Pollen analysis and the vegetational history of Barra and South Uist in the Outer Hebrides, Scotland

Volume 1

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Abstract

This study examines contemporary vegetation, pollen taphonomy and Holocene vegetation history across east-west trending environmental transects in the southern Outer Hebridean islands of South Uist and Barra.

The pollen depositional characteristics of sixteen plant communities are described and modern pollen deposition is found to reflect the distribution of major vegetation types on the islands. The history of Holocene vegetation is investigated at a number of sites which include exposed west coast inter-tidal peat deposits, wooded loch islands and pre-peat soils associated with archaeological features.

These studies indicate that Holocene vegetation development followed a pattern typical for the region at similar latitudes. The early post-glacial vegetation mosaic of *Empetrum* heath, herb-rich grassland and dwarf shrub communities was progressivly altered by the subsequent establishment of predominantly deciduous woodlands. The pollen diagrams record an ordered sequence of tree migration to the islands in which *Betula* then *Corylus* were the first colonists followed later by *Ulmus, Quercus, Pinus Alnus* and *Fraxinus.* The scales of analysis employed in the study indicate that very 'local' pollen deposition is a characteristic of the islands' micro-fossil record - a feature which could be exploited in further archaeologically related studies.

Woodland appears to have persisted in sheltered locations until *c*.5,000 B.P. A gradual reduction of woodland from c.5,000 B.P.was accompanied by an expansion of the herb-rich grassland and blanket bog communitiues which had been present on the islands from the early Holocene After *c* 4,000 B.P.woodland decline accelerated and the grassland and blanket peat communities increased to attain their present dominance in the islands vegetation. The vegetation changes recorded in the pollen diagrams are attributed to a combination of factors changing environmental conditions - such as the pedological effects of Holocene climatic conditions, sea level rise and human impacts.

There is no archaeological evidence for mesolithic occupation of the islands, however at a point in the 'early' Holocene a brief episode of fluctuating woodland disturbance, charcoal and 'cereal type' pollen is noted at one east coast site, Loch Hellisdale. This data contributes to an increasing body of information which suggests some mesolithic presence along the eastern coast of South Uist.

The true histories of the past uncover the buried potentialities of the present.....History, in this sense, explores the field of 'imaginative' variations which surround the present and the real that we take for granted in everyday life. Such is the way in which history, precisely because it seeks to be objective, partakes of fiction. (Ricoeur 1981 in Moore 1990)

Chapter 1.

Introduction.

Introduction

The Outer Hebridean islands of South Uist and Barra are located on the extreme western coast of north west Europe (Figure 1) and offer great potential for the study of "post-glacial" and Late-Glacial vegetation change in remote oceanic islands. The isopol maps for Britain and Europe 0-13,000 years ago (Huntley and Birks 1987) and Holocene isochrone maps showing the patterns of tree spreading in the British Isles (Birks 1989) indicate that these islands have been distant from main centres of plant dispersal throughout the Devensian Late Glacial and Holocene (Figure 9). Despite the authority of these maps, in practice little detail is known of the history of vegetation on these islands. Similarly discussions of the relationships between the ecological history of these islands, and broader relationships to regional and continental patterns are based on rather limited palynological data in what is likely to be a biologically and taphonomically complex region.

Previous botanical and palynological studies undertaken in these remote and windswept islands have raised a number of diverse and interesting questions which are of interest in relation to inter-related theories of biogeography and palaeoecology.

The contemporary flora of the Outer Hebridean islands appears to be relatively impoverished when compared with the Scottish mainland where the species complement numbers 805 species of vascular plants compared with 470 species on South Uist and 407 on Barra (Perring and Walters 1962). This apparent lack of diversity in the islands' flora is in itself worthy of further study. There are indications from the modern floras that the situation may have been different in the past. For example there is the presence on the islands of plant species with disjunct phytosociological provinces. These include the southern Atlantic and north American Jubula huchinsiae and Dryopteris aemula as well as Najas flexilis,

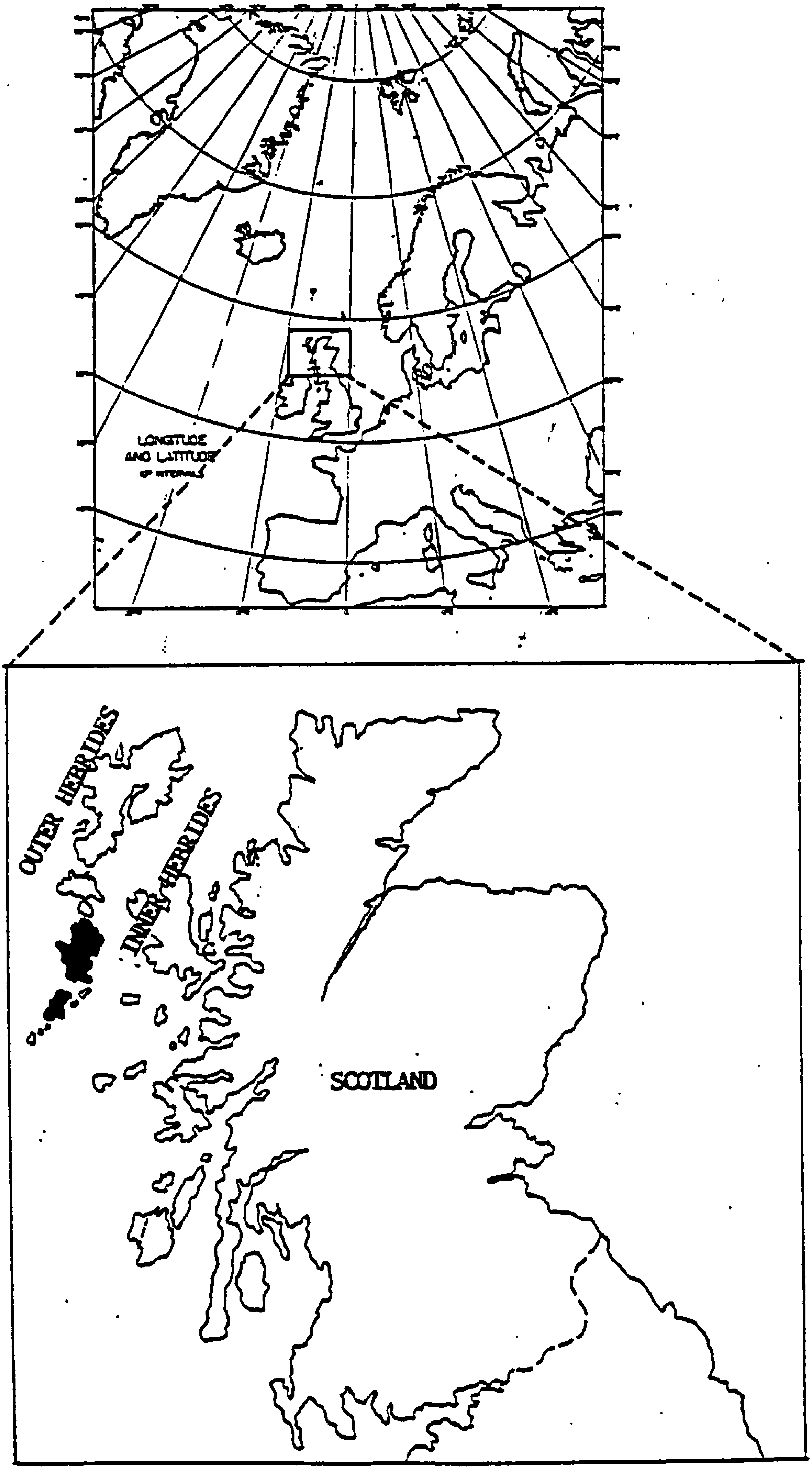


Figure 1. South Uist and Barra, location map

Spiranthes romanzoffiana and Potamogeton epihydrus (see Birks 1991, Curry 1979, Ratcliffe 1968).

The islands are remote, windswept, bleak and of ecological importance because of their unusual geographical location on the Atlantic fringes of western Europe. The relative poverty of the flora could be due to any number of reasons. Plant migration may have been limited by sea barriers particularly as sea levels rose throughout the Holocene. The Sea of the Hebrides and the Minches are deep sea channels yet the islands are only 38.2 km from mainland Scotland at their nearest point. The bleakness and exposure of the islands to Atlantic gales and salt laden precipitation, illustrated in Table 1, may make the islands inhospitable to certain species, many of which are already at the north-western edge of their european range in the Hebrides, for example Osmunda regalis, Dryopteris aemula, Hypericum elodes and Anagallis tenella (see Curry 1979).

The marginality of the Western Isles suggested by the isopol and isochrone maps of plant migration rates in the north Atlantic region are also of interest in relation to previous studies of island biogeographical theory. The dispersal, colonisation , and adaption of plant species on isolated oceanic islands has been the subject of considerable research and controversy since the pioneering work of McArthur and Wilson (1967). In proposing the equilibrium theory of island biogeography they sought to establish a quantitative relationship between the richness of island biotas, island area, and distance from the nearest mainland. The theory suggests that at any time the diversity of an island's biota represents the relationship between species immigration rates, extinction rates and habitat heterogeneity. The vast majority of research into the theory comes from the Pacific Ocean, not the north Atlantic. Consequently there are few geographical tests for the theory relevant to the Hebridean study region. Nevertheless as a first line of enquiry the theory offers some interesting insights into factors limiting the diversity of the flora on these

	Month												
Variable	J	F	M	A	M	J	J	A	S	O	N	D	Year
Mean monthly temperature (°C)	4.5	4.3	5.6	7.2	9.7	12.0	13.1	13.3	11.9	10.0	6.7	5.5	8.7
Rainfall (mm)	129	86	88	62	65	76	83	83	119	137	140	132	1024
Mean hourly wind >17.1 ms^{-1} (h)*	18.8	15.4	12.0	4.6	2.8	0.6	0.8	2.1	7.4	13.8	16.8	24.4	10.0
Mean daily sunshine (h)	1.31	2.54	3.74	5.78	6.52	6.53	4.67	4.87	3.81	2.56	1.57	0.85	3.73

Calculated from data in Monthly Weather Report

*1957-1980

Table 1 Selected climatic variables at Balivanich, Benbecula 1951-1980

(Source Bennett et al. 1990)

islands. In an island biogeographical study of floristic diversity in British offshore islands, Johnson and Simberloff (1974) suggested that although isolation and latitude are contributory factors restricting the diversity of island biotas;

> "Area may be correlated to island species number because it is an index of environmental heterogeneity" (Johnson and Simberloff 1974 p.45)

This implied that environmental heterogeneity contributed to floristic diversity, and this is in turn reflected in the species - area relationship. In the case of the Scottish islands the species number/island area relationships indicate that islands with a wider range of bedrock and soil types supported a larger number of species and that the larger islands in general have a wider diversity of geology and soils. The greatest floristic diversity is recorded on larger islands near to the Scottish mainland (for example Skye). The islands in the Outer Hebrides have a comparatively limited range of geology and soil types than those of comparable size in the Inner Hebrides (Table 2) and this could contribute to their low floristic diversity. However as Edwards (1990), points out many of the smaller, species poor Inner Hebridean islands have low relief and experience greater exposure to Atlantic gales, which may be the dominant limiting factor. Johnson and Simberloff's (1974) study highlighted the importance of habitat diversity and climate (expressed as latitude) as limiting factors affecting the range of plant species on British islands. This statistical analysis of species numbers however obscures the richness of Hebridean island flora's for as Birks (1983 p.269) states,

> 'Nowhere else in the world can one find South Atlantic species with Macronesian or even tropical affinities such as Hymenophyllum tunbrigense and Dryopteris aemula growing at or near their northern most localities in the world on the same islands as Arctic-Subarctic species such as Koenigia islandica, Cerastium arcticum, and Arenaria norvegica growing at or near the their

Table 2. Scottish island area, relief, soils and species number. (source Johnson and Simberloff 1974)

Island	A	E	ST	L	D	S
Arran	429.4	874	4	55.6	5.2	577
Barra	18.4	384	2	57.0	77.4	409
Canna	12.7	210	1	57.1	40.6	300
Coll	74.1	103	3	56.6	14.5	443
Colonsay	44.8	143	1	56.1	31.1	482
Eigg	29.0	393	1	56.9	12.3	453
Foula	13.5	418	1	60.1	177.4	149
Gigha	15.5	101	1	55.7	3.4	401
Hoy	154.1	477	2	58.9	13.1	354
Iona	9.1	101	1	56.3	37.1	388
Islay	605.3	409	3	55.8	22.4	581
Jura	379.4	784	3	56.0	4.8	444
Lewis	2137.3	800	5	58.1	38.2	527
Mingulay	9.6	272	1	56.8	85.5	269
Muck	5.4	137	1	56.8	8.5	284
Mull	909.6	967	4	56.5	2.1	517
N.Ronaldsay	7.3	15	2	59.4	85.5	131
N.Uist	305.6	347	3	57.6	57.1	433
Orkney	489.5	269	6	59.0	28.1	446
Rona	10.4	123	1	57.5	6.5	159
Rhum	106.7	810	3	57.0	24.8	425
Sandray	50.2	66	3	59.3	62.9	162
Shetland	984.2	450	6	60.3	188.7	421
Skye	1735.3	1009	5	57.3	0.6	594
S.Ronaldsay	60.9	119	2	58.8	9.7	207
South Uist	365.2	620	3	57.2	82.3	470
Tiree	76.4	140	2	56.5	36.8	378

A Island area (km)^2

E Elevation

ST Soil types

L latitude

D Distance from mainland (km)

S Observed species number

southernmost localities in Europe'

Johnson and Simberloffs'(1974) study also fails to account for the effects of changing environmental factors through time which may have influenced both plant dispersal and survival on the islands. The flora may have been considerably more diverse in the past.

The contemporary vegetation could, for example, result as much from the effects of Holocene climatic change on soils as island remoteness or habitat heterogeneity. The natural deterioration of soils through time, for example by acidification and leaching may also have reduced habitat diversity in this extreme oceanic environment.

Evidence of past human activity on Barra and South Uist is abundant, the rich, diverse and widespread occurrence of archaeological remains in landscapes - previously assumed to be 'wild and natural', and often impoverished or covered in blanket peat or sand is surprising. Unfortunately relatively little is known about the pre-peat and early machair landscapes of the islands (Barber 1987) and the implied extent of past human activity raises questions which have considerable relevance to understanding the course of vegetational history in the area. The present bleakness and floristic poverty of the landscape could also be the result of past land use, rather than island biogeographical factors. The diverse impacts of people over time may have led to the loss of some habitats. In this context it is worth considering the impact of nineteenth century agriculture particularly in relation to 'clearance' for sheep grazing. Buckland (1990) has emphasised the ovigenric nature of the Hebridean landscapes. The low diversity of contemporary vegetation could be the result of human activity and influence distorting relationships which are therefore not representative of natural processes.

The contemporary landscape of the islands is characterised by a series of distinctive settlement, land use and geomorphic divisions which trend from north to south as shown in Figures 2 & 3. Topographically these islands are relatively diverse with land ranging from sea-level with significant areas of upland above 150 m. O.D. The west coast has a 'soft' coastline with extensive dune systems backed by floristically rich, calcareous dune pasture or 'machair' which is used extensively by the islanders for cereal cultivation and pasture. Machair is described and discussed at length in Ritchie (1976, 1979, 1991) and Boyd and Boyd (1990). This area provides the main focus for contemporary settlement location. Freshwater peats now exposed in the inter-tidal and sub-tidal zones from the west coast of South Uist and Benbecula suggest that sea levels were once lower than today (Ritchie 1976, 1979, 1991) which conforms to general expectations from models of global sea-level change even when moderated by isostatic rebound as in the Hebrides (as discussed in Dawson 1982, Jardine 1982, 1987). Wood remains in these deposits indicate that woodland once existed in areas exposed to the full force of Atlantic gales. Rising sea level and the ingress of sand onto the west coast (Ritchie 1991) had the effect of submerging many Holocene landscapes beneath sand and salt water and may have had impacts on the wider landscape, for example through changing palaeohydrological systems by impeding drainage and raising the water table. The extent and implications of these processes for understanding settlement and vegetation have yet to be fully explored.

The east coast is dominated by mountains and sea cliffs, with a series of corrie lakes and east-west trending valleys extending from the uplands to the rocky coast. This area is now uninhabited although abandoned crofts, cultivation ridges, archaeological sites and historical accounts indicate a history of human occupation in the area. The mountainous east coast and the western machair of South Uist are separated by a loch-studded expanse of blanket peat and wetlands known as "the Blacklands"

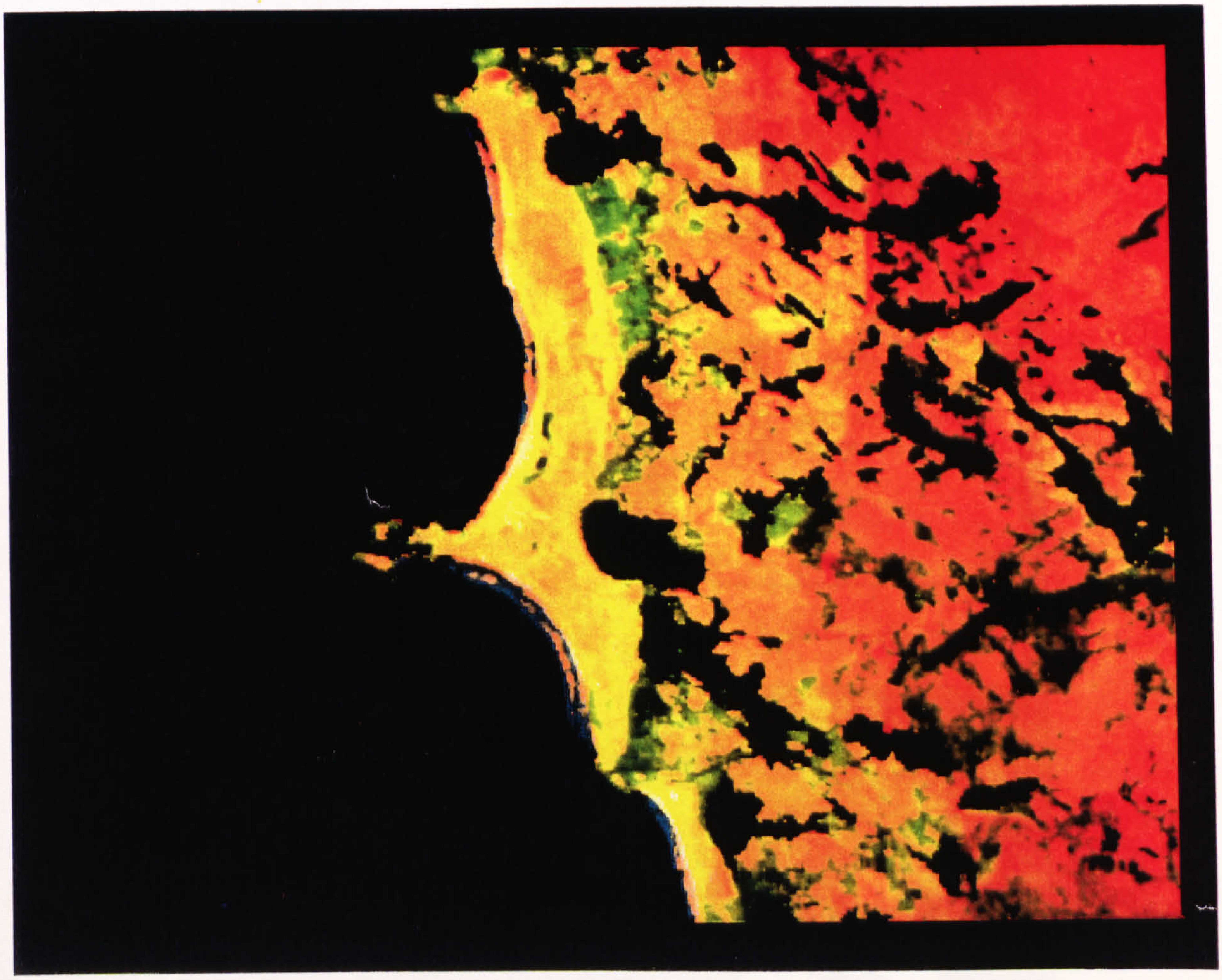
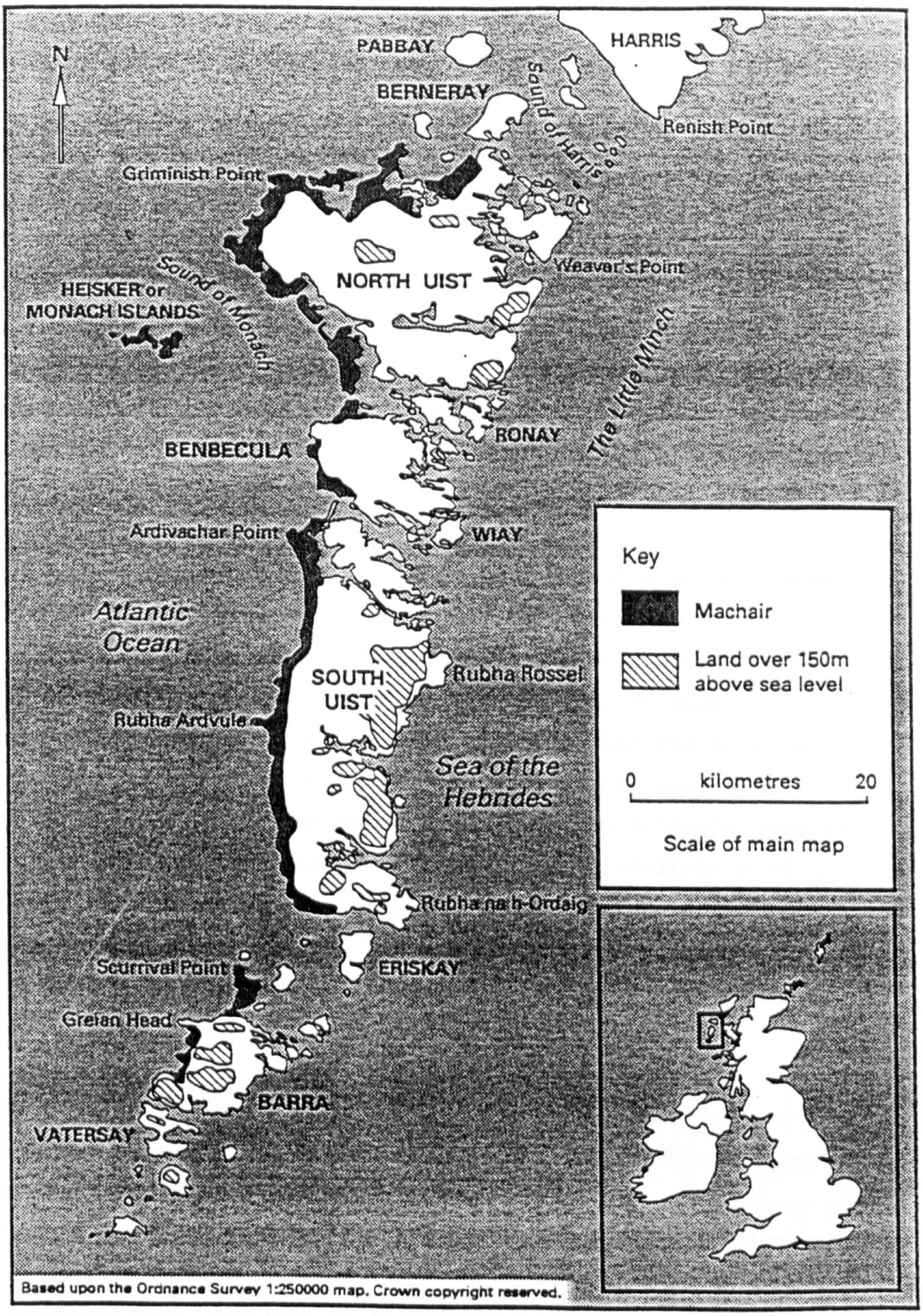


Figure 2. Satellite photograph of South Uist



Based upon the Ordnance Survey 1:250000 map. Crown copyright reserved.

Figure 3. Major landscape units; Southern Outer Hebrides.

where peat is cut extensively by the islanders for fuel. The term "blacklands" owes its origin to the the blacker fen peats produced by the natural or artificial inclusion of shell sand to the peats of the area immediately inland from the machair. Woodland in South Uist and Barra is restricted to a few isolated stands in sheltered locations, typically on loch islands such as occur at the National Nature Reserve, Loch Druidibeg, South Uist, and on terrestrial 'islands' such as in the remote gorges of the National Nature Reserve woodland at Allt Volagir, also on South Uist.

Large areas of the present day landscape are dominated by blanket peat which extends from the uplands of South Uist and Barra down to sea-level in some areas. The history of peat growth and any relationships with climatic change, pedogenesis, or past anthropogenic activity are unknown. In particular the notable absence of woodland on the islands is of more than ecological interest, in that if it pertained throughout the Holocene then it would raise questions about the abundance and distribution of woodland in prehistory - specifically about the nature of ancient resource management and early settlement on these islands.
Thus the contemporary landscape raises a number of multi-faceted questions which are of local and regional significance:

Has the flora of the islands' always been species poor?
Were soils more fertile in the past and therefore able to support a greater diversity of plant species?
What were the environmental impacts of Holocene climatic change on the islands?
Was woodland more abundant in the past, and if so what was the species composition, how has it changed, and what caused the decline to it's present status and distribution.
What was the role of past human activity in producing the present landscape?
When did the contemporary pattern of vegetation become established?
What are the controlling factors in the physical environment which

maintain this pattern of plant distribution and how have these changed in the past?

Do island biogeographical theories have a role in explaining the present flora of these islands ?

Many of these questions can be addressed through palynological investigation.

Previous palynological research in the Outer Hebrides.

a) **Pre-Devensian.** Palynological analysis of pre-Devensian deposits from the Outer Hebrides is restricted to Tao Galson Lewis, (Figure 4), at the extreme north west of this island chain (Sutherland & Walker 1984). Analysis has revealed a glimpse of a past interstadial pollen flora dominated by Gramineae, Cyperaceae, *Empetrum* and open ground herbs. The age of the deposit is unknown as it is outside the range of radiocarbon-dating (Sutherland and Walker 1984). The lack of arboreal pollen in the deposits led Sutherland and Walker (1984) to suggest that these islands were as treeless in previous interstadials as they are "at present".

Two sites, one in northern Lewis and one on Hirta, part of the St.Kilda island group, provide some information about the late Devensian flora. At Tolsta Head, Lewis (Birnie 1983) a polleniferous organic-silt deposit dating to 27,000 B.P. indicated a vegetation mosaic of grassland, herbaceous and arctic Alpine scrub with *Salix herbacea* and *Juniperus*. On Hirta, Sutherland *et al.*, (1984) similarly found a pollen flora dominated by herbaceous species.

b) The Devensian Late-Glacial and the Holocene

There is limited information available from previous pollen analytical studies covering the Late Glacial and Holocene period in the southern Outer Hebrides. The most important publication is by Bennett *et al.* (1990) which appeared towards the end of this research programme. This study reported results of pollen, chemical, magnetic susceptibility and radiocarbon analyses from

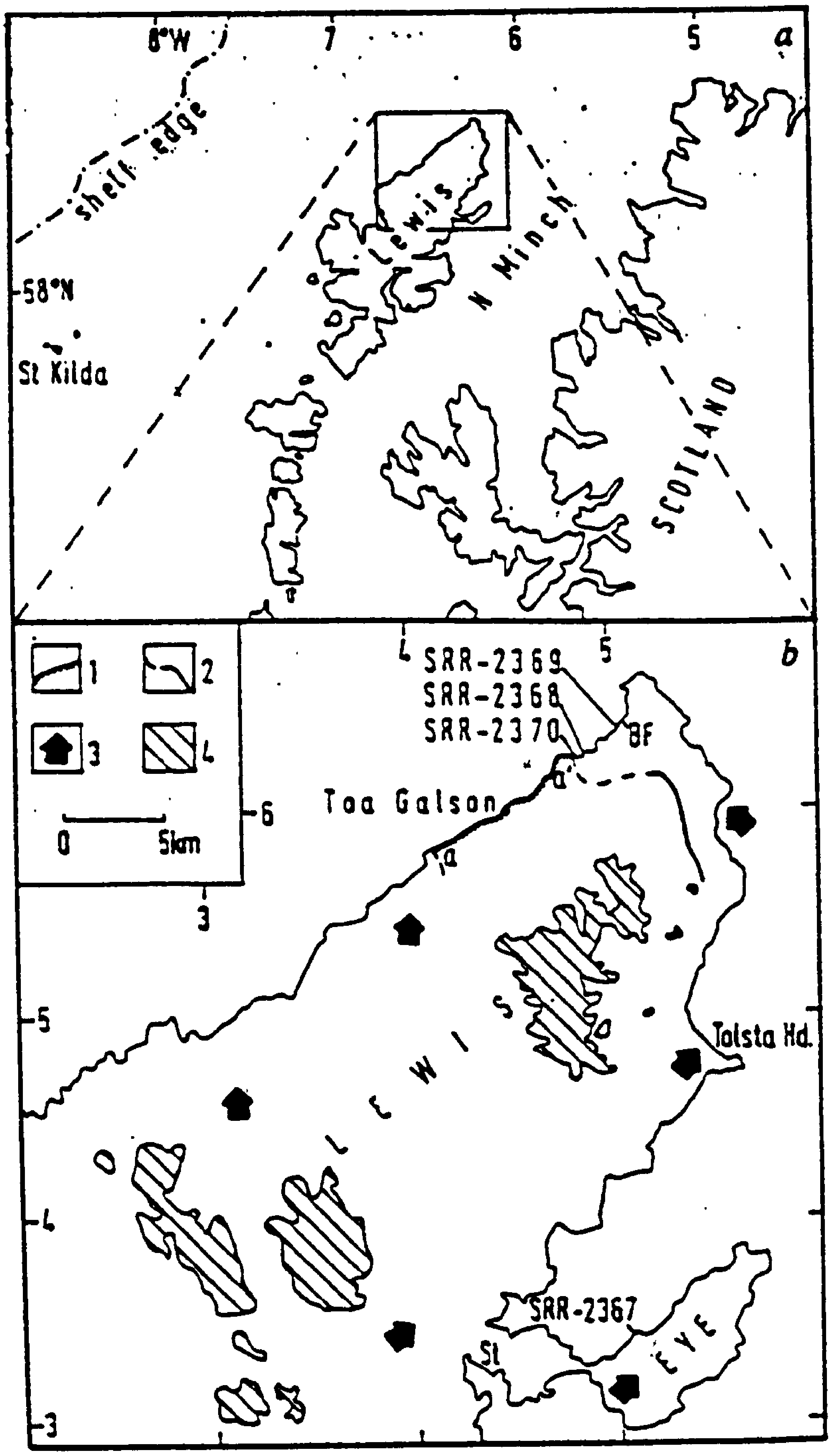


Figure 4. Location of Lewis a) and b) Galson Beach, northern Lewis. 1, stretch of coast (a-a') where the Galson beach is in-situ and not over-lain by glacial deposits; 2, ice margins, continuous line representing the end moraine in north Lewis; 3, generalized direction of last ice movement; 4, land over 122m.
(source Sutherland and Walker 1984)

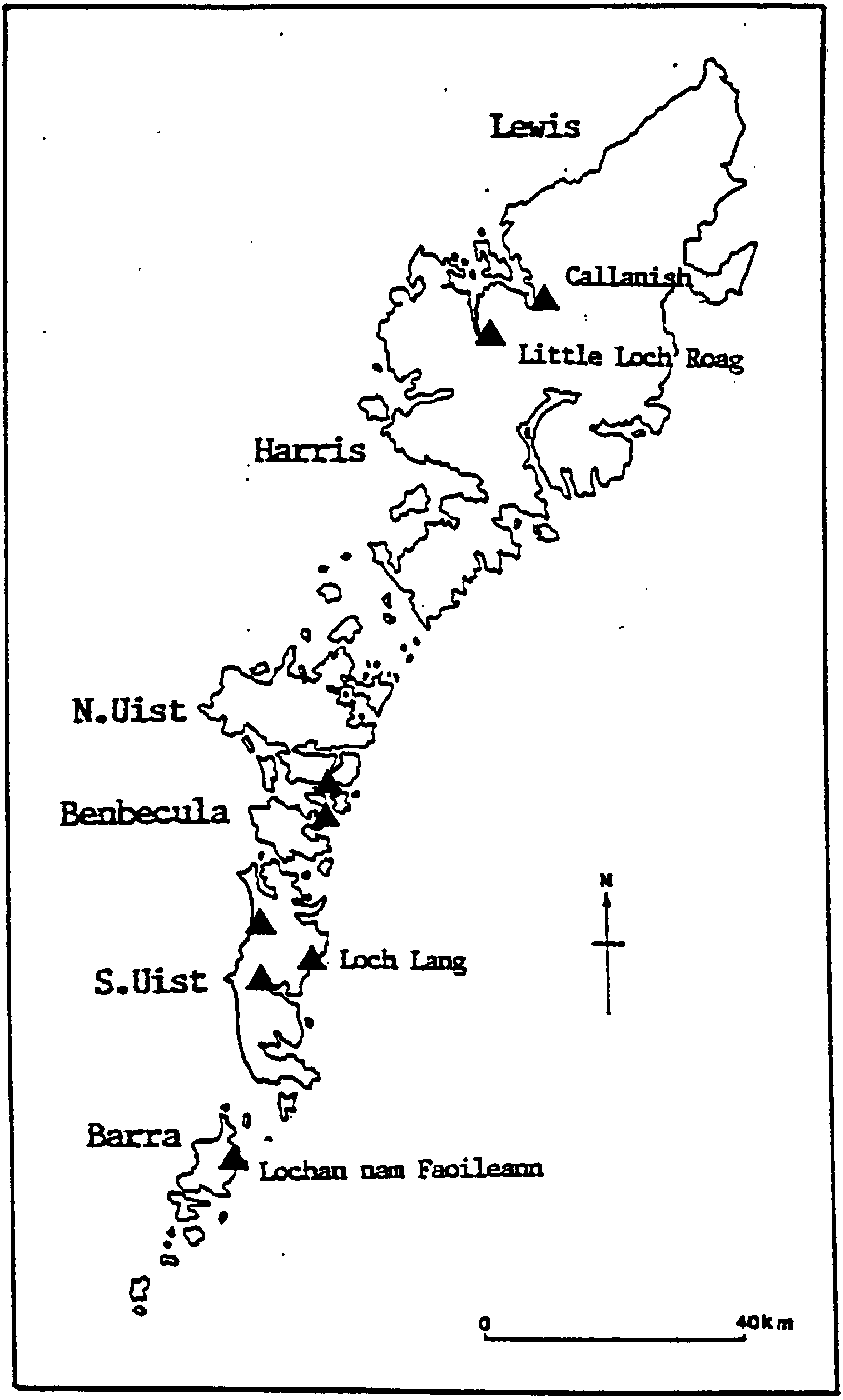


Figure 5. Palynological study sites in the Outer Hebrides.

Loch Lang, South Uist, (Bennett et al. 1990). Before this article appeared, the only previously published palynological data from South Uist and Barra was that of Blackburn (1946) and Heslop-Harrison (1948). These comprised summary diagrams obtained from peat samples from Barra and South Uist, respectively. These diagrams are now rather dated in terms of both theory and practice. The pollen diagram by Blackburn from Barra shows high frequencies for non-arboreal pollen and spore types throughout the period of peat growth. However *Corylus* and *Betula* are recorded in consistently high frequencies with *Ulmus* and *Pinus* occurring in the lower part of the profile. Later *Alnus* and *Quercus* are well represented. Blackburn made two important observations in her discussion of these results. Firstly she suggests that peat accumulation began here 'early in the Boreal period', and that the rate of accumulation was very slow. Secondly, arboreal pollen frequencies were high enough for Blackburn to suggest that;

> ' ...quite considerable numbers of forest trees grew on the better drained parts of the island during that period' (Blackburn 1948 pp.48)

Blackburn made no reference to archaeological history or human impact on the vegetation, possibly because of the coarseness of sampling and limitations in pollen identification of the time gave no reason to suspect human interference with the observed pattern of vegetation change.

These early studies on Barra and South Uist were followed by a palynological study with radiocarbon dates from Little Loch Roag (Figure 5) an exposed west coast site on the Isle of Lewis (Birks and Madsen 1979) - the first modern palynological study from the Outer Hebrides. It provided a detailed vegetation sequence which showed a virtually treeless landscape throughout the Holocene period. This particular study was influential in placing the Outer Hebrides outside the limits of Holocene tree migration patterns in continental scale isopol mapping studies, (Huntley &

Birks 1983) and regional studies (Bennett 1989, Birks 1989), reinforcing the view derived from its modern treeless state, that the Outer Hebrides has remained treeless throughout the Holocene - largely as a result of exposure to Atlantic winds.
Despite Blackburn's (1948) findings, this notion of treelessness became well established in the literature. However subsequent studies from the Isle of Lewis showed that vegetation history on the islands was not as simple as was first thought.

A study by Wilkins (1984) found low pollen frequencies for _Pinus_, _Betula_ and _Salix_, essentially similar to those found in the pollen record at Little Loch Roag (Birks and Madsen 1979). These low tree pollen frequencies were obtained from peats which contained _in situ_ wood macrofossils. Forty wood samples were collected and radiocarbon dated. _Salix_ macrofossils ranged from 9,140-8,550 B.P., _Betula_ macrofossils ranged from 7,980-5,030 B.P. and _Pinus_ macrofossils ranged from 4,870-3,910 B.P. A number of hypotheses were proposed to account for the disparity between the microfossil and macrofossil record. These included;

a) Tree pollen is essentially unrepresented because it is largely "blown off" the islands which are subject to constant strong winds and recurrent Atlantic gales (see Table 1 this study and Angus 1991).
b) The tree stumps represent isolated individuals of different dates which never formed a closed wood and hence there was little pollen produced. (This idea was noted and rejected by Wilkins because of the abundance of wood at some sites).
c) Ecological conditions which inhibited flowering of these species and reduced pollen productivity would result in their absence from the pollen record.
d) That the peat sampled and studied by pollen analysis was not contemporaneous with the tree stumps which may have sunk through the peat of those sites.

In addition to these essentially taphonomic and biological explanations of pollen sparseness, Birks (1991) has added that 'scales of analysis' may be responsible for this effect. The pollen record primarily provides a picture of regional vegetation over a large area whereas macrofossils provide detail of local patterns. In essence he concludes that the islands were still predominantly treeless;

> 'It is perfectly feasible to have sparse tree populations at densities of 0.25 trees ha^{-1} (= 200 trees or less within 2-5 km radius of a pollen site) that are largely undetected pollen analytically' (Birks 1991).

Palynological investigations at Callanish, Lewis (Bohncke 1988) provide further insight into the issue of local variability in the pollen record raised by Birks (1991). Bohncke's study demonstrated the development of locally abundant Betula and Corylus woodland with evidence of anthropogenic burning and clearance at 8,400-7,650 B.P., c. 5,035 ± 60 B.P. and 4,225 ± 65 B.P.

The most recent palynological study from Loch Lang, South Uist (Bennett et al. 1990) a sheltered east coast loch, suggested a history of Holocene woodland development which is very similar to the vegetational record from mainland Scotland and Skye at similar latitudes. At Loch Lang, Devensian Late-Glacial pollen spectra representing open grassland and Empetrum nigrum dominated heath were replaced by Betula and Juniperus scrub with Corylus expanding rapidly at c.9,400 B.P. This early Holocene woodland became increasingly diverse as Quercus and Ulmus are established locally at around 7,800 B.P., followed by Alnus glutinosa at c.7,200 B.P. and Fraxinus excelsior at c.4,400 B.P.

The only other account of Holocene vegetation history in the Outer Hebrides is the work of Walker (1984) which is unfortunately not a complete sequence. Importantly it shows the presence of Salix scrub on the remote island of St. Kilda in the early Holocene but there is no record of later more diverse woodland.

These palynological studies of the Holocene also revealed an early existence of bog communities - with several subsequent phases of expansion to reach its present dominant extent comparatively recently in the Holocene. At Little Loch Roag described by Birks and Madsen (1979), the mosaic of species-rich grassland, tall-herb communities and patches of Birch and Hazel scrub were gradually replaced by acidophilous species such as Calluna heath, acid grassland and blanket bog from c.5,000 B.P. Anthropogenic impacts on the vegetation were noted from 4,000 B.P. but cereal-type pollen was not recorded until c. 1,700-1,100 B.P. Similarly the study by Bennett et al. (1990) dated the onset of the Calluna curve to c. 4,200 B.P. and the expansion of the blanket peat communities from c.4,300 B.P. There were no clear pollen signatures for disturbed or arable biotypes in the Loch Lang pollen record and it was suggest that the area around the loch was never within a cultivated area, but had been part of common grazings.

Other palynological studies have focused on the origins and development of the machair. Records of inter and sub-tidal organic deposits from sites along the west coast of the Outer Hebridean islands date from Sinclair (1794), and include Martin (1695), MacRea (1845), Beveridge (1911), Jehu & Craig (1927), and Elton (1938). Samples of wood from the submerged forest at Pabbay, (Elton, 1938) were identified at the Royal Botanic Gardens, Edinburgh as Betula alba. Pollen grains of Betula and Quercus were found in the accompanying peat together with Ericales, Caryophyllaceae, Compositae and spores of Polypodium and Sphagnum. All these sites were located on the western Atlantic machair coastline (Figure 6).

More recent smaller scale stratigraphic and palynological studies of intertidal deposits in the Outer Hebrides have been published by Ritchie (1966, 1979, 1985), Von Weymarn (1974) and Whittington and Ritchie (1988). Von Weymarn (1974) examined stratigraphy and plant macro-fossils at sites near Stornaway on the Isle of Lewis.

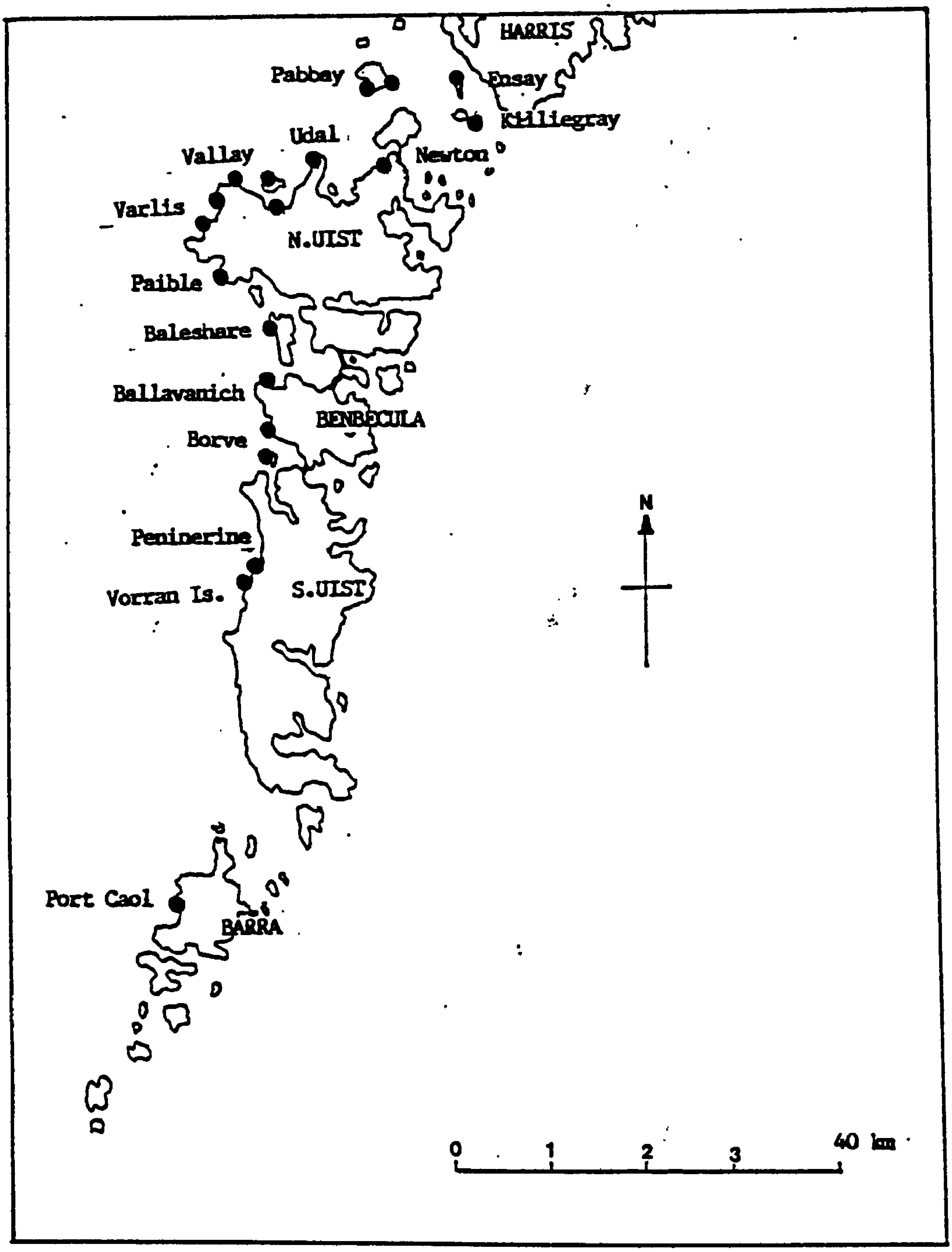


Figure 6. Inter tidal and sub-tidal peat deposits.
(source Ritchie, 1979)

The sites studied contained sand layers and sub-fossil wood remains in stratified - organic deposits. Ritchie (1985) suggested that these deposits provide evidence for a period of sea level rise and land submergence of at least 4-5 metres since c. 8,800 B.P., followed by a period of stability up to c.5,164 B.P. during which time sea level was 3-5m lower than at present. This was followed by a relatively rapid rise of a similar magnitude. A large ingress of aeolian sand at Pabbay (Ritchie 1985) is dated at c.4,366 B.P. and this may be associated with the original ingress of the coastal dune and machair system in this area. The peat which yielded the basal palynological data from Pabbay, immediately north of North Uist Ritchie (1985) has been radiocarbon dated to c.7,703 B.P. at the Jetty and c.8,330 B.P. at Forvath Reef. The pollen spectra at these sites indicated the presence of plants indicative of open water and marsh environments, but there was also a high representation of species associated with "dry, terrestrial peat communities". Arboreal pollen, particularly Betula and Coryloid with Ulmus, Quercus, Pinus and Alnus were also recorded. High Ericaceae pollen values dominated the pollen spectra with Gramineae, Cyperaceae and Sphagnum, suggesting that the vegetation of the area was dominated by acid heath with some woodland. The pollen data reported were limited to the basal samples from the two sites.

Importantly these studies were said to indicate an increase in storm frequency and renewed machair formation after 4,000 B.P. (Ritchie 1985, Birks 1991). Pollen analysis from these deposits suggest that woodland had once developed in locations now exposed to the full force of Atlantic gales.

The contemporary configuration of the coastline of South Uist is considered to be the product of sea level rise since c.5,100 B.P. which is associated with a change towards a more oceanic climate (Ritchie 1985). Birks (1991) suggested this resulted from shifts in the Atlantic storm tracks due to the relative locations and strengths of the Azores "high" and Icelandic "low" pressure systems. Other evidence for such climatic shifts in the mid to late Holocene, indicated from palynological studies in Scotland, has been suggested by a marked decline in woodland growth, particularly of Pinus and an increase in the area of blanket bog (Bennett 1984). On Lewis, Wilkins (1984) found no wood fossils in peat above the Pinus remains at c.4,870 B.P., leading him to conclude that Lewis has been devoid of woodland since that date.

The archaeological record from interbedded palaeosols in the machair has provided information relevant to the history of occupation in these areas. At Rosinish, east Benbecula, for example, Neolithic, Bronze age, Iron age, Viking / Medieval and historic occupation layers have been identified. Settlement has obviously been extensive and sometimes intensive, but although it has left some remarkable monuments, we still know little of the people involved or the manner in which they treated their environment (Shepherd, 1976, Barber 1987).

Analyses of organic deposits now found offshore are limited despite the possibility that these sites contain valuable information relating to sea level rise and sand ingress. These events have transformed the western Outer Hebridean coastline during the Holocene and have considerable relevance to theories of climatic change and human settlement of the North Atlantic since the mid Holocene.

Palynological research ; a wider Atlantic perspective.

The paucity of palynological data from the southern Outer Hebrides stands in contrast to the richness of studies from the Inner Hebrides and other islands. Many diverse and complex issues arise in consideration of this record and the local importance of these records does make extrapolation to the present Outer Hebridean study difficult. However, within the present context there are wider issues of interest. Of paramount importance are the migration and colonisation patterns of Holocene woodlands. Was there a general discernible pattern of development on the edge of the British Isles or was everything varying locally? This question of local variability is again seen to be important. For example, what was the degree of inter-island variability? How variable was the natural Holocene vegetation within one island?

Currently there is only scant radiocarbon dating evidence for woodland macrofossils on the Outer Hebridean islands which was described above (Wilkins 1984, Ritchie 1976,1985). Consequently it is difficult to identify reliable evidence with which to address these questions of within and between island correlation, succession, change and variation. A more critical issue concerns the development of a pollen - biostratigraphic framework for palynological research in the area. Such a framework is currently becoming increasingly needed, as a result of the numerous archaeological excavations and surveys which are now underway e.g. Sheffield Environmental and Archaeological Research in the Hebrides (S.E.A.R.C.H.).

