CHAPTER 2

MATERIALS AND METHODS

Chapter Outline

A. Study Area

References to useful literature on several aspects of the study area are listed in Table 1. Many of these topics are discussed and illustrated in the *Reader's Digest Illustrated Atlas of southern Africa* (Reader's Digest 1994). In his recently published *South African Atlas of Agrohydrology and -Climatology* Schulze (1997a) provides maps of many climatic parameters as well as some physical features of the study area. Unfortunately these two publications only cover the Republic of South Africa. The recently published *Biological diversity in Namibia: a country study* (Barnard 1998), provides useful and up to date information on physiographic, climatic and ecological features of Namibia.

1. Geographic limits

The study area occupies the southern tip of the African continent or Africa south of the Cunene, Okavango and Limpopo Rivers (Fig. 1). It includes the countries of South Africa, Swaziland, Lesotho, Namibia and Botswana and covers an area of c.2.7 million km² (Cowling *et al.* 1997a). The Indian Ocean forms the boundary on the eastern and southern sides while the Atlantic Ocean runs along the west coast. The northern border is not entirely natural as it follows the political boundaries between Namibia and Angola, Namibia and Zambia, Botswana and Zimbabwe, South Africa and Zimbabwe, and South Africa and Mozambique (Reader's Digest 1994).

2. Geology and geomorphology

Geological maps of the region have recently been compiled by Visser (1984) for South Africa, and Hammerbeck & Allcock (1985) for the whole of southern Africa. The geology of South Africa has been summarised in simple terms by Day & King (1995). The handbooks *The Geomorphology of Southern Africa* by Moon & Dardis (1988) and *Biological Diversity in Namibia* by Barnard (1998) have been freely drawn upon in the compilation of the following account.

The geological development of southern Africa can be divided into five major phases or stages (Tankard *et al.* 1982). In the first or Archean crustal development stage the granitic basement of the subcontinent (e.g.the Barberton Sequence) was formed. This phase lasted to the end of the Archean Eon c. 2500 million years ago. The second stage is kown as the Early Proterozoic supracrustal development stage and lasted from 2500 to c. 1500 Ma. During this stage the crystalline basement was covered by sediments and volcanic rocks of the Pongola, Transvaal and Griqualand West sequences, the Witwatersrand and Ventersdorp Supergroups, and the Waterberg and

Soutpansberg Groups. The Bushveld Igneous Complex was formed on top of the transvaal Sequence. During the third phase Proterozoic orogenic activity disturbed the crystalline and cover rocks in the south and west of the subcontinent. Deformation was accompanied by intrusion of granitic rocks from the mantle and partial melting of older crust. Rifting of the crust resulted in the opening of a proto-South Atlantic Ocean which closed again c. 700 Ma. Stage four is known as the Gondwana era. Deposition of the Cape Supergroup sediments was followed by glaciation as Gondwana moved across the south polar region. The Karoo basin was filled with sediments of the Ecca and Beaufort Groups, and the Molteno, Elliot and Clarens Formations, capped by thick lavas of the Drakensberg Formation. The Karoo volcanicity lasted to about 105 Ma. Deformation of the Cape Supergroup rocks gave rise to the Cape fold belt. Fragmentation of Gondwana occured during the fifth and most recent stage of crustal development, known as the Post-Gondwana era. Pitman *et al.* (1993) provided an useful account of the fragmentation of Pangea and Gondwana.

The southern African land-mass achieved its present general outline during the break-up of Gondwana (Moon & Dardis 1988). At that time the subcontinent had an absolute elevation of 2350 m (Lesotho) to 1800 m (Kimberley). The eastern coastline was formed by rifting which started between 142 and 133 million years ago and the south Atlantic was formed when South America started drifting away from Africa c. 127 Ma. Because of the high elevation of southern Africa at the time of rifting, a substantial escarpment was created as the adjoining continental masses drifted away. An erosional face was soon produced by rivers operating to the newly created oceanic base levels. Partridge & Maud (1987) have summarised the geomorphic development of southern Africa since the Mesozoic as follows:

