Postglacial Changes in Scottish Pteridophyte Distribution

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Abstract

This thesis examines changes in range and abundance of pteridophytes in Scotland. The earliest species expanded their range approximately 14,000 years ago at the end of the most recent phase of glaciation. The establishment of pteridophytes and subsequent changes in their distribution are described through published pollen diagrams. These suggest that pioneering pteridophytes enjoyed especially favourable conditions in the vegetational succession. The pollen diagrams span the postglacial periods until recent historic time when anthropogenic changes have become even more pronounced.

As man's activities increased, natural habitats rapidly declined, especially since the agricultural improvements which began in the mid-eighteenth century. Clearance of woodland, widespread drainage, and severe over-grazing become major factors in influencing pteridophyte habitats. Different aspects of land use are examined, ranging through agricultural to industrial changes, with a consideration of how each aspect has affected pteridophytes.

A short field study was conducted on the effects of moorland burning on pteridophytes, with especial reference to *Lycopodium clavatum*. It was found that in the particular area examined, with a regime of infrequent muirburn, the *Lycopodium* did not appear to be diminishing.

The final chapter discusses how future changes in farming practice might affect pteridophytes. There is the prospect of the countryside being less intensively farmed and the opportunity for a greater area to be available for the less common species which have suffered from an ever-decreasing range. It is impossible to ignore the effect that global warming could have on Scottish pteridophytes. Some predictions can be made about climatic changes, using alternative models to give an indication of how various species of pteridophytes might be affected.

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Chapter 1

The Background to the Problem

1.1 Introduction

Field observations and references in the literature indicate that many species of ferns and fern-allies (clubmosses, horsetails and quillworts) are declining in abundance quite dramatically. This is seen both regionally and more extensively throughout the British Isles. In some cases these losses are very substantial.

The overall pattern of change is summarised in the *Atlas of Ferns* (Jermy et al 1978). From the *Atlas* the species suffering the greatest range reduction can be identified in the overall context of the British Isles. These help to show the general picture of decline from which those causes most relevant to Scotland can be selected.

The *Atlas* shows general ranges but only on a coarse scale within ten kilometre squares. It distinguishes between pre-1950 and post-1950 records. It provides background evidence which implies that all species show some decline in range during the last two centuries. The percentage decline which is quoted is the number of squares with only pre-1950 records as a percentage of the total number of pre and post-1950 records. The *Atlas* helps to set the general scene and shows that significant changes are still taking place in both pteridophyte range and abundance.

The percentages of species lost as derived from the *Atlas of Ferns* do not, however, represent a simple picture. While empty circles on the map indicate a record only known from before 1950, black circles are for records in ten kilometre squares which may have been recorded before 1950 and have been recorded since, or are new records. Furthermore, the lack of confirmation of a species after 1950 may be the fault of recording. There is also no indication of species abundance. One population in a square will constitute a record, but may nevertheless mean it has diminished greatly from a previous abundance.

According to the *Atlas* the decline of several species has been extensive and quite recent and some species which have never been very common are now even less so. *Selaginella selaginoides* has lost 10% of its squares, *Cryptogramma crispa* has lost 22%, *Botrychium lunaria* has lost 36%, *Isoetes echinospora* has lost 40%, *Equisetum hyemale* has lost 54% and *Pilularia globulifera* has lost 60% of its pre-1950 records.

Very few habitats have remained unchanged since the end of the last phase of glaciation. The loss of habitat implied by the *Atlas* has accelerated in recent decades. Very few people have considered the subject of changing distributions of British native pteridophytes in any detail, or have tried to explain why some are declining so much more than others. Sometimes pteridophytes are excluded from a general consideration of changing vegetation or little detail is presented (Tansley, 1953. Burnett, 1964). Apart from several studies on *Pteridium aquilinum*, pteridophytes are usually considered in relation to overall changes in vegetation. The only known specific studies are Mitchell (1979) who analysed the decline and subsequent recolonisation of *Woodsia* in the Moffat area and also Marren (1984) on *Cystopteris dickieana*.

In order to study in some depth as wide a range of species as possible, this thesis concentrates on Scottish pteridophytes which include most of the British species. Scotland has been well travelled by botanists, especially in selected areas, over at least the nineteenth and twentieth centuries. The earliest herbarium material dates from the last decade of the eighteenth century. There are supporting field notes and accounts in journals which often correspond to herbarium specimens. The country as a whole encompasses a wide range of habitats and yet also has its share of the problems associated with industrialisation. Modern floras frequently outline the spread of pteridophytes into man-made habitats such as shale bings which were not available for colonisation in the nineteenth century. Such instances help to illustrate the continuing ability of pteridophytes to occupy new kinds of habitats.

There is a perpetual dynamic process of both decline of old habitats and expansion into new ones. Overall decline comes about when the native population is excessively weakened by changes to the landscape caused by man and there is insufficient opportunity for re-establishment. There is a substantial amount of information about changing habitats in the general vegetation studies which are available. I will draw this information together to produce an account of changing habitats which, although based especially on Scottish species, is nevertheless applicable to the whole of the British Isles.

This thesis will:

a) Detail patterns of change in range of native pteridophytes.

b) Detail patterns of change of abundance in native pteridophytes.

c) Identify possible major causes of change in range and abundance.

d) Select a particular example of a native pteridophyte, *Lycopodium clavatum*, which is subjected to a more detailed investigation.

e) Make general recommendations for the future conservation of pteridophytes.

In each case the objectives are more closely focussed on the situation in Scotland where my own field observations have been most extensive. References from broader geographic contexts are brought to bear where this furthers the understanding of the Scottish scene.

1.2 Patterns of Change in Range

A selection of species has been made from the *Atlas of Ferns*, using records based on the whole of Britain, to illustrate the variety of species from montane to coastal habitats which are all suffering a reduction in range. This is shown in **Table 1.1**.

Table 1.1 Selected species representing a variety of habitats which show a reduction in range

Species name	% Decline	Comments on Habitat
Lycopodium annotinum	30%	Old Pine woods very local
L. clavatum	28%	*Calluna* moorland
Lycopodiella inundata	66%	Acidic bog. Now very local
Isoetes lacustris	25%	Unpolluted freshwater
Equisetum variegatum	37%	Sand-dune and montane habits. Local
E. pratense	33%	Montane Woodland Streambanks. Local
Botrychium lunaria	36%	Calcareous grassland. Occasional to rare
Ophioglossum vulgatum	25%	Damp undisturbed pastures. Occasional to rare
Hymenophyllum wilsonii	14%	Oceanic climate. Increasingly restricted to west
Asplenium marinum	16%	Unpolluted rocky coasts
Athyrium flexile *A. distentifolium*	50% 25%	Acidic montane. Rare Local to rare
Cystopteris montana	18%	Basic montane gullies. Rare
Woodsia ilvensis *Woodsia alpina*	66% 35%	{ Montane cliffs and screes. Now rare to very { rare
Dryopteris carthusiana	14%	Wet lowland woodland. Now local although widely distributed
Pilularia globulifera	60%	Silty muds and clay ponds. Rapidly diminishing all over Europe

It is not very productive to group species according to percentages of decline as recorded in the *Atlas*. Of greater significance is the distribution of areas where the decline seems to be occurring. This is most easily seen by examining the maps in the *Atlas* and looking for a pattern in the distribution of the old records. *Oreopteris limbosperma* with a 15% loss is an example of a fern with a more northern distribution which has lost many habitats in the south. *Osmunda regalis* with a 23% loss seems to have been more widely distributed but is now more western. *Ophioglossum vulgatum* with a 25% loss has always been more southern and has lost many of its habitats from the south of Scotland. A reduced range over only a hundred years may be due to climatic factors, but is more probably an indication of human interference in the areas showing the greatest decline.

For most declining species, more than one factor may be having an influence. It is important to consider whether these factors may have operated over long periods and to add the additional present-day factors which may be only the last in a series. Species which flourished in immediate postglacial times may not find the present climate suitable.

Climate affects the range, either extending or reducing the area in which particular species may successfully grow and spread. A very small population may be so reduced as to be very vulnerable and all too easily exterminated. The following chapters will demonstrate the progression through time of this varying range, illustrating the effect the prevailing conditions had particularly on the more sensitive species. In Chapter 2, pollen diagrams from around Scotland are used to describe the changes from open ground vegetation to forest and on to the present landscape. Changes in soil composition and climate allow different species to flourish at various times and places. Sometimes there is good evidence from pollen diagrams about the pteridophyte component and where available this is given. Deductions are also made about which species were probably present in identifiable communities based on knowledge of modern communities.

In Chapter 3 the story of progressive clearance of forest by early man is continued through Roman times until the major changes of land improvement which began in the eighteenth century. The likely implications of the effect on the types of general vegetation are outlined with specific reference to the pteridophytes involved.

Chapter 4 is an examination of the changes wrought by new farming methods which continue into the twentieth century. The eighteenth and nineteenth centuries saw the beginning of many modern practices and probably changed the countryside more than in all the preceding centuries. The human element accounts for more changes than just those derived from the farmers who managed the land. The expansion of the railway network gave easier access to remote areas and the pressure of collectors became a new hazard for the "choicer", more horticulturally desirable, pteridophytes. While illustrating the selective distribution of botanists in well-known areas the mass of information generated at this time makes a solid basis for comparisons with present-day distributions within these areas. In Chapter 5 there is discussion of the possible effects of industrial workings on pteridophyte range.

A consideration of the restriction in range imposed by environmental factors is seen in Chapter 6 in a field examination of the distribution of *Lycopodium clavatum.* This species brings together many of the factors which have influenced the distribution of pteridophytes in general. It has a long history in pollen diagrams. It was also a popular plant with a variety of traditional uses and can in consequence be supposed to have been widely distributed.

Chapter 7 brings together some of the overall lessons to be learned about conservation and gives recommendations for the future with reference to the effects of pollution. Many of the species which have most declined, notably *Lycopodiella inundata, Dryopteris cristata* and *Pilularia globulifera,* inhabit very wet places and their decline suggests that the purity of the water may have an effect on their distribution. There is also an examination of the possible effects of acid rain, changing sea-levels and the "greenhouse effect" in Chapter 7. But pteridophytes can adapt remarkably well to new man-made habitats and with adequate encouragement they could be distributed more widely.

1.3 Patterns of Change in Abundance

The advantage of beginning the survey on the basis of the *Atlas of Ferns* is that it was compiled by recorders and observers all over the British Isles. They often had access to contemporary records and early floras, and there is interest in comparing these old records with the present range and abundance of species.

An unexpected feature in the *Atlas* is the recorded decline of such species as *Dryopteris filix-mas, Pteridium aquilinum* and *Equisetum arvense.* These species have declined by one or two percent and considering their common distribution, especially the notorious Bracken, this may indicate that very low percentages of loss are not significant and could be due merely to errors or omissions in recording. Possibly the commoner species are not recorded so frequently as they are not thought to be so interesting. Certainly the species with up to three or four percent decline do not seem from field evidence or old floras to be declining substantially.

In an historical consideration of abundance, the pteridophytes present can be given an inferred abundance relative to the other species present, but it is difficult to be more precise. It is possible to make some estimates of the abundance of species from knowledge of the available habitats.

In Chapters 2 and 3 these inferences can be made but it is not until some supporting archival information is used in Chapters 4 and 5 that a better quantification is possible. Comparisons of abundance can be made between old and new floras. Individual floras were often the work, very largely, of one individual who had a close knowledge of the area concerned and made useful comparisons with their own observations through time, and other people's observations in the past.

1.4 Identifying Possible General Causes

Archibald Geikie wrote in "The Scenery of Scotland" (1887 p417):

> Man, too, has come upon the scene, and set his mark on well-nigh every rood of the land from mountain-top to seashore. He has helped to demolish the ancient forests; he has drained innumerable fens and mosses, and turned them into fertile fields; he has extirpated the wild beasts of the old woods, thus changing both the aspect of the country and the distribution of its plants and animals. He has engraved the land with thousands of roads and railways, strewn it with villages and hamlets, and clothed it with cities and towns. And thus more has been done by him in altering the aspect of the island, than has been achieved, during the brief period of his sojourn, by all the geological agencies put together.

Changes in vegetation, and the species which compose it, are also affected by natural causes. The initial changes were natural ones due to changing climatic and edaphic factors, as will be discussed in Chapter 2, but human influence has now become the major consideration. Changes in land use extend back over the centuries and are still taking place with a good or bad influence on pteridophytes. More recently, excessive leisure use has led to erosion of sand dunes affecting dune slack habitats. Recreational interests have placed golf courses on many of the old links near the sea but have also preserved large areas from being built upon. Montane habitats represent the fragile remnants of ten thousand years of growth and yet insensitive management can cause erosion and desolation which is not easily remedied, if at all.

There have been changes in the pressure of grazing and the species of animals involved. Former habitats have been built on, ploughed, drained and forested. These changes are examined from an historical point of view in Chapters 3 and 4. It is hoped to gain an impression of the relative importance these factors may have in their effect on particular habitats and on the pteridophytes involved.

The industrial revolution had a marked influence on many pteridophyte localities and the habitats created and altered by industrial activities are investigated in Chapter 5.

Muirburn is a long-established practice which has inevitably modified the species present. To provide young new growth, particularly of *Calluna*, a system of rotational burning has been evolved which means the vegetation is burnt every ten to fifteen years. In Chapter 6 there is an examination, including field studies of *Lycopodium clavatum*, based around the hypothesis that decline is due to repeated muirburn.

There is increasing public awareness of the general changes which seem to be occurring in the climate and the environment. In Chapter 7 the future is considered. There is now land which has been "set-aside," which could suffer the same fate as the better farming land around abandoned crofts which has been inundated by Bracken, but alternatively could mean a reversal of the habitat reduction which has occurred over thousands of years.

1.5 A Particular Example That Can Be Subjected To A More Detailed Investigation

Lycopodium clavatum is an interesting species with an unusually long-lived subterranean gametophyte stage which is often found growing among *Calluna vulgaris*. *Calluna* moorland in its present form is the result of a particular kind of land management for sheep, deer or grouse which involves regular burning and intensive grazing. The moorland habitat as such is maintained by the burning and would not otherwise exist. Colonies of *L. clavatum* have been examined to investigate the relationship between the age of the *Calluna* and the extent of the *Lycopodium* patch. A selected area on Ben Vrackie in Perthshire has been chosen to study the history of burning at this site since 1947, making use of aerial photographs. The hypothesis proposed is that repeated burning has restricted the distribution of *Lycopodium*. In Chapter 6 the distribution and ecology of this species are discussed together with measurements and experiments based on Ben Vrackie and other sites in Scotland.

1.6 Possible Future Recommendations

In Chapter 7 a constructive approach is taken, looking to the future of pteridophytes. Some habitats will inevitably continue to be further reduced but others will become available. The species which first colonised around fourteen thousand years ago are often in a very different environment, which, while satisfying their basic requirements has been largely modified by man. Some pteridophytes have adapted to new man-made niches with remarkable success. Other species may require more deliberate assistance to remain part of the British flora.

Chapter 2

Changes in Pteridophyte Distribution from the Postglacial to the Neolithic Period

2.1 The Postglacial Scene

Immediately after the most recent phase of glaciation in the British Isles an extensive land surface was left available for colonisation. As large volumes of water were still locked up in ice sheets further north, the sea level was considerably lower than at present. At the lowest sea levels the Irish sea was much reduced and Northern Ireland was connected to Britain. The British Isles were also connected to Europe with land extending over a large part of the southern North Sea and the English Channel (Godwin 1975). The weight of ice over the glaciated part was such that the land in the north of Britain was isostatically depressed. Correspondingly the extreme south of Britain was elevated by the displaced mantle. This led to high sea levels in the immediate postglacial period in the north, and low sea levels in the south, relative to present-day sea levels.

The southern part of Britain was never glaciated. The glaciers at their maximum never extended beyond a line running approximately from the Thames to the Severn and the most recent phases did even not reach as far as that. Periglacial conditions prevailed near the ice margin and a tundra type of vegetation existed. There may also have been local areas of tundra further north uncovered by the main ice sheets. The south west of Ireland was not covered by the more recent phases of glaciation and had an especially favourable climate. There is a Lusitanian element in the vegetation which may have migrated north along an unglaciated coastal fringe which has long since been submerged (Pennington 1969).

In correlating the phases of deglaciation across the northern hemisphere, many factors such as altitude, latitude and proximity to oceanic circulation systems combine to produce local effects. But approximately fourteen thousand years ago the temperature began to rise appreciably. In Scotland, Price (1983) names this period the Lateglacial Interstadial. By examining pollen and spores taken from lakes and bogs it is possible to gain an impression of the plants growing in the area around a site. The pollen may represent very local conditions, especially in woods, but wind-borne pollen can travel a long way and wrongly imply that inappropriate species are growing more locally in a particular habitat. The presence of this "background" pollen is recognised and allowances are made for it. The relative proportions of herbaceous and tree pollen present are used to construct pollen diagrams showing which types of vegetation were present and how they change over a period of time. There are unfortunate gaps from some pollen diagrams, especially from the base, before there existed a suitable means of natural preservation to contain the spores. This does not mean that there was no vegetation before a certain point, merely that there is no direct evidence of its presence at that particular locality. Particular assemblages of plants have been recognised in distinct zones and together with radiocarbon dating, approximate dates can be given to these zones.

Table 2.1 Divisions of the postglacial periods

Period	Pollen zone	Approximate Dates	Climate
Lateglacial Interstadial — Older Dryas / Allerød	Zone 1 Zone II	14,000 to 11,000 BP *	Cold to Temperate
Loch Lomond Stadial Younger Dryas	Zone III	11,000 to 10,000 BP	Glacial and Periglacial
Pre-Boreal	Zone IV	10,000 to 9,000 BP	Temperate
Boreal	Zone V and VI	9,000 to 7,000 BP	Warmer and Dryer
Atlantic	Zone VIIa	7,000 to 5,000 BP	Warm and Wet
Sub-Boreal	Zone VIIb	5,000 to 2,500 BP	Cool and Dry
Sub-Atlantic	Zone VIII	2,500 BP to present	Cold and Wet

Dates taken from Price (1983). The Jessen-Godwin pollen zones I to VIII are shown with the dates and names of the postglacial periods according to the Blytt and Sernander classification. *BP = Before Present

This thesis correlates results from the different postglacial periods shown in **Table 2.1**. **Tables 2.2** and **2.3** show a selection which has been made from published pollen diagrams to illustrate the main types of vegetation and any pteridophytes mentioned in the various periods.

Information is not available for every period, due either to non-deposition or to erosion. The allocation to period may not have been made by individual authors who described their own pollen zones, especially in more recent work. Unfortunately this means that the diagrams as published are not directly comparable. In order to be able to use as wide a range of pollen diagrams as possible, it was felt that some correlation was essential. In these cases the Blytt and Sernander periods have been applied where possible by locating changes in the vegetation which follow the general date and trend of that period. In **Table 2.3** the authors' own pollen zones have been inserted, indicating either the Blytt and Sernander classification, or local zones. Obviously even one zone may cover a wide period in time and the divisions are only very approximate. Radiocarbon dating has given various dates for the change to different kinds of vegetation across Scotland. In the north of Scotland a species which has had to migrate the length of the country would appear in pollen diagrams later than in the south although conditions may have been similar for a considerable length of time. Some species would be most unlikely to grow in certain soils and could never be expected to become common in these areas.