In lowland Britain, there is a well known and documented pattern of vegetation change which was established initially by such workers as Godwin and improved by many later workers (see Godwin 1975). Recent studies have shown that pollen zone boundaries are often diachronous in any one region (for example see the discussion in Birks 1989). Inevitably such pollen - biostratigraphy will be a useful aid to correlation and dating but obviously cannot be a source of reliable chronostratigraphy. Nevertheless in the Outer Hebrides and Scottish islands, such a pollen biostratigraphic approach is nowhere near as useful as it might be because of limited and delayed plant colonisation which restricts the detail of such a biostratigraphy. Progress towards a relevant pollen biostratigraphy for the area is slow and expensive and critically radiocarbon dates for pollen zone boundaries are not transferable. In the Hebridean context, for example, Ritchie's (1985) work on providing radiocarbon dates for peat and tree remains associated with the development of machair on South Uist is valuable but cannot be extrapolated elsewhere.

It does however provide a useful local framework for understanding the origins of the machair and its relationship to the vegetation history of the area.

Two dominant and related problems emerge from a consideration of pollen analytical evidence from the other remote and marginal islands off Scotland - e.g., Shetland, (Johansen 1975, Birnie 1983), Orkney, (Moar 1969, Keatinge and Dickson 1979, Davidson and Jones 1985) and Lewis (Birks and Madsen 1979). These are the long distance transport of pollen onto the islands, and the relationship between local vegetation and the pollen produced. In studies from Shetland (e.g.Johansen 1975, Birnie 1983), Orkney (e.g.Moar, 1969), and Lewis, (e.g.Birks and Madsen 1979) significant problems arose with respect to the interpretation of low frequencies of tree pollen contained in the samples. Pollen types with high pollen productivity, particularly those which are wind-transported, can be represented in the pollen rain in areas where the species does not occur as a result of long distance dispersal from source. This effect can be particularly significant in areas of inherently low pollen productivity (Birks 1973b). In the studies from these more remote and exposed Scottish islands, it has been thought that significant amounts of long distance input occurred. Surface samples at Little Loch Roag on Lewis (Birks and Madsen 1979), contained similar pollen frequencies of arboreal pollen types as those recorded in the early Holocene pollen record from the site. As the island is now devoid of trees, Birks and Madsen (1979) suggested that the low percentage frequencies for Alnus, Fraxinus, Pinus, Quercus, and Ulmus found in the fossil pollen record are from long distance input and that the Holocene pollen record indicates a similarly treeless environment.

The almost treeless Shetland Isles were the subject of a study of the pollen rain in the air above ground level by Tyldesley (1973). This study showed that pollen values of as much as 30% arboreal pollen occurred above the Shetland islands. The source area for these types was suggested as the modern boreal forests of Scandinavia. This conclusion may be debatable, but its general importance requires consideration.

To illustrate the second problem of pollen / vegetation relationships, the study by Wilkins (1984) is of especial interest and has previously been mentioned above. He found that low pollen and spore frequencies of Pinus, Betula and Salix, similar to those found in the pollen record at Little Loch Roag, were also found in peats which contained in situ wood macrofossils. No simple explanation for this disparity was apparent although a number of hypotheses which focussed upon the relative absence of tree pollen have been proposed to account for this (see above).

The problem is however of much wider scope and significance. The pollen record of the Holocene across all the Hebrides and western Scotland is often diverse and varied (see Chapter 2 this study). Should it be taken at face value or is it to be explained in terms of further "taphonomic processes" or "scale of studies" as discussed above. These problems of pollen provenance and productivity have focused interest on the extent of woodland on the islands during the Holocene, particularly on the pattern of tree migration. The equally interesting questions concerning Holocene vegetation history in non-wooded landscapes, particularly in identifying anthropogenic effects, remain under-researched (Barber 1987). These issues have never been fully addressed and consequently the vegetational histories of these Outer Hebridean islands tend to have been assumed rather than demonstrated.

These issues highlight the problem of how to recognise past plant communities in the area from pollen-preserving sites. Two sets of distortions have already been considered; those of pollen provenance and under-representation. However these are relatively small issues in comparison with the fundamental lack of relevant information on the modern vegetation of these islands. The flora and general pattern of vegetation of the Outer Hebrides have been described by a number of authors (Currie 1979, Boyd and Boyd 1990, Pankhurst and Mullin 1991). However, only a few detailed accounts of the phytosociology and environmental relationships of the major plant communities have been completed, notably the machair and shell-sand communities, (Dickinson et al. 1971, Randall 1972,1976, Ranwell 1974,1977, Dickinson and Randall 1979). A full account of the machair of the Monach Isles was also given in Randall 1972,1976). In contrast other community types are not well described, although full accounts exist of the peatlands of the Isle of Lewis (Goode and Lindsay 1979), St.Kilda (Gwynne and Milner 1974), the Flannan Isles (Gilbert and Wathern 1976) and several islands of the Inner Hebrides, including the vegetation of Skye (Birks 1973); Rhum (Nature Conservancy Council 1974, Clutton-Brock and Ball 1987) and Mull (Jermy and Crabbe 1978). Vegetation communities strongly associated with soil types are briefly described by Hudson et al. (1982). This is a major shortcoming for attempts to reconstruct the vegetational history of the area. An ecological survey of the contemporary vegetation of the islands, information not currently available, is clearly required. With this information it would become possible to begin to determine the factors which influence the pattern of contemporary plant distribution. Knowledge of patterns of pollen and spore dispersal and deposition and the identification of the pollen and spore 'signature' of the contemporary vegetation units found would begin to resolve some of the major taphonomic issues raised in previous studies and to see to what extent past plant communities and palaeoenvironments have analogues in the present. However, attempts to understand the modern vegetation or past vegetation should avoid the assumption that past or present plant populations are or were maintained in equilibrium by or with environmental conditions. As many plants did not reach the Hebrides the evidence for late colonisation, (and the impossibility of colonisation created by sea level rise) suggests that plant populations were not in an environmentally controlled equilibrium in the past.

The archaeological dimensions, like the ecological dimensions of present knowledge also need elaboration. Frequently archaeologists have expressed the view that conventional palynology has appeared to avoid the actual sites in which people were living. The tradition has always been to investigate the bog or lake most representative of the natural environment where the character of regional vegetation could be discerned. However Dimbleby (1984) has shown that in specific circumstances there is considerable valuable information to be obtained from archaeological sites themselves. Issues of taphonomy, representativeness and interpretation become more difficult in these circumstances, but such information could be of great significance as there is a paucity of published palynological accounts from wetland archaeological sites in the Outer Hebrides. As so little is known about the impact of human settlement on the history of vegetation in these islands the richness of the archaeological record provides an opportunity to examine the fossil record at sites where it may be possible to establish links between human activity and vegetation change.

Therefore the considerations discussed above indicate that the islands of the Outer Hebrides provide a geographically coherent, diverse and under-researched location in which to investigate numerous questions of importance in relation to ecological history and environmental archaeology, and particularly the interpretation of pollen diagrams from this area.

The remoteness and marginality of the area provides a situation where the vegetation is less diverse than on mainland sites and its distribution definable within a given unit of area, thus lending itself more readily to research study. In particular, on these islands the abundance and composition of the contemporary woodland cover is known so that identification of long distance input of certain arboreal pollen types would be less of a problem than was experienced in most other palynological research in these exposed Scottish islands.

As many of the species studied are at the northern and westerly limits of their range in the British Isles, it is possible that they might have responded to changing environmental gradients more quickly than in other more sheltered areas where the vegetation is more stable. Factors of island size and geological uniformity also usefully served to restrict habitat diversity. Similarly the distinct contrasts in pedological substrates and their distinctive plant communities (e.g. machair and acid tills) aid in the definition of vegetation units.

A study of the vegetational history of Barra and South Uist therefore contains numerous worthwhile challenges of both a theoretical and applied character. Further details of the various issues and problems involved are described in the following chapter which provides further important information on relevant previous work in the Scottish islands. A combination of archaeo-environmental studies on the islands was therefore planned in 1987 at the commencement of this project, in order to provide a multidisciplinary approach to understanding the history of Holocene vegetation in South Uist and Barra. This would also contribute to our understanding of plant migration patterns, successional relationships, and past human activity which may be of wider local and regional significance.

(For information, the conventions used to describe radiocarbon dates used in this text follow those used for their publication in the journal Radiocarbon. Unless otherwise indicated B.P. indicates uncalibrated radiocarbon years "before present").

Chapter 2.

Literature Review.

Previous vegetational and palynological studies

The aim of this Chapter is to review previous vegetation and palynological studies from north west Scotland and the Scottish islands, together with hypotheses emerging from these studies which attempt to explain the past and present distribution of the regional vegetation, in order that this present study of southern Outer Hebridean vegetation and its history may be placed within its regional context.

This review will concentrate on the nature of the contemporary woodland and its history, and the spread and development of blanket bog in the region. This is because the almost total absence of woodland and the predominance of blanket bog are of primary importance to this present study, particularly as the history of these two vegetation elements probably has the greatest implications for understanding the palaeoenvironmental setting of any cultural / archaeological period of settlement on South Uist and Barra. This review will focus in from the general regional context to examine more closely the literature concerning aspects of vegetation and vegetation history of the Inner Hebrides and the Northern Isles.

The contemporary environment and vegetation of the Outer Hebrides and its history (already introduced in Chapter 1) are reviewed in subsequent chapters.

The Regional Context ; Woodland distribution and history

McVean and Ratcliffe (1962) used the composition of existing woodland stands in Scotland to reconstruct the potential distribution of native woodland in the region. Their study produced a division of Scotland into potential vegetation zones which described the extent and composition of woodland in the region in the absence of afforestation and agriculture (Figure 7). This study provides a useful framework in which to consider the

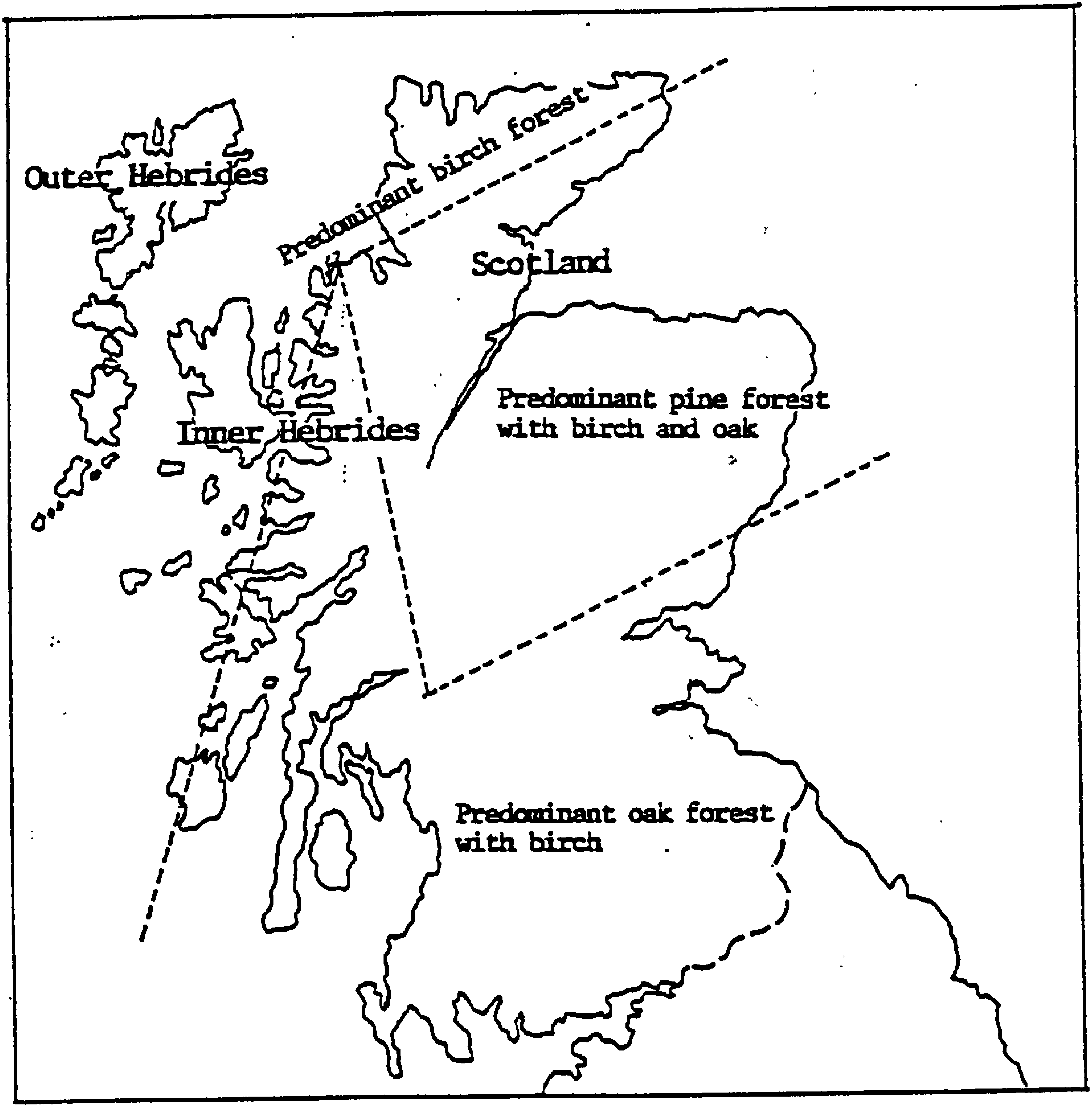


Figure 7. The position of the Outer Hebrides in relation to the potential woodland zones for Scotland. (Source McVean and Ratcliffe 1962)

occurrence of native woodland in the Scottish islands and the pollen analytical studies which investigate its history.

1) The area south of the Grampian highlands and extending up the west coast to southern Skye.

In this region oak and birch woodland would predominate. The composition of existing woodland stands in this area consist of a mosaic of communities differentiated by local conditions with Oak and Birch as important elements of the canopy. Other arboreal species present include; Alnus glutinosa, Populus tremula, Salix spp., Prunus padus, Prunus spinosa and Viburnum opulus. In areas with basic soils the understorey is, if ungrazed, species rich with Lonicera periclymenum, Rubus fruticosus, Vaccinium myrtillus, Anemone nemorosa, Anthoxanthum odoratum, Hyacinthoides non- scriptus, Holcus lanatus, Oxalis acetosella and Primula vulgaris. Where the understorey is grazed species of Gramineae and Pteridium aquilinum become dominant. In areas with acid soils the ungrazed understorey contains Vaccinium myrtillus, Luzula sylvatica and ferns such as Dryopteris borreri, Dryopteris aemula and Blechnum spicant.

2) The central Highlands and east coast.

In this zone the oak / birch woods of the south and west coast change to Pine and Birch woodland, with Birch more dominant in the central highlands and Pine becoming more dominant in the east.

The eastern pine woods are characterised by the canopy trees Pinus sylvestris, Betula verrucosa and Quercus petraea with Vaccinium myrtillus, Vaccinium vitis-idaea and Calluna vulgaris as understory in dense forest and Juniperus communis in more open forest. Where Pine is more dominant, Sorbus aucuparia, Prunus padus, Betula pubescens and B. verrucosa occur with Ilex aquifolium, Juniperus communis, Calluna vulgaris and Sphagnum spp. common in the understorey. The birch woods of the central highlands have Betula pubescens and B. verrucosa with a similar understorey to the Pine woods with the addition of Potentilla erecta, Oxalis acetosella, Melampyrum pratense and Anthoxanthum odoratum. Heavy grazing and burning produces species poor Calluna moorland or Agrostis - Festuca grassland.

3) The North and the Western Isles.

This zone is potentially an area of birch woodland with Betula pubescens, Corylus avellana, Sorbus aucuparia, Prunus padus, Salix cinerea and Lonicera periclymenum.

4) The far north and west and the offshore islands of Shetland and Orkney.

The woodland /scrub vegetation is limited in extent, predominantly Salix aurita, S. cinerea, S. caprea scrub with Rubus fruticosus, Lonicera periclymenum and Rosa spp.

The Hebridean islands

The Hebridean islands are interesting in relation to this pattern, as their location (Figure 7) as island chains off the west coast of Scotland means that they transgress at least two of these potential vegetation zones. Despite an apparent lack of trees, studies of Inner Hebridean woodland (for example, Gilbert 1984, Rose and Coppins 1983, Ball 1983, Bramwell and Cowie 1983, Jermy and Crabbe 1978, Ratcliffe 1977, Birks 1973) indicate considerable local diversity in the abundance and species composition of existing woodland. Shelter from gale force winds, altitude, drainage and soil base status are thought to be the most limiting factors affecting tree growth in the region (Ball 1983). The general pattern indicates that islands with a greater degree of topographic and geological diversity support more diverse woodland (Figure 8.)

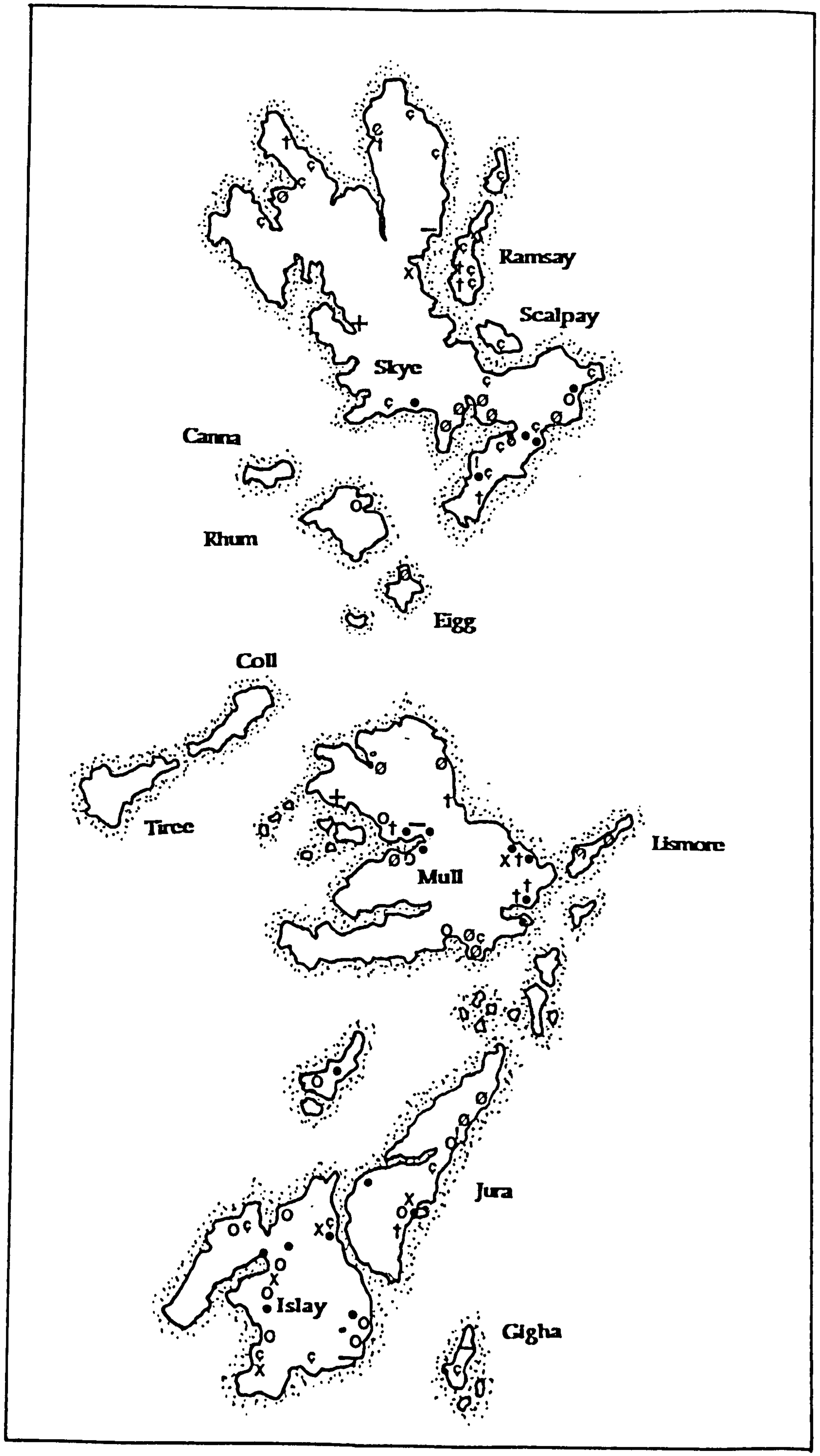
Species vary with soil type, typically Quercus, Betula, Sorbus aucuparia are dominant with Populus, Corylus and Salix on acid soils associated with bedrocks of schists, gneiss, sandstone and granites. In areas with calcareous bedrock, for example on the Dalradian limestones of southern Skye, Ulmus glabra, Fraxinus and

Corylus are more common. An *Alnus-Salix* association is common in areas with wet, gleyed soils.

Islands within the predominantly oak with birch woodland zone of the MacVean and Ratcliffe model; (Gigha, Jura, south-eastern Mull, south eastern Islay, Arran, Coll, Tiree, Eigg, Rhum, Bute, Canna, Colonsay, Oronsay and Southern Skye) can be subdivided into two main groups, comprised of wooded and non-wooded islands. Tiree, Canna, Rhum, and Coll are virtually treeless except for isolated *Quercus*, *Betula*, *Corylus*, *Sorbus*, *Crataegus*, and *Ilex aquifolium* individuals in rock clefts and gorges near sea level, protected from grazing (Ball 1983).

The wooded islands also display a degree of inter- and intra-island variation, for example, Eigg has remnants of *Quercus* woodland but more commonly *Corylus avellana* dominates. *Ulmus glabra*, *Sorbus aucuparia*, *Crataegus monogyna* and *Prunus spinosa* plus *Populus tremula* are locally abundant (Ball 1983). These two main types of woodland are also represented on larger, or more topographically or geologically diverse islands such as around Loch Spelve, south-east Mull, and on Islay. Jura has representatives of all stand types occurring in the Hebrides (Ball 1983).

Islands in the predominantly birch zone, for example, northern Skye, north western Mull and north-western Islay, have a predominance of *Betula* rich woodland. In contrast some of the other smaller islands support *Quercus* dominant and *Quercus* / *Betula* stands, for example on Colonsay (Ball 1983, Ratcliffe 1977, Rose and Coppins, 1983, Andrews *et al.*1987). *Quercus petraea* - *Corylus avellana* - *Betula pubescens* are dominant species with some *Sorbus aucuparia*, *Ilex aquifolium*, *Fraxinus excelsior*. In *Quercus* dominant stands the field layer contains herb rich grass communities containing *Anthoxanthum odoratum* and *Agrostis canina* with *Circaea intermedia*, *Geum rivale*, *Ajuga reptans*, *Anemone nemorosa*, *Hyacinthoides non-scriptus*, *Oxalis acetosella*, *Viola*



Key

- ø *Ulmus glabra-Brachypodium-Galium odoratum*
- ! *Ulmus glabra-Mercurialis-Allium*
- + *Fraxinus-Corylus-Brachypodium*
- † *Fraxinus-Corylus-Mercurialis*
- o *Quercus-Betula-Vaccinium myrtillus*
- • *Quercus-Betula-Corylus-Oreopteris*
- — *Alnus-Salix-Carex*
- ∘ *Betula-Sorbus aucuparia-Vaccinium myrtillus*
- ç *Betula-Corylus-Fragaria*
- x *Salix atrocinerea-Betula-Molinia*

Figure 8. Existing woodland stands in the Hebrides.
(Source Ball 1983)

riviniana, *Primula vulgaris*, *Oreopteris limbosperma*, *Luzula sylvatica*, *Solidago virgaurea*, *Vaccinium myrtillus* and *Lysmachia nemorum*. Ferns are common in shady, rocky clefts and on rocky outcrops, *Dryopteris aemula*, *D. pseudomas*, *D. borreri*, *D. carthusiana*, *Athyrium filix-femina*, *Hymenophyllum wilsonii* and *H. tunbrigense*. In *Betula* dominant stands *Calluna vulgaris*, *Vaccinium myrtillus*, *Deschampsia flexuosa* are more abundant in the field layer. These woodlands have strong affinities with the predominantly 'oak with birch' zone rather than the predominantly birch zone to which they are assigned by MacVean and Ratcliffe (1962).

The distribution of woodland on the island of Skye illustrates the interplay of local characteristics in determining the species composition and abundance of woodland which is seen to gradually decline to the north of the island. *Betula pubescens*, *Corylus avellana* with *Quercus petraea*, *Ulmus glabra*, *Sorbus aucuparia*, *Alnus glutinosa*, *Ilex aquifolium* and *Fraxinus excelsior* stands are limited to the sheltered Sleat Peninsula and Kyleakin area of southern Skye, on the acid Lewisian gneiss and Torridonian sandstone bedrock. Unusual *Fraxinus*-*Corylus* woodland occurs at Thocabhaig National Nature Reserve on the Durness Limestone which outcrops to the south east of the Cullin Hills (Ratcliffe 1977, Ball 1983). *Betula* - *Corylus* scrub with *Sorbus aucuparia*, *Salix aurita* and *Populus tremula* are more common on the Tertiary Basalts of central Skye whereas woodland is almost absent from the Cullin hills and northern Skye.

To the north and west of the island chain several species reach their range limits in Scotland, for example *Quercus* reaches its northern limit in central Skye and *Pinus sylvestris* is virtually absent from records of Scottish island vegetation (Williams and Birks 1983).

Woodland on islands in the far north and west is scarce. Berriedale Wood, Hoy, Orkney is the most northerly woodland in

Britain (Ratcliffe 1977). It contains *Betula pubescens*, *Sorbus aucuparia*, *Salix cinerea*, *Populus tremula* and *Corylus avellana* with a species rich ground flora of ferns and tall herb species including *Filipendula ulmaria*, *Geum rivale* and *Angelica sylvatica*. Such tall herb and fern communities described by Bullard (1973) are potentially areas of past woodland (Keatinge and Dickson 1979). Spence (1960) describes Shetland as a treeless landscape with some scrub vegetation occurring in isolated localities such as sheltered gorges and loch islands. Species composition is typically *Salix aurita*, *Salix atrocinerea*, *Rubus fruticosus*,*Betula pubescens*, *Rosa canina*, *Rosa coriifolia*, *Sorbus aucuparia*, *Hedera helix*, *Lonicera periclymenum* and *Juniperus communis nana*.

Overall the dominant woodland type recorded on the Scottish islands is a *Betula-Corylus* association which includes *Crataegus monogyna*, *Prunus padus*, *Ilex aquifolium* and less commonly *Sorbus aucuparia* and *Populus tremula* (see Ball 1983).

The degree to which the contemporary distribution of woodland reflects "potential natural" woodland cover is difficult to ascertain. The magnitude of past climatic change, rising sea level, together with prehistoric and historic clearance and agriculture may have all contributed to changes in the regional pattern of woodland distribution, such that it may have been considerably different in the past. The changing climatic conditions during the Holocene, plus the effect of grazing animals and the consequences of clearance, for example on soils and woodland rejuvenation are processes which can only be investigated directly through palaeoecological studies.

The dominance of blanket bog communities in large areas of north west Scotland extends from sea level in the Outer Hebrides. The blanket bog and heather moorland communities are characterised by a group of plant associations. The Erico-Sphagnetum papillosum characterises much of the typical and northern forms of blanket bog found in the region ; species include *Calluna vulgaris*, *Sphagnum* spp., *Drosera rotundifolia* and *Narthecium ossifragum*.

Palynological Studies.

Birks (1977) and Walker (1984) reviewed the palynological data for Scotland and suggests that the regionally differentiated pattern of vegetation described above was established by 6,000 B.P. The Holocene isochrone maps of Birks (1989) provide a summary of regional tree spreading, and the pollen maps of Huntley and Birks (1983) provide similar information, including non arboreal plant species. The isopol maps are particularly useful in that by synthesising the palynological record from numerous sites they graphically provide a detailed picture of the direction, and rate of spread of plant species in the region during the Holocene (Figure 9).

The general pattern of woodland succession shown by the isopol maps indicates that *Betula* was the first tree to reach Scotland in the early post-glacial. It was expanding northwards and westwards at 10,000 B.P. probably from the European mainland via the North Sea Basin (Birks 1989). The presence of ice in the Scottish highlands during the Loch Lomond Stadial (Sissons 1981) delayed the spread of *Betula* into these areas (see Birks 1989 and Figure 9a) but by 9,750 B.P. it was well established in peripheral ice free areas of Skye and the west coast and by 9,500 - 9,000 B.P. *Betula* was present in the Highlands.

Corylus avellana was migrating up the west coast of Scotland and onto the Inner Hebridean islands by 9,500 B.P. Birks (1989) suggests that *Corylus* had a rapid rate of spread, perhaps 500 m. yr^{-1}, so that by 8,500 B.P. it had colonised much of mainland Scotland forming a major component of the early Holocene woodland except in eastern Scotland.

The initial rapid spread of *Ulmus glabra* in southern Scotland slowed after 8,500 B.P. and expansion from the south to far north took 2,000 years between 8,500 and 6,200 B.P., as *Ulmus glabra*

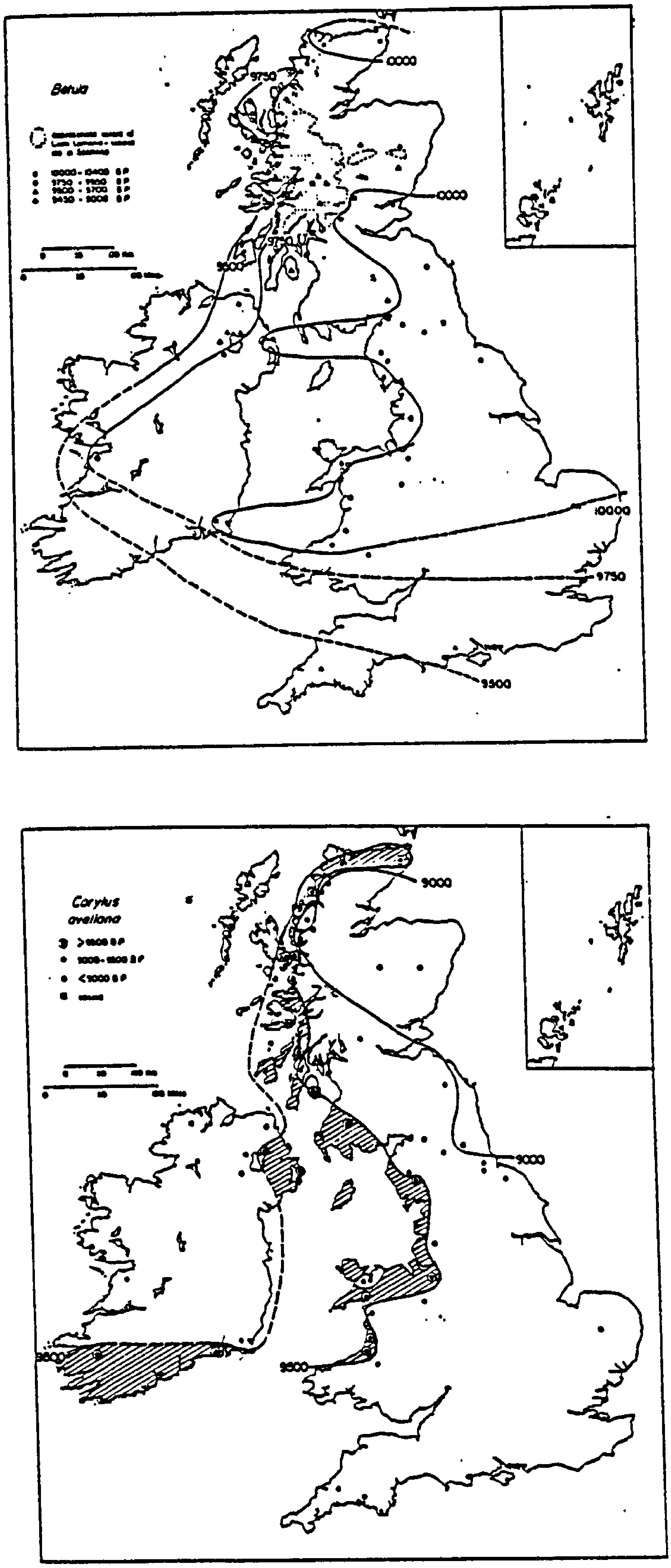


Figure 9a. Isopol maps showing patterns of tree presence and spreading in Britain : **Betula - Corylus.**
(Source Birks 1989)

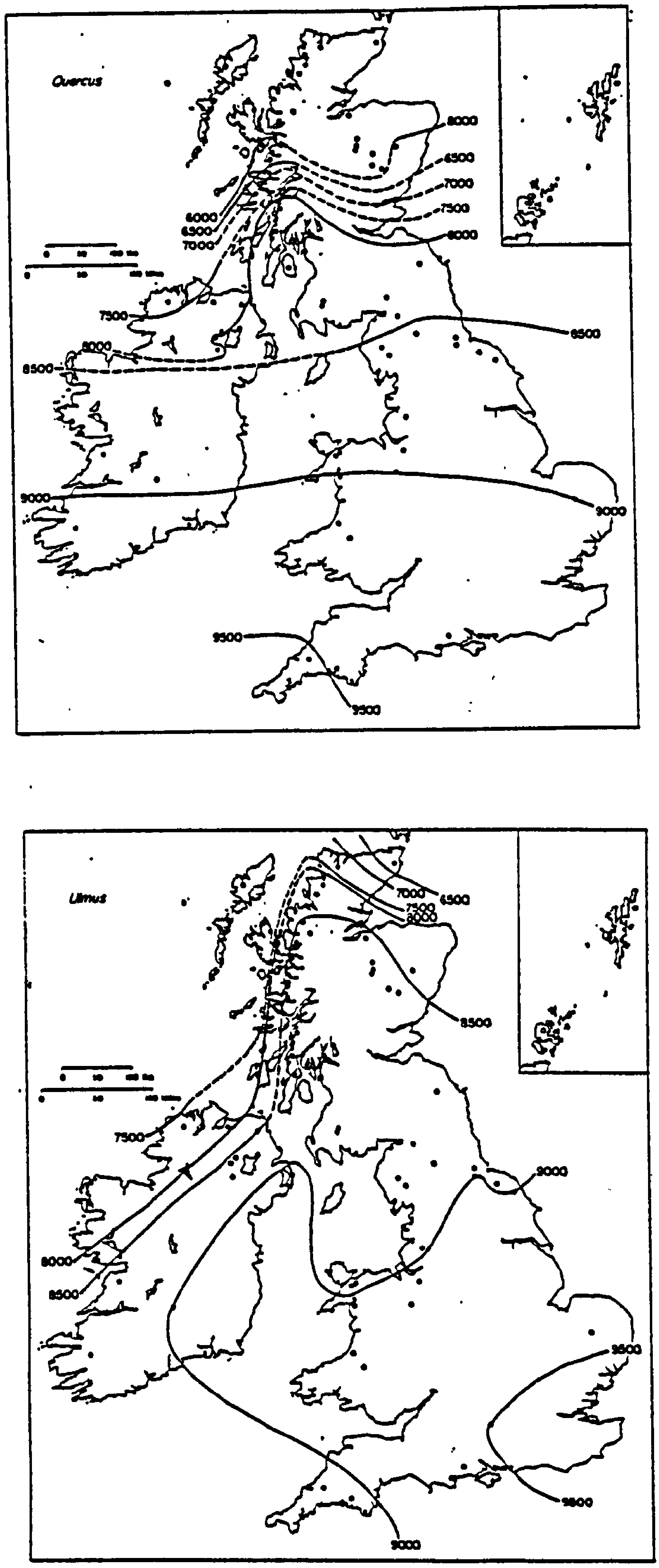


Figure 9b. Isopol maps showing patterns of tree presence and spreading in Britain : **Quercus - Ulmus**
(Source Birks 1989)

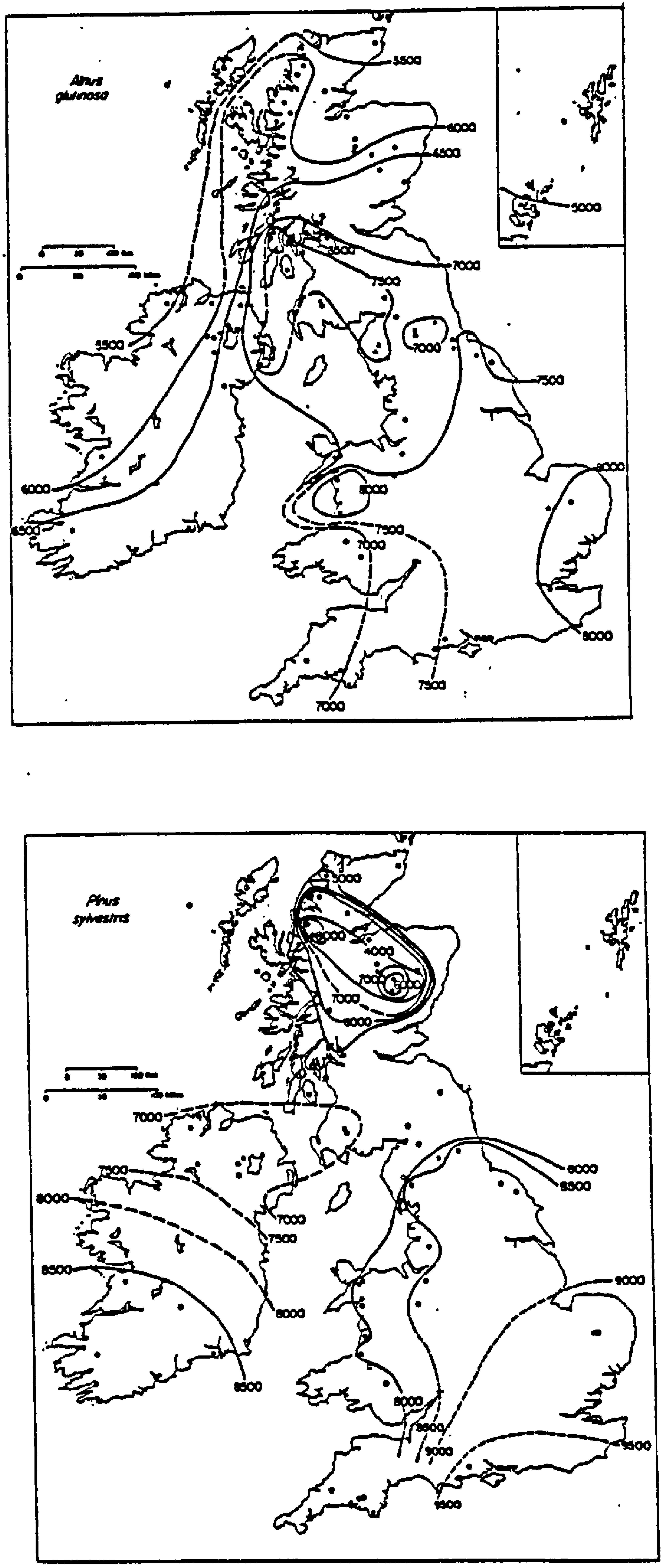


Figure 9c. Isopol maps showing patterns of tree presence and spreading in Britain : **Alnus - Pinus**
(Source Birks 1989)

reached its northern and western range limits in the British Isles.

The history of Quercus in Scotland follows a similar pattern to Ulmus. After a period of rapid spread through the British Isles, Quercus was present in southern Scotland from 8,500 - 8,000 B.P., forming the 'oak with birch' woodland zone of McVean and Ratcliffe (1964). The rate of spread then slowed to 50 m. yr^{-1} reaching its range limit in Northern Scotland by 6,000 B.P.

Pinus sylvestris differs from other woodland species in that an independent, Scottish population of Pinus sylvestris was established in the north west as early as 8,500 - 8,000 B.P. (Birks 1989, Bennett 1984). Biochemical studies of Scots Pine (Kinloch, Westfall and Forrest 1986) further substantiate this theory by providing evidence that the Scottish population is genetically distinct from other European populations. Moore (1987) considers it a possibility that the Caledonian Pine forests did not represent the northwards and eastwards extension of the English Pine population but rather the spread of a distinct, isolated Scottish genotype with origins,

> 'In western refugia, perhaps in the region of the Hebrides' (P.D.Moore 1987 p.545).

Consequently Pinus was able to colonise rapidly in the region before the arrival of Ulmus and Quercus. The isochrone maps show a pattern of Pinus expanding eastwards and northwards until 5,000 B.P. when it was an important element in the 'pine with birch' woodland zone (McVean and Ratcliffe (1962). Just prior to 4,000 B.P. Pinus populations in the west of Scotland declined very rapidly although it remained important in the east.

The important Holocene woodland component Alnus glutinosa arrived in southern Scotland at around 7,500 B.P. (Birks 1989) and had spread to the far north possibly as far as Orkney by 5,300

B.P.(Keatinge and Dickson, 1979). Birks (1989) cites cool winds which inhibited fruiting as a major limiting factor which slowed the spread of *Alnus* in the north of Scotland.

The isochrone maps show that during the early and mid Holocene woodland composition in Scotland was varying at a regional scale of analysis. If, however one examines the pollen analytical data from any one of the Scottish regions it is possible to discern patterns of local variability which are masked by the broad scale of spatial and temporal resolution employed in the published isopol and isochrone maps.

This review shows that the vegetation history of the Scottish islands has been researched extensively. A synthesis of the available pollen data shows a degree of variability which indicates differentiation of the vegetation following the regional zones of McVean and Ratcliffe (1962) with the islands falling within the 'predominant oak forest with birch and 'predominant birch forest' zones. There is however a considerable degree of 'inter-island' and 'on-island' variation within this general pattern. 'Inter-island' variation primarily splits the islands into two main groups, those which supported some canopy woodland in the Holocene and those that did not. 'Within-island' variation reflects local topographic and pedological characteristics which affect woodland development on any one island.

Skye is perhaps the most intensively researched of all the Scottish islands. There are two in depth studies of late-glacial environmental history (Birks 1973 & Walker *et al*.1988) and several other related studies of Holocene vegetation history, (Vasari & Vasari 1968, Birks 1970, 1973, 1977, Williams 1977, Birks & Williams 1983). These records indicate that vegetation history on the island of Skye differs from the predicted pattern in that there is little evidence of *Quercus* dominant woodland at Loch Moedal in southern Skye and that woods on eastern Skye had affinities with the pine-birch woods of Wester Ross.

In a review of Late-glacial and Holocene vegetation history on Skye, Birks and Williams (1983) divided the island into six major geological and topographic regions and investigated Late-glacial pollen records in four of the regions;

(1) at Loch Fada, northern Skye on the Tertiary Basalt bedrock.
(2) Lochan Coir'a'Ghobhainn in the "gabbro lowlands" in the Cullin Hills.
(3) Loch Cill Chriosd on the granite / limestone boundary near Kylekin.
(4) Loch Moedal on the acid Lewisian gneiss, Torridonian sandstones and Moine schists of the Sleat Peninsula.

Essentially these studies showed that the earliest flora of the region was diverse and reflected the impact of local geological and hence pedological controls. Some recent debate over the Late-glacial age of these sequences has been raised by Walker _et_ _al_. (1988) which they now assign to the early Holocene. However the Birks study shows that the only area initially supporting scrub woodland was in the sheltered south-east at Loch Moedal.

The Holocene record described by Birks and Williams (1983) provided a detailed reconstruction of vegetation history from the east coast of the island, discussing the sites at Loch Cleat, Loch Cuithir and Loch Fada which are located in the Tertiary basalt region in the north, Loch Ashik in the Tertiary sandstone region near Kyleakin, south eastern Skye, and Loch Moedal in the Lewisian lithologies of the Sleat peninsula. This record is summarised briefly below:

Loch Cleat :

10000-8900 B.P.	_Juniperus_, _Salix_, _Betula_ scrub with tall herb communities and ferns.
8900 B.P.	_Betula_, _Salix_ scrub with _Sorbus_ _aucuparia_, _Prunus_ _padus_ and species-rich

	grassland and tall herb communities. Low *Ulmus*, *Quercus* and *Pinus* values are recorded.
6300 B.P.	*Alnus glutinosa* rises, but with lower values than in south eastern Skye.
5000 - 700 B.P.	Expansion of Gramineae, *Potentilla*, Chenopodiaceae, Cruciferae, Cereal-type, *Plantago lanceolata*, and *Trifolium*, with decreased arboreal representation indicating arable and pastoral agriculture.
700 B.P	Clearance of remaining woodland and contemporary vegetation becoming established.
Loch Moedal, Sleat :	
9700 B.P.	*Betula*, *Corylus* woods with *Salix*, *Populus tremula* and *Viburnum*.
9000 B.P.	*Quercus* and *Ulmus* were present in low frequencies.
6500 B.P.	*Alnus glutinosa* expanded, some *Fraxinus*, *Sorbus aucuparia*, *Prunus padus*, *Hedera helix* and *Ilex aquifolium* were present, *Salix* declined.
5200 B.P.	Woodland clearance phase began, grassland and heath increase.
2700 B.P.	Little change recorded until 300 BP.
300 B.P.	Widespread forest clearance and spread of *Calluna* and grassland vegetation.

Loch Ashik:

9600 B.P.	*Juniperus* scrub with tall herb communities, grassland and *Betula*, *Corylus* scrub with *Salix*, *Prunus padus* and *Sorbus aucuparia*.
9000 B.P.	*Ulmus* and *Quercus* present in small amounts, *Calluna vulgaris* heath and bog increase.
6300 B.P.	*Alnus glutinosa* rises.
4600 B.P.	*Pinus sylvestris* rises.
3900 B.P.	*Pinus sylvestris* declines.
2700 B.P.	Widespread bog and heath vegetation.

These palynological data show that Skye was an essentially wooded island and suggests that the modern vegetation is largely the result of anthropogenic activity in clearing woodland for agriculture, which began as early as 5000 B.P in Sleat and Trottenish.

In contrast to the local diversity of Holocene woodland on Skye, the pollen record from Mull (Walker and Lowe 1982, 1985, 1987, Walker, Gray and Lowe 1985, Lowe and Walker 1986), indicates a much more uniform pattern of vegetation cover in the Holocene. The geology of Mull is less diverse than Skye and the island is within the 'predominantly oak with birch' zone. The general pattern of vegetation succession was broadly similar at all the sites studied. However there is some indication of 'within-island' variation in that woodland was less abundant and diverse at exposed sites such as Beinn Reudle where very low arboreal pollen counts were recorded (Lowe and Walker 1986). The low arboreal pollen counts at Beinn Reudle are significant as they provide evidence that the pollen record on the islands is representative of the local vegetation and not just reflecting pollen input from the forested mainland.

The site considered by Walker and Lowe (1987) as having the longest and most representative record is at Gribun where the sequence dates back to the Loch Lomond Stadial. Before 10,200 B.P. arctic alpine communities occurred with Artemisia, Rumex, species of Caryophyllaceae, Chenopodiaceae, Compositae, Gramineae and Cyperaceae. This period was followed by the establishment of Empetrum and Juniperus communis dominated communities in the early Holocene with Betula slowly expanding from 9,500 B.P. From 9,000-8,000 B.P., Corylus became established and between 8,000-6,200 B.P. mixed deciduous woodland developed with Betula, Corylus avellana, Quercus, Ulmus and Pinus was locally abundant in sheltered locations. The pattern of vegetation development during this period on Mull indicates that woodland was less extensive on the exposed northern and western coast and Ross of Mull (Walker and Lowe 1987).

The period 6,200 - 4,000 B.P. on Mull is characterised by gradually diminishing arboreal pollen values for all woodland species with the exception of Alnus glutinosa. This decline in tree pollen representation accelerates from 4,000 B.P. to the present and is accompanied by a corresponding increase in pollen representation of acid grasslands, heaths and ombrogenous blanket bog.

In an incomplete Holocene pollen sequence from Kinloch, Rhum, an island now largely devoid of native woodland, Hirons and Edwards (1990), found evidence of Corylus and Salix scrub from 7,800 B.P. Alnus then expanded from c.6,430 B.P. to form the major woodland vegetation with Salix and Corylus until 4,000 B.P. after which time woodland was reduced and evidence for agriculture and peat expansion is discernible in the pollen record. Hirons and Edwards (1990) considered Rhum to have been as well-wooded as areas of Skye and Mull that supported woodland in the Holocene but Betula, Ulmus, Quercus and Pinus were thought not to have occurred locally. This diagram shows that the woodland vegetation of Rhum was broadly similar to that found on the more exposed sites on the larger islands of Skye and Mull but had a distinctive lack of *Betula* and locally abundant *Alnus glutinosa* at Kinloch in the mid Holocene.

The vegetation record from Arran (Robinson 1983, MacIntosh, 1986, Boyd and Dickson, 1987, Boyd and Dickson 1988, Afleck, Edwards and Clarke 1989) indicates that this island was previously wooded. At Machrie Moor (Robinson and Dickson 1988) the Late-glacial tall herb, sedge and grassland vegetation is succeeded in the early Holocene (*c*.10,000 B.P.) by *Juniperus* and *Empetrum* heath. *Betula* woodland then expands between about 9,600 - 8,865 B.P. and is invaded by the spread of *Corylus* at *c*.8,665 B.P. The diversification of the woodland is recorded by the establishment of firstly *Quercus* and *Ulmus* at *c*.7,825 B.P. and later *Sorbus* and *Fraxinus*. *Calluna vulgaris* and charcoal are first recorded at 8,665 B.P., indicating the onset of acid heathland which Robinson and Dickson (1988) interpret as a possible indication of the impact of Mesolithic populations on the vegetation and soils of Arran. The Mesolithic pitchstone and flint site at Auchareoch confirms the presence of Mesolithic people on Arran at this time, and Edwards (in Affleck *et al*. 1988) found evidence of pre-peat clearance and agricultural impacts during the Mesolithic. Small scale woodland clearance is also associated with subsequent peaks in *Plantago lanceolata*, *Pteridium aquilinum* and *Calluna vulgaris*. The regional expansion of *Alnus* is dated at about 6,630 B.P. and the intensification of agricultural land use during the early Neolithic period is associated with another phase of forest clearance at *c*.5,750 B.P. and pre-elm decline cereal pollen at *c*.5,375 B.P. At about 4,310 B.P. there is a change in the pollen spectra as woodland temporarily regenerated and there was possibly a reduction in agricultural activity during the late Neolithic period. At approximately 3,950 B.P. woodland decline accelerates once more, *Plantago lanceolata* attains some very high values together with *Hordeum* type pollen at *c*.3,000 - 2750 B.P. In subzone MM-6c at Machrie Moor *Cannabis* / *Humulus* type pollen occurs. Human impact on the landscape was thought to be reduced during the later Bronze Age and early Iron Age. During this period Calluna heath expanded as soils acidified and deteriorated. Renewed agricultural activity associated with the Viking and early medieval period continued to reduce woodland to contemporary levels.

