climate and habitat. Atmospheric pollution is worse here than anywhere else in the Highlands, because these hills are closest to Edinburgh and Glasgow (Thompson & Baddeley 1991). It would be worth analysing samples of the species from this area for abnormal tissue concentrations of nitrogen and sulphur, and monitoring changes in existing populations.

Ecology of the community

The world distributions and history of the species might be better understood if the relatedness of the different populations was known. It would be valuable to compare the genetics of material from the Himalayas, British Columbia, Norway, the Faroes, Britain and Ireland.

There is still potential for more exploration of the distribution and variation of the hepatic community in the British Isles, especially in Ireland, England and Wales. The study of Beinn Eighe suggests strongly that the hepatic mat species might be more widespread than previously assumed on slopes facing other ways than north and it would be worth doing a survey of a number of hills to find out whether this is so and, if it is true, whether there is any relationship with latitude, altitude or distance inland. It would also be useful to do transplant experiments to see what happens to hepatic mat species, for example on south-facing slopes, or in south-east Scotland.

In this study I did not make a detailed study of the microclimate of the hepatic mat community, largely because the small-scale variation on rocky hillsides is so great as to make measurements meaningless. Nevertheless an analysis of radiation climates at more sites would be valuable. It would also be interesting to do some field experiments to find out whether - and how fast - bare ground is colonised by these species, and how fast they grow. Competition between hepatic mat species and with other bryophytes could also be studied.

There is plenty of scope for studying the physiology of these species. Their response to low temperatures would be worth studying. Rates of water loss from intact cushions could be measured at different windspeeds, as in the work on boundary layers by Proctor (1980a). Growth in relation to water content could be assessed using a simple method described by Noakes & Longton (1988). Tolerance of base-status and minerals could be tested.

Although this study has generated more questions than it has answered, the results challenge the existing ideas that the Northern Atlantic hepatic mat is peculiar to the British Isles, that the characteristic species are calcifuges growing in stable habitats and confined to steep, north-facing slopes and that they are plants on the verge of extinction. Although they undoubtedly need a cool, moist climate, they seem to be successful plants which are able to take advantage of a variety of habitats. Many of these habitats are not at all stable and the hepatic mat community is probably quite dynamic.

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Please note that A M Hobbs and A M Averis are both me: before and after I was married.

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APPENDIX 1. Species recorded in ten 25cm x 25cm quadrats on north-facing slopes at each of 15 sites in western Scotland, England and Wales between 1990 and 1993.

	BS	Q	CM	BMC	F	L	LB	GN	BMB	BEM	SG	BF	BC	HC	CI
Hepatic mat liverworts															
Anastrepta orcadensis	5	2	5	7	4	3	4	10	8	3	6	2	6	2	4
Anastrophyllum donnianum		2	1	1	8	1									
A.joergensenii					4										
Bazzania pearsonii	1	5	2	4	2	1	2								
B.tricrenata	10	9	10	10	9	10	5	9	9	3	10	5	10	10	5
Herbertus aduncus	7	8	7	9	0	10	8	10	10	5		9	4	7	10
Lepidozia pearsonii		2	1	2	1	3	2	4	1		4	1			
Mastigophora woodsii	3	6		6		3	4								
Mylia taylorii	3	4	4	2	3	4	3	4	4	1	7	3	8	7	8
Plagiochila carringtonii	8	8	7	6	4	10	4	1	6						
P.spinulosa	1								1				2	1	2
Pleurozia purpurea	7	9	7	7		10	7	9	8	4		7	2		
Scapania gracilis	10	10	10	9	3	6	6	9	2	2	1	9	8	3	9
S.nimbosa	1		1		2	2									
S.ornithopodioides	3	5	3	4	4	5	7	2	5		2				
Vascular plants															
Alchemilla alpina											1			2	
Agrostis canina									1		1				
A.capillaris	2		1	5	4	0	4	1	6	3	3	1	6	3	
Blechnum spicant		1	1		1		1	1	1		3		2		
Brachypodium sylvaticum									1						
Calluna vulgaris	7	6	9	8	1	3	2	1		2		7			5
Campanula rotundifolia	1								2						
Carex bigelowii	1		1	1	2										
C.binervis											2				
Cornus suecica		1				1									
Deschampsia cespitosa					1		1								
D.flexuosa	4	2	4	9	5	3	5	8	2	3	5	7	8	6	
Dryopteris dilatata											2		1		
Empetrum nigrum	6	3	2	1	6	3							1		
Erica cinerea		2	2	2				1				4			
Eriophorum angustifolium		1				1									
Festuca ovina							2		1					2	7
F.vivipara									3	3			1		
Galium saxatile	1	1	1	1	7	1	2	1	3	3	6	2	6	6	
Hieracium spp													1		
Huperzia selago	1				2		1	1			1		1		
Hymenophyllum wilsonii	3			1			4		6				2	4	1
Hypericum pulchrum				1											
Listera cordata	1	1		1		1									
Melampyrum pratense								1							
Molinia caerulea		1	1				3	2			3				
Nardus stricta	1				4		1				4		1		
Narthecium ossifragum		1		1											
Polygonum viviparum				1											
Potentilla erecta		2	4	2			2	2	2	1	2	4			

