Holocene vegetation history and the palaeoecology of Pinus sylvestris in northern Scotland

In two volumes.

Volume 1.

By

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One of the last surviving pine trees at Glen Einig -
believed to be the most northerly contemporary
native pine woodland

This thesis results from entirely my own work and has not been previously submitted for any other degree.

A. Gear

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ABSTRACT

The present vegetation is described using the techniques of continental phytosociology, mapped using Thematic Mapper imagery and related to a spatially arranged pollen surface-sample survey. The vegetation classification based on the techniques of continental phytosociology relates poorly to both the vegetation classification based on the Thematic Mapper imagery and the surface pollen spectra, although at a low taxonomic level regression lines are established that relate the percentage vegetation cover for *Betula, Pinus, Calluna*, and Gramineae. The results suggest that pollen production of *Betula* is lower in northern Scotland than has been found by other workers in the Highlands.

The regional vegetation history for central-northern Scotland is reconstructed using pollen analyses from both coastal and inland lake sites showing that the vegetation history of the area is complex.

Previous studies have suggested that *Pinus sylvestris* was rare or absent from northern Scotland (Bennett, 1984). Preliminary pollen results from the two lake sites appeared to confirm this view. However, the pollen evidence conflicted with the abundant and widespread distribution of *Pinus sylvestris* macro-fossils. Maps of the spatial distribution and density of sub-fossil *Pinus sylvestris* are presented for the 10 km, 1 km and spatially-precise (tree to next nearest tree or seedling) scales. These maps suggest that *Pinus sylvestris* grew 70-80 km beyond its present range at approximately 4,000 B.P. and that regeneration patterns within *Pinus sylvestris* woods were and still are both spatially and temporally discontinuous. Fine-resolution pollen analysis on a monolith associated with an interstratified *Pinus sylvestris* stump located high concentrations of pine pollen in two peaks spanning 7 mm and 15 mm peat depth respectively. Charcoal analyses suggest that an intensive fire preceded the colonisation of the blanket bog by *Pinus sylvestris*. Dendrochronological analyses from the same site show that tree productivity and average tree age were very low in sub-fossil stands and canopy cover was between 30-47% as *Pinus sylvestris* formed an open canopy over a heath-like understorey. The total period of growth of *Pinus sylvestris* on the blanket bog was less than 350 years. The extinction of *Pinus sylvestris* from northern Scotland was associated with an increase in the evapo-transpiration balance.

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ABBREVIATIONS

greater than or equal to	>
less than or equal to	<
approximately	c.
^{14}C years before present	B.P.
centimetre	cm
centistoke	cs
chi-squared	χ^2
correlation coefficient	r
degree Celsius	$^{\circ}$C
degrees of freedom	df
degrees of latitude and/or slope	$^{\circ}$ (Eg. 20 $^{\circ}$N)
edition	edn
editor(s)	ed. (eds)
experiment	expt.
figure(s)	Fig. (Figs.)
hectare	ha
kilometre	km
logarithm	log
logarithm (base e)	$\log_e$
maximum	max.
metre	m
minimum	min.
minute (angle)	' (Eg. 30')
Ordnance Survey grid reference	O.S.
number of observations	n
page(s)	p. (pp.)
per cent	%
probability	P
radiocarbon	^{14}C
second (angle)	" (Eg. 30")
species	sp. (plural, spp.)
standard deviation	S.D.
standard error of the mean	S.E.
Student's *t* (statistic)	t
sub-species	ssp. (plural, sspp.)
time, period cycle	T
variety	var.
Fisher's *Z* (statistic)	Z

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CHAPTER 1

Introduction

1.1 Introduction

The extinction of the dinosaurs 67 million years ago is a classic example of a mass extinction. However, extinction does not only occur on a global scale, extinctions also occur within restricted geographical areas as species expand and contract their ranges. Plant species combine together individualistically over large geographical areas to form "communities" that are in a constant state of flux as individuals die and reproduce. It is the aim of palaeoecologists to document and explain the vegetation history of geographic areas at varying spatial and temporal scales. The time period to be investigated in this palaeoecological study is the Holocene (0-10,000 years B.P.) and the setting is northern Scotland.

Northern Scotland is presently one of the most treeless areas of Britain (Fig. 1.1). The present geographical treeline is found in northern Scotland and is marked by a transition between birch woodland and treelessness. Treeline or treelimit is here defined as the northern-most limit to the growth of trees and its position will usually be controlled by climatic factors.

In order to understand why this area is predominantly treeless, reference must be made to the vegetation history of the area. The vegetation history of this area is complex and is summarised by Birks (1977a; 1988). Essentially, in north-western Scotland woodlands dominated the landscape from between 10,000 and 9,000 B.P. until 4,000 B.P., whereas in north-eastern Scotland no extensive woodland ever developed during the Holocene. On the basis of the pollen evidence *Pinus sylvestris*[*] has been considered never to have been an important component of the Holocene vegetation of central-north and north-eastern Scotland (Birks, 1977; Bennett, 1984).

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[*] Nomenclature follows Clapham, *et al* (1987) for vascular plants, Smith (1980) for mosses, Watson (1981) for liverworts and James (1965) for lichens.

The absence of *Pinus*[*] pollen from northern Scotland conflicts with the widespread distribution of *P. sylvestris* macro-fossils in north-western and north-eastern Scotland (Bennett, 1984). A similar situation occurs on the island of Lewis (Wilkins, 1984). The absence of *Pinus* pollen (Birks and Madisen, 1979) has been explained by: either the transportation effects of off-shore winds (Wilkins, 1984); or the physiological response to harsh climatic conditions resulting in reduced pollen production (Bennett, 1984). Alternatively, the conflict between the presence of *P. sylvestris* macro-fossils and the absence of *Pinus* pollen may be resolved if pine trees only grew in particularly sheltered and favourable sites (Bennett, 1984; Birks, 1988). We do not know:

1. Whether, and if so when, where, and under what conditions, woodlands were formerly more extensive in central-northern Scotland at any time during the Holocene
2. What these woodlands were like and whether *P. sylvestris* was ever an important component of the Holocene woodlands of central-northern Scotland
3. Why the Holocene vegetation history differs between north-east and north-west Scotland
4. Why there are so few trees in northern Scotland

1.2 Aims

The aims of this study are therefore as follows:

1. To increase our knowledge of vegetation history by studying the region of central-northern Scotland. This is one of the few remaining areas in Britain where a Holocene regional vegetation history has not been established.
2. To ascertain the role that *P. sylvestris* has played in the vegetation history of the area.
3. To supplement the pollen data by establishing the geographic extent and hence the former treeline of *P. sylvestris* by mapping its macro-fossil remains. Previously, no extensive searches have been made with the aim primarily of resolving either the broad-scale (northern Scotland) or fine scale (1km) distribution of sub-fossil *P. sylvestris* macro-fossils on the mainland of northern Scotland. If the former tree limit of *P. sylvestris* can be established, along with the factors that controlled it, then this might give some indication of past climates.
4. As a series of further subsidiary but related aims: to attempt to answer the following questions: (a) What palaeoenvironmental factors enabled *P. sylvestris* to temporarily colonise the blanket bogs? (b) What was the duration of the phase of pine growth on the bogs? (c) How old were individual trees? (d) How well did they grow? (e) Were they able to regenerate? (f) Why did they become extinct?

[*] Pollen nomenclature follows Moore and Webb (1978) unless stated otherwise.

These aims have been achieved by analysing pollen, macro-fossil, charcoal, dendrochronological, phytosociological, and satellite data. There are a total of seven chapters which are organised as follows.

Chapter two briefly outlines the main geographical characteristics of the study area that provide the background for the following chapters.

In chapter three the present vegetation is described and mapped using both the techniques of continental phytosociology and a satellite image obtained by the Thematic Mapper sensor. These results are related to a spatially-arranged pollen surface-sample survey. This has aided the interpretation of the pollen diagrams and provided data on the present treeline.

The regional vegetation history for central-northern Scotland is reconstructed in chapter four. Pollen diagrams are presented from both coastal and inland lake sites showing that the vegetation history of the area is complex.

Chapter five describes a mapping project that was designed to establish the spatial distribution and density of sub-fossil *P. sylvestris* macro-fossils. 10 km , 1 km, and spatially-precise dot maps document the distribution, density, and pattern of *P. sylvestris* macro-fossils. This survey was complemented by producing spatially-precise density maps of contemporary pine woodlands in northern Scotland. This enabled comparisons to be made of regeneration patterns and tree productivity from both extant and sub-fossil stands of *P. sylvestris.*

Chapter six provides details of the pine phase in the blanket peat. Fine temporal-resolution pollen, macro-fossil, and charcoal analyses were carried out on a peat monolith associated with pine macro-fossils. The macro-fossil analyses on the peat monolith provided complementary information about the presence of local taxa. Dendrochonological methods were used to build a chronology based upon *P. sylvestris* remains. This was employed in order to reconstruct the composition, duration, continuity and growth patterns of the pine trees growing on the blanket bog. A variety of techniques are used to reconstruct the frequency and intensity of fires in these fossil woods and their influence on regeneration patterns. The three main potential causes of the extinction of *P. sylvestris* are discussed in the light of the evidence from chapters five and six.

In the final chapter the results are discussed and compared with previous studies.

CHAPTER 2

The Study Area

2.1 Location

Northern Scotland is defined as the area north of latitude 57° 49' N. This area can be divided into three geographical areas: north-western Scotland, north-eastern Scotland and central-northern Scotland (Fig. 2.1a). Figure 2.1b shows the locations of places mentioned in the text.

2.2 Topography

North-western Scotland is characterised by a mountainous topography. North-eastern Scotland, especially Caithness, has a predominantly flat landscape. Central-northern Scotland is comprised of a plateau that is on average between 122 and 244 metres above sea level, rising in isolated peaks to over 427 metres and in a more consistent form along the western and southern watersheds (Fig. 2.2a). The plateau is dissected by a series of river valleys that run in a predominantly north-south direction. (Fig. 2.2b).

2.3 Geology

North-western Scotland is predominantly composed of acidic, Gneisses of the Lewisian metamorphic complex. Smaller areas are composed of sandstones and grits. North-eastern Scotland is dominated by sedimentary rocks, mainly Jurassic sandstones, shales and some limestones. The underlying geology of central-northern Scotland is mainly metamorphic granulites and schists of the Moine series, although there are patches of Lewisian Gneiss, and areas of quartzites and limestone just east of the Moine Thrust .

2.4 Superficial geology and soils

Fig. 2.3b illustrates the superficial geology and Quaternary deposits of northern Scotland. Drift is absent from a large proportion of north-western Scotland because of the steep slopes and mountainous topography. North-eastern Scotland is predominantly covered by peat and morainic deposits. Central-northern Scotland is dominated by boulder clay and morainic deposits in the west, whereas peat deposits dominate in the east.

Peat soils are the most common soil type in northern Scotland. There are several types of peat soil in northern Scotland, but by far the most extensive are blanket or deep bog deposits so called because they blanket the landscape (Ratcliffe and Oswalde, 1988). Blanket peats overlie mineral substrate whereas peat or peaty gley soils are mixtures of organic remains and weathered rocks on the Moine series. Several other soil types occur but the most important are the alluvial soils that occur locally in river valleys (Fig. 2.4).

2.5 Climate

Northern Scotland has a cool, wet climate (Birse and Dry, 1970a) characterised by high levels of precipitation and atmospheric humidity, and low annual temperatures (Figs2.5a and b). There are marked declines in both precipitation and January temperature from west to east. Climatological stations are relatively sparse in northern Scotland. Data from 3 stations are documented in Table 2.1 Of these sites, Lairg is an inland site and records the highest and lowest mean July and January temperatures respectively for the district, whereas the ocean has a moderating influence on temperatures at the coastal stations.

Wind exposure has a pronounced effect on the vegetation of the study area. The data in Table 2.2 illustrates that even stations in north-eastern Scotland receive winds of the same order of magnitude as do those on off-shore islands.

Table 2.2 Average annual wind speeds

Station	wind speed in metres per second
<u>Off-shore islands</u>	
Lerwick (Shetland)	7.3
Kirkwall (Orkney)	6.7
Stornoway (Outer Hebrides)	7.4
Benbecula (Outer Hebrides)	7.5
<u>North-eastern Scotland</u>	
Wick	6.3
Dounreay	7.1
Halkirk	4.8
<u>Central-northern Scotland</u>	
Fort Augustus	2.5

Although inland areas, namely Halkirk, are more sheltered, they are still characterised by moderately strong winds on average in comparison with other parts of mainland Scotland. In addition predictions made by White and Smith (1982) suggest that wind speeds increase in an easterly direction (Fig. 2.5c).

2.6 Vegetation

Fig. 2.6a is a generalized vegetation map of northern Scotland showing that the area is dominated by blanket bog and moorland communities. Localized areas of grassland occur in river valleys and arctic and alpine vegetation on the mountain peaks. Heather moor dominates part of the east coast. Scattered stunted birch woods (mostly *Betula pubescens* subsp. *carpatica*) are located within the river valleys (Fig. 2.6b). In the extreme north, adjacent to the coast the landscape is predominantly treeless. The "northern" native pine woods (*Pinus sylvestris*) are located to the south of this area (Fig. 2.6c). Although most of the area is covered by semi-natural vegetation, the north-east Caithness is dominated by agricultural activity. Fig. 2.6d illustrates the transition from pine, through birch and hazel, to treeless juniper scrub.

2.7 Land-use and Settlement

As a result of the harsh climate, population density has always been low over the region as a whole, although locally high in some of the major river valleys (Fig. 2.7a,b,c, and d). Pre-historic man first colonised the area in Neolithic times (Fig. 2.7a). The population increased to a peak just before 1770 A.D. when there were many small settlements distributed throughout the major river valleys (Fig. 2.7c). Between 1770 and 1870, sheep farming became the dominant land-use and the landlords removed or cleared the inhabitants from the land. As a result, the present population is predominantly restricted to the coastal margins and odd localities in the river valleys that are frequently associated with the sites where sheep farms were established during the eighteenth and nineteenth centuries (Fig. 2.7d).

The majority of northern Scotland is classified as land of little agricultural value, capable of use as rough, or improved, grazing. As a result, sheep farming, deer stalking, forestry, fishing and tourism are the main industries in northern Scotland today. Only in restricted areas, of north-eastern Caithness is arable agricultural production of importance.

CHAPTER 3

The present vegetation and contemporary pollen rain

3.1 Introduction

In order to reconstruct past plant communities the techniques of palynology are used throughout this thesis. If an ecological interpretation of the fossil pollen diagrams is to be made then it is essential that the relationship between percentage vegetation cover (and/or plant communities) and the surface pollen spectra is understood. Pollen analysis can be thought of as a remote sensing instrument (Prentice, 1988). Remote sensing instruments record the composition of the vegetation past and present at different spatial and temporal resolutions and with varying degrees of sensitivity (Prentice, 1988). The resolution of these images depends on the sensor being used. Table 3.1 shows the varying qualities of the phytosociological, Thematic Mapper (satellite), and pollen "sensors" used in this study. Fig. 3.1 illustrates the geographical areas covered by the three sensors used in this study.

Satellites have provided images of the earth every 18 days since 1972 (Curran, 1985). The Thematic Mapper is a sensor carried by Landsat satellites numbers 4 and 5. It is one of the finest scanners in operation (Curran, 1985) and has a spatial resolution of 25 x 25 m. The temporal resolution of pollen data is dependent on sample thickness, but probably at best between 1-5 years, but unlike the satellite imagery pollen can be analysed over thousands of years. The spatial resolution of pollen data depends on the "sensor" or the pollen source area which can be as small as 20 x 20 m in closed woodland canopies. Phytosociological data provide detailed descriptions of 2 x 2 m plots at spatially discrete points from which plant communities are classified at the regional or global scales.

The aims of this study were to :

1. Analyse the relationship between present pollen rain and vegetation cover in Strathnaver and its surrounding area and so to aid the interpretation of the fossil pollen spectra.

2. Describe and classify the main types of woodland in northern Scotland.

These aims were achieved by combining satellite, pollen and phytosociological data. In order to achieve aim 1 it was necessary: (a) to discover and characterise the present pollen rain in Strathnaver and the surrounding area by analysing a spatially arranged series of surface samples. (b) to characterise the vegetation around the surface sample sites by using a Thematic Mapper image to map the distribution of vegetation communities and a systematic phytosociological survey to systematically ground truth the image in Strathnaver and its surrounding area. Aim 2 required in addition an extensive, stand based phytosociological survey of the woodland communities of northern Scotland.

This chapter is organised as follows. The data from both the extensive and intensive phytosociological surveys have been combined and, as they are fundamental to both aims 1 and 2, they will be considered first. The phytosociological survey from Strathnaver and its surrounding area was then used to ground truth the Thematic Mapper image in terms of nodal colours and the probability estimated of obtaining a given Thematic Mapper colour from a particular nodal class. The surface pollen survey is then described and a series of isopoll maps for Strathnaver presented and compared with isopoll maps from northern Scotland. The pollen surface samples are then both subjectively and objectively classified and compared with the noda from which they were derived. Finally, the relationship between percentage vegetation cover (estimated from the Thematic Mapper image) and % total land pollen was assessed by calculating Pearsons's Product Moment Correlation Co-efficient.

3.2 The phytosociological survey of the woodland, scrub and upland vegetation units

3.2.1 Methods

The majority of the woods are small isolated fragments located in remote and isolated localities. The birch woodlands are predominantly composed of a single canopy layer of small, diffuse, many-trunked specimens of *Betula pubescens* subsp. *carpatica.* They are of little economic value and floristically incomparable to most British woodlands. The techniques of continental phytosociology were adopted in order that a comprehensive survey of the birch and pine woods could be made in the available time, and would provide results that were directly comparable with previous studies of Highland vegetation (Birks, 1973a; Birse, 1980, 1982a, 1984; Burnett, 1964; and McVean and Ratcliffe, 1962).

Continental phytosociological methods are based on the random sampling of "stands". A stand is defined as a uniform and homogeneous area of vegetation (McVean and Ratcliffe, 1962). A standard plot size of 2 x 2 metres has been adopted throughout the present study. The description of each of these plots is termed a relevé. Species occurring within the plot were listed and their percentage cover estimated on the 10-point Domin scale (Table 3.2).

Table 3.2 The 10-point Domin Scale

+	present in the stand adjacent to the quadrat, but absent within the quadrat
1.	<4% cover - one or two individuals
2.	<4% cover - scattered individuals
3.	<4% cover - frequent individuals
4.	4%-10% cover
5.	10-25% cover
6.	25-33% cover
7.	33-50% cover
8.	50-75% cover
9.	75-90% cover
10.	90-100% cover

The methodology used follows Birks (1973a) with the exception that aspect, slope angle, and soil type were not recorded in the field. All the phytosociological surveying was carried out in July/August 1987/1988.

The deciduous woodlands in northern Scotland were located using the 1:25,000 Ordnance Survey Landranger map series. A wood was defined as an area of land of at least 16 x 16 metres spatial extent covered by trees. In addition to this, smaller spatial areas were surveyed for willow scrub on the mainland and woody species on islands. A tree is defined as a woody plant, with one or many trunks, greater than 2 metres tall. The native pine woods sampled were those in the "Northern" and "Wester Ross groups" (Steven and Carlisle, 1959). The following types of stand with trees were not recorded:

1. Scattered and isolated trees occurring on rock faces and hill tops
2. Trees that form narrow, linear geographic features, often only 1-2 trees wide; these features are important aesthetic and ecological contributors to the landscape and usually follow river banks or loch sides. They possess a unique set of hydrological, edaphic and micro-climate conditions. These conditions generally result in the proliferation of *Alnus glutinosa* and *Salix* spp. at the expense of *Betula pubescens* which characterises the majority of woodlands of this area.
3. Coniferous plantations

After permission of access was obtained, most of the deciduous woods, including a few wooded islands, were surveyed in Strathnaver and a number of samples were taken from each of the major river valleys in northern Scotland. Many of the sites were inaccessible by car and the majority of each day was spent walking out to sites. Fig. 3.2 illustrates the location of all the relevés on a 1 km grid square basis. In total 288 relevés, containing 284 species, were recorded. On returning to the laboratory, all uncertain bryophyte identifications were confirmed using a microscope (Smith, 1980; Watson, 1981). All *Sphagnum* spp. were identified in the laboratory.

The following definitions are used throughout the descriptions and discussion of the results. A constant species occurs in 81-100% of the relevés of a nodum (Braun-Blanquet, 1951 class V). A dominant species has the highest cover-abundance (Domin scale) value for a given field layer. A stand is an area of vegetation from which a relevée has been recorded. A relevé is a list of species and site characteristics that describes the vegetation of a homogeneous stand. A community is equivalent to a nodum. A nodum (plural, noda) is used to refer to a group of similar relevés of uncertain, undetermined or undefined syntaxonomic rank. An association can be defined as a plant community with "*the number of taxa in constancy class V greater than or equal to the number of taxa in constancy class IV, and which differs from other communities in its floristic composition, particularly in its constant, dominant, and faithful taxa*" (Birks, 1973a p.25). However, no attempt has been made to raise any of the noda defined in this study to the status of association. A sub-association is a division of an association that differs in the occurrence and abundance of certain taxa. Average numbers of species per relevé are classified as follows: low = <10; medium = 10-15; high = >15. Altitudes were derived from the 1:50,000 and 1:25,000 Ordnance Survey maps and are grouped as follows: low= 0-100 metres; medium=100-200 m; high= >200 m (Fig. 3.3). Soil categories were defined from the 1:50,000 and 1:25,000 Soil Survey maps. A list of the soil categories and special variables used can be found in Appendix 1. Solid geological information was obtained from the 1:50,000 Geological Survey maps.

3.2.2 Results - The vegetation classification

The relevés from both the woodland and upland communities were combined into one data set. In total 288 relevés containing 284 species were recorded. These data were classified into noda using TWINSPAN (Hill, 1979b). The results are displayed in Fig. 3.4. The noda were divided into 6 categories: birch woods, pine woods, alder woods, willow scrub, dwarf-shrub heath and bog, and grasslands. The noda within each of these categories will be described below. Table 3.3 lists the noda in each of these categories, Table 3.4 is a conspectus of the plant communities and Table 3.5 is a summary of the affinities of noda to published vegetational units referred to in the text. Fig. 3.5a-y illustrate the location of the relevés within each nodum, on a 1 km grid square basis.

The data were re-arranged using PHYTOPAK (Huntley and Birks, 1981) to produce a table with the relevés and species in a specified order reflecting the nodal classification. This table was divided into nine more manageable sized tables (Tables 3.6-3.15). A synoptic table of constancy values for the noda was also prepared (Table 3.16). The species in Tables 3.6-3.15 are arranged in alphabetical order. Noda have been named according to their most notable species. The tables are located in volume 2. The arrangement and nomenclature of the phytosociological units follows Birks (1973a) and Birse (1984; 1988) with some modifications.

Table 3.3

List of noda

THE BIRCH WOODS

Betula pubescens - Rumex acetosa nodum (nodum 3).

Betula pubescens - Potentilla erecta nodum (nodum 8).

Betula pubescens - Rhytidiadelphus squarrosus nodum (nodum 9).

Betula pubescens - Deschampsia flexuosa nodum (nodum 10).

Betula pendula nodum (nodum 11).

Betula pubescens - Vaccinium myrtillus nodum (nodum 12).

Betula pubescens - Juniperus communis nodum (nodum 13)

Betula pubescens - Thuidium tamariscinum nodum (nodum 14).

THE NATIVE PINEWOODS

Pinus sylvestris - Deschampsia cespitosa nodum (nodum 15).

Pinus sylvestris - Molinia caerulea nodum (nodum 16).

Pinus sylvestris - Vaccinium myrtillus nodum (nodum 17).

Pinus sylvestris - Calluna vulgaris nodum (nodum 18).

THE ALDER WOODS

Alnus glutinosa nodum (nodum 5).

WILLOW SCRUB

Salix nodum (nodum 4).

DWARF-SHRUB HEATH and BOG

Calluna vulgaris - Potentilla erecta nodum (nodum 19)

Calluna vulgaris - Agrostis canina nodum (nodum 20)

Calluna vulgaris - Eriophorum angustifolium nodum (nodum 21)

Erica tetralix - Sphagnum nodum (nodum 22)

Calluna vulgaris nodum (nodum 24)

Calluna vulgaris - Cladonia impexa nodum (nodum 25)

Trichophorum cespitosum - Myrica gale nodum (nodum 23).

Juniperus communis nodum (nodum 6)

GRASSLANDS

Dryas octopetala nodum (nodum 1)

Nardus stricta nodum (nodum 2)

Anthoxanthum odoratum - Rhytidiadelphus squarrosus nodum (nodum 7)

THE BIRCH WOODS

The birch woods are predominantly composed of old, contorted trees usually less than 5 metres tall. Many of these woods have open canopies and are showing signs of senility eg. dead and dying trees with rotten wood covered by bracket fungi. McVean and Ratcliffe (1962) recognise only 2 noda within the birch (*Betula pubescens*) woods; namely the Vaccinium-rich and herb-rich birch woods. This two-fold division was based on only 18 relevés. The larger database that has been obtained in the present study (142 relevés from the birch woods) has enabled a finer level of discrimination and the birch woods are here grouped into 8 noda. Each will now be considered in turn.

Betula pubescens - Rumex acetosa nodum (nodum 3).

The constancy and abundance of *Betula pubescens* and the presence of *Rumex acetosa* and *Euphrasia scottica* characterise this nodum. Stands occur on a wide variety of soil types, but usually on freely drained soils including brown forest soils. The nodum is found at low altitudes within Strathnaver.

8 relevés have been placed in this group. A total of 91 species was recorded with an average of 21 per relevé. Only *B. pubescens* is recorded as a constant. Four species are recorded in class IV, namely *Rumex acetosa, Holcus lanatus, Salix* sp., and *Euphrasia scottica. Rumex acetosa* is indicative of grasslands and open places in woods (Clapham, Tutin, and Moore, 1987) and its presence may indicate that these stands have suffered disturbance.

Betula pubescens - Potentilla erecta nodum (nodum 8).

This nodum is characterised by the following constants: *B. pubescens, P. erecta, Oxalis acetosella, Pteridium aquilinum, Viola riviniana, Thuidium tamariscinum, Mnium spinosum* and *Pseudoscleropodium purum.* The nodum is found in lowland areas of river valleys predominantly in far northern Scotland.

26 relevés are placed in this nodum that contains a total of 105 species and is one of the species richest noda identified. There are on average 22 species per relevé.

Dominants in different stands include *Anthoxanthum odoratum, Primula vulgaris, Prunella vulgaris, Oxalis acetosella, Cerastium fontanum, Hieracium pilosella, Pteridium aquilinum, Thuidium tamariscinum,* and *Agrostis capillaris.*

Sites occur on a wide variety of soil types on freely-drained soils including brown forest soils, and fluvio-glacial sands and gravels, as well as occasionally on peat deposits.

This nodum is nearest to McVean and Ratcliffe's herb-rich birch wood nodum but has a number of different constant species. Of the eight constants of McVean and Ratcliffe's nodum the following are not constants in the *Betula pubescens - Potentilla erecta* nodum; *Blechnum spicant, Anthoxanthum odoratum, Galium saxatile,* and *Hylocomium splendens.*

Betula pubescens - Rhytidiadelphus squarrosus nodum (nodum 9).

The dominance of *B. pubescens* in the canopy layer and the constancy of *Oxalis acetosella, Viola riviniana, Rhytidiadelphus squarrosus* and *Thuidium tamariscinum* characterise this nodum.

There is usually no shrub layer present. *Corylus avellana* and *Populus tremula* occasionally dominate the canopy layer. Field layer dominants include: *Holcus lanatus, Festuca ovina, Rhytidiadelphus triquetris, Geum* sp., *Pteridium aquilinum, Prunella vulgaris,* and *Primula vulgaris.*

This nodum comprises 26 relevés and has a total of 101 species with an average of 22. This is geographically the most widely distributed nodum, being found throughout northern Scotland including sites at Loch Choire, Loch Hope, Loch Eriboll, Loch Brora, Helmsdale, and Loch Loyal.

This nodum is found on brown forest soils, freely drained drift, iron-humus podsols, fluvio-glacial sands and gravels and peaty soils. Sites are found at a wide range of altitudes from 4 to 243 metres. Topographically the sites are found in a wide variety of situations including steep and gentle slopes and flat areas, although often near to large lochs.

This nodum is related to the *Betula pubescens - Potentilla erecta* nodum but has a wider geographical range, the moss layer is characterised by fewer species, *Festuca* spp. are more frequently present and *Rhytidiadelphus squarrosus* is an exclusive constant.

Betula pubescens - Deschampsia flexuosa nodum (nodum 10).

The canopy layer is usually dominated by *B. pubescens* and occasionally by *Sorbus aucuparia* with *Salix* sp. and *Alnus glutinosa.* Constants include *B. pubescens, Potentilla* *erecta, Anthoxanthum odoratum, Rhytidiadelphus squarrosus* and *Odontoschisma sphagni.*

There is a wide variety of field-layer dominants including *Carex* sp., *Deschampsia flexuosa, D. cespitosa, Pteridium aquilinum, Conopodium majus, Carex nigra, C. echinata, Molinia caerulea, Holcus mollis, H. lanatus, Sphagnum subnitens and S. palustre.*

Deschampsia flexuosa is often found in acid open woods and here reflects the fact that most of these relevés come from senile birch woods with open canopies.

This nodum comprises 39 relevés with a total of 118 species and an average of 22 species. This is the most species-rich nodum identified, that is it contains the largest total number of species.

Brown forest soils predominate but the nodum is also found on peats, freely-drained drift, mixed bottom land, and humus-iron podsols.

There are at least two distinct facies within the nodum, namely *Pteridium aquilinum - Agrostis capillaris* rich and *Sphagnum - Carex* rich (relevés 90, 120, 121, 122, 123, 133, 134, 142, 145, 147, 149, and 151, and 20, 40, 41, 47, 51, 52, 53, 54, and 67 respectively). The former are widely distributed across north-western and central-northern Scotland and occur on a wide variety of soils including peats, humus-iron podsols, and fluvio-glacial sands and gravels. The latter group are predominantly restricted to the brown forest soils of Strathnaver. This latter facies resembles the *Sphagnum palustre-Betula pubescens* community of Birse (1982a).

This nodum is found at a wide altitudinal range from lowland coastal locations (relevé 108), to upland plateau areas (relevé 103). Sites are predominantly distributed in far northern Scotland but are also found at Loch Shin (relevés 133, 134), Strathfleet (relevé 135) and Loch Brora (relevé 142).

This nodum resembles some of McVean and Ratcliffe's "high-lying" woods which are classified into their herb-rich nodum. However, it has the following additional constants - *Rhytidiadelphus squarrosus* and *Odontoschisma sphagni*, and lacks the following constants - *Blechnum spicant, Galium saxatile, Oxalis acetosella, Viola riviniana* and *Hylocomium splendens.*

Betula pendula - nodum (nodum 11).

This nodum is geographically restricted to north-western Scotland and the south of the study area. *Betula pendula* dominates the canopy and *Corylus avellana* and *Sorbus aucuparia* are present occasionally.

The nine constants are *Betula pendula*, *Hylocomium splendens, Oxalis acetosella, Potentilla erecta, Pteridium aquilinum, Rhytidiadelphus squarrosus, Thuidium tamariscinum,* and *Viola riviniana*.

The western distribution of this nodum leads to an abundance of bryophytes including *Hypnum cupressiforme, Polytrichum* sp., *Dicranum scoparium, Plagiothecium laetum, Pseudoscleropodium purum* and *Thuidium tamariscinum.*

Topographically, the nodum is situated at medium altitudes. The soils are variable and include brown forest soils and peats.