Pollen analytical data from Oronsay and Colonsay (Andrews et al. 1987) indicate that Betula / Corylus woodland with some Ulmus and Salix was present on these islands by about 9,700 B.P. and that woodland containing Quercus, Ulmus, Alnus and Salix was more widespread in south east Colonsay between 6200 and 4,000 B.P., placing these islands in the Quercus / Betula ecotype. Agricultural impact on the vegetation is in evidence from c.4,000 B.P. with woodland clearance and an expansion in species rich grassland indicated in the pollen record. Andrews et al.(1987) associate the presence of Papaver and Calystegia type pollen between 3,500 - 2,600 B.P. with arable fields near Loch Cholla, Colonsay. These dates correlate well with the period of inferred early Bronze Age activity at Machrie Moor, Arran described by Robinson and Dickson (1988) as does the subsequent regeneration of woodland in zone LCv (2,600-1,500 B.P.) at Loch Cholla and MM-6c at Machrie Moor.

The pollen records from other smaller islands in the Inner Hebrides, for example Canna (Flenley and Pearson 1967), seem to indicate that closed woodland was unable to establish itself successfully on some islands during the Holocene. The pollen record from Tiree is limited to a sequence of samples from Dun Mor Vaul, an Iron Age broch (Pilcher 1974), and consequently provides no information on the status of early-mid Holocene woodland. AP/NAP ratios are low indicating an open, non-wooded landscape around the site. Analysis of charcoal from archaeological contexts revealed the remains of Alnus, Corylus, Salix, Quercus and Picea. The origin of Picea in the assemblage was thought to be from driftwood but the other species may have been locally derived. Plantago lanceolata, Artemisia and Cereal type pollen were recorded in high frequencies in floor deposits leading Pilcher (1974) to speculate that there were possibly two phases of agricultural activity which preceded a major cultivation phase which declined in intensity during the secondary occupation of the site in the late Iron age.

The vegetation record from the northern islands of Orkney and Shetland is similar to that found on the smaller less wooded Inner Hebridean islands where birch-hazel woodland was locally present, but these northern islands appear to have been outside the range limits of other deciduous tree species. There has been some debate over the provenance of arboreal-pollen types found in the sedimentary record in Shetland. At Muraster, Shetland, Johansen (1975) concluded that Betula and Corylus woodland reached a maximum, but limited extent in the early Holocene. The low values for other arboreal-pollen types, such as Pinus, Quercus, Ulmus and Alnus were thought to be of 'off island provenance'. Johansen states,

> ' From the Alnus curve it is quiet clear that this tree did not grow in Shetland in post-glacial times' (Johansen 1975 p.381).

However more recent palynological studies, particularly at Scourd of Brewster (Keith-Lucas 1986), provide some indication that the Shetland pollen record exhibits a degree of local variability (similar to that found in the Outer Hebrides). Total pollen frequencies for Betula and Corylus at Scourd of Brewster in Subzone SBS-2b Betula-Corylus, radiocarbon - dated to between c.6,000-4,680 B.P., consistently exceed 20% tlp (total land pollen), higher than those recorded by Johansen (1975) at Murraster. These findings are further substantiated by macrofossil evidence for past woodland on Shetland;

> '....In contrast to the scarcity of living trees and shrubs the remains of branches, trunks and root systems are widespread in the peat of both upland areas and valley basins. In upland areas the

wood consists of remains restricted to a single 10 - 20 cms. basal layer underlying true blanket peat' (Birnie 1984 pp.156).

Keith-Lucas (1986) also suggests that the status of Alnus may not be so clear cut as Johansen thought due to the higher frequencies of Alnus pollen recorded at Scourd of Brewster. Lewis (1911) described Alnus wood remains and Alnus catkin-scales from within peat which he used to illustrate the presence of the species on Shetland. Birnie (1984) also suggests that the radiocarbon dating of wood remains from Shetland has provided a time span for known woodland from approximately 7,870 to 4,586 B.P. (Hoppe 1965,1974). The maximum pollen frequencies for woodland species occur between two regionally recognisable pollen biostratigraphic horizons, those of the 'elm decline' at c.5,000 B.P. and the Alder rise which occurs after 7,800 B.P., leading Birnie (1984) to suggest that the duration of tree and shrub growth extended between the two dates, approximately 1,450 years later than on the Scottish mainland. However the evidence for such time lags is uncertain. For example the Betula rise on Shetland has been dated to c.7,800 B.P. (Birnie 1984), but Bennett (unpublished B.E.S. Conference Paper 1990) provides a date of 9,400 B.P. for the Betula rise at Dallican Water, Shetland.

At Scourd of Brewster a multi-phase Neolithic-Bronze Age occupation site on Shetland, the combined pollen analytical data from the site and an adjacent lake basin reveals a history of vegetation around the site during the occupation period (Keith - Lucas 1986). An initial phase of woodland decline with corresponding increase in Gramineae and herbaceous taxa representative of the first phase of early Neolithic settlement c. 4,680 B.P. to 4,180 B.P. was followed by a regeneration of woodland and increased representation of herbaceous pollen, which is interpreted by Keith-Lucas as a response to a decrease in agricultural activity to a reduced level of intensity. A second phase of increased land use pressure is indicated by a subsequent reduction in woodland and an increase in grassland and arable indicator species to levels greater than in the first clearance phase. Calluna vulgaris also increased at this time indicating the acidification of soils around the site which may have resulted in the clearance of more land for cultivation or pasture, possibly as a result of a climatic change as Holocene sea levels rose, perhaps affecting local weather conditions, soil drainage and pedogenic processes.

The Holocene palynological record from Orkney includes long stratigraphic sequences from the Loons and Yesanby (Moar 1969) and at Glims Moss and Loch Skaill, Mainland, Orkney (Keatinge and Dickson 1979). This record has been augmented by further pollen analytical studies from archaeologically-related sites (Godwin 1956, Caseldine and Whittington 1976, Davidson, Jones and Renfrew 1979, Jones 1979,) and is reviewed in Davidson and Jones (1985). Wood remains within peat were demonstrated by Traill (1868).The pollen data shows a typical Post-Glacial succession for the region with Late-glacial open grassland and heaths giving way at the onset of the Holocene to Empetrum / Juniperus heath then Betula and Salix scrub.

The Corylus rise is recorded at all the sites. The low pollen representations of Ulmus, Quercus and Pinus are thought to be of 'off-island' provenances. The local Betula / Corylus woodland declined at 4,700 B.P. (see PAZ GM-2, Glimms Moss, LS-2a, Loch Skaill (Keatinge and Dickson 1979) and PAZ F- IV, Yesanby and The Loons (Moar 1969)) as species-rich grassland became more widespread. The tall-herb and fern communities of the woodland understory decline possibly as a result of grazing. The possibility that settlement by Neolithic people may have been instrumental to some degree in this vegetation change is considered probable, given the archaeological evidence of significant Neolithic settlement on Orkney. Davidson and Jones (1985) also cite molluscan evidence from Skara Brae, just south of Moar's (1965) Yesanby site, where woodland indicator land snail species Carychium and Discus are replaced by Vallonia excentrica and Pupilla muscorum, open habitat species in contexts contemporaneous with the first Neolithic occupation.

Intensification of clearance is indicated during the later Neolithic Period when the remaining scrub woodland was cleared and the pattern of contemporary vegetation was established. Archaeo-environmental analyses from a number of settlement and funerary sites provide some interesting evidence for the pastoral element in farming practise which is corroborated by the pollen record. Pollen analysis of the soil/peat interface at Mid-Hill and Braes of Aglath (Keatinge and Dickson 1979) shows a decline in Betula, Coryloid, Polypodium and Filicales and an increase in Gramineae, tall herb and grassland indicators which are replaced by a short phase of species rich grassland with Plantago lanceolata which itself preceeded peat development which began at c.3,400-3,000 B.P. There are few archaeological remains representing the period during which peat initiation began, between the end of the Neolithic and mid-Bronze Age. Increasing pressure from the "deteriorating" climate and continuing land use pressure may have led to the final demise of Orcadian woodland from the Iron Age to the present day.

Synthesis

The palynological record from the Scottish islands is difficult to synthesise because of the richness of studies from some of the islands such as Orkney, Skye and Arran which contrasts with the limited data available from others, especially in the Outer Hebrides. However despite these limitations a number of patterns emerge. Principally the data shows that few if any of the islands were outside the range limits of some species such as Betula and Corylus, which were widespread if not always abundant in the region during the early to mid-Holocene. Betula is seen to decline in all the palynological records from the area after the arrival of Corylus; Quercus and Alnus remain locally important however particularly in marginal localities and in the Northern Isles often in a Betula-Corylus association. Arboreal pollen frequencies are lower in the north and west of the region and in exposed locations on the littoral fringes of the Inner Hebrides and Outer Hebrides. The initial spread of closed canopy woodland appears to have been restricted by factors such as altitude and exposure (Boyd and Dickson, 1986). Deep sea channels may have delayed or slowed the rapid mainland spread of some taxa but do not appear to have prevented migration. For example the rational limit for Corylus occurs some 400-800 years later on Arran than on the Scottish mainland (Boyd and Dickson 1986).

In some areas competitive interaction may have affected the persistence of other species, for example Pinus sylvestris which was well established in north west Scotland and the Scottish highlands between 8-7,000 B.P. but was in decline by approximatly 4,000 B.P. It was never a major component of Hebridean island vegetation and appears to have failed to compete successfully with invading deciduous species such as Betula, Corylus and Quercus in the mainland forests.

The extent of early/mid Holocene woodland in the region (which contrasts with the almost treeless landscapes of the present) is thought to represent vegetation response to the rapid climatic warming which followed the Loch Lomond Stadial (Coope 1977).

Birks (1987) proposed that tree and scrub development was possible on these islands as a result of lower gale frequencies and more equitable climate in the early Holocene. Lamb's (1966) post-glacial atmospheric circulation model supports this theory, by suggesting that gale frequencies were low after 8,500 B.P. as a result of weaker circulation in the North Atlantic as temperature contrasts between North America and Scandinavia lessened. Huntley and Prentice (1988) modelled summer temperatures at 6,000 B.P. and proposed warmer (+2°C) July temperatures in the British Isles. A study of the contemporary and fossil shell-form of Nucella lapillus (the Dog Whelk) from Oronsay, also provides independent evidence of reduced storm frequencies in the Inner Hebrides during this period (Andrews _et al_. 1987).

After _c_.4,000 B.P. natural woodland decline occurred and could have been precipitated by a sudden and widespread change to a more oceanic climate on the Atlantic fringes of north west Europe which could have brought to the islands increased precipitation causing soil degeneration, waterlogging and blanket peat development, all creating an inhospitable environment for tree growth. A brief period of _Pinus_ expansion such as that recorded at Loch Ashik on south-eastern Skye between 4,600 to 3,900 B.P., has been construed as evidence of _Pinus_ expanding onto dried peat surfaces (see H.H.Birks 1975, Birks and Williams 1983) prior to its decline in the region. This decline, which is coincident with an increase in blanket peat vegetation, is thought to represent vegetational response to an increasingly oceanic climate at this time (Bennett 1984).

Forest clearance has similar effects to this type of inferred climatic shift. Evapotranspiration decreases, soil nutrient depletion acceleration and waterlogging occur on poorly drained sites as a result of increased run off. This encourages the development of blanket bog (Moore 1975). The archaeological record from the islands shows evidence of human settlement from _c_.8,500 B.P. and there is increasing evidence that human activity has been partially responsible for fluctuations in woodland populations and species-rich grassland dating from this period. Later phases of agricultural activity in which woodland was cleared seem to have stronger links with the spread of bog and acid heath vegetation particularly after 4,000 B.P.

Inferring human impact as a cause of vegetation change is fraught with difficulties, especially in open landscapes such as those found in the Scottish islands. Often the choice of study site has not helped this type of research. Many palynological studies have focused on forest history and have favoured pollen sampling sites with undisturbed sedimentary sequences remote from archaeological sites, for example on Skye (Birks and Williams 1983) and Mull, Walker and Lowe (1985,1987).

Several palynological studies from sites more closely associated with human settlement have provided some interesting detail for an anthropogenically orientated study programme (Davidson et al. 1976, Andrews et al.1987, Hirons and Edwards 1990, Keith-Lucas 1986, Bohnke 1988, Affleck et al. 1988). Human impact has been recognised in the pollen record to a greater or lesser degree in these studies, typically associated with the decline of some species and the spread of others. The relationship between human settlement, woodland development and peat formation is a complex issue as it takes place in the context of varying species dispersal rates, directions of spread (Birks 1989), climatic fluctuations and sea level rise in the Holocene, making any single causal explanation of change difficult to test. This has encouraged workers to interpret vegetation change as the result of multi-causal effects. For example, Robinson and Dickson (1988) suggested that woodland and early settlement on Arran were concentrated in sheltered locations and the combined influence of exposure and the continued stress of human occupation limited forest development and led to soil acidification and peat formation:

> 'The combination of high settlement pressure from very early times with the inherent ecological sensitivity of the island would explain why the forest canopy never fully developed and why later agriculture had the impact on the vegetation which is so clearly evident in the pollen diagrams' (Robinson and Dickson 1988 p.235).

A series of regional biostratigraphic features have been identified by palynologists which are thought to have significance in relation to human impact on forest development, either through deliberate clearance and burning, (the Scottish evidence is reviewed in Edwards 1990), or through human activity acting as a dispersal mechanism (Boyd and Dickson 1986). For example the early Holocene Corylus rise has been associated with forest clearance and burning which could have facilitated the spread of Corylus in the absence of other competitors and because it was thought to be resistant to forest fires (Smith 1970). This hypothesis was based on the fire resistance of Corylus cornuta, an American species of Corylus. This hypothesis is now thought to be untenable (Andrews et al. 1987, Huntley and Birks 1983, Birks 1987 and Rackham 1980,1986), whose views are summarised in the quote from Rackham 1986:

> 'British woodlands (except Pine) burn like wet asbestos' (Rackham (1986 p.72).

There is no reason to suppose that the early settlers of Scottish islands were fire-adapted or were so profligate with their critical resources that they cleared woodland by burning. It seems more plausible that in such sparsely-wooded island environments trees were felled and the timber used for domestic fires and construction.

In a study of charcoal remains and pollen from a variety of sites in Scotland, Edwards (1990) found no causal relationship between charcoal frequencies and the Corylus rise. However in a study of Corylus spread in western Scotland, Boyd and Dickson (1986) suggested that mesolithic people gathering and travelling with stores of hazel nuts may have assisted the regional spread of Corylus particularly onto the islands of Mull and Arran. Birks (1989 p.75) however states that;

> ' hazel luxuriated as a result of the absence of dense shade from well grown trees such as oak, elm or lime even on the most fertile soils'.

Similarly the Alnus rise has been associated with clearance and burning which was thought to favour the spread of Alnus (Smith 1970, 1984, McVean 1956, Chambers and Elliott 1989, Hirons and Edwards 1990, Edwards 1990). Clearance of woodland and reduced competition could have allowed Alnus to expand into uncultivated areas. The relationship between Alnus abundance and anthropogenic activity is demonstrated by high charcoal concentrations associated with fluctuations in the Alnus pollen curve at Kinloch, Rhum (Hirons and Edwards 1990, Edwards 1990). Alnus was reduced at about 5,950 -5,700 B.P. - a clearance phase of c.250 years after which Alnus then regenerated briefly prior to its' final decline.

Alternative hypotheses (Godwin 1940,1975) suggest that climatic wetness favoured the spread of Alnus. Smith (1984) however argues against a climatic cause because radio-carbon dating has shown the rise to be time transgressive i.e. between 7,500 - c.5,000 B.P. However such a generalised increase in surface wetness could not produce the same type of effect everywhere, simultaneously, on such a diverse set of islands as occur off western Scotland.

Perhaps the most widely discussed palynological biostratigraphic marker is that of the decline in Ulmus at c.5,100 B.P. which occured across at large area of north-western Europe (Huntley and Birks 1983). Anthropogenic causes for the Elm decline are much discussed (e.g. Edwards 1987, 1991). The appearance of Plantago lanceolata and Cerealia type pollen at and around the decline were thought to signify the transition to agriculture from the 'ecocentric Mesolithic' to the 'agrocentric culture' of the Neolithic as elm was putatively, selectively cleared for arable cultivation or lopped to provide elm leaf-fodder for domestic animals. Such a widespread synchronous event would require a large population to achieve such a result (Huntley and Birks 1983) and as Edwards (1988) points out;

> ' ...it is difficult to imagine people everywhere in Europe doing the same thing for the first time at the same time'.

Alternative explanations for the phenomenon include soil deterioration, climatic change and disease analogous to the present elm decline, a theory which has been given some credence by the dicovery by Girling and Greig (1985) of Scolytus scolytus F. a vector of the dutch elm fungus Ophiostoma ulmi (Buis.) Moreau.

Recent palynological studies from Scotland (Edwards 1991) and western Ireland (Molloy and O'Connell 1987, O'Connell 1987, O'Connell et al. 1987) show pollen sequences with multiple decline and regeneration phases in Ulmus records which led Edwards (1991 p.86) to suggest that;

> 'multi-causal explanations for the decline in Ulmus in prehistoric times need to be further explored'.

In terms of the present study, the elm decline is recorded in most of the palynological records from the area, reflecting either decline in local Ulmus populations, for example on Mull and Skye (Birks and Williams 1983, Walker and Lowe 1986,1987), or mirroring the decline in the reduction of Ulmus pollen of long distance provenance as in Shetland and Orkney (Birnie 1984, Keating and Dickson 1979). There appears to be no 'proven' causal relationship between the spread of Neolithic culture and the regional decline of Ulmus.

Studies of contemporary pollen taphonomy which attempt to define plant species associated with particular agricultural practices, provide the basis for interpreting similar activities in the fossil pollen record. Hicks (1989) for example has developed a model which utilises contemporary pollen spectra and historical records to provide a provisional key for distinguishing different agricultural practices in the northern boreal forest zone.

In pollen studies from the Scottish islands reference is made to the occurrence of anthropogenic indicator species and peaks in the pollen or spore representation of Pteridium aquilinum, Urtica, Papaver, Calystegia, Artemisia, Cannabis / Humulus type, Cereal type and particularly Plantago lanceolata pollen which are strongly (but not invariably) associated with human presence. Plantago lanceolata pollen and its expansion following woodland clearance is strongly correlated with the expansion of species-rich grassland for grazing and as a weed of cultivation. It has gained prominence as a useful potential anthropogenic indicator in Scottish island studies because of its association between its expansion on Shetland and cultural change in the Neolithic period. Sporadic grains of Plantago lanceolata at Murraster, Shetland preceeding the onset of a continuous pollen curve were assigned by Johansen (1975) to possible long distance provenance. However Keith-Lucas (1986) suggests that they may be derived from coastal species-rich turf growing on Shetland prior to clearance which expanded with the arrival of Neolithic culture and pastoral and arable agriculture denoted otherwise by a continuous pollen curve. Plantago lanceolata also occurs in numerous types of temporary habitats produced by natural erosion and soil instability in mountains and coastal areas as well as natural openings in woodland. Obviously interpretation of 'so-called' cultivation indicators is problematic in the Scottish island context. Anthropogenic causes for increased pollen representation of ruderal species may have some credence in wooded landscapes in lowland Britain, but may not be so appropriate in the Scottish island context. Hirons and Edwards (1990 p.719) caution;

> 'The stress of proximity to marine conditions or exposure to climatic extremes, both physiographic norms over large proportions of the Hebridean islands, can provide ready niches for apophytic taxa. Thus changes of maritime influences such as sea level fluctuations, exposure or anthropogenic activity may all have similar expression in pollen diagrams'

In brief, it can be seen from the preceeding review of the palynological record from the Scottish islands that the interpretation of vegetational history in the area is full of challenges. A number of important theoretical issues are raised which are of direct relevance to the present study of the Outer

Hebrides. Most important are issues of scales and causes of variation and change depicted in the pollen record, coupled with the problems of identifying and interpreting the diverse impacts of climatic change and human settlement through time.

Chapter 3.

Research Design.

Research design

This chapter outlines the research strategy and aims and objectives of the study. The theoretical and methodological approaches which underpin the research design are discussed and are followed by more detailed discussion of the research aims and objectives of the individual aspects of the research strategy.

In a recent review of palaeocological studies of past cultural landscapes, H.J.B Birks (1987) emphasises the value of multi-disciplinary approaches to landscape reconstruction;

> ' there is more to the study of past cultural landscapes than reconstruction, description and chronology of changing patterns, just as there is more to present day landscape ecology than description, classification, and monitoring of patterns. There is the interpretation of observed temporal and spatial patterns of human impact on landscape development in terms of underlying ecological and sociological processes. Such interpretations require interdisciplinary studies' (Birks 1987 pp 181).

The great potential of this study is that it provides an opportunity to contribute to the interdisciplinary approaches of the S.E.A.R.C.H. project in the Outer Hebrides. Exciting opportunities exist within such a research framework for the palynologist to participate in archaeological as well as palaeoecological problem solving - and also for the archaeologist to participate in palaeoecological problem solving. An appropriate research strategy could thus address the relationships between people and landscape within a richer theoretical framework, thus avoiding the criticism levelled against environmental archaeologists by Thomas (1990) that they draw,

> 'conclusions about human activity which are naive in the extreme'.

The archaeological context of the present study also has significant influence on the present research design. The reconstruction of past vegetation and ecological conditions provides archaeologists with information concerning the material conditions of existence and survival in the past - information which may be of significance in modelling past human culture. The first requirement however is the temporally and spatially precise 'description, classification and chronology of the changing patterns' of landscape history.

The present study incorporates contributions from ecological and palynological theory to provide a detailed reconstruction of past landscapes in one part of the Outer Hebrides. The principles of methodological uniformitarianism as defined by Gould (1965), Walker (1978), Birks and Gordon (1985) lie at the heart of the research design. Contemporary botanical and environmental investigations which describe modern ecological systems are extended into the past in the assumption that the principles governing these systems have not changed through time. They also provide relatively objective methodologies (for example phytosociology) which can be of use in giving order and meaning to the interpretation of stratigraphic pollen-analytical data. Hence the emphasis in this study on contemporary pollen / plant / environmental relationships.

Research aims and objectives

The review made of currently available literature at the start of this dissertation from published studies of the past and present vegetation of the Outer Hebrides shows a number of important gaps in the present state of knowledge. The studies of Blackburn (1948), Birks and Madsen (1979) and Wilkins (1984) provided a starting point for further palynological work. The important issues arising from these studies can be summarised by a series of problems which can be tested using pollen-analytical methods.

1. That vegetation in the past (notably the tree flora) may have been more diverse / different to that of the present.
2. That the islands may have supported woodland in the past.
3. That the vegetation of the islands was unaffected by human impact before 5000 B.P.
4. That the natural vegetation of the islands has been considerably modified by human impact.
5. That the scales of analysis may be of great significance to the nature and reliability of interpretations that can be made in these particular islands.

In considering a research strategy with which to address such hypothesis testing, a series of important questions arise with reference to the particular geographical and biological character of the Outer Hebridean islands. Information concerning the diversity of the modern flora and its controlling factors within the past and present physical environments are important for an understanding of the present patterns of plant distribution. It is important to fully understand the various roles of environmental and human activities. This type of approach would provide a good starting point for questions concerning past vegetation. For example when was the pattern of contemporary vegetation established? What were the patterns of change and chronology in past plant communities? What does such information tell us about past environments and human activity?

Previous palynological studies in the Hebrides have raised questions concerning both pollen taphonomy and scales of analysis. These highlight a set of problems which relate to the interpretation of pollen analytical data from the area. These issues need to be addressed before further palynological investigations are undertaken. Is it possible to identify the dispersal patterns of contemporary plant communities and use this information to interpret the fossil pollen record?

Many questions also arise concerning Holocene vegetation history (discussed in Chapter 1 this study) such as the migration and colonisation patterns of Holocene woodlands, the onset and growth of peat development and the effects of climatic change, pedogenesis or past human activity on vegetation which have produced the existing pattern of contemporary vegetation. Equally interesting questions concerning Holocene vegetation history in non-wooded landscapes, particularly in identifying anthropogenic effects, also remain under-researched. These are issues which have never been fully addressed and are considered to be not only of local importance but also of wider significance particularly as the regional Holocene vegetation record is often diverse and varied.

These groups of questions are used to define the present research strategy and in combination with the theoretical and methodological issues raised below form the basis of the research design. The objectives of this dissertation focus upon elucidating the historical dimensions of the vegetation in order to better understand its present status. These objectives are;

1. To examine the contemporary vegetation of the islands, related to its environment.
2. To examine patterns of modern pollen deposition and relate this information to pollen taphonomic problems.
3. To examine the vegetation record contained in pollen preserving sediments found in each landscape and geomorphic division on the islands in order to provide a detailed picture of the degree of local variability in the vegetation record, and produce an integrated study of vegetation history at a detailed local level of resolution.
4. To identify periods of vegetation stability and change during the Holocene and discuss these in the light of climatic and anthropogenic impacts during this period.

Important recent developments in the theory and practice of pollen analysis have provided a number of new theoretical and methodological approaches with which to address questions concerning the reconstruction of past vegetation from pollen-analytical data. A paucity of contemporary palynological studies in the Outer Hebrides with reference to these trends has prompted the present study. Those of particular relevance to the research design of this study include:

1. The development of comparative or analogue models based on the use of surface samples from known modern vegetation communities as a tool in interpreting fossil data.
2. Theories of pollen representation resulting from studies of pollen productivity, dispersal and sedimentation which has led to greater awareness of site characteristics and their effect on the spatial and temporal resolution of pollen data (e.g. discussed below).
3. The application of multivariate data-analytical techniques for detecting patterns in pollen data.
4. The move away from the classic regional models of Mitchell (1951),Godwin (1975) and West (1977) towards the establishment of local biostratigraphic frameworks and the evaluation of local variability.
5. The establishment of independent chronostratigraphic frameworks using radiocarbon dating.

Surface pollen sample studies

The assumption that there is a diagnostic relationship between plant communities and pollen spectra underpins the reconstruction of past vegetation and the interpretation from pollen-analytical data of effects such as vegetation response to climatic and environmental change and the effects of human activity. This relationship has been demonstrated by studies of contemporary surface samples and pollen deposition (for example

Janssen 1966, Lichti-Federovich and Ritchie 1968, Birks 1973, Heide and Bradshaw 1982). Prentice (1988) describes pollen analysis as a remote sensing instrument, which shows differential sensitivity to different components of the vegetation dependent on their relative pollen production rates and how well their pollen is dispersed. Prentice (1988) suggests that the approximate temporal and spatial resolution of pollen analysis can be deduced from physical principles and its relative sensitivity can be measured and corrected by calibration against modern vegetation. Vegetation characteristics such as relative abundance, community structure, pollen productivity and dispersal characteristics, together with climatic and ecological factors affecting flowering and dispersal, have been shown to influence pollen representation. Site characteristics such as basin size and local vegetation may distort pollen representation which can be further complicated by post depositional processes of transportation, sedimentation and preservation (see Birks and Birks 1980; Birks and Gordon 1985, Tauber 1965,1967,1977; Davis and Brubacker 1973, Peck 1973, Bonny 1976,1978,1980, Jacobson and Bradshaw 1981, Prentice 1982). The complexity of the variables affecting pollen recruitment to sediments and their influence on pollen representation are at present poorly understood. Interacting factors such as pollen production, dispersal, sedimentation and preservation influence the pollen representation of individual plant species in pollen spectra. Birks and Gordon (1985 pp 142) suggest that;

> " as yet no quantitative explanatory models of pollen production, dispersal, sedimentation, and preservation and hence pollen representation have yet been devised that can assist in the reconstruction of past floras, populations and / or communities from fossil pollen spectra".

As a consequence palynologists have attempted to model plant / pollen relationships by examining modern pollen spectra which characterise vegetation and form a basis for comparative studies. Surface sample studies have shown that patterns in the vegetation are actually reflected in pollen data, for example, contemporary pollen spectra correspond with the known distribution of forest types (Huntley and Birks 1983). This approach is also particularly useful when used to interpret pollen spectra from non-wooded landscapes and in modelling cultivation practices in anthropogenicaly modified landscapes (Behre 1989) - such as those found in the Outer Hebrides.

Site characteristics / sampling strategies.

Surface sample studies have shown that the spatial resolution of pollen-analytical data is also influenced to a high degree by the sampling strategies employed in the selection of sites for analysis. The pollen 'source area' of a sampling site has been shown to change in relation to factors such as the pollen dispersal and production characteristics of vegetation, sediment recruitment processes and basin size. Conventionally preferred pollen sampling sites (lakes and mires of between 1-100 hectares) have been shown to reflect 'regional' vegetation composition i.e. within 20-30km. of the sampling site (see Tauber 1965, Jacobson and Bradshaw 1981, Bradshaw and Webb 1985, Prentice *et al*.1987). Finer levels of spatial resolution can be achieved through the selection of sites which reflect more 'local' vegetation (see figure 10). Edwards (1982) also discusses the relationship between site selection and the detection of anthropogenic impact on vegetation and suggests that

> ' impact on the local woodland edge may not be detected unless profiles are prepared from sites less than 30m from the nearest disturbed woodland'

In the context of the present study which places emphasis on the nature of local vegetation the selection of sites for analysis was determined by factors arising from previous studies in the Hebrides and others which suggest that the fine spatial scale studies required are best achieved from small local sites within a single component of the landscape mosaic (Birks 1989). This

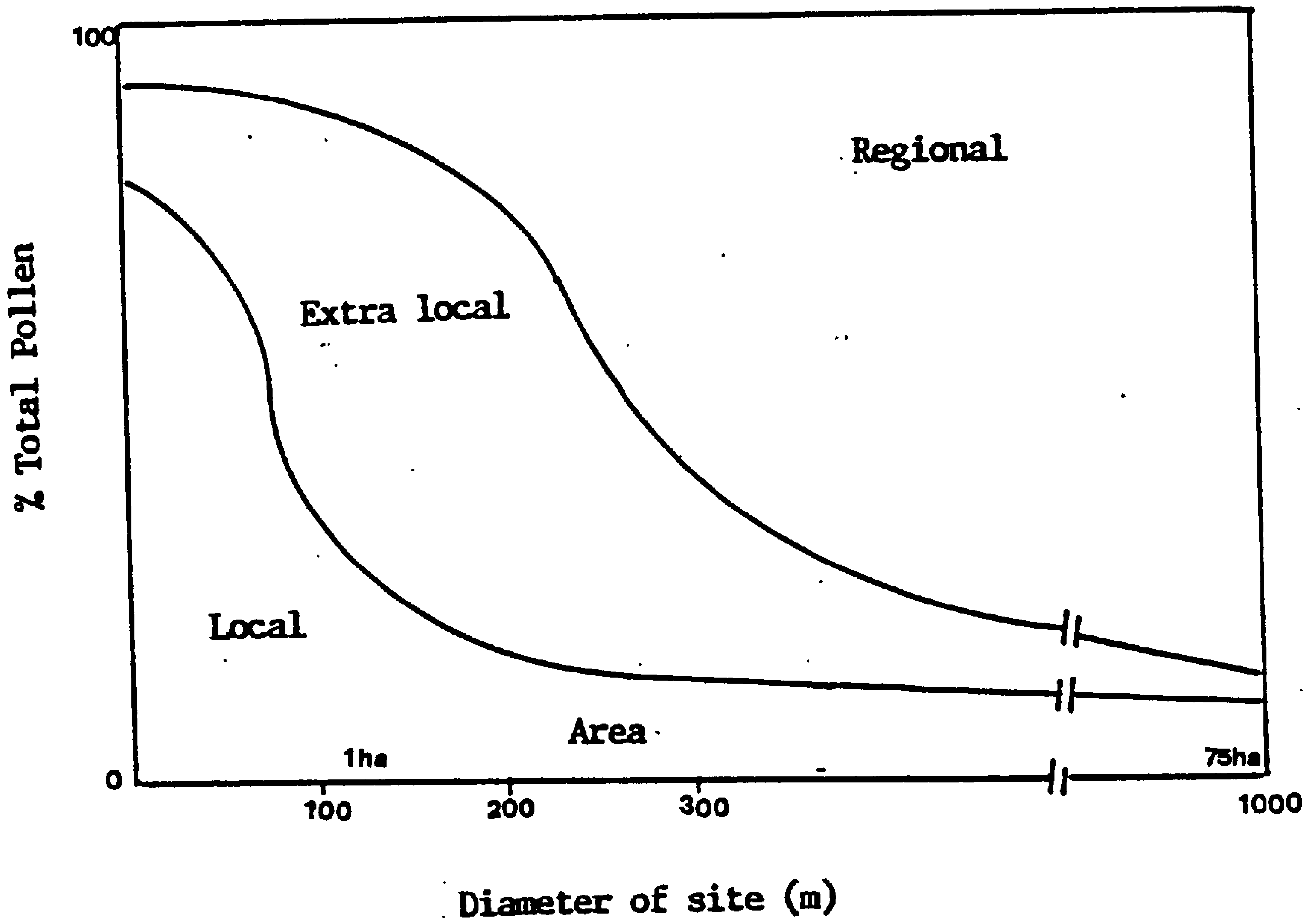


Figure 10. Relationship between the size of a site that has no inflow streams and the relative proportions of pollen originating from different areas around the site.
(Source Bradshaw 1987)

emphasis on local variation in time and space is clearly central to the other sets of issues mentioned above which focus on the role of traditional pollen biostratigraphic models and the importance of independent chronologies - both issues which we addressed more fully later with the benefit of the information found in the present study.

Methodological issues and research strategy

Data analysis.

The application of multivariate data-analytical techniques for detecting patterns in pollen and vegetation data is primarily a device which aids the description of often large and complex data sets, although there is an acknowledgement that the patterns and groupings defined by these techniques are artificial in the sense that vegetation is 'continuously variable in time and space' (Gleason 1927). The use of such techniques also aims to increase objectivity in description. In the present study multivariate data-analytical techniques are applied to floristic vegetation data to define plant communities, to examine the relationships between plant communities and environmental factors such as soils, exposure and topography and to detect patterns (pollen zones) in pollen data. These issues are discussed further in Chapter 4.

The transect

The research objectives outlined above have been approached here with the use of a research strategy based upon a series of carefully chosen east-west aligned survey transects on Barra and South Uist (Figure 11). The east-west orientation is a critical aspect of the study design and is intended to include all major land use and geomorphic divisions observed on the islands which are characterised by their north-south orientation. This particular type of transect study will facilitate a detailed investigation of contemporary vegetation, pedological and environmental variables, pollen deposition and stratigraphy

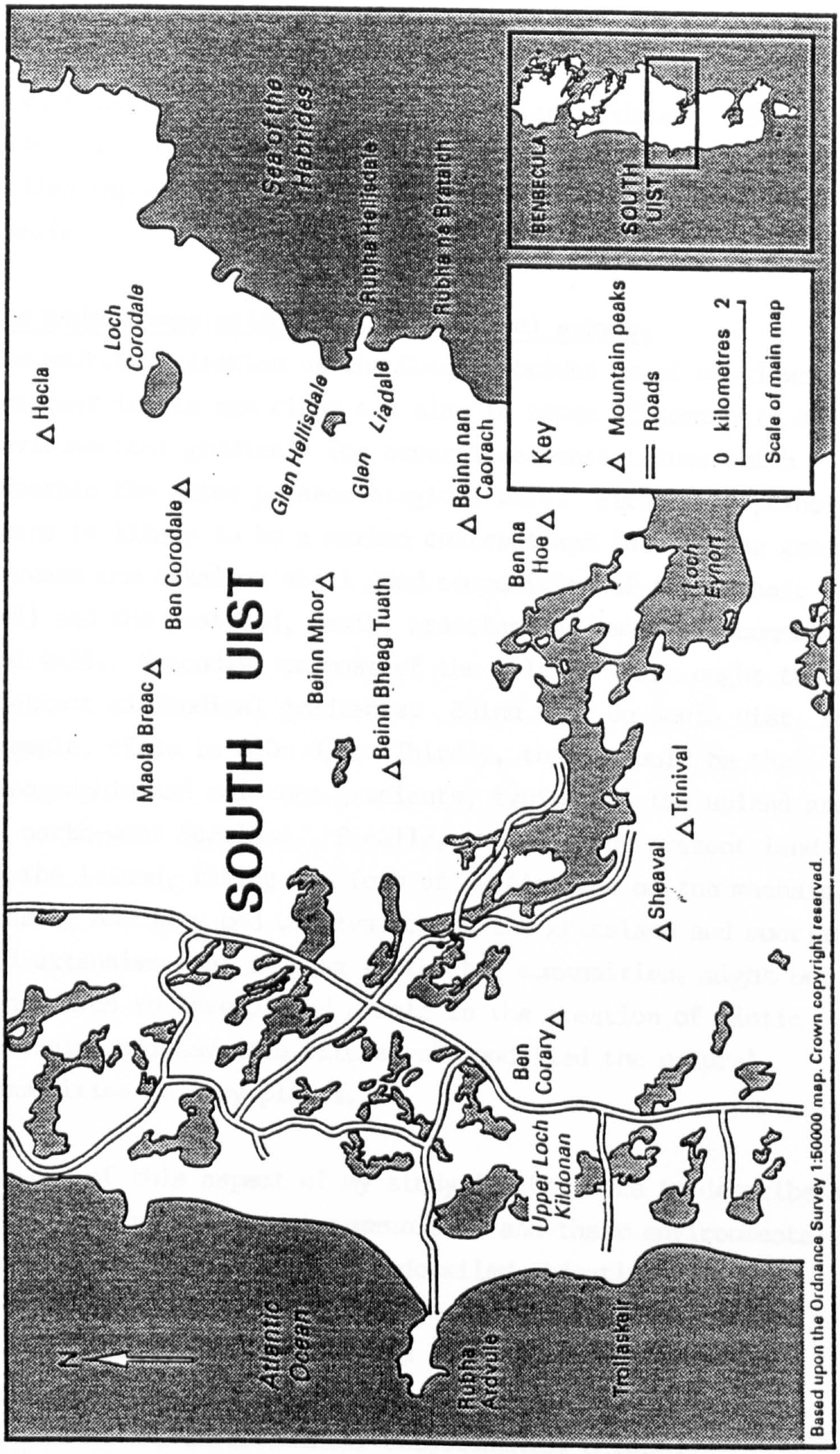


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Figure 11. The South Uist transect.

across the landscape, in this particular landscape. Because of time constraints only the details of the vegetation survey and pollen taphonomy studies from South Uist are included in this thesis.

The modern vegetation and environmental survey.

The modern vegetation of the Outer Hebrides is of considerable interest in its own right and also in terms of community and environmental gradients for several reasons: issues which underpin the later palaeoecological work. Firstly in principle there is likely to be a marked contrast and interesting gradient between the alkaline shell sand communities of the machair (pH 7-8) and the peatland, heath, grassland and mountain communities (pH 4-5). Secondly, on most of the islands there ought to be distinct altitudinal gradients. Beinn Mhor on South Uist, for example, rises to 620m O.D. Thirdly, there should be the topographic and moisture gradients, typical of the upland areas of north-west Scotland. Finally, the past and present land use of the island, taking the form of cultivation of the machair, grazing and lazy bed cultivation on the grassland and moorland and extensive peat digging in the bog communities, might be considered to have played a role in the creation of biotic diversity and may have extensively modified the natural communities in many places.

The aim of this aspect of my study is therefore to describe a detailed survey of plant communities and their environmental controls on South Uist. More detailed objectives were to:

a) define the plant communities along the transect (Phytosociology).
b) examine the environmental relationships between community composition and the environmental controls and gradients discussed above.
c) To compare the results of the phytosociological and environmental survey with existing published

literature.

d) evaluate the extent to which the data from the transect were indicative of the vegetation of the island of South Uist as a whole.

e) and finally in the broader palaeoecological context of the Ph.D to provide information on the contemporary vegetation to relate to other research on the Quaternary vegetation history of the area.

The pollen taphonomy study

The aims of the South Uist taphonomy pollen study are therefore derived from the problems concerning pollen representation identified in previous studies of Holocene pollen sequences and tree macrofossil studies from the Outer Hebrides (see Birks and Madsen 1979, Wilkins 1984 and Chapter 1 this study). These studies suggest that there is some doubt as to the 'meaning' or 'integrity' of the pollen record from this exposed and wind swept region. Sites from Lewis and South Uist record pollen sequences which demonstrate contrasting non-wooded (Birks and Madsen 1979) or wooded (Bohncke 1988, Bennett et al. 1990, Edwards 1990) vegetational aspects within close proximity to each other and pollen taphonomic issues are raised by Wilkins (1984) findings of surprisingly low tree / shrub pollen frequencies in peats associated with fossil wood remains. Consequently before embarking on further palaeo-palynological analyses a study of contemporary pollen deposition designed to examine pollen representation in relation to local vegetation is required. This study therefore aims to describe the pollen representation characteristics and pollen depositional patterns of major plant communities on South Uist: plant communities which have also been identified in this Ph.D. More detailed objectives were to:

a) Describe the pollen representation characteristics of plant species present on the transect.

b) Examine the relationships between species and community pollen representation in each of the communities defined by the vegetation survey.

c) Examine the pollen depositional patterns of tree pollen from within local woodland stands and dispersal patterns of tree pollen along the transect.

d) generate hypotheses concerning specific aspects of pollen deposition in relation to local vegetation on South Uist which may aid the interpretation of fossil pollen spectra.

Vegetation history

Previous palynological studies from the Outer Hebrides had consisted of a number of disparate, individual sites. None had specifically addressed the question of local variability in vegetation development. The present study therefore aims to address this particular issue through a series of integrated pollen studies each from representative sites located in each of the landscape zones of the island which seek to investigate the associated problems outlined in 1.1 above. Stratigraphic investigations located a series of such sites (figure 13). Several of these sites appropriate to these problems were analysed for the purposes of this present study. More detailed objectives in these studies were:

a) To examine the vegetation record contained in pollen preserving sediments found in each landscape and geomorphic division on the islands in order to provide a detailed picture of the degree of local variability within its particular vegetation record, and produce an appropriate and integrated study of vegetation history at a detailed local level of resolution.

b) To identify periods of vegetation stability and change during the Holocene and discuss these in the light of local variation, climatic and anthropogenic impacts during this period.

A set of separate but inter-related studies as outlined above were to be undertaken which it was hoped would contribute new information and new ideas about the landscape history of the southern Outer hebridean islands. Ultimately such information will stand in its own right but it is hoped that it will contribute useful information to archaeological studies in the area.

Chapter 4.

Methodology.

Methods.

This chapter describes the field and laboratory methods used in the study. The collection and analysis of the vegetation and environmental data involved the co-operative effort of a number of co-workers. Dr. M. Kent, Dr. P. Wathern and Dr. R. Weaver were involved in the collection and processing of the vegetation / environmental data.

1. The vegetation survey.

Sampling.

Once the vegetation zone had been mapped out the vegetation survey was completed by walking the length of the transect and locating quadrats at regular intervals and wherever a distinctive change was noted in the flora. Sampling was thus biased, not random, with the specific aim of maximising descriptive difference in species composition. This approach is widely used in vegetation survey (Smartt et al. 1978, Caldas and White 1983), and gives maximum efficiency in terms of description of variability in relation to sampling effort. The position of the quadrats is shown in figure 12.

Vegetation description.

A quadrat size of $1m^2$. was selected, with abundance measured using subjective assessment of percentage cover by eye. This abundance measure is generally acknowledged as combining accuracy together with speed of recording (Smartt et al. 1974, 1976). All species of higher plant together with bryophytes, hepatics and lichens were identified and recorded.

In the peatland and bog communities, the bryophyte flora was seen as of particular importance. Data were collected during June 1988 and June 1989. Identifications were checked using Clapham et al. (1989), Watson (1982) and Smith (1978). Bare sand, bare peat, bare rock, litter and standing water were also recorded as percentage cover.

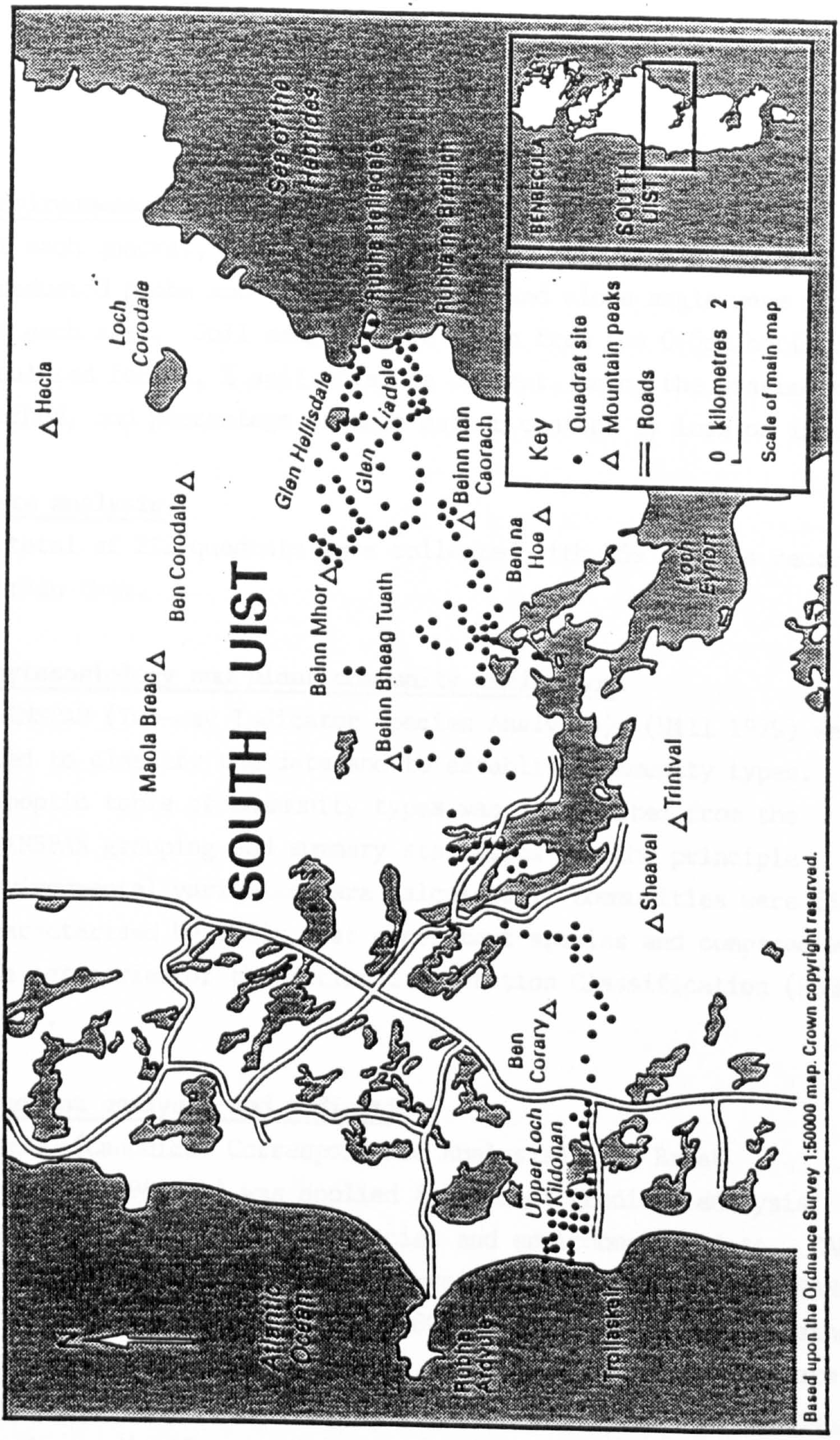

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Figure 12. The location of vegetation quadrats on the South Uist transect.

Environmental data collection.

At each quadrat, data were collected on soil/peat depth, using a graduated probe and altitude, aspect and slope angle were recorded at each site. Soil samples were taken from the 0-5cm horizon and analysed for pH, % soil moisture content, using the gravimetric method, and percentage organic matter content by loss on ignition.

Data analysis.

A total of 212 quadrats were collected with 259 species recorded within them.

Phytososiology and plant community definition.

TWINSPAN (Two-way Indicator Species Analysis), (Hill 1979) was used to classify the data and to establish community types. A synoptic table of community types was constructed from the TWINSPAN grouping and summary statistics for the principle environmental variables were calculated. Communities were finally characterised by their most consistent species and compared with the categories of the National Vegetation Classification (Rodwell 1991).

Gradient analysis and ordination

CANOCO (Canonical Correspondence Analysis) (Ter Braak 1986,1987,1988a,b) was applied for direct gradient analysis ordination using both the species and environmental data. CANOCO is an extension of Detrended Correspondence Analysis (DECORANA) (Hill, 1979, Hill and Gauch, 1980), which is an indirect method utilising only the species data. In CANOCO, species data are directly related to a set of environmental variables and the species ordination axes are constrained to be linear combinations of the environmental variables. The method produces a species/environment bi-plot which enables species distributions to be related to environmental variables. This latter facility greatly enhances the interpretation of environmental gradients. In figure 22, (chapter 6) the points represent individual species and the arrow representing each environmental variable points in the direction of maximum environmental change of that variable across the diagram. The length of the arrow is proportional to the magnitude of change in that direction and for interpretation purposes, each arrow can also be extended backwards through the central origin. Those environmental factors which have long arrows are more closely correlated with the ordination than those with short arrows and thus are more important in controlling community variation. A point representing an individual species can be related to an arrow representing an environmental factor by drawing a perpendicular from the line of the arrow to the point. The order in which points project onto the arrow from the tip downwards, through the origin and into the extension of the line of the arrow beyond the origin, is an indication of the position of the species in relation to the environmental factor. Species with their perpendicular projections near to or beyond the tip of the arrow will be strongly correlated with and influenced by the factor. Those at the opposite end will not. Aspect data were transformed using sines prior to data analysis.