	BS	Q	CM	BMC	F	L	LB	GN	BMB	BEM	SG	BF	BC	HC	CI
Rubus chamaemorus		2													
Saussurea alpina				1											
Scirpus cespitosus					1										
Selaginella selaginoides				1											
Solidago virgaurea	1			1			1	1	2						
Sorbus aucuparia								1	2	1					
Succisa pratensis	1					1	5		2						
Thelypteris limbosperma									1						
Thelypteris phegopteris									1		1				
Thymus praecox	1														
Vaccinium myrtillus	8	9	9	7	8	9	8	10	9	4	10	5	7	6	6
V.vitis-idaea		1	2		2	3					2		1		
Viola riviniana											1				
Other bryophytes															
Anastrophyllum minutum					1										1
Anthelia julacea													1		
Barbilophozia floerkii															1
Breutelia chrysocoma							4	1	1				1		
Bryum alpinum											1				
Campylopus atrovirens			1									2	1		
C.paradoxus						2	1	3	1		1	4		2	2
C.setifolius															5
Chiloscyphus polyanthus													1		
Dicranodontium uncinatum				2		1									
Dicranum majus		1			1				2					1	
D.scoparium	4	2	4	2	4	1	3	5	4	2	7	2	1	1	5
Diplophyllum albicans	4	1	5	4	2	2	5	1	5	3	7	6	9	6	10
Hylocomium splendens	5	7	5	5	5	1	2	4	3	1	2		1		
Hypnum cupressiforme		4	5	2		6	8	6	9	4	7	7	7	7	7
H.jutlandicum				3								1			
Lepidozia reptans				1				2			1				
Lophocolea bidentata									1						
Lophozia ventricosa			1		1	1	1	2	1	1				2	4
Marsupella emarginata											1				
Mnium hornum									2		2		3	1	
Odontoschisma sphagni			2						1						
Plagiothecim undulatum			1	2	1						1				1
Pleurozium schreberi	2	1	3		1	1	1	3	3	1	1				1
Polytrichum alpinum		1				1					1				1
P.commune				2	5	1	2		1		1	2	1		
P.formosum								4	2	1	4	1	6	9	4
P.juniperinum									1	1			1		
Ptilidium ciliare					1										
Racomitrium canescens											1				
R.heterostichum										1					
R.lanuginosum	8	9	7	7	9	7	9	5	6	5	10	9	9	4	10
Rhytidiadelphus loreus	6	7	6	5	9	6	4	3	3	4	5	3	7	6	3
R.squarrosus											1				1
Saccogyna viticulosa									1					1	2
Sphagnum auriculatum				1			1								
S.capillifolium	6	6	8	10	8	5	6	10	5	1	4	3	5	1	6
S.recurvum			1												
S.subnitens							1						1		

	BS	Q	CM	BMC	F	L	LB	GN	BMB	BEM	SG	BF	BC	HC	CI
Sphagnum tenellum						1						3			
Thuidium tamariscinum									1		1		1	1	
Tritomaria quinquedentata	1	1	1	1	2			1	4	1	3		2		1
Lichens															
Cetraria islandica	1	1		1											
Cladonia arbuscula	2	5	4	4	3			2			3				2
C.gracilis	1	1	4	1	2	2		1			2		1	1	1
C.portentosa						3						1		2	
C.uncialis	4	8	6	3	4	4					6	1	2	1	
Cornicularia aculeata						2					1				

Key to sites: BS Ben Stack, Q Quinag, CM Cul Mor, BMC Ben More Coigach, F Fannich Hills, L Liathach, LB Ladhar Bheinn, GN Glen Nevis, BMB Bidean nam Bian, BEM Buachaille Etive Mor, SG Stob Gabhar, BF Beinn Fhada (Mull),BC Ben Cruachan, HC Honister Crag, CI Cader Idris.

The table shows the number of quadrats in which each species was recorded at each site.

APPENDIX 2: Species recorded in 165 5m x 1m quadrats on Beinn Eighe, West Ross in 1992 and 1993.

Hepatic mat species	Total	N	NE	E	SE	S	SW	W	NW
Anastrepta orcadensis	62	13	10	5	11	6	1	6	10
Anastrophyllum donnianum	32	10	9	3				2	8
A.joergensenii	2	2							
Bazzania pearsonii	31	10	7	1				1	12
B.tricrenata	50	16	10	1		2		8	13
Herbertus aduncus	36	15	5	2	1			2	11
Lepidozia pearsonii	23	8	5					3	7
Mastigophora woodsii	15	1	6					2	6
Mylia taylorii	50	16	7	5	3	3	1	4	11
Plagiochila carringtonii	39	15	7	1	1	3		3	9
P.spinulosa	6	1			3	1			1
Pleurozia purpurea	112	20	11	20	13	20	4	10	14
Scapania gracilis	83	17	12	11	10	9	3	8	13
S.nimbosa	20	3	8	3		2			4
S.ornithopodioides	33	10	10	3		1		1	8

Vascular plants

Agrostis canina	8	Festuca ovina	6
A.capillaris	27	Galium boreale	1
Alchemilla alpina	11	G.saxatile	40
Antennaria dioica	3	Huperzia selago	48
Anthoxanthum odoratum	2	Hymenophyllum wilsonii	1
Arctostaphylos alpinus	1	Hypericum pulchrum	1
A.uva-ursi	14	Juncus bulbosus	1
Blechnum spicant	46	J.effusus	1
Calluna vulgaris	156	J.squarrosus	26
Carex bigelowii	24	J.trifidus	3
C.binervis	16	Juniperus communis nana	17
C.demissa	1	Listera cordata	15
C.nigra	11	Loiselurea procumbens	3
C.pilulifera	11	Luzula multiflora	1
C.pulicaris	2	L.sylvatica	4
Chrysosplenium oppositifolium	1	Melampyrum pratense	10
Cornus suecica	7	Molinia caerulea	96
Dactylorhiza maculata	24	Montia fontana	1
Deschampsia cespitosa	5	Myrica gale	7
D.flexuosa	79	Nardus stricta	37
Diphasiastrum alpinum	7	Narthecium ossifragum	50
Drosera intermedia	1	Pedicularis sylvatica	8
D.rotundifolia	3	Poa alpina	1
Dryopteris dilatata	1	Polygala serpyllifolia	41
Empetrum nigrum	62	Potentilla erecta	134
Epilobium anagallidifolium	1	Prunella vulgaris	8
Equisetum sp	2	Pteridium aquilinum	1
Erica cinerea	68	Rubus chamaemorus	7
E.tetralix	41	Rumex acetosa	1
Eriophorum angustifolium	18	Saxifraga stellaris	1
E.vaginatum	8	Scirpus cespitosus	129
Euphrasia officinalis	2	Selaginella selaginoides	2

Solidago virgaurea	24
Sorbus aucuparia	7
Succisa pratensis	50
Thelypteris limbosperma	2
Thymus praecox	5
Vaccinium myrtillus	100
V.uliginosum	16
V.vitis-idaea	22
Valeriana officinalis	1
Viola palustris	3
V.riviniana	6