6 relevés with a total of 58 species and an average of 22 species characterise this noda. A greater number of relevés from this site type might enable further subdivision of this nodum.

This nodum is unlike any of McVean and Ratcliffe's noda; in both of their birch wood communities *Betula pubescens* is the only constant canopy component whereas *B. pendula* forms the canopy in stands of the present nodum.

Betula pubescens - Vaccinium myrtillus nodum (nodum 12).

27 relevés with a total of 96 species and an average of 20 species per relevé were included in this nodum.

The constant species are *Betula pubescens, Potentilla erecta, Rhytidiadelphus squarrosus* and *Vaccinium myrtillus. Betula pubescens* dominates the canopy along with varying quantities of *Sorbus aucuparia, Alnus glutinosa, Pinus sylvestris* and *Salix* sp.

The soils are variable and include humus-iron podsols, mixed bottom land, fluvio-glacial sands and gravels, brown forest soils and peats.

The sites occupy a wide altitudinal range from 15-297 metres. They are located primarily in Strathnaver, although with some relevés from Loch Eriboll (relevé 115), Loch Hope (relevé 119), Glencalvie (relevés 124, 125 and 139), Torroy (relevé 132), Loch Loyal (relevés 146, 148) and Nedd (relevé 205).

This nodum is similar to McVean and Ratcliffe's (1962) Betuletum Oxaleto-Vaccinetum and Birks' (1973a) *Betula pubescens-Vaccinium myrtillus* association. McVean and Ratcliffe (1962) recognise 8 additional constants to those listed for nodum 12 as constants namely: *Sorbus aucuparia, Blechnum spicant, Deschampsia flexuosa, Galium saxatile, Oxalis acetosella, Hylocomium splendens, Pleurozium schreberi* and *Thuidium tamariscinum*. Inaddition McVean and Ratcliffe (1962) is not recognised *Rhytidiadelphus squarrosus* as a constant.

Betula pubescens - Juniperus communis nodum (nodum 13)

Betula pubescens dominates the canopy layer, *Juniperus communis* the shrub layer and *Hylocomium splendens* the moss layer of this nodum. They are the three constant species.

8 relevés comprise this species-poor nodum that has a total of 35 species and an average of 13 species.The canopy layer is usually dominated by *Betula pubescens* with a proportion of *Sorbus aucuparia* in some relevés.

Dominants include *Rhytidiadelphus squarrosus, Vaccinium myrtillus, Hylocomium splendens, Juniperus communis* and *Pteridium aquilinum.*

Peaty soil types predominate but vary depending upon the peat depth and the nature of the underlying substrate.

The sites are located on the plateau of Strathnaver and >75% of the relevés are located on islands within lochs. This suggests that grazing pressure and/or fire suppression is/are sufficiently low to enable *Vaccinium myrtillus* and *Juniperus communis* to remain at >81% and <41-60%> constancy respectively.

This nodum is closest phytosociologically to McVean and Ratcliffe's (1962) Betuletum Oxaleto-Vaccinetum. Only three constants are recognised in comparison with the 11 found by

Although nodum 13 may be compared with both to Huntley and Birks's (1979) *Juniperus communis-Vaccinium vitis-idea* nodum and Birse's (1982a) Trientali-Betuletum pendulae association, both of these communities contain a number of additional species, eg. *Trientalis europaea* and *Ptilium crista-castrensis*, that make them floristically distinct from nodum 13.

This nodum is similar to nodum 12 but is characterised by the presence of a shrub layer of *Juniperus communis* and lacks *Potentilla erecta* as a constant species. In addition the average number of species per relevé is much lower (13 in comparison with 20).

Betula pubescens - Thuidium tamariscinum nodum (nodum 14).

Only 2 relevés are included in this nodum. It is related to nodum 13 and is characterised by the same constants, namely *Betula pubescens*, *Hylocomium splendens* and *Juniperus communis.* Indeed relevé 89 may be best considered as a variant of nodum 13 characterised by a greater abundance of *Juniperus communis* and *Thuidium tamariscinum*, whereas in relevé 102 *Luzula sylvatica* dominates the field layer.

Both relevés are located on islands within lochs on the plateau between 99-129 metres. Peat/silty soils predominate.

Relevé 102 has a very distinctive nature. *Salix* sp. and *Sorbus aucuparia* dominate the canopy layer, although *Betula pubescens* is present. *Juniperus communis*, *Luzula sylvatica* and *Thuidium tamariscinum* dominate the scrub, herb and ground layers respectively.

Relevé 102 is the northernmost wood recorded in this survey. This senile wood is very small in area (<16m^2) and is situated on a raised mound. The wooded area seems to have been significantly reduced in size by a rise in the lake level/water table which has killed/partly submerged several *Salix* trees. This is perhaps the most northerly "relict" of a birch-juniper woodland. Rising water levels have probably resulted in *Betula pubescens* being replaced by *Salix* sp. at this site.

Relevé 102 does not fit well with any published nodum. It is perhaps nearest to the *Salix lapponum-Luzula sylvatica* nodum recognised by McVean and Ratcliffe (1962). However, they do not include *Betula pubescens* and *Juniperus communis* in their lists of species. In addition they include: *Vaccinium myrtillus*, *Hylocomium splendens* and *Rhytidiadelphus loreus*. *Salix lapponum-Luzula sylvatica* communities are not present on Skye (Birks, 1973a) but Birks (1973a) describes two stands with *Salix* as the dominant canopy species with understoreys dominated by tall herb communities including *L.sylvatica*. However, although these communities have affinities with the present nodum they contain a number of sub-alpine and low-alpine species eg. *Saussurea alpina* not present in relevé number 102. Alternatively, nodum 14 might be placed in the *Luzula sylvatica* subassociation of the Blechno-Quercetum (Braun-Blanquet and Tüxen (1952). This is where Birse (1982b) places the *Salix* communities of Orkney (Prentice and Prentice, 1975) and mainland Scotland (Birse, 1982a, 1988). The difficulty of placing noda 14, 3 and 4 into any published noda is primarily because of the scarcity of published records for *Salix* scrub (Birse, 1988).

THE NATIVE PINEWOODS

42 relevés were collected from the native pinewoods. McVean and Ratcliffe (1962) recognise two *Pinus sylvestris* associations, namely Pinetum Hylocomieto-Vaccinetum (Pinewood-*Vaccinium*-moss association) and Pinetum Vaccineto-Callunetum (Pinewood-*Vaccinium-Calluna* association). However, Birse (1980, 1984) argues that these two noda are best considered as subassociations of the Pinetum scoticae association (Steven and Carlise, 1959; Birse 1980, 1984). 4 noda have been identified in the present study and are as follows:

Pinus sylvestris - Deschampsia cespitosa nodum (nodum 15).

The dominance of *Pinus sylvestris* and the constancy of *Deschampsia cespitosa* and *Dicranum scoparium* in the field and moss layers characterise this nodum.

The 12 relevés contain a total of 58 species with an average of 13 species per relevé. This is the species-richest of the noda dominated by *Pinus sylvestris*.

Dominants include *Vaccinium myrtillus, Anthoxanthum odoratum, Agrostis capillaris* and *Rhytidiadelphus triquetrus*. Canopy cover varies between 40-90%, with an average of 66%. The canopy layer is dominated by *Pinus sylvestris* with varying proportions of *Betula pendula* and *Sorbus aucuparia*. *Vaccinium myrtillus* is often more abundant when canopy cover is reduced.

Sites can be found at a wide range of altitudes from 80-330 metres. Brown forest soils predominate, with some peaty soils and humus-iron podsols. Topographically, sites are found in a variety of situations including steep slopes, beside rivers in valleys, and on cliffs. The relevés are from 3 of the 4 northern pine woods, namely Amat, Glen Einig and Rhiddoch but not from Strath Vaich.

This nodum bears some resemblance to the Pinetum-Hylocomieto-Vaccinetum association (McVean and Ratcliffe (1962). However, the abundance and dominance of Gramineae spp., especially *Deschampsia cespitosa/flexuosa* are not characteristic of this association but rather of Pinetum scoticae (Birse, 1984). This nodum is therefore probably a subassociation of Pinetum scoticae.

Pinus sylvestris - *Molinia caerulea* nodum (nodum 16).

6 relevés contain 49 species with an average of 18 species per relevé in this dense canopy nodum. The dominance of *Pinus sylvestris* and the constancy of *Calluna vulgaris*, *Hylocomium splendens*, *Molinia caerulea* and *Potentilla erecta* characterise the nodum.

The canopy cover is between 40-90%, with an average of 82%, and is dominated by *Pinus sylvestris*, although it may contain *Betula pendula/pubescens* and *Sorbus aucuparia*.

Sites are found at medium altitudes in the Amat and Shieldaig pinewoods. Soil types are as found in nodum 16.

The field and moss layers are dominated by *Calluna vulgaris*, *Molinia caerulea* and *Hylocomium splendens*. In wetter hollows *Molinia caerulea* dominates the field layer with the occasional presence of *Juncus* sp., *Carex sp.,* and *Sphagnum* spp., whereas on steeper slopes or drier ground *Calluna vulgaris* dominates the field layer and is often associated with an increase in the abundance of *Betula pubescens* in the canopy.

This nodum differs from nodum 16 in its constant species. The closest phytosociological equivalent is Pinetum Hylocomieto-Vaccinetum (McVean and Ratcliffe,1962). This is characterised by four constants: *Calluna vulgaris*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and *Hylocomium splendens*. The present nodum differs from this association by the absence of *Vaccinium* spp. as constants and the addition of *Molinia caerulea* and *Potentilla erecta*. However, the dominance and abundance of *Molinia caerulea* suggests some affinity to the *Molinia caerulea-Pinus sylvestris* plantation community (Birse, 1988) and the Pinetum scoticae (Birse , 1984). All the other constants that characterise the nodum described here are either absent or are found at low frequencies in Birse's (1988) plantation community. This nodum is therefore best reguarded as a variant of the Pinetum scoticae.

Pinus sylvestris - Vaccinium myrtillus nodum (nodum 17).

This nodum is characterised by the abundance, constancy and dominance of *Pinus sylvestris* and *Vaccinium myrtillus*. Other constants include *Deschampsia flexuosa, Dicranum scoparium, Rhytidiadelphus squarrosus* and *Sorbus aucuparia*.

14 relevés containing a total of 60 species with an average of 17 species per relevé were included in this nodum. Dominants include *Molinia caerulea* and *Vaccinium myrtillus.*

Canopy cover varies between 30-90%, with an average of 60%, and is composed almost entirely of *Pinus sylvestris* although some quantities of *Sorbus aucuparia* seedlings were found in the field layer. *Vaccinium myrtillus* and *Hypnum cupressiforme* increase in abundance with increasing canopy cover, whereas *Molinia caerulea* tends to decrease with canopy cover. These stands contain significant quantities of *Empetrum nigrum*, and in wetter hollows *Sphagnum* spp. occur.

Sites are found at a wide range of altitudes. Distribution is limited to the "Wester Ross" pine woods, namely Loch Maree and Coulin, and the more southerly "northern" woods namely Straith Vaitch and Rhiddoch.

Peaty soils predominate although with brown forest soils locally present.

Nodum 17 is similar to nodum 18 but differs in its constant species. It has affinities with Pinetum Hylocomieto-Vaccinetum (McVean and Ratcliffe, 1962). However, apart from *Pinus sylvestris* and *Vaccinium myrtillus*, it does not contain its other constants as constants namely *Calluna vulgaris, Hylocomium splendens* and *Vaccinium vitis-idaea*; however all these species are intermittently present.

Pinus sylvestris - Calluna vulgaris nodum (nodum 18).

The open canopy and the abundance and constancy of *Pinus sylvestris, Calluna vulgaris, Hylocomium splendens* and *Vaccinium myrtillus* together characterise this nodum.

Canopy cover is very variable, between 2-80%, with an average of 42%. *Pinus sylvestris* dominates the canopy with the occasional presence of *Betula pubescens/pendula*. *Eriophorum angustifolium* and *Sphagnum* spp. are typical of bog communities and suggest that some of these open canopy communities form a transition between bog/heathland and pine wood communities.

Dominants include *Vaccinium myrtillus*, *Calliergon cuspidatum* and *Aulacomnium palustre*. The wide range and abundance of mosses are characteristic of moist, acid environments. The 12 relevés that comprise this nodum are species poor.

Brown forest soils dominate the area although peaty soil types are locally dominant. Sites are found at medium to high altitudes at Amat, Rhiddoch and Loch Maree.

This nodum is related to Pinetum Vaccineto-Callunetum (McVean and Ratcliffe, 1962). However, of their eight constants the following are not found as constants in nodum 18; *Vaccinium myrtillus*, *Deschampsia flexuosa, Plagiothecium undulatum* and *Ptilium crista-castrensis.* However, all but the latter species are intermittently present within this nodum.

THE ALDER WOODS

Alnus glutinosa nodum (nodum 5).

The 5 relevés of this nodum are species poor, containing a total of only 23 species. The nodum is characterised by the abundance and constancy of *Alnus glutinosa* and *Ranunculus acris.*

The canopy layer is dominated by *Alnus glutinosa* with varying proportions of *Corylus avellana, Salix* sp. and *Sorbus aucuparia*. Dominants include *Holcus lanatus,* Gramineae undif., *Carex* sp., and *Filipendula ulmaria.*

Sites are found at low altitude in Strathfleet and near Syre in Strathnaver. These are topographically low-lying areas with silty soils.

This nodum is similar to the *Alnus glutinosa* woodland fragments described from Skye (Birks, 1973a) because of the abundance of *Alnus glutinosa* and *Ranunculus acris.* However, the one relevé that characterises Birks' (1973a) alder woods does not contain *Holcus lanatus, Carex* sp., or *Filipendula ulmaria.*

WILLOW SCRUB

Salix nodum (nodum 4).

Only one constant taxon, *Salix* sp., is found in the 11 relevés that contain a total of 57 species (with an average of 20 species per relevé). These areas of *Salix* scrub are often less than 16 m^2.

Canopy cover is frequently dense, between 50-90%, and is composed mainly of *Salix* sp. with varying proportions of *Alnus glutinosa* and *Betula pubescens*. Tree height is generally low, but varying between 2 and 7 metres.

Dominants include: Gramineae, *Agrostis capillaris, Anthoxanthum odoratum, Holcus lanatus, Deschampsia flexuosa, D. cespitosa* and *Juncus effusus.* The wide range and abundance of Gramineae spp. probably indicates that grazing influences the composition of the field layer.

Brown forest soils predominate with some peats and fluvio-glacial sands and gravels. Most stands are on poorly-drained sites that are located at low altitudes in Strathnaver and in north-western Scotland.

This nodum is difficult to place phytosociologically although it is comparable with the species-rich scrub communities on Orkney (Prentice and Prentice, 1975; Birse, 1982b) that Birse (1982b) places in his subassociation with *Luzula sylvatica* of Blechno-Quercetum (Braun-Blanquet et Tüxen, 1952; Birse, 1982b, 1988).

DWARF-SHRUB HEATH and BOG

This category is composed of the dwarf-shrub heath and bog communities that are dominated by shrubs, monocotyledons, bryophytes and lichens.

Calluna vulgaris - Potentilla erecta nodum (nodum 19)

The 19 relevés are characterised by the constancy and abundance of *Calluna vulgaris* and *Potentilla erecta* although with the occasional dominance of *Molinia caerulea* in wetter hollows.

Sites are distributed throughout Strathnaver at low to medium altitude on shallow, well-drained peaty podsols and peaty gleys.

There are two facies within this nodum. The first facies is characterised by species of moist peatlands including *Carex* sp., *Hypnum cupressiforme, Narthecium ossifragum, Pseudoscleropodium purum* and *Trichophorum cesitosum*, whereas the second facies is distinguished by the abundance of herbaceous species, namely *Viola* sp. *Potentilla erecta*, *Agrostis canina*, and *A. stolonifera*. The first species group is found in almost all relevés whereas the second is restricted to relevés 212, and 229.

This association has affinities with nodum 25 but occurs in drier locations. It is floristically closest to Callunetum vulgaris (McVean and Ratcliffe, 1962) because of the almost complete dominance and abundance of *Calluna vulgaris*. Their other constants include *Dicranum scoparium* and *Hypnum cupressiforme.*

Calluna vulgaris - Agrostis canina nodum (nodum 20)

Nodum 20 differs from nodum 21 in the replacement of *Eriophorum angustifolium* and *Sphagnum* spp. by *Agrostis canina* and *Hypnum cupressiforme.* The constants are *Agrostis canina*, *Calluna vulgaris*, *Hypnum cupressiforme* and *Potentilla erecta.*

There are 6 relevés containing a total of 36 species with the following dominants: *Calluna vulgaris, Erica tetralix* and *Molinia caerulea.*

Geographically sites are distributed as in nodum 22, that is at low to medium altitude throughout Strathnaver. Sites are mostly found on shallow peaty podsols and peaty gleys.

This nodum has affinities with Callunetum vulgaris (McVean and Ratcliffe, 1962) and species-poor Agrosto-Festucetum (McVean and Ratcliffe, 1962) and may represent a transitional form between these two associations. Grazing pressure is possibly higher than in nodum 19 with an increase in the abundance of Gramineae spp.

Calluna vulgaris - Eriophorum angustifolium nodum (nodum 21)

This species-poor nodum contains a total of 28 species in 6 relevés. The constants are *Calluna vulgaris*, *Erica tetralix*, *Eriophorum angustifolium*, *Potentilla erecta* and *Sphagnum* sp. The dominant species are *Eriophorum angustifolium* and *Sphagnum capillifolium* var rubellum.

Soils are similar to those of noda 19 and 20 except that they include some deep peat. Sites are found predominantly near the north coast at medium altitude.

This nodum is floristically nearest to the Trichophoreto - Eriophoretum typicum (McVean and Ratcliffe, 1962) that has the following constants: *Calluna vulgaris, Erica tetralix, Myrica gale, Eriophorum vaginatum, E. angustifolium, Molinia caerulea, Trichophorum cespitosum, Narthecium ossifragum, Drosera rotundifolia* type, *Sphagnum papillosum, S. rubellum* and *Hypnum cupressiforme.* However, nodum 21 is floristically poorer than Trichophoreto - Eriophoretum typicum. It differs from nodum 20 in the increase in the abundance of moisture-loving species, eg. *Erica tetralix* and *Eriophorum angustifolium.* This suggests that the water table is higher in nodum 21 than in noda 19 or 20.

This species-poor nodum contains few notable species excepting *Juncus bulbosus* and *Vaccinium oxyoccus*, both of which occur locally in Sutherland and Caithness and are perhaps related to *Sphagnum*-rich areas with stable water tables (Ratcliffe and Oswalde, 1988).

Erica tetralix - Sphagnum nodum (nodum 22)

Only 3 relevés comprise this species-rich nodum. It is characterised by the following constants: *Erica tetralix, Potentilla erecta* and *Sphagnum* spp. Dominants include *Erica tetralix*, *Sphagnum* spp., *Eriophorum vaginatum, Molinea caerulea* and *Myrica gale.*

This nodum is found from near sea level on the coast to 144 metres inland. It is predominantly found on the plateau throughout Strathnaver on peaty gleys, podsols and rankers. However, relevé 179 is from Rhiddoch pine forest and has probably been misclassified; it perhaps ought to be included in nodum 17.

The nodum contains *Carex* sp., *Dactylorhiza maculata, Drosera rotundifolia* type, *Molinia caerulea, Narthecium ossifragum, Pedicularis palustris, Pinguicula vulgaris, Potentilla erecta, Trichophorum cespitosum* and *Succisa pratensis.* In drier areas *Erica tetralix* is replaced by *Calluna vulgaris*.

It has affinities with Trichophoreto-Eriophoretum typicum (McVean and Ratcliffe, 1962), the only dominants of which are *Sphagnum* spp. There appears to be a wider range of variation in nodum 22 than in Trichophoreto-Eriophoretum typicum and it is also more species rich than nodum 21.

Calluna vulgaris nodum (nodum 24)

The constants are *Calluna vulgaris*, *Molinia caerulea*, *Sphagnum* sp. and *Trichophorum cespitosum*. The 24 relevés contain the following dominants: *Molinia caerulea*, *Myrica gale*, *Sphagnum* sp., *Cladonia impexa*, *Racomitrum fasciculare* and *Trichophorum cespitosum*.

There is considerable variation within this nodum. Two facies are recognised with the following dominants: *Sphagnum capillifolium var. rubellum*; and *Trichophorum cespitosum* associated with an increase in the abundance of *Narthecium ossifragum*.

The first facies has affinities with Molinieto-Callunetum (McVean and Ratcliffe, 1962). Molinieto-Callunetum contains the following constants: *Calluna vulgaris*, *Erica tetralix* and *Hypnum cupressiforme*. This facies is usually found where there is water movement through the bog.

The second facies has affinities with Trichophoreto-Callunetum (McVean and Ratcliffe, 1962) and is found in drier locations than the first facies. The change in moisture status results in the replacement of the dominant *Molinia caerulea* by *Trichophorum cespitosum*.

Trichophoreto-Callunetum and Molinieto-Callunetum are widely distributed throughout the highlands (McVean and Ratcliffe, 1962; Birks, 1973a). The relevés of the present nodum are predominantly found at medium altitude in Strathnaver.

Calluna vulgaris - *Cladonia impexa* nodum (nodum 25)

The 4 relevés are characterised by the dominance of *Cladonia impexa*. The constants are *Cladonia impexa*, *Erica tetralix*, *Hypnum cupressiforme* and *Trichophorum cespitosum*. *Cladonia impexa* and *C. uncialis* are co-dominants.

Stands occur predominantly on shallow peaty podsols and peaty gleys. They are found at medium altitude and are geographically restricted to two localities on the east and west of Strathnaver.

This association has affinities with Cladineto-Callunetum (McVean and Ratcliffe, 1962) and with the moist lichen heaths of Orkney (Prentice and Prentice, 1975). *Cladonia impexa* is however dominant instead of *C. sylvatica* and *Erica tetralix* and *Trichophorum cespitosum* are constants. This suggests that these stands are wetter than the typical Cladineto-Callunetum although *Trichophorum cespitosum* is present in low quantities in the *Cladineto-Callunetum* typicum heaths of Orkney (Prentice and Prentice, 1975).

Trichophorum cespitosum - Myrica gale nodum (nodum 23).

The constancy and abundance of *Calluna vulgaris*, *Myrica gale* and *Sphagnum* spp. characterise this nodum. The other constants include *Erica tetralix, Narthecium ossifragum, Sphagnum* sp. *Potentilla erecta, Trichophorum cespitosum*, *Sphagnum papillosum* and *S. subnitens*. *Trichophorum cespitosu*m and *Sphagnum* sp. are the only dominant taxa.

The 6 relevés are species poor, containing a total of 25 species and an average of 14 species per relevé. This nodum is found on peaty soils that vary in character depending upon soil depth and the nature of the under-lying substrate. Topographically the sites are flat, often with standing water, and are found at low to medium altitude.

This nodum has affinities with Trichophoreto-Eriophoretum (McVean and Ratcliffe, 1962). Nodum 25 contains 4 of the same constants but the following species although being present (with the exception of *Sphagnum capillifolium var rubellum*) are not constants - *Eriophorum angustifolium, Molinia caerulea, Drosera rotundifolia* type, *Sphagnum capillifolium var rubellum* and *Hypnum cupressiforme.* In addition, nodum 23 has *Nardus stricta, Potentilla erecta* and *Sphagnum subnitens* as constants.

The relevés collected in this study are predominantly restricted to Strathnaver. However, Trichophoreto-Eriophoretum is widely distributed throughout Scotland (McVean and Ratcliffe, 1962; Birks, 1973a).

Juniperus communis nodum (nodum 6)

Only 2 relevés comprise this nodum that is characterised by an abundance of *Juniperus communis*. It contains a total of 13 species and had the following constants: *Bellis perennis, Juniperus communis* and *Plantago lanceolata*. Gramineae spp. dominate the field layer of this nodum.

This nodum is restricted to the coastal area on the Bettyhill National Nature Reserve. Calcareous soils predominate.

The phytosociological position of this stand is discussed in McVean and Ratcliffe (1962). They suggest that the junipers are of intermediate form between sub-species *nana* and *communis*, but that perhaps the stand lies closest floristically to Juniperetum nanae. Noda 6, 13 and 14 represent a transition from juniper-rich birch woodlands to low alpine juniper heaths (McVean and Ratcliffe (1962). All of these communities are sensitive to fire and were probably once more widely distributed (McVean and Ratcliffe, 1962).

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Dryas octopetala nodum (nodum 1)

This single relevé contains only 7 species namely: *Botrychium lunaria, Cirsium vulgare, Dryas octopetala,* Gramineae undif., *Nardus stricta, Taraxacum* sp. and *Thymus praecox* subsp. *arcticus.* The dominant species are *Thymus praecox* and *Nardus stricta.*

The relevé was collected at 100 m altitude adjacent to the coast on the Bettyhill National Nature Reserve. Calcareous soils predominate.

This nodum has affinities with published *Dryas octopetala* noda (McVean and Ratcliffe, 1962). The absence of dwarf shrubs other than *D. octopetala* probably reflects the moderately-intensive grazing that occurs on the Bettyhill National Nature Reserve.

Nardus stricta nodum (nodum 2)

2 relevés comprise this species-poor nodum. The constants are *Bellis perennis, Carex echinata, Carex sp., Holcus lanatus, Juncus effusus, Nardus stricta, Poa sp., Potentilla erecta* and *Trifolium repens/T. pratense.* The dominant species are *Nardus stricta* and *Hylocomium splendens.*

The 2 sites are at medium altitude on acidic peaty soils and the 2 relevés were collected in heavily-grazed, managed upland plateau areas of Strathnaver. This nodum is closest floristically to the species poor facies of Nardetum sub-alpinum (McVean and Ratcliffe, 1962; Burnett, 1964) as it contains three of their constant species as constants namely *Nardus stricta, Carex* sp., and *Potentilla erecta.* However, the species mix suggests that this community has been obtained by a combination of seeding and intensive grazing and is therefore not apparently comparable with previously described phytosociological communities.

Anthoxanthum odoratum - Rhytididiadelphus squarrosus nodum (nodum 7)

This species-poor nodum is characterised by three constants: *Anthoxanthum odoratum*, *Potentilla erecta* and *Rhytidiadelphus squarrosus*.

The 10 relevés have the following dominants: *Caltha palustris, Festuca* sp., *Pteridium aquilinum, Calluna vulgaris* and *Anthoxanthum odoratum*.

A variety of soil types are present including brown forest soils, but they are predominantly peaty gleys, peaty podsols and humus iron podsols.

Floristically, this associatation is closest to Nardetum sub-alpinum (McVean and Ratcliffe, 1962). This association is characterised by the following species: *Anthoxanthum odoratum*, *Agrostis tenuis, Festuca ovina* agg., *Carex pilulifera, Galium saxatile* and *Rhytidiadelphus squarrosus.* It tends to be associated with hills that have supported sheep grazing for some considerable time (McVean and Ratcliffe, 1962).

This nodum is located at low-medium altitude throughout Strathnaver.

Few of the present noda fit well into previously described associations, communities and noda. It is therefore pointless to try to fit them rigidly into the classification schemes of the central European phytosociologists (McVean and Ratcliffe, 1962; Birks, 1973a; Birse, 1988).

The interrelationships between the noda defined in this study were investigated by ordination using DECORANA (Hill, 1979a) upon the percentage constancy data of all the species present. Fig. 3.6 shows that the noda have been well separated except for an overlap between the birch woodlands and the willow scrub. In summary, the following groups are separated on the plot: Group A (ai and aii), B, C, and D are the birch, pine and alder woods and willow scrub respectively; group E contains the heathland/bog communities that are confined to peaty soils; group F comprises the anthropogenically-modified grassland noda; group G contains the grassland communities found on calcareous soils. Groups A to D inclusive are predominantly species rich and restricted to the lowland river valleys, whereas groups E-F are predominantly species poor and are found on plateaux above the major river valleys.

The first axis separates noda from wet, acidic (high altitude and/or inland) sites and those from dry, calcareous (low-medium altitude coastal) sites. The second axis separates isolated sites (islands) with reduced grazing and/or burning pressure from areas that are intensively grazed and dominated by Gramineae. The two axes of variation show the effects of soil moisture, pH, altitude and grazing pressure/fire suppression.

In order to investigate the effects of environmental/ecological variables on individual relevés an ordination plot using DECORANA (Hill, 1979a) upon Domin values for spp. was produced. This plot has been broken down by plotting each nodum separately on axes 1 and 2 (Figs. 3.7a-y). The following groups of noda are separated along the first axis in an east or NNE direction. Group 1 contains nodum 14; group 2 contains noda 12 and 13; group 3 contains noda 15, 16, 17 and 18; group 4 contains nodum 7; and group 5 contains noda 19, 20, 21 and 22. Groups 1 and 2 contain the *Betula pubescens-Vaccinium myrtillus/Juniperus communis*-rich and *Betula pendula* woods. Group 3 contains all the pine noda, group 4 is an *Anthoxanthum*-rich grassland, and group 5 includes the heathlands dominated by *Calluna vulgaris* and *Erica tetralix*. This transition from groups 1 to 5 in part reflects a transition from basic to acidic soils and increasing soil moisture content and grazing pressure.

Along the second axis the plots are grouped as follows: group 6 contains noda 8, 9, 10 and 11; group 7 - noda 3, 4; and group 7 contains noda 1, 2, and 6. These groups of noda mark a transition from predominantly Gramineae/herb-rich birch woods; through *Rumex*-rich birch, alder and willow scrub; to *Nardus stricta* and coastal grasslands. The transition along this axis reflects increasing grazing pressure (and/or reduced fire frequency) and increasing alkalinity in a northwards direction. The species by species ordination has not been included as it simply reflects the site ordination.

Throughout the discussion of the spatial separation of noda on the DECORANA plot (Fig. 3.7a-y) it has up to now been assumed that these woods are of similar age ie. relicts of long-establised woodland communities. In order to try to assess whether this assumption is true a number of the relevés from the birch and pine woods (noda 3,8,9,10,12,13, 14 and 15) were categorised according to whether the woodland was established before 1750 (ancient) or between 1750 and 1860 (long established woodland) from the woodland inventories compiled by Walker (1985, 1986 and 1988) based on historical evidence.

Approximately 60 relevés were classified in this way and their positions marked on the DECORANA plot (Fig. 3.7z). Before discussing these results it must be emphasised that data are unavailable for many sites and therefore these results must be treated with caution. Fig. 3.7z shows that axis 1 separates ancient (-ve) from semi-natural (+ve) stands, although there is a "grey" transitional area on the plot where ancient woodland cannot be separated from semi-natural woodland. This suggests that noda 12 and 13 are of relatively recent origin compared with nodum 3 whereas noda 8,9 and 10 are of uncertain (or mixed) age. This may be further substantiated by the fact that noda 12 and 13 contain on average fewer species per relevé (20 and 14 respectively) than noda 3,8,9,10 (21,22,22, and 22 respectively). However, it must be remembered that species richness is related to many factors (eg. edaphic, hydrological conditions and management) and cannot be easily related to age.

If these results are correct then they might provide evidence to refute the hypothesis that the *Betula pubescens-Juniperus communis* stands are not relicts of a formerly more widespread community (McVean and Ratcliffe, 1962) but have been artifically created and/or managed by man within the last 239 years. However, this evidence must be treated with caution as the *Betula pubescens-Juniperus communis* woods may have been accidentally omitted from the 1750 maps and may in reality be ancient woodland which cannot be proven from the historical evidence (Walker, 1986). As the historical evidence is potentially imprecise and incomplete these findings can only be substantiated and/or refuted by fine temporal resolution pollen and/or dendrochronological analysis from sites located within the *Betula pubescens-Juniperus communis* nodum.