Surface sample studies.

The surface samples of lake mud, peat, raw humus or moss polsters were collected from each $1m^2$. quadrat. The samples represented a 1mm. sediment 'slice', measuring 5cms. x 5cms. The samples were stored in sealed polythene bags at 4^oC prior to laboratory preparation. Samples for taphonomic analysis were selected on the basis of the phytosociological groupings identified in the TWINSPAN analysis. Samples from each of the TWINSPAN groupings were selected from across the transect (figure 12). The east-west orientation of the transect also allowed the effects of topography, particularly degree of exposure to be considered by the research design. Pollen samples were prepared and analysed using the methods outlined below.

Further analysis of the surface sample pollen data has adopted the methods used by Randall et al. (1986) in their broadly similar study of pollen catchment in relation to local vegetation on Carn

Ear on the Monach Isles. The sites and study objectives of both studies share many similarities and adopting a similar methodological approach allows direct comparisons to be made between the results of both studies. Consequently further analysis of the pollen data are at this stage essentially descriptive and qualitative (see Chapter 7). The pollen data are presented as a conventional pollen diagram which is followed by discussions of pollen representation for;

(i) individual species.
(ii) each of the TWINSPAN groupings identified from the results of the vegetation survey.
(iii) out-community / off-island pollen depositions.

These analyses are supported by a series of corresponding Pollen Representation tables. In all diagrams and tables, the plant species, pollen taxa and TWINSPAN groupings are ordered, where possible, in relation to their location on the study transect across South Uist.

Vegetation history ; sample collection.

A series of sites suitable for palynological investigation were identified in Barra and South Uist. A preliminary survey of each site selected for investigation was undertaken using an Eijkelramp Gouge corer to assess sediment depth and lithostratigraphy. A core was then retrieved from each site with a Russian peat corer. Core sections were extruded into clean plastic tubing, wrapped in plastic film, aluminium foil and thick plastic. On return to the Sheffield laboratory all cores were stored at 4°C prior to sub-sampling.

Sub-sampling.

1cm. slices of sediment were removed from the core sections at 4cm intervals. This close sampling interval was thought appropriate in order to achieve high levels of temporal resolution in the pollen data and to detect possible short lived vegetational

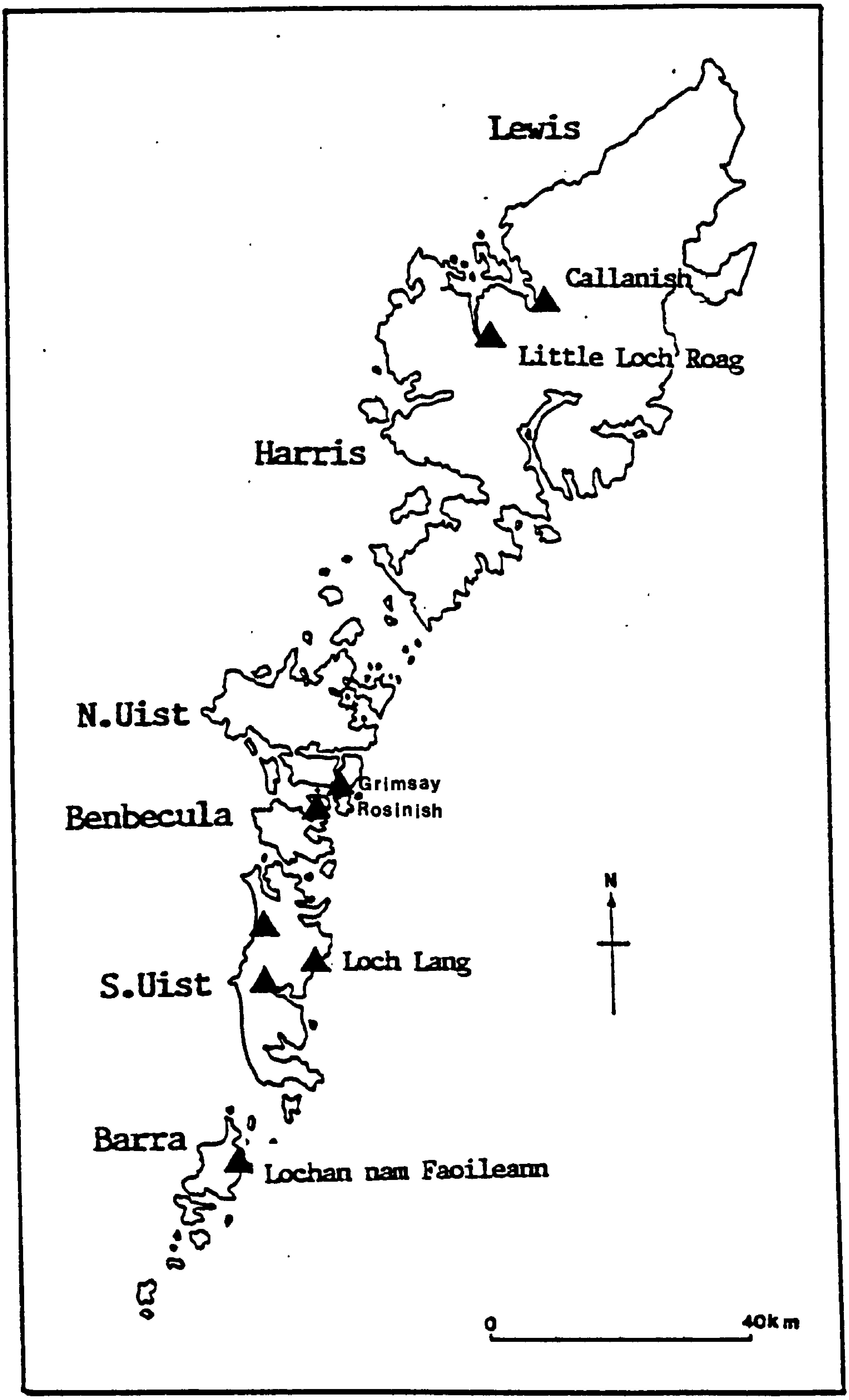


Figure 13. Location of palynological study sites.

developments. Leaving 4cm. intervals between sub-samples also facilitated re-sampling at closer intervals of 2cms. or 1cm. if required.

Laboratory preparations

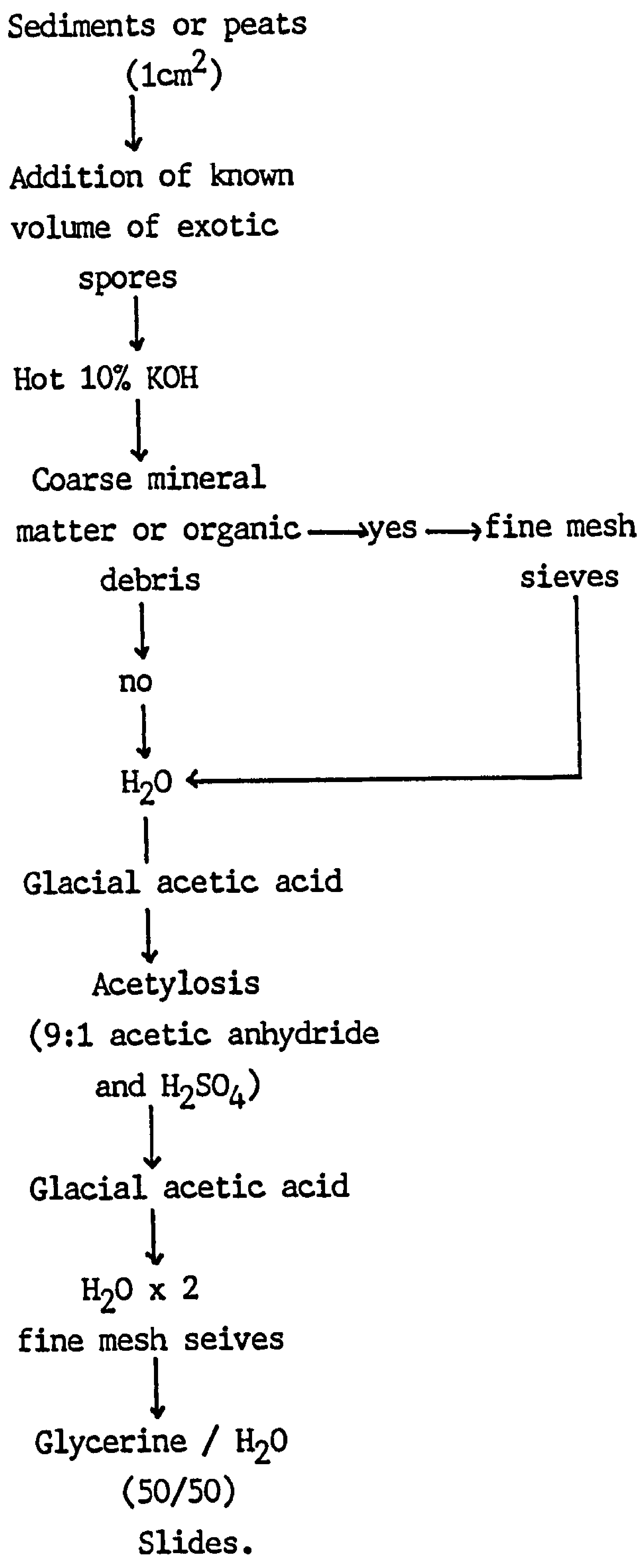
Procedures of sample preparation were modified versions of those used by Faegri and Iversen (1975) and Ralska-Jasiewiczowa (1986) Method B (figure 14).

All samples were prepared by extracting $1cm^3$. of sediment from the centre of each 1cm. 'slice' of sediment in order to avoid any contamination which may have occurred at the outer edge of the core sections. Lycopodium clavatum spores contained in tablets of known concentration (Stockmarr, 1971) were added to the samples. Samples were prepared using deflocculation in NaOH followed by standard acetolysis. All samples were then washed through micro sieves (aperture 100 and 10µ) to increase pollen concentration and remove fine residues. Counting was then undertaken using an Olympus BH microscope at x400 magnification, with some grains examined under oil immersion at x1000 magnification. Pollen and spores were identified using the keys of Faegri and Iversen, (1975), Moore and Webb, (1978) and Andrew,(1984) and using comparisons with the departmental reference collection.

The pollen sum

An important methodological consideration arose from preliminary results of the vegetation survey which indicated that a large proportion of characterising species in the communities were herbaceous taxa with either low pollen productivity and / or entomophilous modes of dispersal. These characteristics suggested the need for high pollen counts to be achieved in order to increase the probability of these types being located and also to maintain constant percentages of more abundant pollen types within the sample. Mosiman (1965) calculated the probability of achieving a count within a sample within a 95% confidence limit

Figure 14. Flowchart showing laboratory techniques for pollen sample preparation



and found that the size of the confidence limit depended on the number of grains counted. The highest confidence limits were achieved with counts exceeding 500 grains (Table 3). Consequently this figure was adopted as a minimum sum for the analysis.

Table 3. 95% confidence intervals for percentages of increasing total pollen counts. Assuming a binomial distribution.
(Data from Faegri and Iversen 1975)

	Number of pollen grains counted.				
Percentages	50	100	200	500	1000
1 ±	4.6	2.7	1.7	1.2	0.6
3 ±	5.8	3.8	2.5	1.6	1.1
5 ±	6.9	4.6	3.2	2.0	1.4
10 ±	8.7	6.0	4.3	2.7	1.9
20 ±	11.1	7.9	5.6	3.6	2.5
30 ±	12.5	9.0	6.4	4.1	2.9
50 ±	13.6	9.6	7.0	4.4	3.1
70 ±	12.5	9.0	6.4	4.1	2.9
80 ±	11.1	7.9	5.6	3.6	2.5
90 ±	8.7	6.0	4.3	2.7	1.9
95 ±	6.9	4.6	3.2	2.0	1.4
97 ±	5.8	3.8	2.5	1.6	1.1
99 ±	4.6	2.7	1.7	1.2	0.6

Diagram preparation.

Both pollen percentage and concentration diagrams were prepared both for individual taxa and composite curves. Pollen percentage data are numerically interdependent because they must sum to 100. As a result an increase in the pollen percentage of one taxon must be accompanied by a decrease in the others, even if the actual abundances of the other taxa remain constant. Pollen concentration data, which provides information on volumetric concentrations of pollen grains in a known volume of sediment, is free of this effect. Thus providing 'independent' information on changes in pollen abundance.

The pollen sum

The pollen sum was made up of those taxa which were taken to be members of the atmospheric pollen rain falling in the catchment area. Local components such as aquatic taxa, Pteridophytes and *Sphagnum* were excluded from the pollen sum. The aquatic component was made up of those taxa that were considered to be obligate aquatic plants, i.e. those that need an aquatic environment for reproduction. So this component included *Potamogeton* but excludes fen species such as *Triglochin*.

Charcoal Estimates

Estimates of microscopic particulate charcoal abundance in sediments were obtained as a method of detecting variations through time in the frequency or abundance of fire (domestic or agricultural), and hence as a potential way of tracing the intensity of human settlement or land-use in the area. Estimates were made by counting all particles of charcoal encountered during routine pollen counting. This method was preferred to point count estimates (Clark 1982) as it was found that the latter method was only suited to samples containing abundant charcoal. As Patterson *et. al* (1987) point out, when the charcoal content is low the point count method will tend to yield zero values.

Diagram Construction and Calculations

The results were computerised by entering the raw pollen data into TILIA 1.10 and TILIA* graph 1.17 (Grimm 1991).
The percentage representation of any one taxon in the pollen sum was calculated using the formula;

$$Px = \frac{Cx}{P} \times 100$$

where Px = Percentage representation of the taxon.
Cx = Count of the taxon.
P = The pollen sum.

The percentage representation of taxa outside the pollen sum is calculated by the formula;

$$Py = \frac{Cy}{P + Sy} \times 100$$

where Py = Percentage representation of the taxon.
P = The pollen sum.
Cy = The count for the taxon.
Sy = The sum of taxa pertaining to that component, e.g. sum of aquatic taxa.

The concentration values of each taxon was calculated by means of the formula;

$$Tx = \frac{Cx.Tm}{Cm}$$

Where Tx = The concentration of each taxon.
Cx = The count for taxon x.
Tm = The number of marker spores (*Lycopodium*) added.
Cm = The count of marker spores in a sample.

All concentration values are expressed as units of pollen grains per cubic cm.

Chapter 5.

The Geographical Setting.

This chapter describes briefly the geographical setting of the study area.

Solid Geology

Accounts of the geology of the Outer Hebrides date back to the early work of MacCulloch (1819), Murchison and Geikie (1861) and Jehu and Craig (1923). More recent studies include Dearnley (1962), Myers (1970, 1971), Coward (1972, 1973), Coward and Graham (1973), Watson (1977), Smith and Fettes (1979), British Geological Survey (1981) and Gribble (1991).

The basement rocks of the study area (figure 15) consist almost entirely of Pre Cambrian (Lewisian) metamorphic gneiss and metasedimentary rocks which were formed during the late Archaean-early Proterozoic eras approximately 2,800 m.y to 1,600 m.y. ago. This period is divided in Scotland into two events, the Scourian which ended at c.2,200 m.y. and the Laxfordian which was ended by the Outer Hebrides Thrust which produced the Outer Hebrides Thrust Zone which runs along the east coast of the island chain (Figure 15). These rocks comprise mostly of grey gniesses which are quartz-rich and contain horneblend streaks and patches. Gribble (1991) suggests that these rocks have been metamorphosed to such a degree such that they are migmatised (melted) in places. Included in the Lewisian complex on South Uist are outcrops of metamorphosed sedimentary rocks, termed metasediments, which include calcareous and graphite bearing gneisses, quartzites, marble bands and garnet-bearing schists. The Lewisian gneisses were eroded during the Tertiary period and now form much of the undulating, low lying landscapes of the islands.

Very resistant, intrusive igneous rocks, the eastern Basic Gniess, form the highest peaks on South Uist such as Hecla and Beinn Mhor and have been dated to c.2,200 m.y. Later, at the end of the Laxfordian, c.1,750 m.y. granite intrusions and pegmatite dykes and veins were emplaced particularly in central Harris and western

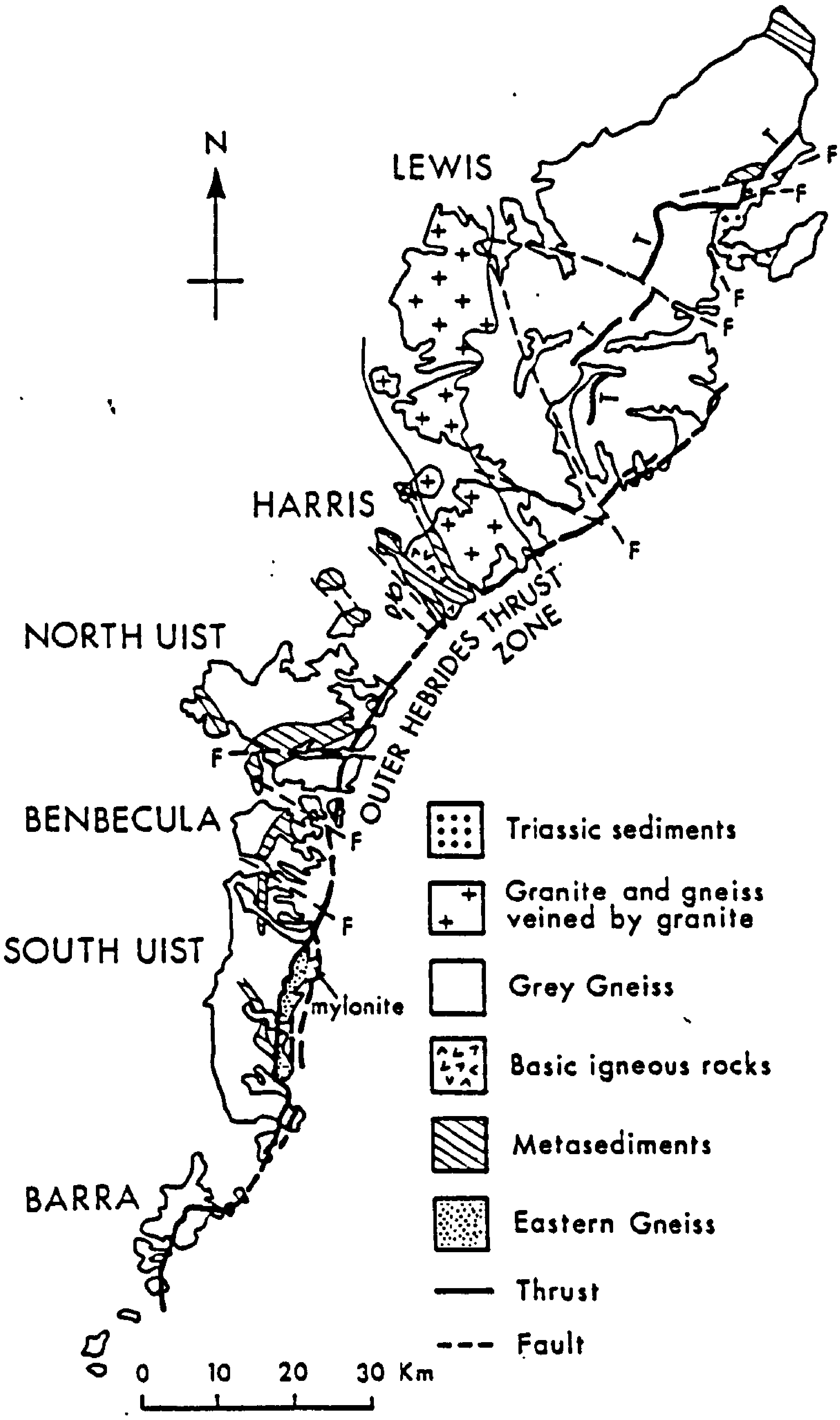


Figure 15 A simplified geological map of the Outer Hebrides.
(source Gribble 1991)

Lewis. Other important igneous intrusions include the Scourie dykes and the Permo-Carboniferous quartz dolorites which occur as groups of east-west trending dykes in the north of Barra and South Uist. The bed of the sea of the Hebrides, the Minches and the Atlantic platform to the west consist of Mesosoic sedimentary rocks, mainly sandstones and shales. Northwest - southeast and east-west trending faults have influenced the landscape forming fault guided valleys and sea inlets. In more recent geological history glacial erosion during the Quaternary period has produced the distinctive ice scoured basins and roche moutonées which characterise large areas of the islands.

The Quaternary Period

The pioneering work of early glaciologists Agassiz (1840) and Geikie (1863,1865) produced the first model of Quaternary glaciation in Scotland which located the main source area for ice accumulation and traced the movement of ice from centres in the Scottish highlands and southern Uplands. They suggested that ice margins lay to the north and west beyond the Outer Hebrides and Orkney islands. It is now known that there were several glacial episodes during the Quaternary period but this early model has been adopted as a framework for the last Devensian ice sheet in Scotland. Modifications to the theory have caused considerable debate which has diverged into two schools of thought concerning the main extent of the late Devensian Scottish ice sheet, either it was as extensive as Geikie first suggested (Price 1983) or as Sissons (1980), Sutherland (1984), Peacock (1984) argue the ice sheet was less extensive with ice margins through the Inner Hebrides and separate centres of ice accumulation in the Cullin Hills, Skye and on the Outer Hebrides.

The Devensian ice sheets

The expansion of polar ice during the early-mid Devensian eustatically lowered sea levels around the Scottish coast by c.120 metres (Denton and Hughes 1981). As a result land area was extended to the west off the coast of the Outer Hebrides and eastwards in the North Sea basin. As the polar front moved to its maximum southward extent off the Portugese coast (Ruddiman and McIntyre 1981) precipitation increased southwards and ice accumulation increased in the Scottish Highlands, Southern Uplands and Hebrides. The ice margins were thought to be confluent with the Scandinavian ice sheet in the central north sea basin (Boulton 1977, Denton and Hughes 1981). However the presence of deposits of interstadial age at Tao Galson (Sutherland and Walker 1984), Cross brae Farm (Hall 1984) and Teindland (Edwards et al. (1976) indicated to these authors that areas in the extreme north and west of Scotland might have remained ice free. Coastal rock cut platforms in the Inner Hebrides caused Sissons (1984) to suggest that the ice margins were fluctuating in their extent in the Minches and Sea of the Hebrides in response to climatic shifts.

A raised platform and cliff of marine erosion found only on the northern and eastern tip of Lewis are the earliest Pleistocene landforms noted in the Outer Hebrides. The presence of glacially transported red sandstone and quartzite erratics in Lewis and in raised beach gravels in the north west of Barra thought to originate in the Permo-Triassic, Torridonian and Cambrian rocks of north west Scotland, have been cited as evidence of former Scottish mainland ice on the north of Lewis and southern islands, possibly of Wolstonian or early Devensian age (Peacock 1984). An alternative explanation (Selby 1987) suggests the Permo-Triassic basins located offshore to the west of the Outer Hebrides as an alternative source for this material.

This was followed by two further glacial periods described by Peacock as "The Hebridean Ice-sheet Phase" (Late Devensian maximum) and the subsequent "Valley glacier phase" possibly of Late Devensian c.11,000-10,000 B.P. age (see table 4). Peacock (1984) suggests two main centres of ice accumulation in the Outer Hebrides, one in the mountains of southern Lewis and northern Harris and the other extending from the west coast of Barra up the west coast of the Uists and Benbecula, from which ice flowed

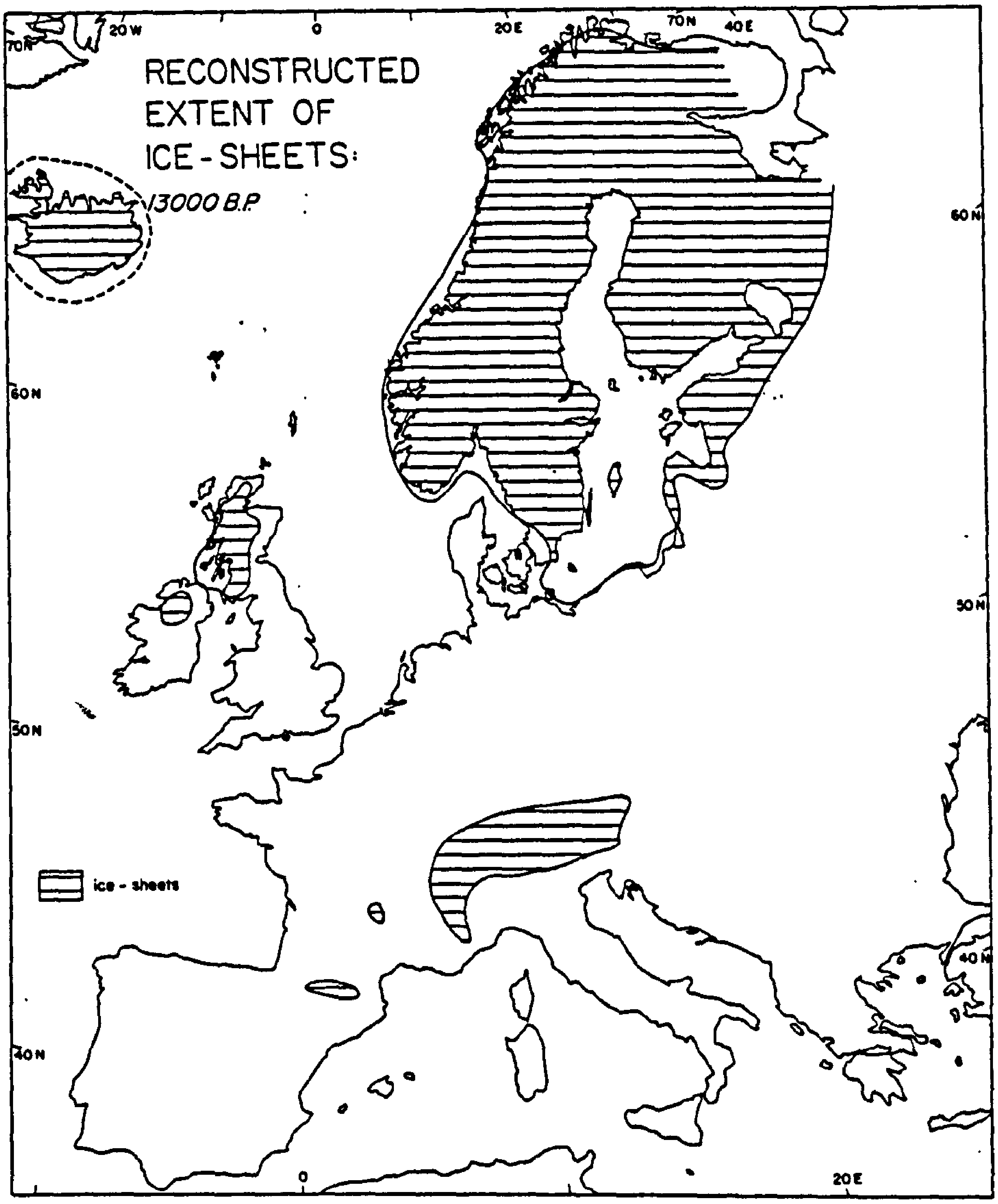


Figure 16. <u>The extent of the late Devensian ice sheet,13,000 B.P.</u> (source Huntley & Birks 1983).

Glacial events	**Extra-glacial events**	**Suggested correlations**
Mountain glaciation of Lewis & Harris (in part?)	Formation of boulder lobes on mountains	Loch Lomond Readvance (Late-Devensian 11,000-10,000 B.P.)
Mountain glaciation of Lewis & Harris in part?)		Wester Ross Readvance (Late Devensian, 13000 B.P.?)
Hebridean ice-sheet glaciation. External ice in North Lewis?	Formation of periglacial features in North Lewis.	Main Devensian glaciation (Late Devensian, 18000 B.P.
	Formation of interstadial deposits on Tolsta Head, Lewis.	
	Formation of raised beach in Lewis and Harris.	Devensian (pre-Late-Devensian) or Ipswichian Interglacial.
	Formation of periglacial features in North Lewis	?Wolstonian or Early to Mid. Devensian.
Scottish mainland ice in parts of the Outer Hebrides.	(Probably entirely glaciated).	
	Formation of raised platform and cliff of marine erosion.	???

Table 4. **Summary of Pleistocene History, Outer Hebrides** (Source Peacock 1984).

eastwards across the islands. Interstadial deposits at Tolsta Head, Isle of Lewis (Von Weymarn and Edwards 1973) indicate that during the late Devensian ice maximum (c.18,000 B.P.) this area remained ice free. (see Figure 16).

The "valley glacier" phase is thought to have been confined to south Lewis and north Harris and is associated with drift and meltwater deposits and landforms, particularly the Valtos meltwater channel in Lewis. Importantly these studies suggest that the last ice sheet phase in South Uist and Barra was the late Devensian and as far as is known ice did not return to these islands following the retreat of the main Devensian ice sheet.

The extent of former ice-margins is of interest to palaeoecologists because the concept of a limited ice sheet is central to theories of glacial refugia and the possibility of the in situ survival of some plant species during the late Devensian. This theory has been evoked to account for the presence in western Ireland of the Hiberno-cantabrian (Lusitanian) elements in the flora (Stelfox and Welsh 1980) and amphi-atlantic species in the Outer Hebrides (Heslop-Harrison 1948b). However Sutherland and Walker (1984) argue that even if such ice free areas did exist on St. Kilda and by inference other Scottish islands, the periglacial climate would be to severe for the survival of plant species.

The period following the late Devensian ice maximum, dated in the north Atlantic at c.14,500 B.P. (Ruddiman and McIntyre 1973), marks the onset of climatic amelioration, the Late-glacial Interstadial. The most compelling evidence of climatic change during this period is found in the terrestrial fossil Coleoptera with warmth demanding beetle species occurring in southern Scotland (Coope 1981).
There are pollen records available from many Scottish Late-glacial Interstadial sites (Donner 1957, Lowe and Walker 1976, 1980,1981, Walker and Lowe 1977,1979,1980,1985,1988, Pennington 1977,1978,

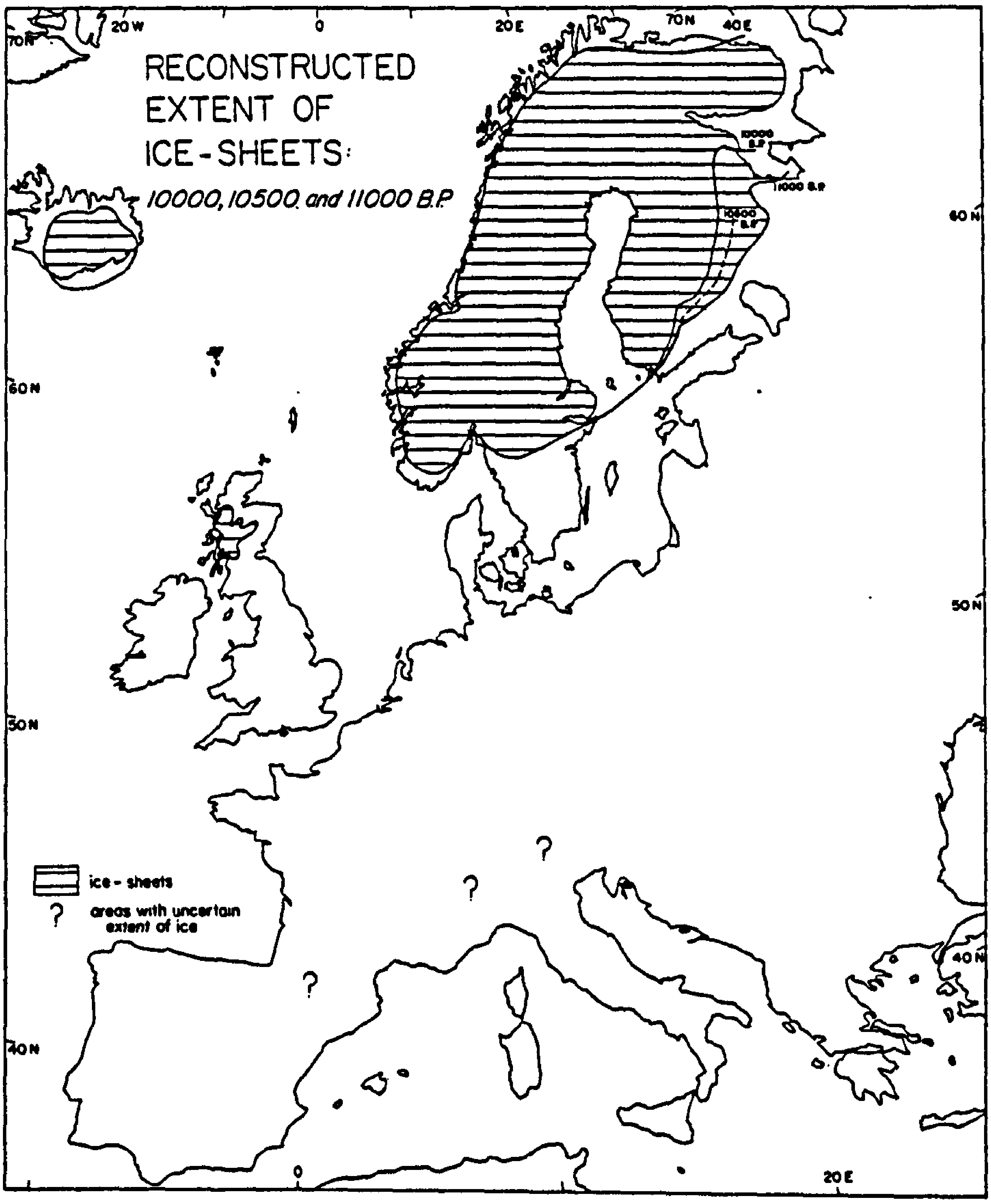


Figure 17. The extent of Loch Lomond ice, 10,000, 10,500 & 11,000 B.P. (source Huntley & Birks 1983).

Tipping 1984,1987) which indicate that ice retreat was not a synchronous event but that it began at approximately 13,000 B.P.

The biostratigraphic sub-division of the period following ice wastage to the start of the Holocene has provided a chronology for glacial retreat and the readvance of ice during the Loch Lomond stadial (see figure 17), a return to a colder climatic regime in the Scottish highlands which ended at the onset of the Holocene c.10,000 B.P.

At the begining of the Holocene the polar front which lay off the west of Ireland coast moved rapidly northwards to eastern Greenland (Ruddiman, Sancetta and McIntyre 1977), resulting in rapid climatic warming, which is indicated in many Scottish pollen diagrams by the expansion Juniperus / Empetrum heath followed by the colonisation of tree species Betula and then Corylus.
The glacial history of the Outer Hebrides as it is currently known is summarised in Table 4.

Sea level change

Evidence for variations in sea-level during the Quaternary period in western Scotland has been recognised in a variety of morphological features such as rock cut platforms, raised beaches, shingle ridges and marine gravels; and in sedimentary sequences located off-shore and in estuarine situations. These features provide evidence of past marine transgression and regression, but a chronology of events is difficult to establish because Devensian ice advance has obscured the evidence from previous periods.

The extent of the late Devensien ice sheet in Scotland is significant as the formation of shoreline features at the ice margin are indicative of the presence or absence of ice and the height of relative sea level. During the process of ice retreat differential uplifting of shoreline features occurred making correlation between sites difficult and leading to considerable debate over the age and origin of many relict shorelines and the western limit of Scottish ice sheets.

The pattern of sea level change in western Scotland since the Devensian glacial maxima reflects the interaction between regional and global effects. At the time of the Devensian ice maximum global sea levels were thought to have been -120 to -130 metres O.D. and in the North Sea levels of -130 to -160 metres O.D. have been recorded (Sissons 1981) indicating that areas of dry land were present in the North Sea basin.

The wastage of the major Devensian ice sheets produced eustatic sea-level rise which is recorded in deep sea cores (Shackleton and Opdyke 1973) indicating a global rise in sea level from the low levels of the late Devensian to present day levels at c.5,000 B.P.

The transition between the low sea levels associated with ice maximum to the high seas of the post-glacial was complicated by the effects of isostatic rebound which began to have regional affects during the Lateglacial interstadial in Scotland. As ice receded isostatic recovery began to exceed eustatic rise and produced various Late-glacial shoreline features. These are differentiated on the east and west coast by their position in relation to the ice sheet margins, the rate of ice retreat and their position in relation to the main centre of isostatic uplift in the west Highlands. The main evidence for sea level during the Late-glacial period are the Main Perth Shoreline with an inferred age of 13-12,000 B.P. and the Late-glacial Shoreline in western Scotland consisting of a wave-cut rock platform and associated marine gravels.

Dawson (1984) suggests that during the Late-glacial Interstadial relative sea level fell rapidly between 13-12,000 B.P. and then more slowly until 11,000 B.P. and that the Lateglacial shoreline was formed by marine erosion during the Loch Lomond Stadial. Other workers (Brown et al. 1983) maintained that the shoreline was formed during the Late-glacial Interstadial when isostatic rebound was in equilibrium with eustatic sea-level. This theory proposes a phase of high relative sea-level following deglaciation, followed by a fall in sea level until c.12,000 B.P. to c.11,000 B.P. when levels were stable and the shoreline was formed. In the subsequent Loch Lomond stadial the deep valleys of the Forth and Tay were incised.

A similar debate has ensued over the formation of the Main Lateglacial Shoreline Platform which is found on the Inner Hebridean islands of Jura, Scarba and northern Islay. This feature was thought to be of interglacial origin but Dawson (1984) argues that it was formed during the Loch Lomond Stadial by shore erosion in periglacial conditions which have modern analogues in polar regions. Sutherland (1981) and Sissons (1982,1983) interpret the coastal landforms in the Inner Hebrides as expressions of former ice margins. Sissons (1986) divides the Inner Hebridean shorelines into three phases on the basis of altitude. The high altitude rock platform fragments, typically at c.18-50 metres O.D. with backing cliffs range in height from 10-90 metres. These features are further differentiated by the presence / absence of glacial characteristics such as ice moulding, striations and till cover. Sissons (1986) suggests that these high altitude features represent glacial periods when the area was isostatically depressed, gaining their present altitude as a response to glacio-isostatic uplift. The fragmented distribution of these features is thought to indicate the presence or absence of ice margins along the coastline.

Similar rock-cut platform fragments also occur at lower altitudes and are assigned to the Loch Lomond Stadial. As with the high altitude platform, the fragmented distribution and presence / absence of glacial features are thought to represent the westward limit of Inner Hebridean Loch Lomond Stadial ice margins. The associated Main Late-glacial Shoreline slopes westward from Oban to Mull, south-west to Jura and through zero isobase on north-west Islay (Sissons 1974, Gray 1978, Dawson 1980).

Also in the Inner Hebrides, marine gravels, raised beaches and shingle ridges occurring at altitudes of up to 30 metres O.D. are associated with falling Late-glacial sea level and are located on Colonsay, Mull, Rhum and Skye.
Further evidence for the pattern of Late Glacial sea-level change has been examined in sedimentary deposits found around the Scottish coast and in offshore basins. Two principal units have been identified. The Errol Beds which are found principally on the east coast and the Clyde Beds which overlay the Errol Beds in some areas but which are concentrated on the west coast, particularly in the Clyde estuary and in boreholes off-shore. The Errol Beds are thought to have been laid down in the period following the late Devensian ice, maximum c.18,000 B.P. Sutherland (1984) suggests that they were deposited in front of a retreating ice sheet. The Clyde Beds contain a suite of boreal type marine molluscan remains which are commensurate with the radio-carbon date of c.13,000 B.P. at the base of the deposit. Peacock (1981) suggests that the sequence of deposition of the Clyde Beds was firstly, lower laminated clays indicating rapid deglaciation, followed by a period of slow sedimentation as the land surface became stabilized by re-vegetation, a phase of increased sedimentation as a result of solifluction and frost action during the Loch Lomond Stadial. Peacock (1981) suggests that the Errol Beds are not present on the west coast because of ice cover in areas where only the Clyde beds occur. Sissons (1974), Peacock (1978) and Sutherland (1981) produced sea level curves based on the depth and salinity tolerance of the fossil marine Mollusca in the Clyde Beds. These curves show an initial rapid fall in sea level c.1.8 metres per 100 years, followed by a period of much slower change after c.11,500 when sea level was thought to have been on average +8 to +4metres O.D. (the period when the Main Late Glacial Platform may have been produced).

Evidence for sea-level change during the Loch Lomond Stadial in the Firth of Forth, consisting of an erosional surface cutting across Late-glacial marine sediments, till and bedrock buried beneath Holocene sediments, is thought by Sissons (1981) to indicate an hiatus in the otherwise uniform depositional sequence created by a switch back to isostatic sea level rise during the stadial. Paterson et al. (1981) have identified a similar feature which correlates with the Main Late-glacial shoreline leading them to suggest that the erosional episode was during the Late-glacial Interstadial.

However the generally accepted pattern of sea level change following deglaciation is one of a rapid fall between 13-12,000 B.P. Renewed marine erosion during the Loch Lomond Stadial which produced the Main Late-glacial Shoreline which declines in altitude from the main centres of glacio-isostatic uplift in the western highlands to the south, west and south-west. This pattern of change is substantiated by the sea level curves based on the analysis of the Clyde Beds. Late-glacial sea-levels are therefore the result of the interaction of eustatic and isostatic processes,resulting from glaciation, the recovery and tilting of the Scottish land mass in response to the unloading of ice, and a isostatic depression caused by ice advance during the Loch Lomond Stadial.

In the Outer Hebrides intertidal peat deposits exposed by coastal erosion, eroding coastal peats and the movement of sand onshore suggest that rising sea levels have been predominant during the last 8,000 years (Ritchie 1975). The effects of glaciation during the Quaternary period produced the distinctive 'Knock and Lochan' topography which characterises large areas of the landscape of the Western Isles. Erosion exploited faults and other lines of structural weakness creating ice scoured basins (lochans) and producing the deposition of lodgement till on the lee slopes of rock outcrops; often to form 'crag and tail' features. Locally derived glacial till was deposited as an extensive plain. As ice receded englacial and supraglacial sediments were deposited as morainic drift and drumlin fields. In the Holocene, the landward movement of aeolian shell sands resulting from rising sea levels formed the sand dune and machair plains of the west coast (Ritchie 1979). These materials provide the substrates upon which the contemporary soils are developed.

Soils and vegetation

The most recent survey of the soils of the Outer Hebrides is that of Hudson *et al*. (1982) for the Soil Survey of Scotland.
The system of classification used in the Soil Survey is based on divisions, major soil groups and sub-groups found in the region. The soils have been grouped into 97 map units each of which may contain several major soil sub-groups. The map units are grouped together on the basis of parent materials into 21 Associations. The map units in each association are broadly grouped by their position in the landscape, that is into catenary sequences.
This brief description of soils is confined to the soils of South Uist and Barra as detailed on the 1:50 000 map, Sheets No.22 and No.33 (Hudson *et al*. 1982).

Soils represented in the southern Outer Hebrides include, Organic soils, soils of the Lochinvar Association and soils of the Fraserburgh Association. The distribution of soils in South Uist and Barra are illustrated in figures 18 and 19 and their main characteristics, listed in table 5, are outlined below.

Organic soils (Map Units 4 and 4u)

This association is comprised of peats formed either as basin / valley mires or as blanket peat. Blanket peat is defined in the Soil Survey as a soil having a surface horizon greater than 50cms thick with an organic matter content of more than 60% (Hudson *et al*. 1982). It is typically present on waterlogged anaerobic sites. High rainfall and low temperatures in the region together

Association	Parent Material	Map Unit	Component Soils
Organic Soils	Organic deposits	4	Blanket peat
Fraserburgh	Shelly sands	259	Brown calcareous soils, calcareous regosols.
		260	Brown calcareous soils, calcareous regosols.
		260N	Brown calcareous soils, calcareous regosols.
		261E	Calcareous regosols.
		261F	Calcareous regosols, brown calcareous soils.
		263	Eutrophic flushed peat, peaty gleys.
Lochinver	Drifts derived from Lewisian gneisses.	386	Brown forest soils, humus iron podzols, noncalcareous gleys, peaty gleys & rankers.
		388	Humus iron podzols, noncalcareous gleys, humic gleys & peaty podzols.
		391	Peaty podzols, peat, some peaty gleys.
		392	Peat, peaty gleys, some peaty podzols and humic gleys.
		394	Peaty gleys, peat, some peaty podzols and peaty rankers.
		395	Peaty gleys, peat, peaty rankers, some peaty podzols.
		396M	Peaty gleys, peaty podzols, peaty rankers.
		396U	Peaty rankers, peaty gleys, peaty podzols.
		397	Subalpine podzols, peat.
		398	Subalpine and alpine soils, lithosols and regosols.

Table 5. Legend for soil map units.
(Figures 18 & 19)
(source Hudson et al. 1985).

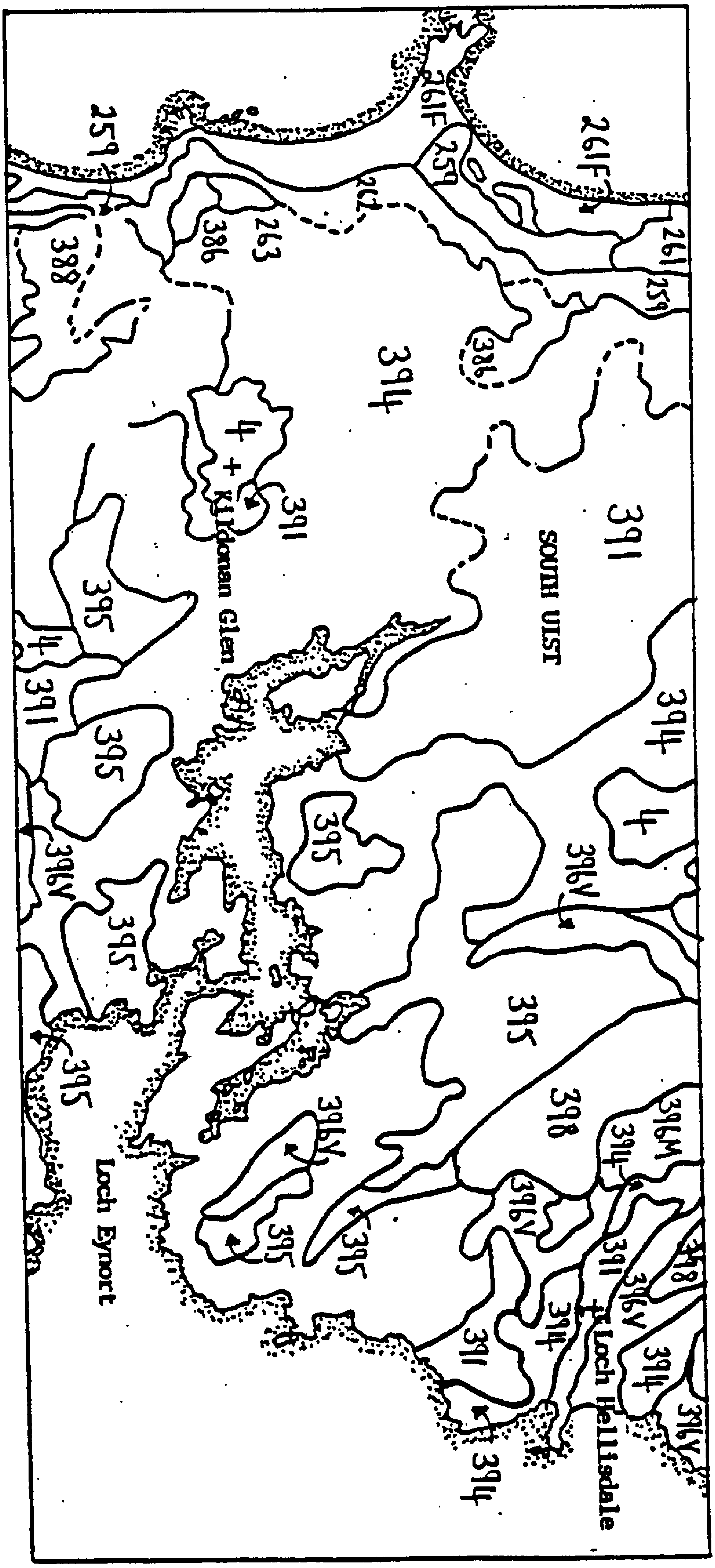


Figure 18. Soil map units ; South Uist transect.
(source Hudson et al. 1982).