The principal geomorphic events in southern Africa since the Mesozoic (Partridge & Maud 1987)

1. The break-up of Gondwana through rift faulting (Late Jurassic/early Cretaceous).
2. African cycle of erosion (Late Jurassic/early Cretaceous to end of early Miocene).
3. Moderate uplift of 150-300 m (End of early Miocene, ~ 18 Ma).
4. Post-African I cycle of erosion (Early mid-Miocene to late Pliocene).
5. Major uplift, up to 900 m in eastern marginal areas. (Late Pliocene, ~ 2,5 Ma).
6. Post-African II cycle of major valley incision, especially in southeastern coastal hinterland.
7. Climatic oscillations and glacio-eustatic sea-level changes. (Late Pliocene to Holocene).

The present land surface of South Africa, Lesotho and Swaziland has been divided into a number of categories (see maps in Reader's Digest 1994, and Schulze 1997a), each of which is classified according to its height above sea level and its surface form. The subcontinent is characterised by a high interior plateau, bounded on 3 sides by the Great Escarpment. The plateau is tilted to the west and consists of elevated mountain massifs like the Lesotho Highlands, exceeding 3000 m in places, and large basins such as the Kalahari and Transvaal Bushveld. The escarpment comprises a number of distinct mountain ranges such as the Kamiesberg of Namaqualand, the Roggeveld and Nuweveld of the Karoo, and the Drakensberg of KwaZulu-Natal, Mpumalanga and the Northern Province. Below the escarpment lies the coastal plain or Marginal Zone, 50 to 200 km wide, in places deeply dissected by river gorges. The Cape Fold Mountains in the south-western corner of the subcontinent provide for the highest altitudes in this zone.

Namibia, with a land area of 823,988 km², can be divided into 4 main geophysical zones (Barnard 1998):

1. the Namib Desert and coastal plain
2. the Namib escarpment
3. the central plateau
4. the Kalahari sandveld

The Namib desert and coastal plain occupies a narrow strip of land between the Atlantic Ocean in the west and the Namib escarpment, 80-200 km to the east. The eastern border of the Namib roughly coincides with the 100 mm annual rainfall isohyet and the 1000 m altitude contour (see maps in Barnard 1998). The Namib Desert is subdivided into three broad landforms: 1) the southern Namib with it's dune sea and inselbergs, 2) the central Namib with gravel plains between the Ugab and Kuiseb Rivers, and 3) the northern Namib with mountains and dunefields. Barnard (1998) describes the Namib escarpment as "... a thin, sometimes poorly defined transition zone between the desert and the central highland plateau." It is a deeply dissected region with some of the highest mountains in Namibia. To the east of the escarpment zone, roughly between 1000 and 2000 m altitude, and running the full length of the country, lies the central plateau. It is stony and flat or mountainous, dissected by deep canyons in some places. The Kalahari sandveld flats to the east of the central plateau consists of a thick layer of red or pale sand in the south and brittle alkaline soils in the north.

Colourful maps of the soil zones of South Africa and Namibia have recently been published in Schulze (1997a) and Barnard (1998) respectively.

3. Climate

Southern Africa can be classified as semi-arid with less than 5% of the region recieving an annual rainfall of greater than 800 mm and, on average, more than 90% of rainfall returned to the atmosphere through evaporation (Cowling *et al.* 1997a). Average runoff only constitutes 9% of the total rainfall (Schulze 1997a). The average mean annual rainfall for South Africa is only c.500 mm, compared to a world mean of

860 mm (Reader's Digest 1994). There is a steep climatic gradient from the hyper-arid and foggy Namib desert along the west coast, to the hot and humid climate along the east coast of southern Africa. There is also a steep gradient from the semi-arid Karoo basin to the wet winter-rainfall mountains of the Cape. The study area can be divided into a *winter rainfall* region in the south-western corner, stretching along the west coast to southern Namibia, an *all year rainfall* area along the southern Cape coast, and a *summer rainfall* region covering the largest part of southern Africa. These climatic patterns are largely the result of the temperate-tropical convergence zone, the cold Benguela Current along the west coast and warm Agulhas Current along the east coast, and the varied topography described under the preceding heading.