3.2.3 Discussion

25 noda were distinguished during the vegetation classification. Few if any of these noda correspond exactly to any published communities. Where they are related to such divisions they are most frequently related to McVean and Ratcliffe's (1962) communities. This is not surprising because few phytosociological surveys have been carried out on the mainland north of Gairloch (Birse, 1988) and those that have are not fully published eg. Ratcliffe and Oswalde (1988) only include summary constancy tables of noda that cannot easily be related to this survey. Phytosociological surveys have been carried out on the off-shore islands of Orkney (Prentice and Prentice, 1975; Birse, 1982b) and Skye (Birks, 1973a) but tend to be characterised by western/Atlantic species, being much richer in bryophytes and *Carex* spp.

3.3 Mapping the vegetation using the Thematic Mapper image.

3.3.1 Methods

Photographs taken from space have until relatively recently only been of value in large-scale vegetation surveys because of their relatively poor spatial resolution. As developments have occurred in satellites so the potential use of satellite imagery has increased. Remote sensors record the amount of radiation in visible and infra-red wavelengths that is reflected from an object or else that is absorbed and re-emitted. The sensitivity of the sensor is related to the radiometric resolution of the sensor, the amount of atmospheric scatter, the surface roughness of the object, and the spatial variability of reflectance within the scene (Curran, 1985).

Because of financial limitations a hard copy image was obtained rather than a tape containing the digitised information. The hard copy image is less satisfactory than the digitised tape; a single pixel can be characterised by at least 256 numbers, whereas the human eye can only detect 20-30 colours (Curran, 1985). This means that the results are both more subjective and less accurate than they might otherwise be.

The Thematic mapper records seven spectral wavebands. The three wavebands used in the production of the image used were: Band 3 (0.63-0.69 micrometres) which discriminates between plant chlorophyll absorption measurements enabling plant species determinations; Band 4 (0.76-0.90 micrometres) which delineates water bodies and determines biomass content; and Band 5 (1.55-1.75 micrometres) for measurement of vegetation and soil moisture (Curran, 1985; Weaver and Jewell, 1987). The image was geometrically corrected in order that it could be directly compared with the 1:25000 Ordnance Survey maps. In order to assess whether the plant communities of northern Scotland could be characterised by pixel colour, or response, the image was ground truthed by surveying the scrub, and upland communities in Strathnaver and its surrounding area by the following methods:

1. Photographs were made of three 7 x 5 km areas of the Thematic Mapper image for use in the field. Each was centred around the position of one of the three lakes cored in Strathnaver for pollen analysis namely Loch Mer, Loch Chealamy, and Lochan by Rosail. Field vegetation maps were then produced for each of these areas by plotting the boundaries detected on the Thematic Mapper photograph onto acetate together with field observations of the dominant vegetation types. Two of these maps will be presented in chapter 4.
2. Short transects were positioned within these 7 x 5 km areas and quadrats placed at 25 m. intervals using a compass and tape measure. The phytosociological data were collected from 2 x 2 m quadrats and the Thematic Mapper image colour, or spectral response, which characterised that point noted.
3.In addition, wherever possible a Thematic Mapper image colour was then assigned for each of the releveès recorded during the survey of the birch woodlands.

3.3.2 Results

In order to investigate the relationship between the vegetation classification and the surface pollen maps a two-fold analysis was required. The first step involved estimating the percentage cover of different vegetation types around surface-sample sites. The second step was to relate the percentage vegetation cover to the surface-pollen spectra. The Thematic Mapper image was used for the first step and will be discussed next.

The variation in the Thematic Mapper colour classification, ie. the range of colours, for a single nodum meant that single noda could not be separated easily from each other by colour alone (Table 3.17). Cluster analysis (a polythetic agglomerative classification) was carried out in order to classify the noda according to their representation by Thematic Mapper colours. The results are displayed in the form of a dendrogram for minimum variance cluster analysis that is based on minimising the sum of squared distances from the centre of gravity (Fig. 3.8). The cophenetic correlation co-efficient, which assesses how well the original dissimilarity patterns are displayed by the dendrogram, is 0.67, suggesting that the original structure is well displayed by the dendrogram. A cut-off at a dissimilarity value of 37% of the maximum was arbitrarily chosen and 7 groups distinguished.

A probability table was constructed in order to assess the probability of a given Thematic Mapper colour being representative of a particular nodal class (Table 3.18). The relationship between Thematic Mapper colour and nodal class is poor when viewed from a statistical point of view. However, although a wide range of colours can be associated with a single nodum there is usually a reasonable probability that any one colour reflects one particular nodum.

3.3.3 Discussion

None of the vegetation communities can be easily related to the Thematic Mapper colours. The estimation of percentage vegetation cover from Thematic Mapper imagery was only partly successful. Previous studies have separated different grassland communities using more spatially-precise SPOT imagery (Wyatt and Jones, 1988) and Thematic Imagery (McMorrow and Hume, 1986), and communities of heather, bracken and sedges using Thematic Mapper imagery (Jewell and Brown, 1987; Ward *et al*, 1987; and Weaver, 1987). However, few studies have tried to discriminate between previously defined phtyosociological communities using satellite imagery (Morton, 1986). It is therefore perhaps not surprising that the classification of pre-defined vegetation communities was only partly successful. The reasons for this include the limitations of the imagery type (hardcopy not digitised tape) and the limited time available that prevented the collection of repetitive samples so that the distance between samples was too great (minimum of 25 metres). In addition, the basis of the two classifications is different; the phytosociological classification is based on presence/absence of species and species abundance whereas the Thematic Mapper classification is related to plant phenology, grazing intensity, moisture content of the ground, surface roughness, and slope angle to name only a few variables (Jewell and Brown, 1987). Classification based on areas rather than single pixel colour, and that took into account relief and the proximity of vegetation boundaries, might improve the relationship between the Thematic Mapper pixel response (colour) and the vegetation communities (Weaver and Miles, 1989). However, the vegetation classification achieved was nonetheless useful and considerably better than anything that could be obtained from aerial photographs (McMorrow and Hume, 1986).

3.4 The surface pollen survey

3.4.1 Methods

In order to investigate the relationship between percentage vegetation cover and surface pollen spectra, a spatially arranged surface pollen survey was carried out. A series of transects (up to 33 km long) running in an east-west direction, was spaced at approximately 10 km intervals down the Strathnaver valley. Along each transect a number of lochans were sampled mostly at intervals of less than 3-4 km (Fig. 3.9b and Table 3.19). Small lochans (ideally smaller than 100 x 100 metres) were chosen as they would be both comparable with the fossil assemblages and because their pollen source area was between 0-5 km radius. The corer was a purpose-designed Hongve sampler (Hongve, 1972; and is described by Wright, 1980); this comprises of a single perspex tube 30 cm long and 4 cm wide with a rubber bung that operated to seal the tube on impact into the sediment. The sample was extruded and the top 1 cm collected in a self-sealing polythene bag.

The samples were prepared using the method recommended by Birks and Peglar (1977). This involved treatment with HCl to remove free calcium carbonate; NaOH to defloculate and remove humic colloids; HF to remove siliceous material; Acetolysis to remove cellulose; followed by staining and suspending in silicone oil to prevent dehydration during storage. Details of the treatment of each sample were recorded on a pollen preparation sheet.

The residues were mounted in 2000 cs silicone oil on slides according to the method described by Birks (1980b). Pollen grains and spores were identified using a Leitz microscope at a magnification of x 400. A total of at least 500 grains was counted on each slide where possible. Nomenclature of the pollen taxa follows Moore and Webb (1978) with the following exceptions: Cyperaceae (Fægri and Iversen, 1964); Caryophyllaceae (Fægri and Iversen, 1964); wild grass and cereal pollen (Andersen, 1978); *Calluna* and *Empetrum* are distinguished from Ericales (Oldfield, 1959; Birks, 1973a); and *Tilia* (Andrew, 1971). The results are expressed as a percentage of the total land pollen (Fig. 3.10) and grouped according to the phytosociological communities they were collected from. 3 main vegetation types were recognised: birch woods, grasslands and dwarf-shrub heath and bog. Within each of these groups the surface samples were arranged according to the noda from which each sample was obtained.

The results from the surface samples were then combined with data obtained from published sites (Fig. 3.9a) to produce a series of isopoll maps at two geographic scales: 1. For Strathnaver and its surrounding area and 2. for northern Scotland. Figs 3.9a and 3.9b show the location of the surface samples used in the construction of these maps and Table 3.19 documents the location of the surface samples analysed by the author. The isopoll maps show the main geographic patterns in the surface sample data and enable comparison of the present pollen rain with the distribution of present vegetation (Grimm, 1988).

3.4.2 The surface pollen maps

The pollen maps show that the percentage pollen values reflect the distribution of plant communities. Contour lines and surface pollen isopoll maps (Fig. 3.11 to 3.17b inclusive) were produced for :

1. DECORANA sample scores on axis 1
2. *Betula* (>25 % total land pollen)
3. Gramineae (>15 % total land pollen)
4. *Calluna* (>40 % total land pollen)
5. Cyperaceae (>10 % total land pollen)

On Fig. 3.11 the DECORANA sample scores for axis 1 have been plotted. Contour lines have been mapped for values of >100 and >50. Values between 50 and 100 are predominantly found below 183 metres and along the coast, whereas values >100 are only located in the northern part of Strathnaver valley coinciding with the comparatively intensive grazing/management that occurs there. Values <50 are primarily found on the plateau (Fig. 3.11).

Pollen values of >25% *Betula* are taken to indicate the local presence of *Betula pubescens/pendula* (Huntley and Birks, 1983). Fig. 3.12a shows that the majority of pollen sites in northern Scotland have pollen values of <25%, suggesting that *Betula* is not locally present in northern Scotland. These values reflect the fact that the majority of these sites are situated on the plateau. This picture is modified when the surface samples from within/around Strathnaver are considered (Fig. 3.12b). A contour line has been drawn for the 25 % *Betula* pollen values. Most of the *Betula* pollen values of >25% occur below 183 metres altitude. The exceptions to this are sites that are within 10-12 km of the coast. Coastal sites are subjected to severe wind exposure and as a result relatively few woodlands are found near to the coast (Fig. 3.12.b).

Fig. 3.13a shows that in northern Scotland high *Calluna* pollen values (>50%) reflect the distribution of peat deposits. Values of between 40 and 50% are often found adjacent to peat deposits. Fig. 3.13b shows that in the area around Strathnaver >40% *Calluna* pollen is usually found on the plateau. However, localised lowland and coastal areas(sites 27, 24, and 20) also have high *Calluna* pollen values. All of these sites are on sloping ground, with better drainage encouraging the proliferation of *Calluna vulgaris*.

Fig. 3.14a documents that only 15% of all sites have Gramineae pollen values of >25%. Huntley and Birks (1983) state that "*values >25% reflect a preponderance of treeless vegetation.*" This conflicts with the evidence presented here because the majority of northern Scotland is treeless natural or semi-natural heath/bog and not the anthroprogenic grasslands that dominate Europe's treeless areas. Pollen values of 6% may be taken to reflect a treeless environment in this area. Gramineae pollen values are contoured for 10% (Fig 3.14b). This illustrates the presence of lowland and coastal grasslands; many of these areas are intensively grazed.

Fig. 3.15a records *Pinus* pollen values consistently <12% in northern Scotland indicating that *Pinus sylvestris* is not locally present in northern Scotland. However, 60% *Pinus* pollen values are recorded from Coire bog indicating the local presence of *Pinus* plantations. Fig. 3.15b depicts the locations of the major coniferous plantations. A number of these plantations in Strathnaver are composed of *P. sylvestris*. Even sites adjacent to these plantations have low *Pinus* pollen values (<15%). This suggests that either these pine trees have not yet reached maturity and therefore and are not yet producing pollen or else that *Pinus* produces only small amounts of pollen beyond its natural limit. *P. sylvestris* produces pollen from 10-15 years (Carlisle and Brown, 1968) and the majority of these plantations are at least that age. This may suggest that *P. sylvestris* produces only small amounts of pollen at its climatic limits.

Fig. 3.16a shows that Cyperaceae pollen values range between 6-25% in northern Scotland. Pollen values >10% are taken to indicate the presence of treeless vegetation (Huntley and Birks, 1983). However, Cyperaceae pollen values from northern Scotland are often below 10% because of the dominance of other pollen taxa namely *Calluna* and Gramineae. A 10% contour line has been drawn in Fig. 3.16b. This documents the presence of Cyperaceae in coastal areas and suggests that inland values of >10% are predominantly found above 183 metres. There are several exceptions to this suggesting that the distribution of Cyperaceae is complex. Some of the variability may be accounted for by the presence of aquatic species of Cyperaceae which may inflate the Cyperaceae pollen values in lowland situations.

Fig. 3.17a shows the presence of *Pteridium* spores in northern Scotland. The presence of spores appears to be spasmodic; no records of *Pteridium* are found at several sites where *Pteridium* is known to be present. The absence of spores from some sites may be because of poor transportation whereas in other cases its absence may be because *Pteridium* is located in shady places where it is unable to produce spores (Tinsley and Smith, 1974; Huntley and Birks, 1983). Fig. 3.17b maps the distribution of all spores around Strathnaver. Spores are present at all sites with values >5% except at sites 22 and 26. *Pteridium* spores are recorded at only 25% of these sites. *Pteridium* forms widespread but localised populations throughout Strathnaver. Poor transportation and/or preservation may account for its absence.

Modern isopoll maps of northern Scotland have previously only been produced at course scales of resolution (Huntley and Birks, 1983). The maps presented show that previously coursely resolved pollen isopoll maps while characterising the upland vegetation fail to distinguish either the birch wood communities, found in the valleys, or the coastal grassland communities. Thus although the pollen percentages do exhibit local variability the surface pollen and DECORANA maps do reflect the distribution of *Calluna, Betula, Pinus,* Gramineae and to a lesser extent Cyperacee, and *Pteridium.*

In order to investigate the patterns in greater detail the pollen spectra from Strathnaver and its surrounding area each surface sample was subjectively classified into the nodum that represented the dominant vegetation surrounding the site. This method was rather crude as the phytosociological surveys showed that up to 6 noda can be found around the edge of a single loch. The noda have already been described and only their important distingishing features are highlighted below.

3.4.3 The surface pollen spectra from the birch woods, willow scrub, dwarf-shrub heath and bog and grasslands.

Pollen spectra from the birch woods

Only one surface sample was collected from a loch completely enclosed by birch (*Betula pubescens*). The woodland types found at Loch Chealamy are:

1. *Betula pubescens - Potentilla erecta* nodum
2. *Betula pubescens - Rhytidiadelphus squarrosus* nodum
3. *Betula pubescens - Deschampsia flexuosa* nodum

Betula pubescens is the only constant species present in all of these noda whose understoreys are dominated by tall herbs. These floristically distinct noda are separated on the constancy and abundance of *Rhytidiadelphus squarrosus*, *Thuidium tamariscinum, Odontoschisma sphagni, Anthoxanthum odoratum, Pteridium aquilinum, Potentilla erecta* and *Viola riviniana.*

The pollen spectrum from Loch Chealamy is overwhelmingly dominated by *Betula* with the occasional presence of other tree taxa including *Quercus, Ulmus, Picea, Acer, Corylus,* and *Salix.* Of these tree species only *Salix* and *Corylus* grow rarely in the wood, whilst isolated trees of *Quercus, Ulmus, Picea,* and *Acer* can be found within 3 kms of the site. *Sorbus aucuparia* is occasionally present in the wood but is absent from the pollen spectrum.

The pollen spectrum suggests that the understorey is dominated by Gramineae and

Cyperaceae with the occasional presence of herbs and ferns eg. *Plantago lanceolata, Ranunculus* type, Compositae Subfamily Liguliflorae, *Rumex acetosa, Hordeum* type, *Ononis,* and Filicales, whereas *Viola*, *Oxalis,* and *Pteridium* are not represented in the pollen spectrum. The absence of *Pteridium* spores from shaded habitats has already been discussed.

The pollen representation of the understorey species is poor This pollen spectrum might be placed into the *Betula pubescens - Rumex acetosa* nodum, which is not recorded within the wood, because of the over-representation of *Rumex acetosa* and *Plantago lanceolata.* The poor separation between different *Betula* understoreys is similar to that found by Birks (1973a) although he recognised that there was a good correlation between *Betula* pollen percentages and canopy cover, whilst recognising that *Sorbus aucuparia, Populus tremula,* and *Salix* spp. were poorly represented.

With the exception of Loch Chealamy, the pollen surface sample sites are dominated by treeless vegetation and will therefore be considered under their respective vegetation communities. However, before doing this a brief consideration will be made of those sites that have birch woods growing locally.

Fig. 3.10 indicates that 12 sites have birch woods within a 1 km radius and that of these sites only 3 have *Betula* pollen values greater than 25%. The remaining 9 sites have *Betula* pollen values as low as 5%. These extremely low *Betula* pollen values are indicative of either low pollen production or poor pollen transportation or preservation. Poor pollen transportation or preservation seems unlikely to account for the low *Betula* pollen values as Birks (1973a; 1980a), Huntley and Birks (1983) and Prentice *et al* (1987) have found that *Betula* is usually well represented with values of >25% taken to indicate the local presence of birch woods (Huntley and Birks, 1983). 3 further sites (site numbers 7 and 8) have pollen values of greater than 25%, but are not located within 1 km of a natural birch wood, however all 3 of these sites are located within 2 km of coniferous plantations that probably contain scattered birch trees.

These results suggest that not only are birch wood understoreys difficult to relate to the pollen spectra but that *Betula* appears to be under-represented by the pollen spectra. Low pollen production may account for the low pollen values because either the trees are physiologically unable to produce pollen at or near the potential treeline or else because these trees are so old that pollen production has substantially declined or ceased.

Pollen spectra from grasslands

7 samples fall into this category namely nos 7, 14, 21, 32, 16, 29, 30, and 33. The grassland types are divided between two noda:

1. *Nardus stricta* nodum
2. *Anthoxanthum odoratum - Rhytidiadelphus squarrosus* nodum

These two noda are separated primarily by the constancy and abundance of *Nardus stricta* and *Carex* sp. in the *Nardus stricta* nodum.

The pollen spectra can not be separated into the two nodal groups as Cyperaceae is consistently present in all the surface samples and *Nardus stricta* can not be separated from the other members of the Gramineae. The pollen spectra are characterised by pollen values of both Gramineae and Cyperaceae of > 10% with *Calluna* being dominant at some sites. There is a wide variety of herb taxa at low pollen frequencies including: *Potentilla* type, *Filipendula, Plantago lanceolata, P. coronopus, Ranunculus* type, *Bidens* type, Umbelliferae type 2, *Artemisia, Succisa, Rumex acetosa, R. acetosella,* Compositae Sub-family Liguliflorae, *Pedicularis, Hordeum* type and *Galium* type. In addition, there are a number of spore types including *Sphagnum, Pteridium, Selaginella selaginoides, Polypodium vulgare* and *Dryopteris carthusiana* type. All these pollen and spore taxa are found at low values (<10%) and appear to be well represented despite their low percentage cover in the vegetation.

Pollen spectra from dwarf-shrub heaths

The 25 surface samples in this category represent 5 noda:

1. *Calluna vulgaris - Eriophorum angustifolium* nodum
2. *Erica tetralix - Sphagnum* nodum
3. *Calluna vulgaris* nodum
4. *Calluna vulgaris - Cladonia impexa* nodum
5. *Trichophorum cespitosum - Myrica gale* nodum

Essentially, 1. is dominated by the dominance of *Eriophorum angustifolium* and *Sphagnum* sp. and the constancy of *Calluna vulgaris* and *Potentilla erecta,* whereas 2. does not have *C. vulgaris* as a constant species.

The pollen spectrum from surface sample number 2 seems to represent well the *Calluna vulgaris - Eriophorum angustifolium* nodum as it is dominated by *Calluna,* and

Cyperaceae, with the occasional presence of *Potentilla* type, *Drosera rotundifolia* type and *Sphagnum*. Although the pollen spectrum from the *Erica tetralix - Sphagnum* nodum (sample 28) does have significantly less *Calluna* pollen than do those from the *Calluna vulgaris - Eriophorum angustifolium* nodum it is dominated by *Betula* pollen (>40%). This is surprising as only small birch woods are present within 1 km of the site, whereas the loch nearest to one of these birch woods has <15% *Betula* pollen (sample 24). In addition, there is less than 5% *Sphagnum* present in the sample which therefore is not really accurately representative of the treeless *Calluna vulgaris - Sphagnum* nodum.

The constancy and abundance of *Calluna vulgaris*, *Myrica gale*, and *Sphagnum* characterise the *Trichophorum cespitosum - Myrica gale* nodum. The pollen spectrum is represented by >20% *Calluna* and constant but low values of Gramineae, Cyperaceae and *Sphagnum*. Both *Myrica gale* and *Sphagnum* sp. appear to be under-represented. The intermittent presence of *Potentilla* type, *Drosera rotundifolia* type, *Melampyrum, Succisa* and *Pedicularis* are characteristic of acid bogs whereas *Plantago lanceolata, Bidens* type and a single grain of *Secale* may indicate disturbance, the local presence of grassland areas around streams or the local cultivation of cereals.

The *Calluna vulgaris* nodum is distinguished from the *Trichophorum cespitosum - Myrica gale* nodum by the replacement of *Molinia caerulea* by *Myrica gale*. The pollen spectra are very similar to those found to be representative of the *Trichophorum cespitosum - Myrica gale* nodum except that *C. vulgaris* is always found at values of <20% in this nodum compared with >20% in the *C. vulgaris* nodum. As *Molinia caerulea* can not be separated from Gramineae pollen, and because *Myrica gale* is usually present at low pollen percentages in surface samples from both of these noda, the pollen spectra from these two noda cannot be separated.

The *Calluna vulgaris - Cladonia impexa* nodum is characterised by the constancy of *Cladonia impexa, Erica tetralix, Hypnum cupressiforme* and *Trichophorum cespitosum*. Obviously neither *C. impexa* nor *H. cupressiforme* can be recognised as pollen taxa. The pollen spectrum is represented by only one sample that is overwhelmingly dominated by *Calluna vulgaris* (>70%) with only small percentages of Cyperaceae and Ericaceae undif. pollen (<5%). This suggests that the *Calluna* dominated understorey has only recently been replaced by the wetter *Erica tetralix - Trichophorum cespitosum* dominated community. This hypothesis was substantiated by the presence of dead and dying bushes of *Calluna vulgaris* around this site.

Pollen spectra from willow scrub

A note should perhaps draw attention to samples 20 (Lochan Chuibhe) and 10 (Loch Rosail). These samples are not grouped under *Salix* scrub on Fig. 3.10 as their pollen catchments are predominantly treeless. Both of these samples were taken from small lochs that contained wooded islands dominated by *Salix* sp. and *Betula pubescens*. However, at both of these sites, *Betula* and *Salix* pollen is found at low frequencies. This apparent under-representation may be because either their pollen catchments are predominantly treeless or because these senile *Betula* and *Salix* trees are poor pollen producers. The pollen percentages found for *Salix* are comparable with those found by Birks (1973a) in moss polsters taken from *Salix lapponum-Luzula sylvatica* scrub in north-western Scotland. The presence of prostrate forms of *Juniperus communis* ssp. *alpina* near to Lochan Chuibhe is also under-represented in the pollen spectrum, perhaps because of their growth form and flowering characteristics (Birks, 1973a).

This very subjective and somewhat crude interpretation of the relationship between pollen spectra and plant communities suggests that whereas broad ecological groups (eg. grasslands, birch woods, and dwarf-shrub heath and bog) can be distinguished using pollen spectra, individual noda can not be reliably separated within these groups. These results are consistent with other studies (Birks, 1973a, 1973b, 1980a; Prentice, 1986, 1988). The reasons for the comparative "inaccuracy" in pollen surface samples are partly the complex interaction of factors that affect pollen representation and partly these lochs are surrounded by a mosaic of vegetation types preventing them being easily characterised by a single phytosociological community. The resolution of the vegetation description and of pollen data will remain at different orders of magnitude until improvements in palynological techniques enable pollen taxa to be more frequently identified to species level (eg. areas dominated by different Cyperaceae cannot be identified) and pollen representation factors to be determined more precisely.

3.4.4 The numerical classification of the pollen spectra

In the preceding section the pollen surface samples were grouped subjectively according to the noda that they were derived from. The pollen spectra will now be grouped objectively using numerical procedures. If these two classification systems are similar then this would suggest that modern pollen spectra can be reliably compared to fossil pollen spectra (Birks, 1973b).

As the pollen surface samples are not in stratigraphic order they can not be zoned in the conventional manner into assemblage zones using programs like CONSLINK, SPLITLSQ, and SPLITINF (Gordon and Birks, 1972). TWINSPAN or two-way indicator analysis (Hill, 1979b) is a method of classification that assumes no stratigraphic constraints and DECORANA or detrended correspondence analysis attempts to display the groups or pattern in the data (Hill, 1979a); both methods are therefore ideally suited to objective classification of, or examination of the patterns amongst, the surface samples (Grimm, 1988).

The surface sample data were classified and ordinated using TWINSPAN (Hill, 1979b) and DECORANA (Hill, 1979a) respectively, based on thirteen taxa namely: *Pinus, Alnus, Betula, Betula/Corylus/Myrica/, Corylus,* Ericales, *Calluna, Myrica,* Gramineae, Cyperaceae, *Sphagnum,* Filicales, and *Pteridium.* TWINSPAN distinguished seven groups (Fig.3.18) that clearly discriminated between: inland and coastal vegetation types; coastal-plateau and coastal-valleys; inland valleys where birch is and is not locally present.

The ordination plots (Fig. 3.19a) show a clear separation between: the coastal and inland groups; and the plateau and lowland groups. However, the inland areas where birch is locally present could not be separated from those areas where birch is not locally present. The species by species plot for axes 1 x 2 illustrates that plateau and lowland areas have been separated by the presence of birch and alder whereas the coastal sites are distinguished by a high percentage of grasses, sedges and spores (Fig. 3.19b).

The pollen classifications based on both the phytosociological communities and the TWINSPAN and/or DECORANA give broadly similar results with birch, grassland and dwarf-shrub heath and bog communities being recognised. No reliable sub-division of these communities can be made using either numerical or subjective techniques to separate them into different noda. These results are similar to those found by Birks (1973b).

3.5 The pollen vegetation relationships

In order that the fossil pollen data could be interpreted in terms of plant communities an assessment was made of the relationship between the surface pollen spectra and vegetation composition. Vegetation cover was estimated using the Thematic Mapper image.

The location of each surface sample was marked on the Thematic Mapper image and the percentage of colour cover assessed using the Domin scale at 0.5, 1.5 and 2.5 km radii from the centre of the loch. Each Thematic Mapper colour was then assigned a vegetation class. This process was somewhat subjective, the colours being interpreted in relation to the known vegetation cover wherever possible.

The next step in quantifying the relationship between percentage vegetation cover and the surface pollen spectra was to produce a series of scatter plots that illustrate the percentage vegetation cover and the percentage total land pollen cover for each site (2.5km radius). Least-squares regression lines were then fitted for the following groups: *Pinus, Betula,* Gramineae, *Calluna*, *Pteridium* and Cyperaceae and Fig 3.20 (a-d inclusive) shows the scatter plots and least-squares regression lines for the first four of these taxa. The scatter on each of these plots is large, and is expressed by the value of Pearsons's Product Moment Correlation Co-efficient or "r". The correlation co-efficient is significant only for Gramineae (Table 3.20). Well-grazed areas are easily distinguished on the Thematic Mapper image and have a high probability of being correctly assigned. Although Gramineae pollen reflects the percentage of estimated vegetation cover, the value of r^2 suggests that only 34% of the variation is accounted for by the trend. Care must therefore be taken when interpreting the distribution of Gramineae dominated areas from pollen data.

The correlation between percentage vegetation cover and percentage total land pollen is not significant for the other taxa considered namely *Pinus*, *Calluna*, *Betula, Pteridium,* and Cyperaceae. The reasons for this include: only 31 surface samples were used which is a small sample and therefore more likely to give a wide range; spore-producing plants that are only locally distributed, for example, *Pteridium*; poor estimation of the percentage vegetation cover from the Thematic Mapper image as some vegetation types are not clearly distinguished from other communities, for example *Pteridium* and *Betula*, resulting in either over or under-estimation of the vegetation cover. Pollen percentages also depend upon the size of the pollen catchment and this is related both to the lake size (Prentice, 1988) and to its geographical position in the landscape. For example, Loch Mer (No. 21), is a large loch (400 m x 87 m) with woodland along one side, with the result that its main pollen input comes from within 2.5 km radius. However, Loch Chealamy (No. 22) is a small loch (125 m x 75 m) surrounded by woodland, as a result its main pollen input comes from within 50 metres of the water's edge. Without specifically adjusting the percentage vegetation cover estimates to relate to pollen catchment size there will always be bias in figures of this kind.

Although there is a poor relationship between the percentage of total land pollen and estimated vegetation cover, a few conclusions can be drawn from the scatter diagrams: Gramineae values reflect percentage vegetation cover of grasses; high *Betula* values only occur at sites where woodland surrounds the loch; *Betula* is only locally present in the Strathnaver catchment and this is reflected in generally low *Betula* pollen values; the intercept of the regression line is significantly lower for *Betula* than that found in western Scotland (Birks, 1980a) and suggests that either pollen production is suppressed near the potential treeline or else that these predominantly senile woodlands are poor pollen producers; *Calluna* appears to be the most prolific pollen producer of the taxa considered. The results from the surface sample survey indicate that *Betula-*, *Calluna-* and Gramineae-dominated communities can be distinguished.

3.6 Summary

1. Using the techniques of continental phytosociology 25 noda were recognised and described in 6 broad categories: birch woods, pine woods, alder woods, willow scrub, dwarf-shrub heaths and bog, and grasslands.
2. A Thematic Mapper image was ground truthed and the results used to construct a probability table for obtaining a given Thematic Mapper colour from a given nodal class.
3. A series of isopoll maps show the main geographic patterns in the surface sample data and enabled a comparison with the present distribution of vegetation.
4. The surface pollen spectra were subjectively related to the noda they were derived from before being classified objectively using numerical techniques. Both methods gave similar classifications.
5. The relationship between the percentage vegetation cover (using estimates derived from the Thematic Mapper image) and the pollen abundance values in surface pollen spectra was assessed using Pearson's Product Moment Correlation Co-efficient.

CHAPTER 4

The Holocene vegetation history of northern-most central Scotland

4.1 Background: The Holocene vegetation history and climate of northern Scotland.

Pollen-stratigraphic and, in some cases, radio-carbon evidence have been used to reconstruct the vegetation history of at least 23 sites in northern Scotland (Fig. 4.1). The vegetation history of the area is complex and is summarised by Birks (1977a). Essentially, in Sutherland, woodlands dominated the landscape from between 10,000 and 9,000 B.P. until 4,000 B.P., whereas in Caithness no extensive woodland ever developed. A series of pie-diagrams have been drawn to display the pollen percentage values of pine, other woody, herbaceous and heath taxa for 0, 2000, 4000, 6000, and 8,000 B.P. for 8 sites in northern Scotland (Fig. 4.2). Figure 4.2 shows that woodland either dominated or played a significant role in the landscape in Sutherland and Orkney between 8,000 and 4,000 B.P.. Open herbaceous vegetation dominated throughout most of this time in Caithness and on the island of Lewis. By 2,000 B.P., these predominantly grassland communities had in part been replaced by the development of blanket bog communities. Surprisingly, woodland increased in importance at An Druim between 4,000 and 2,000 B.P., whereas it declined at nearly every other site in northern Scotland. Between 2,000 B.P. and the present day there has been a clear reduction in the woodland cover at nearly all sites, accompanied by an increase in the percentage of open grassland, moorland and blanket bog communities.