Other bryophytes

Anastrophyllum minutum	12
Andreaea alpina	1
A.rothii/A.rupestris	19
Aneura pinguis	2
Anthelia julacea	1
Barbilophozia floerkii	5
Blasia pusilla	1
Breutelia chrysocoma	24
Bryum pseudotriquetrum	2
Calliergon sarmentosum	2
Calypogeia fissa	3
Calypogeia muellerana	6
Campylopus atrovirens	9
C.fragilis	3
C.introflexus	1
C.paradoxus	41
C.pyriformis	1
C.setifolius	3
Cephalozia bicuspidata	7
Ctenidium molluscum	1
Dicranella palustris	1
Dicranodontium uncinatum	18
Dicranum majus	11
D.scoparium	72
Diplophyllum albicans	115
Frullania fragilifolia	2
F.tamarisci	26
Funaria obtusa	1
Herbertus borealis	14
Hookeria lucens	1
Hylocomium splendens	93
H.umbratum	3
Hypnum cupressiforme	29
H.jutlandicum	110
Isopterygium elegans	2
Isothecium myosuroides	3
Kurzia spp	6
Lepidozia reptans	1
Leptodontium recurvifolium	1
Lophocolea bidentata	2
Lophozia bicrenata	1
L.ventricosa	6
Marsupella emarginata	4
M.sphacelata	1
Mnium hornum	3
Nowellia curvifolia	11
Odontoschisma sphagni	11
Oligotrichum hercynicum	1
Oxystegus hibernicus	1
O.tenuirostris	5
Pellia epiphylla	5
Philonotis fontana	3
Plagiochila porelloides	1
Plagiothecium undulatum	48
Pleurozium schreberi	53
Polytrichum alpinum	10
P.commune	5
P.formosum	5
P.juniperinum	2
Pseudoscleropodium purum	3
Ptilidium ciliare	19
Ptilium crista-castrensis	1
Racomitrium aciculare	1
R.fasciculare	4
R.heterostichum	2
R.lanuginosum	146
Rhytidiadelphus loreus	79
R.squarrosus	2
Riccardia chamaedryfolia	1
Riccardia latifrons	1
R.multifida	1
Scapania undulata	6
Sphagnum auriculatum	19
S.capillifolium	89
S.compactum	1
S.palustre	2
S.papillosum	8
S.recurvum	7
S.subnitens	3
S.tenellum	4
Splachnum sphaericum	1
Thuidium tamariscinum	6
Tortella tortuosa	1
Tritomaria quinquedentata	20

Lichens

Cetraria islandica	23
Cladonia arbuscula	133
C.gracilis	43
C.portentosa	1
C.rangiferina	1
C.uncialis	132
Cornicularia aculeata	8
Parmelia omphalodes	1
P.saxatilis	1
Rhizocarpon geographicum	1
Sphaerophorus globosus	1

Algae

Zygogonium sp.	10

Figures show number of quadrats in which each species was recorded. For hepatic mat species this has been subdivided into the numbers found on each aspect. N - north, S - south, E - east, W - west.

Appendix 3: Species recorded in 160 25cm x 25cm quadrats on Liathach.
West Ross, in May 1990.

Hepatic mat species

Anastrepta orcadensis	34
Anastrophyllum donnianum	8
Bazzania pearsonii	19
B.tricrenata	107
Herbertus aduncus	157
Lepidozia pearsonii	23
Mastigophora woodsii	32
Mylia taylorii	60
Plagiochila carringtonii	121
P.spinulosa	3
Pleurozia purpurea	147
Scapania gracilis	125
S.nimbosa	35
S.ornithopodioides	64

Mosses

Campylopus paradoxus	16
Dicranodontium uncinatum	21
Dicranum scoparium	22
Hylocomium splendens	31
Hypnum jutlandicum	87
Plagiothecium undulatum	3
Pleurozium schreberi	5
Polytrichum alpinum	1
P.commune	8
P.formosum	6
Racomitrium lanuginosum	129
Rhytidiadelphus loreus	70
R.squarrosus	2
Sphagnum auriculatum	3
S.capillifolium	50
S.subnitens	0
S.tenellum	24
Splachnum sphaericum	1

Liverworts

Anastrophyllum minutum	1
Diplophyllum albicans	39
Frullania tamarisci	2
Odontoschisma sphagni	0
Ptilidium ciliare	1
Tritomaria quinquedentata	1

Vascular plants

Agrostis capillaris	33
Alchemilla alpina	5
Blechnum spicant	6
Calluna vulgaris	62
Campanula rotundifolia	2
Carex bigelowii	7
Cornus suecica	6
Dactylorhiza maculata	1
Deschampsia cespitosa	3
D.flexuosa	92
Dryopteris dilatata	0
Empetrum nigrum	34
Erica cinerea	3
E.tetralix	1
Eriophorum angustifolium	1
Festuca rubra	1
Galium saxatile	36
Huperzia selago	13
Hymenophyllum wilsonii	9
Listera cordata	5
Molinia caerulea	8
Nardus stricta	2
Narthecium ossifragum	3
Potentilla erecta	14
Selaginella selaginoides	1
Scirpus cespitosus	5
Solidago virgaurea	1
Sorbus aucuparia	1
Succisa pratensis	7
Thalictrum alpinum	2
Vaccinium myrtillus	136
V.vitis-idaea	31

Lichens

Cladonia arbuscula	12
C.furcata	1
C.gracilis	23
C.portentosa	22
C.uncialis	75
Cornicularia aculeata	3

Figures show the number of quadrats in which each species was recorded.

APPENDIX 4. Water content (as percentage of oven-dry weight) against time for six liverworts dried at 20°C in front of an electric fan. Figures show means of five replicates +- standard error. Time in minutes from start.