Bennett constructed tables which showed the distribution of pollen zones of some tree species through the last 10,000 years, from the north to the south of the British Isles and wrote: "The resulting impression is that interacting climate and topography produced a mosaic of woodland cover across the British Isles which has varied almost continually in time and space during the Holocene." (Bennett 1988 p251).

2.2 The Lateglacial Interstadial

2.2.1 Climate, Landscape and General Vegetation

By 13,000 BP the climate was very similar to the present day. As there was a succeeding cooler phase there was not sufficient time for the development of forest. The highest sea levels at this time occurred in areas of maximum isostatic depression. This gave levels of up to forty metres above present sea levels in the west of Scotland, but varied considerably throughout the country (Price 1983).

Pollen evidence showed the initial spread of tundra plants like *Betula nana*, Willows (*Salix* spp), grasses and sedges. The mineral soil sustained a varied flora such as is now found only on ungrazed basic mountain ledges. Because of the subsequent depletion of the vegetation mainly by grazing, these ledges are thus the only remnants of the sub-arctic flora which was found extensively at lower altitudes at that time. The melting ice left numerous pools in hollows and moraine dammed lakes. This early part of the interstadial has been correlated with the Older Dryas period elsewhere and placed in Pollen Zone I. Newey (1970) described plants from Corstorphine in Edinburgh with pollen from Cyperaceae and Gramineae, abundant *Empetrum nigrum* and spores from *Selaginella selaginoides*. The pollen which fell on to the lake bed was mixed with hill wash from Corstorphine Hill. The soil was made unstable by solifluction which disturbed the surface by repeated freeze and thaw action. As the interstadial continued there was a rise in tree pollen progressing into Pollen Zone II. This period can be equated to the Allerød Interstadial. Small birch copses grew on the sunny south-facing hillside with *Juniperus communis* and tree Willows. There was a high proportion of herbaceous pollen but the presence of *Salix herbacea* pollen showed that there were snow patches still in the neighbourhood.

Pollen diagrams from other localities around Scotland (**Table 2.2**) show a considerable variety of species. Newey suggested that Corstorphine suffered from cold east winds which limited the vegetation. Further south at the Whitlaw mosses near Melrose, *Salix* and *Betula* made an earlier appearance. There is a richer species list with *Thelypteris palustris* and *Dryopteris filix-mas* -type spores. Both indicate a basic environment, the former in very wet conditions, the latter less so. Another tall fern, *Osmunda regalis* is recorded from Little Lochans in Galloway.

These pollen zones can be divided to show a similar sequence in the stages of development from tundra to the beginning of woodland. But the stages did not occur at exactly the same time throughout the country. Migration takes time and in some parts of the country the soil or climate may never be suitable for some species to grow.

By studying the beetles present another indication of climatic change is available (Price 1983). Around 12,000 BP there is evidence of cooling. This was a thousand years before there was a clear change in the vegetation and illustrates how the vegetation changed slowly while insects, being mobile, could respond more rapidly.

2.2.2 Pteridophytes Known to have Occurred from Fossil Evidence

Species which were found from this period include *Lycopodium clavatum*, *L. annotinum*, *Huperzia selago*, *Selaginella selaginoides*, *Diphasiastrum alpinum*, *Botrychium*, *Ophioglossum*, *Cystopteris fragilis*, *Osmunda regalis*, *Polypodium*, *Thelypteris palustris*-type, *Dryopteris filix-mas* -type, undifferentiated ferns and *Equisetum*. (See **Table 2.2** for localities)

2.2.3 Other Pteridophytes Possibly Present by Inference from Modern Species and Habitats

The lack of spore evidence is a reflection of the difficulty in precisely identifying to species level material which may be in a poor state of preservation and at most perhaps only identifiable as a genus. Poor preservation is likely in an unstable frost-heaved soil. Species like *Selaginella* with robust and identifiable megaspores are frequently recorded, but without a suitable bog to retain spores a record has not necessarily been made of other species. This does not mean that they were not present, especially if more durable fragments of associated species are found.

The surface created during the Older and Younger Dryas would have offered ideal conditions for colonisation by ferns and mosses. With their minute spores, lighter than any seeds, such plants are typically the earliest pioneers. The present day montane species derive from species which colonised more than ten thousand years ago. During the present-day milder conditions these species are found only on the higher mountains or near the sea, where these extreme habitats offer less competition and occasional erosion surfaces suitable for colonisation. In postglacial times such species would have been distributed more widely at all altitudes.

Botrychium lunaria, *Equisetum variegatum* and *Selaginella selaginoides* are three pteridophytes which are still found today in calcareous dune slacks and basic montane habitats but are less frequent at intermediate altitudes. *Equisetum variegatum* and *Selaginella selaginoides* still require an open habitat. All three would have been widely distributed in postglacial times. An Arctic species, *Equisetum scirpoides*, could well have been present in the Lateglacial Interstadial but could only be identified from careful examination of macro-fossils which has not been done. Three other *Equisetum* may also have been present. The ubiquitous *E. arvense* can occur at relatively high altitudes in common with all the deciduous species but only *E. pratense* and *E. sylvaticum* have a marked preference for higher habitats. *E. pratense* in Scotland is now at the south of its range in the northern hemisphere and *E. sylvaticum* is also much more common in the north of Britain.

Today some ferns are found more commonly at lower altitudes but are also found higher. *Polypodium vulgare* is one of these. *Polypodium* is commonly quoted in pollen diagrams from the Lateglacial Interstadial.

Ferns which require protection by winter snow cover suggest species which would have been well suited to Lateglacial times. *Oreopteris limbosperma* and *Blechnum spicant* grow in the central and eastern part of the Highlands and require the over-winter protection of snow (Poore and McVean 1957). *Cryptogramma crispa* grows at higher altitudes on more acidic rocks. It is a notable early stabiliser of screes within areas protected by winter snowdrifts. *Athyrium distentifolium* also requires snowbed protection as does *Athyrium flexile.* Peter Hainsworth (unpublished) has located varieties of *A. distentifolium* that show how the fern has evolved in small isolated populations. These two species would originally have been widespread but have long since been isolated. The diversity of varieties is good evidence of a former wider distribution.

Still at high altitudes today, *Cystopteris montana* grows in very damp base rich areas, with *Cystopteris fragilis* in dryer habitats up to slightly lower altitudes. Other pteridophytes growing at higher altitudes are *Dryopteris expansa, Polystichum lonchitis, Asplenium viride, Lycopodium annotinum, Huperzia selago, Diphasiastrum alpinum* and *Selaginella selaginoides* (Page 1982). All these species exist today only in sites with little competition and would have benefited from the lateglacial conditions. They were probably among the earlier colonists. The widespread abundance of *Selaginella* suggests that the mineral soil was generally more basic than at present and it would not yet have been affected by leaching. The effects of humification and the formation of an acidic layer of peat would take several centuries to influence the vegetation.

2.3 The Loch Lomond Stadial

2.3.1 Climate, Landscape and General Vegetation

The Lateglacial Interstadial was followed around 11,000 BP by a colder period characterised in Scotland by the Lateglacial or Loch Lomond Stadial (Sissons 1976) equivalent to the Younger Dryas, (Pollen Zone III). Glaciers reappeared on higher ground and areas which were not covered by ice were affected again by solifluction. Sea levels fell again as more water was locked up in the ice. On the east coast the levels were five to ten metres below the present levels but the continuing effect of isostatic depression on the west coast, from the greater weight of ice on that region, gave levels up to ten metres higher (Price 1983).

This climatic change is seen as at Corstorphine as the formation of marl was replaced by the results of hill wash. Loch Mahaick near Callander also has solifluction deposits washed in during this period. Vegetation was limited and tundra again prevailed with *Salix herbacea* and *Betula nana* indicating an open treeless landscape.

2.3.2 Pteridophytes Known to Have Occurred from Fossil Evidence

Selaginella selaginoides, Huperzia selago, Diphasiastrum alpinum, Botrychium lunaria, Polypodium, Dryopteris filix-mas, D. carthusiana, Pteridium aquilinum, Equisetum, Osmunda regalis and other undifferentiated ferns are recorded. (See **Table 2.2** for localities)

2.3.3 Other Pteridophytes Possibly Present by Inference from Modern Species and Habitats

The observations made under the previous section on the early Lateglacial Interstadial apply equally to the species involved in the Loch Lomond Stadial.

Table 2.2 Some species known at lateglacial sites from pollen evidence.

Author	Locality	The Lateglacial Interstadial		The L.L.Stadial
		Older Dryas	Allerød	Younger Dryas
Kirk and Godwin (1963)	Loch Droma Ross and Cromarty		No woodland. *Ferns* and *Huperzia selago* then *Empetrum* heath. *Betula nana* *Salix herbacea* Snow patch communities. *Selaginella* *Diphasiastrum alpinum* *Botrychium*	
H J B Birks (1973)	Loch Cill Chriosd Skye	Cyperaceae Undiff Ericaceae *Salix herbacea* *H. selago* *Botrychium* *Selaginella*	Gramineae Previous plants less. *Juniperus*	Gramineae more. Low *Betula nana* Low count other dwarf shrubs

Author	Locality	The Lateglacial Interstadial		The L.L.Stadial
		Older Dryas	Allerød	Younger Dryas
Rymer (1977)	Drimnagall North Knapdale	Cyperaceae Gramineae *Calluna vulgaris* present. ***Lycopodium annotinum*** ***L. clavatum*** ***C. fragilis*** ***Selaginella*** ***H. selago***	Cyperaceae Gramineae increasing *Salix* peak. *Calluna* present ***Undiff. Ferns*** high	*Calluna* declining. Cyperaceae and Gramineae falling. ***Botrychium.*** ***Dryopteris carthusiana*** type. Some ***Pteridium***
Donner (1958)	Loch Mahaick Near Callander		Significant amounts of *Betula* *Juniperus* high. ***Polypodium*** ***Ferns Undiff.*** ***Selaginella*** ***H. selago***	Solifluction disturbed deposits
Newey (1970)	Corstorphine Edinburgh	Cyperaceae Gramineae Open ground vegetation ***Selaginella***	*Betula and Salix* copses. *Empetrum* heath Low frequencies. *Salix herbacea* *Juniperus* Herbs, ***Lycopodium*** ***Selaginella***	Gramineae Cyperaceae ***Selaginella*** ***Lycopodium***
Dickson (1984)	Straloch Perthshire	*Empetrum* Gramineae *Rumex* and *Artemesia* *Salix* ***Undiff. Ferns*** ***Selaginella*** ***H selago*** ***Botrychium*** ***D. alpinum***	*Betula nana* *Salix herbacea* *Juniperus* *Helianthemum* More *Empetrum* and Gramineae. ***Selaginella*** ***H. selago*** ***D. alpinum*** ***Botrychium.*** ***Undiff. Ferns*** becomes less	*Empetrum* *Salix herbacea* ***Undiff. Ferns*** increasing. ***D. filix-mas*** ***L. annotinum*** ***L. clavatum*** ***D. alpinum*** ***Selaginella*** ***H. selago*** ***Botrychium*** ***Polypodium***
Moar (1968)	Little Lochans Galloway	Some *Juniperus,* *Betula* and *Salix* ***Ferns Undiff.*** ***Equisetum*** ***Osmunda*** ***Polypodium*** ***Selaginella***	*Juniperus, Betula* and *Salix* ***Ferns Undiff.*** ***Ophioglossum*** ***Selaginella*** ***Equisetum***	*Betula, Salix* Less *Juniperus* ***Botrychium*** ***Equisetum*** ***Ferns Undiff.*** increasing. ***Osmunda*** ***Selaginella*** ***Polypodium*** ***Selaginella*** less

Author	Locality	The Lateglacial Interstadial		The L.L.Stadial
		Older Dryas	Allerød	Younger Dryas
Webb and Moore (1982)	Whitlaw Mosses Near Melrose Borders	Thin *Salix* and tree *Betula* scrub Gramineae Dwarf shrub heath *Betula nana* *Dryas* heath *Undiff. Ferns* *Thelypteris palustris* -type *D filix-mas* *Botrychium* *Ophioglossum* *L. clavatum* Some *Equisetum*	Similar to (1) but more Gramineae. *Juniperus* scrub and *Helianthemum* Dryer open grass land. *Selaginella* Some *Equisetum*	*Salix herbaceae* Bare ground communities. *Juniperus* low frequency. *H. selago* *Botrychium* *Selaginella* *Equisetum* and *Undiff. ferns* increasing into Pre-Boreal.

2.4 The Pre-Boreal

2.4.1 Climate, Landscape and General Vegetation

Around ten thousand years ago the temperature began to rise sufficiently to allow other plant communities to migrate into the area. Winter temperatures especially were higher. Pennington (1969) refers to some arctic-alpine species like *Papaver alpinum* which were present in Late-glacial times but are no longer found in this country so that some losses as well as additions to the flora occurred at this time.

In this Pre-Boreal period which is Pollen Zone IV, an abundance of *Filipendula ulmaria* in the pollen record indicated that the climate was both basic and wet and becoming warmer (Pennington 1969). Fossil evidence shows that conditions were still suitable for many of the earlier Postglacial Interstadial pteridophytes like *Selaginella* with *Botrychium lunaria* and other ferns.

During this time Hazel (Corylus) and Birch (*Betula*) began to appear in the south of Scotland. They are recorded at approximately 9,700 BP at Din Moss in Roxburghshire (Price 1983). *Juniperus communis* began to increase rapidly especially further north where areas which were later dominated by *Pinus sylvestris* had initial colonisation of Juniper with

Empetrum nigrum and some Birch. H.H. Birks (1972a) suggested that the Loch Maree Juniper at its best had a fern understory. Juniper pollen and fern spores reached a maximum and then declined into the Boreal.

2.4.2 Pteridophytes Known to have Occurred from Fossil Evidence

Selaginella selaginoides, Gymnocarpium dryopteris, Dryopteris filix-mas, Polypodium, Cryptogramma crispa, Cystopteris fragilis, Huperzia selago, Botrychium lunaria, Lycopodium, Equisetum, Osmunda regalis, and other ferns have all been recorded. (See **Table 2.3** for localities)

2.4.3 Other Pteridophytes Possibly Present by Inference from Modern Species and Habitats

Better preserved areas of Juniper today have some interesting species which suggest former communities. At Creag Fhiaclach, Poore and McVean (1957) recorded an unburnt area beneath the canopy, with carpets of mosses, *Blechnum spicant* and *Lycopodium annotinum.* This *Lycopodium* also grows among Juniper at Glen Feshie. *Gymnocarpium dryopteris* is another species McVean (1964) records among fern-rich Juniper scrub and there are several occurrences in the pollen record in the Pre-Boreal.

There are several species which would have occupied the pools which were still basic. Analogies based on the species which are known, suggest other species belonging to the same assemblage. The fenland in the south-east of England, for example, suggests possible species. *Equisetum fluviatile* would have been a prominent and vigorous component. *Dryopteris cristata* is now only known from one station in Scotland, with one other older record. It would have grown well, before the natural seral succession led to increasing acidification. *Thelypteris palustris* is also now very rare and only recorded from a few localities in Scotland but would most likely have been abundant. *Dryopteris carthusiana* would probably have been very widely distributed while it is not now common. *Osmunda regalis* is the final species which would have been a conspicuous member. Except for a restricted area in the south east of Britain it is now limited in its distribution towards the west coast. *Pilularia globulifera* would probably have grown on any exposed muddy areas before the vegetation became too dense. In suitable base-rich flushed areas *Equisetum telmateia* could also have been found.

2.5 The Boreal

2.5.1 Climate, Landscape and General Vegetation

Around 9,000 years ago another change was apparent as the climate became both warmer and dryer and the Boreal period commenced (encompassing both Pollen Zone V and VI). Relative sea levels were low in Scotland but as ice sheets further north were melting, the sea level was rising in the south of Britain which was no longer linked to the Continent. While some migration was still possible, this was the end of the major influx of species by land. Lime (*Tilia*), for example, grew in the south of England but did not have time to migrate across the country to Ireland before the Irish Sea was flooded (Pennington 1969). Further colonisation would also be difficult after this time as habitats were already colonised and competition was much greater (Page 1988).

Oak and Birch became well established in the south and especially the west of the country. By 9,000 BP Hazel (*Corylus avellana*) was the dominant species in areas later to be dominated by Pine (*Pinus sylvestris*). A thousand years later mixed Birch and Hazel and Pine woods were beginning to become established. Oak and Elm (*Ulmus*) grew in sheltered valleys as far north as the Great Glen. By 8,300 BP Pine was found in the west around the Loch Maree area and was the dominant species in the Abernethy area by 7,200 BP and further east by 7,000 BP.

The spread of *Pinus sylvestris* raises some problems concerning recolonisation. From pollen records, Pine was first found in the south of England 9,500 BP and seems to have spread separately into the south of Ireland by 8,500 BP. When it was first recorded in the north west of Scotland, around 8,000 BP, it had only reached the north of England and even less far north in Ireland (H.J.B. Birks 1989). This implies an alternative local source of colonisation in the north west. It also suggests that small colonies in this area may have survived glaciation and has interesting implications for the survival of other associated pinewood species.

In the north of Sutherland, Caithness and southern Skye, Birch and Hazel were established by 9,000 BP. Other species did not become dominant until the Atlantic period. There was some Elm on the Durness limestone. Caithness only had patches of woodland in sheltered places with Willows, tall herbs and ferns (Price 1983). A similar vegetation developed on Orkney and Shetland.

Towards the end of this period, the climate generally became dryer and lake levels fell. The frequency of *Osmunda regalis* spores became less which suggests both that fens were drying up and also perhaps growing over. H.H. Birks (1972a) described a large quantity of *Isoetes* spores at Loch Maree but these declined, possibly due to increasingly organic muds. *Diphasiastrum alpinum* recorded from Loch Maree indicated that some open vegetation was still present on higher ground. Birks suggested that the Juniper persisted as an understory in the forest, and also above the tree-line with sub-alpine species. At Snibe Bog in Galloway, *Lycopodium clavatum* was the *Lycopodium* which best survived into more closed vegetation, presumably of an upland heathy type (H.H. Birks 1972b). *Lycopodium clavatum* grows on the dryer tops of any undulations and benefits from open gaps in the vegetation. It can also grow through moderately tall heath.

Pteridium aquilinum first appeared at Loch Maree (H.H. Birks 1972a) after the Juniper had begun to decline along with the general reduction of ferns. At the Nick of Curleywee, Moar (1968) observed the same phenomenon of *Pteridium* only appearing after other pteridophytes are past their maximum. Juniper only produces abundant pollen when there is little shade competition. With a greater tree cover it produces more vegetative growth, cones less frequently and consequently appears less in pollen diagrams, before it is eventually shaded out of very dense woods. This indicates the general increasing density of vegetation which reached a climax in the Boreal. The early advantage of open habitats that pteridophytes had enjoyed was no longer available and they thereafter colonised actively eroding habitats or became more minor members of the general vegetation.

Pteridium aquilinum requires shelter, deep soil, good light, and suitable edaphic conditions, neither waterlogged nor liable to dry out. In the dense woodland interior there would not have been enough light, although there would have been adequate moisture and shelter from wind. With large fronds *Pteridium* cannot tolerate a lot of wind. Outside the wood there is inadequate shelter so that the margin or glades are best. The smaller subspecies, *Pteridium aquilinum* subsp. *latiusculum* described later, would have been better able to survive in wind. There were many factors influencing the early stages of colonisation and an explanation for the observed sequence of high pollen and spore frequency is not always easily found with the limited information available.