Figure 4.1 illustrates eight *Pinus sylvestris* and accompanying Ericales or *Calluna* pollen curves for northern Scotland. The following conclusions emerge with respect to the pine (*P. sylvestris*) phase in northern Scotland:

1. Pine never colonised the islands off-shore of Sutherland or Caithness.
2. Pine grew extensively in the Loch Maree area between 8,000 and 4,000 B.P.
3. Pine was present at Coire bog between 7,000 and 5,000 B.P. but became locally extinct for 200 years in the middle of this period between approximately 6892 and 6731 years B.P..
4. Elsewhere in north-western Scotland the pine phase was "transitory", occupying a relatively short period of time between 6,000 and 4,000 years B.P. (Moar, 1969a), although Loch Sionascaig and Suisguill form exceptions to this rule. Pine was still dominant at both Loch Sionascaig and Suisgill sites, at 2,000 B.P. whist being absent elsewhere, suggesting that relict pine communities were able to persist in isolated areas until 2,000 years B.P..

5. If Bennett (1984) and Birks (1988) were correct in basing their conclusions upon the two pollen-analytically studied lake sites of Lochan An Druim and Loch of Winless, then pine was never an important component of the vegetation history over most of central-northern Scotland and Caithness. This, however, is at variance with the macro-fossil evidence for central-northern Scotland (Bennett, 1984).

4.2 Methods

4.2.1 The values and limitations of the palynological investigation

Previous studies have demonstrated marked differences between the forest histories of north-west (Birks, 1977a) and north-east Scotland. The general aim of the present study is to document the forest history of the intervening area, central-northern Scotland. A palynological study of two enclosed lake sites, namely Loch Mer and Lochan by Rosail, was the first step in achieving this aim. These two sites are presently located in quite distinct geographical environments but are both located in predominantly treeless areas. By studying their Holocene vegetation histories it was hoped to increase our knowledge of the spatial distribution and composition of the woodlands in this area. The study of the former distribution of tree-limits is known as palaeo-treeline reconstruction.

Whether or not pollen analysis can be considered to be a useful tool in palaeo-treeline reconstruction depends on the spatial, temporal and floristic-resolution it can provide and the available alternative methods. Fossil pollen grains and spores may provide some indication of the species composition and treeline fluctuations in altitude and latitude, but there are many factors that influence pollen production, transport, sedimentation and preservation. Changes in treelines can take at least two forms namely: 1. spatial displacement of the boundary between woodland and treeless vegetation without any change in the species composition and relative abundance of taxa in the two communities; 2. changes in species composition and/or abundance of taxa in the woodland community forming the treeline. Often both 1 and 2 occur together (Huntley, 1988; Huntley and Webb, 1989).

The spatial distributional limits of tree species can take several forms depending on the scale under consideration:

1. An altitudinal tree-limit, either abrupt or diffuse from dense tall stands, through scattered isolated trees to stunted individuals (Tranquillini, 1979). That is, scattered or continuous woodland may occupy lowland, but trees are absent from hills and/or mountain peaks.

2. Latitudinal or longitudinal tree-limits, either sharp or diffuse, from one dominant tree species to another, or from areas with trees to areas where trees are absent.

Species composition and relative abundance at individual points in time and space are influenced by environmental and biotic factors. Changes in species composition and relative abundance can be considered to occur on at least two scales: 1. community cycles occur over short timescales, usually following disturbance by an allogenic process, and result in the re-establishment of the original community (by regeneration) following the disturbance phase, eg. the short-lived formation of gaps or clearings in a forest canopy and the subsequent closure of the gap by means of regeneration; 2. community succession is considered to be a uni-directional process whereby one community is replaced by another community, eg. the development of a pine forest on a previously treeless blanket bog.

The extent to which any of these boundaries can be detected depends on the sensitivity of the "sensor" being used. If pollen analysis can be considered as a sensor (Prentice, 1988), then its sensitivity is related to the size of the pollen source area, that is in turn dependent upon the dispersal efficiency of individual pollen grains and site size (Jacobson and Bradshaw, 1981; Jacobson, 1988; Prentice, 1988). For small lake sites, the majority of the pollen rain is obtained from the surrounding 1-2 km (Jacobson, 1988), although pollen grain size, shape, weight, dispersal mechanism and the height from which the pollen grain is released all influence the distance travelled by individual grains. In addition, the size of the pollen source area for an individual site changes with plant succession (Andersen, 1970; Jacobson and Bradshaw, 1981). Pollen source area is much larger for treeless late glacial sites than when a closed canopy formed during the succeeding post glacial period.

Many other factors influence pollen representation and include times of flowering, plant density, flowering success, pollen predation, morphological, physical and environmental conditions of the parent plant, as well as an array of factors that influence sediment focusing and preservation. These include annual variations in water density, wind speed and direction and bioturbation (Moore and Webb, 1978). As a result we "*cannot distinguish between a few individuals* (eg. pine trees) *near the pollen site and many individuals at a greater distance*" (Jacobson and Bradshaw, 1981 p.83).

Pollen source area varies with basin size, time, place and even between individual tree species whose pollen grains are differentiated by weight or aerodynamic properties. Thus, Jacobson and Bradshaw's (1981) claim that site size and characteristics determines the size of the pollen source area should be treated with caution (Prentice, 1988). However, having considered the limitations of their work, their advice (the best available for the purposes of the present study) on site size and characteristics was used as a general guide when selecting sites.

Lake sites were chosen in preference to peat deposits because the aim of this part of the study was to reconstruct Holocene regional/local environmental change. Peat deposits are not ideal for palaeoenvironmental reconstruction on either of these time or spatial scales. Peat deposits often offer only a relatively short palaeoenvironmental record in comparison with lake deposits. Hiatuses may occur in both peat and lake records during warm, dry phases, but they are generally more likely in peat deposits. Furthermore, it is easier to separate the contribution of local pollen in lake sites because of the morphological distinctiveness of the pollen of aquatic plants. Thus lake deposits often provide long, continuous records of regional vegetation fluctuations.

The criteria used to select limnic sites included the loch's geographical and geological position, size and nutritional status and anthropogenic influence. The lochs had to be between 10^4 and 10^5 m^2 or smaller if they were to represent a basin size of between 0.01 and 0.05 km^2 (Jacobson, 1988). Loch depth was an important secondary consideration because lochs that were deeper than 9 metres would necessitate the building of a raft for coring in order to operate a hoisting device. Eutrophic and calcareous lochs were specifically excluded, as were lochs that appeared to suffer from serious erosion whether natural or anthroprogenic. Using these criteria, two lake sites were chosen (Fig. 4.3), one in the river valley near the coast (Loch Mer) and the second inland on the plateau (Lochan by Rosail). It was hoped that this combination of sites would enable a comparison of the woodland histories of these two geographic areas, giving some insights into both the general woodland history of central-northern Scotland and into fluctuations in palaeo-treelines during the Holocene.

4.3 The sites

4.3.1 Loch Mer

4.3.1.1 Site description and sediment lithology

Loch Mer is situated at the mouth of Strathnaver (O.S. reference NC 703600). This loch is long and narrow being approximately 400 x 87 metres (Fig. 4.4a). Along the eastern side of the lochan lies a steep scarp slope that shields the lochan from north-westerly winds. Inflow during the summer months is via seepage from the fen, located to the south of the loch, and from a tiny stream off the scarp face. The outflow is from a small, slow moving stream located to the north of the loch. Fig. 4.4b shows the dominant vegetation of the area surrounding Loch Mer. The coastal outline was drawn from the 1:25,000 Ordnance Survey maps and the vegetation communities plotted from the Thematic Mapper image (with the exception of the location of the birch woodlands that were located with the 1:25,000 Ordnance Survey maps). Because of the difficulties of reliably assigning noda to Thematic Mapper colours the vegetation has been grouped into 4 broad categories: birch woods, grasslands, dwarf-shrub heath/bog and willow scrub. (It should be noted that there are a small number of alder/willow woods located along the river Borgie that cannot be precisely mapped from either the Thematic Mapper image, nor the Ordnance Survey maps and have therefore been omitted). It is believed that these categories are reflected reasonably well by the pollen record (see previous chapter) and therefore are vegetational units that may be directly compared with the surface pollen spectra.

Grassland communities dominate the river valleys and lowland coastal areas surrounding Loch Mer, whereas dwarf-shrub heath/bog blankets the plateau and shallow peaty soils near the coast. Along the eastern and southern sides of the loch are a number of small moderately dense *Betula pubescens* woods. The bed of the loch itself is partly covered with vegetation including *Isoetes* sp., *Littorella uniflora* and *Lobelia dortmanna*.

The core was collected from the deepest part of the loch using a 5 cm diameter Livingstone corer (Wright, 1967) in October 1986, from below 3 metres of water. To obtain the superficial unconsolidated sediments a 5 cm diameter perspex tube surface sampler was used and the samples extruded at 1 cm intervals into self-sealing polythene bags (Birks and Birks, 1980). The cores were double wrapped in film-wrap and aluminium foil to conserve moisture and exclude light and stored in a cold room at 4^0 C.

Sediment stratigraphy was described using the method advocated by Troels-Smith (1955). The water content of the samples was determined by drying samples in an oven at 105^0 C for 24 hours. The organic and carbonate content was obtained by placing the samples in a muffle furnace at 550^0 and 1000^0 C respectively for 24 hours. Water loss was calculated as a percentage of fresh weight, and organic and carbonate loss are expressed as a percentage of dry weight.

Fig. 4.5 records the sedimentological and chemical records for Loch Mer. The profile is an almost uniform, homogeneous sediment dominated by Ld 4 from 3 to 11 metres. From 8 to 9.2 metres the sediment stratigraphy is more complex, a number of thin organic layers being interstratified with sandy laminations. This is reflected in marked fluctuations in water and organic loss of the sediments.

Pollen samples were prepared and counted in the way described in chapter 3 (Fig. 4.6a). All the pollen and sedimentological diagrams throughout the thesis were plotted using POLLDATA.MK5 (Birks and Huntley, 1978). All herb and tree taxa were calculated as a sum of total land pollen excluding spores (when the total percentage of spores was >5% total land pollen) and aquatics that were calculated as a percentage of the total land pollen plus spores.

Charcoal analysis was carried out on the residues remaining after seiving following the NaOH digestion of the pollen samples. The supernatant was passed through a 0.214 mm sieve and the residue washed into a petri-dish. The residues were examined using a stereo microscope (X12 and X50) and all the macro-fossil remains were identified and the total number of charcoal particles for six x 1 cm^2 squares were classified into two groups - particles whose longest axis was >2mm versus those <2mm. The results are expressed as the total number of charcoal particles of each class counted per 6 cm^2 (Fig. 4.6a).

Eight radiocarbon determinations were made upon bulk sediment samples from the core by D.D. Harkness at the Natural Environmental Research Council Laboratory, East Kilbride, Scotland. The dates are presented in tabular form (Table 4.1), as well as being indicated on the left of the pollen diagram (Fig. 4.6a).

4.3.1.2 The Holocene vegetation history of Loch Mer

The pollen diagram from Loch Mer extends to at least 7,920 years B.P. although the anomalous lowermost dates leave in doubt the timing of the initial colonisation of the area by juniper-scrub and birch-hazel woods. A detailed discussion of the initial post-glacial colonisation of this area must therefore be left until further investigations have been carried out.

To aid interpretation and discussion of the pollen diagram (Fig. 4.6a) it was divided into a series of pollen zones. A pollen zone is here defined as a number of adjacent levels whose fossil pollen and spore content is distinguished from those of adjacent zones by major differences in pollen taxa and their relative abundance. The pollen and sedimentological diagrams were first visually inspected and divided into the 4 pollen zones. In order to objectively assess the position of these zones a number of numerical techniques were also used. Different numerical techniques, although providing quantitative methods of zonation, gave varying results (Grimm, 1988). As a result several techniques were used including:

1. CONSLINK or constrained single-link cluster analysis (Gordon and Birks, 1972)
2. SPLITINF or constrained divisive analysis using information content (Gordon and Birks, 1972)

3. SPLITLSQ or constrainded divisive analysis using sum of squares deviation (Gordon and Birks, 1972)
4. DECORANA or detrended correspondence analysis (Hill, 1979a)

All four of these methods have been frequently used by palynologists (eg. Gordon and Birks, 1972; Birks, 1974; Birks, 1986; Birks and Berglund, 1979; Jacobson and Grimm, 1986; and Stevenson, 1984) and will not be described in detail here.

Methods 1 to 3 (inclusive) are based upon a maximum of 18 taxa and constrained so that clusters only contain stratigraphically adjacent clusters, whereas method 4 can utilise data from all taxa and groups together with similar pollen samples irrespective of their stratigraphic position. Methods 1 to 3 (inclusive) applied using the following 18 taxa: *Betula, Alnus, Pinus, Ulmus, Corylus, Salix, Juniperus, Myrica, Calluna,* Gramineae, Cyperaceae, *Pteridium, Polypodium,* Filicales, *Dryopteris, Isoetes echinospora, Isoetes lacustris* and *Sphagnum.* Method 4 was applied using all 99 taxa.

2 of the 4 pollen zones were subdivided into 3 and 2 sub-zones respectively on similar but more minor criteria. Although, the lowermost dates are anomalous they suggest that colonisation of the site by juniper and herb-rich grassland communities was unlikely to have occurred after 8,000 B.P.. Table 4.2 documents the macro-fossil records from Loch Mer in relation to the pollen zones.

The lowermost sample in LM-1 is characterised by a brief phase of high values of *Juniperus* pollen and moderate values of *Corylus, Betula, Salix* and a number of herbaceous taxa including *Potentilla* type, *Ranunculus* type, *Galium* type, *Thalictrum* type and *Pedicularis.* Spores include *Pteridium, Osmunda, Dryopteris filix-mas* type and *Gymnocarpium dryopteris.*

The other 4 samples included in LM-1 have a similar overall composition although they lack the abundance of juniper found in the lowermost sample. There is a peak in birch pollen values together with low values of pollen taxa that are characteristic of open grassland communities eg. *Artemisia, Cirsium, Plantago lanceolata* and *P. maritima.* A wide range of the spore-producing taxa were found including *Cryptogramma crispa, Lycopodium clavatum, Lycopodiella inundatum* and *Polypodium.* Low pollen concentration, poor pollen preservation and highly minerogenic sediments made accurate recording difficult and time consuming.

These pollen spectra are interpreted as representing a treeless landscape where dwarf-shrubs, herbs and ferns dominated with the local presence of birch-hazel woods and willow scrub, perhaps along the water courses.

LM-2 is distinguished from LM-1 by the rise in arboreal pollen as *Betula* and *Corylus* come to dominate the pollen spectra attaining values of >20% and >10% respectively. *Juniperus*, *Polypodium*, *Drypoteris* pollen and spores are consistently found throughout this zone. A number of rare pollen and spores are occasionally found in this zone and include: *Prunus* type, *Empetrum*, *Triglochin* and *Botrychium*.

These pollen spectra are interpreted as reflecting the development of a birch-hazel wood. *Prunus padus* is typically under-represented in the pollen spectra (Birks, 1973a) and therefore the occasional grain of *Prunus* type suggests that *P. padus* may have been present in the *Betula-Corylus* canopy. *Juniperus* may have formed an understorey to the birch wood together with herb-rich communities which included a number of ferns eg. *Polypodium* and *Drypoteris*. *Salix* scrub probably occurred along water courses and *Juniperus communis* subsp *communis or Juniperus communis* subsp *alpina* may have formed a shrub heath over considerable areas of this coast. *Empetrum*, *Triglochin* and *Botrychium* pollen grains and spores are only occasionally found in the fossil pollen spectra from northern Scotland and probably represent the local presence of these taxa. *Botrychium lunaria* and *Triglochin maritima* occur today on base-rich soils which are only found along the coast in this area. This may suggest that either the coast line was higher than today or that wind blown calcareous deposits were locally present.

LM-3a is dominated by high *Betula* pollen values and is characterised by an abrupt rise in arboreal pollen, notably *Alnus* to values >5%. This is accompanied by a reduction in the pollen values of *Ulmus*, *Salix*, *Juniperus*, *Calluna* and herbaceous taxa. *Juniperus*, *Sorbus* and *Prunus* type pollen is intermittently present at low values within this zone. There is a peak in *Pinus* pollen within this zone that lies between 4,500 and 3,500 B.P., but pollen values are always <20%.

This suggests that the area was dominated by birch-hazel woodland with the occasional presence of *Sorbus aucuparia* and *Prunus padus* possibly with an understorey of *Juniperus*. There are a number of taxa indicative of base-rich soils including *Plantago coronopus*, Chenopodiaceae and *Botrychium*. The low *Pinus* pollen values probably indicate that *P. sylvestris* did not grow locally within the catchment.

Pollen zone LM-3b is characterised by the abundance and constant presence of *Betula*, *Alnus*, *Corylus* and an increase in the abundance of *Calluna* and Gramineae compared with the previous zone. *Pinus*, *Salix*, *Alnus* are found at low pollen values. *Salix* and *Juniperus* pollen are intermittently present.

This suggests that between 3,500 and 2,900 B.P. the landscape was occupied by a mosaic of communities with *Salix* and *Alnus* growing in the wetter hollows and/or along stream sides; *Juniperus* scrub-heath along the calcareous rich coastal soils; *Calluna*-heath along the drier peaty soils; and grassland communities probably along the coastal margins.

LM-3c is distinguished from LM-3b by a decline in *Betula* pollen values from consistently >25% to consistently <25% and a rise in the abundance of dwarf shrubs and herbs notably *Calluna*, Gramineae and Cyperaceae. *Betula, Corylus* and *Alnus* still dominate the arboreal pollen spectra together with the occasional occurrence of *Populus tremula*. The frequency and occurrence of *Salix, Juniperus* and *Crataegus* type (which can include poorly preserved grains of *Sorbus aucuparia*) pollen does not appear to differ markedly from that found in LM-3b. A wide range of herbaceous pollen taxa are present within this zone including: *Artemisia, Filipendula, Plantago lanceolata, P. coronopus, Potentilla* type, *Succisa, Stellaria holostea, Knautia* type *Hordeum* type and *Cerastium* type.

Birch still dominated the canopy cover together with the presence of alder, probably along the lochs-side or along water courses. *P. tremula* is usually under-represented in pollen spectra and is difficult to relate to cover (Birks, 1973a); *P. tremula* is found on rock ledges and cliffs on Skye (Birks, 1973a) and rarely in the woods of Strathnaver, but was found at low pollen values in Skye and not at all in the surface pollen spectra from Strathnaver. This suggests that *P. tremula* may have been present in clearings in the birch-hazel woods. The intermittent presence of *Hordeum* type grains may indicate the local cultivation of crops between 2,900 and 2,600 years B.P.. However, as a number of the Gramineae species that fall within this category are wild grasses and not cultivated species (Andersen, 1978), and because their is little other evidence from the pollen diagram that might indicate cultivation this interpretation must remain speculative.

Between 2,600 and 1,830 B.P. (zone LM-4a) arboreal pollen declined as *Betula, Alnus* and *Corylus* pollen frequencies declined. *Betula* and *Corylus* pollen values remain at >20% and >10% respectively. There is an isolated occurrence of *Ilex*. The herbaceous pollen taxa are very similar to those found in LM-3c, although less frequent and wide ranging. The herbaceous pollen taxa include: *Plantago major, P. coronopus, P. lanceolata, Filipendula, Potentilla* type, *Rumex* undif., *Succisa, Ranunculus* type, Caryophyllaceae undif. and Chenopodiaceae.

This zone is interpreted as representing a gradual reduction in the area covered by woodland as the blanket bog and grassland communities expanded. *Betula* was still the dominant canopy species in the woods interspersed with varying proportions of *Corylus*. *Salix* pollen was almost absent during this zone and may/may not have been present within the catchment. *Ilex aquifolium* was probably growing as an understorey species within the birch wood as it does occasionally today in northern Scotland. A number of ferns and club mosses probably grew along the lake shore including *Polypodium vulgare, Pteridium aquilinum, Lycopodium clavatum* and *Selaginella selaginoides*. The presence of *Juncus* seeds suggests that *Juncus* sp. were growing locally in wet hollows or beside streams. Both the pollen and macro-fossil evidence show significant rises in the abundance of *Isoetes lacustris* together with pennate and elliptical diatoms. This probably indicates a change in the productivity of the loch which may be either due to a rise in water temperature or a decline in the nutrient or base status of the loch.

After 1,830 +/- 70 B.P., during LM-4b, arboreal pollen falls again to lower levels as the pollen values of *Betula* decline and those of *Calluna,* Gramineae, Cyperaceae and *Juniperus* increase. The proportion of *Betula* to *Corylus* pollen varies significantly through this zone. The herbaceous pollen include: Compositae Subfamily Tubuliflorae undif., Compositae Subfamily Liguliflorae undif., *Artemisia, Cirsium* type, *Filipendula, Plantago lanceolata, Potentilla* type, *Succisa, Ranunculus* type, *Sinapis* type, Umbelliferae type 2 (possibly *Conopodium majus*), *Knautia* type, *Bidens* type (possibly *Bellis perennis* or *Solidago*) *Rumex acetosella, Oxyria* type (possibly *Rumex* spp.), *Thalictrum* type and *Hordeum* type.

The areas covered by grassland, dwarf-shrub heath and blanket bog communities continued to expand during this zone, while birch-hazel woodland remained locally present, although the proportion of birch and hazel in the tree canopy probably varied over this time. Relatively recently *Betula* came to dominate the canopy with a small proportion of *Corylus*. The herbaceous pollen taxa are characteristic of fields and the field layer of woods on acid soils, although, as it has already been discussed in chapter 3, it is very difficult to relate pollen spectra to the field layer communities of woodlands. *Alnus* and *Salix* communities were probably found along stream sides and in wet hollows throughout this zone as they are today. *Juniperus*-heath grows extensively on the plateau above Loch Mer and the decline in birch woodland may have enabled an increase in the transport of *Juniperus* pollen to Loch Mer, without there being an increase in the spatial extent of *Juniperus communis* on the plateau.

Isoetes echinospora and *I. lacustris* pollen is found in abundance in zone LM-4b, together with the presence of *Nymphaea, Myriophyllum spicatum* and *M. verticillatum* pollen taxa. This suggests that lake productivity was similar to that found in the previous zone.

The pollen influx diagram (Fig. 4.6b) for Loch Mer shows that there was a rapid rise in the sediment accumulation rate between approximately 3,500 and 3,250 years B.P. and again between approximately 3,000 and 2,750 years B.P. Surprisingly, there is no change in the sediment stratigraphy that relates to this period with the exception of a decline in the percentage of carbonate loss. This may suggest that overland- and through-flow have increased resulting in a "diluting" of the available carbonate material. The timing of this greatly increased accumulation rate is after the extinction of pine from northern Scotland and indicates a change in the evapo-transpiration balance of the catchment. As the pollen samples were taken at regular intervals down the core, the rapid accumulation rates, between 900 and 500 cms, have resulted in over half the pollen samples being located in the 1,000 year period between 3,500 and 2,500 years B.P. This unfortunately results in the time interval between samples being very variable, which results in difficulties in calculating fire-index estimates.

Fire-frequency estimates for Loch Mer are based on 8mm wide samples with varying inter-sample distances. The available radiocarbon dates enable the calculation of sediment accumulation rates in terms of cm. yr^{-1} (Table 4.1). The results show that 1 cm of sediment can represent between 3.95 and 45.10 years. In addition the time interval between adjacent samples varies between 12 and 721 years. This will result in fire frequency being greatly under-estimated and the charcoal curve varyingly smoothed along its length. Whilst bearing these points in mind, fire frequency has been crudely estimated for Loch Mer using a series of fire indices. A fire is considered to have occurred locally if charcoal particles >2mm are found. This is based on Clark's (1988a) work, that suggests that charcoal particles >0.2 mm are unlikely to have travelled >50 metres from their source.

The fire indices were calculated as follows:

Probability of a sample containing evidence of a fire (P_F):

$$P_F = S' / S$$

where, for pollen zone x:

S' is the number of samples that record >2mm charcoal and

S is the total number of samples.

Fire index 1:

$$F_1 = {}_{i=1,S'} \Sigma C_i / T$$

where, for each sample i:

C_i represents the number of charcoal particles >2mm and

$$T = {}_{i=1,S} \Sigma t_i \times (P / L)$$

where:

t_i is sample thickness in cm,
P is the number of years that a pollen zone spans and
L is the length of the zone in cm
(ie. P / L = the accumulation rate in $yr.cm^{-1}$).

Fire index 2:

$$F_2 = S' / T$$

(ie. S' / T = the number of fires per year).

Of these fire indices F_1 is the most appealing theoretically, as it takes into account both sample thickness and the accumulation rate, therefore enabling estimates of fire frequency to be more "realistic". P_F and F_2 are tentative estimates of the maximum and minimum number of fires per pollen zone. There are theoretical limitations with all these fire indices and only consecutive samples from varved sediments can over come these problems. The fire indices in turn cannot be readily interpreted as estimates of fire frequency, as C_i may relate to fire frequency, fire intensity, distance from fire source or wind direction. Caution must therefore be used when interpreting the fire indices.

The fire indices appear to have changed considerably over time. Between 8330 and 8000 years B.P. (LM-1) mean fire index (F_2) was a minimum of 0.06, with local fires being recorded in 40% of samples. Between 8,000 and 5,500 (LM-2) years B.P. the fire index (F_1) appears to have increased. However, this figure conceals the fact that the fire index was high between 7,920 and 7,730 years B.P., with local fires being recorded in every sample, while between 7,730 and 5,500 the fire index was very low. Between 5,500 and 3,500 years B.P. (LM-3a) no local fires are recorded. Between 3,500 and 2,500 years B.P. (LM-3b) local fires are recorded in 30% of the samples found in this zone. Between 2,900 and 2,600 years B.P. (LM-3c) and 2,600 and 1,830 years B.P. (LM-4a) the fire indexes (F_1) increase respectively, although the probability of fires being recorded declines during LM-4a. No local fires are recorded between 1,830 and 0 years B.P. (LM-4b).

Whilst admitting that both inter-sample ages and sedimentation rates vary enormously between samples, these figures do give some idea of the changes in fire indices over the past 8,000 years at Loch Mer. The inaccuracies of this data set make direct comparisons with other work very difficult, although they are comparable with figures presented by Robinson (1987) for north-eastern Caithness. The charcoal curve for Caithness has a number of similarities with that obtained from Loch Mer. In essence the charcoal diagram from north-eastern Caithness shows:

1. The most intense fires and the greatest number of microscopic charcoal particles (<2mm) are found at the base of the profile between 8,000 and 7,800 B.P.
2. Fire indices were generally low between 7,800 and 5,500 years B.P. although there may have been a number of fires around 6,500 years B.P.
3. Between 3,500 and 1,000 years B.P. fire frequency increased.
4. Since 1,000 B.P. few, if any, local fires are recorded.

Fire indices in both north-eastern Scotland and at Loch Mer appear to be broadly similar (Table 4.4):

1. High fire indices occur in both areas between 7,900 and 7,700 years B.P., perhaps suggesting that the most intensive and frequent fires occurred in both these areas between 7,900 and 7,700 years B.P.
2. A notable decline in fire indices between approximately 7,800 and 3,500 years B.P., perhaps suggesting a decline in the fire frequency and intensity during this period.
3. An increase in fire indices between 3,500 and 2,685 years B.P.
4. Very low fire indices frequencies and intensities between 1,000 and 0 years B.P., perhaps suggesting a decline in fire frequency and intensity.

The major difference between the fire histories of north-eastern Scotland and Loch Mer seems to be that the decline in fire index appears to begin earlier at Loch Mer (2,685) compared with Ackhorn (1,000 B.P.).

The occurrence of high fire indices in two quite distinct geographical areas suggests that the occurrence of fires was widespread across northern Scotland between 7,900 and 7,700 years

B.P.. Robinson (1987) interpreted the high fire indices that occurred at Ackhorn between these dates as "*almost certainly the result of man*" (Robinson, 1987 p.195). However, the sparsity of Mesolithic sites and the scarcity of mainland evidence of Neolithic cultivation (between 5,000 and 3,000 years B.P.), together with the widespread occurrence of fires, perhaps suggests that these fires were natural and not man-made.

Climatic conditions must have been such as to firstly have enabled fuel to be dry enough to burn and secondly to provide an ignition agent (lightning). The usual weather conditions for fire in the northern forests are:

> "*1. Rainless periods of at least two weeks*
> *2. Occasional dry days of low relative humidity, high temperature and high wind speeds*
> *3. Lightening storms of limited extent.*" (from Van Wagner, 1983 p. 68)

High fire frequencies could readily be accounted for by the frequent occurrence of these weather conditions during this period, suggesting that the climate at this time was characterised by the more frequent occurrence of high pressure systems (anticyclones) in the summer and autumn.

The vegetation history and fire frequency estimates from Loch Mer provide insights into the different vegetation histories and climate over central-northern and north-eastern Scotland over the past 8,000 years. However, a regional vegetation history of central-northern Scotland can not be based on a single palynological site and, therefore, all comparisons of this kind must remain tentative until other data are available from both central-northern and north-eastern Scotland.

4.3.2 Lochan by Rosail

4.3.2.1 Site description and sediment lithology

The primary aim of this part of the study was to document the forest history of central-northern Scotland. The palynological study of Loch Mer was the first step in achieving this general aim. In order to complete this aim further palynological work was undertaken at a second site, Lochan by Rosail (National Grid reference NC 721463). This site is situated some 20 km south and inland from Loch Mer upon the blanket peat-covered plateau to the east of Strathnaver (Fig. 4.3). Few trees are in view except the afforested area of Rimsdale Forest. The basin is a particularly small site (Fig. 4.7a) leading to speculation that it might have periodically dried up causing hiatuses in the pollen record. However, the lochan was chosen because:

1. It was the only suitable lake in the desired area, in terms of size and access for coring
2. There appeared to be no evidence of human interference with the surrounding peat or lake level
3. The site lies upon bedrock and has a relatively flat bottom; it was therefore a good site for sediment deposition
4. The lochan has a gentle seepage in and out that results in very little through flow

The surrounding vegetation has been tentatively mapped from the Thematic Mapper image. The vegetation of this area seemed particularly difficult to relate to the Thematic Mapper image. Field knowledge was used to interpret the distribution of the Thematic Mapper image colours and a vegetation map of the area was produced (Fig. 4.7b).

Several communities grow in the immediate vicinity of Lochan by Rosail, including the *Trichophorum cespitosum-Myrica gale* nodum (nodum 23), *Calluna vulgaris* nodum (nodum 24) and *Calluna vulgaris-Cladonia impexa* nodum (nodum 25). Together these communities form a mosaic across the landscape dominating the majority of the vegetation of the area. Along the stream-sides, *Molinia caerulea* dominates the vegetation communities.

After the deepest part of the loch had been located a series of parallel overlapping cores were obtained using a 5 cm diameter Livingstone corer (Wright, 1967) in the way described for Loch Mer. The sediment stratigraphy was described and the results displayed in Fig. 4.8. The sediment stratigraphy of Lochan by Rosail is fairly uniform, being dominated by finely divided organic matter (Ld4) with the occasional inclusion of small quantities of mineral material. Towards the bottom of the core (330 cm) mineral material and *Betula* macro-fossils are found.