Schulze (1997) identified light, temperature and moisture as the climatic factors of greatest importance in vegetation development. Maps of these as well as other climatic parameters in South Africa can be found in Schulze (1997, 1997a).

In Namibia the climatic gradient runs from tropical semi-humid in the northeast to hyper-arid in the west. Overall, 69% of the country is regarded as semi-arid and the remaining 16% as arid (Barnard 1998). Average annual rainfall is c. 250 mm of which about 83% evaporates and 14% is transpired by plants. Only c. 2% enter drainage systems. Mean annual rainfall varies from c. 700 mm in the eastern Caprivi to less than 50 mm along the coast. Temperatures can be extremely variable with greatest fluctuations in the hyper-arid zone. Mean water deficit (mean annual rainfall minus mean annual evaporation) is greatest in the south-eastern part of Namibia. The convergence of the cold Benguela (subantarctic) upwelling and the hot subtropical interior is responsible for the arid conditions in the Namib Desert. It has been established that the Namib and adjacent plateaus have been arid or semi-arid for 55 to 80 million years (Barnard 1998).

4. Flora and vegetation

For a predominantly warm temperate, semi-arid region, southern Africa is exceptionally rich in vascular plants. It contains approximately 21137 indigenous species in 1930 genera and 226 families (Cowling & Hilton-Taylor 1997). The south-western Cape, 'mesic parts of the Tongaland-Pondoland Region' and the Afromontane areas in the north-east of the study area are particularly rich in vascular plants. Species density (species/km^2) in the Cape Region is amongst the highest in the world. At 80% vascular plant species endemism is unusually high for a continental region (Cowling & Hilton-Taylor 1994, 1997). The flora is also characterised by numerous large genera, most of which are centred in the Cape region. Species/genus ratios in southern Africa and the Cape Region are consequently among the highest in the world, comparable with those of oceanic islands (Goldblatt 1978 in Cowling & Hilton-Taylor 1997). Centres of vascular plant diversity and endemism in the FSA area are discussed in detail under *Historical perspective*, Chapter 3.

In the preface to *Vegetation of southern Africa*, Cowling *et al.* (1997a) provide a short overview of the vegetation classifications of the region. The most important works were written or edited by Pole Evans (1936), Adamson (1938), Acocks (1953), Werger (1978c) and White (1983). The most recent works on the region's vegetation were edited by Low & Rebelo (1996) and Cowling *et al.* (1997a). The vegetation maps provided by Acocks (1953) and Low & Rebelo (1996) only cover the Republic of South Africa (as well as Lesotho and Swaziland) while White (1983) mapped the vegetation types of the whole continent.

Rutherford & Westfall (1986) and Rutherford (1997) identified seven biomes in southern Africa (Fig. 2) in accordance with dominance or codominance of plant life forms at the biome scale: 1) Desert, 2) Grassland, 3) Succulent Karoo, 4) Forest, 5) Nama-Karoo, 6) Savanna, and 7) Fynbos biomes. The Desert Biome is only found in Namibia while the Grassland and Fynbos Biomes are restricted to South Africa. Grassland covers the Highveld, from Mpumalanga in the north down to the Eastern Cape in the south.
Savanna vegetation covers a large area in the north and a narrow strip along the east coast, as far south as Port Elizabeth in the Eastern Cape. Fynbos vegetation is largely restricted to the Cape Fold Mountains in the extreme south-west of the study area.

Low & Rebelo (1996) added an 8th biome, the Thicket Biome, consisting of subtropical thicket vegetation in the dry river valleys of the south-eastern Marginal Zone, roughly from Melmoth in KwaZulu-Natal to Port Elizabeth in the Eastern Cape, and inland to Ladismith in the Klein Karoo.