2.5.2 Pteridophytes Known to have Occurred from Fossil Evidence

Isoetes, Osmunda regalis, Pteridium aquilinum, Polypodium, Dryopteris filix-mas, Lycopodium, Equisetum and other ferns were all present. (See **Table 2.3** for localities)

2.5.3 Other Pteridophytes Possibly Present by Inference from Modern Species and Habitats

Poore and McVean (1957) described the present-day Durness limestone flora as typical of a northern woodland. Including as it does such species as *Dryas octopetala, Trollius europaeus, Sanicula europaea* and *Polystichum lonchitis,* the flora would have been similar to those early base-rich woodlands. Another genus not normally associated with woodland is *Woodsia*. Both species of *Woodsia* are found on montane rocks but are now very rare. With a higher treeline and more general forest cover, *Woodsia ilvensis* could have grown on screes and rocks within the mixed Pine and Juniper woods. As screes extend a considerable distance down the side of a mountain from the unstable rock face, the habitat which screes provide can be found at comparatively low altitudes. The provision of periodic new habitats due to the unstable surface, prevents permanent colonisation and favours species like *Woodsias*. It has been found among relict Juniper in Glen Feshie (Page 1988).

Similarly flushed areas would always remain open habitats suitable for species like *Selaginella, Equisetum variegatum* and *E. hyemale.* The present-day Morrone Birkwood near Braemar, with mixed Juniper and Birch, has flushes with these species.

The possibility of a warmer dryer climate would favour different ferns from those now present. Those which now grow in the south of Britain would have been found very much further north. There are several species which have adaptations to resist drought, usually growing on rock faces. They include *Asplenium septentrionale,* now very local, *Asplenium billotii,* now only found in the south-west of England, *Ceterach officinarum,* now mainly western, and *Polypodium australe* now from the south and west. These could have grown in suitable rocky habitats much more widely than at present.

Due to more extensive woodland shade, *Pteridium aquilinum* would have been a minor component of the undershrub. Recent discoveries of different subspecies of Bracken (Page 1989b), suggest that from this early time there would have been two subspecies. Where the natural vegetation was an open mixture of Scots Pine and Juniper, *Pteridium aquilinum* subsp. *latiusculum* would have grown. This subspecies is found around the northern hemisphere in conifer woodland and was probably the first subspecies to arrive. The few known sites from Speyside and Perthshire represent remnants of what may have once been an extensive distribution. The other subspecies has western affinities and possibly migrated from the south of Britain later during the Atlantic period.

2.6 The Atlantic

2.6.1 Climate, Landscape and General Vegetation

After almost two thousand years, the Boreal period was succeeded by the Atlantic, (Pollen Zone VIIa), which was still warm but with much more precipitation. It has been suggested that the closed forest cover absorbed this increased precipitation (Price 1983). The continued rising sea level reached a maximum during this time. There was no date at which the levels were equally high around the country, as again the areas of maximum isostatic depression from the weight of the ice took longest to recover. The highest points of sea level transgressions are found with younger dates the further they are away from the main areas of depression. On the east coast the maximum was reached just before 6,000 BP, but the maximum was earlier further north in the west. The Solway Firth did not experience the maximum transgression until 5,000 BP. Around 6,000 BP Scotland was nearly cut in two and was connected by only a narrow piece of land to the east of the present Loch Lomond, which was then a sea loch (Price 1983).

In the Outer Hebrides the sea level had been rising continuously since 13,000 BP until 5,700 BP. Shell sand on the continental shelf was swept before the rising seas and when blown by the wind gave rise to the present machair (Price 1983). Similarly the sand dune systems and shingle banks around the entire coastline owe their origin to the higher sea levels from around 6,000 BP. This dates the earliest vegetation found in these areas. Twenty percent of the Scottish coastline is made up of dunes, links and machair (Price 1983). The dynamic nature of the dune systems offer frequent new habitats which combine with the effects of wind and exposure to reduce the competition.

Orkney and Shetland, by way of contrast, have been experiencing a transgression since 6,600 BP. Before that time more land was emergent and submerged peat has been found nine metres below the present sea level (Price 1983).

The carselands in the Forth, Tay, Upper Clyde and Solway were flooded. Earlier peats were covered by carse clays. When the sea level fell again, as isostatic equilibrium was established, marshes developed. These were colonised by sedges, mosses, more peat and then woodlands (Price 1983).

By 7,600 BP peat bogs were growing, especially above 360 metres (1,200 ft), where Alder (*Alnus glutinosa*) and Birch woods were replaced by peat covered by *Eriophorum* and *Sphagnum*. Pine and Birch remains of this period have been found at up to 790 metres (2,600 ft) in the Cairngorms Price 1983). Much of the country was covered by forest except for mountain tops where *Calluna vulgaris* made its first significant appearance at this time. The appearance of *Calluna* marks the beginning of extensive acidic areas and shows a significant change in available habitats. Pine was the dominant tree in the Cairngorms, Strathspey and the area north-west of the Great Glen (Pears 1966). The only open habitats available were on mountain tops, shingle beaches, river banks and screes, although Caithness, Orkney and Shetland never attained a complete forest cover but had tall herbs and ferns with some scrubby Birch and Hazel (Price 1983). In the southern part of Scotland Alder replaced Willows between 7,000 and 6,500 BP. There was another rapid increase in Alder at 6,000 BP which occurred rather earlier further north at 6,500 BP. Raised bogs grew over old lake sites.

Towards the end of the period the climate deteriorated and there was an increase of Birch at the expense of other trees, such as Pine.

2.6.2 Pteridophytes Known to have Occurred from Fossil Evidence

Pteridium aquilinum, Polypodium, Osmunda regalis, Dryopteris carthusiana, Selaginella selaginoides, Huperzia selago were all present. (See **Table 2.3** for localities).

2.6.3 Other Pteridophytes Possibly Present by Inference from Modern Species and Habitats

There are some species which now grow only in extreme habitats but which could have been more widespread with a more favourable climate. With the Atlantic climate, a second subspecies of Bracken, *P. aquilinum* subsp. *atlanticum* (Page 1989b) would have grown well. It is now present in the west of Scotland and the colonies are thought to be relict. It may have arrived by migrating up the west coast. In its present habitat it grows on flushed basic rocks. This is not usual for *Pteridium* as it prefers acidic habitats. The fronds are very late in expanding and require a longer growing season than the plants currently experience, suggesting that it grew more successfully when the climate was warmer. The other subspecies, *P. a.* subsp. *latiusculum,* flushes very early in the spring and seems better adapted to a shorter high-latitude season. Unfortunately it is not possible to identify the various subspecies from the spores collected in pollen diagrams.

The appearance of more acidic habitats and a more humid environment would favour many species which could only have grown on rocks or screes which were themselves acidic. The Filmy Ferns, *Hymenophyllum wilsonii* and *H. tunbrigense* would have been less restricted towards the west coast than at present. The small remnants further east indicate that most of the country may have been colonised in suitable places. *Trichomanes speciosum* has a very restricted distribution now. During the Atlantic period the climate would have favoured the establishment of the west coast colonies. *Dryopteris aemula,* also now very western, would have been found in acidic woods over the lowlands within Scotland generally.

The brackish marshlands left by falling sea levels would have offered extensive new habitats. *Equisetum palustre* grows at the top of the present-day saltmarshes at Aberlady in East Lothian and would have been very probably found in those marshes. As the marshland became freshwater, *E fluviatile* would occupy pools and other species like *Dryopteris carthusiana* and *Osmunda regalis* would enjoy the Atlantic climate.

The climatic deterioration at the end of this period would possibly have reduced the eastern distribution of the more frost-sensitive species like the Filmy Ferns.

2.7 The Sub-Boreal

2.7.1 Climate, Landscape and General Vegetation

This period (Pollen Zone VIIb) was cool but dryer. Around this time, 5,000 years ago, the first farmers began to make an impression on the vegetation. There had been Mesolithic hunters from the early Boreal. Some early fires indicated by charcoal horizons in both the Boreal and Atlantic at Loch Maree (H.H. Birks 1972a) may have been hunters deliberately making use of fire (Piggott 1982) but they would have had a small impact compared with the effect of agriculture (Millman 1975). In the north east of Scotland the earliest agricultural clearances were near the coast, often on raised beaches which were left as the sea level continued to fall until 2,000 BP. Here, the light soil would have supported a scrubby vegetation which was more easily cleared. The clearances are identified in pollen diagrams by a fall in tree pollen. The people used already well-developed methods of agriculture. Their culture identifies them with the Late Neolithic or Bronze Age period. (Durno 1957)

In north Europe generally there is a decline in tree pollen at this time. Earlier fluctuations can be attributed to climatic factors but these reductions have associated features. There is a marked "Elm Decline " implying a selective use of the tree, possibly as animal fodder. But the decline also seemed to occur where there is no evidence of human interference and was more probably caused by something like Dutch Elm Disease. However, as the Elm and other tree pollen declines there is often an increase in the pollen of *Plantago lanceolata*, a typical weed of cultivation (Pennington 1969). When the Beaker Folk were living in the north east (approximately 4,000 BP) the clearances extended further inland with the use of bronze axes (Durno 1957). The typical "slash and burn" method employed involved small clearances in the forest which were cultivated until the soil became impoverished. Evidence for this is found all over the country. In Galloway the reduction in tree pollen is first most notable at 5,000 BP. In Roxburghshire it is seen at 5,440 BP, while it is 5,014 BP in the Forth Valley and 5,300 BP near Loch Lomond (Price 1983).

Durno (1965) described typical sequences from Dalnaglar in Glenshee, Perthshire. Using pollen taken from a raised moss basin Durno described undisturbed forest cover below peat 3.6 m deep. At 3.2 m and again between 2.6 to 2.4 m, *Plantago* pollen appears and the amount of Elm diminishes. There are irregular quantities of Elm between 2.4 m and 1.3 m and above this there is always *Plantago* present and very low amounts of Elm. This indicates a first episode of clearance at 3.2 m, and a longer phase at 2.6 m. Moar's pollen diagram (1968) of the Moss of Cree described a high correlation between tree cover and fern abundance. There is a sporadic appearance of *Pteridium* which is a frequent feature following land clearance and subsequent abandonment.

In upland areas, or on the light soils of the lowlands, podsols developed after clearance, supporting a heath vegetation instead of regenerated forest (Pennington 1969). In the Cairngorms there is no evidence of anthropogenic activity but the proportion of tree pollen still declines at the transition from the Atlantic to Sub-Boreal (Pears 1966). The dryer climate favoured the development of grasses, sedges and *Calluna* instead of trees. This suggests that the decline in tree cover was a natural change due to climate but in certain areas it was accentuated by man's activities.

This period saw the most significant increase in *Calluna vulgaris*. It had been present since the early postglacial but increasing podsolization and a drying peat surface encouraged the large scale colonisation. Very occasional fires would have occurred from lightning or human agency but the *Calluna* would usually be able to follow its own cycle with plants of different ages offering variously open habitats.

2.7.2 Pteridophytes Known to have Occurred from Fossil Evidence

Pteridium aquilinum, and other ferns were present. (See **Table 2.3** for localities) As the pollen diagrams become more recent less information is available.

2.7.3 Other Pteridophytes Possibly Present by Inference from Modern Species and Habitats

Page (1989b) suggested that at some point after the arrival of both *Pteridium aquilinum* subsp. *latiusculum* and *P. a.* subsp. *atlanticum* hybridisation occurred. With areas being cleared and then left with only pioneer vegetation, abundant habitats were made available for hybridisation. The change from the dryer Boreal to the wetter Atlantic climate would have left relict areas of *P. a.* subsp. *latiusculum* in localities later colonised by *P. a.* subsp. *atlanticum,* Probably the same hybridisation occurred in many different places giving a range of types more or less like either parent. Page proposed that it is the vigorous hybrid which is now the commonest form of Bracken and that the two parent subspecies have been largely displaced.

As few of the pollen diagrams cover more recent material there is not very much spore evidence of former species. In view of the increase in *Calluna* moorland at this period, it is appropriate to look at present day species-rich *Calluna* moorland. Here, the pteridophytes include *Blechnum spicant, Lycopodium clavatum, L. annotinum* on slightly flushed slopes and *Huperzia selago* colonising any exposed or eroded area. On higher ground at the upper limit of *Calluna, Diphasiastrum alpinum* occurs, and open peaty areas with permanent flushing are suitable for *Lycopodiella inundata*. These species would probably all have been more abundant than at present.

2.8 The Sub-Atlantic

2.8.1 Climate, Landscape and General Vegetation

By 2,500 years ago the comparatively cold and wet Sub-Atlantic period had commenced, which still continues. Peat bogs started to grow again, sometimes very rapidly. Higher level Birch was swamped by the spreading bogs and the area occupied by Pine was also reduced. Shallow-rooted Pine would be particularly vulnerable to being blown over. H.H. Birks (1972a) suggested that at Loch Maree 4,200 BP, *Pteridium* was able to expand into the areas created by exposed roots. The tree line was around 700 metres (2,300 ft) compared with 500 metres (1,600 ft) today. Pears (1966) demonstrated a similar tree-line in the Cairngorms 4,000 BP. The highest tree-line Pears discovered was 800 metres (2,600 ft) 7,000 BP. Strong winds in the Atlantic Period depressed the tree line, and the Sub-Boreal conditions have further affected the optimum level. The removal of trees has also affected the remaining tree line by removing shelter. Leaching due to the high rainfall has led to poor regeneration and increased podsolization.

The geographical distribution of ferns was coming closer to the present distribution. Minor climatic variations would have had local influences but the main effect came from changes brought about by human agency in modifying the environment and generally reducing the species variety. In the next chapter the anthropogenic effect is followed, through changing methods of agriculture and the demands made upon the environment to provide the raw materials for a developing civilisation.

Table 2.3 Showing changes in the Flandrian vegetation in different parts of Scotland

Author	Locality	Pre-Boreal 10,000-9,000 BP	Boreal 9,000-7,000 BP	Atlantic 7,000-5,000 BP	Sub-Boreal 5,000--2,500 BP	Sub-Atlantic 2,500 BP-present
Durno (1958a)	Loch na Moine Jessen-Godwin pollen zones	IV *Betula* with rising amounts of *Corylus*	V & VI *Betula* and *Corylus* with rising amounts of *Pinus*. *Quercus* and *Ulmus* very infrequent	VIIa *Alnus* rising *Corylus* present Falling *Pinus* High Ericaceae rising to very high *Betula* replacing *Pinus*		
Durno (1958a)	Cnoc a Broillich Jessen-Godwin pollen zones	IV *Corylus* and *Betula* scrub	V & VI *Betula* and a little *Pinus* Ericaceae peak just before Atlantic	VIIa *Alnus* small increase *Pinus* higher all other trees lower Gramineae Cyperaceae Ericaceae and *Betula*		
Durno (1958a)	Braehour Jessen-Godwin pollen zones	IV Gramineae Cyperaceae Ericaceae High count *Selaginella* before rise in *Corylus*. *Pinus* and *Betula*	V & VI *Pinus* and *Betula* *Corylus* maximum. Low *Ulmus* *Tilia* *Quercus*	VIIa *Alnus* slowly increase with *Betula*. *Pinus* and *Corylus* less	VIIb Ericaceae Gramineae *Betula* all increasing	
Durno (1958a)	Quintfall Jessen-Godwin pollen zones	IV Rising *Corylus*	V & VI *Pinus* high but falling. *Betula* high. *Quercus* and *Ulmus* very low	VIIa *Alnus* rise *Betula* remains high	VIIb Ericaceae and *Sphagnum* fluctuating but increasing. *Betula*	
Durno (1958a)	Flows of Leanas Jessen-Godwin pollen zones	IV *Betula* high	V & VI *Corylus* and *Betula* high then declining. *Pinus* fluctuating	VIIa *Alnus* rising *Corylus* fluctuating and declining *Quercus* and *Ulmus* very sparse		

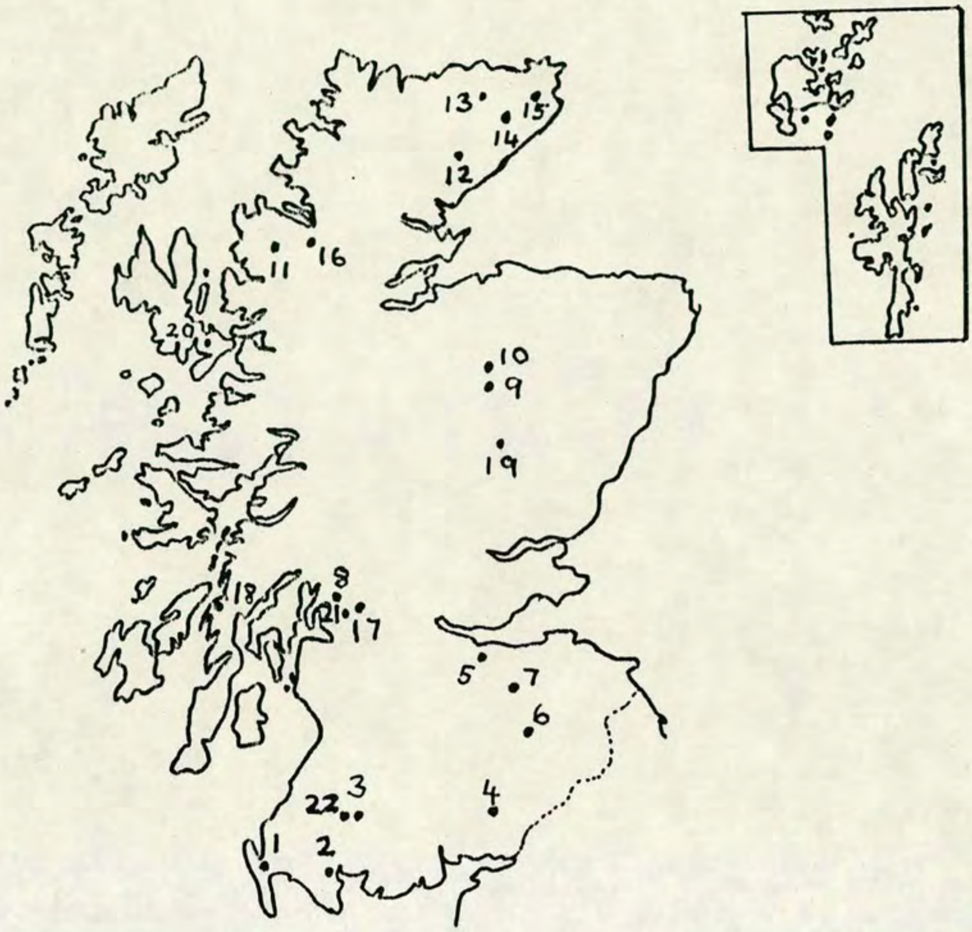
Author	Locality	Pre-Boreal 10,000-9,000 BP	Boreal 9,000-7,000 BP	Atlantic 7,000-5,000 BP	Sub-Boreal 5,000--2,500 BP	Sub-Atlantic 2,500 BP-present
Pears (1966)	Carn Mor Cairn-gorms Author's pollen zones		VI *Corylus* and *Betula* give way to *Pinus*. *Ferns* high and then decline	VIIa & VIIb Rise in *Alnus*. Ericaceae and *Sphagnum* high. *Betula* more successful than *Pinus*. Large *Pinus* stumps. No *Elm* Decline No *Plantago* Ericaceae high		VIII Slight *Alnus* rise Increase in Gramineae Cyperaceae *Sphagnum* and Ericaceae
H H Birks (1972a)	Loch Maree Author's pollen zones	LME-1 Later than in south *Empetrum* decreases as *Juniperus* expands. 9,085 BP at max. Undiff *Salix* scrub Cyperaceae Gramineae Montane spp ***Gymno-carpium dryopteris Dryopteris filix-mas Polypodium Crypto-gramma crispa Cystopteris fragilis Huperzia selago***	LME-2 &-3 8,950 BP for base *Betula* with some *Corylus* and *Myrica Salix* scrub and similar ferns less. **Isoetes** high 9,000-8,100 BP ***Osmunda*** abundant Tall herbs. *Quercus Sorbus* and *Ulmus* low values. *Pinus* becomes abundant 8,250 BP.with ***Pteridium*** *Juniperus* on upper forest margin with sub-alpine flora ***D alpinum H. selago G dryopteris D filix-mas*** Some *Calluna* ***General ferns*** and ***Osmunda*** declining at end	LME-4 6,513 BP for base *Alnus* higher ***Dryopteris carthusiana Osmunda*** increase *Pinus* high then falling 7,000 BP. *Betula* higher Gramineae and *Calluna* rising 6,000-5,000 BP ***Pteridium*** still present ***Selaginella H selago*** continue Elm Decline of possibly only distant pollen to half previous level. 5,150 BP First *Plantago Corylus* and *Myrica* high	LME-5 4,200 BP First signs of possible human disturbance. *Pinus* and *Quercus* rapidly lower. 4,000 BP More herbs grass and dwarf shrubs A little *Plantago*. No settlements known very near. More *Alnus* and *Betula*. Natural bog expanding. Less ***Pteridium*** and ***D.filix-mas*** as tree cover diminished	*Pinus* on south shore *Quercus* on north shore. Gradual decrease of forest and increase of Ericaceae