Eight bulk samples from the core are currently being processed in order to provide radiocarbon dates for this profile, but the results are as yet unavailable. The stratigraphic positions of the samples are marked on Fig. 4.9.

4.3.2.2 The Holocene vegetation history

The vegetation history recorded at Lochan by Rosail is estimated to span the last 8,500 years B.P. The area around the site appears to have been initially colonised by a dense birch woodland that was succeeded in turn by birch-hazel woodland, pine-birch woodland, and dwarf-scrub heath dominated by heather, before finally becoming a blanket bog area dominated by *Calluna*, Cyperaceae and Gramineae.

The pollen diagram has been divided into 7 zones using the numerical techniques of CONSLINK, SPLITINF AND SPLITLSQ (Gordon and Birks, 1972). DECORANA was also run on the data and produced very similar results that are not included here.

The pollen diagram is difficult to date as it is quite unlike any other radiocarbon dated pollen diagrams far northern Scotland. All dates during this account are therefore tentative estimates based on the available radiocarbon dates from Loch Mer.

Zone LR-1a probably spans between 8,500 and 7,600 years B.P.. The zone is characterised by high values of *Betula* (40-60%) and the abundance of *Betula* macro-fossils and varying percentages of *Corylus*, *Salix*, *Alnus* and *Juniperus* pollen. The dwarf-shrub and herbaceous pollen taxa include *Potentilla* type, *Succisa*, *Ranunculus* type, *Calluna* and *Empetrum*.

These pollen spectra are interpreted as representing a dense birch-hazel wood with the local presence of *Salix* and possibly *Alnus*. The understorey was characterised by a wide variety of shrubs and dwarf-shrubs indicative of moist acid heathlands, including *Juniperus*, *Calluna* and *Empetrum*. Where the drainage was impeded *Calluna*/Cyperaceae (probably *Trichophorum cespitosum*) or *Calluna*/Gramineae (probably *Molinia caerulea* or *Nardus stricta*) predominated, with localised areas of *Sphagnum* bog. *Juniperus* was probably found throughout the wood but was perhaps more abundant in open places.

Zone LM-1b probably spans between 7,800-6,550 years B.P. The zone is characterised by a decline in *Betula* pollen (40-55%) values and a rise in *Salix*, Cyperaceae and Gramineae. The herbaceous pollen taxa are characteristic of grasslands and include *Bidens* type, *Filipendula*, *Potentilla* type, *Succisa*, *Campanula* type, *Armeria* and *Ranunculus* type. Spores include *Polypodium*, *Dryopteris filix-mas* type and *Pteridium*.

This suggests that whilst a birch-hazel wood was still locally present, the drainage of the area had become slightly impeded as *Salix*-scrub and Cyperaceae dominated communities become more prolific. This may suggest that there had been a change in the evapo-transpiration balance. The understorey of the wood and the surrounding areas was probably dominated by *Trichophorum cespitosum*, *Eriophorum* sp., *Nardus stricta* or *Molinia caerulea*.

Zone LR-2 (6,300 to 5,600 years B.P.) is characterised by a decline in *Betula* pollen values (25-45%) and an increase in *Calluna* pollen values to between 20-45%. *Ulmus* and *Alnus* pollen values rise, but both remain at <5% total land pollen. *Salix* pollen values decline to <1%. *Pinus* pollen values fluctuate within this zone up to 20% total land pollen. *Calluna* pollen values rise during this zone. Herbaceous pollen taxa include *Hypericum* cf. *H. pulchrum*, *Potentilla* type, *Succisa, Sinapis* type and *Pedicularis.*

These pollen values are interpreted as indicating that an open canopy birch-hazel wood was locally present, together with the local presence of *Salix* and *Alnus* in areas where the drainage is impeded. The herbaceous taxa are characteristic of herb-rich heathland areas and are usually under-represented in terms of both frequency and occurrence of species. The presence of *Menyanthes, Potamogeton, Equisetum, Isoetes lacustris* and *Nymphaea* pollen suggests that *Menyanthes* was growing locally, probably on the loch itself, together with *Potamogeton, Equisetum, Isoetes lacustris* and *Nymphaea.*

Zone LR-3a (5,600 to 5,200 B.P.) is characterised by an initial decline in the pollen percentages of *Betula* and a decline in the pollen values of *Pinus* and *Calluna. Betula, Calluna* and *Corylus* pollen values fluctuate widely during this zone. The herbaceous pollen and spore taxa include *Potentilla* type, *Succisa, Ranunculus* type, *Sinapis* type, *Rumex acetosella, Umbelliferae* undif., *Sphagnum* and *Dryopteris filix-mas* type.

This zone is interpreted as representing an open-canopy *Betula-Corylus* wood with *Alnus* and *Salix* communities near water courses. The *Pinus* pollen values of <20% are interpreted as indicating that *Pinus* was not locally present at the site. *Calluna* dominated the field layer together with the presence of *Myrica gale* and a number of herbaceous taxa including *Potentilla erecta* and *Succisa pratensis* at low cover values (<4%). *Sphagnum* was present in wet hollows and fern species, probably including *Dryopteris filix-mas,* were growing locally.

Zone LR-3b (5,200 to 4,700 B.P.) is distinguished from LR-3a by an increase in *Betula* pollen values from 15-35% to 30-50% respectively. This is accompanied by an increase in *Alnus* pollen and a decline in *Calluna* and Cyperaceae pollen. Herbaceous pollen and spore taxa are very similar to those found in LR-3a. The change in the abundance of *Betula* pollen may indicate that the birch woodland became more dense during this zone. *Salix* pollen is not recorded in this zone although as *Salix* pollen is usually under-represented (Birks, 1973b), it may have been growing locally.

At the beginning of zone LR-4a (4,700 to 4,500 B.P.) there is a marked rise in *Pinus* pollen values to >30%, although *Pinus* pollen values fluctuate markedly through this zone. The pollen and spores found include: *Calluna,* Cyperaceae *Potentilla* type, *Succisa, Ranunculus* type, *Galium* type, *Armeria* type, *Plantago lanceolata, Rumex acetosa, Pedicularis, Sphagnum, Polypodium vulgare, Dryopteris filix-mas* type and *Pteridium.*

This zone is interpreted as a period when a pine-birch woodland had developed at this site with *Alnus* and *Salix* being locally present. The low pollen values for *Quercus, Ulmus* and *Tilia cordata* are interpreted as being derived from long-distance transport with these trees not growing locally. A herb-rich heathland community perhaps formed an understorey to the birch-pine wood that was growing near the loch.

The fluctuating high pine and birch pollen values (>30% and >40% respectively) were probably short-lived in LR-4a (4,700 to 4,500 years B.P.). These fluctuations may represent changes in the canopy cover and structure of the birch-pine wood that was growing around the site (eg. a clearing in the wood may have enabled the temporary proliferation of *Pinus sylvestris*), or they may represent fluctuations in the treelimit of pine at the regional scale. However, until the radiocarbon dates are available, it is difficult to establish between these two hypotheses, although the gradual decline in arboreal pollen during this pollen zone suggests that progressive deforestation was occurring during this time. Towards the end of this zone *Pinus*, *Betula* and *Calluna* pollen values fall. The decline in *Pinus* is accompanied by an increase in the percentage of Gramineae and Cyperaceae pollen. This may indicate a temporary disturbance to the canopy cover.

There appears initially to be a fairly smooth transition between LR-4a and LR4b. It is estimated that LR-4b spans the period between 4,500 and 4,100 B.P. Periods of low *Pinus* and *Betula* pollen values (approximately 20% and 25% respectively) are followed by successive peaks in *Pinus* (to >30%) and *Betula* pollen (>35%). These marked fluctuations in the arboreal pollen taxa are accompanied by high, but fluctuating values of *Calluna* and a consistent presence of *Myrica,* Cyperaceae and Gramineae pollen. Herbaceous taxa include *Filipendula, Potentilla* type, *Succisa, Ranunculus* type, *Sinapis* type, *Artemisia, Galium* type, *Plantago lanceolata, Rumex acetosella* and Compositae Subfamily Liguliflorae undif.. Spores include *Sphagnum* and *Polypodium.* Towards the end of LR-4b *Pinus* pollen values decline to being consistently <15%. *Ulmus* declined immediately following the first peak in pine pollen in this zone.

Zone LR-4b is interpreted as representing a short-lived succession from an open-canopy *Pinus-Betula* dominated wood through to an open canopy *Betula* dominated wood. The temporary fluctuations in the *Betula* and *Pinus* pollen values, at the beginning of this zone, are interpreted as reflecting the formation of natural clearings within the birch-pine wood which reduced the percentage canopy cover temporarily. *Alnus* and *Salix* were locally present. The field layer was dominated by a herb-rich heath dominated by *Calluna* with *Sphagnum* being dominant in the wetter hollows. The decline in the total percentage of arboreal pollen towards the end of this zone suggests that the area was continuing to undergo progressive deforestation. The gradual decline in *Pinus* pollen during this zone suggests that the pine trees became extinct locally during this time.

Zone LR-5 (4,100 to 3,150 years B.P.) is distinguished by a steady decline in *Pinus* pollen values to less than 5%. *Betula* pollen values remain consistently at approximately 25%. *Alnus* and *Salix* pollen values decline and *Calluna* pollen maintains moderate values of between 25-30%. This is accompanied by a rise in Gramineae and Cyperaceae pollen. Herbaceous pollen taxa included: *Filipendula*, *Campanula* type, *Saxifraga oppositifolia* type, Compositae Subfamily Liguliflorae, cf. *Cerastium* type, *Artemisia*, *Plantago lanceolata*, *Rumex acetosa* and *Pedicularis*.

This is interpreted as suggesting that *P. sylvestris* was not growing in woodland communities within the catchment during LR-5. There appears to have been a birch wood growing locally together with herb-rich heath and/or grassland communities. A single grain of *Hordeum* type pollen was found in this zone. Whilst this may indicate the presence of man in the area, this is unlikely because there are a number of wild grasses that fall into this category. In addition, if man had significantly affected the vegetation immediately surrounding Lochan by Rosail then it is expected that the percentage of *Plantago lanceolata* would be much greater (at least 5%).

Zone LR-6 (3,150 to 2,000 years B.P.) is distinguished from the previous zone by a general decline in *Betula* pollen values to 15% and a marked increase in the percentage of *Calluna* (40-60%). *Juniperus*, *Alnus*, *Salix*, *Potentilla* type, *Succisa*, *Campanula* type, *Armeria*, *Ranunculus* type and *Sinapis* type are found at low pollen values.

The area of woodland had become significantly reduced and birch was probably only locally present within the catchment at this time. *Alnus* and *Salix* were still locally present in small quantities. The combination of the dwarf-shrub and herbaceous species suggests that a herb-rich heathland dominated by *Calluna* blanketed the landscape. *Juniperus* may have been present in the catchment. *Sphagnum* formed dense mats where edaphic/hydrological conditions were suitable.

During the final zone, LR-7 (2,000 to 0 years B.P.) *Betula* values continue to fall (to less than 15%), as do the pollen percentages of *Alnus* and *Calluna*. This is accompanied by a rise in Cyperaceae and Gramineae pollen values. Herbaceous pollen taxa include *Potentilla* type, *Succisa, Galium* type and *Pedicularis*. This zone marks the transition from a dry heathland environment to a *Trichophorum-Eriophorum* dominated blanket bog.

The fire history of Lochan by Rosail can only be discussed very generally without the ability to calculate sediment accumulation rates. Local fires (indicated by the presence of charcoal particles >2mm) appear to have been absent during zones LR-1a and LR-1b when *Juniperus* was most frequently abundant at the site. As soon as a local fire is recorded in zone LR-1b (318cm) then *Juniperus* pollen values decline rapidly. This is not surprising as *Juniperus* is destroyed by intensive fires (Diotte and Bergeron, 1989).

Local fires are recorded in most samples in zones 2, 3a, 3b and 4a, which may suggest that fire index was high during this time. Although local fires are recorded in a smaller proportion of samples in zones 4b, 5, 6 and 7 than in the previous group they nevertheless appear to occur frequently. The fire index increases during LR-6 when the number of charcoal particles of >2mm is high in comparison with the previous zone. Fire index may have declined during zone LR-7 except that the surface sample seems to record a very intense fire in recent years.

Unfortunately, until radiocarbon dates are available, there is little point in comparing the fire histories of Loch Mer and Lochan by Rosail, as estimates of sediment accumulation rate may be highly erroneous.

4.4 Comparison of the modern and fossil pollen spectra

The main aim of the pollen surface sample survey was to aid the interpretation of the fossil pollen spectra. The relation between present percentage vegetation cover in the plant communities and pollen percentage values in surface pollen spectra has already been discussed in section 3.4 and 3.5. If the surface sample spectra are to provide useful modern analogues for the fossil spectra they must be shown to be floristically similar. Because of the complexity of the data sets involved, an objective method of comparison that would group together similar samples was considered essential. In order to achieve this aim a DECORANA ordination was carried out of the fossil pollen spectra from Loch Mer and Lochan by Rosail together with the surface sample data. It was essential to combine the data sets, as DECORANA separates dissimilar samples only on a relative basis (Jacobson and Grimm, 1986). The data were compiled as described below using the following 12 taxa for each data set: *Pinus, Betula, Alnus, Corylus, Calluna,* Ericaceae, *Myrica,* Cyperaceae, Gramineae, *Sphagnum, Pteridium* and Filicales:

A. The raw surface pollen data were entered and the samples grouped together on the plot to represent the major different vegetation units found in Strathnaver namely: dwarf-shrub heath; coastal grasslands; samples that contained 25% *Betula* pollen, but where dwarf-shrub heath dominated the surrounding area; and sites where dense birch wood had developed around the lochan. These groups are clearly separated on the DECORANA plot (Fig. 4.10).

B. Smoothed (5-sample moving average) data from both the Loch Mer and Lochan by Rosail fossil samples were joined in chronological order. Smoothed samples were preferred as, whilst showing the major trends in the data, this removed "noise" in the form of high frequency variability that would make a plot of this nature with 147 points unnecessarily complex.

The results (Fig. 4.10) show that all the samples from Loch Mer and Lochan by Rosail form spatially discrete groups on the plot and suggest that the fossil pollen spectra from Loch Mer and Lochan by Rosail are dissimilar. The bottom sample from Lochan by Rosail (dense birch-hazel wood) is nearest to Loch Mer's zone LM-3B, but both samples vary significantly in the abundance of their major taxa (Table 4.5).

TABLE 4.5 Comparison of the pollen spectra from Loch Mer zone LM-3b, Lochan by Rosail zone LR-1a and Loch Chealamy's surface pollen sample.

SITE	*BETULA* (%)	*CORYLUS* (%)	*CALLUNA* (%)	GRAMINEAE (%)
Lochan by Rosail	45-65	5-10	10-20	1-10
Loch Mer	30-45	10-20	<10	5-20
Loch Chealamy	60-65	<5	5-10	15-20

As the two fossil sites can not be directly compared because of major differences in the species composition and abundance between the two sites each will be considered separately in their relationship to the surface pollen spectra.

Not later than 8,000 B.P., the area surrounding Loch Mer was initially colonised by a treeless juniper-scrub heath that has no analogues with the present surface pollen spectra, but is nearest to present day coastal grassland environments. This was succeeded by a birch-hazel woodland, fragments of which have persisted until the present day. The site underwent succession through time with fluctuating birch values that culminated in a peak in zone LM-3b (3,500-2,900 years B.P.). This zone is most similar to the dense birch woodland that surrounds

Loch Chealamy's at the present day. Thereafter, the percentage of birch in the woodland progressively declined until the site was nearest to the present day coastal grassland communities. It might therefore appear that the community succession almost goes in a circle, from a treeless environment to a dense birch-hazel woodland and back to a tree-less environment similar to that present initially.

The fossil pollen spectra from Loch Mer have no good analogues with the present pollen spectra from the area around Strathnaver. However, Lochan by Rosail records a unidirectional successional sequence, from a wooded environment to a treeless environment, both of which have analogues with the present environment. The original birch-hazel woodland (LR-1a) was most similar to the dense birch woodland that surrounds Loch Chealamy that falls within the area defined by >25% birch pollen. Zones LR-1b, 2, 3a, 3b, 4a and 5 do not correspond with any of the surface samples from Strathnaver, but are grouped closest to present day predominantly treeless areas with >25 birch pollen. Zone LR-6 falls within the present day treeless zone with >25% birch pollen and zone LR-7 within the dwarf-shrub heath bog communities.

It is concluded that the pollen diagrams from Loch Mer and Lochan by Rosail are different and suggest that the vegetation history of the area is complex. It is perhaps not surprising that there are few, if any, analogues that equate to the Holocene birch-hazel woods of Loch Mer, as the majority of surface samples were classified as treeless communities. Lochan by Rosail, however, does appear to have analogues for some pollen zones. Lochan by Rosail is located on an exposed plateau, as are the majority of surface samples, and therefore, the climatic and environmental conditions should be more comparable than to a comparatively sheltered lowland coastal site.

4.5 Discussion

Having compared the 2 fossil pollen diagrams with the surface samples, a brief comparison will be made with the other published pollen diagrams from far north-eastern and north-western Scotland.

As has already been mentioned, large areas of Caithness have never supported widespread woodland for extended periods of time eg. Auckhorn (Robinson, 1987) and Hill of Harley (Huntley, 1989). Both of these sites span at least the last 7,800 years and never record values >20% for *Betula* pollen. Loch of Winless (Peglar, 1979) does periodically have *Betula* pollen values of >20% between 11,000-5,000 B.P., although these are all relatively short-lived events.

In contrast, in far north-western Scotland (Birks, 1980a) birch woodland and then birch-hazel woodland dominated the area around Loch Eriboll between 10,500 and 6,000 years B.P.. Between 6,000 and 3,000 B.P. *Alnus* dominated the tree taxa, although *Betula/Alnus/Corylus* woods were locally present between 3,000 and 0 years B.P. Deforestation occurred progressively from 5,000 B.P. (Birks, 1977a). *Pinus* was never considered to have grown locally in any abundance (Birks, 1977a).

It can be seen that the two pollen diagrams from central-northern Scotland presented in this chapter are very different, not only from each other, but also from those published from far north-eastern and north-western Scotland. The pollen diagrams from Loch Mer and Lochan by Rosail suggest that extensive birch-hazel woods developed at approximately 8,000 B.P.. In the river valleys of north-western and central-northern Scotland, woodland communities have remained of importance for the last 8,000 years although with progressive deforestation from 5,000 and 3,000 B.P. respectively. In contrast the plateau areas of central-northern Scotland underwent progressive deforestation from 8,500 years B.P., with areas becoming predominantly treeless by 4,000 B.P. The relative importance and abundance of different tree species varies markedly between all of the sites mentioned. *Ulmus* is not considered to have grown locally at either Loch Mer nor Loch by Rosail although it was growing locally at An Druim (Birks, 1977a). Whilst *Alnus* was locally present at Loch Mer and Lochan by Rosail it never dominated the tree taxa which is in direct contrast to An Druim where *Alnus* dominated the tree taxa for the last 3,000 years (Birks, 1980a). *Pinus* pollen values of >20% were not found at either Loch Mer nor An Druim and may suggest that *Pinus* never grew locally although the pine pollen may have been "missed" because of the stratigraphic resolution of these pollen diagrams. However, birch-pine woods were locally present on the blanket peat covered plateax of central-northern Scotland between 5,000 and 4,000 B.P..

This brief comparison of the 2 fossil pollen diagrams presented with the present day surface samples and other available evidence from far northern Scotland shows that the woodland history of Strathnaver is complex with Loch Mer and Lochan by Rosail having quite distinct woodland histories. The former woodland communities of Loch Mer were incomparable with present day analogues found in Strathnaver although the earliest woodland communities of Lochan by Rosail were similar to present dense birch woodland communities found in Strathnaver.

Extensive woodland communities had developed across both north-western and central-northern Scotland at 8,500 B.P., but were not found in north-eastern Scotland. Differences in the occurrence and abundance of different tree taxa varied markedly across far north-western and central-northern Scotland. *Pinus* pollen appears to be absent (<20% total land pollen) from the immediate vicinity of all the sites in far northern Scotland except Lochan by Rosail where the *Pinus* pollen values fluctuate widely. This still leaves unanswered the question as to what role *Pinus sylvestris* has played in the vegetation histories of far northern Scotland since the absence of pine pollen appears to be incompatible with the macro-fossil evidence that indicates *P. sylvestris* once grew within a few kilometres of both Loch Mer and An Druim. This issue will be addressed in chapters 5 and 6.

CHAPTER 5

The Late Holocene Distribution and density of Pinus sylvestris in northern Scotland

5.1 Macro-fossils versus micro-fossils the Pinus sylvestris problem

The widespread distribution of *P. sylvestris* macro-fossils has long been known (Lewis, 1906). It is only during the 1980's, however, that the distribution of pine macro-fossils has been mapped systematically (Bennett, 1984). When Bennett's (1984) macro-fossil map is compared with the present distribution of pine woods (Fig. 5.1) it can be seen that pine trees once grew 70-80 km further north. However, if Bennett's criterion of 20% pine pollen to represent the local presence of *P. sylvestris* within the catchment is accepted, then the available published pollen diagrams reveal no evidence to substantiate the presence of *P. sylvestris* woods in the far north of Scotland during the Holocene (Fig. 5.2).

The apparent conflict between the absence of pine pollen and the presence of pine macro-fossils might be resolved if the pine macro-fossils represented only a sparse presence of trees over a long time period. The low pine pollen values might then reflect a sparse population of scattered trees. However, all of the radiocarbon-dated pine stumps in northern Scotland have yielded dates of between 3,976 and 4,393 B.P., suggesting that they are approximately synchronous. Fig. 5.3 illustrates the locations of all previously known radiocarbon-dated pine stumps along with the locations of the stumps upon which radiocarbon dates which have been obtained for this project.

Faced with the conflicting pollen and macro-fossil evidence Bennett (1984) suggested that: .

"this may be because Pinus sylvestris *produces very low amounts of pollen at its climatic limits, or may indicate that it is not common occurring in only particularly sheltered and favourable sites"* (Bennett, 1984 p. 144).

To evaluate Bennett's hypothesis a project combing pollen, stratigraphic analyses and macro-fossil mapping was designed. The detailed pine-woodland reconstruction using fine temporal-resolution pollen analyses will be discussed in Chapter 6. The pine macro-fossil survey will be considered next.

5.2 Mapping the late Holocene distribution of Pinus sylvestris

An assessment of the changes in the *P. sylvestris* tree-limit must take into account the following problems:

1.The present tree-line cannot be precisely determined
2.The factors which limit the present distribution of *P. sylvestris* are not fully understood
3.The nature of the evidence for the formerly more extensive distribution of *P. sylvestris*.

Each of these factors will be considered in turn.

Steven and Carlisle (1959) reconstructed the natural tree-limit of *P. sylvestris* using historical records, age-structure, pattern of individual trees, the composition of the field layer communities, the morphological variation of trees themselves, and the accessibility or rather the inaccessibility of individual sites. Other workers have used the techniques of monoterpene (Forrest, 1982), and pollen analysis (O'Sullivan, 1977) to assess the historical status of individual sites.

The number and distribution of native pine woods is a matter of debate. Steven and Carlisle (1959) recognize eight sites in the "northern" and "Wester Ross" groups. However, Perring and Walters (1962) and Forrest (1982) each propose different locations for the native pinewoods. The historical status of these sites can only be established by pollen and radiocarbon analysis. This has only been done for a limited number of sites from the "northern" and "Wester Ross" groups, notably Loch Maree (Birks, 1972a) and Coulin (Pennington *et al*, 1972). Due to the total absence of pollen studies of the forest dynamics from the majority of the proposed native pinewood sites their historical status remains unknown.

Available pollen evidence, however, suggests that the "northern" and "Wester Ross" pine woods (as defined by Steven and Carlisle, 1959) are relict communities and that after 4,000 B.P. these areas became predominantly treeless (O'Sullivan, 1977). Relict pinewoods, or geographically isolated fragments, have survived in these areas because of shelter, favourable soils or chance factors relating to anthropogenic exploitation. For example, the relict pinewoods on the islands and slopes adjacent to Loch Maree are presently confined to the localised areas in the river valley and only isolated trees can be found on the mountain slopes. However, the pollen evidence would suggest that before 4,000 B.P. pine formed continuous communities in the valley and on the lower slopes of the mountains (Birks, 1972a).

These "relict" communities were formerly more widespread before human clearance. An atypical pollen diagram from the Helmsdale (Andrews *et al,* 1985) shows that between approximately 6,700 B.P. and 1,700 B.P. pine or pine-birch woodlands were consistently present despite a number of clearance phases. At approximately 1,700 B.P. pine became extinct in this area, probably because of the activities of man.

It is certain that man has reduced the area of northern Scotland dominated by pine over the last 4,000 years, but it is impossible to assess how much man has accelerated a trend caused by a change in climate. In view of this fact and the fact that vegetation boundaries are in constant flux it is considered impossible to reconstruct accurately the present potential natural treeline in Scotland as Eronen (1979) has found in Lapland. However, for the purposes of this discussion, the fragments of *P. sylvestris* woodland recognized by Steven and Carlisle (1959) are used as the baseline from which to assess the potentially more widespread distribution.

Evidence for the former distribution of *P. sylvestris* can be gained from a number of sources including:

1. Place names
2. Historical records
3. The distribution of phytosociological communities associated with pine woods
4. The distribution of *P. sylvestris* macro-fossils
5. Pollen and macro-fossil analyses at specific locations

The value and reliability of each of these sources of information will now be assessed in turn, with the exception of pollen analysis as this was dealt with in chapter 4.

A list of the locations of "pine" place names has been compiled for Sutherland (Nature Conservancey Council, 1987; see Appendix 2). The distribution of pine place names is interesting. Although most of them are located in southern Sutherland, one is located in the far north west. The origin and meaning of these names is, however, often uncertain. A name may relate to either living or sub-fossil trees, to either a single, isolated tree or an entire forest growing historically or in living memory. The evidence derived from place names should therefore be treated with caution.

There are a number of historical records that refer to the former location of both extant and fossil pine woodlands. These records are of varying quality in terms of accuracy and reliability. Some of the earliest records referring to fossil pine trees date from 1791, for example,

"In many mosses there are roots of fir trees dug up.....often large fir trees quite fresh and sound, and of considerable length, have been dug up, and when split they are useful for rafters in building houses and last very long" (from The (Old) Statistical Account of Scotland Ed. J. Sinclair - 1791 - listed in Andersen, 1967. See Appendix 3).

Sub-fossil material of *P. sylvestris* has been utilised by humans since that time and has probably been used since the very earliest colonisation of this area by humans. Another quotation, from 1845 referring to the parish of Farr serves to emphasize this point:

"where extensive forests of fir grew in this country, the remains of which are still deeply embedded in the moss, and are raised by the parishioners for roofing their houses, and other domestic purposes." (From the New Statistical Account of Scotland. Anon, 1845. In Andersen, 1967, see Appendix 3).

These records are, however, of limited value in recording the former distribution of *P. sylvestris* for two reasons. Firstly, the occurrence of pine macro-fossils is only recorded in a number of parishes, and absence of a record does not mean absence of pine stumps. Secondly, the records have only been made at the parish scale and are therefore imprecisely located. Full details of all such records referring to fir (*P. sylvestris*) are recorded in Appendix 3.

Pears (1968) argued that the potential altitudinal treeline in the Cairngorms, formed by *P. sylvestris*, is characterised by areas of Juniperetum nanae that grow between 305-610 metres (McVean and Ratcliffe, 1962). Pears (1968) assessed the effects of wind exposure on tree growth from a series of flag tatter experiments. He argued that because of wind exposure *P. sylvestris* would be unable to grow above 610 and 685 metres in exposed and sheltered localities respectively.

There is no palaeoecological evidence to substantiate whether or not *P. sylvestris* ever formed woodlands at this height in the Cairngorms. Long distance *Pinus* pollen can be misinterpreted as representing the local presence of trees. While *P. sylvestris* macro-fossils younger than 3,200 B.P. have not been found above 530 metres (Dubois and Ferguson, 1985), although today *P. sylvestris* seedlings are found up to 730 metres, but above 531 metres the climate is so severe that *P. sylvestris* fails to grow to maturity (Miller and Cummins, 1982). This suggests that either *P. sylvestris* has not grown above this altitude in the last 3000 years or else that their macro-fossils have not been preserved.

Whether or not Pears (1968) hypothesis is correct, his work is strictly related to altitudinal treelines and his criteria cannot be reliably applied to latitudinal tree limits. Many areas of northern Scotland suffer wind exposure of the same order of magnitude (4-6 metres per second) as that found between 408-448 metres (Pears, 1968). This suggests that if wind exposure is the limiting factor controlling the latitudinal distribution of *P. sylvestris* then pines should be able to grow on the north coast. However, other factors, namely the evapo-transpiration balance, limit their potential distribution.

Sub-fossil *P. sylvestris* macro-fossils in the form of trunks, stumps and cones provides indisputable evidence for the presence of pine trees at some time during the past. Only under exceptional flood conditions could macro-fossils of this size be moved any considerable distance along river courses. However, macro-fossils may not accurately reflect the past distribution of *P. sylvestris* because :

1. Spatial discontinuities in the preservation of sub-fossil remains of *P. sylvestris* might mean that pines growing at either the altitudinal or latitudinal range margins, as well as at sites within these boundaries, might not be preserved. Spatial differences in preservation may be the result of differences in the rate of peat growth, the depth of the water table, slope angle, temperature, precipitation, the distribution of soil types, underlying geology, and site accessibility that would influence their utilization by local inhabitants.
2. They may not have been continually preserved through time. Pine stumps, and other woody macro-fossils, might only represent the death assemblage and not the entire period for which the pine trees grew on the bog surface (Wilkins, 1984). In addition, pine macro-fossils are notoriously difficult to date by means of biostratigraphic correlation and radiocarbon dating is essential to prevent serious mistakes in interpretation being made (Pears, 1970).
3. They can only give information that is site specific and cannot easily be used to reconstruct a picture of the regional vegetation history, the forest density or the plant communities in which they grew without being complimented by pollen, dendrochronological and radiocarbon analyses. Time and financial constraints allowed only one site to be investigated using several techniques. The results from this site will be discussed in chapter 6.

Nonetheless, a number of studies have used macro-fossils to assess the former distribution of *P. sylvestris*. The earliest studies were made by Lewis (1905, 1906, 1907, and 1911) and by Samuelson (1910). Although giving excellent descriptions of peat stratigraphies, these studies were restricted to small geographical areas. Birks (1975) re-examined Coire Bog, one of the six sites examined by Lewis (1907) in northern Scotland. Interestingly Lewis found two layers of pine macro-fossils, whereas Birks (1975) found only one layer, although she did have at least two peaks in pine pollen at 7,000 and 5,000 B.P. respectively. In addition she included a map showing the known distribution of pine stumps on a 10 km grid square basis. This was the first attempt to produce a map delimiting the former distribution of *P. sylvestris* in Scotland. This map greatly underestimated the former distribution of *P. sylvestris* as Bennett's map (1984) showed. Bennett's map was predominantly based on an extensive review of the available literature. A literature review of this kind has a number of limitations. Firstly, no assessment could be made of how systematically *P. sylvestris* macro-fossils had been searched for in different areas, leaving doubts about whether the described distribution merely reflected the areas visited by research workers. Secondly, it is impossible to question the reliability of some of the records. Since Bennett's (1984) publication a number of the sites have been re-examined and research workers failed to find *P. sylvestris* macro-fossils (Keatinge and Dickson, 1979), whilst other studies have shown that wood specimens had been mis-identified and were not *P. sylvestris*, but were *Salix* sp. (Wilson and Carter, 1988).