	Scapania gracilis		*Pleurozia purpurea*		*Mastigophora woodsii*	
Time	mean	se	mean	se	mean	se
0	342.2	37.6	358.9	10.6	376.8	9.8
5	286.9	40.7	246.1	4.5	247.7	17.4
10	265.7	42.2	199.2	4.4	186.1	12.1
15	251.0	43.0	175.2	4.2	159.7	11.1
20	237.6	44.0	155.9	4.8	146.4	10.5
25	226.8	44.7	141.8	5.2	135.6	9.7
30	216.3	45.1	130.9	4.6	127.7	8.4
35						
40	202.3	45.6	120.3	2.9	118.2	6.2
45						
50						
55						
60	184.4	45.6	112.7	1.5	114.1	4.0
65						
70						
75						
80	171.5	43.8	110.5	0.7	111.4	2.2
85						
90						
95						
100	164.0	41.7	109.6	0.7	109.4	1.1
105						
110						
115						
120	157.3	38.9	109.6	0.7	107.1	0.6
125						
130						
135						
140	151.8	35.7			107.1	0.6
145						
150						
155						
160	168.7	40.4				
165						
170						
175						
180	159.0	34.7				
185						
190						
195						
200	151.1	30.9				
205						

	Plagiochila carringtonii		*Herbertus aduncus*		*Scapania ornithopodioides*	
Time	mean	se	mean	se	mean	se
0	362.8	11.4	325.1	18.9	215.2	12.3
5	249.0	6.5				
10	186.7	7.9				
15	162.7	6.8	241.8	14.2	154.6	9.6
20	145.3	5.8				
25	133.1	6.0				
30	123.3	5.4				
35						
40	114.5	4.0				
45			177.4	12.5	114.8	5.8
50						
55						
60	110.0	1.6				
65						
70						
75			140.0	12.0	106.4	4.3
80	108.2	0.3				
85						
90						
95						
100	107.3	0.4				
105			121.8	8.5	105.1	3.9
110						
115						
120	107.3	0.4				
125						
130						
135			113.5	4.0	104.9	3.9
140						
145						
150						
155						
160						
165						
170						
175					104.9	3.9
180						
185						
190						
195						
200						
205			105.5	3.1		

APPENDIX 5: Publications

Conservation of leafy liverwort-rich *Calluna vulgaris* heath in Scotland

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INTRODUCTION

Sub-montane heaths dominated by *Calluna vulgaris* cover about $1{\cdot}2 \times 10^6$ ha of Scotland (Tivy 1973). Most of these, however, are the large, dry grouse moors of central and eastern Scotland (Hobbs & Gimingham 1987). In the west, the cool and wet climate is more favourable for the development of damp heaths: *Calluna vulgaris* with an understorey of *Sphagnum capillifolium* and *Racomitrium lanuginosum*, rather than the *Hypnum*-type mosses which characterize the drier heaths. In particularly damp, shady places in the west there is a form of *C. vulgaris* heath with a ground flora of large leafy liverworts, first recognized by McVean & Ratcliffe (1962) and classified by them as Vaccineto-Callunetum, hepaticosum facies. Subsequently the National Vegetation Classification (J. Rodwell, pers. comm.) referred these heaths to its *Calluna vulgaris–Vaccinium myrtillus–Sphagnum* heath, *Pleurozia purpurea–Bazzania tricrenata* sub-community. The typical species, which include *Herbertus aduncus* (usually dominant), *Anastrepta orcadensis, Mastigophora woodsii, Bazzania tricrenata* and *Scapania nimbosa,* grow in large cushions, made conspicuous by the bright orange colour of *Herbertus aduncus.*

This hepatic heath is limited in its distribution by the rather narrow ecological tolerances of the liverworts. The species belong to the Northern Atlantic phytogeographical group (Ratcliffe 1968). They grow only in regions with an oceanic climate, which has high atmospheric humidity and equable temperatures throughout the year. Ratcliffe (1968) found that the liverwort community develops only in climatic regions where there are more than 220 wet days, days with more than 1 mm of rain, a year. Ratcliffe (1968) found a further marked bias towards the most shaded and humid places within this region; on steep, north-facing or east-facing slopes, cliffs and in boulder-fields. The heath is only found in the mountainous districts of western Scotland and western Ireland, making its occurrence in Britain internationally important (Ratcliffe & Thompson 1988).

Although formerly widespread, the heath has proved very susceptible to grazing and burning (McVean & Ratcliffe 1962; Ratcliffe 1968). This paper discusses and quantifies the distribution and decline of the hepatic heaths.

Nomenclature for vascular plants follows Clapham, Tutin & Warburg (1981) and for bryophytes either Jones (1958) or Watson (1978).

FIG. 1. The hill areas in Scotland surveyed by the Upland Vegetation Survey. (a) Location of all areas surveyed, and (b) areas where leafy liverwort-rich *Calluna vulgaris* heath was found. Numbers refer to areas listed in Table 1, and the line shows the eastern limit of 220 wet days year^{-1} (Ratcliffe 1968).

METHODS

The Nature Conservancy Council's Upland Vegetation Survey (UVS) has mapped the vegetation on 96 upland areas in Scotland (Fig. 1a), 81 of which are Sites of Special Scientific Interest. Examples of hepatic heaths which were found during this work were mapped on to aerial photographs at a scale of 1:25,000. These were then transferred to 1:25,000 scale Ordnance Survey maps. The surface areas of heath were measured using a Tamaya 'Planix' digital planimeter and converted from square centimetres to hectares.

RESULTS

Distribution of hepatic heath

Fig. 1b shows the distribution of hepatic heath on the hill areas mapped by the UVS. The heath is confined to the western parts of Scotland and has been found on only 14 of the 96 areas surveyed.

Table 1 shows that the heath is not evenly distributed on these 14 areas. The largest continuous patches are on the Torridon Hills; Liathach, Beinn Eighe and Beinn Alligin. On North Harris there are many small patches. The heaths on

TABLE 1. The number and surface area of patches of leafy liverwort-rich *Calluna vulgaris* heath on 14 upland areas. Site numbers are shown in Fig. 1

Site	Number of patches	Total area (ha)	Mean area (standard error)
1. Beinn Alligin	5	161	32·1 (10·1)
2. Beinn Eighe/Liathach	1	111	—
3. Foinaven	6	72	12·0 (5·5)
4. North Harris	14	65	4·5 (1·1)
5. Beinn an Oir	1	50	—
6. Beinn Bhàn	3	23	7·7 (2·5)
7. An Teallach	3	17	5·6 (1·3)
8. Letterewe Forest	3	17	5·6 (2·3)
9. Cuillin Hills	2	6	3·0 (1·1)
10. Ben More Assynt	1	5	—
11. Monar Forest	1	3	—
12. Fannich Hills	2	2·5	1·3 (0·4)
13. North Hoy	1	<1	—
14. Glas Cnoc	1	<1	—

North Hoy and Glas Cnoc cover too small an area to measure at the scale of these maps.