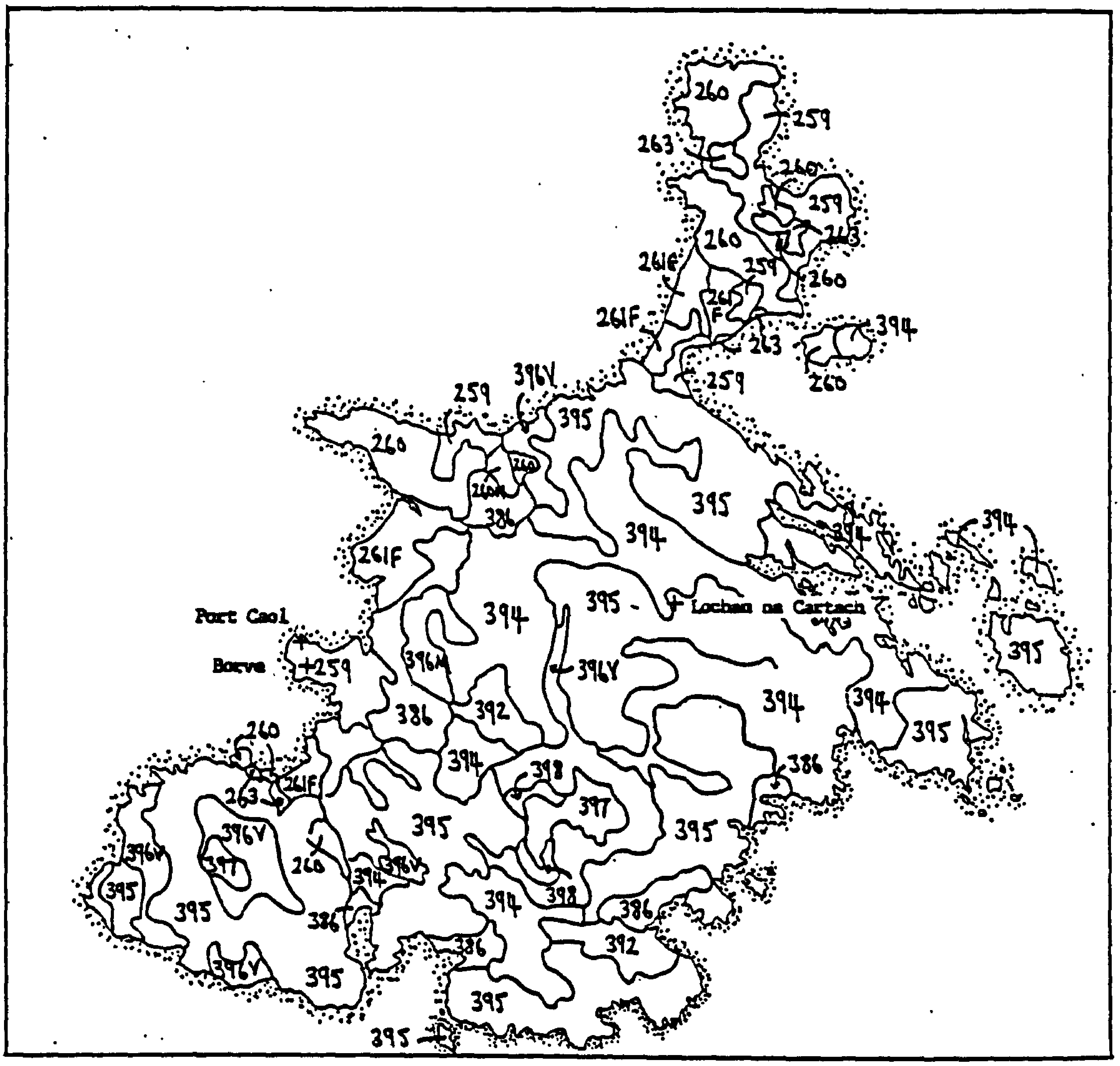


Figure 19. <u>Soil map units ; Barra</u>.
(source Hudson <u>et</u> <u>al</u>. 1982).

with acid, low base status substrates contribute to the dominance of peat and peaty soils on the islands. Distribution is extensive as peat occurs within an altitudinal range from sea level to 350m O.D. The peat is acidic (pH typically 3.5-4.0, Chapter 6 this study, Kent et al. in press). Local topography influences peat depths with the deepest peats occurring particularly in valley bottoms. Vegetation is typically Eriophorum angustifolium bog pool community of Chapter 6 this study, Kent et al (in press) in deeper waterlogged peats and Molinia caerulea - Scirpus cespitosus - Erica tetralix - Calluna vulgaris wet heath, (Chapter 6 this study, Kent et al. in press). On better drained slopes and shallower peats Calluna vulgaris dry heath (Chapter 6 this study, Kent et al. in press) occurs.

The Lochinvar Association (Map Units 386, 388. 391, 392, 394, 395, 396M, 396V, 397,398)

This association occurs extensively in South Uist and Barra. Parent materials for the soils of the Lochinvar Association are drifts derived from Lewisian gniesses and schists and the soils are typically peaty podzols, peaty gleys and humus iron podzols formed in areas underlain by colluvium, till and moraine. On steeper slopes and well drained sites brown forest soils occur.

The Organic soils and the soils of The Lochinvar Association are the dominant soil types in the landscape of the islands. Humus iron podsols occur widely in better drained sites such as steeper slopes and moraine mounds. Peaty and non calcareous gleys are associated with depressions and water receiving sites. Soil units adjacent to the machair soils of the Fraserburgh Association (for example Map Units 386 and 388 of the Lochinvar Association) have in some cases been modified by the addition of shell sand and provide areas of permanent pasture with some arable and rootcrop cultivation. Further inland the peaty gleys and peats are utilised for domestic peat burning.

In mountain areas (above 350 metres) stony drift produced by freeze-thaw action forms the substrate for subalpine soils, alpine lithosols and regosols (e.g. Map Units 397 and 398).

Peatland, wet heathland and bog communities are widespread vegetation types associated with the more organic soils of the Lochinvar Association together with neutral acid grassland communities such as *Agrostis capillaris* - *Festuca ovina* grasslands and *Pteridium aquilinum* - *Potentilla erecta* - *Anthoxanthum odoratum* bracken infested grassland of Chapter 6 this study, Kent *et al*. (in press.)

The Fraserburgh Association (Map Units 259-263)

Parent materials for soils of the Fraserburgh Association are the windblown shell sands which extend up the western coast of South Uist and Barra. The land area in which these soils occur is lowlying. Mather and Ritchie (1977) suggest that 87% of the machairs on the Outer Hebrides are below 50m. O.D. and 18% below 10m. O.D. Typically pH values range between 6.5 - 8.0. In the classification of soils occurring on the machair, undulating and plain surfaces are grouped together, as is hilly machair.

Soils of the stable and active dune are thin calcareous regosols with calcareous groundwater gleys present in dune hollows and slacks where the land surface is at or near the water table. *Elymus farctus* foredune community (Chapter 6 this study, Kent *et al*. in press) is present on the foredunes with *Festuca rubra* - *Galium verum* dune / machair community (Chapter 6 this study, Kent *et al*. in press) occurring on stable dune and dune slack areas.

Behind the dune systems freely draining brown calcareous soils and calcareous regosols are present where the land surface is above the water table (Hudson 1991). Vegetation is typically *Festuca rubra* - *Galium verum* dune / machair community (Group H, Chapter 6 this study, Kent *et al*., in press). Cultivation is developed around 2-5 year crop rotation systems and includes arable and root crops.

In low lying areas in the machair where deflation has lowered the land surface to the water table calcareous ground water gleys are typical and vegetation includes Potentilla anserina - Carex nigra - Vicia cracca inner machair community of Chapter 6 this study, Kent et al. (in press).

Climate

Accounts of the climatic environment of the Outer Hebrides can be found in Manley 1979, Hudsen et al. 1982 and Angus 1991. Manley (1979) summarises the climatic situation of the islands as,

> '...Decidedly windy, often cloudy, and with frequent though not exceptional amounts of rainfall on the low ground' (Manley 1979 pp 48).

In the generally maritime climate the seasonal temperature range is relatively small, wind speeds are high and rainfall distributed relatively evenly throughout the year (see table 1).

Precipitation, derived from Atlantic depressions, increases with altitude (Figure 20) and has high salinity levels. Importantly the area has relatively low potential water deficit due to the effects of high levels of precipitation and humidity which reduces potential evapo-transpiration (Hudsen et al. 1982).

The most dominant climatic characteristic of the islands, the stong and frequent winds, are amongst the highest in the world (Hudson et al. 1982) with mean speeds of 10 metres per second in winter and 5 metres per second in summer. It has been suggested that wind frequency, velocity and salinity have restricted the development of woodland on the islands. Existing stands are typically low growing and wind-contoured (Birks and Madsen 1979, Angus 1987, Birks 1991, Angus 1991).

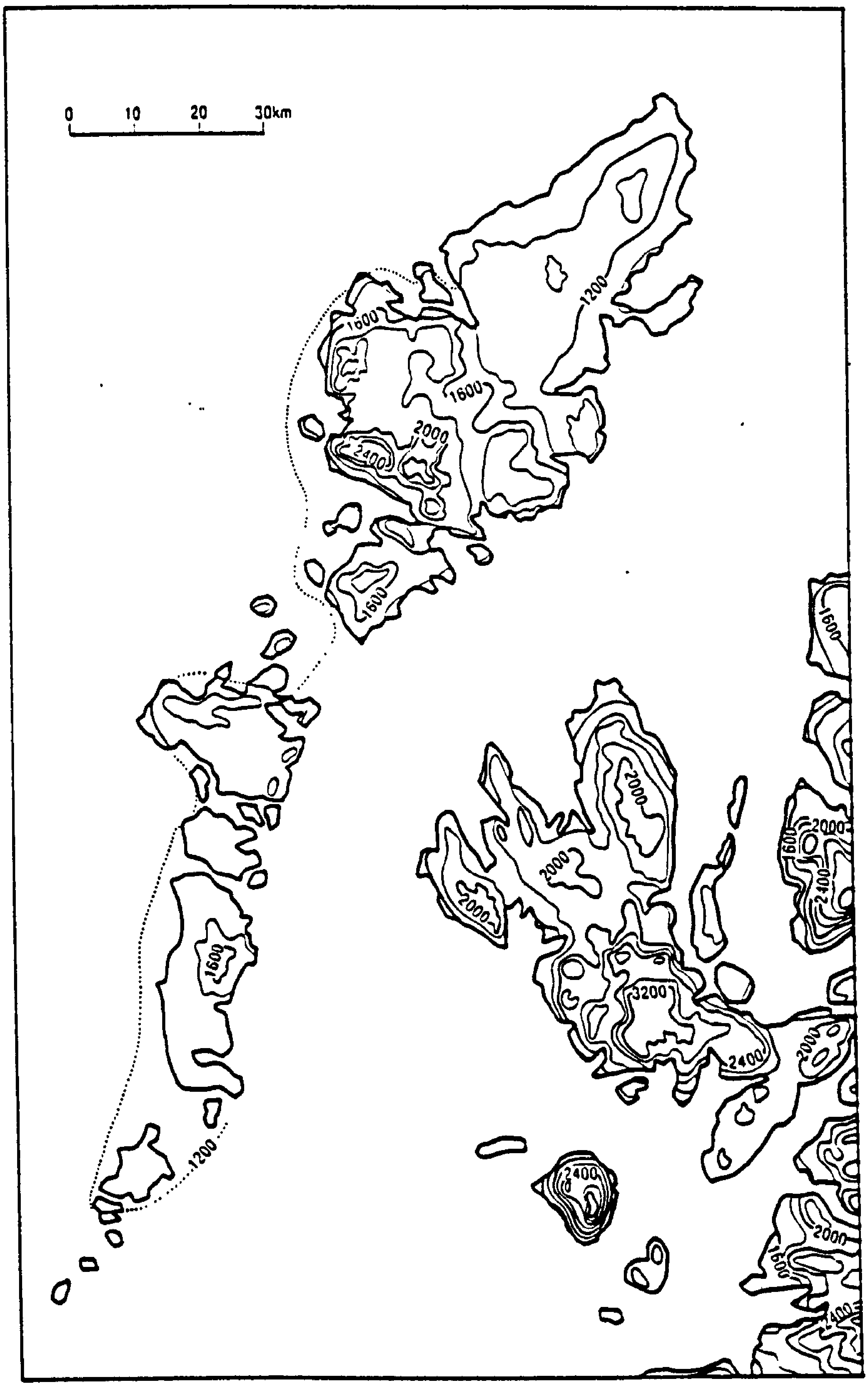


Figure 20. Rainfall (average annual, mm.)
(source Hudson et al.1982)

Angus (1991) discusses the influence of the climate of the Outer Hebrides on vegetation and suggests that salt laden winds induce prostrate growth forms in some species such as Calluna vulgaris and Juniperus communis. Plant distribution patterns also reflect the influence of the climate, for example, montane species can be found growing at or near sea level. The influence of high rainfall and low temperatures in the area is reflected in the widespread distribution of organic soils, peats and gleyed soils. Such a predominance of acid waterlogged soil types (outside the machair) limits habitat diversity and as a result floristic diversity.

Chapter 6.

Vegetation and Environmental Survey.

The plant communities of the South Uist transect

This chapter describes the plant communities identified by TWINSPAN from the South Uist environmental transect survey data. The methods used in the analysis are detailed in Chapter 4 of this study.

A total of sixteen plant communities were identified by TWINSPAN, these are summarised in Table 6 and their location on the transect illustrated in Figure 21. The following description of communities is related to the primary habitats of the island and is also placed within recognised syntaxonomic categories, as well as the groups of the National Vegetation Classification (NVC), Rodwell (1991). Comparison is also made with the communities of Pankhurst and Mullin (PM) (1991). In addition, the environmental characteristics of each group have been summarised in Table 7.

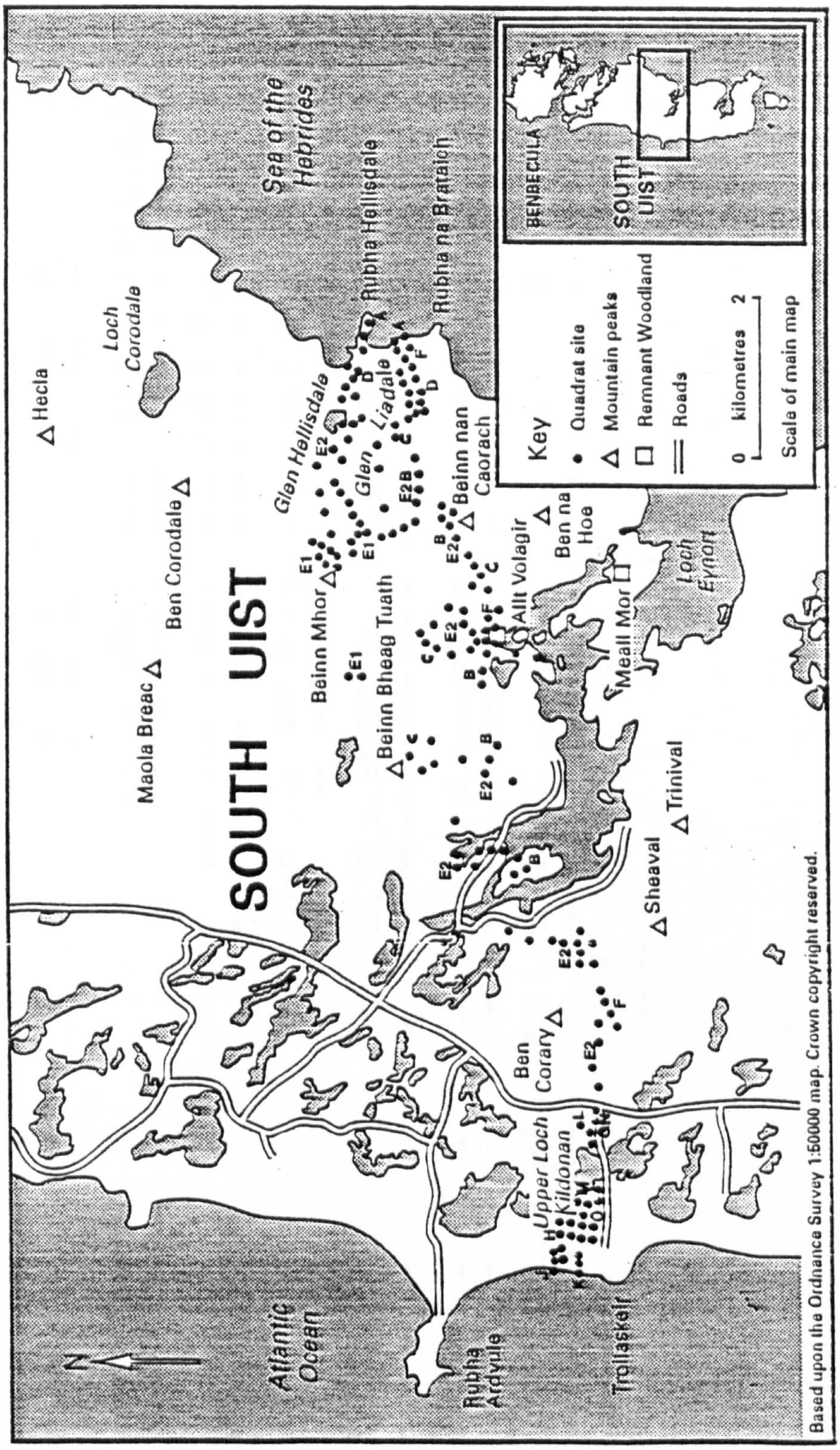
Coastal communities

Festuca rubra - Armeria maritima - Plantago coronopus maritime grassland community (Group A).

This community occurs above the tidal zone of the sea lochs and sheltered bays of the east coast. Festuca rubra, Armeria maritima and Plantago coronopus are the main characterising species with Glaux maritima, Plantago maritima and Poa annua as associated species. It equates with category MC8 Plantago coronopus sub community of the NVC and PM. The pH of quadrats in this group is relatively high (mean 6.4) but species diversity is low (mean 4.5) due to salinity effects.

Elymus farctus foredune community (Group J/K).

The fore dunes of the west coast are characterised by this type. Elymus farctus and bare sand are the constants with Atriplex hastata, Plantago lanceolata, Cakile maritima and Taraxacum officionale as common associates. The equivalent NVC group is SD5 and this community is recognised by PM. The fresh shell sand characteristic of these quadrats gives the highest mean pH (7.84),



Based upon the Ordnance Survey 1:50000 map. Crown copyright reserved.

Figure 21. Location of plant communities on the South Uist transect

Species	TWINSPAN GROUP										
	A	B	C1	C2	D	E1	E2	F	G	H	I
Pedicularis palustris			II 1	I 1	+ 1		+ 1				
Drosera intermedia			IV 2	+ 1							
Drosera rotundifolia		+ 1	III 2	II 2	+ 1						
Erica tetralix		III 2	IV 2	V 3	+ 1	+ 1	+ 1				
Listera cordata			+ 1								
Narthecium ossifragum			V 3	III 2	II 2	I 3					
Pinguicula vulgaris			I 1	II 1		+ 1					
Polygala serpyllifolia			+ 1	+ 1			+ 1				
Polygala vulgaris			IV 2	IV 2	II 2		II 1	+ 1			
Juniperus communis				+ 1							
Molinia caerulea		IV 5	VI 5	III 4			II 4	II 5	+ 1		
Eriophorum vaginatum		+ 1	III 4	IV 4	III 3	+ 1					
Schoenus nigricans			V 4								
Scirpus cespitosus			VI 4	V 5	II 5	+ 1					
Campylopus atrovirens			IV 4	+ 1		III 1					
Leucobryum glaucum			+ 1	I 3							
Pleurozia purpurea			IV 4	I 3		I 1					
Racomitrium lanuginosum			IV 4	III 3	II 3	IV 2					
Sphagnum cuspidatum			+ 5	+ 5							
Cladonia portentosa			VI 2	III 3							
Cladonia uncialis			VI 1	III 3	+ 1	I 1					
Antennaria dioica				+ 1							
Calluna vulgaris		III 4	VI 4	VI 4	VI 5	III 3	III 4	III 4			
Dactylorhiza maculata				I 1	I 1		+ 1				
Empetrum nigrum					I 3	+ 1					
Erica cinerea			II 2	III 3	III 2	I 1	I 1				
Hypericum elodes		+ 1									
Potamogeton polygonifolius		IV 4									
Eriophorum angustifolium		V 4	IV 3	III 4	III 2		II 2		III 5		
Bazzania trilobata					+ 4						
Hypnum cupressiforme			II 3	III 4	VI 5	III 1	II 1	+ 5	+ 2		
Sphagnum capillifolium			IV 5	IV 5	IV 5	III 2	I 3	+ 3			
Sphagnum palustre		IV 3									
Menyanthes trifoliata		II 3		+ 5							
Plantago coronopus	VI 4										
Deschampsia flexuosa			+ 3	+ 3		+ 3		+ 5			
Juncus squarrosus			+ 3	+ 3	III 4	II 5					
Lepidozia setacea			+ 1			+ 1					
Scapania nemorea			+ 2	II 1	I 1	II 1	+ 1				
Armeria maritima	VI 5					II 3					
Glaux maritima	IV 5								+ 3		
Plantago maritima	IV 3										
Rhytidiadelphus loreus			+ 1	+ 1	IV 3	V 3	II 2				
Pedicularis sylvatica		+ 1		+ 2			+ 3				
Potentilla erecta		IV 3	V 2	V 3	V 3	V 3	VI 3	IV 4	+ 2		
Dicranum scoparium			II 1	II 2		II 1	II 2	II 2			
Sphagnum papillosum			III 4	II 3	III 4	III 3	III 4	III 5			
Sphagnum recurvum		III 5	I 5				II 5		III 5		
Carex echinata		II 3		I 2		+ 2	II 2		+ 3		
Vaccinium myrtillus					II 4	III 3	+ 3	+ 4			
Nardus stricta			+ 5		III 5	III 5	I 2				
Carex binervis				+ 2	III 5	III 2	+ 4	I 3			
Carex dioica		II 4		+ 2		+ 4	+ 4	+ 1			
Carex pilulifera				+ 2		III 2					
Breutelia chrysocoma			+ 1	+ 1	+ 1	II 1		+ 1			
Dicranum majus					I 1		I 1	+ 1			
Sphagnum auriculatum			+ 3			I 1					
Cladonia fimbriata				+ 2		II 1					
Saccogyna viticulosa				+ 1			+ 1	+ 1			
Aulacomnium palustre				+ 3		II 2	+ 5				
Plagiothecium undulatum				+ 3	II 1	III 3	III 1	I 1			+ 1
Allium ursinum					+ 2		+ 1	+ 5			
Hypericum pulchrum					+ 1	+ 1	+ 1	+ 1			
Luzula sylvatica					+ 5	III 2		I 2			
Polytrichum commune				+ 2	III 3	V 3	III 3	III 4			
Brassica rapa									I 1		
Cardamine amara									III 4		
Scutellaria minor							+ 2		+ 2		
Eleocharis uniglumis									+ 5		
Juncus effusus		IV 4					III 3	III 4	V 4		+ 4
Hylocomium splendens					II 3	III 1	III 3	II 5	+ 3		+ 2
Digitalis purpurea								III 3			
Fragaria vesca								+ 3			
Hedera helix								I 3			
Hyacinthoides non-scripta								II 4			
Hypericum perforatum								II 1			
Lonicera periclymenum								+ 3			
Oxalis acetosella								III 2			
Primula vulgaris							I 1	III 3			
Rubus fruticosus agg.								II 2			
Teucrium scorodonia								I 2			
Valeriana officinalis							+ 2	+ 1			
Betula pubescens								II 4			
Corylus avellana								II 2			
Populus tremula								I 4			
Sorbus aucuparia								+ 4			
Salix aurita						+ 3	I 5	III 4			
Holcus mollis								+ 4			
Luzula pilosa								I 1			
Atrichum undulatum								I 1			
Camptothecium sericium								I 4			
Tortula intermedia						+ 1		+ 3			
Asplenium adiantum-nigrum								+ 2			
Blechnum spicant				+ 1	+ 3	+ 2	I 2	III 3			
Cystopteris fragilis								+ 3			
Osmunda regalis								+ 3			
Pteridium aquilinum					+ 2		II 3	VI 4			
Alchemilla glabra						+ 1	+ 1				
Cochlearia officinalis						I 3					
Hieracium pilosella						+ 3					

Table 6. <u>Plant communities of the South Uist transect</u>

Species	A	B	C1	C2	D	E1	E2	F	G	H	I
Oxyria digyna						I 1					
Sedum rosea						I 1	+ 2	+ 2			
Saxifraga stellaris						II 2	+ 1				
Thalictrum alpinum						II 3					
Thymus serpyllum						III 3	II 3	+ 3			
Carex panicea						II 3	+ 1				
Juncus bufonius						I 1	+ 1				
Andreaea rupestris						+ 1					
Bartramia pomiformis						+ 1					
Brachythecium rivulare						+ 1	+ 1				
Bryum pseudotriquetrum						+ 1					
Dicranum squarrosus						+ 4	+ 3				
Diplophyllum albicans						I 2					
Lycopodium selago						II 2					
Preissia quadrata						+ 1					
Riccia fluitans						+ 1					
~~*Sphagnum squarrosus*~~						~~+ 2~~					
Selaginella selaginoides						III 1					
Asplenium trichomanes						+ 1					
Hymenophyllum wilsonii						I 1	+ 1				
Cladonia furcata						+ 1					
Psoroma hypnorum						II 1					
Stereocaulon vesuvianum						I 1					
Philonotis fontana						I 3					
Polypodium vulgare						+ 1					
Solidago virgaurea						+ 1					
Plagiochila spinulosa						+ 1					
Anagallis tenella							I 1				
Cardamine flexuosa							I 1				
Cirsium palustre							I 1	+ 2			
Lysimachia nemorum							I 1				
Rumex acetosella							I 5				
Stellaria alsine							+ 1				
Viola riviniana						IV 2	IV 3	II 2	+ 1		
Aira praecox							+ 1				
Festuca ovina		II 4		+ 5		V 4	V 5	III 5			
Carex caryophyllea				+ 1		III 2	III 2	+ 3			+ 1
Carex pulicaris							+ 2				
Plagiochila asplenioides							+ 1				
Pseudoscleropodium purum							II 2	II 1			
Ophioglossum vulgatum							+ 1				
Sedum anglicum							+ 1				
Triglochin palustris							+ 3				
Galium saxatile						III 2	III 3	IV 3			
Hieracium spp.				+ 2			III 1	I 2			
Rhytidiadelphus triquetrus							I 1	+ 3			
Dicranella heteromalla						+ 2	+ 3	+ 3			
Thuidium tamariscinum				+ 2	I 1	III 2	III 2	III 3			
Dryopteris dilatata				+ 1			II 2	II 5			
Agrostis capillaris			+ 2	+ 4	II 3	VI 3	VI 4	IV 5	III 4		II 5
Ranunculus ficaria							III 3	III 4			II 2
Veronica officinalis							+ 1	II 2			+ 1
Anthoxanthum odoratum						II 2	V 3	V 4			III 3
Rhytidiadelphus squarrosus				+ 3	I 3	III 1	IV 3	IV 4	+ 2	+ 5	+ 2
Lophocolea bidentata					II 1	+ 1	II 1		III 4		+ 1
Agrostis canina					III 2	III 3	II 4	II 2	+ 5	+ 4	II 1
Luzula campestris				+ 3		II 1	III 3	+ 1			III 1
Eurhynchium praelongum					+ 1	+ 2	+ 1	II 4	I 3		II 2
Prunella vulgaris						I 1	II 1				+ 2
Peltigera rufescens						I 1	II 2			+ 3	
Pellia epiphylla							+ 3				
Carex nigra			+ 2	III 3	I 3	IV 3	IV 4	+ 1	IV 3		
Cardamine pratensis						II 1	+ 1		IV 3		II 1
Epilobium palustre		II 1				+ 1	II 1		V 3		
Rumex acetosa						II 4	III 2	III 3	V 2		III 2
Holcus lanatus							IV 3	III 4	IV 4	+ 4	V 3
Pleurozium schreberi			+ 1	I 1	III 1	II 1	III 2	+ 2	III 4	III 4	II 1
Sedum acre							I 2	+ 3		+ 1	+ 3
Stellaria media								+ 2			+ 1
Carex flacca		III 3				I 4					II 3
Sagina procumbens						+ 1	II 3	+ 2	+ 3		+ 5
Poa pratensis							I 3		III 1		II 2
Hydrocotyle vulgaris		V 3					II 2	+ 1	III 4		
Potentilla palustris		III 4					I 3		III 4		
Iris pseudacorus							I 2		V 5		
Stellaria palustre											
Eurhynchium striatum								+ 1	III 4		
Mnium punctatum						II 1	I 1				
Bellis perennis							II 5			III 1	III 3
Cerastium glomeratum						III 1	II 1	I 1		III 2	IV 2
Trifolium repens							IV 4			V 4	VI 4
Poa trivialis						+ 1	I 3	+ 5	+ 1		II 4
Leontodon autumnalis							II 2			III 2	II 2
Taraxacum officinale						II 1	+ 1			III 1	
Achillea millefolium							+ 1	+ 5		III 2	II 1
Atriplex hastata										+ 1	
Anthyllis vulneraria										+ 5	
Cakile maritima										+ 1	
Capsella bursa-pastoris											+ 1
Centaurea nigra										II 3	II 2
Centaurea scabiosa											+ 5
Cerastium semidecandrum										III 3	+ 1
Cirsium vulgare										+ 1	
Crepis capillaris										II 1	+ 1
Daucus carota											
Erodium cicutarium										II 1	+ 3
Erophila verna											+ 1
Euphrasia officinalis agg.						I 1	II 1			IV 2	III 2
Galium verum										IV 4	+ 1
Geranium molle										+ 3	+ 2
Heracleum sphondylium										IV 4	
Honkenya peploides										II 5	
Lotus corniculatus							I 2	+ 5		IV 3	II 3
Myosotis arvensis										III 1	+ 1
Plantago lanceolata							III 3	+ 5		V 3	III 3
Polygonum persicaria											+ 1
Saxifraga tridactylites										III 1	
Senecio jacobaea							I 1			IV 2	II 1

Species	A	B	C1	C2	D	E1	E2	F	G	H	I
Silene alba										+ 1	
Sinapis arvensis										III 2	III 2
Sonchus asper											+ 1
Thalictrum minus							+ 3			III 2	
Trifolium pratense										+ 2	+ 1
Urtica dioica								+ 3		II 3	
Veronica agrestis										II 2	
Viola tricolor										III 1	+ 1
Elymus farctus											
Ammophila arenaria										IV 3	
Avena strigosa										+ 3	
Cynosurus cristatus											II 1
Festuca rubra	IV 5						I 5			VI 5	VI 5
Poa annua	IV 2									II 2	
Poa subcaerulea										III 3	IV 4
Brachythecium albicans										+ 1	I 2
~~*Tortula ruraliformis*~~										~~III 2~~	~~+ 2~~
Ranunculus acris						II 2	III 1		III 3	III 1	IV 3
Ranunculus repens							+ 1			III 3	III 4
Rhinanthus minor							I 1			IV 1	IV 5
Carex arenaria										III 3	+ 2
Anacamptis pyramidalis											II 1
Potentilla anserina							+ 2		III 3	+ 3	IV 5
Equisetum arvense							I 1		III 1		III 5
Vicia cracca										II 2	IV 1
Brachythecium rutabulum							+ 3			+ 5	III 2
Angelica sylvestris	–						+ 1	II 4			I 3
Dactylorhiza majalis							I 1				III 1
Agrostis stolonifera							+ 4	+ 4	III 4		IV 5
Juncus articulatus											+ 4
Montia fontana						+ 2	+ 1				+ 4
Glyceria fluitans											+ 1
Caltha palustris									I 2		
Filipendula ulmaria									III 2		
Filipendula vulgaris											
Galium palustre							+ 1		III 1		
Hippuris vulgaris											
Mentha aquatica									+ 4		
Polygonum bistorta											
Triglochin maritima											
Phragmites australis									II 2		+ 2
Carex demissa											
Eleocharis palustris											
Typha latifolia											
Calliergon cuspidatum						+ 1	+ 1				+ 1
Fontinalis antipyretica											
Equisetum palustre									II 1		
Equisetum fluviatile											
Rumex crispus											
Ranunculus flammula		III 3				II 1			II 1		
Viola palustris		II 4		+ 1	+ 3		+ 4		II 2		+ 2
Bare peat		II 5	III 4	III 4	+ 3	I 3	II 3		III 4		
Bare rock			II 3	+ 3		IV 3	II 3	II 3			
Bare sand										IV 3	+ 5
Litter			+ 2	IV 5	III 4		+ 2	IV 5	+ 5	II 3	+ 4
Standing water		VI 5	I 4	+ 5							

Group (N)	Statistics	Altitude (m)	Aspect (Cos deg)	Slope (deg)	% Soil moisture	Soil O.M.	Sand/soil/ peat depth (cm)	pH	Species richness
A (2)	Mean	0.5	0.85	7.5	264.5	57.98	41.3	6.40	4.5
	S.E.mean	0.5	0.15	7.5	59.5	0.98	33.7	0.60	0.5
	Max	1.0	1.00	15.0	323.9	59.00	75.0	6.80	5.0
	Min	0.0	0.71	0.0	205.0	57.00	7.6	5.80	4.0
B (5)	Mean	45.4	0.07	21.8	1985.0	72.26	71.2	6.36	8.8
	S.E.mean	16.2	0.41	17.2	285.0	3.80	3.3	0.16	2.0
	Max	75.0	1.00	25.0	2710.0	85.36	75.0	6.80	13.0
	Min	2.0	-0.97	0.0	1308.0	62.46	58.0	5.80	4.0
C1 (17)	Mean	66.4	0.49	4.59	839.2	80.73	58.1	4.35	13.2
	S.E.mean	18.6	0.19	1.76	46.0	3.38	6.6	0.10	0.7
	Max	300.0	1.00	25.00	1209.6	95.26	75.0	5.20	20.0
	Min	10.0	-0.77	0.00	540.9	42.64	8.2	3.30	9.0
C2 (39)	Mean	65.0	0.00	10.0	906.0	82.93	59.2	4.40	10.3
	S.E.mean	9.3	0.12	1.4	101.0	1.75	3.6	0.08	0.4
	Max	250.0	1.00	40.0	3132.0	97.51	75.0	5.60	16.0
	Min	1.0	-0.99	0.0	193.0	53.75	3.4	3.60	6.0
D (21)	Mean	195.6	-0.07	12.7	594.3	81.36	60.2	4.50	9.3
	S.E.mean	42.4	0.17	1.5	55.7	2.59	3.7	0.11	0.7
	Max	605.0	1.00	27.0	1192.7	97.81	75.0	6.00	14.0
	Mean	4.0	-1.00	1.0	16.6	57.00	24.2	3.80	3.0
E1 (20)	Mean	445.7	0.16	30.45	470.3	54.74	24.4	5.21	18.8
	S.E.mean	25.7	0.14	5.39	63.7	3.95	5.3	0.14	1.7
	Max	610.0	1.00	90.00	1142.5	89.79	75.0	6.80	35.0
	Min	280.0	-0.99	10.00	72.4	16.39	1.8	4.20	10.0
E2 (29)	Mean	65.1	0.25	13.33	417.0	53.59	37.1	5.09	17.6
	S.E.mean	15.3	0.13	3.42	71.6	4.40	4.7	0.11	1.2
	Max	325.0	1.00	75.00	1637.5	93.05	75.0	6.40	34.0
	Min	0.0	-1.00	0.00	16.7	10.34	4.2	4.20	9.0
F (18)	Mean	38.4	-0.16	20.56	404.3	60.13	33.9	4.60	13.3
	S.E.mean	10.7	0.13	4.43	59.7	5.84	3.8	0.18	1.1
	Max	150.0	0.77	80.00	921.5	88.93	75.0	6.20	24.0
	Min	1.0	-0.97	3.00	41.3	12.56	1.6	3.80	6.0
G (8)	Mean	8.1	-0.01	3.12	738.0	60.33	53.3	5.56	12.1
	S.E.mean	3.0	0.29	1.08	153.0	5.97	9.2	0.31	1.0
	Max	21.0	1.00	9.00	1546.0	78.94	75.0	7.40	16.0
	Min	0.0	-1.00	0.00	172.0	30.24	18.6	4.60	8.0

Table 7. Summary environmental statistics of the 16 TWINSPAN plant community groups from South Uist transect (212 quadrats)

Group (N)	Statistics	Altitude (m)	Aspect (Cos deg)	Slope (deg)	% Soil moisture	Soil O.M.	Sand/soil/peat depth (cm)	pH	Species richness
H (14)	Mean	6.36	0.16	6.4	4.4	3.11	57.3	7.36	12.7
	S.E.mean	1.58	0.16	1.6	0.3	0.51	5.1	0.07	0.9
	Max	15.00	1.00	20.0	10.3	6.81	75.0	7.80	17.0
	Min	3.00	-0.87	0.0	0.7	0.81	25.2	6.80	7.0
I (16)	Mean	5.37	0.06	4.0	39.6	9.38	37.8	6.98	13.8
	S.E.mean	0.66	0.16	0.9	7.8	1.78	5.9	0.19	0.9
	Max	14.00	1.00	10.0	117.5	22.08	75.0	7.60	20.0
	Min	3.00	-0.94	0.0	3.2	1.19	18.0	5.40	8.0
J/K (5)	Mean	3.00	-0.03	31.0	2.6	0.82	73.2	7.84	7.0
	S.E.mean	0.63	0.02	2.2	1.5	0.04	1.6	0.10	1.8
	Max	5.00	0.00	35.0	8.7	0.90	75.0	8.00	12.0
	Min	2.00	-0.09	23.0	0.4	0.66	67.0	7.60	2.0
L (5)	Mean	3.00	-0.30	4.0	320.7	36.97	59.3	7.12	13.0
	S.E.mean	0.32	0.17	1.6	71.6	8.67	9.0	0.10	0.9
	Max	4.00	0.34	10.0	542.3	60.64	75.0	7.40	15.0
	Min	2.00	-0.70	1.0	128.1	9.34	31.0	6.90	10.0
M (5)	Mean	1.92	0.03	3.0	124.5	8.16	73.6	7.32	10.4
	S.E.mean	0.74	0.32	0.8	68.3	4.96	0.9	0.10	1.6
	Max	4.00	0.87	6.0	392.1	27.25	75.0	7.60	16.0
	Mean	0.10	-0.50	1.0	34.1	1.05	71.0	7.00	6.0
N (4)	Mean	4.00	0.32	3.0	406.0	43.00	65.9	5.90	9.3
	S.E.mean	0.71	0.43	1.1	113.0	9.11	9.1	0.39	2.0
	Max	6.00	1.00	5.0	620.0	63.78	75.0	6.90	14.0
	Min	3.00	-0.94	0.0	128.0	25.39	38.6	5.20	5.0
O (3)	Mean	3.33	-0.07	1.0	638.0	33.61	75.0	7.33	14.3
	S.E.mean	0.33	0.54	0.6	252.0	7.46	0.0	0.18	0.3
	Max	4.00	1.00	2.0	997.0	42.25	75.0	7.60	15.0
	Min	3.00	-0.64	0.0	152.0	18.76	75.0	7.00	14.0

along with the lowest mean soil moisture content (2.6%) and soil organic matter (0.82)

Festuca rubra - Galium verum dune/machair community (Group H).
These quadrats occur inland from the foredunes and represent the machair type found nearest the sea. *Festuca rubra* and *Galium verum* are the diagnostic species but *Plantago lanceolata*, *Trifolium repens*, *Achillea millifolium* together with bare sand are also common. There is a sizeable list of associated species including *Ammophila arenaria*, *Bellis perennis*, *Carex arenaria*, *Carex semidecandrum*, *Euphrasia officinalis*, *Heraclium sphondylum*, *Leontodon autumnalis*, *Lotus corniculatus*, *Pleurozium schreberi*, *Poa subcaerulea*, *Ranunculus acris*, *Ranunculus repens*, *Rhinanthus minor*, *Senecio jacobaea*, *Sinapis arvensis*, *Taraxacum officinale*, *Thalictrum minus*, *Tortula ruraliformis* and *Viola tricolor*. The NVC category SD10 is closest to this community type (*Festuca rubra*-*Galium verum* dune but it represents the first of two special sub-groups for high diversity machair. PM recognises this type although with *Koeleria gracilis* as a characteristic species. However this was not recorded as present in this part of South Uist. Robertson (1984) described this type as eyebright-red fescue dune.

The diagnostic environmental factors of this group are high pH (mean 7.36); low soil moisture content (mean 4.4%) and organic matter content (mean 3.1%) and relatively high species richness (mean 12.0; maximum 17.0).

Festuca rubra - Potentilla anserina - Trifolium repens - Agrostis stolonifera inland grassland community (Group I).
The majority of the machair shell sand quadrats located further inland are contained in this group which is distinguished by its very high species diversity (mean 13.8; max 20.0). Eleven of the most distinctive machair species are dominant *Festuca rubra*, *Potentilla anserina*, *Trifolium repens*, *Agrostis stolonifera*, *Holcus lanatus*, *Plantago lanceolata*, *Rhinanthus minor*, *Poa*

subcaerulea, Cerastium glomeratum, Vicia cracca and Ranunculus acris. Anthoxanthum odoratum, Bellis perennis, Dactylorhiza majalis, Sinapsis arvensis, Euphrasia officinalis, Equisetum arvensis, Rumex acetosa, Luzula campestris, Ranunculus repens and Brachythecium rutubulum are common associates. TWINSPAN also defined two sub-groups containing combinations of the above species together with Agrostis stolonifera, Ranunculus repens and Sinapis arvensis or Agrostis canina, Agrostis capillaris and Rumex acetosa. The first sub-group comprised quadrats nearer the sea and the second further inland. As a specialised community type, the first community sub-group appears to lie close to the NVC category MG11 (Festuca rubra - Agrostis stolonifera- Potentilla anserina lowland grassland subject to inundation by fresh or brackish water). The second sub-group represents a specialised high diversity shell sand sub-community with Agrostis canina, and Agrostis capillaris replacing Agrostis stolonifera as characteristic species. As such it remains a variant of category MG11. There appears to be no exact match in the community types of PM.

Environmentally, the quadrats of this group are typical of the machair plain. Compared with Group H, the mean pH is lower (I: 6.98, H: 7.36). Soil moisture and organic matter content are slightly increased and mean species richness is slightly higher (I: mean 13.8, Max 20.0; H: mean 12.7, max 17.0).

Machair lake margin communities.

Iris pseudacorus inner machair communities (Groups G and N).

Scattered iris clumps are a significant community type of the inner machair plain. They tend to occur in wet or damp basins within the inner machair and on the margins of lochs and small ponds. Iris pseudacorus is the principal species but as Table 6 (Groups G and N) shows there is a large number of associated species and overall diversity of these communities is high. Commonest associates in both groups are Cardamine pratensis, Epilobium palustre, Rumex acetosa, Holcus lanatus and Carex nigra.

Differentiation between the two groups is shown primarily by the presence of *Montia fontana* in Group N together with a wide range of loch-side species such as *Caltha palustris*, *Galium palustre*, *Ranunculus repens*, *Potentilla anserina*, *Brachythecium rutubulum* and *Caliergon cuspidatum*. In Group G *Hydrocotyle vulgaris*, *Potentilla palustris*, *Ranunculus acris* and *Filipendula ulmaria*,are distinguishing species, as is bare peat. This type corresponds in part with the NVC category M28 - *Iris pseudacorus* / *Filipendula ulmaria* mire within the general class of fen meadow. In this situation, however, *Filipendula* is not widely represented. PM agrees with this state and Adam (1981) believes this type to be commonplace on marshes in western Scotland.

The environmental conditions typical of both groups are similar. The pH is significantly lower (G: mean 5.56, N: mean 5.90) when compared with the machair communities. As they are found on lake margins and in wet basins, soil moisture and soil organic matter values are high.

Phragmites australis machair swamp community (Group O).

These swamp communities occur in infilled machair loch areas and on the transect were located adjacent to Upper Loch Kildonain (GR NF729280). *Phragmites australis*, *Angelica sylvestris*, *Dactyloriza majalis* and *Caltha palustris* are the most constant species, with a diversity of associates, including *Carex nigra*, *Rumex acetosa*, *Pleurozium schreberi*, *Stellaria palustris*, *Agrostis stolonifera*, *Equisetum palustre* and *Viola palustris*. This group corresponds well with the NVC category S4 (*Phragmites australis* swamp and reed beds) but it difficult to allocate it to any sub-community. Situated on the machair these wet sites have a relativley high pH (mean 7.33) and species richness (mean 14.3).

Potentilla anserina - Carex nigra - Vicia cracca inner machair community (Group L).

This group constitutes a distinct sub-community of the machair occurring on the damper areas above the machair lochs. It is characterised by a dominant cover of Potentilla anserina, Carex nigra and Vicia cracca with a high diversity of other species, some of which are characteristic of drier machair areas (Group I), for example, Rhinanthus minor, Rumex acetosa, Leontodon autumnnalis and Dactylorhiza majalis, while others are indicative of the true lake margin types (Groups M,N and O), for example, Caltha palustris, Hydrocotyle vulgaris, Equisetum arvense, Filipendula ulmaria, Mentha aquatica, Caliergon cuspidatum and Equisetum fluvatile. This is a transitional community within the dune grassland and lake margin classes of the NVC and is represented in the classification by category SD17 (Potentilla anserina- Carex nigra dune slack). This type is clearly recognised by PM. As with group O both pH and species richness is high.

Eleocharis palustris lake margin community (Group M).

In the five quadrats in this group Eleocharis palustris is 100% constant with Ranunculus flammula, Caliergon cuspidatum, Mentha aquatica and Agrostis stolonifera as associated species. Such communities occur on the margins of lochs in the inner machair plain. They correspond to community type S19 of the NVC.

Neutral / acid grassland communities.

Agrostis capillaris - Festuca ovina grasslands (Group E).

This very large group has three diagnostic species; Agrostis capillaris, Festuca ovina and Potentilla erecta with Viola riviniana, Rhytidiadelphus loreus, Polytrichum commune, Rhytidiadelphus lanuginosum and Nardus stricta as associates with high constancy along with bare rock. The second (E2) included Anthoxanthum odoratum, Luzula campestris, Holcus lanatus and Trifolium repens. Both groups have other species in common, notably Agrostis canina, Calluna vulgaris, Galium saxatile, Thuidium tamariscinum and Plagiothecium undulatum.

The first group (E1) is generally more acidic in nature and represents typical upland Agrostis - Festuca pasture (mean altitude 446m.). They are located on steep slopes at middle to higher altitudes across the Beinn Mhor massif. The second group (E2) are found at lower altitudes (mean altitude 65m.) in the zone between the machair and the uplands. Soils of quadrats in both groups E1 and E2 are acidic (E1: mean pH 5.21, E2: mean pH 5.09) and both groups have significantly higher soil organic matter content than the machair communities previously described. Species richness is the highest of all groups (E1: mean 18.8, max 35.0, E2: mean 17.6, max 34.0)

The whole group corresponds with section U4 of the NVC with E1 representing the typical sub community and E2 the *Holcus lanatus* - *Trifolium repens* sub community. This division is also recognised by PM.

Pteridium aquilinum - *Potentilla erecta* - *Anthoxanthum odoratum* bracken infested grasslands (Group F).

Pteridium aquilinum patches occur in a variety of locations across the transect primarily on the peatlands at lower altitudes. Usually, bracken has invaded areas of *Agrostis* - *Festuca* pasture (Group E). Associated species are *Potentilla erecta*, *Anthoxanthum odoratum*, *Agrostis capillaris*, *Agrostis canina*, *Festuca ovina*, *Rhytidiadelphus sqarrosus* and *Galium saxatile*. Litter accumulation is common. A number of these quadrats also contain *Salix aurita* demonstrating that they may be indicative of former woodland areas. Several quadrats were recorded from Allt Volagir (GR NF799291) described as the best example of natural woodland in the Outer Hebrides by Spence (1960) and Curry (1979).

Group F correlates closely with NVC category U20 (*Pteridium aquilinum* - *Galium saxatile* community; *Anthoxanthum odoratum* sub-community) and is also recognised by PM. These bracken infested pastures are typically found at low altitude (mean 38m) and have a lower pH than the previous grassland group (E; mean 4.6). Species richness is also distinctly lower.

Peat, wet heathland and bog communities.

A large part of the eastern half of the South Uist transect is covered by blanket mire with the surface broken by rock outcrops, lochs and lochans. The vegetation of the area is distributed as a mosaic of two major communities (Groups B and C) with group C being further sub-divided.

Eriophorum angustifolium bog pool community (Group B).

Within the blanket mire there are frequently pools of standing water over considerable depths of peat. These are colonised by Eriophorum angustifolium together with Hydrocotyle vulgaris, Juncus effusus, Potentilla erecta, Molinia caerulea, Potamogeton polygonifolius and Sphagnum palustre. This type is clearly recognised in the NVC as M3 (Eriophorum angustifolium bog pool community) and similarly by PM.

Molinia caerulea - Scirpus cespitosus - Erica tetralix - Calluna vulgaris wet heath.

This vegetation type occurs extensively in the upland eastern two-thirds of the transect. They correspond to the Scirpus cespitosus- Erica tetralix wet heath of the NVC category M15. The four characteristic species are found in varying combinations depending on local site conditions. The TWINSPAN analysis separated two distinct sub-groups, both of which contain the four main species as constants together with Potentilla erecta and Cladonia uncialis, Cladonia portentosa, Eriophorum angustifolium, Eriophorum vaginatum, Rhacomitrium lanuginosum, Sphagnum capillifolium and bare peat. However, a large sub-group (C1) containing only these species could be seperated from a second smaller group of 17 quadrats (C2) which had Cladonia uncialis, Cladonia portentosa, Narthecium ossifragum, Schoenus nigricans, Polygala vulgaris and Drosera intermedia as associated species with 50% constancy, as well as Drosera rotundifolia, Pleurozium purpurea, Campylopus atrovirens and Sphagnum papillosum as associated species. Schoenus nigricans is a particularly good indicator for this second sub-group. The dominance of Calluna vulgaris also tends to be higher. Within the NVC category M15, this sub group (C2) would appear to correspond to the Cladonia spp sub-community. PM agrees with this classification.

The pH of soil/peat samples in this group were the most acid of the transect (C1; mean 4.35; C2 mean 4.40). Soil moisture and organic matter content is high in the peat dominated soils and in the basins the peat is regularly over 75cm. in depth. Altitude, however, is comparitively low (C1; mean 66m. C2; mean 65m.) and these quadrats correspond to the middle plateau lands below the Beinn Mhor massif and the peatland areas between the machair and the uplands.