The aims of the this mapping project were twofold:

1. To assess the former range margins of *P. sylvestris*.
2. To map the woodland transition from a baseline in central-northern Scotland, where it was believed that *P. sylvestris* dominated the landscape in the past, eastwards to where it was either absent or was found in only small scattered localities.

Pine macro-fossils were mapped at two scales. A systematic, but extensive survey of far northern Scotland was made on a 10 km grid square basis. Far northern Scotland is defined as the area north of NC 14 and the area to the south of this extending as far south as NC 00 is included in the definition of northern Scotland (Fig. 5.1). A more intensive survey, on a 1 km grid square basis, was conducted along a 10 x 50 km belt originating from NC 7045 (Fig. 5.4a). In addition, a random survey was made in northern Scotland by recording all the locations were *P. sylvestris* macro-fossils were seen during my travels in the summer of 1987 and 1988 and the results were combined with those of other research workers (Huntley, J.P., Huntley, B. and Keatinge, T. personal communication). The results of these surveys are plotted at a 10 km scale in Fig. 5.1.

During the search for pine macro-fossils in far northern Scotland particular attention was paid to coastal areas and off-shore islands (A list of the off-shore islands that were searched can be found in Appendix 4), in order to assess the most northerly extent of *P. sylvestris* during the Holocene. As a general rule, as soon as a pine stump was located in a 10 km grid square the search was abandoned in that square and started afresh in the adjacent 10 km grid square. By following this method, 87% of all the 10 km grid squares were surveyed in far northern Scotland and a 100% increase achieved in the number of 10 km grid squares where *P. sylvestris* macro-fossils have been found (Fig. 5.1). A list and diagrammatic representation of the 4 figure grid references for all 1 km squares containing *P. sylvestris* macro-fossils can be found in Appendix 5a and 5b.

The choice of sites where sub-fossil *P. sylvestris* was searched for was governed by accessibility, suitable soil types, local knowledge, and sampling strategy. Permission of access was gained from all estates. A significant proportion of each day was spent walking on the hills, but even so some sites remained remarkably inaccessible. Claridge (1988) has made an assessment of the accessibility of peat deposits in the highland region on a 1 km scale. In order to direct the search suitable soil types were located using 1:25,000 (where available) and 1:50,000 Ordnance Survey maps. Organic, basin and valley peats were highlighted on the maps and as many of these 1 km grid squares visited as possible. Crofters, highland workers, foresters and other local people often saved much time and effort by being able to pin-point the location of *P. sylvestris* stumps.

Wherever macro-fossil remains were found, notes were made on location, density, depth, presence of tree roots, stumps, trunks, cones, and altitude. Samples were brought back for microscopic examination if there was any doubt about the identification of the sample or where only branch or root material was found (Jane, 1970; Cutler *et al,* 1987; Schweingruber, 1978).

Most of the sub-fossil pine stumps found would once have been interstatified in the peat. Pine stumps were rarely found on the mineral surface overlain by peat. The later occurrences were almost entirely restricted to the steeper slopes of the plateau, where the development of blanket bog probably was initiated later. As a result, fossil pine stumps could only be found where natural or artificial erosion had taken place in recent centuries, for example in river banks or gullies, drainage ditches, at the side of road workings, quarry faces, or at the sides of lochs. Particularly good sites for locating *P. sylvestris* macro-fossils were areas where afforestation has recently been taking place. It was largely due to the large scale afforestation that has taken place in Sutherland and Caithness between 1986-1988 that this survey was able to be carried out comprehensively.

In order to try to overcome the problem of not being able to assess whether sub-fossil wood was present in the peat in areas where peat faces had not been exposed by either natural or artificial means, a probe was designed by Dr. B. Huntley. An assessment of the efficiency of the probe in locating sub-terranean stumps was made, the details and results of which can be found in Appendix 6. Although, statistically speaking the probe did hit pine stumps as often as would be expected in relation to pine stump density and surveying strategy, it was nonetheless decided that it would be a more efficient use of my resources of time if the probe was not used in routine surveying. The results of this study are therefore dependent on the distribution of erosional features.

5.2.1.1 An assessment of the former range margins of Pinus sylvestris

Fig. 5.1 shows that *P. sylvestris* occupied a substantial area of northern and far northern Scotland at some time in the past. The following discussion is based upon an assumption that all the macro-fossils date from approximately 4,000 B.P..

It has already been mentioned that at Coire bog, in the area to the south of the study area, two pine layers have been found (Lewis, 1906). Other research workers (Dr. D. Patterson, personal communication) have noted the presence of two layers of *P. sylvestris* macro-fossils in far northern Scotland. Despite extensive searches only two localities are tentatively suggested as containing two layers of *P. sylvestris* on present evidence. These occur at Badanloch (Ordnance Survey grid ref. NC 789331) and near Syre (NC 669445). Field observation suggests that these layers may have been formed by re-working or sinking of stumps. At Badanloch two layers of *P. sylvestris* were found interstratified within the peat at only one locality. As only one layer of pine stumps can be traced for some considerable distance and because there has been extensive erosion and reworking of this shore line, this occurrence may be due to sinking or reworking of the deposit (Plates 5.1a and 5.1b). At Syre the upper layer is located at the present surface. The stratigraphy at Syre could be interpreted in one of three ways:

1. Excavation of the road has resulted in the stump being thrown onto the top of the peat profile.
2. The stump represents the remains of a tree that was planted in recent centuries.
3. An isolated population of *P. sylvestris* persisted until recent decades at this site.

At present there is insufficient evidence to distinguish between these hypotheses. Radiocarbon evidence would be required to evaluate whether there are two layers of *P. sylvestris* macro-fossils either at Badanloch or at Syre.

In addition, to these two sites, where two discrete layers of *P. sylvestris* were found interstratified within the peat, there were several locations where a number of woody remains of different species were found, usually below, but occasionally above, the pine layer (see Appendix 7).

The distribution of *Betula* sp. and *Salix* sp. macro-fossils are recorded on a 10 km grid square basis for far northern Scotland (Fig. 5.5 and Appendix 8). This survey is far from complete as systematic notes were not always made on the location of *Betula* sp. macro-fossils, but the map is included as it gives some indication of the relative distribution of sub-fossil *Betula* sp. and *P. sylvestris* macro-fossils in the area north-east of NC 73. Given the problems of using macro-fossils in reconstructing the past distribution of tree species mentioned above, and especially because of the lack of dating control, little can as yet be said firmly about the distribution of these former woodland communities in time.

The number of layers containing wood macro-fossils, and their species composition, varies between sites within relatively small geographic areas. The presence of up to 6 discrete layers of woody taxa interstratified within the peat suggests that some sites have been colonised by tree species at several times in the past when climatic/edaphic conditions were suitable. Alternatively, some sites might have been occupied by woody taxa continuously for an extended period and the layers of macro-fossils may reflect only the occasional periods when conditions were suitable for macro-fossil preservation.

Irrespective of the lack of dating control, *Betula* sp. and *Salix* sp. macro-fossils have only on one occasion been found in the same horizon as *P. sylvestris*. This was at Badanloch (Ordnance Survey grid. ref. NC 789331). The infrequent occurrence of *Betula* together with *P. sylvestris* perhaps suggests that *P. sylvestris* was the dominant species on the upland sites. This is a point that will be discussed in chapter 7.

Betula sp. macro-fossils occur frequently in the far north-east (John O'Groats) and in the far north west (Cape Wrath) of Scotland where no records of *P. sylvestris* have been found to date. This suggests that *P. sylvestris* did not colonise these areas, or that if it did then probably scattered trees only occupied very small, isolated patches of ground. The reasons for this are not known, but may be because either these areas were always too harsh, exposed and wet to support pine trees or, alternatively, chance factors might have prevented the colonisation of these areas during periods of suitable climatic conditions. It is also suggested that the Cape Wrath area is more likely than the John O'Groats area to have supported *P. sylvestris* because of its relative proximity to some relatively dense populations of the species. The presence of a military defence outpost at Cape Wrath has prevented detailed surveying of this area.

5.2.2 The woodland transition

The 10 km grid square maps (Fig. 5.1 and 5.5) summarise the distribution of *P. sylvestris* and *Betula* sp. macro-fossils, enabling tentative suggestions to be made about the species composition at this latitudinal tree-line at 4,000 B.P. The results from the intensive survey confirm the general picture, but also suggest that there is a marked decline in the number of localities in an eastwards direction (Fig. 5.4a and 5.4b).

An assessment of whether the distribution of *P. sylvestris* macro-fossils was a reflection of the sampling technique or of the distribution of soil types was made for the area of the intensive survey (Table 5.1 and Fig. 5.6). Each 1 km grid square, that is for a total of 500 grid squares, was categorised according to whether :

A. *P. sylvestris* macro-fossils were found.
B. It was searched for macro-fossils, but no remains of *P. sylvestris* were found.
C. It was not searched for macro-fossils.

For each 1 km grid square in categories A and B, an assessment was made of the soil types that dominated that square and a soil category assigned. Four soil categories were designated as follows: 1=peat <50cm depth; 2=blanket peat >50cm depth; 3=alluvium and freely drained soils; 4=soils derived from sandstone.

For each 10 X 10 km square the numbers of 1 km squares in each of the following categories were expressed as percentages of the total number of 1 km squares contained in categories A and B:

1. Number of squares dominated by each of the following soil types 1 (E), 2 (I), 3 (K) and 4 (M) soils.
2. Number of squares where *P. sylvestris* macro-fossils were located (D) .
3. Number of squares dominated by each of the following soil types 1,2,3, and 4 and in which *P. sylvestris* macro-fossils were located (G,J,L, and O respectively).

The alphabetical categories defined in brackets are found in table 5.1.

From the total number of 1 km squares that contained *P. sylvestris* macro-fossils, for each 10 km square, the percentage of squares that contained soil categories 1,2,3, or 4 was calculated (P, Q, U, and R).

Fig. 5.6 and Table 5.1 show that, east of ND 0045, there is a 45.5 % decline in the number of *P. sylvestris* records found in relation to the number of 1 km grid squares searched . This decline is accompanied by a reduction in the proportion of peat soil types. However, the percentage of *P. sylvestris* records found in peat and blanket peat deposits declines by 62.5% and 37.1% respectively between NC 9 and ND 0.

Table 5.1 illustrates that *P. sylvestris* macro-fossils are most frequently found on blanket peat (Category 2). The sporadic occurrence of stumps on the supposedly freely-drained soils of category 3 is illusory as these stumps were preserved in small pockets of peat found within these grid squares. This example emphasises the problems of categorising grid squares into general soil categories. The fact that no *P. sylvestris* macro-fossils have been found in category 4 soils is probably because this soil type is derived from sandstone and is therefore unsuitable for the preservation of macro-fossils.

Nonetheless, these results show that it is not because of a lack of suitable soil types for the preservation of *P. sylvestris* macro-fossils, that pine macro-fossils become rare or absent in far north eastern Scotland. It is assumed, however, that blanket peat has been growing over most of this area for the past 4,000 years. If, this assumption were untrue, and blanket peat did not begin to colonise significant parts of this landscape until after 4,000 B.P., then *P. sylvestris* macro-fossils might not have been preserved.

An indication of the date of blanket peat development, and the continuity of preservation conditions across the landscape, can be gained from three sources of information. Firstly, a few radio-carbon dated peat profiles indicate that blanket bog was widely distributed at 4,000 B.P. (Andrews *et al*, 1985; Birks, H.H. 1975; Huntley, J.P. 1989; Pennington *et al*, 1972; Robinson, 1987). Secondly, pine trunks are preserved across large geographic areas in northern Scotland (Fig. 5.7). Thirdly, evidence from the distribution of pine with altitude may indicate the continuity of preservation across the landscape.

An assessment was made of the distribution of pine with altitude within a 10 x 63 km area defined by the grid co-ordinates NC 5745 to ND 2055. This area is comprised of the area of the intensive survey plus a 13 x 10 km band west of NC 70. Thus for each 1 km grid easting there are 10 potential 1 km grid squares that could have been searched for *P. sylvestris*. Within each 1 km grid square where pine was found, notes were made on the maximum and minimum potential altitude at which pine could be found. The maximum and minimum potential altitude were defined as the absolute lowest and highest elevations within each grid square. These results were combined and an absolute maximum and minimum potential altitude defined for each 1 km grid easting where pine stumps were found. In addition, for the 1 km grid eastings where no pine macro-fossils were found, maximum and minimum potential altitudes were defined from the searched 1 km grid squares. Finally, a note was made of the major north-south trending river valleys.

Figure 5.8 illustrates that pine is found both on the plateau and in the river valleys, suggesting that pine macro-fossils are widely preserved in the landscape. However, pine macro-fossils in the far west are considerably below their maximum potential range, indicating that conditions were unsuitable either for their preservation or for their growth. When pine is found east of ND 0 it is frequently found near to its maximum potential altitude, suggesting that pine could have grown at higher altitudes at these longitudes. East of ND 0, pine stumps are often located around water courses and less frequently on the higher plateau. This may or may not reflect preservation conditions. East of ND 10, however, pine is only intermittently present in the prevailing flat lowlands.

The regression lines for maximum and minimum potential altitude clearly show that the potential altitudinal range reduces considerably with grid easting. Although, the correlation co-efficient between the altitude at which pine stumps are found and grid easting is significant at the 99 % level the value for r^2 indicates that less than 11.5 % of the variation can be accounted for by the regression line. The biological significance of the relationship between pine and altitude is therefore doubtful.

There is clear evidence for the northward migration of pine and birch tree limits at 4,000 B.P. Nonetheless, the former range margins of *P. sylvestris* can never be known precisely and will continue to be modified in the light of future research. The evidence presented suggests that as one moves eastwards from far, central-northern Scotland a widespread and more or less continuous belt of *P. sylvestris* gradually breaks up to become increasingly fragmented until it reaches its maximum extent, perhaps being replaced by *Betula* sp. at its most extreme range margins.

The retreat of the pine forest by approximately 70-80 km since 4,000 B.P. is almost exactly the same as the 70 km latitudinal decline recorded in Finnish Lapland (Eronen, and Hultunen, 1987). Unfortunately, there are few published records mentioning sub-fossil remains of *Betula* sp. in Lapland, although *Betula pubescens* ssp. *tortuosa* forms the latitudinal tree limit beyond *P. sylvestris* today (Kullman, 1987a; 1988a). Assuming that the decline of *P. sylvestris* occurred in far northern Scotland between 4,000-3,500 B.P., this would be approximately synchronous with the pine declines in Lapland and Ireland (Eronen and Hultunen, 1987; Eronen, 1979; Kullman, 1987a; and Bradshaw and Brown, 1987). The environmental factors that enabled its expansion and then caused its extinction from northern Scotland will be considered more fully in Chapter 6.

5.3 The density and pattern of Pinus sylvestris individuals at a number of sites past and present

The density and age-class distribution of former stands of *P. sylvestris* may yield some indication of regeneration patterns and of environmental conditions for particular geographic locations in the past. There were two main aims when surveying the density of both sub-fossil and extant trees of *P. sylvestris.* Firstly, it was hoped to be able to infer and so compare the age-class relationships and regeneration patterns at different fossil sites. Secondly, it was hoped that a comparison of the regeneration patterns and tree productivity between sub-fossil and contemporary sites may yield some insights into the factors influencing fluctuations in the treeline.

If evidence from pine stump density is to be used to infer differences in age-class relationships between fossil sites then a relationship between age and tree diameter must be established. Although ring width varies annually tree diameter is often a good reflection of age (Goodier and Bunce, 1977; McNally and Doyle, 1985). Two assumptions will be made in the following discussion:

1. That mean productivity and conditions of preservation at all sub-fossil sites, usually found on blanket peat, are approximately equal.
2. That mean productivity curves for all contemporary sites, usually found on mineral soil, are approximately equal.

The density of *P. sylvestris* individuals was routinely assessed at each location where macro-fossils were found according to the number of individuals encountered in approximately a 100 metre stretch. If only one stump was found then the location was defined as "rare", 2-5 stumps as occasional, 6-10 stumps as frequent, and more than 10 stumps as abundant. There are two main problems in using this method to assess former woodland density. Firstly, there is not always a 100 metre stretch of peat available for study. As an alternative measure, wherever possible the density of stumps was based on a 10 x 10 m area. Secondly, in order to make this survey as comprehensive as possible as soon as *P. sylvestris* remains were located in a 1 km grid square I proceeded to the next grid square. Thus tree density was often being estimated on only one sample per 1 km square. This rough estimate method of assessing tree density was used as a quick means of comparing over 200 sites. The results were analysed in relationship to grid easting and northing. No relationship could be discovered between tree density and geographical location.

At a limited number of localities, pine stumps were exposed in such a way as to enable surveys to be made of the exact spatial positions and tree diameters of the sub-fossil pine. Compass bearings, on objects identifiable on the 1:25000 scale maps, were used to locate each site precisely (Fig. 5.9). The diameter of each stump was measured and the distance and orientation to the next stump assessed using a compass and tape measure. For comparative purposes this exercise was repeated, except that tree girths were measured and not tree diameter, for a number of stands in contemporary woods. The results for each site have been plotted in terms of x-y space and the diameters classified into 6 groups using a series of computer programs written by Dr. Brian Huntley.

The results from the spatially-precise determination of fossil and extant tree density suggest that within both fossil and extant woods there are stands that show the following regeneration patterns:

1. A significant number of small trees, diameters <25 cms, with an absence of large pine trees, diameters >70 cms (Fig. 5.10a and Fig. 5.10d).
2. A small number of small trees, a predominance of trees with diameters >11-50 cms, plus a few large trees with diameters of >70 cms (Fig. 5.10b and Fig. 5.10c).

This suggests that patterns of regeneration were and still are spatially and temporally discontinuous.

Although there are notable differences between stands within individual woods, there are also notable differences between regeneration patterns in different woods. Figs. 5.11a and 5.11c show both fossil and extant woods that are characterised by a number of seedlings whereas Figs 5.11b and 5.11d characterise woods that are dominated by older, larger trees with a total absence of *P. sylvestris* seedlings.

When interpreting the sub-fossil localities, care must be exercised due to the different ways in which pine stumps have been exposed. At Badanloch and "Loch Loyal" the stumps have been exposed along the shores of lochs, enabling more comprehensive surveys to be carried out

(Plates 5.1 and 5.2). At Inchkinloch and Melness, however, pine stumps have been exposed by peat cutting, resulting in some stumps being fully exposed whereas others remain buried within the peat. Often, roots are exposed in the peat profile, along the trenches, enabling an approximation of the spatial position of the stump to be made. Thus at some sites, for example Melness and Inchkinloch, there are many stumps that have been recorded with unknown diameters. Therefore, when the plots of basal area (Fig 5.12a and d)are compared with those showing the approximate spatial position of all trunks (Fig. 5.12b and c) then there is a substantial increase in tree density.

In order to quantitatively compare sub-fossil and extant sites the number and basal areas of trees were calculated for each site using the method recommended by Mueller- Dombois and Ellenerg (1974). The area occupied by one tree (A) was calculated by : $A = (\bar{D} \text{ X } 1.67)^2$, where $\bar{D}$ = sum of D / n minus 1, where D = the sum of the intertree distances and n = the number of trees. The number of trees per hectare was calculated by dividing A by 10,000.

Some of the plots from extant sites illustrate that basal area estimates are not good indicators of age-class distributions. Figs. 5.13 a and b show two stands from different woods with approximately similar basal area estimates, but quite different age-class distributions. Conversely Figs. 5.13 c and d show two stands in the same wood with quite different basal area estimates, but with similar age-class distributions.

Tables 5.2 and 5.3 show that woodland density in modern forest stands ranges between 14 and 751 trees per hectare, whereas that in extant stands is between 91 and 627 trees per hectare. Direct comparisons of this kind yield little information as the variability within localities can be enormous. For example, the two modern stands in Amat yielded density estimates of 152.3 and 522.4 trees per hectare and there are similar differences between the stands that were analysed from the sub-fossil Badanloch site. The variation in tree density is partly related to regeneration patterns, for example the densities at the second site at Amat and Clyneliss moss are similar and reflect that both are sites where pine is naturally regenerating from plantations.

Tables 5.3 and 5.4 show that the range in sub-fossil tree density is comparable to that from modern sites. However, the basal area estimates are consistently lower in the sub-fossil localities. In addition, the sub-fossil tree density estimates have not been corrected to account for the fact that from the total macro-fossil assemblage upto 50% of stumps represent trees that were not alive at the time of maximum density. If the estimated figures for basal area and number of trees per hectare are reduced by 50 % then the tree density and basal area estimates are very low indeed. It is therefore suggested that these sub-fossil woodlands were of an open character with few scattered trees.

To evaluate whether or not the pine canopy layer was closed in the sub-fossil localities it is necessary to try to establish a relationship between basal area and the percentage of land area covered by canopy cover at extant sites. Percentage tree canopy cover was plotted against basal area estimates for the contemporary sites (Fig. 5.14 and Table 5.2). Canopy cover estimates were based on the 2 x 2 metre square quadrats used in the phytosociological survey. Regression and correlation co-efficients were calculated. If the two most outlying sites, Einig and Strath Vaich, are excluded then the correlation co-efficient of 0.8543 is significant at the 0.02 percent level. Einig was an exceptional site with widely scattered trees in a heavily grazed grassland community that hardly constituted a wood. The quadrat had to placed under one of the trees and was therefore not a reasonable representation of canopy cover. Strath Vaich was a dense wood with a large basal area estimate due to the large tree girth measurements, but the tree canopy estimate was low due to the recent death of the tree crowns.

Using the regression line of percentage tree canopy cover as a guide (Fig. 5.14) the tree canopy was estimated for each of the sub-fossil sites (Table 5.3). The percentage tree canopy was extremely low ranging between 1 and 28 %.

The evidence presented in this chapter suggests that at most of the sub-fossil sites there was an open canopy with a few scattered pine trees. Caution must be emphasized when interpreting the fossil patterns because of discontinuities of preservation within sites and because man has undoubtedly removed some of the stumps for his use. More importantly, it has been assumed that all the fossil trees were of a contemporary age. This question will be addressed in chapter 6.

CHAPTER 6

The Late Holocene pine wood communities of northern Scotland - The Lochstrathy example

6.1 Palynological and macro-fossil evidence for the pine rise, occupation and extinction at Lochstrathy

Lochstrathy is situated in an area of extensive blanket bog (Ordnance Survey grid reference NC 796491). The location of Lochstrathy in relation to Loch Mer and Lochan by Rosail can be seen in Figure 4.3. The area is predominantly undulating and at approximately 160 metres above sea level (Fig. 6.1 and Plate 6.1). A large proportion of the bog has been drained and afforested between 1985-1988. In the past, peat cutting has been carried out in parts of the area, but the site from which the monolith was collected had not been exploited by peat cutters.

The present vegetation is dominated by *Eriophorum angustifolium* and *Calluna vulgaris*, interspersed with *Myrica gale*. *Sphagnum* spp. do not dominate the flora at Lochstrathy.

A forest road exposes a discrete layer of *Pinus sylvestris* stumps interstratified within the peat that can be traced for a distance of at least 1 km. The macro-fossils are well preserved and include pine trunks and bark. The density of pine stumps appears to be high, although this will be discussed in section 6.4. The main aim of this investigation was to "locate" the pine pollen associated with these macro-fossils.

A peat monolith was cut that spanned the horizon with the stumps. Plate 6.2 shows the location of the monolith in relation to a pine stump. After the site was located, the peat face was cut back, using a spade, and the sample obtained by isolating a 30 x 30 x 76 cm block of peat. The monolith was double wrapped in cling film and aluminium foil.

On return to the laboratory, a 10 x 10 x 76 cm block was cut from the main monolith, re-wrapped and stored in a cold room at 5° C. The block was periodically unwrapped and samples taken for pollen, macro-fossil and charcoal analyses.

Pollen analysis was carried out at two scales of resolution. Firstly, in order to locate the *Pinus* pollen a relatively coarsely-resolved pollen diagram was obtained by sampling at 80, 40, 20, and 8 mm intervals through the part of the profile adjacent to the pine stump and roots. It was assumed that the associated pine pollen was unlikely to occur below the lowest roots, and therefore no pollen samples were prepared below this depth. The coarse-resolution pollen samples were obtained using an 8 mm wide calibrated brass sampler and the results are displayed in Fig. 6.2. A rise in pine pollen values was located between 328 and 354 mm (56 mm in total). It was apparent that a finer resolution pollen diagram was essential if insight was to be gained into the short-lived changes that enabled pine to colonise the blanket bog surface.

Fine-resolution pollen samples were obtained by sampling at 1 mm intervals using a 25 mm diameter brass microtome. 125 samples were prepared between 300 and 425 mm (Fig. 6.3). Unfortunately, there are breaks in this record because some of the samples were extremely humified and did not contain any pollen. Further limitations arise from the sampling method. The barrel of the microtome is only 20 mm long and at the end of every 20 mm section two samples must be combined. Pollen samples were stored in glycerol and prepared and counted in the way described in chapter 4.

The fine-resolution pollen diagram has been zoned using a combination of visual and numerical techniques. The numerical analyses include: Constrained Single Link (CONSLINK, Gordon and Birks, 1972), Sum of Squares Criterion (SPLITLSQ, Gordon and Birks, 1972), Information Content Criterion (SPLITINF, Gordon and Birks, 1972), and Detrended Correspondence Analysis (DECORANA, Hill, 1979a).

Plant macro-fossil analyses were carried out in order to locate precisely the pine horizon in relation to the pine pollen peak and to discover what plants were growing on the bog surface prior to its colonisation by pine, during the phase of pine growth, and after the extinction of pine. A finely-resolved macro-fossil diagram was essential if it was to be linked with the fine-resolution pollen diagram.

Fine-resolution macro-fossil and pollen diagrams from a single peat deposit can not be resolved to the same temporal scale while still maintaining species determination. A pine pollen grain, excluding sacci, can be up to 0.06 mm long (Moore and Webb, 1978), and therefore peat could be sliced to this thickness and still contain identifiable pollen. However, *P. sylvestris* seeds are between 3 and 5 mm, excluding the wing that is about 3 times this length (Beijerinck, 1947; Clapham Tutin and Moore, 1987). *P. sylvestris* needles are between 3-8 (10) cm x 1-2 mm (Clapham, Tutin and Moore 1987). Therefore, it is essential not to slice the peat to less than 4 mm if *P. sylvestris* macro-fossils are to remain identifiable. Even at this thickness, if pine needles or seeds are not lying horizontally then they will be sliced and may be rendered unidentifiable.

Samples were cut at 4 mm intervals, from a 10 x 10 cm block, for the entire length of the core using a stainless steel guillotine. A course-resolution macro-fossil diagram was prepared at

20 cm intervals. Contiguous samples were prepared at 4 mm intervals between 300-364 mm. The macro-fossil samples were dissociated by suspending in NaOH for 2-3 minutes and washed through sieves at 0.125 and 0.425 mm. A Wild dissecting microscope with a x 12 magnification, was used in combination with a reference collection of modern plant material, to identify most specimens to species level. Critical determinations were made at x 50 magnification.

Interpretation of the pollen and macro-fossil diagrams is dependent upon a knowledge of the variability of the source area of these different fossils and the changes in the property of the sedimentary environment over time (Jacobson, 1988). Beneath a forest canopy, the pollen source area is between 0-10^2 metres (Bradshaw, 1988). Plant macro-fossils are unlikely to travel more than a few metres from their source area due to their size, weight and aerodynamic properties (Jacobson, 1988). As a bog is colonisized by trees the pollen source area is reduced, although the macro-fossil source area will remain unchanged. Interpretation of the pollen diagram is further complicated because of the inability to distinguish between a small amount of pollen produced locally and a large amount of pollen produced at a distance (Bennett, 1984).

Fig. 6.4 illustrates the macro-fossil diagram for Lochstrathy. The presence of pine needles and bark at 352 mm indicates that *P. sylvestris* must have been growing within a few metres of the site at this time. Only 4 *P. sylvestris* needles were found in one discrete layer, perhaps suggesting that during the majority of the phase of pine occupation the conditions for the preservation of this type of macro-fossil were poor. The stratigraphic relationship between pine stump, pollen and macro-fossils is displayed in Fig. 6.5.

Before the rise in pine pollen values, the area was dominated by a *Calluna-Eriophorum* bog with local presence of *Erica tetralix* in wetter hollows (Figs. 6.2 and 6.5 and Table 6.1).

The first pollen zone, Ls-1a, in the fine-resolution pollen diagram (Fig. 6.3) confirms that immediately before the pine event the landscape was dominated by a *Calluna-Eriophorum* bog and that pine pollen values were low. The frequent presence of pollen *Sinapis* type and *Plantago lanceolata* might indicate a moist grassland/fen community was present near the stream.

Ls-1b is distinguished from Ls-1a by the consistent rise in *Pinus* pollen values, in both the percentage pollen and concentration diagrams. *P. sylvestris* was colonising the pollen catchment of the site (Fig. 6.3 and 6.6).

Pinus pollen increases abruptly to 40%, and remains consistently above 30%, in Ls-2. This indicates that *P. sylvestris* was locally present. There is a reduction in the percentage of

Cyperaceae pollen as *Calluna* came to dominate the woodland understorey. Low percentages of *Sphagnum* spores, *Potentilla* type and *Pedicularis* indicate a moist heathland environment.

In Ls-3a there is a marked decline in *Pinus* pollen values below 20%, and a rise in *Calluna* pollen values. *Sphagnum* spores are only intermittently present and there are only occasional occurrences of herbaceous pollen types including *Ranunculus* type, Chenopodiaceae, *Potentilla* type, and Compositae Sub-family Liguliflorae.

Low, fluctuating values of *Pinus* pollen continue in Ls-3b. They are accompanied by a rise in the percentage of *Sphagnum* spores, as well as the consistent presence of Gramineae and Cyperaceae. Herbaceous pollen taxa include *Ranunculus* type, *Sinapis* type, *Filipendula* and *Pedicularis*.

In Ls-3c *Pinus* pollen values rise and remain consistently greater than 20%. They are accompanied by high *Sphagnum* values. Herbs include *Succisa, Rumex* and *Sinapis* type. Pine bark is present in this horizon.

There is a rise in *Pinus* pollen values in Ls-4a, to between 35 and 47 %. The woodland understorey was dominated by moisture loving plants including *Sphagnum*, Cyperaceae and Ericales, with the local presence of *Pteridium* and *Polypodium*. The high percentage of *Sphagnum* spores in association with *P. sylvestris* was unexpected, as it had been assumed that the bog surface must have dried to enable pine to become established. The observed high *Sphagnum* spore values, in Ls-4a, can be explained by either of two hypotheses:

1. Either a closed pine canopy that developed during Ls-4 enabled shade-tolerant species of *Sphagnum* to grow, and suppressed higher plant competitors.
2. Or an open-canopy pine woodland had already become established during Ls-2 on a dry bog surface, with a relatively low water table. A subsequent increase in precipitation, or a change in the evapo-transpiration balance, resulted in a rise in the water table enabling *Sphagnum* and moisture-loving species to proliferate and simultaneously affecting seedling germination and survival of *P. sylvestris* .

To evaluate whether or not the pine canopy was closed or open during the second pine phase it is necessary to establish the percentage of land area covered by the canopy layer. Birks (1973a; 1973b; 1980a) analysed a series of surface pollen samples from small lakes, bogs, or clearings in present day woodlands in western Scotland. He analysed the pollen percentage data in relation to percentage canopy cover and suggested that the percentage of pine tree canopy could be estimated from the following formulae: *Pinus* as a % of the total land pollen.