Table 2 shows that most of the hepatic heaths are on rocky slopes. They often grow on cliff ledges and in boulder-fields within the area of the slope. The altitudinal range is from almost sea-level (North Harris) to nearly 900 m (Liathach) but these are extremes and most lie between 300 m and 600 m above sea-level. The aspect in all cases was between north-west and east.

Loss of hepatic heaths

Altogether the UVS has mapped 44 patches of hepatic heath. Ratcliffe (1968) gave 55 records. McVean & Ratcliffe (1962) gave grid references for eleven heaths; the UVS team has visited 10 of these and has found that 4 no longer exist. Two more have been damaged by recent grazing and burning, with the loss of

TABLE 2. Occurrence of leafy liverwort-rich *Calluna vulgaris* heath according to aspect and habitat (there were no south-east, south, south-west or west occurrences)

	Habitat				
Aspect	Rocky slope	Boulder-field	Cliff	Corrie	Total
North-east	14	6	3	—	23
East	2	2	—	1	5
North-west	4	—	—	—	4
North	7	4	—	1	12
Total	27	12	3	2	44

most of the liverworts, and 4 remain. The damage must have been done in the last 25 years, between McVean and Ratcliffe's visit and our own.

DISCUSSION

The distribution and quantity of hepatic heath on each of the 14 massifs is probably a result of the topography and geographical position of each. For example, there is probably one large patch on Liathach because this mountain has a single long, steep, north-facing slope. North Harris is made up of many small hills, most of which provide a suitable but small site.

All 14 areas with the hepatic heath are within the climatic region where there are more than 220 wet days a year, and most of them are towards the west of this region. The more easterly localities, Monar Forest, the Fannich Hills and Ben More Assynt, do not have very much of the heath and it may be because these hills are close to the limit of the suitable climate.

All our examples were found on rocky slopes, cliffs or in boulder-fields facing between north-west and east, and always with tall *C. vulgaris*. In these places the effects of the oceanic climate are amplified. A northerly to easterly aspect is in shade for much of the day, and the rocks and tall shrubs further decrease the amount of light reaching the ground. Slopes with these aspects are sheltered from the prevailing winds, and the combination of still air and little direct sunlight makes evaporation into the atmosphere almost negligible (Ratcliffe 1968). Constant atmospheric humidity seems to be one of the most important factors in the ecology of the hepatic heath.

According to Ratcliffe (1968), the hepatic heath was once widespread from the Reay Forest and Ben Hope in Sutherland to Glen Coe and possibly to Ben Cruachan in Argyll. There is good evidence for this. Throughout the region there are fragments of heath on cliffs, in boulder-fields and on islands, existing as isolated patches in places which look suitable for more widespread development but which have obviously been burned, intensively grazed, or both. The effects of burning and grazing, although often obvious in the field, are difficult to quantify. The charred wood of *C. vulgaris* persists for several years after a fire. The liverworts are destroyed by burning and seem to be unable to recolonize without the shelter of tall *C. vulgaris*. Instead, they are typically replaced by *Racomitrium lanuginosum* and *Hypnum*-type mosses. For example, at NC 350495 on Foinaven there are signs of recent burning, with the *C. vulgaris* dead and the liverworts reduced to a few scattered plants (A. Brown, pers. comm.).

The long-term effect of grazing is to promote the conversion of *C. vulgaris* heath to grassland, a far less favourable habitat for liverworts (Ratcliffe 1968). Hepatic heaths on Ben More Assynt and Beinn Bhàn may have been reduced in extent by deer-grazing. In both cases hepatic heath is bordered by *Nardus stricta* grassland in which there are a few closely-grazed plants of *C. vulgaris* and *H. aduncus*.

D. A. Ratcliffe (pers. comm.) has recorded hepatic heath on the island of Loch an Eoin in the Beinn Damph Forest, Ross-shire, where there is neither grazing nor burning and the heath grows on flat ground. This suggests that the heaths were once more widespread on flat ground as well as on steep slopes and that their present distribution is an artefact of destruction in places which are more easily burnt and grazed. Boulder-fields, steep slopes and cliffs are difficult to burn because there is too little continuity of vegetation and in most cases shepherds try to discourage sheep from using these dangerous places.

The usual way of managing moorland in the west of Scotland is to burn large areas so as to improve the quality of the forage by encouraging the growth of young *C. vulgaris* and grasses. This, together with intensive grazing, is probably threatening the survival of the hepatic heath.

This heath is one of the most distinctive forms of upland vegetation, and in areas which can be safeguarded for nature conservation it could be located and protected from burning. Some grazing may be necessary to prevent colonization by trees. Britain is one of the richest places for Atlantic bryophytes in the world, and nowhere else do they form this type of vegetation. These liverworts are ideal candidates for the study of plant distribution in relation to climate (Ratcliffe 1968) and their scientific interest cannot be overestimated. Their survival probably depends entirely on the way that they are managed in future.

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Bryological Notes

Mylia taylori *producing sporophytes in cultivation*

A clump of approximately twenty shoots of *Mylia taylori*, collected in the field on 22 May 1989 and maintained in cultivation had mature sporophytes by 3 July 1989. All had dehisced by 11 July. *M. taylori* is a western British species (Ratcliffe, 1968). It is widely distributed in the northern hemisphere but has a markedly western bias in Britain. In Wester Ross and Sutherland (Scotland) it is often abundant in a liverwort-rich heath dominated by *Calluna vulgaris* L. with *Vaccinium myrtillus* L. and *V. vitis-ideae* L. The liverwort component is mostly made up of northern Atlantic species such as *Herbertus aduncus*, *Bazzania pearsonii* and *Mastigophora woodsii*.

M. taylori is dieocious and capsules are rare (Hill, 1988; Watson, 1978; R. Woods, personal communication; B. Averis, personal communication).