Author	Locality	Pre-Boreal 10,000- 9,000 BP	Boreal 9,000- 7000 BP	Atlantic 7,000- 5,000 BP	Sub-Boreal 5,000- -2,500 BP	Sub-Atlantic 2,500 BP- present
Dickson (1984)	Straloch Perth-shire Author's pollen zones	S4 Fen *Salix* *Betula nana* *Gramineae* *Empetrum* heath Gramineae **Polypodiaceae** increase with ***D. filix-mas*** - type	S5 & S6 *Juniperus* scrub replaced by **ferny** *Betula* woods. *Empetrum* *Betula nana* **Polypodiaceae** and ***D. filix-mas*** then declining. Later *Betula* and *Corylus* woodland *Salix Ulmus* and *Quercus*	S7 Large aquatics then Cyperaceae Later higher values of *Pteridium* and *Calluna*. Peaty deposits thereafter		
Lowe (1982)	Mollands near Callander Perth-shire Author's pollen zones	Mo-b,c & d *Betula* and *Juniperus* 10,670-10,480 BP *Betula* becoming dominant. varying amounts of *Corylus*. Mo-d 9,365 BP High *Corylus* *Ulmus*, *Quercus*, *Alnus* present ***Equisetum*** particularly well represented	Mo-e & Mo-f *Corylus* declining, *Salix, Alnus* and *Pinus* increasing. More Gramineae and Cyperaceae. Eventually *Pinus* and *Betula* dominant	Mo-g *Alnus* dominant *Quercus* and *Ulmus* at maximum. *Betula* lower, *Pinus* almost disappears at top of zone. Elm Decline at boundary. *Plantago lanceolata* found. ***Polypodium*** and ***Equisetum*** high	Mo-h Very little *Pinus* and *Ulmus*. Increase of *Betula* and *Corylus, Alnus* still important. *Quercus* reduced More Ericaceae, Gramineae and *Sphagnum*. *Salix* almost disappears. *Plantago* pollen ***Filicales*** decline	
H J B Birks (1973)	Loch Cill Chriosd Skye Author's pollen zones	LCC-6 &7 *Gramineae* *Juniperus* ***G. dryopteris*** ***Undiff.Ferns*** Abundant 9,650 BP *Corylus,Betula, Sorbus, Populus*. ***Undiff Ferns*** less abundant. ***Polypodium*** and ***Pteridium***	LCC-8 *Corylus* more abundant than *Betula*			

Author	Locality	Pre-Boreal 10,000- 9,000 BP	Boreal 9,000- 7,000 BP	Atlantic 7,000- 5,000 BP	Sub-Boreal 5,000- -2,500 BP	Sub-Atlantic 2,500 BP- present
Stewart, Walker and Dickson (1984)	Dubh Lochan near Loch Lomond Authors' pollen zones	DL-1 *Empetrum* Dwarf shrubs and herbs Gramineae Cyperaceae *Juniperus* rising then falling to *Betula* High fern count ***Lycopodium*** and ***Selaginella*** ***D.filix-mas***	DL-2 &-3 9,356 BP *Betula* *Corylus* wood Tall herbs *Ulmus* and *Quercus* in sheltered places near end of DL-3 A little ***Pteridium*** Rise in *Pinus.* Fall in herb and shrub pollen	DL-4 Mixed *Quercus* ***Polypodium*** spores increase 5905 BP *Alnus* rise Elm Decline end of period at 4900 BP. No obvious agricultural link. Fluctuating abundance of ***Isoetes*** spores	DL-5 *Quercus* woodland with *Ulmus* and *Betula.* Gramineae proportion rises. High *Salix* count	DL-6 Mixed woodland until 1,000 BP Clearances 1,600 to 950 BP and from 800 BP Pollen from agriculture, *Calluna* and bog species Tree pollen declining except for coppiced *Oak* in last 400 years High *Myrica,* and *Sphagnum* pollen
H Birks (1972b)	Snibe Bog Galloway Author's pollen zones	SB-1 Species-rich grassland Flowering *Juniperus* ***C. crispa*** ***H. selago*** ***D alpinum*** ***Botrychium*** ***Selaginella*** ***L.annotinum*** ***Polypodium*** ***G. dryopteris***	SB-2 & 3 *Juniper* falls *Betula* and *Corylus* expand Closed vegetation. *Pinus* expanding 7,400 BP	SB-4 Forest Equilibrium between 7,000 and 5,000 BP. *Pinus* f alls as *Alnus* rises *Quercus* and *Ulmus* present	SB-5 *Elm* Decline 5,000 BP Two zones of *Plantago* with ***Pteridium.*** Mixed woods *Betula* and *Pinus* on higher ground	Increased sediment implies clearance and erosion
Newey (1966)	Side Moss Southern Uplands Jessen-Godwin pollen zones	IV Mineral solifluction deposits *Empetrum* *Betula* woodland	V and VI *Corylus* with *Betula* then high *frequency of Quercus.* Low *Pinus*	VIIa High *Alnus.* *Quercus* still present but beginning of raised bog	VIIb *Elm* decline. Bronze Age forest clearance *Plantago lanceolata* found	VIII Peat. Some *Betula* and *Corylus* scrub. *Quercus* and *Alnus* decline. Ericaceae, Gramineae, Cyperaceae

Author	Locality	Pre-Boreal 10,000-9,000 BP	Boreal 9,000-7,000 BP	Atlantic 7,000-5,000 BP	Sub-Boreal 5,000--2,500 BP	Sub-Atlantic 2,500 BP-present
Moar (1968)	Little Lochans Galloway Author's pollen zones	FI *Betula*. Increasing *Juniperus*. ***Equisetum*** declining. ***Undiff Ferns*** increasing ***Botrychium Polypodium***	FII & FIII *Juniperus Betula* and *Corylus*. ***Osmunda regalis*** several high counts	FIV *Alnus* increasing. *Betula* decreasing. *Sphagnum* ***Osmunda*** abundant ***Polypodium*** *Corylus* more at end		
Moar (1968)	Nick of Curley-wee Galloway Author's pollen zones	FI *Juniperus Salix* and *Betula Empetrum* heath ***H.selago*** abundant ***Undiff Ferns*** Abundant ***Selaginella Lycopodium Botrychium***	FII & FIII *Corylus* and *Betula* Less *Juniperus* Some *Pinus* and *Ulmus*. Less ***Lycopodium*** and ***Ferns***. ***Equisetum***	FIV *Alnus* increase. Some *Pinus Quercus* and *Ulmus*. Less *Corylus* and *Betula* ***Ferns*** less ***Pteridium*** and *Calluna* more	FV Declining *Ulmus Pinus* and *Quercus* ***Pteridium*** and *Calluna* increasing. *Corylus* and *Alnus* increase at end of Sub-Boreal	
Moar (1968)	Bigholm Burn Galloway Author's pollen zones	FI 9,470 BP *Juniperus Betula Salix Pinus*. *Corylus* rise ***Equisetum***. ***Fern*** increase and decline. ***Osmunda***	FII & FIII *Salix Juniperus* and *Betula* declining. *Pinus*. *Corylus* at maximum. FIII 7,735 BP ***Equisetum Pteridium***	FIV 5,475 BP *Alnus* increase. *Ulmus* and *Quercus* present Less *Corylus* and *Pinus* ***Pteridium***	FV More *Corylus Calluna* increasing *Alnus* continues. ***Pteridium***. ***Ferns*** declining	

Figure 2.1 Map of Scotland showing localities for pollen diagram sites



1. Little Lochans
2. Moss of Cree
3. Nick of Curleywee
4. Bigholm Burn
5. Corstorphine
6. Whitlaw Mosses
7. Side Moss
8. Dubh Lochan
9. Carn Mor
10. Abernethy
11. Loch Maree
12. Loch na Moine
13. Cnoc a Broillich
14. Braehour
15. Quintfall
16. Loch Droma
17. Loch Mahaick
18. Drimnagall
19. Straloch
20. Loch Cill Criosd
21. Mollands
22. Snibe Bog

Chapter 3

The Impact of Man on Pteridophyte Habitats from Neolithic Times to the Eighteenth Century

3.1 The Causes: Exploitation of the Land

In the following sections there is a chronological consideration of the impact which man's farming activities and use of natural resources, together with small scale climatic variations have had on the vegetation. References to the occurrence of pteridophytes are incorporated within the general background. Many agricultural and industrial practices had very early origins and continued with little change for thousands of years. While more recent farming and other practices have irretrievably altered some habitats, many other semi-natural habitats which have been created during the last five thousand years have survived until the present day as a product of the continuing management regimes.

3.1.1 Agriculture

Like the hunters before them, the farmers colonised coastal areas which were more accessible than were the densely forested inland areas. Large forest trees were more difficult to clear than scrub, which may have influenced the choice of earlier settlements. Areas preferred for cultivation were the lighter soils near the coast which extended up the estuaries, along river margins and lochsides. The falling sea levels after 6,000 BP had left a coastal fringe of light soil suitable for early agricultural methods (Morrison 1985).

The Neolithic farming economy seems to have been well developed before it was introduced to this country. Wheat (*Triticum* spp.) and barley (*Hordeum* spp.) were grown and the people kept cattle (*Bos primigenius* later *B. longifrons*), sheep (*Ovis* spp.), goats (*Capra hircus*), pigs (*Sus scrofa*) and dogs (*Canis lupis* derived). Part of their food on Orkney, for example, was derived from the sea but the people had brought sheep and goats which were presumably thought most suitable. Pigs which were at that time kept in woodland were not found among the remains on Orkney which suggests that the woods were not sufficiently extensive to support them (Piggott 1982). On Shetland the settlements were more spaced out with distributions very similar to modern crofts. Traces have been found of five or six fields enclosing a total of about one hectare (2.5 acres) (Piggott 1982). The sheep and goats would have an immediate effect on the vegetation, reducing taller herbage. If they were not too abundant they could have fulfilled a useful role maintaining open habitats for the smaller species of pteridophytes like *Botrychium lunaria* and *Ophioglossum vulgatum* which could not flourish below dense vegetation.

It appears that the earliest methods of cultivation did not return nutrients into the soil and relied heavily on using new sites until they became exhausted, probably after two years. Domestic animals would have provided some fertility. The forest took up to sixty years to regenerate after being cleared (Whittington 1980). This would have provided an opportunity for other species to expand at the appropriate point in the seral succession. In these clearings, abandoned after the short phase of cropping, there would have been tree seedlings which without excessive grazing can regenerate satisfactorily. In the thin shade of saplings the typical woodland species would begin to re-establish: *Dryopteris filix-mas* in more basic woods, *Athyrium filix-femina, Blechnum spicant, Dryopteris dilatata* and *D. affinis* subspp. on more acidic soil. *Pteridium aquilinum* subsp. *aquilinum,* may have found newly abandoned areas very favourable for expansion. As ferns are pioneer species, and the disturbances would be on a small scale, at least initially, there should always be local plants to provide spores for new plants.

There is also the possibility of spores remaining in the soil from the previous woodland phase. Samples taken from a present-day woodland have contained spores to a depth of at least 95 cm. Cultured soil samples have usually produced gametophytes most abundantly in the top 15 cm with diminishing numbers growing in the lower samples (Lindsay and Dyer 1990). As cultivation would have disturbed this surface layer it is possible that even without a local source of spores new sporophytes could have grown in the regenerating woodland.

Excavations at Balbridie on Deeside demonstrated the existence of a large wooden building with carbonised cereal grains of emmer (a form of wheat), barley and breadwheat which gave radio-carbon dates of 5,500 BP (Beith 1990b). This indicates that cereal plants were grown from early times as a staple crop until the large-scale introduction of turnips and potatoes which was comparatively very recent. Arable weeds accompanied agriculture and it is possible that *Equisetum arvense* began its long association with cultivated ground at this time. Cultivation lessens competition, with which *E. arvense* cannot compete, but with a deep underground rhizome *E. arvense* can survive shallow cultivation.

Stone axes were used at first, with bronze and copper introduced around four thousand years ago. Iron was coming into general use by 700 BC but an ard plough with a sharp pointed stone was still used to break up the ground. Below a Roman fort at Elginhaugh near Dalkeith there were marks left by such a plough although the area had actually been grassland when the Romans built on top (Hanson 1986).

Remains found in water-logged artificial island homes called crannogs at Loch Tay have been dated 595 to 190 BC. Ploughs and digging implements were found, together with materials used for spinning, weaving and working iron. A map which Morrison (1985) made shows the close correspondence between old pre-improvement field systems and the distribution of the crannogs along Loch Tay. Most of the crannogs are near good arable land. This indicates the establishment of a pattern of agriculture which continued with very little change until the improvements in the eighteenth century. The land was divided into strips running up the hill away from the loch. The lower part would have been cultivated and the higher ground used for summer grazing. Some old ploughed rigs from more recent eighteenth century farming can still be seen on the better land.

In the concluding chapter of *Scotland Before History* Piggott (1982 p90) wrote "..the whole structure of the pre-industrial agrarian economy, and with it the basic rural technology of carpenter, wheelwright and blacksmith, potter, thatcher and hurdle-maker, could be said to have been fully formed at the advent of Agricola."

The Roman era was dryer and warmer than at present (Lamb 1966). This would have influenced the crops which could be grown. But general agricultural change was very slow and seems to have changed very little over thousands of years. From the Western Isles, there are remains of sheep bones and weaving combs indicating a continuing history of sheep-grazing on these islands (Piggott 1982).

From 400 to 1200 AD there was a second climatic optimum which was most favourable between 800 and 1000 AD (Lamb 1966). It is perhaps significant that the main Viking raids began just before the ninth century AD. The climate would have been more appropriate for wider ranging travel in comparatively small boats than it is now. The Vikings, too, brought their contribution to house types and local customs.

The monasteries founded by the Normans from the twelfth century owned large estates and had a strong influence on the surrounding people and countryside. In the south of Scotland they introduced some improved farming methods, most notably large-scale sheep farming in the Borders. They had orchards, gardens and rabbit warrens. They were also involved in the earliest ventures into coal mining and the extraction of salt from sea water (Mackie 1962).

Materials found in excavations in medieval Perth showed that people shared at least part of their houses with animals. They had sheep, cows, and goats, but only a few pigs. They also kept hens. They ate wheat, oats (*Avena sativa*) and barley. Turnip (*Brassica rapa*) seeds were found representing new introductions which were later re-introduced with a greater impact. Hazelnuts (*Corylus avellana*) were discovered in quantity in addition to local apples (*Malus sylvestris*), blackberries (*Rubus fruticosus* agg.) and strawberries (*Fragaria vesca*), all identified from their seeds (Perth Archaeology Support Group 1984). The flourishing Hazel trees suggest an ideal habitat for ferns. Preferring slightly basic soil *Dryopteris filix-mas* would do well and possibly also *Gymnocarpium dryopteris* and *Phegopteris connectilis. Polystichum aculeatum* could have been found in adequately basic soil and if it was warmer, *P. setiferum* would have had a wider range than now. An abundance of nuts does suggests a good climate to ripen them.

Dodgshon (1980) found that by 1100 AD there were extensive settlements and subsequent expansion was into the surrounding "waste". This demonstrated the encroachment on to land which had previously been more difficult to cultivate, such as moorland, forest and rough grazing. But from 1200 to 1400 AD the weather was very changeable with alternating floods and droughts, mild and severe winters. With this climatic deterioration some of the higher settlements were abandoned although traces of field systems can still be seen on aerial photographs. Also at the end of the thirteenth and beginning of the fourteenth century the thirty year War of Independence was fought and the country suffered badly. The better farming land tended to be on the routes despoiled by invading armies. Birks (1972) referred to some regeneration of forest in Galloway around this disrupted period so that some areas must have been very severely depopulated. Abandoned farmland was ideal for *Pteridium aquilinum*, the ridge and furrow system of ploughing providing the drainage which Bracken requires. Damp, neglected hollows on upland areas were suitable for *Oreopteris limbosperma* and *Blechnum spicant*, although they would require adequate drainage. From 1400 to 1550 AD the weather was warmer than the preceding colder period (Lamb 1966) so that agriculture would have been more successful again.

Mackie (1962) described the landscape at the beginning of the sixteenth century. The southern part of the country had few trees. This had an influence on the success of agricultural practices. Small "ferm touns", groups of a few houses, were distributed at irregular intervals along the valley-sides. There were no field divisions as the traditional farming runrig field pattern was in use. The runrig system of intensively cultivated ground was organised so that individuals had shares of strips of land in different aspects which may or may not have been redistributed at intervals. Their wooden ploughs were pulled by eight oxen. Several neighbours had to combine to make a plough team (Mackie 1962). Owing to drainage problems cultivation was usually not directly on the valley floor. When ploughed, the soil was ridged into the centre of the rig to encourage drainage as there were no field drains. During wet periods any hollows between rigs would have had more or less permanent standing water forming ponds or boggy areas (Fenton 1987). There were alternate strips of weedy ground as paths in between the cultivated rigs (Grant 1961). These ridges and furrows can still be seen where modern ploughing has not destroyed the pattern. Duddingston golf course in Edinburgh is a well-preserved example (Fig 3.1). De Wit's plan of Edinburgh shows the pattern of these rigs outside the city wall.

Figure 3.1 Runrig on Duddingston Golf Course seen from Arthur's Seat, Edinburgh.