Using the above equation it can be estimated that canopy cover was between 35-47 % during Ls-4a. This figure would suggest that pine heathland was present (O'Sullivan, 1973a; McNally and Doyle 1984b). This figure is very different from that obtained by the basal area estimates (discussed in section 5.3; Tables 5.2 and 5.3) that suggested that percentage canopy cover varied between 1 and 16 percent for sites A,B, and C. The canopy cover figures based on the basal area estimates are somewhat lower than expected and cannot easily be explained unless pine stumps were not consistently preserved.

If the percent canopy cover estimate based upon the pollen data is accepted then it can be argued on the basis of the pollen percentage figures that the two pine woodland phases were "open" and that therefore hypothesis two should be accepted. If an open heath was present then it might also be suggested that pollen production from these sub-fossil communities was more or less equivalent to that from modern pine communities.

Ls-4b is distinguished from Ls-4a by the high but fluctuating values of *Pinus*, a marked decline in the percentage of *Sphagnum* and an increase in *Calluna*. This might reflect an old, sparsely-populated pine wood that had good flowering years related to periods that were more favourable to pollen production by the existing trees.

Ls-5 is characterised by low, fluctuating *Pinus* pollen values with *Calluna* pollen dominating the pollen spectra. Cyperaceae and *Sphagnum* are consistently present at low values. There appears to be a short period at the beginning of this zone when the plant assemblage resembles that at the beginning of Ls-1b and the pollen spectra are dominated by low pollen values of Gramineae, Cyperaceae and *Sphagnum*. This then poses the question as to why *Pinus* was able to regenerate during Ls-1b and Ls-2 and not during Ls-5. The fluctuations in the pollen peaks during Ls-5 may either represent local regeneration within the catchment, or else fluctuations in the pollen production of either small isolated pockets of *Pinus* within the catchment, or else of the retreating pine forest limit, perhaps positioned some 30 or more kilometres further south. The failure to regenerate during this period was probably due to the operation of chance factors determining the coincidence of good seed years together with periods when environmental factors would have enabled seedlings to become established on the bog. The presence of *Rumex* sp., *Sinapis* type and *Plantago lanceolata* in this zone may reflect some local disturbance by either natural or artificial factors.

The final zone, Ls-6, shows a decline in the dominance of *Calluna* and a marked rise in pollen values of Cyperaceae as the area reverted to being dominated by an *Eriophorum* bog. The bog flora probably included *Rubus chamaemorus* and *Drosera rotundifolia.* The herbs included several disturbance indicators, amongst them were *Sinapis* type and *Rumex* sp..

Given the above summary of available pollen and macro-fossil evidence it is concluded that the two pinewood communities represented by Ls-2 and Ls-4a and b were quite different from each other. The first pine woodland community, Ls-2, had an understorey dominated by *Calluna* with herbs that indicate a moist heathland environment. This may have been similar to existing areas of the northern pinewoods that have open canopies on peat with good drainage. During the second pine woodland phase, Ls-4, the understorey is dominated by *Sphagnum*, with the local presence of *Erica tetralix*.

These two pine woodland communities are quite different and occupy only very small stratigraphic lengths, being 7 and 15 mm respectively. The short length of these sequences explains why *Pinus* pollen has previously not been found using routine pollen sampling intervals, often of 8 cm. The distance between the 2 peaks in pine pollen is only 45 mm.

The two peaks in pine pollen may be considered to represent:

1. A single period of pine occupation at the site, the fluctuations in *Pinus* pollen during Ls-3 being accounted for by changes in pollen concentration or preservation.
2. One regional phase of colonisation, the fluctuations in the *Pinus* pollen curve representing patchiness in the forest dynamics.
3. Two regional phases of colonisation, reflecting alternate expansion, contraction and re-expansion of the range margins of *P. sylvestris*.

The first hypothesis seems unlikely. Pollen concentration does not vary markedly over the course of the diagram (Fig. 6.6); although fluctuations in pollen concentration coincide with the exceptionally high peaks in *Calluna* pollen in zones Ls-1b and Ls-3a suggesting that pollen production was greater in these years. *Pinus* concentration values drop in zone Ls-3a and remain at very low values thereafter. These low concentrations of *Pinus* pollen are difficult to explain. One hypothesis is that environmental conditions resulted in pollen taxa being preserved differentially. If peat growth is suspended or drastically reduced, because of a lowering of the water table, the decay rate would increase. During periods of relatively rapid decay the less resistant taxa would be destroyed leaving the more resistant pollen taxa. Differential pollen preservation may account for the absence of minor herbaceous taxa in zone Ls-3a, but *Pinus* is renowned for its over-representation in pollen diagrams due to its aerodynamic properties and its robust nature (Fægri, K. and Iversen, 1964).

Either hypothesis 2 or 3 seems plausible. The presence of pine needles at 352 mm, just before the second peak in pine pollen, might be used to argue in favour of 3. In order to distinguish between these hypotheses, however, two types of data would be useful. Firstly, pollen diagrams from other sites showing two pine pollen peaks confirming that this was a regional phenomena. Secondly, radiocarbon or other dating evidence to show that the pine decline in Ls-3 is of a sufficiently short duration, 100 years or less, for the phase to represent hypothesis 2 but not 3.

Estimates of the duration of the *P. sylvestris* phase at Lochstrathy have been obtained by two means. Firstly, 6 radiocarbon dates have been obtained on peat associated with the local pollen zones and 1 radiocarbon date on the *P. sylvestris* stump associated with the monolith (Fig. 6.3). Secondly an attempt has been made to establish a floating dendrochronological sequence from as many suitable macro-fossils as could be gathered from the site. The results from the latter approach will be discussed next.

6.2 Dendrochronological evidence for changes in the population dynamics at Lochstrathy

The Lochstrathy site has been divided into four areas: A, B, C, and D (Fig. 6.1). Each of these sites was surveyed in turn and density maps and histograms prepared in the way described in section 5.3. Fig. 6.7a, b, c, and d illustrate that basal area estimates are low at all sites. The size class histograms indicate that no seedlings were found at any of the four sites. However, 4 *P. sylvestris* seedlings were found elsewhere at Lochstrathy (Plate 6.3). It is concluded that there was only a relatively low density of pine seedlings in the area, although this may be an artefact of the depositional environment. The majority of the measured pine stumps fell into the basal area categories 2 and 3, being 4-50cms diameter, although all 4 stumps found at site D were between 51-70 cm diameter. These figures suggest that the age structure was skewed towards a middle-aged population that had failed either to regenerate or to produce any long-lived trees. This hypothesis was tested using dendrochronological methods.

At sites A and B, all of the stumps were located *in situ*, interstratified within the peat. All of the samples from these sites were dug out of peat faces. At sites C and D, peat depth was shallower and the stumps had been exposed by the cutting of drainage ditches. Although some remained *in situ*, the majority had been dug out by the plough and turned over to form the adjacent ridge.

Using a 16-inch bar Stihl 024-Woodboss chainsaw, discs were cut from all suitable stumps/trunks. 60 samples were obtained in total. Samples were air dried and then levelled using a commercial sander. They were finished by hand using 50, 100 and 150 grade sand papers on a Black and Decker orbital sander. Sanding continued until individual cells could be distinguished across the entire diameter of the sample.

Ring measurements were made using a Wild dissecting microscope with a X 25 magnification. Ring width was measured using a mechanical stage that enabled measurements to be made to an accuracy of 0.02 mm. All ring measurements were recorded by hand, together with notes on the position of fire scars, abnormal growth, potential missing and/or false rings, and whether the core and/or bark were present. 3 radii were measured on each sample whereever possible. A total of 48 samples proved to be suitable for measurement.

Cross-dating techniques are used to establish the relative temporal positions of individual samples by correlating ring patterns. It is assumed that if two trees grew at the same time, and hence under similar climatic conditions, and providing that there are no missing or false rings, then their relative ring width patterns should be similar. Many workers, eg. Bridge *et al* (1986), use the Baillie and Pitcher (1973) cross-dating program to compare ring width series.

Baillie and Pitcher (1973) calculate the product moment co-efficient (PMCC) for each potential match position as sample A is slid past sample B. This co-efficient is parametric and takes into account the magnitudes of yearly width variations. The PMCC is expressed as a value of "r". "r" takes no account of the length of the overlap and Baillie and Pilcher (1973) therefore used the Students "t" test to evaluate the significance of the cross-match in relation to the length of the overlap. The number of degrees freedom is based on the number of years overlap between the specimens. For values of "t" to be used to assess significance, the tree-ring data from the specimens must be approximately normally distributed. To satisfy this condition, any long-term trends must be removed from the raw data. This is achieved by converting, or "transforming", each raw ring width to a percentage of the mean of the five widths of which it is the centre value. Normalization is achieved by taking $\log_e$ of the percentage figures.

There are many alternative methods for transforming ring-width data. Most methods can be referred to as filters. Low-pass filters are intended to emphasize trends of long duration; as these trends can be the result of tree aging, as well as of longer wavelength climate fluctuations, they are of little use in cross-dating (Wigley, 1987). High-pass filters, in contrast, filter out low frequency data, and emphasize high-frequency interannual variations. As interannual variation is largely controlled by high-frequency climate effects that extend over large geographical areas, high-pass filters are generally used for cross-dating (Wigley, 1987).

Before cross-correlations were performed, a number of filters were applied to the data in order to assess their relative value. Dr. B. Huntley wrote a program, RINGWID5, that calculates the following ring width statistics and filtered values:

1. Mean ring width per radius (sum of ring widths divided by the number of rings)
2. Standardized ring widths (ring width minus mean ring width and divided by the standard deviation of ring widths)
3. Natural logs of ring widths
4. Baillie and Pilcher (1973) 5-point filtered, normalized values.
5. Fritts' (1976) 13-term low-pass filtered log widths
6. Fritts' (1976) 13-term high-pass filtered log widths
6. Munrow's (1984) 23-term 8-year cut-off filtered log widths
7. Munrow's (1984) 23-term 9 year cut-off filtered log widths
8. Munrow's (1984) 23-term 10 year cut-off filtered log widths
9. 5-point high-pass tricube-weighted filtered log widths
10. 9 point high-pass tricube-weighted filtered log widths
11. 13 point high-pass tricube-weighted filtered log widths

The equations and terms used for each of these filters are given in Appendix 9. The results of applying each of these filters were plotted for 5 samples. Many of the filters produced remarkably similar results, for example, Fritts' high pass, and Munrows's 8- and 9-year cut-off and the 5-, 9-, and 13-term tricube filters. Of the 9 filters, 4 were chosen to perform the cross-matches. These were:

1. Baillie and Pilcher's 5-point filtered normalized values
2. Fritts' 13-term high-pass filtered log widths
3. Munrow's 23-term 10-year cut-off filtered log widths
4. 9- point high-pass tricube-weighted filtered log widths

In addition, standardized log transformed widths were also used to perform cross-matches. Each filter emphasizes the high-frequency component of the data slightly differently.

CROSSDAT, written by Dr. Brian Huntley, was used to perform the cross-matches by sliding one tree-ring sequence past another. The significance of the correlations, that is, the goodness of fit is assessed by calculating Fisher's "Z" statistic and from this the associated probability level. The probability value must take into account the fact that during the cross-dating a large number of comparisons are made as the sequences are slid past each other. This problem is known as that of "multiplicity" and Wigley (1987) recommends a method that takes it into account.

Fisher's Z transformation is given by:

$$Z = 1/2 \log_e *((1+r)/1-r))$$ with N minus 2 degrees freedom. (Wigley, 1987).

In cases where N is large, Students "t" and Fisher's Z are almost identical. Z has a normal distribution, enabling the probability level for any value of Z to be estimated analytically.

The probability level, P, for each potential match position is given by:

$$P = 1 - (1-p)^m$$

where P = The significance level P
p = case
M = number of cross-match positions attempted

The best match has both the lowest value of P, that is the most probable, and an isolated value of P. The degree of isolation of the P value was obtained by calculating the ratio of the probability for the least likely and that for the next least likely.

The results from one cross-match using CROSSDAT are summarised in table 6.2.

CROSSDAT was used to cross-match:

1. Individual radii from a single sample with each other.
2. The oldest tree (S050) radius number 4 individually with every other radius from all available samples.

All samples with more than 15 rings were crossmatched using CROSSDAT. As the filters vary in the number of terms they use, the length of the tree ring sequence and the minimum overlap determines which filters can be applied (Table 6.3). The need for caution must be emphased when using a range of filters because the chances of obtaining spurious significant cross-correlations statistics increase with the number of filters used (Monserud, 1989; Yamaguchi, 1989).

Table 6.3 Tree ring sequence lengths and the filters used

Number of rings	Filters used
>30	Munrow's 10 year 9-point tricube Fritts' High-Pass Baillie and Pilcher's normalised values
<15-30	9-point tricube Fritts' High-Pass Baillie and Pilcher's normalised values
<15	No crossmatching applied

In 50% of the cross-matches, the minimum overlap was less than 30 rings. Short ring sequences, <30 rings, are more easily crossmatched than longer sequences and are not traditionally used by dendrochronologists (Ward *et al*, 1987).

The reliability of the crossmatching positions is fundamental to any conclusions drawn from these data. Matches that were significant at *the 95% confidence level (allowing for* multiplicity) were accepted. This led to 6 samples (stumps) being rejected because either: rings were badly damaged because of fire and the stumps contained missing and/or false rings; or abnormal growth patterns were present; or ring sequences were too short <15 rings in total.

35 stumps could be cross-matched with the longest sequence (s050) at significant multiple probabilities. 7 stumps had insignificant multiple probabilities, but were included as the individual probabilities for the best matches were very high. Most dendrochronologists only assess significance of individual probabilities (Wigley, 1987); and the fact that 80% of the stumps could be cross-matched with significant multiple probabilities confirms beyond doubt the significance of the present cross-matching results.

Using the crossdating statistics, the individual radii were positioned for each stump and the results checked with the laboratory notes and the positions of the fire scars and traumas noted for each radius. The validity of the relative chronological sequence based on the 4 filters used was checked by constructing a second plot of the relative match positions based upon only the Baillie and Pilcher normalised values. The results were very similar and are not included here.

The dendrochronological record spans 344 years (Fig. 6.8). Recruitment occurred over a total of 241 years. In order to date and check the duration of the pine phase of the Lochstrathy chronology, 5 radiocarbon dates upon samples of wood have been applied for. These dates are not yet available.

Without firm dates to fix the "floating" dendrochronological sequence it is difficult to be able to verify the accuracy of the chronology. However, six radiocarbon determinations were made upon bulk sediment samples from the peat core and one on the *P. sylvestris* stump associated with the monolith. The dates were processed by D.D. Harkness at the Natural Environmental Research Council Laboratory, East Kilbride, Scotland. The dates are presented in tabular form (Table 6.8), as well as their stratigraphic positions being indicated on the left of the pollen diagram (Fig. 6.6).

These determinations show that the high pine pollen concentrations occur between 3,930 +/- 55 and 3,525 +/- 65 years B.P.. This suggests that pine trees occupied the Lochstrathy site for 405 years +/- 85 years. The standard deviation on this last date is calculated by squaring the standard errors on both the radiocarbon determinations and then calculating the square root of the sum of the two variances. These two estimates of the duration of pine of phase at Lochstrathy of 405 +/-85 and 344 years respectively lie within one standard deviation of each other ie. there is a 66% chance that the timespans represented correspond. However, caution must be expressed when interpreting these figures as the pine chronology is "floating" and can not easily be reliably related to the pine pollen chronology. In addition it is surprising that the only available date on pine macro-fossil from the Lochstrathy site is considerably older than the oldest date on the peat. This is probably because of contamination of the peat samples by humic acids from overlying younger sediments. The radiocarbon determinations on the other pine macro-fossils from Lochstrathy will test this hypothesis.

Finally the radiocarbon dates have been calibrated using Pearson and Stuivers's (1986) high precision calibration program CALIB (Revision 2.0, 1987). These results (Table 6.8) suggest that the pines occupied Lochstrathy between 4,413 and 3,833 cal.yrs B.P.. The magnitude of the time period spanned between 333-400 mm, (the location of the high concentrations of pine pollen), is 580 cal. years. However, it must be remembered that both the conventional and calibrated radiocarbon determinations are based on peat samples each side of the pine pollen peaks. The middle values of the radiocarbon samples span 83.5 mm whereas the pine pollen samples span 67 mm inclusively. If the radiocarbon dates are then re-calculated so as to represent the 67 mm pine pollen span the results would suggest a 325 and 465 year spans for the conventional and calibrated B.P. dates respectively. These figures add further confirmation to the fact that the dendrochronological sequence is a reliable estimate of the duration of the pine phase at Lochstrathy; it is to be expected that a few widely scattered pioneering trees may not have been sampled for dendrochronological processing.

It is presently suggested that the dendrochronological sequence is a reliable estimate of the duration of the pine phase at Lochstrathy. The dendrochronological sequence has therefore been used to estimate the dates of colonisation of the four sites at Lochstrathy. Table 6.4 shows that colonisation occurred consecutively at sites C, D, A and B.

Table 6.4 Dates of site occupation for Lochstrathy sites A,B,C and D

Site	Date of site colonisation (yr)	Date of last surviving tree (yr)	Total length of site occupation (yrs)
A	26	241	215
B	61	275	214
C	0	258	258
D	11	248	237

Sites C and D are located on thinner peat, approximately 0.6 metre deep, whereas at sites A and B peat depth was >1.5 metre. This suggests that the shallower peat soils were colonised first. Root systems from site C and D occasionally reached the mineral substrate indicating that these trees were probably situated on slightly better drained land. Using Fig. 6.8, Table 6.5 was constructed to indicate the number of births and deaths in 25-year intervals. These data were then used to construct Figs. 6.9a, b, and c.

Fig. 6.9a is a cumulative plot of births and deaths. It shows that germinations were approximately equal to deaths for most of the period of site occupation.

Fig. 6.9b shows 3 periods of population expansion interspersed with 3 periods of decline. Each consecutive period of expansion occupies a shorter period with durations of 75, 50 and 25 years respectively. Additionally, the magnitude of each phase of expansion is smaller as progressively more deaths occur than births. After year 200 pine goes into decline as the number of births does not equal the number of deaths.

Fig. 6.9c shows the relationship between the 3 phases of population growth and tree longevity. The trees that colonise the site during periods of population growth (phases 1, 3 and 5) live for longer periods on average than trees that become established during the 3 periods of decline (phases 2,4, and 6).

In order to assess tree productivity, the average age and annual increment rates have been calculated for each part of the Lochstrathy site (Table 6.6).

Table 6.6 Average age and ring widths for the Lochstrathy sites A, B, C and D.

Site	Average number of rings	Average ring width (mm)
A	57.0	0.788
B	54.0	0.595
C	64.9	0.738
D	63.1	0.843

McNally and Doyle (1985) produced plots of mean annual increment for both sub-fossil and extant stands of pine in Ireland. Their two sub-fossil sites have average annual increments of between 1.125 and 2.25 mm respectively, whereas their figures for contemporary sites were almost double these figures. This suggests that both tree age and annual growth rate at Lochstrathy were extremely low.

In order to look at the patterns of regeneration at a finer spatial scale a plot was made of the relative temporal and spatial positions of all trees at Lochstrathy site A (Fig. 6.10). This figure is unfortunately based upon a sample of only 12 trees and the conclusions must therefore be tentative. Sites A and B were colonised asynchronously. The first colonising trees within sites A and B were established in small groups within 5 years of each other, perhaps in response to fire events. Two other regeneration events may be distinguished: at each of years 81 and 192 there are two trees that germinated within 8 years of each other. Both periods of regeneration may be widespread as they occur over 80 metres apart and/or cross the River Strathy. In order to assess these discrete phases of regeneration the fire history of the site must be considered.

6.3 The role of fire in the pine woodland history at Lochstrathy

The frequency and intensity of fires determines the species composition and age structure of the present day boreal forests of northern Sweden (Zackrisson, 1977). In order to assess the role of fire in influencing regeneration at Lochstrathy it was hoped to be able to assess fire frequency and intensity.

The amount of charcoal produced by a fire depends on the material being burned; the peat, the field layer of *Calluna*, and/or the pine trees themselves. The distance travelled by charcoal particles has been studied intensively and will not be discussed in depth here (Clark, 1988a; Patterson, 1987). Clark (1988a) argues that charcoal particles larger than 0.2 mm are not likely to be carried further than 50 metres from the site and are almost certainly deposited locally, whereas microscopic charcoal, 0.005-0.022 mm, is deposited as dust from the atmosphere at regional or sub-continental scales.

As the main aim was to assess the influence of local fires on pine regeneration three studies were made. Each of these methods will now be considered in turn.

Clark (1988a) suggests that a sedimentation rate of 1 mm per year is a reasonable estimate for lake sediments and that if the fire intervals are to be accurately resolved then closely spaced sampling must be adopted. According to Clark (1988a), soil thin sections, provide a method by which charcoal can be analysed at 0.18 mm intervals enabling single fire events to be studied accurately. Duplicate 16.5 x 5 cm thin sections were prepared using the acetone vapour exchange (Fitzpatrick, and Gudmundsson, 1978) and liquid exchange with acetone (Fitzpatrick, 1984; Murphy, 1986) methods of dehydration. This was followed by impregnation with Crystic Resin 17449 using the catalyst Methyl Ethyl Ketone Peroxide (in 50% solution with phthalate UN2550). The sample that had been dehydrated by the liquid exchange method failed to impregnate successfully and therefore had to be discarded. The remaining sample was lapped, polished with a Logitech PM2 polishing machine, and finished in the manner described by Fitzpatrick (1984). The section was reduced to a thickness of 0.0275 mm. Unfortunately, the length of the peat had shrunk differentially along its length by >30 % during the phases of dehydration and impregnation. As the stratigraphic position of the samples measured could not be related precisely to the pollen samples the results could not be used.

After the NaOH wash, pollen samples were passed through a 0.214 mm sieve. The residue on the sieve was washed into a petri-dish. A piece of graph paper was placed beneath the petri-dish and using a Wild dissecting miscroscope at x 12 magnification, all charcoal particles were counted in each of the six 1 x 1 cm squares closest to the centre of the petri-dish. Charcoal was defined as opaque carbonised material, usually angular fragments but also including recognisable plant fragments, for example leaves and flowers of *Calluna.* Charcoal was classified into particles whose longest axis was either <0.214-2.0> mm or >2.0 mm. The results are presented as total number of charcoal particles counted per 6 cm^2. This method is quick and enables charcoal estimates to be precisely stratigraphically related to the pollen curve. Empirical evidence suggests that pollen grains are unlikely to move more than 1 mm in peat deposits (Clymo and Mackay, 1987) and if the criteria defined by Turner and Peglar (1988) are accepted, then sediment mixing is considered unlikely to have occurred in this peat profile. Assuming that the pine chronology (Fig. 6.8) spans the entire period of high pine pollen values then it is estimated that each 1 mm sample represents 3-5 years. Each peak in the charcoal curve may therefore represents between 3-5 years of charcoal input, compared with the potential 0.5 year resolution of the thin section traverses.

The third method used to assess the frequency and intensity of fires was via a record of fire scars made during the dendrochronological analysis. A fire scar was recognized, viewed in cross-section, as a black charcoal layer marking the outer margin of an annual ring (Zackrisson, 1977). A fire chronology was first produced for each sample using the method described by Arno and Sneck (1977). A master fire chronology was then produced by combining the relative dates of all fires identified on individual trees. No attempt was made so as to shift dates to correct for the fact that a fire may have occurred either in the autumn of one year or in the early spring of the next (McBride, 1983). The relative dates of fires are therefore accurate plus or minus 1 year. A series of fire statistics was then produced (Figs. 6.12a,b, and c). The results from the fine-resolution charcoal diagram and from the fire-scar based statistics will now be considered in turn.

The fine-resolution charcoal diagram from Lochstrathy (Fig. 6.11) indicates that intensive fires occurred at the beginning of Ls-1b, perhaps enabling a few scattered trees to colonise the area. An intensive fire at 401 mm apparently triggered off the first pine phase. If 1 mm represents 3-5 years, then there was a lag between the fire and the date of regeneration. This is in line with Dimbleby's (1953) findings on contemporary pine regeneration on the heather moors of Yorkshire. Fire may enable regeneration to occur immediately, either because of the temporary increase in mineral nutrients or else because of the reduction in heather growth that in turn reduces the competition for water, light and nutrients. Dimbleby (1953) argued that a short lag, of up to 5 years, may be favourable to colonisation immediately following a fire because a small percentage of *Calluna* may provide protection to seedlings from high summer temperatures and/or from frost damage.

9 mm before the second pine phase, Ls-4a, there is a high peak in the charcoal curve. This is 27-47 years before the second peak in pine pollen. As pine pollen is produced in male cones which are not produced until the tree has reached 10-15 years (Carlisle and Brown, 1968), it seems unlikely that this particular fire incident triggered this period of pine regeneration.

Clark (1988c) used the 15 year running means to evaluate the mean interval between high intensity fires. Fire frequency was analysed by calculating a weighted running mean on 5 samples. If each 1 mm sample is taken to represent 3 years then the average fire frequency is 32.5 years, with intensive fires occurring every 128 years (Fig. 6.11). There is no change in fire frequency over time.

In order to examine the fire frequency at Lochstrathy with greater temporal precision, the fire-scar records from the dendrochronological samples are considered next. Fire-scar frequency is influenced by many factors, including bark thickness, tree diameter, fuel conditions and wind velocity (Gill, 1974; McBride, 1983). Once a tree has been fire scarred then it becomes more susceptible to further fire scar formation (Zackrisson, 1977) as shown in Fig. 6.12a.

Mean fire frequency was calculated for 25 year intervals using the master chronology (Table 6.7). Fires became progressively more frequent up to year 150, with mean fire intervals varying between 2 and 25 years. These figures are high by comparison with Zackrisson's (1977) results from northern Swedish boreal forests where the most frequent mean interval between fires was 45.8 years in the Pine-lichen *Calluna* forest of flat, sandy river terraces between years 1300-1975.

Zackrisson (1977) recognizes a fire year <u>only</u> when fire scars are found in <u>two</u> independent areas. Using his criterion he estimates a fire frequency of 155.2 years for the years between 1300-1975 using 281 0.25 hectare sample plots.

On only three occasions can fires at Lochstrathy be cross-dated between trees. These were at years 99, 208, and 210 (Fig. 6.13). Cross-matches occur in so few trees that the probability that by chance one fire could be crossed-matched on three occasions should not be ruled out. As only a relatively small number of trees record fires in the area it is suggested that the majority of fires were light and low burning and therefore not recorded as fire scars. Only two of these fires were "widespread", that is they are recorded in at least two of the sub-units of the site. The fire at year 99 appears to have crossed the River Strathy, whereas that at year 210 was restricted to the western side of the river Strathy.

The fact that only two widespread fires are recorded is perhaps not so surprising in the light of Zackrisson's (1977) statement that only 1% of the forest stands in northern Sweden burn annually; it is therefore not unreasonable that, using 42 short-lived trees, only 2 "widespread" fires are recorded.

There appears to be no clear relationship between fire frequency, based on fire scars, and the ratio of births to deaths. After year 250 no fire scars are recorded, whereas the ratio of births to deaths increases substantially.

At a finer spatial scale, the fire-scar chronology for Lochstrathy sites A and B indicates that the regeneration episodes at years 81 and 150 may have been responses to fire events occurring up to 10 years previously. However, it must be stated that the majority of the dates of germination cannot be related to dates of fires.

6.4 The potential regeneration ability of these sub-fossil woods

Evidence for two periods of regeneration has been presented from the palynological record, whereas dendrochronological evidence suggests three phases of pine colonisation. Further evidence for the regeneration ability of these sub-fossil woods is provided by the distribution of *P. sylvestris* cones and seedlings (Fig. 6.14 and Plates 6.3, 6.4a and 6.4b). The presence of pine cones, including seeds, proves that, at least at some stage in the past, trees were growing sufficiently well not only to produce pollen, but to produce seed as well. Some seedlings undoubtedly grew to maturity whereas others died and ultimately became preserved within the peat.

The most common reason for failure of *P. sylvestris* to regenerate or grow to maturity on blanket bog is the high water table causing asphyxiation of roots, seedlings, and mycorrhiza. The nature of the sub-fossil pine roots may give some indication of the depth of the water table at different sites. Most of the pine samples that were examined had superficial or horizontal root systems composed of many long, branchless roots. Laitakari (1927) noted that root systems of this type are usually caused by excessive moisture.

Apart from horizontal root systems, other root types were rare. Finely divided roots, that according to Laitakari (1927) are usually associated with mycorrhiza, were found on only one pine seedling from Lochstrathy. The presence of bark meant that the species determination of this specimen was certain. Tap roots were found only at the Badanloch locality (Plate 6.5); their presence at this site may be explained in one of three ways:

1. The pine seedlings in question became established on top of decaying pine stumps and developed tap roots in response to either better nutrient availability or better drainage.
2. Tap roots may have developed in response to conditions of excessive moisture as the trees tried to "escape" from rising water tables.
3. Tap roots may have developed in very dry conditions as a response to water deficit.

3 seems unlikely when the majority of root systems of *P. sylvestris* are horizontal indicating high water tables producing anaerobic conditions. However, as the root systems of pine seedlings are short a hot/dry summer could easily result in the surface layers of peat drying out. Therefore both 1, 2, and possibly 3 are plausible, although in the absence of pollen and/or dendrochronological data no firm conclusions can be drawn.

6.5 The implications for the cause of the extinction - man/paludification/fire.

Extinction of a species is caused by death of existing individuals and failure of offspring to grow to maturity. A number of biotic and abiotic factors may affect the birth and death rates of *P. sylvestris*. Biotic factors include fire, disease, man and grazing. Abiotic factors include air temperature, precipitation, wind, soil moisture content, plant nutrient relationships, storm frequency and oceanity (via the effects of wind and fire).

Three hypotheses can be advanced to account for the extinction of *P. sylvestris* at Lochstrathy:

1. The forest was cleared by man, either by felling or else using a slash and burn technique.
2. A natural catastrophe, for example, either a fire, storm or wind event, or else a disease, killed most of the trees suddenly.
3. Climatic change resulted in a change in the evapo-transpiration balance and hence in rising water tables that affected seedling growth and establishment.

There is little evidence at present to substantiate the first hypothesis. It is believed that the human population was low during the Neolithic period, and the prehistoric remains, notably burial chambers, are largely confined to coastal sites and river valleys (Henshall, 1985). Stone axes have, however, been found in of Sutherland (Henshall, 1985). Some of the sub-fossil pine trees at Lochstrathy had axe marks on their surfaces. However, these axe marks were not comparable to the marks usually made by stone axes (Jørgensen, 1985). One stump at Melness did show axe marks that could be interpreted as indicating an attempt to fell the tree. Unfortunately, this specimen was destroyed by fire. Pre-historic humans probably did fell occasional trees in northern Scotland, but the pollen and dendrochronological evidence does not substantiate a hypothesis that the pine wood at Lochstrathy was felled. Even if prehistoric humans felled this site, evidence would be needed indicating that continued management of this site, perhaps using fire, prevented it's recolonisation by *P. sylvestris*. Presently, this evidence is lacking.