The Namibian terrestrial biome classification of Irish (1994) differs only slightly from that of Rutherford (1997). Both schemes distinguish four biomes in Namibia: 1) Desert, 2) Succulent Karoo, 3) Nama-Karoo, and 4) Savanna. At a finer scale the classification of Giess (1971), who divided the area into 14 major vegetation types, are widely accepted (Barnard 1998). The annual precipitation determines the three main vegetation zones of Namibia: 1) desert, 2) savanna, and 3) woodlands, while environmental variables such as temperature, seasonality of rainfall, and topography and soil are responsible for the 14 major subdevisions of these zones (Barnard 1998). The Namib can be subdivided into true Namib to the north of Lüderitz and the Succulent Steppe vegetation zone in the southern, winter rainfall area. To the east of the Namib is a Semi-desert – savanna transition zone. Most of Namibia is covered by thorny shrub and tree savanna. Forest Savanna and Woodlands cover the moist northeastern region. The Southern African Bird Atlas Project (SABAP) used a biome map of four major and two minor biomes, divided into nine Avi-vegetational Zones, to explain bird distribution and abundance in Namibia (Barnard 1998). However, the major biomes of this scheme do not differ significantly from those of Irish (1994).

B. Data Compilation

The MOSSLIT and MOSS databases were set up specifically for this study using the ISI Sci-Mate (Anon 1985) personal computer program:

1. MOSSLIT database

This searchable literature database contains more than 2000 references to publications on the taxonomy, nomenclature, ecology and phytogeography of bryophytes, with particular emphasis on African and southern African mosses. The following fields were entered for each record:

- **Author:** Name of the author(s).
- **Date:** Date of publication.
- **Title:** Title of the article or book.
- **In**: Name(s) of the editor(s).
- **Public:** Name of the journal or book in which the article appeared.
- **Publishr:** Publisher of the book and place of publication.
- **Keyword:** The keywords and phrases used are not very extensive but include major categories of scientific, mostly botanical, research (e.g. *phytogeography, taxonomy*, *ecology*, *nomenclature, geology*), important research topics (e.g. *species, monograph, mountains, classification, ordination, DNA*), scientific names of taxa, and geography (continents, regions, countries etc.). All words entered for a specific record, and not only the keywords, determine whether a record is retrieved during a search.
- **Notes:** Notes such as the whereabouts of the publication or reprint.

2. **MOSS database**

This database contains the names and distributions of mosses recorded and accepted for the FSA area and is also fully searchable. Information has been entered in the following fields:

- **Family:** Name of the family.
- **Genus:** Name of the genus.
- **Species:** Name of the species and infraspecific taxon.
- **Grids:** The ½° grid squares (Edwards & Leistner 1971) in which the moss has been collected. The grids were recorded directly from specimens in PRE (incorporating specimens from NH, Compton ex SAMH, and STE on permanent loan), specimens in other southern African herbaria (see Magill 1980), and type

specimens received on loan from other herbaria such as BM, C, E, G, H, NY etc. (see Holmgren *et al.* 1990 for herbarium acronyms). The PRECIS database (Morris & Manders 1981, Magill *et al.* 1983, Arnold 1997) contained too many errors at the time (Rebelo & Cowling 1991, Rebelo 1994) to be useful in this regard. The bryophyte distribution data in PRECIS has since been checked and should now be more reliable.

- **Dist SA:** The FSA distribution of the taxon according to the geographic regions in the *Moss Flora of Southern Africa* (Magill 1981, 1987).
- **Dist Wo:** The total or world distribution of the taxon by region (e.g. Europe), country (e.g. Zimbabwe) and occasionally subdivisions of a country (e.g. western Australia). The most important and most recent checklists and related publications consulted for the world distributions of southern African mosses are listed in Table 2. In addition to these, many monographs, revisions and taxonomic notes were also consulted (see Van Rooy, 1997 for useful taxonomic literature).
- **Subs:** The substrate recorded on the specimen label (e.g. terricolous).
- **Alt:** The altitude recorded on the specimen label in metres.
- **Biome:** The Biome/s (Rutherford & Westfall 1986) in which the taxon has been recorded.
- **Comment:** References to literature on the taxonomy, phytogeography and ecology of the taxon.
- **Synonym:** The most important and most recent synonymy.