Even in full cultivation, the rigs must have offered a habitat for many kinds of wild plants. The boggy areas like small ponds may have been occupied by *Equisetum fluviatile, E. palustre, Dryopteris carthusiana*, and, if kept open by occasional trampling, perhaps even *Pilularia globulifera*. The dryer areas like paths between the rigs, described above as "weedy", were very likely occupied by *E. arvense.*

With regional variations and different names, the lower part of the hillside up to the level of the head-dyke was cultivated and the hillside beyond was used for grazing. The rigs on the infield or inbye low down on the hill, were manured regularly and cropped annually. Animal manure from the byres was used as well as seaweed, peat-ash and the smoke-saturated turf removed when the houses were re-roofed. Oats and bere, (a form of barley), were the major crops grown. The rigs in the outfield or outbye, on the higher valley sides beyond the head-dyke were manured by the animals which were penned in by temporary turf dykes and were cultivated less frequently (Fenton 1987). In the more populated lowlands the outfield would be cropped more often and the people may not have had the benefit of distant grazing or common pastures beyond the head-dyke found in more Highland regions (Dodgshon 1980). There was careful regulation of the stock on the infield. All animals were excluded to beyond the head-dyke, from the time crops were planted. Permanent pasture beyond the occasionally cultivated areas could be heathland with a predominance of *Calluna vulgaris.*

Very small houses called shielings were used on the higher ground beyond the head dyke where the people lived while herding the cattle in the summer. The cattle formed a substantial part of the farming economy. Some sheep and goats were also kept and individuals were allowed to keep so many sheep or cows according to the "soum" they had been allocated. The total number of stock for the grazing available depended on the animals' ages and varied from region to region. Some terrain could obviously support more animals than others. In the Outer Hebrides, for example, one cow was the grazing equivalent of eight sheep (Fenton 1980).

The traditional Highland sheep were small animals with a thin fleece and were kept in "sheep cotes" at night. They were kept for milk as well as their wool and were mainly for the people's own use. Grant (1961) suggested that approximately the same number of cows as sheep were kept. Goats also seem to have been kept in quite large numbers and their destructiveness was recognised as they were not in favour once the improvements were being introduced from around 1745. Pigs were not generally very popular or extensively kept (Grant 1961).

1550 to 1850 has been called the Little Ice Age and Mackie (1962) records that when the Earl of Leven crossed the Tweed in the mid-seventeenth century, bringing men to fight in the Civil War, the Tweed was frozen. This incident indicates the extreme cold which would have been encountered and again has implications for agriculture.

By the sixteenth century a market was beginning to be established for cattle which were driven to England. After the Union of the Parliaments in 1707 many drove roads were used to herd the cattle on their way south. These tracks were not always well defined and were more like broad through-routes. In Lowland areas the routes were restricted to preserve the crops (Haldane 1952). Overnight stops were at ten to twelve mile intervals (16 - 19 km.). Haldane states that greener parts of the countryside showing the drove roads and the stopping places can still be identified. Such enrichment of permanent pasture would have been beneficial for *Ophioglossum* and *Botrychium*. It was usual to drive the cattle in a lean state and they were fattened in English fields. Fenton (1980) suggested that this practice resulted in over-grazing and that people did not necessarily adhere to their allocated souming.

More intensive grazing meant that pteridophytes would be under increasing pressure. Over-grazing would restrict the range to inaccessible ledges and implies that such remaining habitats have been refuges for many centuries. Alpine ferns like *Athyrium distentifolium* may also be affected by the fluctuations in the weather. A series of prolonged, wet, damp years could cause many plants to rot and die. Erratic weather with late frosts also has a marked effect on most ferns which have frost-sensitive foliage. While another flush of fronds is produced after an unusual spring, weakening of the plants is inevitable if the pattern is repeated. If at the same time the hills are suffering from overgrazing the range would be reduced yet again.

At the beginning of the eighteenth century political events combined to bring to an end the system of farming which had not greatly changed in the Highlands for hundreds of years. After the 1715 Rebellion, General Wade set about building roads and bridges from 1724 onwards, in an attempt to subdue the Highlands by providing easy access for troops and incidentally opening up the country to new ideas. Then in 1745 there was a second Rebellion.

The effects of the Forty-five Rebellion were very far reaching. The people who had been involved were dealt with very harshly. Their homes and crops, sometimes their woods, were burned. Many were taken prisoner and executed, transported, exiled or died of ill-treatment. The chiefs lost their traditional role of judge and were no longer able to call upon their people to make up what had effectively become a private army. This weakened the links within clans and hastened the end of former loyalties. Many estates were forfeited from 1715 and when more were annexed in 1745, Commissioners were appointed who took a very deliberate managing role in an attempt to change the Highlands (Mackie 1962).

In the Lowlands changes had already begun to take place. From before the end of the seventeenth century the success of the cattle trade had encouraged early enclosures in Galloway. Although the "Levellers" were actively destroying dykes from 1724-25 it was only when the land became enclosed that major changes were effected on the landscape (Donnachie and Macleod 1974).

3.1.2 Timber and Turf Construction

<u>Turf</u>

The stripping of turf must have been one of the earliest forms of disturbance. A Neolithic barrow at Fettercairn used an estimated 0.73 hectares of turf which effectively impoverished the ground for some time to follow (Whittington 1980). The Antonine Wall built by the Romans between the Forth and Clyde had a stone base but was mainly constructed of turf. It was 3 metres high (10 feet), 1.8 metres (6 feet) wide on top and there was a 3.6 metres (12 feet) deep, 12 metres (40 feet) wide ditch on the north side (Ritchie 1972). For nearly 60 kilometres (37 miles) across Scotland it represented a considerable disruption of the local soil and vegetation with tree felling and turf stripping. It has been estimated that a strip of turf extending 50 metres from both sides of the line of the wall would have been required. Pollen information showed that the countryside was open grassland and heathland (Keppie 1986). Such stripped areas would have offered another opportunity for the establishment of *Pteridium aquilinum* from spores.

Turf was a traditional material for the poorest kind of hut dwelling. In the absence of an abundant local source of stone it was used to build head-dykes which can still be seen. Hunter (1883) refers to turf dykes used by tenants for surrounding their corn-yards in the more populated lowlands. Again, such open ground was suitable for more *Pteridium*. This practice may well been another encouragement in its early spread following the first clearances. Traditionally turf was taken from the outfield for use as fuel in areas where there was a very poor supply of wood and no peat. This depleted the fertility which had been built up over the years. Brien (1989) suggests that this practice contributed to the impoverishment of many upland areas. It would also make the topsoil less deep.

Cromwell took turf for the ramparts of a citadel he built at Perth in 1651 from the North and South Inch (N.S.A. 10 1845) and turf continued to be used as a common building material until at least the nineteenth century. In the nineteenth century the North Inch was noted for the occurrence of *Botrychium lunaria*. "This singular fugitive is found plentifully on the much-trodden North Inch of Perth" (M'Nab 1920 p72). Presumably turf removal would not extend deep enough to affect the deep rootstock although the fertility of the ground would be reduced. It is possible that the exposure of such a large area of bare ground facilitated the establishment or rapid spread of the *Botrychium*. Weed seeds would have been removed with the turf and would have had to blow in from elsewhere. The competition in a closed turf community would have been less for at least one season.

Timber

The earliest farmers have left few remains to indicate their types of houses. Probably they made a greater use of wood than later builders and this has not been preserved. In the absence of abundant timber supplies most houses and internal fixtures were made of stone. Skara Brae is a well-known example. The hill forts which were built from early Sub-Atlantic times used timber to consolidate the rubbly core. It has been estimated that at least 24 hectares (60 acres) were felled to build a small fort at Abernethy (Ritchie and Ritchie 1972).

A hill fort built at Hayhope Knowe in Roxburghshire during this period had palisades and fences. These seemed to have been made primarily of Alder and it has been estimated that 3.6 hectares (9 acres) of woodland would have been required to obtain the necessary wood (Ritchie and Ritchie 1972). At Harehope the timber was set into an earth bank which would have required less wood. This may have been a development as the wood supply became less abundant.

An early Sub-Boreal site estimated to be five thousand years old has been discovered in North Uist (Dean 1989). Built on an island which became waterlogged, the organic material present has not decayed. Seeds including grain and hazelnuts were found along with querns and stone axes. There were thick stone outer walls with wattlework for internal partitions and fences. This indicates that there may have been management of woodlands by coppicing from very early in settlement history. Coppicing would have been the easiest way to obtain a large quantity of branches of uniform thickness.

The North Uist site is similar to the type known as crannogs. These were settlements built on either heaps of stones, wooden piles or a mixture of both on the shallow shelves of lochs. Their position offered defence from enemies, protection for stock from wild animals and reduced the danger of rodent attacks on food supplies. The crannogs could have been in permanent use or only inhabited during particular need. Crannogs in various forms were inhabited until comparatively recent times. There are references to seventeenth century occupations at least during times of unrest. Morrison (1985) mentions these later records and although he gives the dates of already substantial early structures in Loch Tay from around 595 BC to 190 BC, new evidence from the same sites at lower levels of occupation may extend the dates back nearer to that of the North Uist settlement. The regular straight lengths of timber used in the Loch Tay crannogs (Morrison 1985) again suggest that pollarding was practised to obtain suitable wood.

Later settlements have remained more conspicuous in our time as they had defensive ramparts. In the early part of the Sub-Atlantic period more substantial settlements were being made. Many of these structures date from around 700 BC (Piggott 1982) which is the approximate date of the arrival of the Celts in another wave of immigration. In the north and west small fortified homesteads were constructed called brochs and duns. In the east, hill forts housing several families were more common while crannogs were still widely occupied in suitable localities.

In constructing roads, timber was cut along the margins of roads. Cadell (1913) refers both to the existence of a Roman road and the marks of Roman axes on felled trees which had grown on Flanders Moss. There was a marked clearance illustrated by Turner at Flanders Moss 100 AD and an anthropogenic cause is suggested (Pennington 1963). The forest was cleared in some cases to minimise danger from wild animals, but the Romans were probably trying to prevent ambush. As it was standard practice to clear an area on either side of Roman roads, this would constitute a substantial de-forestation. Anderson (1967) estimated that the Romans spent a large part of their time clearing the woods, especially the thin birchwoods of the Southern Uplands.

The first church on Iona in the sixth century was made of wattle and daub, until logs were floated over from the forests on the mainland and a larger structure built (Mackie 1962). Most of the other buildings were beehive-shaped huts made from stone without mortar, or wattle and daub.

The Viking houses varied according to the materials available, with flag-stones in Orkney and local field-stones or volcanic rock on the west coast (Brøndsted 1965). They were also known in their own countries to have made use of turf, driftwood, wattle and daub, rough planks of wood or logs joined in something like the log cabin style. Their habitations were not unlike the later blackhouses, first with a single room shared with the animals and later with internal partitions.

Excavations in medieval Perth have revealed the structure of the ordinary people's houses. There was a basic frame made from large pieces of timber. These were in short supply and had been re-used. The walls were made of wattle from coppiced Hazel or Alder. The roofs were thatched with straw, *Calluna, Pteridium* or coarse grasses. Samples of all these have been found on the site. (Perth Archaeology Support Group 1984).

The choice of materials for building houses gives an indication of the availability of timber. The massive timber hall at Balbridie (5,500 BP) was 28m long by 14m wide and would have required a considerable amount of wood. It also illustrates the Neolithic ability to cut timber with stone axes (Beith 1990b). While other examples of this type have only been tentatively suggested, there must have been many structures of this kind, all requiring timber. The crannogs built on Loch Tay from at least 600 BC used large oak timbers. But in medieval Perth there was evidence that the larger pieces of wood were in sufficiently short supply to merit re-use. This was the case with the few roof timbers used in the construction of the blackhouse type of dwelling, which were the most valuable part of the house. The Normans must have had access to substantial timber supplies to build their wooden towers in the twelfth century but the Abbeys were being built of stone and it is probable that the forests were already very much reduced to distinct localities.

By the fifteenth century timber supplies in the Southern Uplands and Midland Valley of Scotland were not adequate. In 1457 an Act of

Parliament was passed which required "that all their tenants plant woods and trees, and make hedges, and saw broom" (Hunter 1883). An Act of Parliament in 1503 specified that landowners should "plant at least ane acre of wood, where there is na great woods of forests" (Hunter 1883), but with limited success. Another Act of Parliament passed in 1535 in James V's time continued the attempt to compensate for the shortage of timber. It said "that every man having an hundred pounds land of new extent, where there is no wood, plant, and make hedges and haining, extending to three acres, and that the tenants of every merk land plant a tree" (Hunter 1883).

James IV had difficulty in finding enough wood for ship-building at the beginning of the sixteenth century (Mackie 1962). The largest ship which he built, the *Great Michael*, reputedly used all the large timber from Fife, except from the Falkland area. In 1651 Cromwell built a citadel at Perth on the South Inch. He used trees from Falkland and stone from existing buildings (N.S.A.S. 10 1845). It is interesting that he used trees from the Falkland area; it is tempting to speculate whether this was the only major source left unexploited.

Heron (1799) records that at Cromarty there had been a large forest in the days of James V of which no trees were then remaining.

Charles II passed an Act of Parliament in 1669 "that every heritor, liferenter, or wadsetter [bondholder], worth £1000 of valued rent, enclose yearly for ten years next ensuing, four acres of ground, and plant the same with oak and other trees, at three yards distance" (Hunter 1883). The Acts requiring tree planting reflect an increasing need, but not until the beginning of the eighteenth century was planting commenced on a large scale.

The common people's buildings did not in any case have a long life as, especially in the west, they were often built of a double drystone wall without mortar infilled with earth or sand with only a small amount of wood in the roof supports (Grant 1961). There would have been several old houses on all the sites at any time. The traditional black house, without windows or a chimney, can be traced back to medieval times (Dodgshon 1980).

Houses in many places were still little changed from the earlier patterns with variations depending on tradition and local building materials. Clay was used, if available, between the stones or sometimes alternate layers of turf and stone (Fenton 1987). There were still clay houses at Errol on the Tay Estuary at the end of the eighteenth century (The Third Statistical Account of Scotland, Perth and Kinross 1979). Clay houses had been built in various parts of the country and Fenton (1987) illustrates a surviving example photographed in 1973.

The roofs were thatched with *Calluna, Juncus, Ulex, Molinia* or *Pteridium* stems laid on large pieces of turf on a framework of branches (Grant 1961). Less durable thatches like the grass ones were replaced annually. The thatch became saturated with peat-soot and was used as a fertiliser. Brander (1980) quoting from the Court book of Glenorchy at the beginning of the seventeenth century referred to the fern which must be cut for the Laird's thatching.

The earliest stone walls like those at Skara Brae were made without mortar. Clay may have been used to fill gaps but a double wall with sand or earth in the middle would have been windproof. The houses must have been very damp, especially where the roof drained into the cavity between the walls. With the thick double drystone walls of the Outer Hebrides type there was often a broad ledge into which the water would drain off the roof. The north side of such a house in a sheltered spot would have offered a suitable habitat to acid-loving ferns like *Dryopteris affinis,* although the habitat would not be very enduring. Present-day remains of these old houses, found as an un-mortared rectangular heap of fieldstones, often have *Dryopteris dilatata,* and *Cryptogramma crispa* has also been seen. *D. dilatata* can grow in the high levels of nitrogen which would be found around old settlements.

By the end of the seventeenth century there were stone houses built with mortar for farm workers of two or even three storeys, as at Lasswade in

Midlothian (Whyte 1980). It was mainly during the improvements of the eighteenth century described in Chapter 4 that mortar became widely used for anything other than important houses or castles.

3.1.3 The Search for Fuel: Wood, Charcoal and Peat

Wood was the first and most easily acquired fuel. With the increasing necessity to provide wood for smelting metal the demand increased. Newey (1966) suggested that the reduction in forest at Side Moss in the Moorfoots was due to a combination of grazing cattle and the use of timber both to build forts and to make charcoal. Iron was smelted at Castlelaw Fort in the Pentlands.

Clearance was started at Ben Eighe in the north west as early as the ninth or tenth century. Timber was being used for charcoal burning from Loch Maree in this area from the twelfth to the seventeenth centuries (Durno and McVean 1959). The Loch Lomond woods had several bloomeries for smelting iron ore (Tittensor 1970). There were also furnaces at Bonawe on Loch Awe (Pennant 1769), Abernethy (Birks 1970), and Inveraray (Heron 1799). As General Wade began to build better roads from the 1720s onwards, access for extracting timber was very much easier.

The earliest written records of coppicing were for monastic land in Perthshire in the 1470s (Lindsay 1980), but the existence of wattlework as much as five thousand years ago has already been referred to on Uist (Dean 1989). Contemporary evidence examined by Lindsay (1980) indicated that the forests were already much reduced before timber was used to make charcoal for iron smelting. The Loch Maree woods were managed as coppice (Bunce 1969). Hunter (1883) refers to coppiced areas within many woodlands in Perthshire, at Dunira, Garvock, Methven and Cambusmore, as an incidental part of his description of woods. Heron (1799) recorded coppices on both sides of Loch Ness. Millman (1975) states that most of the woods around the Firth of Clyde were being managed on a short rotation for Oak but the Upper Forth Valley rotated on a twenty-four year cycle. Most of the trees were cut to regenerating boles but a few trees were left to provide larger timbers which would also provide bark for tanning. Birch was also grown to be burned for potash (Pennant 1769).

The woods were usually cropped in sections which would allow recolonisation into adjacent areas should the species there have suffered unduly. With a period of rotation somewhere in the order of twenty to twenty-five years, there would be ample time for ferns to establish and mature. With proper management, and exclusion of stock in the earliest stages of regeneration, a more productive woodland would be encouraged than the degenerate scrub with grazing animals which would otherwise have prevailed. This would benefit the maturation of sporelings on disturbed ground until they reached maturity. All the woodland species could have benefited from these conditions, with perhaps only a check in the earlier years until a reasonable amount of shade was re-established. Coppicing continued in some form into the early twentieth century but was at a peak at the end of the eighteenth (Lindsay 1980).

As the people had little ability to drain bogs such a habitat would not have been substantially disturbed. Peat cutting would have accounted for a certain amount of disturbance of the habitat. These effects would have been small-scale and may have had a beneficial result in the new flooded areas which were thus created. A sphagnum bog is an appropriate habitat for *Lycopodiella inundata*. This species is not at all common now but was known in more sites last century and may have been much more extensive with suitable habitats available. There are references to this species growing in England, often associated with "turf cutting" (Newman 1844, Branfield 1852). This may have lead to a greater abundance in the past when such activities were on a smaller scale than now.

3.1.4 Traditional Uses of Pteridophytes

Traditional uses imply that a species was abundant, as uncommon species would soon have disappeared altogether and their continued use would not be possible.

Bracken is the most commonly found pteridophyte with numerous uses. One of the earliest recorded findings was at Vindolanda, a Roman Fort near Hadrian's Wall in the north of England. Bracken had been strewn on the floor, presumably with a similar function to rushes. Because Bracken is toxic it is of use in providing a form of bedding with built-in insecticide. Its widespread usage by Roman times suggests a long history. It was used for both human and animal bedding. From the evidence of one small room used to store Bracken, it has been estimated that at least one hectare (2.5 acres) would have been cut annually (Seaward 1976). Bracken was also found at Perth dating from the thirteenth or fourteenth century. It was laid on the floor and used as bedding, in common with other materials like straw (Perth Archaeology Support Group 1984).