Dry heathland.

Calluna vulgaris heath community (Group D).

These quadrats correspond to communities of pure heather, often in the degenerative phase of the Calluna cycle (Gimingham 1964a). Most of these quadrats lie in Glen Liadale and Glen Hellisdale on the east side of the island (GR NF830300 and NF825313), where more sheltered and slightly drier conditions occur and grazing and burning pressure is reduced. Hypnum cupressiforme, Potentilla erecta, Sphagnum capillifolium and Rhytidiadelphus loreus are the main associated species. In the NVC classification these occur in type H9 (Calluna vulgaris - Deschampsia flexuosa heath). On the South Uist transect, Deschampsia is virtually absent however due to the maturity of the stands and consequently this group would appear to correspond to the NVC species-poor sub-community. PM do not list Deschampsia as a common associate.

Ordination and the definition of environmental gradients.

The joint biplot of species and environmental analyses of the CANOCO ordination is presented in Figure 22 and the matrix on correlation coefficients within and between ordination axes and environmental factors is shown in Table 8. For ease of interpretation, only those species mentioned in the above

characterisation of plant community groups have been plotted on the ordination diagram (Figure 22).
The highest correlations with the first axis are pH (r = 0.902) and soil organic matter content (r = 0.578) (Table 8). Species typical of the high pH environment of the machair are found to the centre right of the biplot (figure 22). Organic matter is negatively correlated with the first axis since the dune soils contain little organic matter - in contrast to the peatlands which are indicated by species at the left end of the first axis. Soil moisture also shows a strong negative correlation with the first axis (r = o.513) being closely correlated with organic matter. The percentage variation in the species data explained by the first axis of the canonical correspondence analysis was 33.5%.

Soil/sand/peat depth (r = 0. 612), soil moisture content (r = 0.578), slope angle (r = 0. 482) and altitude (r = -0.480)are most strongly correlated with the second axis. The high positive intercorrelation between slope and altitude is to be expected, as are the negative ones between slope and soil moisture and slope and soil depth. Aspect emerges as being of little or no significance. Percentage explanation of variability in the species data on this second axis is 19.5%.

Altitude is also even more strongly correlated with the third axis (percentage explanation 15.2%) with no other high correlations. This almost certainly reflects a biotic gradient, with high degrees of ecosystem modification at lower altitudes, declining as height increases. The cumulative explanation of the first three axes is approximately 68% with the explanatory power of the fourth axis reduced to 11.4%.

In Figure 22, the species mentioned as characterising each of the 16 TWINSPAN groups have been plotted on the CONOCO biplot and their TWINSPAN group membership (A - O) has been superimposed on Figure 23. This shows the relative positions of the 16 plant communities.

	AX 1	AX 2	AX 3	AX 4	ALT	SLOPE	AS	SM	OM	SSPD	PH
AX 1	1.000										
AX 2	-0.009	1.000									
AX 3	0.011	0.042	1.000								
AX 4	-0.005	-0.007	-0.007	1.000							
ALT	-0.368	-0.480	0.616	0.018	1.000						
SLOPE	-0.144	-0.483	0.064	0.555	0.416	1.000					
AS	0.030	0.042	0.030	0.140	-0.101	-0.022	1.000				
SM	-0.513	0.578	0.196	0.286	0.047	-0.105	0.079	1.000			
OM	-0.856	0.338	0.022	-0.070	0.137	-0.093	-0.069	0.644	1.000		
SSPD	-0.011	0.612	0.156	-0.267	-0.267	-0.401	0.005	0.355	0.297	1.000	
PH	0.902	0.105	0.204	0.133	-0.241	-0.095	0.044	-0.315	-0.784	-0.008	1.000

AX 1 - Ordination axis 1
AX 2 - Ordination axis 2
AX 3 - Ordination axis 3
AX 4 - Ordination axis 4
ALT - Altitude
SLOPE - Slope angle

AS - Aspect
SM - Soil moisture
OM - Soil organic matter content
SSPD - Mean sand/soil/peat depth
PH - pH

Table 8. Matrix of Pearson product moment correlation coefficients between ordination axes and environmental factors across the South Uist transect. (n = 212; correlations >+/-0.20 are significant at the 0.01 level)

Key to plot

Environmental variables

ALT - altitude
SLOPE - slope
AS - aspect
SM - soil moisture
OM - soil organic matter content
SSPD - mean soil/sand/peat depth
pH - pH

Species

Ami - *Achillea millifolium*
Aca - *Agrostis canina*
Ac - *Agrostis capillaris*
As - *Agrostis stolonifera*
Aa - *Ammophila arenaria*
Asy - *Angelica sylvestris*
Ao - *Anthoxanthum odoratum*
Am - *Armeria maritima*
Ah - *Atriplex hastata*
Bpt - *Bare peat*
Bp - *Bellis perennis*
Br - *Bare rock*
Bs - *Bare sand*
Cc - *Caliergon cuspidatum*
Cv - *Calluna vulgaris*
Cpa - *Caltha palustris*
Cm - *Cakile maritima*
Ca - *Campylopus atrovirens*
Cp - *Cardamine pratensis*
Cn - *Carex nigra*
Cg - *Cerastium glomeratum*
Cpo - *Cladonia portentosa*
Cu - *Cladonia uncialis*
Dm - *Dactylorhiza majalis*
Di - *Drosera intermedia*
Dr - *Drosera rotundiafolia*
Elp - *Eleocharis palustris*
Ef - *Elymus farctus*
Ep - *Epilobium palustre*
Ea - *Equisetum arvense*
Epa - *Equisetum palustre*
Ec - *Erica cinerea*
Et - *Erica tetralix*
Ea - *Eriophorum angustifolium*
Ev - *Eriophorum vaginatum*
Eo - *Euphrasia officinalis*
Fo - *Festuca ovina*
Fr - *Festuca rubra*
Gpa - *Galium palustre*
Gs - *Galium saxatile*
Gv - *Galium verum*
Gm - *Glaux maritima*
Hs - *Heracleum sphondylium*
Hl - *Holcus lanatus*
Hv - *Hydrocotyle vulgaris*
Hc - *Hypnum cupressiforme*
Ip - *Iris pseudacorus*
Je - *Juncus effusus*
Lc - *Lotus corniculatus*
Lca - *Luzula campestris*
Lit - *Litter*
Ma - *Mentha aquatica*
Mc - *Molinia caerulea*
Mf - *Montia fontana*
No - *Narthecium ossifragum*
Pa - *Phragmites australis*
Pu - *Plagiothecium undulatum*
Pc - *Plantago coronopus*
Pl - *Plantago lanceolata*
Pm - *Plantago maritima*
Ppu - *Pleurozium purpurea*
Psc - *Pleurozium schreberi*
Pa - *Poa annua*
Ps - *Poa subcaerulea*
Pv - *Polygala vulgaris*
Pcm - *Polytrichum commune*
Pp - *Potamogeton polygonifolius*
Pan - *Potentilla anserina*
Pe - *Potentilla erecta*
Pta - *Pteridium aquilinum*
Ra - *Ranunculus acris*
Rf - *Ranunculus flammula*
Rr - *Ranunculus repens*
Rla - *Rhacomitreum lanuginosum*
Rm - *Rhinanthus minor*
Rl - *Rhytidiadelphus loreus*
Rua - *Rumex acetosa*
Sau - *Salix aurita*

Sn - *Schoenus nigricans*
Sc - *Scirpus cespitosus*
Sj - *Senecio jacobaea*
Sa - *Sinapis arvensis*
Sca - *Sphagnum capillifolium*
Spal - *Sphagnum palustre*
Spa - *Sphagnum papillosum*
Sw - Standing water
Sp - *Stellaria palustris*
To - *Taraxacum officinale*
Tm - *Thalictrum minus*
Tt - *Thiuidium tamariscinum*
Tru - *Tortula ruraliformis*
Tr - *Trifolium repens*
Vc - *Vicia cracca*
Vp - *Viola palustre*
Vr - *Viola riviniana*
Vt - *Viola tricolor*

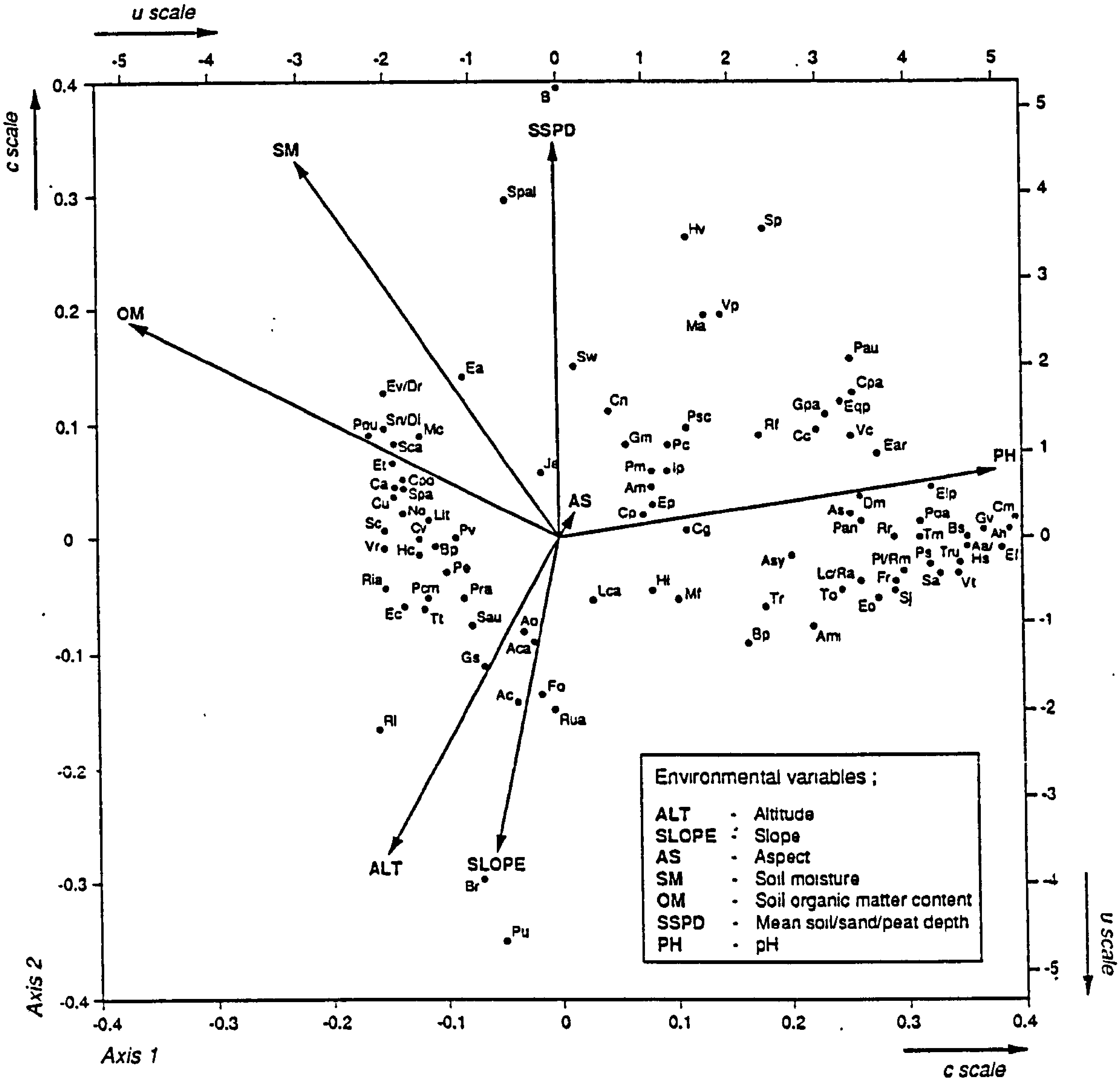


Figure 22. Canonical correspondance analysis - joint biplot of the first two axes of the species ordination with environmental factors. Eigenvalues: Axis 1 - 0.785; Axis 2 - 0.456. Variance explained by the first two axes 53%. Axis scales: u scale - species scores; c scale - environmental variables.

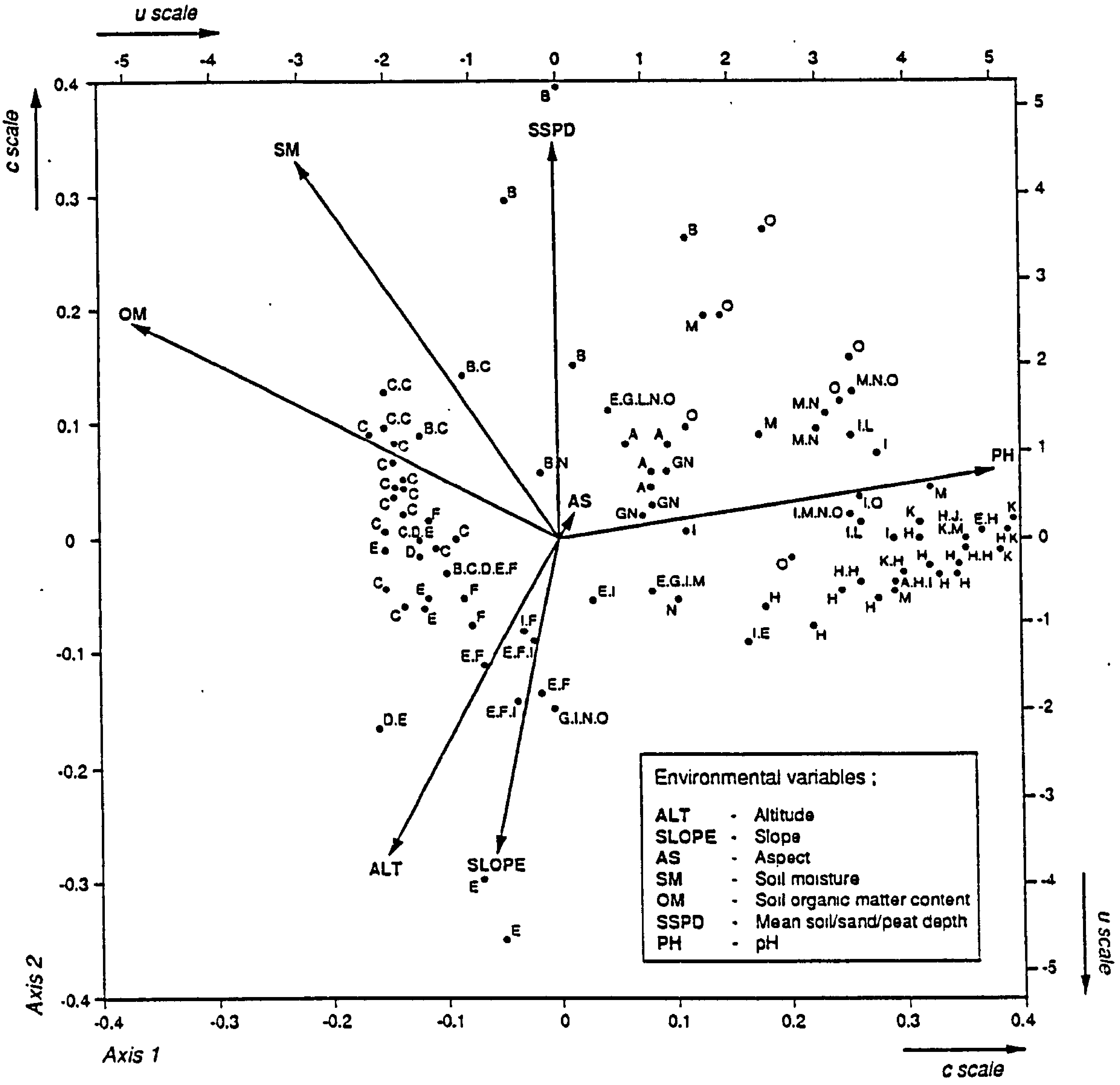


Figure 23. Canonical correspondance analysis - joint biplot of the first two axes of the species ordination with environmental factors. TWINSPAN group membership of the diagnostic species plotted in figure 22.

The seaward machair communities (Elymus farctus foredune community - Group K) and the Festuca rubra - Galium verum dune machair community - Group H) are clearly shown to the centre right of the diagram at one end of the first axis. The wet heath communities - Group C occur at the opposite end. The east coast maritime grassland type (Group A) form a tight group in the upper centre right. The various machair and swamp communites (L,M,N,O) occupy the top right quadrant of the plot, while species typical of Group I (Inner machair grassland) lie between the machair species and the acidic Agrostis-Festuca upland pasture (Group E) - with Group E species being widely spread, corresponding to the two subgroups of Agrostis - Festuca pasture already identified. Species of subgroup E1 occur towards the left and bottom of the plot - high altitude upland grazings, while those in E2 occur further right on the diagram, closer to the various machair types at much lower altitudes.

The wet heaths (Group C) are clustered to the left of centre with the wet Eriophorum pools (Group B) towards the top centre. Dry heath species (Group D) are found at the bottom of the Group C cluster.

Discussion

Community types and environmental gradients.

Sixteen plant community types have been recognised on South Uist distributed along a primary gradient of substrate pH, organic matter and soil moisture. This gradient reflects the marked contrast between the machair shell sand communities and the peat and upland environments characterised by wet heathland and acidic grassland and is indicative of soil chemistry and biology. A secondary gradient corresponds to soil moisture, soil depth, slope angle and altitude, all of which are significantly intercorrelated amongst themselves representing a response to altitude and geomorphology. The third axis only correlates with altitude and probably represents a response to biotic pressure.

Conclusion

Following this detailed survey of vegetation on a transect across South Uist, a number of ideas for further work can be suggested:

a) The communities of the machair need to be examined in much greater detail. The broader divisions which are recognised here include a number of interesting sub-divisions which reflect both the origins and present day geomorphology of the machair as well as the history of their management for grazing and cultivation. Hypotheses may be generated concerning relationships between the dynamics of sand movement during and following cultivation and disturbance.

b) The machair lake margin communities include some of the most diverse and ecologically interesting vegetation (Groups G and N). From the standpoint of botanical conservation, the maintenance of species richness in these communities is very important.

c) Arctic-alpine communities - these occur above 500m O.D. on Beinn Mhor and other mountains on the islands, such as Hecla (GR NF825345) particularly on north and east facing crags and slopes. In the TWINSPAN classification, these are seen to form a distinct sub-group with a number of the rarer species present and high species richness.

d) Relict woodland communities of any size occur at only two sites on the island: Alt Volagir and Meall Mor. The ground floras of these woodlands are of considerable interest as they contain species which are rare on the island (although not elsewhere). Their rarity is attributable to the relict nature of the woodland.

In conclusion, although the flora of the Outer Hebrides has been previously quite well described, survey of the community types has been comparatively neglected. The work described here presents a full inventory of vegetation types as they occur on the South Uist transect and clearly demonstrates their relationships with prevailing environmental factors and gradients.

Chapter 7.

Pollen Taphonomy in Relation to Local Vegetation.

Pollen taphonomy in relation to local vegetation.

This chapter describes an investigation of the relationship between the vegetation of South Uist as recorded by the modern quadrat-based study presented in Chapter 6 and the contemporary pollen recovered from surface materials in those quadrats. It is proposed to provide baseline information to aid in the interpretation of pollen diagrams presented later. As discussed previously the Outer Hebrides is poorly known in terms of its pollen taphonomy. The approach used here in the palynological analysis of surface samples from vegetation survey quadrats on the South Uist transect has adopted the methods used by Randall et al. (1986) in their broadly similar study of pollen catchment in relation to local vegetation on Caenn Ear, on the Monach Isles, off the coast of North Uist. In the Caenn Ear study of Randall et al. (1986) the vegetation / pollen relationships were investigated using phytosociological criteria (frequency and abundance) to describe the modern vegetation, and surface sample studies from a variety of pollen trapping media as sources of trapped pollen. This study identified a number of interesting problems affecting pollen deposition and dispersal in relation to local vegetation in a geographic location similar to South Uist in terms of degree of exposure and vegetation structure. The isolated location of the Monach Isles and the relatively limited flora, which forms a mosaic of distinctive plant communities facilitated the assignation of pollen types to "in community", "out-community" and "off-island" sources. Of the 178 species of flowering plants growing on the Monach Isles, 68 pollen taxa were recorded in 12 samples from 10 plant communities. An important feature of pollen deposition was that in none of the communities were the pollen spectra;

> "a reasonably full reflection of the constitution of the community" (Randall et al. 1986 pp 307).

So called characteristic pollen types were absent from the samples ; in some instances this could be accounted for on the basis of low pollen productivity, poor preservation of fragile types or the weak dispersal characteristics of certain plants. Difficulties of pollen identification to species level also reduced the resolution of the pollen data but some morphologically distinct pollen types were absent. Despite these limitations each community had a pollen spectrum which was individual and the mosaic of plant communities produced a corresponding mosaic of pollen rain (Randall et al. 1986 pp 308). Some species emerged as 'faithful' only to the communities in which the plant occured, for example, Triglochin palustris, Caltha palustris, Potentilla palustris, Hippuris vulgaris, Ranunculus flammula, Cerastium, Galium verum, Selaginella and Spergularia marina. Other well represented species were widely distributed - for example Bellis perennis and Plantago lanceolata.

Significantly, pollen of long distance provenance constituted only a small proportion of the pollen rain (c.1.6% tlp = Total land pollen) with Betula and Pinus consistently present and most abundant in the "off-island" pollen rain. The nearest source of these types was identified as forestry plantation and natural woodland stands in the Outer Hebrides. The study also highlighted the problems which arise in attempting to establish quantitative relationships between the spatial extent of plant communities, the number of individuals present in the community and pollen representation. There appears to be no explanatory relationship between species frequency, species abundance and pollen frequency at community level in the Ceann Ear study. Rather pollen deposition appears to be affected by the pollen dispersal and production characteristics of individual species, which can vary in relation to the spatial and physiognomic characteristics of the community in the vegetation mosaic. The pollen trapping medium was also found to influence representation, for example, lake mud surface samples reflected a wider source area than moss polsters which reflected a very local source area. Pollen representation in samples from moss polsters may also be affected by losses caused by post-depositional oxidation (Randall et al. 1986 pp 308).

The aims of the present South Uist pollen taphonomy study are derived from problems concerning pollen representation identified in previous studies of Holocene pollen sequences and tree macrofossils from the Outer Hebrides (see Chapter 1 and Birks and Madsen 1979, Wilkins 1984). Primarily a study of modern pollen taphonomy aims here to provide information about patterns of pollen deposition which may may help to elucidate some of the questions concerning pollen deposition in this exposed and wind-swept region - with particular attention to questions concerning the under-representation of arboreal pollen in Outer Hebridean Holocene spectra. Additionally analysis of contemporary pollen spectra from grassland, machair and blanket bog vegetation would provide an opportunity to study pollen spectra from herbaceous and heathland communities which have been modified by agricultural practice. These spectra may prove particularly useful as comparisons for defining similarly anthropogenically modified landscapes in the past in this region.

In the present study no attempt is made to quantify the relationship between pollen frequency and the spatial extent of the plant communities or the number of individuals present. Rather this study sets out to characterise the depositional and dispersal patterns of pollen from the known plant communities on the South Uist study transect. It also attempts to identify possible "taphonomic distortions" caused by the interactions of local and longer - distance processes.

Pollen identification

In this attempt to ascertain the provenance of pollen found in the surface samples, a number of pollen types normally only identified to 'family level' were tentativley assigned to species on the basis of presence in the vegetation. These types are recorded in the pollen diagram (Figure 24) under the family or genus name but suggestions as to species are discussed in the description of each community type below. Examples include *Leontodon autumnalis* (Compositae tubuliflorea), *Potentilla anserina*, *Potentilla erecta*, (*Potentilla*), *Angelica sylvestris*, *Heracleum spondylium* (Umbelliferae), *Polygala* (Rubiaceae), *Galium* spp.,*Cerastium* spp. *Stellaria* spp. and *Sagina* spp. (Caryophyllaceae). Gramineae and Cyperaceae type grains were separated into morphological classes (listed below) based on size characters as defined by Randall *et al.*(1986) and with reference to Andrew (1984), Andersen (1979), Dickson (1988) and Hall (1991).

Gramineae and Cyperaceae pollen grain size classification.

Gramineae Class 1 (18-20 μ)
Poa trivialis.

Gramineae Class 2 (21-25 μ)
Poa annua, *Agrostis capillaris*, *Agrostis stolonifera*, *Agrostis canina*, *Molinia caerulea*, *Phragmites australis*

Gramineae Class 3 (27-30 μ)
Festuca rubra, *Festuca ovina*, *Poa subcaerulea*, *Anthoxanthum odoratum*, *Holcus lanatus*, *Nardus stricta*

Gramineae Class 4 (40-55 μm)
Glycera fluitans, *Ammophilla arenaria*.

Cyperaceae Class 1 (<27 μ)
Carex piluliflora.

Cyperaceae Class 2 (36-39 μ)
Carex nigra, *Carex caryophyllea*, *Scirpus cespitosus*, *Eriophorum*

vaginatum, Eriophorum angustifolium, Schoenus nigricans

Cyperaceae Class 3 (40-42 µ)
Carex binervis, Carex paniculata, Carex flacca

Cyperaceae Class 4 (>45 µ)
Eleocharis palustris

Categories of pollen representation.

Pollen production and dispersal characteristics of individual species are key elements in an attempt to interpret the pollen spectra of the phytosociological groups defined by the TWINSPAN classification. In order to examine this relationship more closely the pollen representation of each of the plant species present in the quadrats chosen for pollen analysis were considered. The plant taxa are divided into a series of categories of pollen representation (see table 9). The categories used in this classification are based on those used by Randall et. al., (1986) and Fredskild (1967) who utilised species frequency and abundance in relation to pollen representation as a basis for the classification. It is important to note the somewhat arbitrary nature of this procedure - in that the categories are not corrected for factors of differential pollen productivity, for pollination processes or for those pollen morphological characteristics affecting dispersal. However despite these limitations this approach illustrates that such categorisation distinguishes between pollen types with deposition confined to within the community in which the species occurs, those which are more widely distributed, and those with weak or no pollen representation. The categories employed in this analysis are defined below (after Randall et al., 1986).

(a) 'Characterising pollen representation' i.e. 10% or more from taxa in the community with:
(a1) High frequency and abundance score.
(a2) High frequency and low abundance score.
(a3) Low frequency and high abundance score.
(a4) Low frequency and abundance score.

(b) Associated pollen representation : less than 10% from taxa in the community with:

(b1) High frequency and abundance score.
(b2) High frequency and low abundance score.
(b3) Low frequency and high abundance score.
(b4) Low frequency and abundance score.

(c) No pollen representation from taxa in the community with:

(c1) High frequency and abundance score.
(c2) High frequency and low abundance score.
(c3) Low frequency and high abundance score.
(c4) Low frequency and abundance score.

(d) Pollen from outside the community sampled.

Sections e,f,g and h of table 9 summarise the total number of sites in the analysis where:

(e) Pollen and plant were present.
(f) Plant was present, pollen absent.
(g) Pollen was present, plant was absent (out community).
(h) Total sites where plant or pollen were present.
(i) Pollen Representation Class (see below).

The pollen representation characteristics of each of the plant species located in the quadrats is presented in table 9. It is recognised that it is not possible to assign pollen in any one sample to a specific point of origin, particularly as there are considerable problems in identifying beyond the generic level many "characteristic species". This is particularly the case with species of Gramineae and Cyperaceae (which have been excluded, [with the exception of *Poa trivialis* and *Eleocharis palustris*] from table 9 in recognition of the uncertainty associated with identification). Other examples include Rosaceae pollen types (notably *Potentilla anserina* and *Potentilla erecta*) and Ranunculaceae (*R. acris*, *R. repens*, *R. flammula*, *R. ficaria*). However given these limitations

Table 9 : Pollen Representation categories (nomenclature follows Clapham et. al 1990).

	Pollen and Plant present								Plant present Pollen absent					Total number of sites				
													Out Comm.	Plant+ Poll.+	Plant+ Poll.-	Out Comm.	Total Sites	Pollen Representation Class.
	a				b				c				d	e	f	g	h	i
Achillea millefolium	-	-	-	-	-	-	-	-	-	2	-	-	1	-	2	1	2	D
Anagallis tenella	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	F
Angelica sylvestris	-	-	-	-	1	3	1	1	-	-	-	-	2	6	-	2	8	C
Armeria maritima	2	-	-	-	-	-	-	-	-	-	-	-	2	2	2	2	4	A/E
Bellis perennis	2	1	-	-	-	-	-	-	-	-	-	-	11	3	-	11	14	A/E
Betula pendula	-	-	2	-	-	-	-	-	-	-	-	-	25	2	-	25	27	A/E
Blechnam spicant	-	-	1	1	-	-	-	-	-	-	-	-	-	2	-	-	2	B
Calluna vulgaris	17	2	-	-	-	-	-	-	-	-	-	-	17	19	-	17	36	A/E
Caltha palustris	5	2	2	-	1	-	-	-	-	-	-	-	-	10	-	-	10	B
Cardamine amara	-	-	-	-	-	-	-	-	-	-	-	3	-	-	3	-	3	F
Cardamine pratensis	-	-	-	-	-	-	-	-	-	2	-	7	-	-	9	-	9	F
Centaurea nigra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	F
Cerastium glomeratum	-	-	-	-	-	-	-	-	-	-	-	1	-	3	1	-	4	D
Cirsium palustre	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	1	D
Corylus avellana	-	-	2	-	-	-	1	-	-	-	-	-	29	3	-	29	32	A/E
Dactylorhiza majalis	-	-	-	-	-	-	-	-	-	5	-	4	-	9	9	-	9	F
Dactylorhiza purpurea	-	-	-	-	-	-	-	-	-	-	-	2	-	2	2	-	2	F
Digitalis purpurea	-	-	-	-	-	-	-	-	-	-	-	2	-	2	2	-	2	F
Drosera	-	-	-	-	-	2	-	1	-	-	-	-	4	3	-	4	7	C
Eleocharis palustris	3	-	-	-	-	1	-	-	-	-	-	-	-	3	-	-	4	B
Empetrum nigrum	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	3	E
Epilobium palustre	-	-	-	-	2	2	-	3	-	-	-	-	3	7	-	3	10	C
Equisetum spp.	2	1	-	1	-	10	-	-	-	-	-	-	-	14	-	-	14	B
Erica cinerea	-	-	-	1	1	-	-	1	-	-	-	-	6	3	-	6	9	E
Erica tetralix	-	-	-	-	-	8	-	1	-	-	-	-	9	9	-	9	18	C/E

Table 9 : Pollen Representation categories (cont.)

														Total number of sites				
	Pollen and Plant present								Plant present Pollen absent				Out Comm.	Plant+ Poll.+	Plant+ Poll.-	Out Comm.	Total Sites	Pollen Representation Class.
	a				b				c				d	e	f	g	h	i
Euphrasia officinalis	-	-	-	-	-	-	-	-	-	-	-	3	-	3	3	-	3	F
Filipendula ulmaria	1	2	1	-	-	-	-	-	-	-	-	-	8	4	-	-	12	A/E
Galium palustre	1	-	-	-	-	5	-	2	-	-	-	-	3	8	-	3	11	C
Galium saxatile	-	-	-	-	1	5	-	-	-	-	-	-	4	6	-	4	10	C
Galium verum	-	-	-	-	-	2	-	-	-	-	-	-	4	2	-	4	6	C/E
Glaux maritima	-	-	-	-	1	-	-	-	-	-	-	-	1	1	-	1	2	C
Hedera helix	-	-	-	-	-	-	2	-	-	-	-	-	3	2	-	3	5	C/E
Heracleum sphondylium	-	-	-	-	1	-	-	-	-	-	-	-	3	1	-	3	4	C
Hippuris vulgaris	-	-	-	-	1	1	-	-	-	-	-	-	1	2	-	1	3	D
Huperzia selago	-	-	1	-	-	-	-	-	-	-	-	-	5	1	-	5	6	A
Hydrocotyle vulgaris	4	1	-	-	1	1	-	-	-	-	-	-	-	7	-	-	7	B
Hypericum pulchrum	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	1	D
Iris pseudocorus	-	-	-	-	-	-	-	-	3	-	2	-	-	5	5	-	5	F
Juncus bufonius	-	-	-	-	-	-	-	-	-	-	-	2	-	2	2	-	2	F
Juncus effusus	-	-	-	-	-	-	-	-	2	2	-	-	-	4	4	-	4	F

Table 9 : Pollen Representation categories (cont.)

														Total number of sites				
	Pollen and Plant present								Plant present Pollen absent				Out Comm.	Plant+ Poll.+	Plant+ Poll.-	Out Comm.	Total Sites	Pollen Representation Class.
	a				b				c				d	e	f	g	h	i
Juncus squarrosus	-	-	-	-	-	-	-	-	2	-	-	-	-	2	2	-	2	F
Juniperus communis	-	-	-	-	-	-	1	-	-	-	-	-	2	1	-	2	3	C
Luzula campestris	-	-	-	-	-	-	-	-	-	4	3	3	-	1	10	-	10	F
Luzula sylvatica	-	-	-	-	-	-	-	-	-	-	-	3	-	-	3	-	3	F
Leontodon autumnalis	-	-	-	-	-	3	-	-	-	-	-	-	-	3	-	-	3	D
Lonicera periclymenum	-	-	-	-	-	-	1	-	-	-	-	-	3	1	-	3	3	C/E
Lotus corniculatus	-	-	-	-	1	-	2	1	-	-	-	-	3	4	1	3	8	C
Lysimachia nemorum	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	1	D
Mentha aquatica	-	-	-	-	-	4	-	-	-	2	-	-	-	4	2	-	6	D
Menyanthes trifoliata	-	-	1	-	-	-	-	-	-	-	-	-	3	1	-	3	4	A
Montia fontana	-	-	-	-	-	1	1	-	-	-	-	1	-	2	1	-	3	D
Narthecium ossifragum	-	-	-	-	-	1	1	-	-	-	-	-	6	3	-	6	9	C
Osmunda regalis	-	-	1	-	-	-	-	-	-	-	-	-	2	1	-	2	3	A
Oxyria digyna	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	1	D

Table 9 : Pollen Representation categories (cont.)

	Pollen and Plant present								Plant present Pollen absent				Out Comm.	Total number of sites				Pollen Representation Class.
														Plant+ Poll.+	Plant+ Poll.-	Out Comm.	Total Sites	
	a				b				c				d	e	f	g	h	i
Pedicularis sylvatica	-	-	-	-	-	-	-	2	-	-	-	-	1	2	-	1	3	D
Plantago coronopus	1	-	-	-	-	-	-	-	-	-	-	-	3	1	-	3	4	A
Plantago lanceolata	3	1	1	-	-	2	-	1	-	-	-	-	23	8	-	23	31	A
Plantago maritima	1	-	-	-	-	-	-	-	-	-	-	-	4	1	-	4	5	A
Polygala serpyllifolia	-	-	-	-	-	3	1	2	-	-	-	-	9	6	-	9	15	C
Polygonum bistorta	-	-	-	-	-	2	-	-	-	-	-	-	-	2	-	-	2	D
Polypodium	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	11	11	OC
Populus tremula	-	-	-	-	-	-	-	-	-	2	-	-	-	-	2	-	2	F
Potamogeton	-	-	-	-	-	2	-	-	-	-	-	1	5	2	-	5	8	D
Potentilla anserina	-	-	-	-	2	4	-	-	-	1	-	-	-	6	1	-	8	D
Potentilla erecta	2	-	-	-	6	12	-	2	-	-	-	-	8	20	-	8	28	C
Potentilla palustris	-	1	1	-	-	-	-	-	-	-	-	-	-	2	-	-	2	B
Primula vulgaris	-	-	-	-	3	-	-	-	-	-	-	-	1	3	-	1	4	C
Prunella vulgaris	-	-	-	-	-	-	-	1	-	-	-	3	-	-	3	-	3	D

Table 9 : Pollen Representation categories (cont.)

	Pollen and Plant present								Plant present Pollen absent				Out Comm.	Total number of sites Plant+ Poll.+	Total number of sites Plant+ Poll.-	Total number of sites Out Comm.	Total number of sites Total Sites	Pollen Representation Class.
	a				b				c				d	e	f	g	h	i
Pteridium aquilinum	5	-	-	-	1	-	-	-	-	-	-	-	8	6	-	8	14	A
Poa trivialis	2	1	-	-	-	-	-	-	-	-	-	-	-	3	-	-	3	B
Ranunculus acris	4	-	-	-	-	5	-	2	-	-	-	-	4	11	-	4	15	A
Ranunculus ficaria	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2	-	2	F
Ranunculus flammula	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	3	D
Ranunculus repens	-	-	-	-	-	1	-	-	-	-	-	-	-	11	-	-	11	E
Rhinanthus minor	-	-	-	-	-	-	-	-	4	2	-	-	-	-	6	-	6	F
Rubus	-	-	-	-	-	-	1	-	-	-	-	2	-	-	2	-	2	D
Rumex acetosa	-	-	-	-	-	9	-	-	-	-	-	-	5	12	-	5	17	C
Rumex acetosella	-	-	-	-	-	2	-	-	-	-	-	-	2	2	-	2	4	C
Rumex crispus	-	-	-	-	-	-	-	1	-	-	-	-	2	1	-	2	3	C
Sagina spp.	-	-	-	-	-	2	-	1	-	-	-	-	-	1	-	-	1	D
Salix	2	-	-	-	1	-	-	-	-	-	-	-	22	3	-	22	25	A/E
Saxifraga stellaris	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	1	D

Table 9 : Pollen Representation categories (cont.)

	Pollen and Plant present								Plant present Pollen absent				Out Comm.	Total number of sites				Pollen Representation Class.
														Plant+ Poll.+	Plant+ Poll.-	Out Comm.	Total Sites	
	a				b				c				d	e	f	g	h	i
Selaginella	-	1	-	-	-	-	-	-	-	-	-	-	4	1	-	4	5	A
Senecio jacobaea	-	-	-	-	-	1	-	-	-	-	-	3	-	1	3	-	4	D
Sinapsis type	-	-	-	-	-	1	-	-	-	-	-	-	7	1	-	7	8	D
Sorbus	-	-	1	-	-	-	-	-	-	-	-	-	10	1	-	10	11	A/E
Sphagnum spp.	9	1	2	-	-	-	-	-	-	-	-	-	9	12	-	9	21	A
Stellaria palustris	-	-	-	-	1	1	-	-	-	2	-	-	-	2	2	-	4	D
Succisa	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	5	5	OC
Taraxacum officinale	-	-	-	-	-	1	-	1	-	-	-	-	-	2	-	-	2	D
Teucrium scorodonia	-	-	-	-	-	-	-	2	-	-	-	-	-	2	-	-	2	D
Thalictrum alpina	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	1	D
Thalictrum minus	-	-	-	-	2	-	-	-	-	-	-	-	-	2	-	-	2	C
Thymus serpyllum	-	-	-	-	-	-	1	2	-	-	-	-	3	3	-	3	6	D
Trifolium repens	2	-	-	-	2	4	-	-	-	-	-	2	-	8	2	-	10	B
Triglochin maritima	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	A

Table 9 : Pollen Representation categories (cont.)

														Total number of sites			
	Pollen and Plant present								Plant present Pollen absent				Out Comm.	Plant+ Poll.+	Plant+ Poll.-	Out Comm.	Total Sites	Pollen Representation Class.
	a				b				c				d	e	f	g	h	i
Typha latifolia	1	-	-	-	-	-	-	-	-	-	-	-	2	1	-	2	3	B
Urtica	-	-	1	-	-	-	-	-	-	-	-	-	6	1	-	6	7	D/E
Umbelliferae undiff.	-	-	-	-	-	-	-	-	-	-	-	-	13	-	-	13	13	OC
Veronica officinalis	-	-	-	-	-	-	-	-	-	-	1	1	-	-	2	-	2	F
Vicia cracca	-	-	-	-	2	2	-	-	-	-	-	-	2	4	-	2	4	C
Viola palustris	-	-	-	-	2	1	-	-	-	-	-	1	-	5	1	-	6	C
Viola riviniana	-	-	-	-	2	2	1	1	-	-	-	-	5	6	-	5	11	C
Viola tricolor	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	F

table 9 represents an attempt to clarify the pollen deposition of species in relation to their status in the vegetation (expressed as frequency and abundance). The pollen representation of "Characterising species" in each of the TWINSPAN groupings is evident in sections a1,a2,b1,b2,c1,c2 of the table. "Associated"and "Less Frequent" species are represented by sections a3,a4,b3,b4. Species which tend to be over represented by pollen are found in categories a2 and a4, while those tending to be under-represented in b1-3. Those present in the vegetation but with no pollen representation are found in c1-4 (Juncus spp., Populus tremula, Iris pseudacorus).

Using the above criteria several broader classes of pollen representation (see table 10) discussed below can be discerned from these data:

Classes of pollen representation

(A) Well represented "in-community" pollen with wide distribution outside the community.

Eighteen pollen types are included in this category, a relatively small percentage (15.5%) of the total sample. Betula, Corylus, Salix and Calluna vulgaris are the most striking examples. Calluna vulgaris pollen was recorded in 36 of the 45 samples analysed. Where the plant was present (19 quadrats) all pollen frequencies exceeded 10% tlp. However in the 17 samples where Calluna was recorded as "out-community pollen" percentage values decline with distance from Calluna dominated communities. Betula, Salix, Sorbus and Corylus are also included in this group as they have pollen values exceeding 10% tlp in samples where they were present in the vegetation (Allt Volagir National Nature Reserve, Kildonan Glen, Loch Eyenort) but were also present as "out-community" pollen in many other samples. For example, Betula was recorded as "out-community" pollen in 25 samples, Corylus in 29 samples, Sorbus in 10 samples and Salix in 22 samples from across the transect. Herbaceous types in this class included Bellis perennis, Plantago lanceolata, Plantago coronopus, Plantago maritima, Ranunculus acris, Filipendula ulmaria, Armeria maritima, Menyanthes trifoliata, and

Table 10 : Classes of Pollen Representation

		Total number of sites				
	Out Comm.	Plant+ Poll.+	Plant+ Poll.-	Out Comm.	Total Sites	Pollen Representation Class.
	D	E	F	G	H	I
A) Well represented in-community pollen with wide distribution outside the community						
Armeria maritima	2	2	2	2	4	A/E
Bellis perennis	11	3	-	11	14	A/E
Betula pendula	25	2	-	25	27	A/E
Calluna vulgaris	17	19	-	17	36	A/E
Corylus avellana	29	3	-	29	32	A/E
Filipendula ulmaria	8	4	-	-	12	A/E
Huperzia selago	5	1	-	5	6	A
Menyanthes trifoliata	3	1	-	3	4	A
Osmunda regalis	2	1	-	2	3	A
Plantago coronopus	3	1	-	3	4	A
Plantago lanceolata	23	8	-	23	31	A
Plantago maritima	4	1	-	4	5	A
Pteridium aquillinum	8	6	-	8	14	A
Ranunculus acris	4	11	-	4	15	A
Salix	22	3	-	22	25	A/E
Selaginella	4	1	-	4	5	A
Sorbus	10	1	-	10	11	A/E
Sphagnum spp.	9	12	-	9	21	A
B) Pollen well represented in the parent communities not widely distributed						
Blechnam spicant	-	2	-	-	2	B
Caltha palustris	-	10	-	-	10	B
Eleocharis palustris	-	3	-	-	4	B
Equesetum spp	-	14	-	-	14	B
Hydrocotyle vulgaris	-	7	-	-	7	B
Potentilla palustris	-	2	-	-	2	B
Poa trivialis	-	3	-	-	3	B
Trifolium repens	-	8	2	-	10	B
Triglochin maritima	-	1	-	-	1	B
Typha latifolia	2	2	-	-	4	A/B
C) Pollen recorded in low frequencies in the parent community with limited distribution outside the community						
Angelica sylvestris	2	6	-	2	8	C
Drosera	4	3	-	4	7	C
Epilobium palustre	3	7	-	3	10	C
Erica tetralix	9	9	-	9	18	C/E
Galium palustris	3	8	-	3	11	C
Galium saxatile	4	6	-	4	10	C
Galium verum	4	2	-	4	6	C/E
Glaux maritima	1	1	-	1	2	C
Hedera helix	3	2	-	3	5	C/E
Heracleum sphondylium	3	1	-	3	4	C

Lonicera periclymenum	3	1	-	3	3	C/E
Lotus corniculatus	3	4	1	3	8	C
Narthecium ossifragum	6	3	-	6	9	C
Polygala serpyllifolia	6	-	9	15	C	
Potentilla anserina	-	6	1	-	8	C
Potentilla erecta	8	20	-	8	28	C
Primula vulgaris	1	3	-	1	4	C
Rumex acetosa	5	12	-	5	17	C
Rumex acetosella	2	2	-	2	4	C
Rumex crispus	2	1	-	2	3	C
Thalictrum minus	2	-	-	2	C	
Vicia cracca	2	4	-	2	4	C
Viola palustris	5	1	-	6	C	
Viola riviniana	5	6	-	5	11	C

D) Pollen recorded in low frequencies in the parent community.

Achillea millefolium	1	2	-	1	2	D
Cerastium glomeratum	-	3	1	-	4	D
Cirsium palustre	-	1	-	-	1	D
Hippuris vulgaris	1	2	-	1	3	D
Hypericum pulchrum	-	1	-	-	1	D
Leontodon autumnalis	-	3	-	-	3	D
Lysimachia nemorum	-	1	-	-	1	D
Mentha aquatica	-	4	2	-	6	D
Montia fontana	-	2	1	-	3	D
Oxyria digyna	-	1	-	-	1	D
Pedicularis sylvatica	1	2	-	1	3	D
Polygonum bistorta	-	2	-	-	2	D
Potamogeton	1	5	2	-	5	D
Prunella vulgaris	-	-	3	-	3	D
Ranunculus flammula	-	3	-	-	3	D
Sagina spp.	-	1	-	-	1	D
Saxifrage stellaris	-	1	-	-	1	D
Senecio jacobaea	-	1	3	-	4	D
Sinapis type	7	1	-	7	8	D
Stellaria palustris	-	2	2	-	4	D
Taraxacum officinale	-	2	-	-	2	D
Teucrium scordium	-	2	-	-	2	D
Thalictrum alpinum	-	1	-	-	1	D
Thymus serpyllum	3	3	-	3	6	D
Sagina spp.	-	1	-	-	1	D
Urtica	6	1	-	6	7	D/E

E) Pollen recorded in more sites from outside their community than within them.

Armeria maritima	2	2	2	2	4	A/E
Bellis perennis	11	3	-	11	14	A/E
Betula pendula	25	2	-	25	27	A/E
Calluna vulgaris	17	19	-	17	36	A/E
Corylus avellana	29	3	-	29	32	A/E
Empetrum nigrum	2	-	-	-	3	E
Erica cineria	6	3	-	6	9	E
Erica tetralix	9	9	-	9	18	C/E
Filipendula ulmaria	8	4	-	-	12	A/E
Galium verum	4	2	-	4	6	C/E
Hedera helix	3	2	-	3	5	C/E

Huperzia selago	5	1	-	5	6	A/E
Lonicera periclymenum	3	1	-	3	3	C/E
Ranunculus repens	-	11	-	-	11	E
Salix	22	3	-	22	25	A/E
Sorbus	10	1	-	10	11	A/E
Urtica	6	1	-	6	7	D/E

F) No pollen representation where the plant is present.

Anagallis tenella	-	-	1	-	1	F
Cardamine amara	-	-	3	-	3	F
Cardamine pratensis	-	-	9	-	9	F
Centuria nigra	-	-	-	-	3	F
Dactylorhiza majalis	-	9	9	-	9	F
Dactylorhiza purprea	-	2	2	-	2	F
Digitalis purpurea	-	2	2	-	2	F
Euphrasia officinale	-	3	3	-	3	F
Iris psuedocorus	-	5	5	-	5	F
Juncus bufonis	-	2	2	-	2	F
Juncus effusus	-	4	4	-	4	F
Juncus squarrosus	-	2	2	-	2	F
Luzula campestris	-	1	10	-	10	F
Luzula sylvatica	-	-	3	-	3	F
Populus tremula	-	-	2	-	2	F
Ranunculus ficaria	-	-	2	-	2	F
Rhianthus minor	-	-	6	-	6	F
Veronica officinalis	-	-	2	-	2	F
Viola tricolour	-	1	-	-	1	F

Umbelliferae undifferentiated. Many spores, *Huperzia selago*, *Polypodium*, *Pteridium aquilinum* and *Sphagnum* spp., were also in this class.

(B) Pollen well represented in the parent communities, not widely distributed.

Ten pollen types are recorded in this class (8.6% of the total sample). *Caltha palustris* is an example of this class with pollen present only in samples from 10 sites where the plant was present in the vegetation. *Eleocharis palustris*, *Poa trivialis*, *Hydrocotyle vulgaris*, *Oxyria digyna*, *Triglochin maritima*, *Potentilla palustris* and *Trifolium repens* are also included in this class. This group are described by Randall *et al.*,(1986) as to some extent 'faithful' in the sense the term is used in phytosociology. These data suggest that when these pollen types occur in a sample they indicate strongly the presence of the plant in local vegetation.

(C) Pollen recorded in low frequencies in the community where the parent plant is present with limited distribution outside the community.

Twenty six pollen types are recorded in this class (22% of the total sample) which includes many herbaceous pollen types, for example, *Angelica sylvestris*, *Drosera*, *Epilobium palustre*, *Galium saxatile*, *Galium palustre*, *Galium verum*, *Potentilla erecta*, *Potentilla anserina*, *Primula vulgaris*, *Rumex acetosa*, *Rumex acetosella*, *Rumex crispus*, *Thalictrum minus*, *Viola palustris*, *Viola riviniana* and *Vicia cracca*. Dwarf shrubs such as *Juniperus communis*, *Erica cinerea* and *Erica tetralix* are also included in this class.

(D) Pollen recorded in low frequencies or absent where the parent plant is present.