3. Data sets

Choice of taxa: The binary or presence/absence data of all the mosses recorded in southern Africa (see Appendix I) were used in the numerical analysis of distribution patterns. White (1965) has argued that a total analysis of the entire flora would tend to blur the picture, and that studies of selected dominant species of the most widespread and characteristic vegetation types would be more profitable. However, Wohlgemuth (1996), in a numerical analysis of the distribution patterns of Swiss plants, found that although a reduced number of species can result in a successful delimitation of floristic regions under certain circumstances, results were best when high numbers of species were used.

Choice of grids: It is usually assumed that if the grids or (the grain) used in a phytogeographic study are too small (too fine), problems of uneven recording (collecting) will introduce 'noise' into the data. If, on the other hand, the grids are large (grain too coarse), it will result in the detection of broad-scale patterns only (Jardine 1972, Birks 1987, Meentemeyer & Box 1987, Wiens 1989, Myklestad & Birks 1993). However, Kadmon & Heller (1998), in a multivariate analysis of faunal responses to climatic gradients, tested the effect of varying the grid size (the grain) in their species x grid data matrix and found that the main patterns of faunal variation were highly consistent over a range of grid square sizes.

Wiens (1989) has noted that "For logistic reasons, expanding the extent of a study (the study area) usually also entails enlarging the grain." of an investigation. However, no matter how large the study area, the grain will effect the accuracy of borders between the floristic regions: the coarser the grain the less accurate the borders will be, which will ultimately effect the floristic composition of the regions. Simmons *et al*. (1998) claims that the use of ½° grid squares in distribution data sets of Namibian plants and birds reduced the effect of sampling (collecting) bias.

I have subjectively chosen the ½° grid square, c. 52 km x 50 km (Edwards & Leistner 1971) for this study to keep the data set within the parameters required for the numerical analysis and to set the grain as fine as possible. All the grid squares considered, and all those eventually included in the complete data set are shown in Fig. 7.

In addition to the complete data set two more data sets were subjected to numerical analyses (see Fig. 3 and the *Discussion* under *TWINSPAN complete classification*, Chapter 4):

Data sets

1. **TWINSPAN Complete:** Data set containing all southern African grid squares in which mosses have been recorded. The presence/absence data matrix consists of 503 species/infraspecific taxa and 416 grid squares.

2. **TWINSPAN 3+:** Data set of grid squares containing three or more species/infraspecific taxa. The data matrix consists of 501 species/infraspecific taxa and 298 grid squares. The two endemics *Pseudoleskeopsis unilateralis* and *Plaubelia involuta* are absent from this data set.

3. **TWINSPAN 5+:** Data set of grid squares containing five or more species/infraspecific taxa. The presence /absence data matrix consists of 501 specie/infraspecific taxa and 251 grid squares. The two endemics *Pseudoleskeopsis unilateralis* and *Plaubelia involuta* are absent from this data set.

4. Shortcomings in the data sets

- There was no standardisation of collecting effort and the number of specimens per grid varies from a single collection (representing a single species) made on a casual visit, to several hundred specimens (representing many species) collected over many years. The geographic distributions therefore tend to reflect historical ranges and collecting biases (Lawes & Piper 1998). However, for the purpose of conservation planning it may actually be desirable to include historical distribution ranges of taxa in biodiversity databases (Van Jaarsveld *et al.* 1998).
- Some grid squares are totally undercollected, e.g. those covering the Afromontane (inland) forests of the former Transkei (Eastern Cape Province) of which grid 3128 A with five species, 3128 C with 0 species and 3127D with three species

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recorded are good examples. Gibbs Russell *et al.* (1984) estimated that some grids have records for only 17% of their flora. The percentage is likely to be lower for bryophytes.