The plants were cultivated in atmospheric conditions as close as possible to those in the field. A week after collection the shoots were separated from other species and placed in a glazed pottery container lined with peat (to absorb excess water). This container was set in a shallow bowl of water inside a propagating case with a clear plastic lid. The case was kept on a north-west-facing windowsill in an unheated room. The plants were sprayed with spring water on 2 days out of 3. Relative humidity inside the propagator ranged from 85 to 95% and the air temperature outside the propagator from 5°C to 33°C.

This seems to be a successful way to cultivate leafy liverworts. *Herbertus aduncus* and *Pleurozia purpurea* have both made new growth in the same period, in identical conditions. Shaw's (1986) method of growing mosses from ground fragments of dried shoots has been completely unsuccessful for leafy liverworts.

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J. Bryol. (1991) **16**, 641–649

Bryological Notes

Acrobolbus wilsonii *and* Anoectangium warburgii *new to the Faroe Islands*

Acrobolbus wilsonii is a rare oceanic species in the Southern Atlantic group of Ratcliffe (1968). It was previously known only in the Azores, western Ireland and western Scotland (Smith, 1990). In the British Isles it is mainly a plant of streamside rocks in low-lying wooded ravines in areas with high rainfall and mild winters. In Scotland it is unknown north of the mid-western Highlands, even though there is much suitable habitat in the north-west. It was most surprising to discover it much farther north, on the Faroese island of Streymoy. We found it in small quantity, close to sea level, in a small ravine. It was growing on steep, rather moist, north-west-facing banks and rock faces between one and two metres above a stream. Associated species were *Lejeunea patens*, *Radula aquilegia*, *Plagiochila porelloides*, *Diplophyllum albicans*, *Thuidium tamariscinum*, *Mnium hornum*, *Plagiomnium undulatum*, *Isothecium myosuroides* var. *brachythecioides*, *Marsupella emarginata*, *Amphidium lapponicum* and *Cerastium fontanum*. The ravine is rich in bryophytes, with a good representation of oceanic species including *Herbertus stramineus* and *Mastigophora woodsii*. These are montane species in the British Isles, where there are no records at such a low altitude as this (Hill *et al.*, 1991). The arctic-alpine vascular plants *Saxifraga oppositifolia*, *Juncus triglumis*, *Alchemilla alpina*, *Oxyria digyna* and *Silene acaulis* also grow in the ravine. This interesting mixture of geographical elements is probably a result of the strongly oceanic climate. The summers are cool enough for some montane vascular plants and bryophytes to grow at very low elevations while the winters are mild enough for some southern species. It was noteworthy that some shoots of *Acrobolbus* were growing mixed with *Herbertus stramineus*.

Anoectangium warburgii was thought to be a British endemic. It is widespread in the Scottish Highlands and very rare in Wales (Smith, 1978). It occurs on rock faces in wooded ravines and on mountains. It has recently been discovered in Norway (H.J.B. Birks, pers. comm.). We were not surprised to find it in the Faroes, where there is a lot of suitable-looking habitat on basalt cliffs and ravines, and the climate appears to be favourable. We found *A. warburgii* at five Faroese sites, on the islands of Bordoy, Eysturoy and Streymoy. It grew on steep, moist rock faces, from 20 to 450 metres above sea level, on a wide range of aspects. Two of the sites were on mountain rocks, and the other three were in low-lying ravines. Associated species included *Frullania tamarisci* and *Diplophyllum albicans*.

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Where are all the Hepatic Mat Liverworts in Scotland?

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Summary

The Northern Hepatic Mat is a community of liverworts which have an Atlantic distribution in Europe. Eleven of these are Northern Atlantic species, confined to the north and west of Britain and Ireland and rare elsewhere in the world. The number of these liverworts recorded in 10 km squares in Scotland can be predicted from the combined effects of rainfall, temperature, humidity and topography, which account for 43% of the variance. Several 10 km squares in Scotland which are apparently suitable for many of the 11 species have fewer records than the model predicts. It is likely that some of these are under-recorded and would be worth further bryological exploration.