The potash-rich ash of Bracken was also used. The burnt remains of young green fronds were mixed with water and made into balls, left to dry in the sun and then used as soap. The ash was also sold to England to be used in the manufacture of soap and glass (Fairweather 1975).

Bracken fronds were used in dyeing to give a yellow colour. Several other pteridophytes were used as well. *Polypodium* fronds also gave a yellow dye. The spores of *Huperzia selago* were used as a mordant instead of alum as were those of *Lycopodium clavatum*. *Equisetum arvense* gave a grey dye (Fairweather 1975).

Among organic remains in medieval York, fragments have been found of *Diphasiastrum complanatum* and *Lycopodium clavatum* (Page 1988). It is assumed that the shoots were for dyeing purposes. *D. complanatum* has not been recorded growing in Britain, but hybrids with *D. complanatum* have been found indicating that the species must have at one time been present. Nevertheless it is assumed that the material from York was imported as it occurred in such large quantities. Remains at Perth gave some additional medicinal plants not previously known from the fourteenth century in Scotland. Both *Diphasiastrum alpinum* and *Lycopodium clavatum* spores were found and these were known to have been used in the treatment of intestinal worms which were apparently found in other remains (Perth Archaeology Support Group 1984).

Diphasiastrum alpinum was also used as a very effective emetic (Thompson 1988).

For general medicinal purposes in use until recent times *Phyllitis scolopendrium* ointment was used for burns. *Polypodium* fronds made a preparation used for catarrh. *Asplenium trichomanes* was used for disorders of the spleen. *Dryopteris filix-mas* was used for worms. *Equisetum arvense* was applied to a wound to staunch bleeding (Fairweather 1975).

Equisetum arvense was used for pot-scouring as the silicious coating on the stems made a useful mild abrasive. It is known that *Equisetum hyemale* was imported from Holland in medieval times for use in fine work like polishing metal and arrows (Page 1988). It would be reasonable to suppose that the native supplies were used in a similar way in Scotland.

There is a particular colony of *Equisetum hyemale* growing on calcareous sand-dunes in Sutherland. These plants are different from the usual upright thick-stemmed British type. With thinner more prostrate stems it closely resembles the Danish ecotype which also grows on calcareous sand-dunes (Page 1988). As this part of the coast-line was frequently attacked by invading Vikings, it is possible that these plants grew from fragments dropped by Danes who had been using the plant to give a final polish to their weapons and armour (McHaffie 1990).

An early use of a pteridophyte is found in the *Osmunda regalis* spores which were used along with large quantities of *Calluna vulgaris* and *Filipendula ulmaria* pollen mixed with honey in the brewing of mead. This is known from remains adhering to pottery found on the Island of Rum (Page 1988).

There is a story about the origin of the name for *Osmunda regalis* told in Gerard's Herbal. Lankester relates the tradition about Osmund "that a waterman of this name, dwelling at Loch Fyne, on one occasion bravely defended his family from the cruel Danes, and sheltered them among the tall branches of this magnificent plant" (Lankester 1903 p85). The story is set in a western area which was much troubled by the Vikings.

3.2 The Consequences: The Changing Pteridophyte Habitat

3.2.1 Man-made Habitats

The Romans were the first people to use mortar in Scotland, principally in the Antonine building phase (AD 142-165) when stone structures were provided for all the more important buildings using dressed stone and mortar. The mortar was made with lime. There was also plaster on the interior of some walls. This would have been the first opportunity for lime-loving species like *Asplenium ruta-muraria*, *A. adiantum-nigrum*, *A. trichomanes* subsp. *quadrivalens*, *Polypodium interjectum* and *P. australe* to occupy the habitat in which they are now so abundant. The lime which was used in the mortar was much softer and decayed more easily than the present portland cement which was only introduced at the beginning of the nineteenth century (Page 1988), although lime mortar continued to be extensively used.

Botrychium has been found growing on Roman camps near Newbattle, Midlothian and at Ardoch in Perthshire. Possibly the local enrichment of lime has made these sites more favourable for its growth.

The widespread use of mortar did not occur again until medieval times when the abbeys were built. Castles, harbours and bridges also were constructed using dressed stone and over the next few centuries the use of mortar increased. Towns like St Andrews, Dundee, Edinburgh and Perth had defensive walls.

Ruined buildings and old walls constructed with mortar made a very different habitat from turf houses. When these buildings fell into disuse, or were deliberately destroyed during times of war, the species which first flourished more abundantly on old Roman walls could expand again and the creation of such calcareous habitats has lead to an enormous expansion of such species, some of which like *Asplenium ruta-muraria* are not very often seen in a natural outcrop.

By the seventeenth century all the mansion houses would have been built of stone. It was not until the eighteenth century that mortar was used generally in buildings when the improved houses were being introduced for farm tenants (Grant 1961).

3.2.2 Woodland

During the last five thousand years woodland has declined and there has probably been a reversal of the relative abundance of woodland ferns and those preferring open habitats. Since the first major advent of human interference, the recurring picture has been one of forest clearance followed by modified forms of regeneration. The process has been a gradual, usually small scale, erosion of the forest, but the cumulative effect has been very substantial. To a certain extent, it would have been an advantage to pteridophyte species to have new habitats created at infrequent intervals. Pteridophytes are, quite notably, pioneering species, but the diversity has been influenced and some species have had the opportunity to spread far beyond their previous limits.

The extensive woodland cover before Neolithic times would at most have been affected by occasional deliberate burning to drive game. Pears (1966) refers to small scale natural fires in the Cairngorms before there was any suggestion of human causes. The "slash and burn" clearances for agricultural purposes would have probably taken some time to seriously diminish the woodland.

Orkney in Sub-Boreal times had at best Birch and Hazel scrub and heathland. There may have been a cooler period around 5,000 BP which discouraged tree growth on more exposed areas like Orkney. Dated occupation on Orkney began around 4,800 BP (Keatinge and Dickson 1979) and it is thought there may have been some open areas before people began to colonise the area.

At Creag na Cailleach just north of Killin in Perthshire, a five thousand year old stone axe factory has provided peat samples for pollen analysis. Below the lowest signs of occupation the pollen showed that the immediate environment was rough pasture, not the woodland which might have been expected (Beith 1990a). This does suggest that quite extensive areas may have been cleared from early times.

When iron was introduced from 1,000 BC bronze axes were still much used. But the advent of iron axes had a major influence on the vegetation. Previously it had been possible to clear land with sufficient time and effort, but now the scale escalated. The largest forests would still essentially remain although grazing animals would encroach on the margins and inhibit regeneration. Any further grazing would have been discouraged by wild animals.

Woodland animals present in Scotland in postglacial times, were Great Elk (*Alces alces*), giant Fallow Deer (*Dama dama*), Reindeer (Rangifer tarandus), wild Horses (*Equus carabalus ferus nel*), the Great Ox (*Bos primigenius boj*), Beaver (*Castor fiber*), Boar (*Sus scrofa ferus*), Wolf (*Canis lupus*), Brown Bear (*Ursus arctos*), Lynx (*Lynx lynx*), Lemmings (*Lemnus* sp), and Variable Hare (*Lepus variabilis*) (Price 1983). The Great Elk became extinct when there was no longer a large enough forest to support it. Many of the other animals gradually disappeared. The Brown Bear was last known from the tenth century, the Reindeer in the twelfth century, the Beaver with the Wild Boar survived into the fifteenth or sixteenth century. The last Wolf in Scotland was killed in the eighteenth century. All these animals imply the former existence of a habitat which is no longer there.

The postglacial Red Deer (*Cervus elaphus*) were much larger than the present smaller variety. At Vindolanda, south of Hadrian's Wall, these larger bones of Red Deer were found, indicating that conditions would still have been very favourable with enough open forest providing ample grazing (Seaward 1976). Pollen diagrams from Vindolanda, show the establishment in the area of open woodland appropriately dominated by Oak with Alder gaining the ascendency during wetter phases. An increase in *Sphagnum* and Alder marked the Sub-Atlantic period. Then there was a clearance episode associated with the Roman occupation but the tree cover had already declined. As the arboreal pollen continued to decrease, there was a large rise in Ericaceae, grasses, sedges and *Pteridium*. There were two phases of *Pteridium* increase. The first is associated with de-forestation accompanying the Roman occupation in the area. The second phase came later when the Angles arrived to colonise the east coast, and the Vikings were active in the west (Seaward 1976).

As part of their plundering and raiding the Vikings set fire to some areas of woodland (Millman 1975). Birks (1972) refers to the Vikings which were based in Galloway around 800 AD. They made use of the Oak trees for ship-building thus adding to the de-forestation which first became apparent four hundred years before in an earlier clearance episode. Evidence from pollen diagrams based on Loch Dungeon, showed that the earlier clearance had led to podsolization and partial de-forestation. So before the Vikings arrived there was already some open grassland and more dwarf shrubs and heathland.

From the eleventh century with the arrival of the Normans, timber towers were built with accompanying earthworks and palisades. Excavations at Yester Castle in East Lothian revealed Boar tusks and gave an indication of nearby forests (Croal 1873).

Tittensor (1970) observed that by 1405 the woods around Loch Lomond had separate names so that the people no longer occupied clearings among woods, but the woods were in open spaces. The Loch Lomond area would probably have remained wooded longer than many areas.

The Drumselch (Drumsheuch) Forest which covered a large area to the south of Edinburgh was given to the Burgh of Edinburgh in 1143 by David I. The area was a common muir, called the Burgh Muir, but remained well-wooded until the trees, including many Oaks, were felled in the sixteenth century (Smith 1978).

Brander (1980) quotes from the Court book of Glenorchy in the seventeenth century that all the tenants were required to plant a specified number of trees annually and not to cut down young trees. Wood was only to be cut by people with a licence. Despite this, there were court cases against people who were still cutting wood. Legislation indicates it must have been a substantial problem.

The period in the 1640s and 1650s during the Civil war had been very unsettled, but the rest of the century was comparatively peaceful. But after Charles II had been restored to the throne in 1660, landowners began to extend their tower houses or build large country houses with gardens and without the fortifications which had previously been necessary. Yester House in East Lothian was built at this time and by the end of the century was surrounded by large plantations of trees (Whyte 1980). These walled parks were the beginning of later much more extensive plantations. A protective enclosure was necessary to exclude stock.

During the eighteenth century more thought given to the countryside as a whole and ambitious planting schemes were initiated by many landowners. "The Society of Improvers" was founded in Edinburgh in 1723 (Hunter 1883) and encouraged its members to plant new woods and save what remained of the existing ones. Large planting schemes were carried out and other societies were founded which offered prizes to who ever had planted the greatest number of trees in a given period.

At Tyninghame in East Lothian in 1705, Thomas, the sixth Earl of Haddington imported Dorsetshire farmers who introduced the first of the new methods which spread from this area. Shelter belts were planted and grass seed was sown. Three hundred acres near the sea were planted with trees. The local people did not expect trees to survive so close to the sea, but they flourished, and the Binning Wood is still a conspicuous local feature (Ritchie 1880).

With a new interest in cultivating plants and using them medicinally, the Physic Garden was founded at Holyrood in Edinburgh in 1670. With several changes of site this later became the Royal Botanic Garden (Fletcher and Brown 1970).

The 1715 and 1745 rebellions caused problems in the creation of a planned landscape. The destruction of houses and crops seems to have been a regular part of warfare. The woods have also suffered. At Rannoch, Pennant (1769) recorded that Robertson of Struan had part of his estate burned and confiscated after the Forty-five Rebellion. Layers of charcoal are not uncommon throughout Highland woods indicating substantial fires through recent historic time (Durno and McVean 1959). After Glenmoriston was forfeited in 1746 the whole area including part of the estate was burnt. The Woods of Leny also suffered in 1749 (Anderson 1967). Mackenzie (1987) has compiled a map based on Roy's map of Scotland showing the small area of woodland left in 1750.

The stable woodland environment, as could perhaps be envisaged before the main human influence began to take effect five thousand years ago, would have been suitable for several genera. In more basic deciduous woods, *Dryopteris filix-mas, Equisetum pratense, Polystichum aculeatum, Phegopteris connectilis, Gymnocarpium dryopteris* and *Phyllitis scolopendrium* would have been found. A remnant of this kind of woodland is still seen at the Hermitage of Dunkeld in Perthshire. With sufficient base-rich flushing *Equisetum telmateia* and *E. hyemale* would also have been present as in the more southerly ravine at Roslin in the Lothians. *Polystichum setiferum* occurs on the east coast further south than Edinburgh, but occasional records northward imply a wider spread in a previously warmer climate.

Acidic areas of deciduous woodland would have had *Dryopteris affinis* subspp. and *Dryopteris dilatata* in the dryer areas. *Dryopteris carthusiana, Athyrium filix-femina, Blechnum spicant, Oreopteris limbosperma* and *Equisetum sylvaticum* would have been found in the lower-lying damper parts. Further towards the west there would have been *Dryopteris aemula*, with Filmy Ferns on old tree trunks. The forests and steep river valleys around Benmore in Argyle still represent these associations.

Oakwood is associated with the more fertile valley-bottoms along with Ash and Elm. Hazel can grow well as an understory to Oak and probably extended on to higher ground with Birch. Alder would have been present in the damper areas. Anderson (1967) estimated that large areas of moderately fertile hillsides would have been covered by Birch-Hazel scrub until grazing pressure eventually caused its decline. Hazel perpetuates a fertile soil, but once it is removed the soil would become progressively leached and acidic. The intermediate to basic soil below Hazel is a suitable habitat for *Dryopteris filix-mas, Gymnocarpium dryopteris, Phegopteris connectilis* and *Equisetum pratense* which is not now at all common. A small strip of woodland beside the River Garry in Perthshire has these species.

Pinewoods on the poorer soil would have had a subdued understory of *Pteridium,* probably with a wider distribution of *Pteridium aquilinum* subsp. *latiusculum* than at present. In a naturally regenerating wood there would have been areas of different degrees of shade as young trees grew up and older ones which eventually died were blown down to produce a temporary clearing. *Calluna vulgaris* grew beneath the trees with only patches of *Pteridium.* No element of the vegetation was solely predominant but there was an ever-changing mosaic as the different species benefited from the various phases of each other's life-cycle. This association can seen naturally regenerating at Rothiemurchus in Strathspey. *Lycopodium clavatum* would have grown among the *Calluna* in the gaps which occurred as the plants matured. In an uneven-aged community the diversity was great. *Lycopodium annotinum* is another species of definite pinewood affinities.

A third probable clubmoss is *Diphasiastrum alpinum.* Several plants have been found which are intermediate between *D. alpinum* and the Continental lower altitude species *D. complanatum.* The Scottish records were found in what is now moorland, but may have once been Pine forest, especially at lower altitudes. The hybrid also occurs in sub-alpine heath. The occurrence of a hybrid implies the former presence of both parents unless the partially fertile hybrid spread by spores (Page 1988). *D. alpinum* would certainly extend down into the upper margins of pinewoods and ample opportunity for hybridisation would have been presented. While the majority of plants of *D. complanatum* must have long since gone, presumably due to a deteriorating climate and progressive loss of habitat, the possibility still remains that some may have been overlooked.

These upper margins of the pinewoods would have had more open habitats suitable for *Juniperus communis* which is found at or above the treeline (Poore and McVean 1957). It is killed completely by fire and with heavy grazing cannot regenerate. Juniper is a more naturally restricted community than many others and seems to have been markedly reduced. Fenton (1935) suggested that the few Junipers found in the Trossachs area may be the survivors of open Pinewood which has long since gone. Junipers standing alone in a field are often all that remains of woodland. McVean (1957) found Juniper on some islands in fresh-water lochs in the west, where there was no longer any Juniper at all in the surrounding country. These islands were not burned, but the occasional presence of deer inhibits regeneration. Burning and grazing have had this effect on Juniper for at least five thousand years. Species particularly associated with Juniper are *Blechnum spicant, Lycopodium annotinum, Gymnocarpium dryopteris* (Poore & McVean 1957) and *Woodsia ilvensis* (Page 1988).

With local disturbance the woodland species would have been able to recolonise into adjacent areas and the earliest farming episodes probably did not make a very big impact. But pressure intensified and areas which had been cleared did not have the same opportunity to regenerate. Quite apart from the initial clearance, the grazing animals would have had a significant effect. While the forests were still inhabited by large predators like wolves the domestic animals would have been herded and their influence more local. The disappearance of the forests and the wolves was effected at the same time because the forests were known to have been burned to destroy the wolves (Millman 1975). Thereafter regeneration was inhibited by the domestic animals especially sheep which could be kept in increasing numbers and although they would not have been so likely to eat ferns, they would have created a more open habitat which would not have been so suitable. Small animals like mice (*Apodemus sylvaticus*) and voles (*Microtis agrestis*) would also have been able to destroy regenerating seeds more than if their natural predators had still been more abundant (Tansley 1953). In the most favourable areas of cultivated land at low altitudes, only steep sided ravines would have remained as woodland. The management of coppiced woodland, on the other hand, would probably have been to the advantage of woodland ferns. When the trees were cut from the slopes below Kinnoull Hill, there was a large increase in the quantity of wild flowers which were found. With replanting, the abundance is already being reduced (3rd S.A.S. 27 1979). In the woods at Methven, *Corallorhiza trifida* was found in the mid-nineteenth century. It had not flowered when the coppice had just been cut but required more shade. Other orchids were listed from the same wood with *Paris quadrifolia* and *Convallaria majus*. These woods have been coppiced for hundreds of years (N.S.A.S. 10 1845).

3.2.3 Moorland

The vegetation which is now associated with open heath would originally have been more restricted in distribution. The heath was confined to windswept ridges and mountain tops. As the forests were gradually cleared, by burning and cutting, the composition of the flora of large areas became considerably modified. Pollen diagrams from Loch Maree in the north west, Carn Mor in the Cairngorms and Dubh Lochan near Loch Lomond, all show an increase in pollen of *Calluna* and that of grasses and sedges at the expense of trees. *Pteridium* spores also increase and the suggestion has already been made that the cleared forest made a very suitable environment for hybridisation and the subsequent rapid spread of *Pteridium aquilinum* subsp. *aquilinum*. The tree decline was apparent as early as the Sub-Boreal and is most pronounced into the Sub-Atlantic. It marks the progressive spread of lower level moorland over former woodland areas. With a lighter, more fertile soil, grassland could develop, with *Calluna* on the more acidic land.

The subsequent management of the land determined the vegetation which has survived to the present day. The better land was farmed to a higher altitude than is usual now. It was used as mixed grazing for sheep and cows. Providing the grazing intensity was not too high, this maintained a species-rich sward supporting species like *Botrychium lunaria*. As the pre-improvement farming was confined to the better-drained valley sides, these areas were also cultivated on the infield and outfield system. *Pteridium* would have been found on the well-drained slopes where it would have been carefully managed as a valuable resource. Regular cutting along with trampling from the cattle would have kept it within reasonable limits. It would probably also have had periods, as during prolonged wars, when it could extend its range unchecked.