Other grid squares are reasonably well collected because they were incorporated in study areas, e.g. the Mariepskop area (grid 2430 D) on the 'eastern Transvaal' or Mpumalanga escarpment (Vorster 1970, 1990). Uneven coverage of the FSA-area by the PRECIS database has been demonstrated by Gibbs Russell *et al.* (1984) and Rebelo (1994).

- The grid squares gradually decrease in size from north to south (Edwards & Leistner 1971) and some only contain a piece of land (along the coastline) or a piece of the study area (along the northern borders).
- Incomplete, imprecise, and incorrect collecting localities on PRE herbarium labels (Rebelo 1994). For example *Drepanocladus sendtneri* and *Meiothecium fuscescens* only known from the 'Cape', and *Pterobryopsis rehmannii* only recorded from 'Natal'. Another example is the mixed localities on *Wager* specimen labels (Magill 1982).
- The taxonomic treatment of the mosses is not quite uniform between groups and between areas. The taxonomy of the pleurocarpous families Fabroniaceae – Polytrichaceae (see conspectus of classification in Magill & Van Rooy 1998) lag behind that of the other families as they have not yet been revised for the FSA.

  Recently collected areas such as the Eastern Cape Wild Coast between the Kei and Mtamvuna Rivers, parts of the KwaZulu-Natal Drakensberg, and some of the Zululand forests, are better represented by acrocarpous taxa in the 1st three fascicles of the the moss *Flora of Southern Africa* (Magill 1981, 1987) as specimens belonging to the 4th fascicle (Orders Thuidiales, Hypnobryales and Polytrichales) are awaiting identification as part of the revision process.

Despite many shortcomings, binary (presence/absence) data sets have been used successfully in many biodiversity and phytogeographic studies and will for the foreseeable future remain the only source of information for broad-scale analysis of plant and animal distributions, not only in southern Africa but also in other parts of the world (Kadmon & Heller 1998, Van Jaarsveld *et al.* 1998).

A measure of abundance, e.g. the number of specimens of each taxon collected in a grid, normally included in phytosociological databases, is not generally considered practical for 'museum type data sets' (Oliver *et al.* 1983).

C. Numerical Analysis

1. Introduction

Quantitative approaches or numerical techniques have been used extensively in plant ecology, and comparatively less often, but increasingly, in phytogeography (Birks 1987, Myklestad & Birks 1993, McLaughlin 1994, Heikkinen *et al.* 1998). Recent examples of quantitative approaches at the fine-scale vascular plant community or phytosociological level in southern African include studies by Coetzee *et al.* (1995), Richards *et al.* (1995), Hill (1996), Van Wyk *et al.* (1996), Brown *et al.* (1997), Eckhardt *et al.* (1996, 1996a, 1997), Sullivan & Konstant (1997), Smit *et al.* (1997), Cilliers & Bredenkamp (1998), Malan *et al.* (1998) and Rubin (1998).

Numerical techniques have proven most useful in delimiting phytogeographic or broad-scale units in many parts of the world (Birks 1987, McLaughlin 1994, Heikkinen *et al.* 1998). The merits of using numerical techniques as opposed to visual pattern detection in biogeography have been pointed out by Jardine (1972), Birks (1987) and Pederson (1990). The following are recent examples involving vascular plants and ferns: Gill *et al.* (1985), Pederson (1990), Myklestad & Birks (1993), Dzwonko & Kornas (1994), Oksanen & Virtanen (1995), Andersson & Weimarck (1996) and Heikkinen *et al.* (1998). One of the most recent developments in quantitative biogeography is the integration of geographic information system (GIS) tools with standard multivariate techniques (Kadmon & Heller 1998).

Quantitative approaches to bryophyte ecology and geography up to the early nineteen 80's have been reviewed by Bates (1982) and Slack (1982, 1984). Additional examples at the bryophyte community level include studies by: Van Reenen & Gradstein (1983), Gignac & Vitt (1990), Duda *et al.* (1990), Vitt (1991), Forbes (1994), Belland & Vitt (1995), Karttunen & Toivonen (1995), Kürschner (1995), Sillett (1995), Nicholson & Gignac (1995), Jonsson (1996), and Odasz (1996). Bryophytes are sometimes included in predominantly vascular plant databases, for example those of Odland *et al.* (1990), Bjarnason (1991) and Dirkse *et al.* (1991).