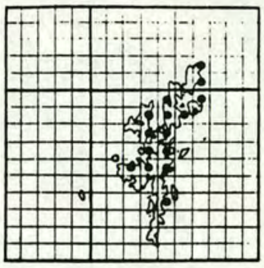
Introduction

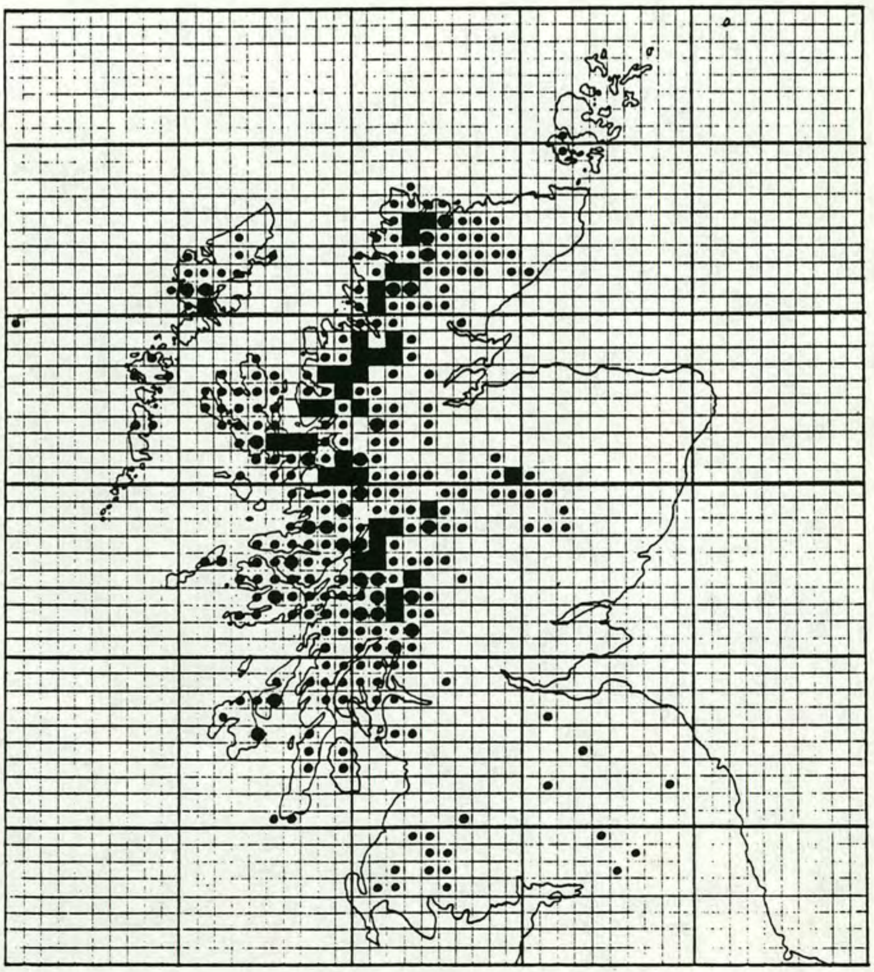
In the north-west of Britain and the west of Ireland there is a community of large leafy liverworts described by Ratcliffe (1968) as the 'mixed Northern Atlantic hepatic mat'. It is characterized by the presence of several of a set of 16 oceanic species with a localized distribution in the British Isles and in the world. Eleven of these species are described by Ratcliffe as 'Northern Atlantic'. In Britain they are confined to the mountainous north and west and they are rare elsewhere in Europe (Ratcliffe, 1968; Hill, Preston & Smith, 1991). The species are *Adelanthus lindenbergianus, Anastrophyllum donnianum, A.jöergensenii, Bazzania pearsonii, Herbertus aduncus* ssp. *hutchinsiae, Lepidozia pearsonii, Mastigophora woodsii, Plagiochila carringtonii, Pleurozia purpurea, Scapania nimbosa* and *S.ornithopodioides*. (Nomenclature follows Smith (1990)). Their geographical distribution, both in the British Isles and elsewhere in the world, suggests that they need an oceanic climate, which has a low annual temperature range, heavy rainfall evenly distributed throughout the year and which is cloudy and windy (McVean & Ratcliffe, 1962). In the British Isles the species show a further bias towards steep, shaded, rocky, north-facing slopes (Ratcliffe, 1968; Hobbs, 1988; Smith, 1990; Averis, 1991; Hill, Preston & Smith, 1991; Rodwell, 1991). On these slopes the hepatic mat usually occurs as an understorey to damp *Calluna vulgaris* (L.) Hull heaths (National Vegetation Classification (NVC) community H21b: *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* damp heath, *Mastigophora woodsii-Herbertus aduncus* ssp. *hutchinsiae* sub-community; Rodwell, 1991) or, at higher altitudes, mossy *Vaccinium myrtillus* L. heaths (NVC H20c: *Vaccinium myrtillus-Racomitrium lanuginosum* heath, *Bazzania tricrenata-Mylia taylorii* sub-community; Rodwell, 1991). Such habitats are restricted to the high mountainous parts of the British Isles: Western Scotland, the English Lake District, Snowdonia in Wales, and Kerry, Connemara and Donegal in Ireland. Scotland is the only

Fig. 1. The combined distributions of 11 Northern Atlantic hepatic mat liverworts in the upland 10 km squares of Scotland. The size of the symbol is proportional to the number of species recorded in the square:

• 1-3 spp, ● 4-6 spp, ■ 7-10 spp.

No squares had all 11 species.





concentrated in the west Highlands, with outliers in the Cairngorms to the east (Fig. 1).

The results of the stepwise multiple regression analysis (Table 1) suggest that high numbers of these species are in squares which have a low annual temperature range, high rainfall evenly distributed throughout the year and irregular topography with a lot of north-facing slopes. The other variables did not make a significant contribution to the amount of variance explained.

Table 1. Stepwise multiple regression analysis of the relationship between the number of hepatic mat liverworts with a Northern Atlantic distribution in a 10 km square and variables of climate and topography.

	Regression coefficient	**t**	**p**
Intercept	0.350		
Temperature range (°C)	-0.065	-5.0	<0.00001
Maximum rainfall (mm)	0.013	3.6	<0.0003
No. of N-facing slopes	0.014	3.6	<0.0003
No. of wet-days (yr^{-1})	0.0029	3.0	<0.002
Area of land (%)	0.036	2.2	<0.02

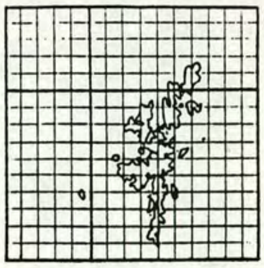
R^2 = 0.430, n = 354. Data log-transformed (log(n+1)).

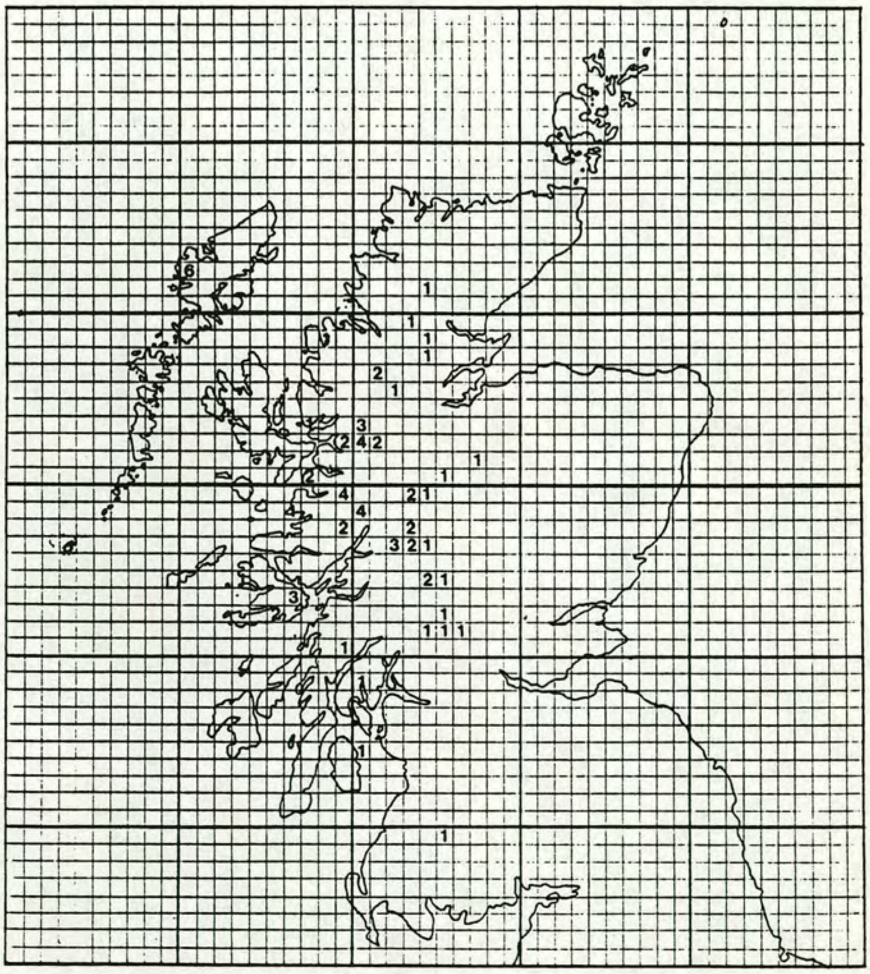
According to the model derived from this combination of variables, some squares have fewer recorded species than one would predict (Fig. 2). In the analysis, these squares have a negative residual value greater than two standard deviations. The model predicts only one more species than have been recorded in squares in the east and south of the country, but further west there are several squares which might be expected to have three or four more species than are recorded.