Hypothesis 2 is dismissed on similar grounds. If a massive fire had killed the majority of the trees at Lochstrathy, then the majority of dendrochronological samples would have fire scars in the outer tree ring; this is not the case. Andersen (1967) quotes Richie (1920) as providing a definite example of an ancient burnt wood in the neighbourhood of Tongue:

> *"When attempts were made late in the nineteenth century to reclaim land in this district, large trees charred for ten to fifteen feet of their length were discovered at a depth of three feet in the peat mosses. Some of the trees were said to be 3 feet in diameter and some were 'cored out with fire for several feet in length as if they had been burnt down'."*

Some sub-fossil woods may have been burned down, but there is no evidence to suggest that pine became extinct at Lochstrathy because of fire. Changes in fire frequency could have effected seed production, germination, and seedling establishment. However, evidence has been presented to suggest that no changes occurred in the mean fire frequency, although no intensive fires occurred after pollen zone LS-3.

Both the pollen and dendrochronological evidence fail to substantiate a sudden and "catastrophic" extinction of the pine population at Lochstrathy and therefore rule out the effects of wind storms, massive fires, plagues of insect pests, or epidemic disease. However, it is not ruled out that fires or wind storms may have caused woodland clearings and/or the local extinction of pine at some localities (Plate 6.6).

Summer temperature is a limiting factor in the present distribution of *P. sylvestris* (Karlén, 1976). Carlisle and Brown (1968) suggested that to ripen seed a mean temperature of $>10.5^{\circ}$ C is required for four summer months. Kullman (1983b) argued that high summer temperatures reduce frost hardiness, resulting in seedling damage with the onset of lower temperatures. Similarly, a reduction in mean air temperature can cause changes in short-term population trends by affecting seed production, germination and establishment (Kullman, 1983b). Perhaps more importantly, a reduction in summer temperature would effect the evapo-transpiration balance and hence the hydrological status of the peat.

Either an increase in precipitation, or else a reduction in summer temperature could have resulted in a threshold being crossed in the hydrological status of the bog that could have prevented seedling establishment and growth.

Until approximately 4,000 B.P., *P. sylvestris* was widely distributed in Ireland (Bradshaw and Brown, 1987), Northern Scotland (Bennett, 1984), Sweden (Kullman, 1987a), and northern Fennoscandia (Eronen, 1979; Eronen and Hultunen, 1987; Eronen and Hyvärinen, 1982). After 4,000 B.P. *P. sylvestris* became relatively infrequent and its macro-fossils are found only within a considerably reduced altitudinal and latitudinal range. Kullman (1987a) has argued that it is impossible to judge whether these macro-fossils represent periods that were unfavourable for the growth and reproduction of *P. sylvestris* or merely periods when pine macro-fossils could be preserved. However, the short pollen diagram from Lochstrathy, and other published diagrams from Ireland, Scotland, and Fennoscandia, substantiate the radical reduction in geographical range of *P. sylvestris* after 4,000 B.P..

Therefore, it is suggested that a climatic change occurred at 4,000 B.P. that influenced the evapo-transpiration balance at Lochstrathy and hence resulted in the local extinction of *P. sylvestris* as a result of pine seedlings failing to grow to maturity. Similar thresholds appear also to have been crossed in many areas of north western Europe at approximately this time. Slight asynchroneity in the extinction of *P. sylvestris* within countries in Europe may have occurred because the change in climatic circulation may be expressed in different ways eg. one country may become warmer whereas another country becomes wetter. Asynchroneity in the extinction of *P. sylvestris* within regions can be explained by either: the factors limiting growth vary locally and therefore critical thresholds will be crossed at different times; or that the lag between climatic change and the resultant change in local environmental conditions will be different at each site depending upon topography, soil type and underlying substrate.

CHAPTER 7

General Discussion

7.1 Introduction

This study was designed to increase our knowledge of the vegetation history of central-northern Scotland. The second aim was to ascertain the role that *Pinus sylvestris* has played in the vegetation history of the area and the third aim was to establish the geographic extent and hence the former treeline of *P. sylvestris*. A series of further subsidiary but related aims attempted to answer the following questions: (a) What palaeoenvironmental factors enabled *P. sylvestris* to temporarily colonise the blanket bogs? (b) What was the duration of the phase of pine growth on the bogs? (c) How old were individual trees? (d) How well did they grow? (e) Were they able to regenerate? (f) Why did they become extinct?

In this chapter the results are discussed and evaluated in terms of the aims and published results.

7.2 The vegetation history of central-northern Scotland

The primary aim of this thesis was to increase our knowledge of the vegetation history of central-northern Scotland using the techniques of palynology. Palynology enables species composition and abundance to be mapped in time and space (Von Post, 1916; Huntley and Birks, 1983; Prentice *et al*, 1987; Prentice, 1988). However, differences in pollen productivity and dispersal rates between different taxa mean that pollen percentages can not be directly interpreted in terms of percent vegetation cover (Bradley, 1985; Moore and Webb, 1978; Prentice and Webb, 1986; Prentice, 1988). Therefore a further subsidiary aim of this study was to analyse the relationship between present pollen rain and vegetation cover in Strathnaver and its surrounding area in order to aid the interpretation of the fossil pollen spectra. This required both the production of vegetation maps and the characterisation of the pollen rain of Strathnaver and its surrounding area.

The phytosociological surveys of the upland vegetation were fundamental in order to firstly characterise the vegetation surrounding each pollen surface sample site and secondly to describe and classify the main woodland types of northern Scotland. The results of the latter will be discussed first.

The vegetation communities of northern Scotland have been classified into 25 noda in 6 broad categories namely: birch woods, pine woods, alder woods, willow scrub, dwarf-shrub heath/bog and grasslands. The relationship of each of these noda to previously defined phytosociological communities was discussed in chapter 3.

The present day natural treeline is almost impossible to define precisely but the native populations of *Pinus sylvestris* are located to the south of the birch zone. The age-class distributions of the majority of extant stands in the "northern" and "Wester Ross" pine woods were positively skewed showing very little evidence of regeneration. These findings confirm previous assessments of the regeneration ability of the Scottish native pine woods (Steven and Carlise, 1959; Goodier and Bunce, 1977; Henman, 1961; Innes and Seal, 1981; MacDonald, 1952; Sykes and Horrill, 1979; Watson, 1983; Whayman, 1951).

Today *Betula pubescens* subsp. *carpatica* forms the tree-line (although being restricted to the river valleys) with small isolated populations of *Sorbus aucuparia* on cliff ledges in the hills. Kullman (1986a) suggests that *S. aucuparia* forms the treeline in Sweden because this species has both good seed dispersal properties and seedlings are easily established even on cliff ledges; whilst its sensitivity to grazing and competition from *B. pubescens* prevents it from forming continuous woodlands. Almost no seedlings or saplings were found in birch woods. This is at least in part because of grazing (Kinnaird, 1974) or other anthoprogenic factors but may also reflect fluctuations in climate (Kullman, 1979; 1989; 1981b). These populations may have become established under periods of more favourable climate but since then seeds have been unable to germinate and/or become established successfully. As a result the present treeline may retreat further unless measures are taken to ensure seedling germination and establishment. Kullman (1989) has indicated that populations of *Betula pubescens* subsp. *carpatica* have retreated in areas of the Scandes Mountains, Sweden because of cooling trend of summers since 1950.

Thus the phytosociological surveys have increased our knowledge of the present treeline of northern Scotland which has aided the interpretation of the fluctuations in the Holocene treeline.

The vegetation around the surface sample sites was mapped using a Thematic Mapper image after being systematically ground truthed using the techniques of continental phytosociology. The relationship between vegetation communities and Thematic Mapper colours was poor. The main reason for this is that the phytosociological survey is based on presence/absence and abundance of plant taxa whereas the Thematic Mapper classification is based on a much wider range of variables including eg. plant phenology, grazing intensity, soil moisture, surface roughness and slope angle (Jewell and Brown, 1987). These results are in line with previous studies and were discussed in chapter 3.

The Thematic Mapper image enabled vegetation classification at a scale analogous to that obtained by pollen surface samples eg. grasslands, dwarf-shrub heath and birch wood communities could be recognised using both methods of classification. This suggests that Thematic Mapper imagery may be of great value in future to palynologists studying pollen representation factors.

A series of surface pollen maps for Strathnaver were presented and compared with isopoll maps from northern Scotland. However, the surface pollen maps presented were for a relatively small geographical area compared with many of the available isopoll maps from Europe (Huntley and Birks, 1983; Prentice, 1978; Prentice, 1987) and North America (Davis, 1963; Davis and Webb, 1975; Delcourt *et al*, 1984; Webb, 1974, 1988). Although these studies show that broad vegetational patterns can be mapped using pollen analysis they have several limitations including the fact that pollen taxa are often grouped and therefore contain several species or even genera which leads to difficulties in interpreting the data in ecological terms (Birks, 1985).

Previous studies have investigated surface pollen samples from a variety of pine and birch wood and treeless communities in Scotland (O'Sullivan, 1973a; O'Sullivan and Riley, 1974; Birks, 1973a; 1980a). All these studies were based on moss polsters and are therefore not directly comparable with samples from lakes as their pollen source areas are quite different (predominantly <30 metres compared with 1-2 km radius for lake samples). Whilst these samples do show a good relationship between vegetation cover and pollen abundance they are not numerous enough to show the variation in vegetation cover across the landscape. This emphasises the need for a spatial network of both surface samples and fossil pollen samples so that vegetation can be mapped systematically in time and space (Grimm, 1988). Previously, most of the fossil sites studied have been located on the plateau areas of northern Scotland. The results from the present study indicate that as a result of the distribution of the pollen sites previous isopoll maps of northern Scotland have "missed" plant communities eg. the *Betula pubescens* woodlands of the river valleys of northern Scotland.

The characteristics of the pollen rain of Strathnaver and its surrounding area and the analysis of the relationship between percentage vegetation cover and pollen abundance has aided the interpretation of the fossil pollen assemblages throughout this thesis. However, it must be remembered that the present vegetation of central-northern Scotland is predominantly treeless. In order to understand why this area is predominantly treeless reference must be made treeless. In order to understand why this area is predominantly treeless reference must be made to the vegetation history of the area.

Previous palynological studies have demonstrated marked differences between the forest histories of north-western (Birks, H.H., 1984; Birks, 1977b; 1980a; 1988) and north-eastern (Peglar, 1979; Robinson, 1987) Scotland. The general aim of the present study was to document the forest history of the intervening area, central-northern Scotland.

The vegetation history of central-northern Scotland was reconstructed from two lake sites in the catchment of the Naver, namely Loch Mer and Lochan by Rosail. Loch Mer is situated in the river valley near the north coast whereas Lochan by Rosail is situated some 20 km inland upon the blanket peat covered plateau.

Pollen evidence from the two sites indicates that the woodland history of the area is complex. *Betula* woodlands were apparently widespread at approximately 8,500 B.P. The river valleys have contained birch or birch-hazel woods from 8,000 B.P. until present, although progressive deforestation has occurred from 3,000 B.P. On the plateau, progressive deforestation occurred from 8,500 years B.P. with the area becoming predominantly treeless by 4,000 B.P. This suggests that the present areas of heathland, bog and grassland on the plateau have been predominantly treeless for the past 4,000 years because of climatic/hydro-edaphic conditions. The fossil samples were directly compared with the surface samples (derived from the area around Strathnaver) and the results suggest that whilst modern analogues could be found for some pollen zones from Lochan by Rosail no analogues could be found for the birch-hazel woods that dominated Loch Mer during the past 8,000 years.

There were differences in the occurrence and abundance of tree taxa not only within central-northern Scotland, but also between central-northern and north-western Scotland. *Pinus* pollen values are not found to exceed 20% total land pollen at either An Druim (Birks, 1980a) nor at Loch Mer and may indicate that *Pinus sylvestris* never grew locally near these sites. However, if the pine phase recorded by the abundant macro-fossil remains was a relatively short temporal event then it may have been "missed" because of the stratigraphic resolution of these pollen diagrams. Birch-pine woodlands were locally present on the blanket peat covered plateaux of central-northern Scotland between 5,000 and 4,000 years B.P.

Caithness, (Huntley, 1989; Peglar, 1979; Robinson, 1987) Orkney (Moar, 1969b; Keatinge and Dickson, 1979) and Shetland (Johansen, 1985; Birnie, 1984) have been predominantly treeless throughout the Holocene with only local development of woodland or scrub communities. North-western and central-northern Scotland supported widespread woodland communities until 4,000 B.P. when extensive blanket bog formation occurred leading to birch and pine woodland fragments being restricted to the river valleys because of the hydro-edaphic conditions of the plateaux areas. Isolated fragments of *P. sylvestris* woodland survived in both north-western Scotland (Pennington *et al*, 1972) and southern central-northern Scotland (Andrews *et al*, 1985) until 2,000 B.P. when probably human activity brought about local deforestation through felling, disturbance or fire. To the south of this area pine woodlands have persisted until the present (Birks, 1972a; O'Sullivan, 1973b, 1977; Pennington *et al*, 1972).

Major differences exist between each of these areas in the occurrence and abundance of tree taxa and the timing of major vegetation changes. Whilst woodlands were widespread at 8,000 years B.P across north-western and central-northern Scotland the total percentage arboreal pollen varies significantly between these two areas. The total percentage arboreal pollen for sites in north-western Scotland usually rises above 50% (Birks, 1980a; Birks, 1972a; Pennington *et al*, 1972; Moar, 1969) rarely rises above 50% in central-northern Scotland and never rises above 50% in eastern Scotland (Huntley, 1989; Peglar, 1979; Robinson, 1987).

The results from the present study have increased our knowledge of the vegetation history of central-northern Scotland. Birch and birch-hazel woods dominated far north-western Scotland and far central-northern Scotland between 8,000 and 4,000 years B.P. with perhaps short-lived pine or birch-pine phases. North-western and perhaps southern central-northern Scotland were dominated by pine or pine birch communities during this period (Andrews *et al*, 1985; Birks, 1972a; Birks, 1975a; Moar, 1969; Pennington *et al*, 1972). However, the results from the present study suggest that the vegetation history of the area is complex preventing the development of broad generalisations. Many more sites need to be investigated before an understanding of how this mosaic of vegetation communities has changed through time in this area.

7.3 The Holocene distribution of Pinus sylvestris

The above description of the distribution of pine woodland in far northern Scotland during the Holocene might suggest that *Pinus sylvestris* never formed an important component of the vegetation cover. However, the widespread distribution of *P. sylvestris* wood remains suggests that *P. sylvestris* once grew between 70-80 km further north of its present limits (Bennett, 1984). One of the aims of this project was to establish the geographical extent and hence the former treeline of *P. sylvestris*.

In order to document the Holocene distribution of *P. sylvestris* in northern Scotland on a 10 km grid square basis a systematic survey was made of far northern Scotland. The northwards extension of the range margins of *P. sylvestris* at approximately 4,000 years B.P. in northern Scotland is coincident with the northwards extension of range of *P. sylvestris* in Finnish Lapland (Eronen and Hultunen, 1987). The Holocene distribution of *P. sylvestris* in Ireland is summarised by Bradshaw and Brown (1987). Essentially by 4,000 years B.P. pine was restricted to areas of blanket bog in the Irish Midlands (McNally and Doyle, 1984a and b) and Connemara (Bowler *et al*, 1987). It is notable that between 4,000 and 3,500 years B.P. pine was radically reduced in geographic extent in Ireland, Scotland, and Fennoscandia. By 2,000 years B.P. only relict, isolated pine populations could be found in Ireland (Dodson and Bradshaw, 1985; Mitchell, 1956; Watts, 1984), England (Turner and Hodgson, 1981) and in northern Scotland (Pennington *et al*, 1972; Andrews *et al*, 1985) where once widespread communities had occurred. Most of these isolated populations appeared to have survived in small areas of mineral material whereas pine had become extinct on the blanket bogs because of changes in the hydro-edaphic conditions that caused asphyxiation of the roots of seedlings and trees.

Bradshaw and Brown (1987) argued that, whereas *P. sylvestris* can tolerate a wide range of environments (Steven and Carlise, 1959), the controlling influence on its distribution is competitive interactions; however this leaves unanswered the following questions:

1. Why did *P. sylvestris* and not *Betula pubescens* grow on the blanket bog at 4,000 years B.P. in northern Scotland when macro-fossil remains of *B. pubescens* are often found interstratified in the blanket bogs of the area usually below and occasionally above the "pine" horizon?
2. Why did *P. sylvestris* become extinct between 4,000 and 3,500 years B.P. in central-northern Scotland?

The "competitive interactions" hypothesis, although able to account for the absence of pine on certain soil types where its competitors grow preferentially (Bradshaw and Brown, 1987) fails to explain either 1. or 2. above. If the hydro-edaphic conditions were suitable for tree-growth then birch should be able to grow on the bog surface and if Bradshaw and Brown (1987) are right then birch should have a competitive advantage over pine in this type of environment. There is no theoretical reason why birch seedlings should not have become established and have grown to maturity as nutrient conditions had been both previously and thereafter suitable for the growth of birch populations on blanket peats in northern Scotland and the presence of birch populations in the river valleys would have always ensured the presence of local seed sources. Alternatively, the absence of pine seed sources can not be used to account for its failure to colonise the bog during previous or subsequent "drier" phases.

Two hypotheses can be put forward to explain the widespread distribution of *P. sylvestris* across North-west Europe on blanket bog surfaces at approximately 4,000 years B.P. but not subsequently:

1. Pine is able to migrate faster than birch and therefore is able to make use of short-lived changes in bog hydrology.
2. Climatic conditions not only reduce water table levels sufficiently to enable their colonisation by trees but that climatic changes (possibly changes in seasonality) resulted in the establishment of pine and not birch.

It has been shown that pine has an inferior ability compared with birch to expand its range margins during short-temporal periods of climatic oscillations (Kullman, 1983b) and therefore 1. can not account for the fact that it was *B. pubescens* that colonised the blanket bogs of far northern Scotland during preceding and subsequent times, but apparently not at all at approximately 4,000 years B.P.

Rather it suggests that 2. is more likely, ie. that some unique climatic change occurred at approximately 4,000 years B.P. that encouraged the germination and establishment of *P. sylvestris* in preference to *B. pubescens*. Perhaps the climatic response surfaces of the two taxa (Huntley, B. 1989; Schweingruber, 1988b) might give some clues. The optimum precipitation conditions for *P. sylvestris* and *B. pubescens* are approximately similar in Europe; however *P. sylvestris* grows best at much higher optimum July temperatures than *B. pubescens*. This together with the suggestion that *B. pubescens* seedlings are more easily established in moist soil conditions and that pine is perhaps better able to establish seedlings on drier surfaces might account for the presence of pine while birch was absent. If summer temperatures had increased sufficiently that not only the water-table level had been lower, but that also the surface layers of peat had dried then conditions may have been suitable for the establishment of pine but not birch seedlings.

This suggests that a "continental-type" had replaced a "maritime-type" climate, resulting in both the reduction of precipitation levels and an increase in summer temperatures. This affected the evapo-transpiration balance sufficiently to cause the bog surface to dry.

This leads to the suggestion that if the bog surface dried then surely peat growth would cease/decline radically resulting in the failure of pine pollen and/or macro-fossils to be preserved. However, soils suitable for the preservation of macro-fossils were widely distributed across far northern Scotland (chapter 5).

Pine was widely distributed across the landscape on both the exposed plateau and in the sheltered river valleys. The marked decline in the number of 1 km grid square localities in an eastwards direction and the presence of macro-fossil remains only near water courses in the east might suggest that wind exposure limited the distribution of pine on the eastern and by implication the north-western range margins. However, pine was found nearer to its maximum potential altitude in the east suggesting that if the land was higher then pine would have been able to grow at higher altitudes.

The northwards extension of pine between 8,000 and 4,000 years B.P. was accompanied by a rise in the maximum altitudinal limit of pine across North-west Europe. Pine grew up to 247 metres higher during the Holocene in the Cairngorms (Pears, 1968) and approximately 200 metres higher in parts of Sweden (Kullman, 1987a) and Finnish Lapland (Karlén, 1976; Karlén, 1983; Eronen and Hultunen, 1987).

Table 7.1 The maximum altitudinal range of Pinus sylvestris during the Holocene

Site	Max. altitude 0 years B.P (m)	Max. altitude Holocene (m)	Miniumum Increase (m)
Ben Loyal	-	300	300
Cairngorms	530[1]	777[2]	247
Kloppanashugan (Sweden) (Kullman, 1987a)	800	990	190
Enontekio (Finnish Lapland) (Eronen and Huttunen, 1987)	370	560	190

1 = Miller (1982); 2 = Pears (1968)

The systematic intensive and extensive searches for pine macro-fossils made during this project have increased our knowledge of the Holocene distribution of *P. sylvestris*. The 10 and 1 km maps will be superceded in time as the processes of natural and artificial erosion will continue to expose more pine macro-fossils. However, the absence or extreme scarcity of pine macro-fossils together with the presence of birch in far North North Western and far North North Eastern Scotland suggests that birch may have formed the treeline at 4,000 years B.P. These results appear to be consistent with those found in Fennoscandia (Kullman, 1988a) except that there few records of macro-fossil remains of birch have been published (Kullman, 1987a; 1988a) and the timing and duration of the pine phase is different. It is therefore difficult to make inferences about the relative distribution of birch and pine tree-limits.

7.4 The role that Pinus sylvestris has played in the vegetation history of central-northern Scotland

The second aim of the thesis was to ascertain the role that *P. sylvestris* has played in the vegetation history of central-northern Scotland. The widespread distribution of pine macro-fossils has long been known and have been known; however published pollen diagrams reveal no pollen evidence to substantiate the presence of *P. sylvestris* woods.

In order to locate the "missing" pine pollen fine-temporal resolution pollen analysis was carried out on a monolith associated with pine macro-fossils. High concentrations of pine pollen were located in two peaks spanning 7 and 15 mm respectively at the Lochstrathy site.

The pine woodland community at Lochstrathy was perhaps analogous to the present pine-heathland communities found around the margins of the present native pine woods (O'Sullivan, 1973a). Early in the successional sequence *Calluna* dominated the under-storey but later *Sphagnum* communities replaced *Calluna* as the dominant field-layer.

Lochstrathy is situated in an area of extensive blanket bog and superficially appears to be similar to many of the other sites where pine stumps are interstratified within blanket bogs. Such sites are widely distributed across Scotland (Birks, 1975; Bennett, 1984), Ireland (Birks, 1975; Bennett, 1984; Bradshaw and Brown, 1987; McNally and Doyle, 1984a) and Fennoscandia (Eronen, 1979). In northern Scotland it is unusual to find birch interstratified in the same horizon as pine although they do occur together in some areas in the Cairngorms and Galloway (Birks, 1975a). However the pollen associated with the pine macro-fossils in Ireland (McNally and Doyle, 1984b) and Scotland (Birks, 1975a; Pennington *et al*, 1972; Moar, 1969) usually suggests that pine/birch wood communities had formed at these sites and that birch grew on the peat surface immediately prior to and often after the local extinction of pine. Prior colonisation of the peat by birch would increase the rate of nutrient cycling, pH and nutrient availability (Miles, 1981) for the young pine populations. However, birch did not colonise the Lochstrathy site either immediately prior to, during or after the phase of pine growth on the blanket bog. The Lochstrathy pollen diagram is therefore unusual in this respect.

Having ascertained beyond doubt that *P. sylvestris* did form woodland communities in central-northern Scotland it was hoped to be able to gain some insights into the period of pine colonisation, growth and extinction. Each of these issues will now be addressed in turn.

7.4.1 What palaeoenvironmental factors enabled P. sylvestris to temporarily colonise the blanket bogs?

An intensive fire occurred immediately prior to the colonisation of the Lochstrathy site by pine. This fire may have increased nutrient availability and decreased the competition from *Calluna* (Dimbleby, 1953) or released seed sources (Birks, 1975a). The sensitivity of bog communities to fires and their role in affecting plant succession is pronounced in marginal bog/heathland/altitudinal habitats (Birks, 1975; Dimbleby, 1953; Kullman, 1983a). Undoubtedly weather conditions had enabled the bog surface to dry out sufficiently to facilitate both the ignition and burning of the bog surface, suggesting that climate-fire interactions were of primary importance in the establishment of pine in this area. Fires occurred at regular intervals (average of 32 years) throughout the period of pine growth on the blanket bog, although many of these fires were confined to separate geographical areas by the presence of a stream or other natural fire breaks. The frequent recurrence of such fires suggests that many of these fires were low burning and that climatic conditions continued to ensure that the "fuel" was dry enough to burn and the ignition agent (lightning) occurred frequently throughout the period of pine occupation. Such conditions are particularly found under periods of high pressure (anticyclones) that are more typical of "continental-type" climates (Heinselman, 1973; Tolonen, 1986).

7.4.2 What was the duration of the phase of pine growth on the bogs?

P. sylvestris occupied the Lochstrathy area for between 350-450 years between 4,000 and 3,500 years B.P. The phase of pine growth on the blanket bog at Glashabaun in Ireland lasted 500 years between 4,000 and 3,500 years B.P. The similarity in both the duration and timing of the phases of pine occupation and local extinction in both these areas strongly suggests that changes in climate or climate-fire interactions across North-west Europe were such as to enable the short-lived temporal expansion and then cause the subsequent contraction of *P. sylvestris* at its range margins, notably on peat deposits.

7.4.3 How old were individual trees and how well did they grow?

Whilst the total period of pine occupation on the blanket peat at Lochstrathy was relatively short the average age of trees was extremely low (between 54-64 years) with annual increment rates of between 0.59-0.84 mm per year. These annual increment rates are much lower than those of pine found growing on peat today (McNally and Doyle, 1985) and even lower than those of the fossil timbers of Glashnabaun (McNally and Doyle, 1985).

Despite the widespread occurrence of *P. sylvestris* in the British Isles and Fennoscandia few authors have published estimates of tree density. This is perhaps not surprising because in many areas *P. sylvestris* macro-fossils span a 4,000 year period between 8,000 and 4,000 years B.P. McNally and Doyle (1984a) use dendrochronological analysis to estimate that length of time that pine occupied the blanket bog and suggested that approximately 500 trees per ha. grew in their sub-fossil pine wood community at Glashabaun between 4,000 and 3,500 years B.P.

The density estimates produced in chapter 5 for both fossil and extant stands are extremely variable between 14 and 751 and 91 and 627 trees per ha. respectively. However, these figures for the fossil sites are probably huge over-estimates and if they are reduced by a factor of 4 (and this is a conservative estimate of the number of generations found at each site) then the density figures vary between 22 and 156 trees per ha. These estimates are lower than those found at Glashabaun (McNally and Doyle, 1984a); however 63% of plots from 26 extant native pine woods in Scotland had <100 trees per ha (Goodier and Bunce, 1977). It is perhaps to be expected that the fossil stands would have had an open nature in the same way as many of the native pine woods have today.

7.4.4 Were the pine trees able to regenerate?

The dendrochronological study of Lochstrathy enabled a detailed study of the population dynamics of the Lochstrathy site. Whereas the ratio of births to deaths remained approximately constant throughout this period at both Lochstrathy and Glashabaun (McNally and Doyle, 1984a), there were 3 distinct phases of pine colonisation at Lochstrathy.

Studies of the recent population dynamics of *P. sylvestris* (Hustich, 1948; Kullman, 1981a, 1983a; 1983b, 1987b, 1987c; 1988b) suggest that regeneration and colonisation by *P. sylvestris* is related to both summer and late winter and spring temperatures and thermal conditions. If, this was true at 4,000 years B.P. then it is suggested that the 3 phases of population expansion at Lochstrathy were related to 3 short-lived oscillations in climate. Each of these oscillations in turn probably had a shorter duration as fewer pines regenerated at each successive stage.

7.4.5 The cause of the extinction of Pinus sylvestris

Pine was able to temporarily grow on peat surfaces between 4,000 and 3,500 years B.P. where both previously and subsequently pine has failed to grow despite the presence of seed sources within 20-30 kms between approximately 6,700 and 1,700 years B.P. (Andrews *et al*, 1985).

P. sylvestris became locally extinct in northern Scotland, the Irish Midlands (McNally and Doyle, 1984a and b) and in northern Fennoscandia between 4,000 and 3,500 years B.P. Both the altitudinal and latitudinal boundaries did regress gradually in many areas between 8,000 and 4,000 years B.P. in parts of Sweden (Kullman, 1987a; Kullman, 1988a), northern Fennoscandia (Eronen, 1979, Eronen and Hyvärinen, 1981, Eronen and Hultunen, 1987), Galloway (Birks, 1975a), and in the Cairngorms (Birks, 1975a; Pears, 1972; Dubois and Ferguson, 1985); however *P. sylvestris* populations were further radically reduced in both altitudinal and latitudinal range between 4,000 and 3,500 years B.P. across North-west Europe eg. Ireland (McNally and Doyle, 1984a and b), Sweden (Kullman, 1987a), and northern Fennoscandia (Eronen, 1979, Eronen and Hyvärinen, 1981, Eronen and Hultunen, 1987), as well as in central-northern Scotland.

It is highly unlikely that man could have caused extensive deforestation over such widespread areas at approximately 4,000 years B.P. and it is suggested that changes in the fire or fire-climate interactions caused the replacement of a more "continental-type" climate with a more "maritime-type" climate resulting in decreased seasonality (Kullman, 1988a). The exact nature of the proximate cause of the local extinctions of pine populations will vary between sites depending upon the local environmental conditions. Therefore the nature of the critical thresholds and the precise timing of their crossing will vary within North-west Europe. Undoubtedly, however, climatic change was the ultimate driving force behind all of these changes.

7.5 Conclusions

As discussed in chapter 5 the widespread abundance of pine macro-fossils in northern Scotland together with the absence of pine pollen data lead Bennett (1984) to suggest that

"*this may be because* Pinus sylvestris *produces very low amounts of pollen at its climatic limits, or may indicate that it is not common occurring in only particularly sheltered and favourable sites*" (Bennett, 1984 p. 144)

Bennett's statement is weakened by the fact that it has long been known that the flowering intensity of both male and female inflorescenes that *P. sylvestris* is high near its climatic limits although the production of viable seed is irregular (Hustich, 1948). In addition Bennett's (1984) hypothesis concerning the role of *P. sylvestris* has played in the landscape of central-northern

Scotland can no longer be supported because of the following findings of this study:

1. Fine-resolution pollen analysis of a monolith associated with an interstratified stump of *P. sylvestris* located high concentrations of pine pollen in two peaks that spanned 7 and 15 mm respectively. Radiocarbon dates and associated dendrochronogical analysis suggest that the total period of pine occupation at Lochstrathy was between 350-450 years between 4,000 and 3,500 years B.P. This suggests that pollen diagrams with routine stratigraphic and temporal-resolution could well have "missed" the period of pine growth in northern Scotland.
2. *P. sylvestris* was widely distributed, colonising both the exposed peat-covered plateaux (up to 305 metres) and the sheltered river valleys in far northern Scotland at approximately 4,000 years B.P.

Previous attempts to reconstruct Holocene pine wood communities across North-western Europe from the distribution of macro-fossil and a few radiocarbon dates are highly unsatisfactory, leading to ambiguity in the interpretation of the results. As Kullman (1987a) states:

> *"It is impossible to judge whether clusters of pine mega-fossils represent periods relatively favourable for pine growth and reproduction or merely periods advantageous for production of dead wood and its long-term preservation"* (Kullman, 1987a p. 21).

The results from the present study show that by combining fine-resolution pollen and dendrochronological evidence, detailed reconstructions can be made of these pine wood communities that can prove that the wood remains in certain areas span approximately the same length of time as the duration of the pine pollen phase in the blanket peat. Further studies of this kind will enable the accurate interpretation of *P. sylvestris* macro-fossils in both climatic and ecological terms for the period between 4,000 and 3,500 years B.P. - probably one of the most important phases of climatic transition that has occurred during the past 8,000 years.

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