One of the first numerical analysis of bryophyte distribution patterns at a broad (regional or subcontinental) scale was carried out on British liverworts by Proctor (1967). Proctor combined classification and ordination techniques to describe the relationships between the 25 vice-county groups and the 47 species groups or elements (Proctor 1967). Other examples of quantitative bryogeographic studies include:

1. The analysis of liverwort distribution patterns in Puerto Rico (Bryant *et al.* 1973).
2. Phytogeographic analyses of the moss flora in the Gulf of St. Lawrence region (Belland 1987, 1989).
3. The analysis of bryophyte distribution patterns in Britain (Hill & Dominguez Lozano 1994, Bates 1995).
4. The analysis of bryophyte distribution patterns in different parts of Australia (Eldridge & Tozer 1997, Fensham & Streimann 1997).

Bryophytes are increasingly used in the development of bioclimatic models (Birks *et al.* 1998); for example the peatland studies in the Mackenzie River Basin, Canada by Gignac *et al.* (1998, 1998a).

Quantitative analyses of African bryophyte distributions are virtually unknown. A few liverworts and mosses were included in a factor analysis of plant distributions in tropical and subtropical Africa by Denys (1980). Kürschner (1995, 1995a) studied floristic discontinuities in epiphytic bryophyte communities along an altitudinal gradient from the eastern Congo basin to the mountains of the Rift Valley and related these to environmental factors.

2. Numerical techniques

Given a presence /absence matrix for a number of taxa in a number of areas (such as grids or relevés) two major types of quantitative analyses are recognised (Jardine 1972, Bryant *et al.* 1973, Pielou 1984, Myklestad & Birks 1993, McLaughlin 1994, Heikkinen *et al.* 1998). The two forms of analysis have been termed R-mode analyses and Q-mode analyses but, as McLaughlin (1994) has recently pointed out, these two terms have been used inconsistently in biogeography to distinguish between the two forms of analysis. The definition of Bryant *et al.* (1973), Sneath & Sokal (1973) and Birks (1987) is followed here:

- **R-mode analyses**. Analysis of the affinities between distributional patterns of taxa. This results in the delimitation of phytogeographic (floristic) elements or groups of taxa with similar geographic distributions. See the definition of a phytogeographic element under *Key Definitions* in Chapter 1.

- **Q-mode analyses**. Analysis of the affinities between the floristic composition of geographic areas. This results in the description of phytogeographic (floristic) regions or groups of areas with similar floristic compositions (floras). See also the definition of a phytogeographic region under *Key Definitions* in Chapter 1.

2.1 Classification

The distribution data in all three data sets were subjected to classification by the FORTRAN computer program TWINSPAN (Hill 1979). TWINSPAN is a divisive, hierarchical classification technique which detects overall patterns of differences in biological data. Although the reliability of this approach has been questioned under certain conditions (Van Groenewoud 1992, Belbin & McDonald 1993, Van der Maarel 1996) TWINSPAN was chosen for its proven combination of effectiveness, robustness and relative objectivity, as well as its availability and speed (Gauch & Whittaker 1981, Myklestad & Birks 1993, Van Der Maarel 1996). Gauch & Whittaker (1981) found that certain advantages "...make TWINSPAN the best general purpose method, especially when a data set is complex, noisy, large or unfamiliar", as in the case of the moss distribution data sets used in this study.

The original TWINSPAN and DECORANA computer programs, also used in this analysis, were recently found to be susceptible to instability and it is recommended that "strict" and "debugged" versions be used (Oksanen & Minchin 1997). How to use these modified versions of TWINSPAN and DECORANA is explained on the web site: http://www.helsinki.fi/~jhoksane/softhelp/readcep.htm by P.R. Minchin. However, Gignac *et al.* (1998) found that the classification of peatlands in Canada by the modified version of TWINSPAN did not vary significantly from that of the original TWINSPAN classification.