Thirty six pollen types are included in this class (31% of the total sample). A number of species which were constants in the TWINSPAN groupings are included in this class, for example, *Achillea millefolium*, *Rhinanthus minor*, *Euphrasia officinalis* and *Iris pseudacorus*. Other important members of the class include species of Juncaceae particularly *Juncus squarrosus*, *Juncus bufonis*, *Juncus effusus*, *Luzula campestris* and *Luzula sylvatica*. The pollen of

these types is fragile and intolerant to preparation (Andrew 1985) which may explain such poor pollen representation.
Populus tremula recorded in the vegetation in the Allt Volagir N.N.R. was not represented by pollen in any of the samples from within the woodland.

(E) Pollen recorded in more sites from outside their parent community than within them.

Seventeen pollen types are included in this class (14.6% of the total sample). Tree, shrub and tall herb pollen types are predominant in this class. However with the exception of Calluna vulgaris all are present in low frequencies where they are recorded as "out community" pollen. Calluna vulgaris, Betula, Coryloid = (Corylus + Myrica undifferentiated), Pinus and Salix appear to be the most widely distributed pollen types as they are present in a majority of samples from right across the transect. Some of this input may be of "off-island" provenance. With the exception of these pollen types most other taxa have relatively limited dispersal outside their parent communities, for example herbaceous types such as Bellis perennis, Plantago lanceolata, Ranunculus repens / acris which are present in the machair and acid grassland vegetation are mostly present as "out community" pollen in other nearby machair or neutral / acid grassland samples (see table 31 "Out-community" pollen representation table). Consequently these pollen types slightly 'blurr' the distinctions between community pollen spectra.

Plant species not represented in pollen spectra.

116 species were recorded in the vegetation quadrats selected for pollen analysis and a total of 130 pollen types were identified (including "Out-community on /off island" pollen and undifferentiated family groups such as Gramineae, Cyperaceae, Compositae Liguliflorae, Compositae Tubuliflorae, Scrophulariaceae, and Rosaceae). The significant 'absentee' pollen types in each of the communities sampled are discussed in the community descriptions below.

A total of 12 pollen types from species not recorded in the vegetation quadrats but present on the transect or listed in the floristic list for the Outer Hebrides (see Curry 1979, Pankhurst and Mullin 1991) were noted. These included, Papaver type, Fagus, Ulmus, Quercus, Sorbus, Ulex, Pinus, Sambucus, Umbelliferae, Compositae, Rosaceae and Filicales (Athyriaceae and Polypodiaceae).

Pollen representation Classes and Community Pollen spectra.

The division of pollen and spore producing species into classes of pollen representation illustrates an important characteristic of pollen deposition on the transect. The two largest classes are Class C (Pollen recorded in low frequencies in the parent communities with limited distribution outside the community) and Class D/F (Pollen recorded in low frequencies or absent from the community where the parent plant is present). Together these 60 pollen taxa constitute c.50% of the total "on-island sample". Well represented pollen taxa (28 types) constitute 24% of the "on-island" sample with only 8% having deposition confined largely to the parent community. A relatively small proportion of the total sample (17 taxa, 14%) are included in Class E (those recorded at more sites from outside their community than within them). The results of the tabulation suggest that a large proportion of species present in the vegetation are likely to have weak pollen representation and that communities with a predominance of these taxa will have a correspondingly weak pollen signature, particulary if characterising species are Class F pollen types. Conversely a proportion of high pollen producing species could have a 'swamping' effect on the community spectra.

The limited proportion of pollen types with wide distribution outside the parent community (Classes A / E) suggests that distortion of community representation by these inputs should be limited and predictable.

Community representation.

Tables 12 - 26 provide details of the pollen representation of each of the communities identified by the TWINSPAN analysis. Species recorded in each quadrat are listed in order of their status in the phytosociological groupings (frequency) together with abundance scores and pollen percentage. All species of Gramineae and Cyperaceae are listed in separate morphological categories because of the uncertainties of identification. "Characterising species" are those which are present in the vegetation and are >50% constant by group, "Associated species" are >25% constant by group and "less frequent" species are <25% constant by group. Abundance scores 1-5 represent percentage frequency of a species in a quadrat where 1 = 2-5%, 2 = 5-10%, 3 = 10-20%, 4 = 21-50 %, 5 = >50% cover.

Pollen from plants present on the islands but absent in the vegetation quadrat are listed as "out community / on island" pollen. Pollen thought to be of long distance provenance is listed as "off-island pollen". This group was perhaps the most difficult to define but pollen from plants not recorded in locations on South Uist (Pankhurst and Mullin 1991, Kent *et al.* in press) are considered to be of "off-island provenance".

Elymus farctus foredune community (Group J/K).

The foredunes of the west coast are characterised by this community type. The bare sand substrate and lack of any pollen trapping medium suitable for analysis resulted in this community not being studied.

Festuca rubra-Galium verum dune machair community (Group H).

Sample from *Tortula ruraliformis* moss polster.

These quadrats occur inland from the foredunes and represent the machair type found nearest the sea. At the time of sampling (June 1989 / 1990) almost all of the species present were flowering and the community was ungrazed. *Plantago lanceolata*, *Trifolium repens*, *Achillea millefolium* and *Galium verum* are the constants with a large group of common associates which include *Bellis perennis*, *Euphrasia officinalis*, *Heracleum sphondylium*, *Leontodon autumnalis*, *Lotus corniculatus* and *Ranunculus acris* (see table 14 and vegetation survey results, chapter 6). Of the "Characterising species",

FIGURE 24

South Uist transect : Surface sample pollen percentage diagram.

see Appendix

Festuca rubra had the highest abundance scores (5-4) and is well represented by pollen (15-23% tlp) in Gramineae class 3. This class also included the much less abundant *Poa subcaerulea* and as a consequence Gramineae class 3 pollen values are thought to reflect *Festuca rubra* rather than *Poa subcaerulea*.

Plantago lanceolata pollen frequencies (5-14 %tlp) reflect the range of abundance scores (1-4) for this species in the quadrats analysed. Other "Characterising species" with high abundance scores included *Trifolium repens* (1-5% tlp) and *Galium verum* (4-7% tlp) had low but significant pollen frequencies. *Achillea millefolium*, a "characterising" but less abundant species in this community, was not represented by pollen.

"Associated species" with high abundance scores and good pollen representation (category a3 types) included *Bellis perennis* (8-12% tlp), *Ranunculus acris* / *repens* (1-12% tlp), *Thalictrum minus* 2-8% tlp, and *Carex arenaria* (10-14% tlp). Whereas the low pollen percentage values recorded for other "associated" species such as *Heraclium sphondylium*, *Leontodon autumnalis*, *Senecio jacobaea* and *Taraxacum officinale* reflect their low abundane scores in the vegetation. Several "associated" species are either not recorded or are present in very low, inconsistent numbers. These include *Euphrasia officinalis*, *Lotus corniculatus*, *Rhinanthus minor*, *Senecio jacobaea*, *Sinapis arvensis*, *Taraxacum officinale*, *Viola tricolor* and *Ammophila arenaria*.

Two "less frequent species" both with high abundance scores (4-5) were recorded in one sample (H1). *Urtica dioica* (7% tlp) was well-represented by pollen in contrast to *Centaurea nigra* (1% tlp) which is poorly represented.

"Out community / on island" pollen constitutes 9% tlp in one sample and 5% tlp in the other. Most of the pollen in this category was derived from nearby coastal and machair communities and comprised scarce grains of *Armeria maritima*, *Rumex acetosa*, *Potentilla*, and

Table 11 ; Festuca rubra - Galium verum - dune machair community (Group H).

1. Characterising species.	Abundance.		Pollen %.		PRC*
Plantago lanceolata	1	4	5	14	A
Trifolium repens	3	1	5	<1	B
Achillea millefolium	1	-	-	-	D
Galium verum	5	2	7	4	C
Festuca rubra	5	4			
2. Associated species.					
Bellis perennis	1	3	8	12	A
Euphrasia officinalis	-	1	-	-	F
Heracleum sphondylum	-	3	<1	2	C
Leontodon autumnalis	-	1	1	4	D
Lotus corniculatus	-	5	-	4	C
Ranunculus acris	-	4	1	12	A
Ranunculus repens	-	1	ND	ND*	D
Rhianthus minor	-	2	-	<1	F
Senecio jacobaea	2	-	<1	-	D
Sinapsis arvensis	-	1	-	3	D
Taraxacum officinale	-	1	-	<1	D
Thalictrum minus	3	5	2	4	C
Viola tricolor	-	1	-	-	F
Carex arenaria	1	1	8	4	
Poa subcaerulea	1	-			
Ammophila arenaria	-	3	-	1	
3. Less frequent species.					
Urtica dioica	5	-	7	-	A
Centaurea nigra	4	-	1	<1	D
4. Gramineae class 3.			23 - 15%		
Festuca rubra	5	4			
Poa subcaerulea	1	-			
Gramineae class 4.			-	1	

Ammophila arenaria	-	3			
Total Gramineae.	6	7	23	16	
5. Cyperaceae class 2.			9	4	
Carex arenaria	1	1			
Total Cyperaceae.			9	4	
6. On island / Out-community pollen.					
Potentilla			<1	-	D
Rumex acetosa			<1	<1	C
Gramineae class 2			2	<1	
Armeria maritima			-	<1	A
Papaver type			-	<1	OT*
Pinus sylvestris			<1	-	OT*
Betula			<1	<1	A/E
Calluna vulgaris			2	1	A/E
Ulmus			<1	-	OT*
Coryloid			<1	-	
7. Out-community / off-island pollen					
Juglans regia			<1	-	
Tilia cordata			-	<1	

Total pollen percentages	**H1**	**H2**
Total In-community	79	85
Total Out-community / on island	9	5
Total Off-island	<1	<1
Total degraded	10	8
Total unidentified	3	2

* OT - On-island off-transect pollen.

* ND. Not differentiated to species.

* PRC Pollen representation class.

Papaver type. *Calluna vulgaris* grains present in both samples are thought to be derived from *Calluna vulgaris* dominated communities located in Upper Loch Kildonan. *Pinus sylvestris*, *Ulmus*, *Salix*, Coryloid and *Betula* were also present in low frequencies (<1% tlp respectively), the nearest local source for these taxa being the local woodland at Allt Volagir N.N.R., the wooded islands in Loch Druidibeg and Forestry Commission woodland on the islands.
"Off island" pollen representation comprised one grain of *Juglans regia* and scarce grains of *Tilia*.

This community was fairly well represented in the pollen spectra with all but one (that is *Achillea millifolium*) of the "characterising species" present. However the relatively high species richness (mean 12.0, maximum 17.0) of the community is less well represented with many common "associated species" such as *Ammophila arenarea*, *Rhinanthus minor*, *Euphrasia officinalis*, *Lotus corniculatus* and *Viola tricolor* absent or present in low inconsistent frequencies. The pollen spectra of this community is similar to that of the stable dune (site 1) described by Randall *et al.* (1986). The pollen spectra contained 3 pollen representation class (PRC) A taxa, (*Plantago lanceolata*, *Bellis perennis* and *Ranunculus* which together with low but significant frequencies of PRC / C and PRC / D taxa, *Thalictrum minus*, *Heracleum sphondylum*, *Urtica dioica*, *Leontodon autumnalis* and *Lotus corniculatus*, characterise the pollen signature of the community.

The vegetation quadrats analysed for pollen contained a total of 23 plant species and of this total 20 species were represented by pollen and 11 "out-community" pollen types were identified. There appears to be some distortion of this community's pollen spectra as a result of "on-island" pollen transfer but the low percentage values recorded for each "out-community" type suggests that this effect is not significant and that local vegetation is the main source of "out-community" input. The presence of *Heracleum sphondylium*, *Thalictrum minus* and *Galium verum* in the pollen spectra distinguishes this community from other machair grassland communities.

Festuca rubra - *Potentilla anserina* - *Trifolium repens* - *Agrostis stolonifera* inland grassland community (Group I).

Samples from moss polsters.
The majority of the shell sand machair quadrats located further inland are contained in this group, which consisted of two sub-groups (Group Ia and Group Ib). The first sub-group comprised quadrats nearest the sea and the second further inland. Mean species richness is slightly higher (Group I, mean 13.8, maximum 20.0; Group H, mean 12.7, maximum 17.0). The "characterising species" of this community include *Festuca rubra*, *Agrostis stolonifera*, *Trifolium repens*, *Potentilla anserina*, *Plantago lanceolata* and *Vicia cracca* and there are a number of "associated" and "less frequent" species.

Pollen representation of two "characterising species" with high abundance scores, *Plantago lanceolata* (12-29% tlp), and *Trifolium repens* (4-14% tlp) is relatively good. However *Potentilla anserina* (<1-4% tlp), *Rhinanthus minor* (0% tlp) and *Vicia cracca* (<1-5% tlp) all particularly characteristic species of the machair grassland communities - with high abundance scores in the vegetation quadrats - are poorly represented in the pollen spectra. Gramineae pollen percentage values compare well with those of abundance in the vegetation, suggesting that Gramineae class 3 pollen types (*Festuca rubra*, *Anthoxanthum odoratum* and *Holcus lanatus*) and Gramineae class 1 (*Poa trivialis*) were deposited near source. An exception to this general pattern is found in *Agrostis stolonifera* / *Agrostis canina* which has values of *c.*11-20% tlp in samples from quadrats where the species was present in the vegetation; in contrast to *c.*4% tlp in quadrats where it was not. Class 2 type pollen values of 2-4% tlp were also recorded in samples from Group H samples where the species was not recorded in the vegetation, suggesting that *Agrostis* pollen is slightly more widely dispersed than *Festuca rubra* and *Poa trivialis*.

Table 12 ; Festuca rubra - Potentilla anserina - Trifolium repens - Agrostis stolonifera - inland grassland community (Group I

1. **Characterising species.**	**Abundance.**	**Pollen %**				**PRC**
Trifolium repens	5 5 4 4	12	14	4	6	B
Potentilla anserina	- 5 5 -	<1	4	4	<1	C
Plantago lanceolata	1 4 4 4	12	29	16	26	A
Rhinanthus minor	- 4 4 5	-	<1	-	-	F
Vicia cracca	- - 3 2	<1	-	5	2	C
2. **Associated Species**						
Bellis perennis	- - - 5	<1	-	-	28	A
Dactylorhiza majalis	- - 2 1	-	-	-	-	F
Rumex acetosa	3 1 1 1	9	<1	6	1	C
Cerastium glomeratum	- 1 - 1	-	<1	-	-	D
Ranunculus acris	2 4 5 5	4	13	11	10	A
Luzula campestris	1 - - -	-	-	-	-	F
Equisetum arvensis	- 3 2 -	-	18	5	-	B
3. **Less frequent species.**						
Sagina procumbens	2 - - -	<1	-	-	-	D
Centaurea nigra	1 - - 2	<1	-	-	<1	D
Cardamine pratensis	1 - 1 1	-	-	-	-	F
Lotus corniculatus	- 4 4 -	<1	<1	3	-	C
Ranunculus ficaria	1 - - -	-	-	-	-	F
Montia fontana	4 - - -	<1	-	-	-	D
Viola palustris	- - - 2	-	-	-	<1	C
Angelica sylvestris	- - - 3	<1	-	-	2	C
4. **Gramineae class 1**		12	-	<1	-	B
Poa trivialis	3 - - -					
Gramineae class 2		4	11	20	3	A
Agrostis stolonifera	- 5 5 -					

Gramineae class 3.		22	6	15	4	B
Festuca rubra	5 - 5 -					
Holcus lanatus	4 1 1 1					
Anthoxanthum odoratum	3 - - -					
Total Gramineae		38	17	36	7	
5. Cyperaceae class 2						
Carex caryophyllea	1 - - -	4	-	-	<1	
Total Cyperaceae		<1	-	-	-	
6. Out-community / on island pollen						
Campanulaceae		<1	-	-	<1	OT
Calluna vulgaris		3	5	<1	3	A/E
Ammophila arenaria		<1	-	<1	-	C/E
Betula		1	<1	3	-	A/E
Corylus		-	-	2	2	OT
Pinus		<1	<1	-	<1	OT
Salix		-	-	<1	1	A/E
7. Out community / off island pollen.						
Quercus		-	<1	<1	-	
Ulmus		<1	<1	-	-	

Total pollen percentages	**I1**	**I2**	**I3**	**I4**
Total In-community	84	85	89	85
Total Out-community / on island %	6	7	6	6
Total Off island	<1	<1	-	<1
Total degraded	9	7	4	6
Total unidentified	1	<1	<1	2

"Associated species" such as *Bellis perennis* (28% tlp), *Rumex acetosa* (1-9% tlp) *Equisetum arvensis* (5-14% tlp) and *Ranunculus acris* (5-18% tlp) are well represented by pollen. Three "associated" species, *Dactylorhiza majalis*, *Cerastium glomeratum* and *Luzula campestris* have no pollen representation. "Less frequent" species present in the quadrats are generally poorly represented by pollen for example, *Sagina procumbens*, *Centaurea nigra*, *Cardamine pratensis*, *Lotus corniculatus*, *Montia fontana*, *Viola palustris*, *Carex caryophyllea* and *Angelica sylvestris*.

"On island / out community" pollen values vary from 6-7% tlp and comprised scarce grains of *Ammophila arenaria*, *Pinus*, Coryloid, *Salix*, *Betula* and *c*.3-5% tlp *Calluna vulgaris*

Of the 26 plant species recorded in the quadrats 21 were represented by pollen but only 7 taxa are in PRC. A and B. 5 "out-community / on island" taxa comprising 6-7% tlp were recorded. This community is distinguishable from Group H by the absence of *Galium verum*, *Thalictrum minus* and *Heracleum sphondylum* and the presence of class character species such as *Plantago lanceolata* and *Trifolium repens* in combination with low but significant proportions of *Potentilla* and *Vicia cracca*. Otherwise the pollen spectra is dominated by a similar suite of machair species *Plantago lanceolata*, *Bellis perennis*, *Ranunculus acris* and *Trifolium repens*.

The vegetation quadrats analysed for pollen contained a total of 26 plant species, and of this total 21 species were represented by pollen and 6 "out-community / on island" pollen types were identified. There appears to be little distortion of the communities pollen spectra as a result of "on-island / off island" pollen transfer which ranges between 7-8% tlp. A relatively high proportion (4-9% tlp) of pollen was classed as degraded and / or unidentifiable in these samples.

Iris pseudacorus inner machair communities (Group G and N).

Samples from moss polsters and surface organic sediment.
Scattered iris clumps are a significant community type of the inner machair plain. They tend to occur in wet or damp basins within the inner machair and on the margins of small lochs and ponds. *Iris psuedacorus* is the main "characterising species" but there is a wide diversity of "associated species". Group N is a loch-edge community, Group G the typical *Iris* patch community.

The five "characterising species" in Group G are poorly represented in the pollen spectra. Three species, *Iris pseudacorus*, *Cardamine pratensis* and *Juncus effusus* were not recorded and *Epilobium palustre* and *Rumex acetosella* are present in very low frequencies. In contrast several "associated species", *Hydrocotyle vulgaris* (8-11% tlp), *Equisetum arvensis*, *Filipendula ulmaria* (19-23% tlp) and *Sphagnum recurvum* are well represented by pollen / spores as are the grasses, *Agrostis capillaris* and *Agrostis stolonifera*; and sedges *Carex nigra* and *Eriophorum angustifolium*.

The floristic diversity of the community is poorly reflected in the pollen spectra as many associated species such as *Potentilla anserina*, *Stellaria palustris*, *Viola palustris*, *Equisetum arvense* and *Cardamine amara* are either scarce or absent.

As with Group G, the similar suite of "characterising species" in Group N are poorly represented in the pollen spectra, notably, *Iris pseudacorus*, *Cardamine pratensis*, *Epilobium palustre*, *Montia fontana*, and *Potentilla anserina* all have pollen frequencies of <1%-3% tlp in all the samples. Of the "characterising species" only *Rumex acetosa* (<1-3% tlp), *Galium palustre* (1-6% tlp) and *Caltha palustris* (13-26% tlp) reflect their abundance in the vegetation.

"Associated species" such as *Equisetum fluvatile*, *Equisetum palustre* (5-5% tlp), *Caltha palustris* (13-22% tlp) and *Phragmites australis* (15% tlp) are reasonably well represented in the pollen spectra. The high pollen frequencies recorded for *Carex nigra* (19-22% tlp)

Table 13: Machair lake margin communities ; *Iris pseudacorus* inner machair communities (Groups G).

1. **Characterising species.**	**Abundance.**		**Pollen %**		**PRC**
Iris pseudacorus	5	5	-	-	F
Epilobium palustre	3	4	2	2	C
Rumex acetosella	3	2	7	<1	C
Cardamine pratensis	4	3	-	-	F
Juncus effusus	5	2	-	-	F
2. **Associated species**					
Galium palustre	1	1	4	<1	C
Potentilla anserina	-	3	-	<1	C
Stellaria palustris	1	1	-	-	D
Hydrocotyle vulgaris	3	5	10	8	B
Ranunculus acris	2	4	2	3	A
Filipendula ulmaria	3	2	23	19	A
Equisetum arvense	1	1	3	<1	B
Sphagnum recurvum	-	4	6	86	A
				*P.Sample.	
3. **Less frequent species.**					
Cardamine amara	1	-	-	-	F
Viola palustris	-	2	-	<1	C
4. **Gramineae class 2.**			15	20	
Poa pratensis	-	2			
Agrostis capillaris	5	-			
Agrostis stolonifera	-	4			
Gramineae class 3.			<1	4	
Holcus lanatus	-	2			
Total Gramineae.			18	24	
5. **Cyperaceae class 2.**			15	33	
Carex nigra	3	-			

Eriophorum angustifolium	-	5	
Total Cyperaceae.	15	33	
6. Out community / on island.			
Calluna vulgaris	<1	-	A/E
Plantago lanceolata	1	-	A/E
Bellis perennis	<1	<1	A/E
Trifolium repens	<1	-	B
Ranunculus acris	<1	1	A
Sinapis type	-	<1	D
7. Out-community / off island pollen			
Ulmus	1	1	
Quercus	<1	-	
Tilia	-	<1	
Alnus	-	<1	
Betula	2	-	
Pinus	<1	<1	

Total pollen percentages		**G1**	**G2**
Total In-community		90	92
Total Out-community / on island	%	6	2
Total Off island		1.8	2.3
Total degraded	%	2	1
Total unidentified	%	<1	2

* P.sample: Pollen sample consisted of this species.

and *Eleocharis palustris* (20% tlp), which have low abundance scores in the vegetation suggests that these types are slightly over - represented in the pollen spectra because of the low pollen frequencies recorded for many herbaceous taxa.

"On island / out comunity" pollen values are low (*c*.2-6% tlp) in each sample and comprise scarce grains of *Bellis perennis*, *Plantago lanceolata* and *Ranunculus* type, thought to originate from nearby machair grassland communities and *Betula* and *Calluna vulgaris* present in woodland and heath communities to the east of Loch Kildonan. These two communities have a pollen spectra which is strongly indicative of loch-edge and fen meadow vegetation but overall the communities are not well represented by pollen. Very little pollen from outside the community is present in the samples in comparison with the open grassland communities of the machair,suggesting that the taller vegetation structure may influence pollen dispersal into the communities.

The vegetation quadrats analysed for pollen in Group G contained a total of 21 plant species, and of this total 18 species were represented by pollen and 6 "out-community / on-island" pollen types were identified. There appears to be little distortion of this communities pollen spectra as a result of "on-island" pollen transfer which ranges between 2-4% tlp. "Off-island" pollen contributes 1.8% tlp and 2.3% tlp and comprises scarce grains of *Ulmus*, *Quercus*, *Tilia* and *Alnus*.

The vegetation quadrats analysed for pollen in Group N contained a total of 22 plant species, and of this total 20 species were represented by pollen and 6 "out-community / on-island" pollen types were identified. There also appears to be little distortion of this community's pollen spectra as a result of "on-island" pollen transfer which ranges between 4-5% tlp. Pollen identified as "off-island" contributes 1.4% tlp and 0.8% tlp and comprises scarce grains of *Ulmus* and *Alnus* respectively.

Table 14 : Iris pseudacorus Inner Machair community (Group N).

1. Characterising species	**Abundance.**		**Pollen %**		**PRC**
Iris pseudacorus	5	5	-	-	F
Cardamine pratense	2	1	-	-	F
Epilobium palustre	3	1	1	<1	C
Rumex acetosa	-	1	<1	3	C
Montia fontana	-	1	<1	-	D
Ranunculus repens	-	2	2	4	D
Potentilla anserina	1	1	<1	<1	D
Caltha palustris	5	2	22	13	B
Galium palustre	4	1	6	1	C
2. Associated species.					
Potentilla palustris	-	1	-	16	B
Angelica sylvestris	2	-	4	-	C
Polygonum bistorta	3	-	<1	-	D
Phragmites australis	4	-			A
Equisetum fluvatile	1	-	6	<1	B
Equisetum palustre	1	-	2	4	B
3. Less frequent species.					
Poa trivialis (see Gramineae class 1.)					
4. Gramineae class 1.			-	14	
Poa trivialis	-	1			
Gramineae class 2.			15	9	
Agrostis stolonifera	3	-			
Gramineae class 3.			<1	<1	
Holcus lanatus	1	1			
Phragmites australis	4	-	15	-	
Total Gramineae.			30	27	
5. Cyperaceae class 2.			15	12	
Carex nigra	2	2			
Cyperaceae class 4.			3	20	

Eleocharis palustris	-	3	
Total Cyperaceae.	18	20	
6. Out community / on island pollen			
Bellis perennis	1	-	A/E
Lotus type	-	<1	C
Betula	<1	-	A/E
Plantago coronopus	-	<1	A
Calluna vulgaris	1	1	A
7. Out-community / off island pollen			
Ulmus	<1	-	
Alnus	<1	<1	

Total pollen percentages		**N1**	**N2**
Total In-community		91	93
Total Out-community / on island		5	4
Total Off island		1.4	0.8
Total degraded	%	1	2
Total unidentified	%	0.7	0.2

Phragmites australis machair swamp community (Group O)

Samples from moss polsters and surface organic sediments.
These communities occur in infilled machair loch areas and on the transect were located adjacent to Upper Loch Kildonon (GR NF729280). Situated on the machair these wet sites have a relativley high species richness (mean 14.3).

Four of the "characterising species" in this community are well represented by pollen, Phragmites australis (10-13% tlp), Carex nigra (10-19% tlp), Agrostis stolonifera (4-17% tlp) and Caltha palustris (12-26% tlp). Other "characterising species" which are present in low but significant frequencies include Angelica sylvestris (c.2% tlp), Rumex acetosa (4-6% tlp) and Equisetum palustre (3-10% tlp) whereas Stellaria palustris, Dactylorhiza majalis and Viola palustris are either absent or present only as scarce grains. With the exception of Typha latifolia and Ranunculus all the "associated species" such as Cerastium glomeratum, Galium palustris, Mentha aquatica and Polygonum bistorta are also poorly represented in the pollen spectra, as are several less frequent species such as Cardamine pratensis, Epilobium palustris, Iris pseudacorus and Potentilla anserina. Phragmites australis, Cyperaceae (Carex nigra), Caltha palustris, Equisetum and Typha latifolia are the strongest indicator species for this community.

However, because of the low pollen frequencies recorded for many "associated" and "less frequent" species the pollen spectra is a poor reflection of the floristic diversity of the community.
The vegetation quadrats analysed for pollen contained a total of 26 plant species, and of this total c.17 species were represented by pollen. 6 "out-community / on-island" pollen types including Plantago lanceolata, Coryloid and Calluna vulgaris were present but in low (<1% -3 tlp) frequencies. There appears to be some distortion of this community's pollen spectra as a result of "on-island" pollen transfer which ranges between 4-16% tlp.
This proportion of pollen in the samples is relatively high in two of the

Table 15 : Pragmites australis Machair Swamp Community (Group 0)

1. Characterising species	Abundance.			Pollen %			PRC
Pragmites australis	5	5	4	13	11	10	A
Angelica sylvestris	2	5	3	2	2	2	C
Dactylorhiza majalis	2	1	1	<1	-	-	F
Caltha palustris	5	4	3	22	12	26	B
Stellaria palustris	3	5	-	1	2	-	D
Viola palustris	5	1	3	4	-	<1	C
Rumex acetosa	-	2	2	-	4	6	C
Agrostis stolonifera	5	5	-				
Carex nigra	2	5	1				
Equisetum palustre	1	3	-	3	10	<1	B
2. Associated species							
Cerastium glomeratum	1	-	-	<1	-	-	D
Ranunculus acris	1	1	-	8	1	-	A
Ranunculus repens	3	3	-	-	-	-	C
Galium palustris	1	-	-	3	-	-	C
Mentha aquatica	-	1	2	-	<1	1	D
Polygonum bistorta	-	3	-	-	<1	-	D
Typha latifolia	-	-	5	-	-	11	B
Eleocharis palustris	1	-	-	6	-	-	B
Equisetum fluvatile	-	1	-	-	4	-	B
3. Less frequent species.							
Cardamine pratensis	1	-	1	-	-	-	F
Epilobium palustris	-	1	-	-	2	-	C
Iris pseudacorus	-	-	5	-	-	-	F
Cerastium glomeratum	1	-	-	1	-	-	D
Potentilla anserina	1	-	-	<1	-	<1	C
4. Gramineae class 2.							
Agrostis stolonifera	5	5	-	14	12	4	
Phragmites australis	5	5	4	13	11	10	
Total Gramineae.				27	23	14	

5) Cyperaceae class 2.				10	19	15	
Carex nigra	2	5	1				
Cyperaceae class 4.				<1	6	-	
Eleocharis palustris	-	1	-				
Total Cyperaceae.				11	29	15	
6) Out community / on island pollen.							
Gramineae class 3.				<1	2	12	
Plantago lanceolata				1	1	-	A
Calluna vulgaris				-	3	2	A/E
Coryloid				-	-	<1	A
Sambucus				<1	-	-	OT
Fraxinus				-	-	<1	
Pinus				-	<1	-	
Betula				<1	<1	<1	
Sorbus				-	-	<1	
Quercus				-	<1	-	
7. Out-community / off island pollen							
Quercus				-	<1	-	

Total pollen percentages	**01**	**02**	**03**
Total In-community	90	89	77
Total Out-community / on island	4	6	16
Total Off island	-	<1	-
Total degraded	2	4	5
Total unidentified	0.6	1	1

samples due high levels of Gramineae class 3 pollen (*Festuca rubra*?) which may have originated in nearby machair grassland communities. "Off-island" pollen contributes <1% tlp and comprises scarce grains of *Quercus*.

Eleocharis palustris lake margin community (Group M)

This community type occurs on the loch margins of Upper Loch Kildonon. Samples from moss polsters.

Two of the five "characterising species" in this community are well represented in the pollen spectra. *Eleocharis palustris* (34%, 23% and 45% tlp) was abundant in the vegetation as was *Caltha palustris* (9%, 17%, 14% tlp). *Ranunculus flammula*, *Mentha aquatica* and *Agrostis stolonifera* which were less abundant have poor pollen representation. The "associated species", *Potentilla anserina*, *Galium palustre*, *Hippuris vulgaris* and *Equisetum palustris* are also poorly represented in the pollen spectra. In contrast the "less frequent" species *Filipendula ulmaria*, *Potentilla palustris* and *Carex nigra* where present in the vegetation had good pollen representation and are dispersed in lower frequencies into samples which were taken from nearby quadrats. "Out community / on island" pollen input includes low frequencies of Gramineae classes 2 and 4, *Bellis perennis*, *Triglochin*, *Plantago lanceolata*, *Rumex crispus*, *Sinapis* type, *Ranunculus* and Umbelliferae (*Angelica* type) thought to originate in nearby machair and lake margin communities. *Calluna vulgaris*, *Betula*, *Corylus* and *Pinus* are also present. The pollen spectra reflects the lake margin character of the community with high pollen frequencies of *Eleocharis palustris*, *Filipendula ulmaria* and *Caltha palustris* but the greater number of low pollen producing species present, and diversity of "out community" input weakens the pollen 'signature' of this community.

Table 16 : *Eleocharis palustris* lake margin community (Group M)

1. Characterising species.	**Abundance.**	**Pollen %**			**PRC**
Eleocharis palustris	5 5 5	27	36	45	B
Ranunculus flammula	1 1 -	<1	<1	-	D
Caltha palustris	4 3 4	9	17	14	B
Mentha aquatica	1 - 1	<1	-	-	D
2. Associated species.					
Potentilla anserina	2 - 1	4	-	-	C
Galium palustre	2 - -	6	-	1	C
Hippurus vulgaris	1 - 4	-	-	<1	D
Equisetum palustris	1 - -	4	-	-	B
3. Less frequent species.					
Filipendula ulmaria	4 - -	17	2	5	A
Potentilla palustris	3 - -	12	3	2	B
4. Gramineae class 2.		5	<1	9	
Agrostis stolonifera	1 - 1				
Total Gramineae.		5	4	9	
5. Cyperaceae class 2.	- 5 -	4	22	9	
Carex nigra					
Cyperaceae class 4		26	29	44	
Eleocharis palustris	5 5 5				
Total Cyperaceae.		30	51	53	
6. Out-community / on island pollen					
Gramineae class 4.		<1	2	1	
Gramineae class 3.		1	3	3	
Bellis perennis		-	1	<1	A
Ranunculus type		-	1	1	A
Plantago lanceolata		<1	1	2	A
Triglochin		-	<1	-	B
Rumex crispus		<1	-	-	D

Sinapis type	-	1	1	C
Umbelliferae	<1	-	<1	
Calluna vulgaris	2	4	<1	A
Betula	-	<1	-	A
Pinus	-	-	<1	OT
Corylus	<1	<1	-	OT
Ulex	-	-	<1	OT
Fraxinus	-	<1	<1	OT
Huperzia selago	<1	-	-	A

7. Out-community / off-island pollen

Alnus	1	1	-
Quercus	<1	-	<1
Carpinus	<1	-	-
Tilia	-	1	-

Total pollen percentages.	**M1**	**M2**	**M3**
Total In-community	88	78	85
Total Out-community / on island	6	14	11
Total Off island	2.8	2	0.6
Total degraded	2	4	4
Total unidentified	1	2	0.4

Potentilla anserina - Carex nigra - Vicia cracca inner machair community (Group L).

Samples from moss polster and surface organic detritus. This group constitutes a distinct sub-community of the machair occurring on the damper sites above the machair lochs. The pollen spectra from this community contains a number of well represented "characterising species." *Filipendula ulmaria* (18% tlp), *Carex nigra* (17-22% tlp), *Triglochin maritima* (27% tlp), *Equisetum* (8-16% tlp), *Hydrocotyle vulgaris* (12-14% tlp) and *Rumex acetosa* (6%-12% tlp) are notable. Of the "less frequent" species *Caltha palustris* (13-17% tlp) is well represented by pollen. "Characterising" species with low but significant pollen representation include *Vicia cracca* and *Potentilla anserina*. As in other machair communities *Rhinanthus minor*, *Iris pseudacorus* and *Dactylorhiza purpurea* are absent from the pollen spectra.

"Out community / on island" pollen input includes low frequencies of Gramineae class 2 and 3, and scarce grains of *Plantago lanceolata*, *Pedicularis* and *Bellis perennis* (all present in the local vegetation). Scarce grains of *Sinapis* type and *Papaver* type were thought to originate from a small cultivated machair strip nearby. However there is a notable change in the "out-community" pollen input with an increase in the diversity of species associated with blanket bog communities (Ericaceae, *Sphagnum*, *Pedicularis* and *Huperzia selago*) even though pollen percentage values for these types are low. Overall the pollen spectra of the community is dominated by a number of well represented and weakly dispersed pollen types such as *Hydrocotyle*, *Triglochin maritima*, *Filipendula ulmaria* and *Caltha palustris* but as with many communities floristic diversity is not well reflected by the pollen spectra.

The stable dune and grassland communities have a group of pollen types which are well-represented in all the samples where the parent plant is present in the vegetation. This group includes, *Plantago lanceolata*, *Bellis perennis*, *Ranunculus acris* and *Festuca*

Table 17 ; Potentilla anserina - Carex nigra - Vicia cracca Inner machair community (Group L).

1. Characterising species	**Abundance.**		**Pollen %**		**PRC**
Potentilla anserina	4	4	3	<1	C
Vicia cracca	5	3	4	1	C
Rhinanthus minor	3	1	-	-	F
Hydrocotyle vulgaris	5	3	12	4	B
Rumex acetosa	3	1	5	-	C
Leontodon autumnalis	1	1	-	<1	D
Dactylorhiza majalis	-	1	-	-	F
Filipendula ulmaria	5	-	18	2	A
Mentha aquatica	2	-	<1	-	D
Carex nigra	5	5			
Triglochin maritima	-	5	-	27	B
Equisetum fluvatile	3	4	8	16	B
2. Associated species					
Iris pseudacorus	1	-	-	-	F
Equisetum palustre	1	-	1	<1	B
3. Less frequent species.					
Caltha palustris	5	5	13	17	B
Galium palustris	-	2	-	<1	C
4.Gramineae class 2.			2	1	
Gramineae class 3.			6	3	
Total Gramineae.			8	4	
5. Cyperaceae class 2.			17	22	
Carex nigra	5	5			
Total Cyperaceae.			19	22	
6. Out-community / on-island pollen					
Sinapis type			2	-	D
Ranunculus type			<1	<1	A

Pedicularis	-	<1	D
Bellis perennis	<1	<1	A/E
Papaver type.	<1	-	OT
Betula	-	1	A/E
Pinus	-	<1	OT
Calluna vulgaris	3	1	A/E
Ericaceae	<1	-	C
Sphagnum	-	2	A/E

Total pollen percentages	**L1**	**L2**
Total In-community	90	89
Total Out-community / on island	7	6
Total Off island	-	<1
Total degraded	2	4
Total unidentified	0.6	1

rubra. Although particularly significant indicators of the stable dune and machair grasslands, this group of pollen taxa are also the most widely dispersed and as a result the machair communities defined by TWINSPAN are difficult to differentiate palynologically. This is partly due also to difficulties with Gramineae identification and the nature of the machair vegetation itself which is a continuum of the "characterising species" growing as a mosaic of herbaceous communities differentiated by local environmental conditions. There are some notable contrasts between vegetation abundance and the pollen frequencies of "characterising species". For example Trifolium repens, Potentilla anserina, Achillea millefolium and Rhinanthus minor which have high abundance scores in many of the vegetation quadrats have inconsistent or very poor pollen records. The distinction between the Festuca rubra - Galium verum dune machair community (Group I) and the Festuca rubra - Potentilla anserina - Trifolium repens - Agrostis stolonifera inland grassland community (Group H) can be seen in the presence of low but significant frequencies of morphologically - distinctive pollen types rather than the pollen representation of "characterising" species which are common to both groups. For example Vicia cracca and scarce grains of Montia fontana in Group I and Galium verum, as well as Thalictrum minus in Group H (see table 11) in association with other characterising taxa, are good community indicators because they appear to have weakly dispersed pollen.

The Iris pseudacorus patch communities which are such a distinctive feature of the machair grassland vegetation were poorly represented in the pollen analysis. The absence of any Iris pseudacorus grains in the samples was suprising as the plant was flowering when the samples were collected.

In contrast the machair wetland communities are characterised by a suite of pollen types which are strongly represented within the community and weakly dispersed outside. This group includes Caltha palustris, Triglochin palustris, Eleocharis palustris, Equisetum arvensis, Filipendula ulmaria and Typha latifolia. Potentilla palustris also belongs to this group but would be difficult to identify with confidence in fossil samples. These findings are in good agreement with the results of Randall et al. (1986) which identified (i) Plantago lanceolata and Ranunculus acris as well represented, widely dispersed pollen types and (ii) Bellis perennis as a well represented, less widely dispersed type on the machair.

Neutral / acid grassland communities.

Agrostis capillaris - Festuca ovina grasslands (Group E1 and E2). Samples from moss polsters and surface organic sediment. TWINSPAN defined two sub-communities within this group. The first group (E2) is located at lower altitudes (mean 65m.) in the zone between the machair and the uplands. The second (E1) is generally more acidic in nature and represents typical upland Agrostis - Festuca pasture (mean altitude 446m.) and is located on the steep slopes at middle to higher altitudes across the Beinn Mhor massif. Species richness is the highest of all groups (E1 mean 18.8, maximum 35.0, E2 mean 17.6 maximum 34.0). The acid neutral grassland communities described here are subject to grazing by sheep, and in the uplands by deer. Such intensive grazing affects the vegetation and as a consequence the pollen spectra of the community. Pollen analysis consequently provides a pollen 'signature' for grazed grassland communities on the transect (see Groenman-van Waateringe 1986, Berglund and Persson 1986, for discussion). This information may be useful for identifying grassland biotypes associated with pastoralism in the fossil pollen record.

The E2 TWINSPAN grouping covers samples located between the transition from the machair grassland communities in Upper Loch Kildonon to the upland grassland communities of group E1. The samples analysed from Group E1 included one from quadrats located on rocky "ledges" at high altitudes on the north facing crags of Beinn Mhor.

The "characterising species" of Group E2 are similar to those of E1 and the pollen spectrum displays a similar pattern to E1 in that Gramineae representation is low in comparison with abundance in the vegetation and with the ungrazed machair grassland communities (see figure 24). *Potentilla erecta*, a "characterising species" in the community is poorly represented by pollen, as are a range of associated herbaceous species including *Polygala serpyllifolia*, *Plantago lanceolata*, *Galium saxatile*, *Viola riviniana* and *Thymus serpyllum*. Also a large group of ten "associated" and "less frequent" species were either absent or very poorly represented by pollen. This group included *Trifolium repens*, *Bellis perennis*, *Achillea millifolium*, *Senecio jacobaea*, *Anagalis tenella*, *Euphrasia officinalis*, *Cerastium glomeratum* and *Luzula campestris*. The pollen values for *Bellis perennis* and *Trifolium repens* were considerably lower in the these samples than in the machair grassland where both taxa were well represented. This probably results from the greater abundance of ungrazed patches of both species in the machair which contrasts with the sparser, grazed vegetation of the acid grassland.

The analysis of the Gramineae and Cyperaceae pollen in these samples was complicated by the number of species present in each group, and therefore the composite values for these types provided the best indication of Gramineae and Cyperaceae representation. There appears to be correlation between Gramineae pollen class 2 and class 3 types and their presence in the vegetation which suggests local deposition (see table 18). However the pollen values (13-23% tlp) are not a good indication of Gramineae abundance in this group and again these values are thought to be a consequence of grazing. Cyperaceae pollen representation reflects species presence in the vegetation, for example, *Carex nigra* (6-32% tlp) is the most abundant species, *Carex pilulifera* and *Carex*

Table 18 : Agrostis capillaris - Festuca ovina grasslands (Group E2)

1. **Characteristic species.**	**Abundance.**			**Pollen %**			**PRC**
Potentilla erecta	3	-	1	2	-	<1	C
Trifolium repens	2	2	-	<1	-	-	B
Agrostis capillaris	5	1	3				
Festuca ovina	5	-	5				
Holcus lanatus	1	-	5				
Anthoxanthum odoratum	2	-	3				
2. **Associated species.**							
Calluna vulgaris	5	-	-	42	29	36	A
Viola riviniana	4	-	3	<1	-	2	C
Galium saxatile	1	-	2	<1	-	1	C
Luzula campestris	2	-	-	-	-	-	F
Carex nigra	1	5	1				
3. **Less frequent species.**							
Polygala serpyllifolia	5	-	-	1	-	1	C
Achillea millifolium	1	-	-	<1	-	-	F
Lotus corniculatus	1	-	-	<1	-	-	C
Plantago lanceolata	2	-	-	4	-	-	A
Galium palustre	-	1	-	<1	<1	-	C
Potentilla anserina	-	2	-	-	1	-	C
Ranunculus acris	-	1	1	-	3	<1	C
Senecio jacobaea	-	1	-	-	-	-	D
Potentilla palustris	5	-	-	12	-	-	B
Epilobium palustre	-	1	1	-	2	3	C
Prunella vulgaris	-	1	1	-	-	-	D
Anagallis tenella	-	1	-	-	-	-	F
Euphrasia officinalis	-	-	1	-	-	-	F
Cerastium glomeratum	-	-	1	-	-	2	D
Thymus serpyllum	-	-	1	-	-	2	D
Lysimachia nemorum	-	-	1	-	-	<1	D
Ranunculus ficaria	-	-	1	-	-	-	F

Nardus stricta	1 - -				
Molinia caerulea	- 4 -				
Agrostis canina	- - 4				
Carex echinata	- 1 -				
Carex pilulifera	- 1 -				
Triglochin palustris	- 3 -	-	6	-	A
4. Gramineae class 2.		5	17	<1	
Agrostis capillaris	5 1 3				
Molinia caerulea	- 4 -				
Agrostis canina	- - 4				
Gramineae class 3.		**16**	**4**	**17**	
Festuca ovina	5 - 5				
Holcus lanatus	1 - 5				
Anthoxanthum odoratum	2 - 3				
Nardus stricta	1 - -				
Total Gramineae.		20	21	18	
5. Cyperaceae class 1.		-	-	-	
Carex pilulifera	- 1 -				
Carex echinata	- 1 -				
Cyperaceae class 2.		6	32	16	
Carex nigra	1 5 1				
Total Cyperaceae.		6	32	16	
6. Out-community / On-island pollen.					
Erica cinerea		-	1	1	E
Campanulaceae		-	<1	-	OC
Chenopodiaceae		<1	-	-	OC
Salix		1	<1	3	A
Pteridium aquilinum		1	-	2	A
Betula		1	3	4	A
Coryloid		-	<1	3	A
Pinus		<1	<1	-	OT
Ilex		-	<1	-	OT
Sorbus		<1	-	1	A

Alnus	<1	-	-	OT
Polypodium	-	-	1	OC
Drosera	<1	-	-	C
Compositae Liguliflorea	-	<1	-	
Compositae Tubuliflorae	<1	-	<1	
7. Out-community / off-island pollen				
Ulmus	-	<1	<1	

Total pollen percentages	**E21**	**E22**	**E23**
Total In-community	91	87	83
Total Out-community / on island	7	6	15
Total Off island	-	<1	<1
Total degraded	-	<1	<1
Total unidentified	-	<1	<1

echinata which have low abundance scores in the vegetation, also have relatively low pollen frequencies.

"On island / out community" pollen values range between 6 -15% tlp, comprising *Erica cinerea* (*c*.1% tlp) and scarce grains of Campanulaceae, Chenopodiaceae, *Ilex*, *Sorbus*, *Pinus*, Umbelliferae, *Drosera*, Compositae Liguliflorea, Compositae Tubuliflorea, and spores of *Pteridium aquilinum* and *Huperzia selago*. *Betula* (3-4% tlp) and *Salix* (1-3% tlp) are the most abundant "out-community" types recorded. The over-representation of *Calluna vulgaris* in the pollen spectra of the E1 and E2 samples tends to repress the pollen frquencies of other less-productive and well-dispersed types. This effect distorts community representation and as a result the pollen spectra reflect to a greater extent the spatial distribution of the E1 and E2 communities as part of the mosaic of grassland, wetland and heath vegetation and the pollen is therefore a good indicator of the surrounding vegetation mosaic.

The pollen spectra of the samples analysed from the E1 grouping contained large proportions of *Calluna vulgaris* which attained values of 12-24% tlp in samples where *Calluna vulgaris* was not present in the vegetation, only 7% less than in one sample in which *Calluna vulgaris* was abundant. The ledge sample had a higher proportion of Gramineae (26% tlp) than the other grassland samples presumably because it was inaccessible to grazing animals. Low but significant frequencies of *Saxifraga stellaris* (<1% tlp), *Thalictrum alpinum* (2% tlp) and *Oxyria digyna* (1.8% tlp) were recorded in the ledge sample. However *Juncus bufonius* and *Juncus squarrosus*, with high abundance scores in the vegetation, were not represented by pollen. Ericaceous shrubs, where present in the vegetation, were represented by pollen, for example, *Vaccinium myrtillus* (4-12% tlp) and *Erica cinerea* (2-3% tlp) but these values are much lower than those recorded for *Calluna vulgaris*. Of the "characterising" species *Potentilla anserina* (3-9% tlp) was recorded together with low but significant frequencies of other

Table 19 : Neutral / acid grassland communities *Agrostis capillaris* - *Festuca ovina* grasslands (Group E1).