Discussion

Ratcliffe (1968) suggested that there was a relationship between the distribution of the hepatic mat community and the regions with more than 220 wet-days a year. While this is certainly supported by these results, there are hepatic mats and squares with a large number of species in places with fewer than 220 wet-days. This may be because the data for wet-days are not corrected for altitude and there may well be more wet-days at the altitudes at which these plants grow than there are at the stations where the measurements are made. Bryophyte recording has also continued since 1968, and some of the species are more widely distributed than they were thought to be then. However it is unlikely that the distribution of the community is limited by just one environmental variable. The model suggests that at least three climatic factors act in combination. For example, a low rainfall or annual number of wet-days in some 10 km squares could be compensated for by a lower temperature range and in particular a lower maximum temperature, so that any rain that falls does not evaporate so quickly.

Fig. 2. The 10 km squares in the uplands of Scotland with fewer records of Northern Atlantic hepatic mat species than predicted by a model relating to the distribution of the species to climate and topography. The figures show the number of extra species that might be expected in each square.





It is clear that climate at the scale of a 10 km square, while important, is not adequate as a predictor of species distribution on its own. As Ratcliffe (1968) suggested, even where the regional climate is favourable a particular sort of topography is still necessary. The virtual restriction of the species to steep north-facing slopes implies that local microclimate is equally important. This is because the high mountains in the north-west Highlands amplify the effect of the generally wet climate. The prevailing south-westerly winds carry low-pressure systems or depressions across the latitude of the British Isles. Associated with these depressions are saturated masses of air which are forced to rise over the barrier of the hills and in doing so they cool and rain falls. The north- and east-facing slopes of the hills are cool and shaded compared with the more exposed aspects, and the steeper slopes experience no direct sunlight at all for much of the year (Proctor, 1981). Conditions on these slopes, especially close to the ground amongst boulders and dwarf shrubs, are sheltered from the prevailing wind and must be extremely humid. In winter the bryophytes on these slopes are protected from the extreme fluctuations in temperature associated with freezing and thawing on sunny days, and in summer they do not dry out as quickly as they would on southern and western slopes.

There is an association between number of species and percentage of the square occupied by land. The squares with a small proportion of land are on the coast. In the west of Scotland the coastal lands are often inhabited and cultivated. Only rarely do high mountains rise directly from the shore, and most of these coastal squares have no steep, rocky slopes. Because of orographic effects the flat lands have less rain than do the adjacent mountains (Meteorological Office, 1977), so their climate is also less favourable for the liverworts.

Several squares which apparently have suitable climate and topography have fewer of the hepatic mat species than the model predicts. There are several possible reasons for this, for example:

1. The species may never have been there. Some of these squares are at the edge of the range of these liverworts. One would expect plants to be more patchily distributed as a result of chance establishment or extinction near to their climatic limits (Ratcliffe, 1968). It would be instructive to visit unoccupied squares to find out whether environmental conditions are unsuitable there. For instance, the soils might be too base-rich, or the vegetation of the mountain slopes could be a grassland rather than a dwarf-shrub heath.

2. The plants could have been there once but have been lost because of unfavourable management, natural disasters or pollution. It has long been suspected (McVean & Ratcliffe, 1962; Ratcliffe, 1968; Birks, 1973; Rodwell, 1991) that these hepatic mat species are adversely affected by excessive grazing and, particularly, by burning. As well as the direct damage to the plants, these treatments reduce the cover of dwarf shrubs and expose the liverworts to a more severe environment. The plants are slow to recolonize. Of these 11 species, only *Anastrophyllum donnianum* has ever been observed with sporophytes in Britain and then only once (D.G. Long, pers. comm.). So the liverworts have to rely on vegetative means for recolonization and this is slow and uncertain. Their place in these communities seems to be taken by larger and more vigorous mosses (Ratcliffe, 1968). Fires can, of course, occur naturally and these together with landslides, rockfalls and flooding may have reduced the range of these species. However only

atmospheric pollution is likely to cause complete extinction in a particular locality unless the plants were always rare. This is a possibility in the south of the Highlands, close to the industrial areas in and around Glasgow, where acidic deposition is greater than it is elsewhere in the Highlands (Thompson & Baddeley, 1991).

Damage by grazing and burning has never been quantified. It would be useful to find out from estate records whether intensity of land management could be correlated with numbers of the hepatic mat species. The extent and speed of recolonization could be measured on hillsides where damage has recently occurred.

3. The squares may be under-recorded. Many of those with fewer species than predicted are remote. Some of them have no bryophyte records at all, suggesting that they are almost certainly unvisited by bryologists. The best test of this model would be to look for hepatic mat species in these squares, to find out whether they are really absent or simply not recorded.

I would be delighted to hear of any new records for these (or any other) 10 km squares in Scotland.

Acknowledgements

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