Default settings were used for all TWINSPAN parameters. The results of the different TWINSPAN classifications (TWINSPAN Complete, 3+ and 5+ classifications of grid squares, and TWINSPAN 3+ classification of species) are presented as dendrograms, plotted on distribution maps, and listed in the appendices. The regions or elements at the different levels of TWINSPAN division have been numbered from left to right on the dendrograms in the order of the two-way matrix.

2.2 Indirect gradient analysis (ordination)

An indirect gradient analysis or ordination is an exploratory approach which aims to produce hypotheses about possible environmental factors causing the observed gradients in the data. However, a suspected correlation between distribution patterns and environmental factors is no proof of a cause-effect relationship and should ideally be tested by experimentation (Bates 1982, 1995; Heikkinen *et al.* 1998, Birks *et al.* 1998).

A detrended correspondence analysis (DCA) ordination was carried out on the moss distribution data in the TWINSPAN 3+ and TWINSPAN 5+ data sets by using the FORTRAN computer program DECORANA (Hill 1979a). Default options were employed and no downweighting took place. The advantages of using DCA are discussed by Gauch (1982), Slack (1984) and Michael Palmer on the Oklahoma State University Web page (http:www.okstate.edu/artsci/botany/ordinate/DCA.htm).

Both TWINSPAN and DECORANA are widely accepted programs and often used in combination in quantitative community ecology as well as phytogeography (Gauch & Whittaker 1981, Gauch 1982, Slack 1984, Pederson 1990, Hill 1996) (see examples listed under *Numerical Analysis*, this chapter). The two programs have the added advantage of performing classification or ordination on grid squares and species simultaneously. They are compatible as both use a reciprocal averaging procedure to derive their results but TWINSPAN divides the grids (and species) according to differences, while the ordination technique tends to group the grids (and species) according to their similarities. Therefore a clustering of grid squares (or species) in ordination space is indicitave of a floristic similarity (or shared geographic distribution) among them.

The distribution of TWINSPAN 5+ grid squares in ordination space was plotted along the 1st and 2nd DCA ordination axes, the two axes with the highest eigenvalues (Fig. 40). The same was done with the ordination of TWINSPAN 3+ species (Fig. 66). TWINSPAN groupings of grid squares at the level of Region, and species at the level of Element were then superimposed on the resultant scatter plots.

The geographic trends in the compositional gradients of the grids were also studied in another way: For each axis of the TWINSPAN 3+ and 5+ ordinations the grid (sample) scores were divided into five and 10 equal intervals respectively. The grids were then assigned to groups (represented by different colours) according to these intervals and plotted on distribution maps (Figs. 41–48). Only the five-interval maps are presented here as both intervals showed basically similar patterns and colour separation on the 10-interval maps became difficult.

The length of the ordination axes or gradient lengths as well as the grid and species scores are given in *average standard deviation of species turnover* or *standard deviation* (SD) units (Gauch 1982).

The geographic trends in the floristic composition of the moss regions, as well as the distributions of the moss elements, were then related to a range of environmental, in particular climatic, variables. With DCA, environmental (climatic) gradients are not studied directly as only the floristic data is ordinated. Care was taken not to propose correlations of variables which are likely to be fortuitous.

2.3 Two-way table

The relationships between the broad scale floristic regions and floristic elements delimited by the TWINSPAN 3+ analysis were studied by summarising the re-ordered data-matrix in a two-way table (Fig. 65). The abundance of each Subelement in each Domain (represented by different sized dots in the figure) was estimated as follows: The total number of species in a particular Subelement was multiplied by the total number of grids in a specific Domain. The actual number of occurrences of the Subelement in the Domain was then counted and the percentage calculated. The percentages were then grouped into 10 classes represented by different-sized dots in the table.

2.4 Distribution maps

The distribution maps presented in Part 2 of this thesis were prepared by hand and scanned into a computer programme for further manipulation. The number of species that occur in each grid square was added to some of the diversity maps and all of the distribution maps of the elements in order to determine main distribution areas and centres.