1. Characterising species.	**Abundance.**	**Pollen %**	**PRC**
Potentilla erecta	1 5 3	<1 9 3	C
Agrostis capillaris	1 1 3		
Festuca ovina	5 3 4		
2. Associated species			
Calluna vulgaris	- - 5	24 12 31	A
Vaccinium myrtillus	- 5 1	- 12 4	C
Viola riviniana	1 - 1	4 - <1	C
Galium saxatile	- 1 1	- 1 1	C
Selaginella selaginoides	- - 1	- - 7	C
3. Less frequent species.			
Saxifraga stellaris	2 - -	<1 - -	D
Thalictrum alpinum	4 - -	2 - -	D
Oxyria digyna	1 - -	4 - -	D
Narthecium ossifragum	- 3 -	- 6 -	C
Thymus serpyllum	- 1 -	- 2 -	D
Erica cinerea	- - 4	- 2 3	C
Taraxacum officinale	- - 1	- - 1	D
Hypericum pulchrum	- - 1	- - <1	D
Juncus bufonius	1 - -	- - -	F
Juncus squarrosus	5 5 -	- - -	F
Sphagnum papillosum	- - 1	13 9 83*	A
		*P.sample	
Huperzia selago	- - 4	2 - 8	A
4. Gramineae class 2.		6 <1 7	
Agrostis capillaris	1 1 3		
Agrostis canina	1 - 1		
Gramineae class 3.		20 10 9	
Nardus stricta	- 3 4		

Festuca ovina	5	3	4				
Total Gramineae.				26	12	16	
5. Cyperaceae class 1.				-	-	-	
Carex piluliflora	-	1	-				
Cyperaceae class 2.				10	12	-	
Carex caryophyllea	-	1	-				
Carex dioica	-	4	-				
Cyperaceae class 3.				-	5	10	
Carex flacca	-	-	4				
Carex binervis	-	3	-				
Total Cyperaceae.				10	17	10	
6. Out-community / on island pollen.							
Succisa pratensis				1	1	-	OC
Plantago lanceolata				-	-	2	C
Armeria maritima				<1	-	-	A
Erica tetralix				-	<1	-	C
Alnus				-	<1	<1	OT
Pinus				<1	<1	<1	OT
Betula				3	2	1	A
Salix				4	3	3	A
Fagus				<1	-	-	OT
Coryloid				<1	3	-	A
Pteridium				-	2	2	A
Botrychium lunaria				1	-	-	OT
Polypodium				1	2	-	OC
Filicales				-	2	<1	OC
Ranunculus				-	<1	-	C
Drosera				-	-	<1	D
7. Out-community / off-island pollen							
Quercus				1	<1	<1	
Ulmus				<1	<1	-	

Total pollen percentages	**E1**	**E2**	**E3**
Total In-community	85	81	86
Total Out-community / on island	12	16	9
Total Off island	1.5	1	0.6
Total degraded	2	2	4
Total unidentified	-	-	-

herbaceous species such as *Galium saxatile*, *Narthecium ossifragum*, *Thymus serphyllum*, *Taraxacum officinale* and scarce grains of *Hypericum* type. The spores of *Huperzia selago* (10% tlp) and *Selaginella selaginoides* (7% tlp) are recoded from samples where the species were present in the vegetation. The absence of *Juncus* spp. from the pollen spectra is significant as the species is abundant in the vegetation at high altitudes on Beinn Mhor. Also there is a degree of distortion caused by the high *Calluna vulgaris* and low Gramineae values. "On island / out-community" pollen values were relatively high for the study ranging from 8-15% tlp with a corresponding increase in the diversity of taxa present. 16 "on-island / out-community" types included grassland species such as *Plantago lanceolata*, *Succisa pratensis*, *Ranunculus* Compositae Liguliflorea and bracken patch species (Group F) such as *Pteridium aquilinum*, *Salix*, *Betula*, Coryloid, *Polypodium* and Filicales undifferentiated, thought to originate from local communities occurring at lower altitudes. Scarce grains of *Pinus*, *Fagus*, *Quercus* and *Ulmus* were also noted. A group of distinctive pollen taxa appear to be good indicators of the sub-communities, notably *Potentilla erecta*, *Thymus serpyllum*, *Thalictrum alpinum*, *Saxifraga stellaris*, *Oxyria digyna*, *Galium*, *Huperzia selago* and species of Ericaceae.

Pteridium aquilinum - Potentilla erecta - Anthoxanthum odoratum bracken infested grasslands (Group F).

Samples from moss polsters and surface organic sediments. *Pteridium aquilinum* patches occur in a variety of locations across the transect primarily on peatlands at lower altitudes. Usually bracken has invaded areas of *Agrostis*- *Festuca* pasture or, as in the east coast valleys, mature degenerative stands of *Calluna vulgaris*. Two woodland sub-groups not identified by TWINSPAN were included in the pollen taphonomic study. These include samples from the woodland at Allt Volagir and from patches of *Salix aurita* scrub located in Kildonan Glen and Loch Eyenort. The "characterising species" *Pteridium aquilinum* and *Potentilla erecta* are present in the pollen spectra from all the samples analysed in this group. *Pteridium aquilinum* (12-27% tlp + Pteridophytes) is particularly well represented. However the TWINSPAN grouping includes a variety of "associated" and "less frequent" species which makes it difficult to characterise the pollen assemblage from the grouping. Quadrats in which tree or shrub species were present were deliberately selected in order to examine the relationship between arboreal pollen representation and existing woodland (see table 20). In one sample from Glen Kildonan where *Salix aurita* forms dense patches around inflow streams a pollen percentage value of 31% tlp is recorded. The figure is if anything under-representative in that it refers to single *Salix* grains counted on the slide and ignores some large clumps of pollen which were impossible to count accurately.

In the samples from Allt Volagir N.N.R., *Salix*, *Betula pendula*, *Populus tremula* and *Corylus avellana* were present in the vegetation. In general arboreal pollen representation was low, reflecting the open nature of this woodland (in contrast to the dense low canopies of the Loch Druidibeg island woods, see Chapter 10 this study). *Betula* (6-23% tlp), *Salix* (15-19% tlp) and *Sorbus* (14% tlp) have the best pollen record, however *Corylus avellana* - a reputedly high pollen producer - had low pollen frequencies (4-12% tlp) whereas *Populus tremula* was not recorded. Of the species associated with the woodland understory, *Hedera helix* (2-9% tlp) and *Lonicera periclymenum* (1-2% tlp) were present in significant proportions. *Rubus fruticosus* was not identified. Other associated species with low but significant pollen values, included *Primula vulgaris*, *Osmunda regalis* and *Rumex acetosa*. Of the less frequent species, *Plantago lanceolata*, *Urtica dioica*, *Viola riviniana*,, *Thymus serpyllum* and *Teucrium scordium* were represented by pollen. In the woodland samples notable absences from the pollen record included *Digitalis purpurea*, *Juncus effusus* and *Hyacinthoides non-scriptus*. *Calluna vulgaris* pollen values range from 12-19% tlp in samples from Allt Volagir. The background levels of *Calluna vulgaris* pollen in the "within woodland" samples was less than those recorded from the acid

Table 20a *Pteridium aquilinum* - *Potentilla erecta* - *Anthoxanthum odoratum* bracken infested grasslands (Group F) ; Kildonan Glen and Loch Eyenort

1. Characterising species.	**Abundance.**			**Pollen %**			**PRC**
Potentilla erecta	4	4	5	3	1	<1	C
Pteridium aquilinum	5	5	5	12	27	19	A
2. Associated species.							
Salix aurita	-	-	5	4	4	31	A
Calluna vulgaris	4	5	-	38	34	13	A
Primula vulgaris	3	-	-	2	-	<1	C
Galium saxatile	4	-	1	<1	-	<1	C
Rumex acetosa	-	-	4	<1	-	1	C
3. Less frequent species.							
Viola riviniana	4	-	-	2	-	-	C
Cirsium palustre	2	-	-	1	<1	-	D
Digitalis purpurea	-	-	2	-	-	-	F
Carex caryophyllea	-	-	3				
Carex nigra	-	-	-				
Juncus effusus	-	-	5				
Blechnum spicant	2	4	-	3	4	-	
Sphagnum capillifolium	-	3	-	3	81	7	
				(* P. sample)			
4. Gramineae Class 2.				6	4	3	
Agrostis capillaris	5	3	5				
Agrostis canina	-	-	5				
Gramineae Class 3.				9	6	<1	
Festuca ovina	1	-	-				
Holcus lanatus	-	-	4				
Total Gramineae				15	10	4	
5. Cyperaceae Class 2.				4	7	<1	
Carex caryophyllea	-	-	3				

Total Cyperaceae	4	7	<1	
6. Out community / on island pollen.				
Scrophulariaceae	1	<1	-	OC
Armeria maritima	-	-	<1	A
Equisetum	-	<1	<1	B
Polypodium	2	1	4	OC
Huperzia selago	-	<1	-	A
Betula	2	4	<1	A
Coryloid	3	<1	4	A
Sambucus	<1	-	-	OT
Pinus	2	<1	<1	OT
Fraxinus	<1	<1	-	OT
Umbelliferae	-	<1	<1	
Compositae Liguliflorea	<1	<1	-	
Ilex	-	-	<1	
7. Out-community / off-island pollen				
Quercus	-	-	<1	
Tilia	<1	-	-	
Ulmus	<1	-	-	
Alnus	-	<1	<1	

Total pollen percentages	**F1**	**F2**	**F3**
Total In-community	85	89	87
Total Out-community / on island	12	9	12
Total Off island	1	.5	1
Total degraded	2	2	4
Total unidentified	<1	<1	<1

Table 20b Pteridium aquilinum - Potentilla erecta - Anthoxanthum odoratum bracken infested grasslands Allt Volagir N.N.R (Group F).

1. Characterising species.	Abundance.	Pollen %			PRC
Potentilla erecta	- 3 -	1	3	<1	C
Pteridium aquilinum	4 5 -	6	8	4	A
2. Associated species.					
Salix aurita	4 5 -	15	19	6	A
Calluna vulgaris	3 - -	19	17	12	A
Primula vulgaris	3 - 5	<1	-	5	C
Rumex acetosa	3 4 -	4	3	-	C
3. Less frequent species.					
Betula pendula	5 4 -	18	23	6	A
Corylus avellana	- 4 1	4	12	8	A
Populus temula	- 3 5	-	-	<1	C
Sorbus aucuparia	- - 4	<1	-	14	A
Hedera helix	4 - 3	6	2	9	C
Lonicera periclymenum	3 - -	2	<1	1	C
Rubus fruticosus	3 - 2	-	-	-	F
Viola riviniana	2 - -	1	-	-	C
Digitalis purpurea	2 - -	-	-	-	F
Teucrium scordium	3 - 3	1	<1	1	D
Thymus serpyllum	3 - -	<1	-	-	D
Ranunculus ficaria	2 - 5	-	-	2	F
Veronica officinalis	4 - 2	-	-	-	F
Plantago lanceolata	- - 5	-	<1	3	A
Urtica dioica	- - 2	-	-	2	A
Angelica sylvestris	- - 2	-	-	1	C
Carex nigra	1 - -				
Osmunda regalis	- 3 -	<1	6	2	
Sphagnum capillifolium	- - 1	4	2	6	
4. Gramineae Class 1.					
Poa trivialis	- - 5	-	-	12	

Gramineae Class 2.		5	3	4	
Agrostis capillaris	4 - -				
Agrostis canina	- 5 -				
Gramineae Class 3.		6	3	10	
Festuca ovina	5 4 5				
Holcus lanatus	- 4 -				
Total Gramineae		11	6	26	
5. Cyperaceae Class 2.		4	2	4	
Carex nigra	1 - -				
Total Cyperaceae		4	2	4	
6. Out community / on island pollen.					
Chenopodiaceae		-	<1	<1	OC
Fagus		-	-	-	OT
Pinus		<1	-	<1	OT
7. Out-community / off-island pollen.					
Ulmus		-	<1	<1	

Total pollen percentages	**F4**	**F5**	**F6**
Total In-community	98	97	96
Total Out-community / on island	.5	.5	1
Total Off island	-	.5	.5
Total degraded	2	.5	.5
Total unidentified	-	-	-

grassland communities (E1 and E2) suggesting that vegetation structure may be affecting pollen transport and deposition. Importantly, the "within woodland" samples demonstrated the presence of arboreal species in the vegetation with pollen percentage values for genera such as Betula, Salix and Sorbus increasing to levels two or three times greater than in the samples from elsewhere on the transect, where these types are recorded as "out-community" pollen.

PEAT, WET HEATHLAND AND BOG COMMUNITIES

The pollen samples in this group are located in the eastern half of the South Uist transect (Figure 21). The area is covered by a mosaic of two major communities (Groups B and C) with two subgroups recognised within Group C.

Eriophorum angustifolium bog pool community (Group B).

Samples from moss polsters from North Loch Eyenort and Kildonan Glen. This community occurs where there are pools of standing water overlying considerable depths of peat. "Characterising species" in this community have generally good pollen representation notably, Eriophorum angustifolium / Carex nigra (18-30% tlp), Hydrocotyle vulgaris (7-16% tlp), Potentilla erecta (4-6% tlp) and Sphagnum spp. (12-46% tlp). Two of the "characterising" or "associated" species are present in low but significant pollen frequencies. This group includes Potamogeton polygonifolius and Erica tetralix (1-6% tlp). Juncus effusus was not recorded. Menyanthes trifoliata (14% tlp) is present in a sample from a site where the species was present in the vegetation. As with many of the pollen spectra from this part of the transect Calluna vulgaris (7-14% tlp) dominates "out-community" pollen in all the samples. Other "on island / out community" inputs included Gramineae class 3 (2-6% tlp), (species belonging to this pollen class were present in nearby vegetation, for example Nardus stricta and Festuca ovina) and scarce grains of Succisa, Rubiaceae type (Polygala), Compositeae Liguliflorea, Narthecium ossifragum and Drosera, all thought to originate in the local vegetation near the sample sites. Betula (1-3% tlp) and

Table 21 ; Eriophorum angustifolium bog pool community (Group B).

1. Characterising species.	**Abundance.**	**Pollen %**			**PRC**
Hydrocotyle vulgaris	2 2 5	7	2	16	A
Potentilla erecta	2 4 3	1	6	4	C
Potamogeton polygonifolius	5 - 4	8	-	6	D
Juncus effusus	2 - 4	-	-	<1	F
Sphagnum palustre	1 5 3	12	76	82	A
			*	*	P.Sample.
2. Associated species.					
Erica tetralix	- 3 1	<1	8	<1	C
Ranunculus flammula	3 - -	1	-	-	C
Sphagnum recurvum	- 5 -	ND	ND	ND	
3. Less frequent species.					
Menyanthes trifoliata	3 - -	7	<1	-	A
4. Gramineae Class 2.		16	19	14	
Total Gramineae.		16	19	14	
5. Cyperaceae Class 2.		18	25	20	
Eriophorum angustifolium	3 5 -				
Carex nigra	- - 3				
Total Cyperaceae.		18	25	20	
6. On island / out community pollen.					
Calluna vulgaris		14	17	21	A
Gramineae Class 3.		1	6	2	
Rubiaceae (Polygala)		<1	-	-	C
Succisa type		<1	-	-	OC
Narthecium ossifragum		-	1	-	C
Drosera		-	-	1	C
Compositae Liguliflorea		<1	<1	-	
Compositae Tubuliflorae		<1	-	<1	

Betula	1	1	3	A
Salix	3	3	2	A
Pinus	<1	<1	-	
Sorbus	<1	-	-	
Fraxinus	-	<1	-	
Coryloid	2	4	1	
Ulex	-	-	<1	
Pteridium	<1	1	-	
Huperzia selago	1	1	2	
7. Out-community / off island pollen				
Ulmus	<1	-	<1	
Quercus	-	<1	-	

Total pollen percentages (* excluding *Sphagnum*)	**B1**	**B2***	**B3***
Total In-community	70	61	65
Total Out-community / on island	25	33	34
Total Off island	<1	<1	<1
Total degraded	1	5	-
Total unidentified	-	-	<1

Salix (2-3% tlp) were thought to be of local origin. The proportion of "out-community / on island" pollen was the highest of the total sample (19-21% tlp) whereas "off-island" pollen was negligible (<1-1% tlp).

Molinia caerulea - Scirpus cespitosus - Erica tetralix - Calluna vulgaris wet heath (Group C).

Samples from moss polsters.

Samples from this community include C1 and C2 quadrats which occur extensively in the eastern uplands of the transect. Samples were analysed from a bog adjacent to Allt Volagir N.N.R., and the area of the Beinn Mhor massif above Kildonan Glen. In group C1 three characterising pollen types were well represented, for example, Cyperaceae class 2 (Scirpus cespitosus, Eriophorum vaginatum, Eriophorum angustifolium) c.17-21% tlp, Calluna vulgaris 20-36% tlp and Gramineae class 2 (Molinia caerulea) 12-17% tlp. Two "characterising" species were represented by low but significant pollen frequencies, Erica tetralix (2-4% tlp) and Potentilla erecta (1-5% tlp). Sphagnum capillifolium spores were also abundant. Pedicularis grains were present in low frequency in one sample.

"On island/ out community" pollen consists of low frequencies of 15 taxa which include Pteridium aquilinum, Gramineae class 3, Betula, Salix, Sorbus, together with scarce grains of Bellis perennis, Narthecium ossifragum and Huperzia selago. The slight increase in arboreal pollen representation in the sample taken from between Allt Volagir and Loch Lang suggests that there is some dispersal by wind of tree pollen from the woodland gorge to the adjoining vegetation.

Group C2 had a similar pollen spectra to C1 with respect to the representation of characterising species. Distinguishing between the different types of Cyperaceae proved difficult due to the diversity of sedges found in these quadrats.

Table 22a ; Molinia caerulea - Scirpus cespitosus - Erica tetralix Calluna vulgaris wet heath (Group C1)

	Abundance.	Pollen %			PRC
1. Characterising species.					
Calluna vulgaris	2 4 4	20	36	47	A
Erica tetralix	2 2 -	2	4	<1	C
Potentilla erecta	1 2 1	1	4	5	C
2. Associated species.					
Sphagnum capillifolium	1 - 2	20	74	67	A
			*	*	P.S.
3. Less frequent species.					
Pedicularis palustris	- - 2	-	-	<1	D
Sphagnum recurvum	- 5 -	ND	ND	ND	
4. Gramineae Class 2.		17	15	12	
Molinia caerulea	4 4 3				
Total Gramineae.		17	15	12	
5. Cyperaceae Class 2.		25	21	27	
Scirpus cespitosus	5 4 5				
Eriophorum angustifolium	1 - -				
Eriophorum vaginatum	3 - 3				
Total Cyperaceae.		25	25	27	
6. Out-community on island pollen.					
Pteridium aquilinum		2	<1	-	A
Plantago lanceolata		<1	2	-	A
Bellis perennis		<1	-	-	A
Narthecium ossifragrum		1	-	<1	C
Huperzia selago		-	-	<1	A
Gramineae Class 3		<1	3	<1	
Salix		1	-	<1	A
Betula		4	4	<1	A
Pinus		1	<1	<1	

Fagus	<1	-	-
Sambucus	-	-	-
Ulex	-	-	<1
Coryloid	-	3	1
Compositae Liguliflorea	-	<1	-
Compositae Tubuliflorae	<1	-	<1
7. Out-community / off-island pollen			
Ulmus	<1	<1	-
Alnus	<1	<1	-

Total pollen percentages (* excluding *Sphagnum*)	**C1**	**C2***	**C3***
Total In-community	86	80	92
Total Out-community / on island	12	14	6
Total Off island	<1	<1	-
Total degraded	3	4	1
Total unidentified	-	1	<1

Table 22b ; Molinia caerulea - Scirpus cespitosus - Erica tetralix - Calluna vulgaris wet heath (Group C2).

1. Characterising species.	**Abundance.**	**Pollen %**				**PRC**
Potentilla erecta	- 2 3 3	4	6	8	6	C
Erica tetralix	3 - 2 2	5	-	<1	2	C
Calluna vulgaris	4 5 5 5	34	31	49	39	A
Molinia caerulea	5 3 2 5					
Scirpus caespitosus	4 - 3 -					
2. Associated species.						
Narthecium ossifragum	3 - - 2	4	<1	-	4	C
Polygala vulgaris	2 1 - 3	<1	<1	-	<1	C
Drosera intermedia	1 1 - -	3	1	-	-	C
Drosera rotundifolia	- 1 1 -	-	2	1	-	C
Erica cinerea	- 4 - -	<1	5	-	-	C
Schoenus nigricans	1 1 - -					
Eriophorum angustifolium	- - - 4					
Carex nigra	- 1 4 -					
Sphagnum capillifolium	5 - 5 5	68	14	59	64	A
3. Less frequent species.						
Juniperus communis	- 5 - -	-	4	-	-	C
Carex caryophyllea	- 1 - -					
Carex nigra	- 1 4 -					
Sphagnum papillosum	- - - 5	ND	ND	ND	ND	A
4. Gramineae Class 2.		16	12	10	18	
Molinea caerulea	5 3 2 5					
Total Gramineae.		16	12	10	18	
5. Cyperaceae class 2.		22	8	14	14	
Scirpus caespitosus	4 - 3 -					
Eriophorum angustifolium	- - - 4					
Carex nigra	- 1 4 -					

Carex caryophyllea	-	1	-	-	
Total Cyperaceae	22	8	14	14	

6. Out-community / on-island pollen.

Betula	-	3	2	1	A
Salix	2	-	4	3	A
Ilex	-	<1	-	-	OT
Coryloid	<1	1	2	-	A
Gramineae Class 3	3	5	1	7	
Plantago lanceolata	<1	-	-	<1	A
Polypodium	2	2	-	<1	OC
Osmunda regalis	-	<1	-	-	OC
Huperzia selago	-	<1	<1	<1	
Succisa	-	-	-	<1	
Compositae Liguliflorea	<1	-	<1	-	
Compositae Tubuliflorae	<1	-	<1	-	
Fraxinus	-	-	<1	<1	
Sorbus	<1	<1	-	-	
Pinus	<1	-	<1	-	

7. Out-community / off-island pollen

Alnus	-	<1	-	<1
Tilia	-	-	-	<1
Quercus	-	-	-	<1
Ulmus	<1	<1	-	-

Total pollen percentages.	C4	C5	C6	C7
Total In-community	88	85	83	86
Total Out-community / on island	10	14	12	14
Total Off island	<1	<1	-	2
Total degraded	-	-	4	<1
Total unidentified	<1	<1	1	-

However, the "associated" species and their pollen representation separate the two C groups. Narthecium ossifragum (c.4% tlp) and Drosera type (1-3% tlp) have their strongest pollen representation in the C2 group and Sphagnum frequencies dominate all the pollen spectra. Other less frequent species with low but significant pollen representation included Erica cinerea, Juniperus communis and Polygala vulgaris.

"On island / out community" pollen representation was 10-14% tlp and included Gramineae class 3 type (possibly Nardus stricta) with pollen frequencies of between 1-7% tlp and scarce grains of Plantago lanceolata, Succisa, Compositae Liguliflorea, Salix, Betula, Sorbus, Polypodium and Huperzia selago thought to be of local origin.

Calluna vulgaris heath community (Group D)

Samples from moss and surface organic sediments.
Most of the quadrats in this group are located in the sheltered, steep sided valleys of Glen Liadale and Glen Hellisdale on the east side of the island. Pollen samples were analysed from quadrats in almost pure Calluna vulgaris stands in the degenerative phase of the Calluna cycle. Inevitably the pollen spectra from the Group D samples were dominated by very high frequencies of Calluna vulgaris (40-66% tlp). Sphagnum spores were present in all the samples with values ranging from c.37% tlp + Sphagnum (where the species was present in the quadrat) to between 12-16% tlp + Sphagnum in samples from quadrats where the species was not present in the vegetation. "On island / out community" pollen values were low (<1-2% tlp) and included 4 herbaceous taxa, Viola type, Hypericum type, Plantago maritima and Umbelliferae all present in the vegetation of the catchment. Scarce grains of Betula, Coryloid, Ulmus and Pinus were recorded and Pteridium aquilinum was present in all the samples.

Table 23 ; Dry heathland Calluna vulgaris heath community (Group D).

	Abundance.	Pollen %				PRC
1. Characterising species.						
Calluna vulgaris	5 5 5 5	62	66	40	55	A
2. Associated species.						
Potentilla erecta	1 - 3 3	1	-	3	2	C
Sphagnum capillifolium	- - 5 -	13	12	36	16	A
3. Less frequent species.						
Pedicularis palustris	- - 1 -	-	-	<1	-	D
Polygala vulgaris	- - 2 2	-	-	<1	<1	C
Dactylorhiza maculata	- - 1 -	-	-	-	-	F
Drosera rotundifolia	1 - - -	1	-	-	-	C
Erica tetralix	1 - - -	4	-	-	<1	C
Molinia caerulea	5 - - -					
Nardus stricta	- - 5 5					
Agrostis canina	1 - 3 -					
Carex binervis	- - 4 1					
Scirpus cespitosus	1 - 3 5					
Carex nigra	- 1 3 -					
4. Gramineae Class 2.		6	7	<1	<1	
Molinia caerulea	5 - - -					
Agrostis canina	1 - 3 -					
Gramineae Class 3.		3	<1	12	8	
Nardus stricta	- - 5 5					
Total Gramineae.		9	8	13	9	
5. Cyperaceae Class 2		6	4	11	10	
Scipus cespitosus	1 - 3 5					
Carex nigra	- 1 3 -					
Cyperaceae Class 3		-	-	<1	<1	
Carex binervis	- - 4 1					
Total Cyperaceae.		6	4	15	11	

6. Out community / on island pollen.

Viola type	<1	-	-	-	D
Pteridium aquilinum	1	<1	<1	-	A
Betula	<1	<1	-	-	A
Pinus	-	<1	<1	-	OT
Coryloid	<1	<1	1	<1	A
Compositae Liguliflorea	-	<1	-	-	

7. Out-community / off-island pollen

Alnus	<1	-	-	-

Total pollen percentages	**D1**	**D2**	**D3**	**D4**
Total In-community	96	94	96	95
Total Out-community / on island	3	3	2	-
Total Off island	-	<1	-	<1
Total degraded	1	1	2	4
Total unidentified	-	1	-	-

Festuca rubra - Armeria maritima-Plantago coronopus maritime grassland community (Group A).

This community occurs above the tidal zone of the sea lochs and sheltered bays of the east coast. Samples from *Armeria maritima* leaf litter.

The "characterising species" of this community, with the exception of *Glaux maritima* are all PRC A taxa (*Plantago coronopus* (18-26% tlp), *Plantago maritima* (16% tlp) and *Armeria maritima* (14-17% tlp), as a result the community is well represented in the pollen spectra. However it should be noted that all species were flowering when the samples were collected. *Festuca rubra* (12-18% tlp) and *Poa annua* (18% tlp) are present. Proportions of "On island / out community" pollen are high in these samples because of the relatively high frequencies of *Calluna vulgaris* (16-23% tlp) and *Pteridium aquilinum* spores. No "off island" pollen types were identified.

Table 24 : Festuca - Armeria maritima - Plantago coronopus maritime-grassland community (Group A).

1. Characterising species.	**Abundance.**		**Pollen %**		**PRC**
Plantago coronopus	3	5	18	26	A
Plantago maritima	-	3	6	16	A
Armeria maritima	5	5	17	14	A
Glaux maritima	-	5	-	<1	C
2. Gramineae class 3					
Festuca rubra	5	-	18	12	
Gramineae class 2.					
Poa annua	-	5			
Total Gramineae			18	12	
3. Out-community / on-island					
Pinus sylvestris			<1	-	OT
Betula			<1	-	A
Calluna vulgaris			22	14	A
Potentilla			<1	-	C
Pteridium aquilinum			4	1	A

Total pollen percentages	**A1**	**A2**
Total In-community	63	68
Total Out-community / on island	30	15
Total Off island	-	<1
Total degraded	10	16
Total unidentified	-	1

Discussion ; An overview of community representation

The relationships between phytosociological criteria (frequency and abundance) and pollen representation identified here are complex and difficult to synthesise. In the present study a number of interacting factors appear to have determined the degree to which each of the TWINSPAN groupings is reflected in the pollen spectra.

Firstly the pollen productivity and dispersal capability of individual plant species in the community appeared to determine the degree to which plant communities were reflected in pollen spectra. For example, the strongest community 'signatures' were detected in communities such as Calluna vulgaris dry heath (Group D) and the machair loch edge and swamp communities (Groups O and M). These had "characterising species" in Pollen Representation Classes A and B. Whereas other communities in which "characterising species" were poorly represented or absent (for example the Iris pseudacorus Inner machair Groups G and N) had weaker pollen 'signatures'. Closer scrutiny of the data shows that in some instances, community representation was distorted because pollen frequencies were biased towards some taxa at the expense of others. This effect was most noticeable when over-represented pollen taxa (those in categories a2, a4, b2 and b4, table 10) are present in the community: Calluna vulgaris, Filipendula ulmaria, Hydrocotyle vulgaris and Equisetum spp. are examples of these types. The acid grassland communities were the most vulnerable to this effect because high Calluna vulgaris pollen frequencies had a 'swamping' effect on the pollen representation of grasses and herbaceous taxa such as Plantago lanceolata, Bellis perennis and Potentilla erecta.

The effects of the various substrates used for sampling also appear to have influenced the representation of the community. Higher levels of degraded pollen were found in samples collected from moss polsters on the machair, whereas samples from wetland

and peat sites had lower levels of degraded pollen. Increasing wetness and acidity appeared to increase pollen preservation. The type of substrate used for sampling similarly had a distorting effect on some pollen spectra. For example, Sphagnum moss polsters and moss polsters from within Calluna dominated vegetation contained very high frequencies of Sphagnum and/or Calluna pollen and as a result percentage calculations were adjusted in some cases in order to reduce this effect. The area of the community and the pollen dipersal capabilities of the surrounding vegetation mosaic also seem to have effected pollen representation. This is illustrated by the influence of large areas of Calluna heath on the pollen spectra of smaller areas of grassland and bracken patch communities.

Arboreal pollen representation is of particular interest in the context of the present study because it has been suggested (Birks and Madsen 1979) that in the generally treeless landscapes of Lewis arboreal pollen present in early Holocene spectra was of "off-island" provenance.

In the present study, all the tree species present in the vegetation of the South Uist transect (with the exception of Populus tremula) were found to be Class A pollen representation types (those with greater than 10% tlp "in-community" pollen with wide distribution outside the community). Betula pollen increased from c.4% tlp outside the community to between 18-23% tlp in Allt Volagir N.N.R. - falling to c.4% tlp in samples from just outside the woodland gorge. A similar pattern can be observed with Salix pollen frequencies in samples from Kildonan Glen which attain levels of 31% tlp in the shrub canopy samples but fall to background levels of c.3-4% tlp in nearby samples beyond the scrub (see Group F, samples F1-5). It can be seen from these data that in the present study, only the within-woodland samples contain a "good record" of arboreal pollen. However the comparatively low percentages (c.30% maximum) recorded for tree species in the woodland samples suggests that the open structure of the woodland may also increase pollen dispersal away from source. Betula, Salix and Coryloid type showed the widest dispersal patterns but when recorded as "out-community" pollen, frequencies did not exceed 4% tlp. Some of the "out-community" arboreal pollen must also include pollen of "off-island" provenance which is the 'tail' of non-local tree pollen dispersal curves. The low but consistent amounts of Pinus, Ulmus, Quercus and Alnus pollen testify to the presence of some local or regional pollen rain which may also include a proportion of Betula which is of "off-island" provenance. Importantly, no samples from treeless parts of the transect had high arboreal pollen frequencies (c.7% tlp) and conversely arboreal pollen frequencies are high enough to demonstrate convincingly the presence of woodland. The contrasts between arboreal pollen frquencies in the "non-wooded" and "wooded" sampling sites in the present landscape is sufficient over relatively short distances to suggest that tree pollen deposition outside the canopy is minimal in these windswept islands. This principle suggests ;

(i) that pockets of woodland will be weakly represented in regional pollen rain and
(ii) arboreal pollen is " convincingly" present at sites where local woodland is present.

Observation suggests that shelter afforded by local topography or a tree canopy appears to increase the pollen representation of tree species. If this observation is used as an analogue or predictive model and applied to the interpretation of fossil pollen spectra, it explains the variability in arboreal pollen frequencies found within relatively close sampling sites such as those from Lewis (Birks and Madsen 1979, Bohncke 1986) and similar variability noted in the analysis of fossil pollen spectra in this study. In the context of such exposed and windswept islands with a relatively small land area, it questions the notion that the fossil pollen record primarily provides a picture of regional vegetation over a large area. It also reinforces Birks (1991) suggestion that 'scales of analysis' may be responsible for this effect and that;

> 'It is perfectly feasible to have sparse tree populations at densities of 0.25 trees ha^{-1} (= 200 trees or less within 2-5 km radius of a pollen site) that are largely undetected pollen analytically' (Birks 1991,P.35).

Out-community / on-island pollen deposition.

Table 25 summarises the "out-community" pollen deposition patterns observed in the pollen spectra from each of the plant communities. In general there is an increase in both the frequency and diversity of "out-community" representation from west to east across the transect presumably as a result of transport by the prevailing winds. Communities with low proportions of "out-community / on-island" pollen include the stable dune and machair grassland communities (Groups H and I), possibly because these groups contain a group of common "class character" species, and the surrounding vegetation mosaic does not contain many well-represented, widely-dispersed pollen types. Widespread taxa such as Calluna vulgaris, Betula and Salix are present in the samples but in low frequencies suggesting that pollen dispersal westwards from the east where these species are located on the transect is limited in extent. Low "out-community" pollen input is also a feature of the machair loch-edge, swamp and Iris patch communities (Groups G, N, O, and L). The taller vegetation structure of these tall-herb communities may trap some airborne pollen and the canopy effect of the vegetation may reduce dispersal from the community, but distance from the Calluna dominated wetland and heath sections of the transect may be a more critical factor in reducing "out-community / on island" inputs. "Out-community / on-island" pollen values begin to rise towards the machair / blacklands ecotone (samples O3, and Group M) lending support to the idea that "on-island" pollen dispersal is essentially local in origin. This effect is most apparent in the acid grassland communities (Group E1 and E2) and Group F bracken patch samples from Kildonan Glen

Table 25 : Out-community / on-island and off-island pollen representation

Dune machair community (Group H)
Machair grassland community (Group I)
Inner Machair Community (Group G)
Inner Machair Community (Group N)

Machair swamp community (Group O)
Lake margin Community (Group M)
Inner machair Community (Group L)

Sample Number.

Pollen taxon.	H1	H2	I1	I2	I3	I4	G1	G2	N1	N2	O1	O2	O3	M1	M2	M3	L1	L2
Betula	<1	<1	1	<1	3	-	2	-	<1	-	<1	<1	<1	-	<1	-	-	1
Salix	-	-	-	-	<1	1	-	<1	-	<1	<1	-	-	-	<1	1	-	-
Pinus	<1	-	<1	<1	-	<1	<1	<1	-	-	-	<1	<1	-	-	<1	-	<1
Fraxinus	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	<1	<1	-
Sorbus	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	<1	-	-
Fagus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-
Coryloid	<1	-	1	<1	3	-	-	<1	<1	-	-	-	<1	<1	<1	-	<1	-
Sambucus	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	<1	<1
Ulex	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-
Calluna vulgaris	2	1	3	5	<1	3	<1	-	1	1	-	3	2	2	4	<1	3	1
Ericaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-
Gramineae class 2	2	<1	4	-	-	3	-	-	-	9	<1	2	13	-	-	-	-	-
Gramineae class 3	-	-	-	6	-	4	-	-	-	-	-	-	-	1	3	3	-	-
Gramineae class 4	-	-	<1	-	<1	-	-	-	-	-	-	-	-	<1	2	1	-	-
Cyperaceae	-	-	P	-	-	<1	-	-	3	P	<1	-	-	4	P	9	-	-
Plantago lanceolata	-	-	-	-	-	-	1	-	-	-	1	1	-	<1	1	2	-	-
Bellis perennis	-	-	<1	-	-	-	<1	<1	1	-	-	-	-	-	1	<1	<1	<1
Potentilla	<1	-	<1	-	-	<1	-	-	-	-	-	-	-	-	-	-	-	-
Ranunculus	-	-	-	-	-	-	<1	1	2	-	-	-	-	-	1	1	<1	<1
Trifolium	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-	-	-
Rumex acetosa	<1	<1	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-
Papaver type	-	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 25 : Out-community / on-island and off-island pollen representation (cont.)

Pollen taxon.	H1	H2	I1	I2	I3	I4	G1	G2	N1	N2	O1	O2	O3	M1	M2	M3	L1	L2
	Sample Number.																	
Armeria maritima	-	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulaceae	-	<1	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-
Cruciferae	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	1	1	2	-
Leguminosae	-	-	<1	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-
Plantago coronopus	-	<1	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-
Plantago maritima	-	-	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Triglochin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	-
Rumux crispus	-	-	-	-	<1	-	-	-	-	-	-	-	-	<1	-	-	-	-
Chenopodiaceae	-	<1	-	<1	<1	<1	-	-	-	-	-	-	-	-	-	-	-	-
Umbelliferae	<1	-	<1	-	-	-	-	-	-	-	-	-	-	<1	-	<1	-	-
Compositae lig.	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Compositae tub.	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vicia cracca	<1	-	P	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Filipendula	-	-	-	-	-	-	-	-	-	-	-	-	-	P	2	5	P	2
Succisa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1
Pedicularis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1
Scrophulariaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rubiaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Narthecium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Drosera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Viola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pteridium aquilinum	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	<1	-	-
Polypodium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Filicales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Equisetum	-	-	-	-	-	-	-	-	-	4	-	-	<1	-	-	-	-	<1
Osmunda regalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Huperzia selago	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	<1
Botrychium lunaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sphagnum	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-

Table 25 : Out-community / on-island and off-island pollen representation (cont.)

Pollen taxon.	H1	H2	I1	I2	I3	I4	G1	G2	N1	N2	O1	O2	O3	M1	M2	M3	L1	L2
Off-island pollen																		
Juglans regia	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tilia	<1	<1	-	-	-	-	-	<1	-	-	-	-	-	-	<1	-	-	-
Quercus	-	-	-	<1	-	-	<1	-	-	-	-	<1	-	<1	-	<1	-	-
Ulmus	-	-	<1	<1	-	<1	1	1	<1	-	-	-	-	-	-	-	-	-
Alnus	-	-	-	-	-	-	-	<1	<1	<1	-	-	-	1	1	-	-	-
Carpinus	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	-
Ilex	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total 'In Community'	79	85	84	85	89	85	90	92	91	93	90	89	77	88	78	85	90	89
Total 'Out Community on-island' pollen	9	5	6	7	6	6	6	2	5	4	4	6	16	6	14	11	7	6
Total 'Off-island'	<1	<1	<1	<1	-	<1	1.8	2.3	1.4	<1	-	<1	-	2.8	2	<1	-	<1

Table 25 : Out-community / on island and off island pollen representation (cont.)

Neutral / acid grassland communities (Group E1 and E2)
Bracken infested grasslands (Group F)

	Sample Number											
Pollen taxon	E1	E2	E3	E4	E5	E6	F1	F2	F3	F4	F5	F6
Betula	3	2	1	1	1	3	4	2	4	-	-	-
Salix	4	3	3	1	<1	3	4	4	P	P	P	P
Pinus	<1	<1	-	<1	<1	<1	<1	1	<1	<1	-	<1
Fraxinus	-	2	-	-	-	-	<1	<1	-	-	-	-
Sorbus	-	-	-	<1	-	1	-	-	-	-	-	-
Fagus	-	-	-	-	-	-	-	-	-	-	<1	-
Coryloid	<1	3	-	-	<1	3	3	<1	4	-	-	-
Sambucus	-	-	-	-	-	-	<1	-	-	-	-	-
Ulex	-	-	-	-	-	-	-	-	-	-	-	-
Calluna vulgaris	-	-	-	P	29	36	P	P	13	-	-	-
Ericaceae	-	<1	-	-	-	-	-	-	-	-	-	-
Gramineae class 2	-	-	-	-	-	P	6	P	-	P	P	8
Gramineae class 3	-	-	-	-	-	-	-	-	-	-	-	-
Gramineae class 4	-	-	-	-	-	-	-	-	-	-	-	-
Cyperaceae	10	5	P	-	-	-	4	7	P	P	2	4
Plantago lanceolata	-	-	2	-	-	-	-	-	-	-	<1	P
Bellis perennis	-	-	-	-	-	-	-	-	-	-	-	-
Potentilla	-	-	-	-	-	-	-	-	-	1	P	<1
Ranunculus spp.	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium	-	-	-	-	-	-	-	-	-	-	-	-
Rumex acetosa	-	<1	-	-	-	-	<1	-	-	-	-	-
Papaver type	-	-	-	-	-	-	-	-	-	-	-	-
Armeria maritima	<1	-	-	-	-	-	-	-	<1	-	-	-
Campanulaceae	-	-	-	-	<1	-	-	-	-	-	-	-

Table 25 : Out-community / on-island and off-island pollen representation (cont.)

	Sample Number.											
Pollen taxon	E1	E2	E3	E4	E5	E6	F1	F2	F3	F4	F5	F6
Sinapis type	-	-	-	-	-	-	-	-	-	-	-	-
Leguminosae	-	-	-	-	-	-	-	-	-	-	-	-
Plantago coronopus	-	-	-	-	-	-	-	-	-	-	-	-
Plantago maritima	-	-	-	-	-	-	-	-	-	-	-	-
Triglochin	-	-	-	-	-	-	-	-	-	-	-	-
Rumux crispus	-	-	-	-	-	-	-	-	-	-	-	-
Umbelliferae	-	-	-	-	-	-	-	<1	<1	-	-	-
Compositae lig.	-	<1	<1	-	2	-	<1	<1	-	-	-	-
Compositae tub.	-	-	-	<1	-	<1	<1	-	-	-	-	-
Vicia cracca	-	-	-	-	-	-	-	-	-	-	-	-
Filipendula	-	-	-	-	-	-	-	-	-	-	-	-
Succisa	1	1	-	-	-	-	-	-	-	-	-	-
Pedicularis	-	-	-	-	-	-	-	-	-	-	-	-
Scrophulariaceae	-	-	-	-	1	-	<1	1	-	-	-	-
Chenopodiaceae	-	-	-	-	<1	-	-	-	-	-	<1	<1
Rubiaceae	-	-	-	-	P	-	1	-	-	-	-	-
Narthecium	-	-	-	-	-	-	-	-	-	-	-	-
Drosera	-	<1	-	<1	-	-	-	-	-	-	-	-
Viola	-	-	-	-	-	-	-	-	-	-	-	-
Pteridium aquilinum	-	2	2	1	-	2	-	-	-	-	-	-
Polypodium	1	2	-	-	-	1	2	1	4	-	-	-
Filicales	-	2	<1	-	-	-	-	-	-	-	-	-
Equisetum	-	-	-	-	-	-	-	-	<1	-	-	-
Osmunda regalis	-	-	-	-	-	-	-	-	-	-	-	-
Huperzia selago	2	-	P	-	-	-	-	<1	-	-	-	-
Botrychium lunaria	1	-	-	-	-	-	-	-	-	-	-	-
Sphagnum	13	9	P	-	-	-	3	P	7	4	2	P

Table 25 : Out-community / on-island and off-island pollen representation (cont.)
Off-island pollen

Sample Number.

Pollen taxon	E1	E2	E3	E4	E5	E6	F1	F2	F3	F4	F5	F6
Juglans regia	-	-	-	-	-	-	-	-	-	-	-	-
Tilia	-	-	-	-	-	-	-	<1	-	-	-	-
Quercus	1	<1	1	-	-	-	-	-	<1	-	-	-
Ulmus	<1	<1	-	-	<1	<1	<1	-	-	-	-	-
Alnus	-	<1	<1	1	-	-	-	<1	<1	-	-	-
Carpinus	-	-	-	-	-	-	-	-	-	-	-	-
Ilex	-	-	-	-	-	-	<1	<1	-	-	-	-
Total In-Community	91	87	83	85	81	86	85	89	87	98	97	96
Total Out-community on-island pollen	7	6	15	12	16	9	12	9	12	.5	.5	1
Total Off-island	<1	<1	<1	1.5	1	<1	1	<1	1	-	<1	<1

Table 25 : Out-community / on island and off island pollen representation (cont.)
Bog pool community (Group B)
Wet heath communities (Group C1 and C2)
Dry heath community (Group D)
Maritime grassland community (Group A)

	Sample Number															
Pollen taxon	B1	B2	B3	C1	C2	C3	C4	C5	C6	C7	D1	D2	D3	D4	A1	A2
Betula	1	1	3	-	4	<1	-	3	2	1	<1	<1	-	-	<1	-
Salix	3	3	2	1	-	<1	2	-	4	3	-	-	-	-	-	-
Pinus	<1	<1	-	<1	<1	<1	<1	-	<1	-	<1	<1	<1	-	<1	-
Fraxinus	-	<1	-	-	-	-	-	-	<1	<1	-	-	-	-	-	-
Sorbus	<1	-	-	-	-	-	<1	<1	-	-	-	-	-	-	-	-
Fagus	-	-	-	<1	-	-	-	-	-	-	-	-	-	-	-	-
Coryloid	2	2	<1	-	3	1	-	<1	1	2	<1	<1	1	<1	-	-
Sambucus	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-	-
Ulex	-	-	<1	-	-	<1	-	<1	-	-	-	-	-	-	-	-
Calluna vulgaris	14	7	11	-	-	-	-	-	-	-	-	-	-	-	22	14
Ericaceae	<1	P	P	-	-	-	<1	P	-	-	P	-	-	<1	-	-
Gramineae class 2	1	3	2	<1	3	<1	3	6	1	7	P	7	P	<1	-	-
Gramineae class 3	-	-	-	-	-	-	-	-	-	-	3	<1	P	P	-	-
Gramineae class 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyperaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plantago lanceolata	-	-	-	<1	2	-	<1	-	-	<1	-	-	-	-	-	-
Bellis perennis	-	-	-	<1	-	-	-	-	-	-	-	-	-	-	-	-
Potentilla	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-
Ranunculus spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rumex acetosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Papaver type	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 25 : Out-community / on-island and off-island pollen representation (cont.)

	Sample Number.															
Pollen taxon	**B1**	**B2**	**B3**	**C1**	**C2**	**C3**	**C4**	**C5**	**C6**	**C7**	**D1**	**D2**	**D3**	**D4**	**A1**	**A2**
Armeria maritima	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanulaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sinapis type	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leguminosae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plantago coronopus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plantago maritima	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Triglochin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rumux crispus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Umbelliferae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Compositae lig.	<1	<1	-	-	<1	<1	<1	-	<1	-	-	<1	-	-	-	-
Compositae tub.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vicia cracca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Filipendula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Succisa	<1	<1	-	-	-	-	-	-	-	<1	-	-	-	-	-	-
Pedicularis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scrophulariaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chenopodiaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rubiaceae	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Narthecium	-	-	-	-	1	-	<1	-	-	-	-	-	-	-	-	-
Drosera	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Viola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pteridium aquilinum	-	-	-	2	<1	-	-	-	-	-	1	<1	<1	-	4	1
Polypodium	-	-	-	-	-	-	2	2	-	<1	-	-	-	-	-	-
Filicales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Equesetum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Osmunda regalis	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-
Huperzia selago	<1	-	<1	-	-	<1	-	<1	<1	<1	-	-	-	-	-	-
Botrychium lunaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sphagnum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 25 : Out-community / on-island and off-island pollen representation (cont.)

	Sample Number.															
Pollen taxon	B1	B2	B3	C1	C2	C3	C4	C5	C6	C7	D1	D2	D3	D4	A1	A2
Off-island pollen																
Juglans regia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tilia	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	-
Quercus	1	1	<1	-	-	-	-	<1	-	-	-	-	-	-	-	-
Ulmus	-	-	-	<1	<1	-	-	-	-	-	-	-	-	-	-	-
Alnus	<1	<1	<1	-	<1	<1	-	<1	<1	-	<1	-	-	-	-	-
Carpinus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ilex	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

where higher levels of out-community input can be related to increasing Calluna vulgaris frequencies and the presence of Calluna dominated heathland in the vegetation mosaic. The trend towards increasing levels of "out-community / on-island" input continues across the transect (Groups C1, C1, and B) but the species present suggest nearby communities as major sources. A further difficulty also noted by Randall et al. (1986) was that many species are characteristic of more than one community (for example Plantago lanceolata and Bellis perennis) and this reduces their usefulness as community indicators in the pollen record.

Exceptions to this general pattern can be seen in the low "out-community / on-island" pollen input at sites such as Allt Volagir N.N.R. (Group F4-6) and the Calluna vulgaris dry heath (Group D) samples from Glen Hellisdale. These sites experience a degree of shelter which is afforded by the gorge at Allt Volagir and the Beinn Mhor massif. These factors may reduce dispersal from the communities and "out-community" inputs. Pollen spectra from patches of maritime grassland (Group A) located on the eastern coast-line at Rhubra Hellisdale have the highest proportion of "out-community" pollen from the total sample. This may reflect low pollen productivity in the community and the nearness of Calluna and Pteridium dominated vegetation in lower Glen Hellisdale.

An important feature of the "out-community pollen" rain was that although varying levels of community distortion resulted from the transfer of pollen between communities, the general pattern of deposition appeared to reflect the major landscape and vegetation divisions present on the transect.

The long distance proportion of the pollen rain was particularly difficult to define because unlike the Monach Islands studied by Randall et al. (1986) the species list for South Uist contains a much greater number of species which may have contributed pollen. Only seven pollen types thought to be of long-distance provenance were identified (see table 25) and the proportion of "off-island" pollen which could be identified did not exceed 3% tlp in any sample.

Summary.

The results of the vegetation survey found approximately 200 pollen or spore-producing plants present on the study transect. This represented slightly less than half that recorded in the floristic lists for the Outer Hebrides (see Curry 1979, and Pankhurst and Mullin 1991). 45 pollen samples were analysed and 118 pollen taxa were identified in the total sample, including 17 recorded as "out-community / on island" taxa and 7 of long-distance provenance. The quadrats analysed for pollen contained c.96 species from the transect list. A number of important species were absent from the pollen spectra notably Juncus spp. Luzula spp. Populus tremula, Rhinanthus minor, Euphrasia officinalis and Iris psuedacorus. In many communities "characterising species" had poor pollen representation yet despite these limitations each had an individual pollen 'signature' in which some of the "characterising species", in combination with low but significant frequencies of others, were present (high pollen counts >600 grains were required in order to detect less frequent species).

Patterns of "in-community" and "out-community" pollen deposition reflected the major vegetation units on the transect and revealed a general harmony between the contemporary pollen rain and vegetation, demonstrating the local nature of pollen deposition, and justify a relatively straight-forward approach to interpreting the pollen analytical evidence described later in this thesis. The adoption of the methods of Randall et al. (1985) to a similar problem in an adjacent landscape has been broadly successful. Its defects have been its length and rather pedantic nature. In future such analysis might profitably adopt statistical techniques of data reduction, and the use of such approaches as Canonical Correspondence Analysis to compare the two data sets - modern vegetation and pollen recovered from the surface samples in the survey quadrats.