The greatly extended areas of *Calluna* moorland still supported a considerable number of species. The pteridophytes which had only been able to succeed on higher ground were able to grow at lower elevations. The smaller species which had grown among the open forests were often able to survive in some form beneath the *Calluna* canopy. *Lycopodium clavatum* is well adapted to the moorlands. *Blechnum spicant* grows among the shrubby undergrowth but sends up its fertile fronds above the other vegetation to shed its spores. *Equisetum sylvaticum*, however, is perhaps one of the less adaptable species and is often found in a yellow stunted form in open moorland, indicating the departure of former woodlands. *E. pratense* is also found at higher altitudes along river banks where there is still some shade. The larger ferns have not been so well able to grow in open exposed positions. Any *Dryopteris affinis* subspp., *D. dilatata* or *Oreopteris limbosperma* found on moorland are usually beside rocks, growing by streambanks, or within a sheltered fold of the hill.

Brander (1980) quoted from the Court book of Glenorchy at the beginning of the seventeenth century and recorded that the moors were only to be burnt in March. This implies that already the moors were being burnt and not in an acceptable way.

3.2.4 Montane Habitats

Provided that there is not excessive erosion or grazing, present-day mountain summits like the high tops of the Cairngorms probably represent vegetation in as near as possible a relict form of the earliest tundra kind of vegetation. *Calluna vulgaris* does not extend above 720m (2400ft) and is very short towards its upper limits. Lichens and mosses, especially *Racomitrium lanuginosum* form the main ground-cover at higher altitudes. Clubmosses are the major pteridological components of these regions. *Huperzia selago* grows in the most barren stony parts with *Diphasiastrum alpinum* among the more vegetated but still acidic areas. *Lycopodium clavatum* can also occur at slightly lower altitudes along with *Blechnum spicant*. Among very short basic turf *Selaginella selaginoides* and *Botrychium lunaria* can be found. *Selaginella* is also found in basic flushes where there is enough gentle erosion to keep the habitat open, as is the upright montane form of *Equisetum variegatum* with the ubiquitous *E. arvense*.

The less accessible mountain cliffs would have retained their distinctive species including *Polystichum lonchitis, Asplenium viride, Cystopteris montana, Dryopteris expansa, Athyrium distentifolium* and *A. flexile, Woodsia alpina* and *W. ilvensis*. Only as the grazing pressure became more acute from ledge-wandering sheep, goats and deer did these species begin to be affected.

3.2.5 Bogs and Marshes

The Romans probably carried out the earliest drainage schemes in Scotland. Anderson (1967) quotes Galen referring to the Roman roads built across drained mosses. The roads formed a network over the area south of the Forth-Clyde line with a few other roads going north. These roads would still have been used long after the Romans had departed. The Romans dug open ditches as field drains, and had sophisticated drainage systems in their buildings, but such systems were not adopted by others in this country for many more centuries.

There would also have been large areas of marshy land which could not be cultivated. Heavy clay could not be ploughed by the earliest kinds of implements. With poor drainage this would have left relatively undisturbed large areas which are now under cultivation. Clay is comparatively basic and with dissolved silica offers a good growing medium for *Equisetum*. The wettest areas would have had extensive stands of *Equisetum fluviatile*, and also *E. palustre* towards the margins of these areas. Seepage lines, constantly damp and yet not stagnant, would have been admirably suitable for *E. telmateia*. *E. hyemale* grows especially well on clay banks. *Dryopteris carthusiana* would have been very common. The single record of *Dryopteris cristata* from Renfrewshire and the hybrid *D x uliginosa* (*D.cristata x D. carthusiana*) near Stirling show the former presence of this species which was presumably more widespread. *Thelypteris palustris* also is now only known from two mainland areas, near Forfar and in Kirkcudbrightshire, but in more basic fens it too would have been far more abundant. *Thelypteris palustris* with *Dryopteris carthusiana* are listed in notes on the flora of Islay, growing in dense Willow carr (Birks and Adam 1977). *Osmunda regalis*, while growing luxuriantly in acidic bogs in the west, also has a smaller form which can grow in more basic fen conditions and is found more towards the east.

Areas lacking in basic groundwaters would naturally become more acidic, especially as organic matter began to accumulate. The first very significant growth of peat bogs began in the Atlantic period from around 7,500 BP. In the Sub-Boreal the climate was dryer and the bogs dried out enough to be colonised by woodland. This dryer climate was favourable to the early farming being practised at this time. The succeeding Sub-Atlantic, being the present colder wetter climate, saw the growth of the bogs as they are known today and in recent historic time.

It is probable that anthropogenic factors have contributed to the widespread development of bogs thereafter. Forest clearance extended the moorland upon which a podsol developed and drainage was inhibited. At the same time, high rainfall would have leached nutrients to speed podsolization and give the same effect. Some Birch and Pine woodland was also engulfed by expanding bogs. At the Moss of Achnacree, Bronze Age field boundaries dated 3,650 - 3,200 BP have been found below peat deposits (Whittington 1980). Stone circles have been surrounded by peat to the extent of only having a small part still visible.

The subsequent development of bogs may have been initiated by the presence of fallen trees. Miller refers to the cut stumps of trees with a Roman axe still embedded. These are now covered by peat and he infers that Roman felling was a common practice (Miller 1887). Miller also described mosses formed when Robert the Bruce laid waste John of Lorn's land. Fallen trees would inhibit the drainage and encourage the growth of bog plants. The strong winds which are associated with the Sub-Atlantic climate would have the same effect in restricting drainage. He also refers to the regular orientation of broken twisted trees, all blown down in the same direction by gales and now thickly covered by peat.

Such a catastrophic event would have a rapid influence on the species involved. From the sheltered security of mature woodland, few species except *Pteridium* could readily survive in the open, but even the *Pteridium* would soon disappear as the site became wetter and the boggy conditions were more suitable for *Dryopteris carthusiana* and *Osmunda regalis*.

Increasing pressure on peat deposits led to the complete removal of many lowland bogs even before the eighteenth century improvements when such clearances were planned on a large scale (Fenton 1979).

3.2.6 Lochs and Ponds

There were many lochs left at the end of the glaciation which survived until comparatively recent times when they were deliberately drained although they have also naturally reduced in size through seral progression.

A map produced by Cadell (1913) shows the lochs present in the Edinburgh area at an estimated time of approximately 6,000 years ago. Their former extent has been demonstrated by excavations which showed lake sediments. Their presence illustrates a vastly greater area of water and wetlands than at present. Such a scene would have been prevalent all over the country. Their margins would have supported the species listed in the section on bogs and marshes.

Human activity has had an influence on sediment entering lakes. *Isoetes* species cannot tolerate a high sediment load and prefer clear, even slightly scoured, lake bottoms. A well-vegetated hinterland provides clear streams, but a clearance episode is clearly shown in the pollen record as the sediment suddenly increases and the *Isoetes* megaspores decline. Price (1983) refers to a large sediment increase in Loch Lomond around 300 AD, and there has been a marked increase over the last three hundred years. At Braeroddoch in the Dee Valley, a forest clearance was apparent 4,500 years ago when the sediment in the core increased to three times the usual amount. Many other episodes were seen by the same means in this area. *Isoetes* at Loch Maree grew well in the immediate post glacial period but grew less well in the Boreal, presumably as more organic mud encroached from the advancing vegetated bank (Birks 1972).

Pilularia globulifera requires a reasonably open habitat and benefits from areas which are kept open by human activity. It grows at the head of lochs, preferably on silty clay and recent records indicate that it is not necessarily very long-lived at a given site. Appropriate loch margins, with the occasional disturbance caused perhaps by launching boats, would have provided the conditions it requires. It would also have appreciated the newly exposed margins of artificial ponds, especially if they had a base of puddled clay. These would have offered suitable wet habitats for the usual wetland species. Fish ponds which were associated with monasteries would have been suitable for *Pilularia* until other vegetation reduced the habitat. Castle moats were another potential location which would have been kept reasonably open to prevent the water being covered by vegetation and eventually being ineffective.

3.2.7 Sand-dunes

The present coastline has been moulded by the high sea levels from around 6,000 years ago. As the sea level rose, shell sand, quartz sand and pebbles were brought in from the continental shelf and subsequently left as raised beaches. On the west coast the calcareous shell sand made the foundation for the productive fixed-dune "machair" which fringes much of the coastline and has been traditionally recognised as species rich. The machair on Lewis, for example, supported woodland until around 4,500 years ago when the woods were cleared and continued as open woodland for around a thousand years. A period of regeneration occurred until the felling associated with the advent of iron (approximately 2,700 years ago) when the machair became the open country which is recognised today (Ritchie 1979). Short, moderately grazed turf, constitutes an ideal habitat for *Botrychium lunaria* and *Ophioglossum vulgatum*. The damper areas are suitable for *Selaginella selaginoides* and the prostrate coastal form of *Equisetum variegatum* is typically found in such a habitat. *E. palustre* is also found with the possibility of *E x litorale* where there is an overlap in the habitats of the parents, *E. fluviatile* and *E. arvense*. *E. x trachyodon*, the hybrid between *E. variegatum* and *E. hyemale*, is also present in Lewis, Rum and Skye. It is of especial interest as both parents are no longer found at these sites, but indicate a past distribution which is no longer maintained (Page 1988).

Well developed sand-dune systems may be found all round the coast. The dunes on the east coast tend to be more acidic, as *Polypodium vulgare* illustrates, growing on stable dunes in East Lothian. But calcareous groundwaters derived from shelly raised beach deposits or more basic local rocks can give a different habitat. Gimingham (1964a) lists damp dune slack communities from Shetland, Sutherland, Caithness, Aberdeenshire, Fife and Wigtonshire, which have *Ophioglossum vulgatum*, *Selaginella selaginoides* and *Equisetum arvense*. There are many old records for *Botrychium* and *Equisetum variegatum* from dune slacks and the flatter "links" which mark more vegetated raised beaches. *Equisetum arvense* is often found, in a prostrate sand-dune form. These links have frequently been used as golf courses and Dornoch, Cruden Bay, Montrose, St Andrews, Elie, Carnoustie, Monifieth and Lundin are all on fixed dunes (Smith 1905).

Some dunes are unstable and have been so for hundreds of years. Hugh Miller described the inundation of the Culbin area in Moray, and an Act of Parliament passed in William III's time (late seventeenth century), which said that "many lands, meadows, and pasturages, lying on the sea-coasts, have been ruined and overspread in many parts of this kingdom by sand driven from sand-hills, the which has been mainly occasioned by the pulling up of the roots of bent, juniper and broom bushes, which did loose and break the surface and scroof of the sand-hills" (Miller 1859 p13). This is also a reflection on the growing scarcity of fuel.

Geikie (1887) lists many sites around the coast of Scotland which are affected by windblown sand. Pennant (1769), in describing Durness, mentions that blown sand has covered several farms and more are endangered. He also describes how the Parish of Forvie has lost all but two farms under shifting sands. It is not a new problem. Keatinge and Dickson (1979) suggested that increased wind speeds from 5,000 BP on Orkney initiated sand-blow and established the machair there. Skara Brae was covered by blown sand and many areas have suffered in this way since that time.

The natural succession of a vegetated dune slack behind the fore dunes offers good habitats for many small species including pteridophytes. Some pteridophytes can only colonise an area with little competition and disappear again with more vegetation. *Lycopodiella inundata* has been found in wet dune hollows on the Sands of Culbin (Patton and Stewart 1924) and also in the actively extending dunes at Tentsmuir in Fife (Sonntag 1894). Provided the area has some habitats able to provide spores to colonise new sites, some active erosion is an advantage and prevents species being crowded out by increasing vegetation.

As the dune slack becomes more vegetated it assumes the character of a heath. Eventually scrub is followed by trees. On the south side of the estuary at Tyninghame in East Lothian there is an area of *Calluna vulgaris* with large patches of *Lycopodium clavatum* (Beattie 1967). *L. clavatum* is also found at the Sands of Forvie and from Tain northward Juniper is found in the dune heath with *Betula* seedlings (Gimingham 1964b). Without rabbit grazing this would be a Juniper-Birch scrub and possibly indicates a type of vegetation which would have been much more widespread in the past and possibly could be in the future. Juniper was mentioned growing at Culbin. These areas of heath near the coast would at the time of maximum forest cover have constituted a substantial part of the country's moorland. It emphasises the close similarity between montane and coastal habitats which are shared by plants like *Lycopodium clavatum*.

3.2.8 Rocky Coasts

Higher sea levels would have eroded the cliffs and created the sea caves which are now only rarely awash. On a vertical cliff *Asplenium marinum* would have extended its range up or down to remain within the splash zone. At higher levels and inland generally *Asplenium adiantum-nigrum* also grows. These two species are both quite widely distributed but are only found on rocky coasts, not on sand. *A. marinum* has an Atlantic distribution. The slight warming effect of the North Atlantic Drift all round the coast of Scotland, provides the necessary protection from frost.

The cave near Aberdeen which contains the rare *Cystopteris dickieana* is something of an anomaly. A distinct species, it has been reported from a few other localities but these have been not been confirmed recently. Growing within the reach of salt spray it is able to tolerate conditions different from *C. fragilis*. As it is deciduous it cannot derive much benefit from winter frost protection unless the rhizomes are especially sensitive. A few intermediate forms have been found elsewhere (Page 1982) and these are perhaps the results of an introgression which has survived. Possibly the milder conditions under which *C. dickieana* first flourished are no longer available. The fluctuating sea levels may have compressed the habitat and allowed other species to share an already restricted habitat, so that there is now only a very small remnant of the original population left.

Chapter 4

Pteridophytes in a Rural Setting from the Eighteenth Century to the Present

4.1 Introduction

This chapter and the succeeding one describe the impact on pteridophytes of changes in the landscape from the mid-eighteenth century until the present. The more obvious rural activites like farming and forestry have been included in this chapter describing the aspects which provide or remove pteridophyte habitats. Grazing is a major factor in species composition over a very wide part of the countryside, especially the uplands which may be commonly thought of as wild and unfarmed. The area which is covered by forestry has sharply declined and then risen again as new plantations bring another element to operate on pteridophyte distribution. Large installations like reservoirs and the different modes of transport which are necessarily placed in a rural setting have been included in the next chapter on industrial development.

As the material used in this chapter is based on recent reports and observations, it is possible to give more examples than has previously been the case. Information is derived from herbarium sheets of material kept at the Royal Botanic Garden in Edinburgh (RBGE), the Botany Departments at Glasgow (BDG) and Aberdeen (BDA) Universities and at Perth Museum (PM). Floras compiled during the nineteenth and twentieth century have been used together with reports of field excursions in various journals. Especially valuable sources on land-use came from the many volumes of the Statistical Account of Scotland (S.A.S.) published at the end of the eighteenth century, the New Statistical Account of Scotland (N.S.A.S.) produced in the mid nineteenth century and the Third Statistical Account of Scotland (3rd S.A.S.) written a hundred years later in the twentieth century. Unattributed statements are based on personal observations by the author.

An historical outline is given to set the pteridophyte scene, and then a more specific account follows with a direct bearing on pteridophytes and their distribution.

4.2 Improvements in the Farming Economy which have Influenced the Distribution of Pteridophytes

As ideas on more efficient land management became known in the eighteenth century, land owners used their home farms to disseminate knowledge about improved farming methods. Introduced first in the Lothians, the ideas spread into other Lowland counties in the east and west. Stone dykes, hedges, or a combination of the two were established as part of the policy of enclosing land. The practice of laying hedges which was used in England never became widespread but shelter belts were planted.

A Board of Commissioners was appointed to oversee the estates which had been confiscated after the 1715 and 1745 Rebellions and it attempted to implement many changes which were typical of those being introduced at the time. Long leases were given subject to the fulfilment of certain conditions. The Board required that land should be drained, animals should be herded in the winter, grass and clover seed should be sown on the outfield, and that turnips and potatoes should be grown. Assistance was provided in building new houses but only if the roof was thatched with fern (*Pteridium aquilinum*), *Calluna* or straw, to ensure that turf was not being stripped for this purpose (Smith 1982).

The practice of sowing grass and clover instead of allowing fallow ground to be vegetated by the most dominant weeds was encouraged. The old systems of cultivation were gradually abandoned. Referring to an area near Coupar Angus the compiler of the first Statistical Account wrote: "Formerly the distinction between *Outfield* and *Infield* was constantly observed. The former was cropped alternately with oats and bear (sic); the latter, after a few successive crops of oats was suffered to lie a number of years in lea. The *run-rigg* prevailed too in many places. These absurd practices are now worn out, and the modern improvements generally introduced " (S.A.S. 17 1796 p3).

By the time the New Statistical Account appeared in 1845 many profound landscape changes had already taken place. The author of the Account of the Parish of Auchtergaven near Dunkeld compared the Moor of Thorn which the old Statistical Account described as "hills and muirs, or waste uncultivated ground" with the new situation where scarcely any muir can be seen from the turnpike road, only a few patches in remote parts which are gradually being reduced. "Draining, planting, enclosing, improved tillage, and judicious cropping have completely changed the face of the country; so that this parish is entitled to rank with the best cultivated districts in the wide country of which it forms a part" (N.S.A.S. 10 1845 p450). At Carmylie Parish near Forfar between eight and nine hundred acres (320 ha to 360 ha) had been brought into cultivation since the previous Statistical account (N.S.A.S. 11 1845).

At Auchterhouse near Forfar nearly 500 acres (200 ha) had been reclaimed from bog, moss and moorland (N.S.A.S. 11 1845). The Vale of Eden had formerly been a barren sandy tract, but was cultivated and improved (Heron 1799). In Stevenston Parish 1,200 acres (480 ha) of sandhills had been reclaimed (N.S.A.S. 5 1845). Cockburn described the changes in the countryside between Stonehaven and Aberdeen which he had travelled through for thirty years up until 1838. He said that it had been a "hopeless region of stone and moss" (Cockburn 1983 p10) but the area had been much improved by clearing the stones and draining. The volume of stones removed from the fields was so great in some places, that very wide consumption dykes were built to accommodate the surplus.

The major change in the distribution of cultivated land is seen in the new areas which were farmed. The lighter soils of hillsides had been ploughed for hundreds of years but the boggy areas in the valleys had not been cultivated. It was these areas which were now drained and improved. There was a limited period of re-occupation of the higher land using new access roads to bring in lime. The land was farmed more intensively without the infield-outfield system especially as new strains of seed led to greater productivity. An indication of the large proportion of the ground under cultivation in a Lowland area is given in the New Statistical Account of Dunlop in Ayrshire where it was estimated that the parish was composed of 5,834 acres (2,333 ha) cultivated, 311 acres (124 ha) natural pasture, 246 acres (98 ha) improved meadow, 30 acres (12 ha) moss and 131 acres (52 ha) planted woods (N.S.A.S. 5 1845).

Small farms continued to be amalgamated until 1835 and thereafter became about the same size as they are now (3rd S.A.S. 3 1953). The Lowland farms were laid out with planned fields. Higher ground was used for grazing. This change of land use, from the small barely viable hill farms to extensive sheep farms managed by comparatively few people, resulted in the clearance of most people from the upland glens. Many people either emigrated, settled in fishing villages located on poor land, or were displaced into the towns where industry was growing. Others were offered land to reclaim like the Moss of Kincardine, but when their leases expired the land was incorporated into larger holdings (Caird 1980). In the north-east, the tenants who were evicted to make way for flocks of sheep were allowed to attempt to cultivate very poor land on the coast. This led to the development at the beginning of the nineteenth century of the smallholdings which were called crofts.

Crofting country is characterised by long strips of land, often beside the sea, each with a house. Some landowners gave assistance in building the houses to a specified size, to be constructed using stone and lime mortar. The crofts were very small and it was expected that the crofter would supplement his income in some other way (Caird 1980).

In very wet, peaty soil, "lazybeds" were cultivated. This involved turning the soil over into raised beds, which made drainage easier and made the most of the available soil. Manure or seaweed was carried in creels and laid on the ground in strips. The soil was then turned over the manure and the crops sown. Bere and oats were grown at first, but the potato became the main crop after 1740 (Fenton 1987).

There were high prices for sheep and grain from the outbreak of war against France from 1793 until 1815, but the cultivation of higher land was not sustained when prices fell (Parry 1980). The production of food for the growing populations in towns continued to expand until the Corn Laws were repealed in 1846 following which the importation of wheat created less demand upon the home farmers (Mackie 1962). There was a change towards more stock rearing and and less arable crops. Three agricultural colleges were founded at the beginning of the twentieth century which helped to research and propagate new methods.

The increase in stock rearing is reflected in a report by Brown (1913) who described an increase in permanent grass in the Shotts Parish. In 1912 there were 3,082 (1,233 ha) more acres under permanent grass than in 1867 and 244 acres (98 ha) more than in 1902. Land was put down to grass in the depression of the 1920s to 1930s and upland areas especially were allowed to deteriorate. The Second World War brought a new urgency to the production of food, and land was ploughed again. There have been continued improvements since. Grassland on the hill has been improved for sheep. There is still a lot of stock rearing both for dairy cows and beef (3rd S.A.S. 2 1979).

Mellanby (1981) gives a modern example of improvement in Angus where agriculturally unproductive land with *Calluna*, *Nardus stricta*, *Cytisus scoparius*, *Ulex europaeus* and *Pteridium* was ploughed, fertilised and reseeded. The pasture which was thus obtained supported 675 well-fed cattle, instead of the 60 which had previously been provided with poor grazing.

A study was commissioned by the former N.C.C. based on changes in vegetation type as shown in aerial photographs in the Lothians comparing the 1940s and the 1970s. The amount of arable farmland has remained similar although distributed differently (Easton 1982). The greatest habitat loss was in dwarf shrub heath including *Calluna* moorland which had lost 61% of its previous area. Deciduous woodland had declined in area by 15%, hedges 18%, permanent grassland 5%, improved grassland 38%, wetland 5% and ponds by 12%. The woodlands and dwarf shrub heath areas had been mainly lost to new conifer plantations, but when the conifers were felled, the land was used for agriculture (Easton 1982).

Some aspects of these improvements had specific effects on pteridophytes which are more precisely detailed in the following sections.

4.3 The Effects of the Improvements on Pteridophytes

4.3.1 Mechanisation

The introduction of improved farm machinery made it easier to cultivate the land. The new swing plough was invented by John Small from Dalkeith in 1750 by adapting the Rotherham plough. It was pulled by two horses and only required one man to operate it. Low cultivation ridges allowed a more efficient use of the land with less area lost in the furrow.

In 1918 the first tractors were used although the depression of the 1920s and 1930s slowed the introduction of mechanisation. The combine harvester arrived in 1932 (Fenton 1987) and was first used in East Lothian, in keeping with so many of the early introductions. Its effective use required large fields and caused the loss of many walls and hedges dividing smaller fields.

In the Parish of Abernyte, mechanisation led to similar results as elsewhere with the gradual removal of dry-stone dykes and hedges to allow for larger fields (3rd S.A.S. 27 1979). This can, however, have a positive effect as there are some areas which cannot be easily cultivated by large machinery and these can be left to provide small wild patches (Jeffrey 1982).

4.3.2 Farm Buildings and Country Estates

More than 300 planned villages were built throughout Scotland late in the eighteenth and early in the nineteenth centuries (I & K Whyte 1987). In some instances local landowners completely re-organised the field boundaries and buildings, bringing a marked change to the character of the countryside.

The building of extensive areas of mortared wall, both in houses and in long estate walls such as can be seen at Tyninghame in East Lothian, created an unprecedentedly large area for the subsequent colonisation of wall ferns. Walls which are near the sea, or within the range of the cooling dampening effect of the coastal "haars" (Page 1988), offer a very suitable habitat for *Asplenium ruta-muraria*, *A. trichomanes* subsp. *quadrivalens* and the less frequent *A. adiantum-nigrum*. The coping on the wall seems to be most commonly colonised by *Polypodium interjectum*, and *Cystopteris fragilis* is often found on the damper more shady side of the wall. All these species have been observed on walls around East Linton in East Lothian. Walls in the south-west of Scotland also include *Ceterach officinarum*.

Remains of ruined crofts are often the only source of lime in an acidic area. As such they offer a habitat for the typical wall ferns, *Asplenium ruta-muraria* and *A. trichomanes*.

The walled gardens of large estates provided a protected environment and cultivated species extended into the stone-work, probably often by design. *Ceterach officinarum* occurs on the walled garden at the House of Dun near Montrose, where it is further north and east than its usual range. From its occasional occurrence on walls in the east of the country it can be supposed to have been deliberately introduced. An example of its deliberate introduction is given in a rescue operation which was organised when the northernmost colony near Inverness was to be affected by a new road. The colony had increased from twelve plants to sixteen between 1962 and 1970. Plants were removed to three different walls nearby although one of the original plants did survive (Webster 1978).

Phyllitis scolopendrium grows on old walls in Perthshire and elsewhere, but the nearest natural locality is often a considerable distance away and this species has probably grown from spores borne by locally cultivated plants.

Many of the large estates, as in Perthshire for example, included ferns in their planting schemes and the introduced species *Matteuccia struthiopteris* can be found at Blair Atholl, Blair-Adam, Kindrogan, Murthly, Taymouth and Bleaton Hallet near Blairgowrie, in addition to *Onoclea sensibilis* on the Tay Estuary. The Victorians planted native ferns and built special ferneries to cultivate the chosen species. An early example of fern planting is given in William Adam's account (1834) of the "Woods and Plantations of Blair-Adam" in Kinross-shire where planting commenced in 1755. As part of the planting of the woods, in previously barren countryside, his grandfather specified that the mixed hardwoods and conifers should be underplanted with "fern, fox-gloves and other wild plants" (Adam 1834 p87). A further footnote describes a collection of ferns. "There are twenty-seven different kinds of fern collected here, and at the north entrance to the Hill behind the house. Twenty-four of these kinds grow wild in the grounds" (Adam 1834 p18). Ballantyne writing in 1985 saw no survivors of this planting scheme except for *Matteuccia struthiopteris*.

Lycopodium clavatum forms an unexpected component of a few lawns. While it is often associated with *Calluna* moorland, it does occur growing among grass as Webster (1978) recorded it in short grassland near Dallas in Morayshire. Webster also gives the record of *L. clavatum* growing on the lawn at Glenferness House also in Morayshire. Dickson (1991) recorded it in a lawn at Ruchill Hospital in Glasgow. Cunningham and Kenneth (1979) reported this *Lycopodium* as a "possible introduction" in lawns at Stonefield Castle Hotel and Inverneill, both in Kintyre. It is easier to understand how *Selaginella kraussiana* could be introduced and maintained vegetatively as a "lawn weed" at Kilberry Castle (Cunningham and Kenneth 1979 p9), than to comprehend the deliberate propagation of *Lycopodium clavatum*.

4.3.3 The Use of Artificial Fertilisers

Marl was used before the spreading of lime had become a general practice. A calcareous deposit formed on postglacial lake beds, it was very popular when it was first discovered but was gradually replaced by alternative fertilisers. Marl was most abundantly extracted between the middle and end of the eighteenth century. The author of the New Statistical Account wrote in 1845 that there was less demand for marl than formerly (N.S.A.S. 11 1845) and marl was reported to have been extracted from Fingask Loch but not used very much any more (N.S.A.S. 10 1845). Marl was obtained either by draining or dredging. To extract marl, the Loch of Forfar was drained to reduce the depth by 16 feet (4.8 m) and reduced in area from 200 acres (80 ha) to 100 acres (40 ha). Lundie Loch formerly covered at least 100 acres (40 ha) and was reduced to 8 acres (3.2 ha) (N.S.A.S. 11 1845). Restenneth Loch and Lundie loch were covered in peat moss which had to be removed first. The Loch of Kinnordy was drained for marl in 1740 and 1741 but proved impossible to drain completely. Also drained were Rescobie, Whitefield near County Angus and Monk's Myre (Brien 1989).

A fern associated with Rescobie and Restenneth is *Thelypteris palustris*. Its present-day scattered distribution over the country as a whole suggests a natural decline as habitats became more acidic through seral progression. Only base-flushed fens could retain *T. palustris* and even then seral growth could eliminate it. As it grows in basic fen it would possibly have benefited by the removal of the peat cover with the consequent creation of a new more basic wet area. It is difficult to estimate its abundance in the Forfar area before the marl extraction took place, but it presumably was present to provide spores for new colonisation once conditions were suitable for establishment. Cultivated plants in the Edinburgh area do not readily produce spores, which may imply that conditions were more favourable for spore production in the eighteenth and nineteenth century. There are several records from around Forfar last century but it is now rare in this area once more.

Table 4.1 Records of *Thelypteris palustris* in the Forfar area

Date	Locality	Recorder
1824	Whitmuir Loch	Arnott
1838	Rescobie Loch	Croal
1839	Restenet (sic)	Croal
1848	Rescobie	Gardiner
1848	Restenet (sic)	Gardiner
1862	Cult mains Dundee	_
1863	Nr Forfar	_
1877	Clocksbridge	Kidston
1903	Rescobie Loch	Somerville
1948	Clocksbridge	Ingram & Noltie

Symson in the seventeenth century described the manufacture of lime from burnt sea-shells in Galloway (Donnachie and Macleod 1974). Lime was used on the fields as early as 1620 (Fenton 1987). Many small lime kilns were built, mainly after 1745, and still provide a locally lime-rich habitat both in their walls and the surrounding enriched turf. At Loch Moraig near Blair Atholl in Perthshire, Smith (1905) mentions the presence of an old lime kiln and suggests that enrichment from it accounts for the local abundance of *Equisetum fluviatile* and *E. palustre* in the adjacent loch. Basic turf around lime kilns is also suitable for *Botrychium lunaria* and *Ophioglossum vulgatum.* Webster recorded *Botrychium* near an old lime kiln at Mid Morile in Strathdearn (1978). Old limestone quarries at Cults in Fife provided a suitably basic and damp habitat for *Ophioglossum vulgatum* (Young 1936). The mortared walls of the kilns are appropriate for the usual wall species like *Asplenium ruta-muraria, A. trichomanes* and *Cystopteris fragilis.*

In addition to small local limekilns there were very large kilns near suitable limestone outcrops in appropriate parts of the country. Heron (1799) described the limeworks at Limekilns near Rosyth as the biggest in Britain. The kilns still survive but are too dry in the present climate to sustain a pteridophyte flora, although other flowering plants in the vicinity are specifically calcareous species.

Both marl and lime were applied with over-enthusiasm and in Berwick County the effect of the lime was to kill the Trout (*Salmo trutta*) and Salmon(*Salmo salar*) (Brien 1989). This was an early example of substantial local changes, presumably short-term, being brought about by a change in the immediate supply of available nutrients. After lime or marl, bonemeal was used and then ground phosphate was introduced by the end of the nineteenth century. The use of phosphates and nitrogen increased by a factor of three between 1900 and 1914 in Perth and Kinross-shire and twice as much potassium was used by 1914 (3rd S.A.S. 27 1979).

Nearly all cereal crops are given nitrogen. Barley yields have been considerably improved by the application of lime to what is often an acidic soil. From 1913 to 1969 there has been a seven-fold increase in the application of balanced plant-food fertilisers ($N+P_2O_5+K_2O$). The most notable increase has been since the beginning of the Second World War (Holmes 1973).

The effect on pteridophytes of artificial fertilisers is to produce an environment in which growth rates are considerably accelerated providing shading which may prove excessive even for species like *Equisetum arvense* which usually are persistent. The repeated cropping of silage several times a season (Mellanby 1981) brings a complete removal of vegetative parts which can weaken the rootstock. Sown grassland may alternate with other crops and only exist for two to four years (Mellanby 1981). *Botrychium lunaria* and *Ophioglossum vulgatum* require moderately grazed pasture. A forced regime of artificial fertilisers alternating with ploughing and intensive crops with the probability of herbicides does not allow these species to grow as they could formerly. An indication of the species which were more common in natural pasture is found in the New Statistical Account from the Parish of Inchture between Perth and Dundee which mentions "the old pastures with the rare *Botrychium lunaria*" (N.S.A.S. 10 1845 p829). Brown (1913) recorded both *Botrychium* and *Ophioglossum* from natural pastures with *Equisetum* *arvense* in artificial pastures and meadowland. On heaths which had been improved to become grassland, he did not record any pteridophytes.

Many of the older floras describe *Botrychium* habitats in the lowland areas as occurring in "pasture". Dickie (1860) recorded this species around Aberdeen in "natural pastures, generally diffused". By 1923 Trail in the same area wrote of "dry pastures; not common". Greville (1824), Balfour and Sadler (1871) and Sonntag (1894) found *Botrychium* around Edinburgh in "dry pastures". In Perthshire, White (1898) mentioned "pastures" and Sadler (1863) specified "pastures near Balvaird Castle". In Forfarshire Mathers (1848) listed "Old pastures, Kinnaird. Old pastures, Kinnordy". Johnston (1833) in the East Borders described *Botrychium* in "old pastures above Butterdean Mill". In Peebleshire, Balfour (1925) wrote "On pasture land beside Manor Water . . . Frequent in old pastures at Glen, Hatton Knowe, Eddleston". More recent authors describe *Botrychium* from more marginal habitats like Bishop Hill, Fife, (Ballantyne 1985) screes on Skye, (Murray and Birks 1980), "Base-rich turf, especially on the hills and near the coast" (Forfar area, Ingram and Noltie 1981).

Ophioglossum vulgatum was similarly described from "old pastures" in the Lothians (Martin 1934), Aberdeen, Banff and Kincardine (Dickie 1860), Perthshire (White 1898), River Clyde and City of Glasgow (Hopkirk 1813), Dumfriesshire (Scott-Elliot 1896). It is now rare or absent in most areas. These floras strongly suggest that the two species have lost many of their former sites which were only in pasture land which had remained unploughed for long periods.

In 1905 Smith described the Long Loch with a typical upland aquatic flora comprising *Isoetes, Lobelia dortmanna* and *Subularia aquatica,* but he said it had since all gone due to "artificial enrichment"(pxxxii). Local enrichment of ponds and lochs has occurred due to run-off from fields. In excessively large quantities this can result in algal blooms which de-oxygenate the water and kill all plant and animal life. This happened in Loch Leven during the 1960s causing the death of both fish and submerged plants (Thom 1986). On a lesser scale, slight enrichment may not be entirely harmful. Chemical fertilisers were washed into Beanrigg Moss and brought about local variations which encouraged flowering plant species diversity (Daniels 1972), although no pteridophytes were recorded in this instance. The nitrogen-based fertilisers used in more recent years have been slow-release and less harmful to other vegetation.

Intensive farming methods when animals are kept indoors has created a problem with the disposal of manure. This can cause excessive eutrophication locally (Mellanby 1981). The rapid increase in colonies of birds like the Herring Gull (*Larus argentatus*) has led to not dissimilar problems. Here the birds have both destroyed local vegetation by gathering material for nesting and have changed the plant associations with additional nutrients. Thom (1986) gave an example of two moorland sites, on Lewis and near Gairloch where the moorland has been radically changed and also described the bright green grass on Rum associated with nesting Manx Shearwaters (*Puffinus puffinus*). A positive association between a pteridophyte, *Ophioglossum azoricum* and sea birds is suggested by Page (1988) when he links this species with the nesting sites of the Storm Petrel (*Hydrobates pelagicus*), the Puffin (*Fratercula arctica*) and the Manx Shearwater and suggested that they may assist in dispersal or in providing local enrichment.

The increase in gull populations is often related to practices in refuse disposal which in itself can cause local problems with high nitrogen levels and other pollutants entering groundwaters.

4.3.4 Drainage Schemes and the Removal of Peat Bogs

In Crieff Parish there is a description of the drainage methods which were introduced as an alternative to runrig ridge and furrows. Ploughing extended deeper than had previously been attempted, extending to 18 inches (45 cm). Stones were blasted with gunpowder to remove them completely. Field drains were dug five feet (1.5 m) deep, filled to within twenty-two inches (56cm) of the top with stones and then filled with earth (N.S.A.S. 10 1845).

In the Lothians the earliest tile-draining was introduced from 1829 (Fenton 1987). Land reclamation continued all over the country through the nineteenth century and into the twentieth especially into the carse lands. St Madoes tile drains were manufactured near Perth and became very popular. Repeated references to drainage are made in the New Statistical Account from the mid nineteenth century such as "every bog and morass drained" (N.S.A.S. 10 1845 p636). At Fordoun in Kincardineshire the compiler wrote "Draining is now understood, and has been so successfully practised, that not a bog, loch, or swamp, remains in the parish" (N.S.A.S 11 1845 p71). The determination to drain and reclaim was such that it seemed necessary to explain areas which had been left, as at Lochbrown near Ayr. "It covers sixty acres of ground. It would have been drained many years ago, had it not been for the two corn mills it supplies with water" (N.S.A.S. 5 1845 p159).

Ten feet of water (3 m) was drained from Loch Lubnaig to reclaim 50 acres (20 hectares) at the head of the loch (Brien 1989). Similarly Loch Leven had its level reduced to reclaim land around the margin at some point prior to the New Statistical Account of 1845 so that 500 acres (200 ha) were brought into cultivation (3rd S.A.S. 27 1979). While more land was made available for agriculture, in the immediate vicinity of the lochs new uncolonised mud would have been exposed. *Pilularia globulifera* was first found at Loch Lubnaig in 1868 (BDA) where it must have established on the new area exposed and has remained in several localities there ever since.

The demand for land during the Second World War led to further drainage in some hill areas as near Blairgowrie. Near Abernethy, land which had been cultivated, but had been used as pasture, was again ploughed with the aid of government grants, and improved pasture resulted (3rd S.A.S. 27 1979). In the Parish of Orwell in Kinross-shire since the Second World War there has been substantial drainage with government subsidies (3rd S.A.S. 27 1979). Methven Moss near Perth has been progressively drained during the nineteenth and twentieth centuries until the last remnants have disappeared. *Dryopteris carthusiana* which had formerly been widespread at Methven, appears in herbarium collections at the Royal Botanic Garden Edinburgh (1856, 1857, 1861), Perth Museum (1861, 1871, 1874, 1885) and Aberdeen University (1854) and this site was a well-known locality for the species.

It is noticeable that many of the old localities of *Pilularia globulifera* no longer exist. Small ponds have either grown over or have been drained. Near Edinburgh it was recorded from "the Braid Hill marshes" (Sonntag 1894), now the site of a large golf course. Perthshire localities with names like "Moss of Cairny" and "Moss of Balgoune" (White 1898) no longer have this species.

In Orkney, Halcro-Johnston annotated a 1922 herbarium specimen (RBGE) with a description of the loss of *Diphasiastrum alpinum* on the 11th July 1924 "through the ground having been ploughed up for cultivation". At Newtyle, near Forfar, much of the previously pasture land had been ploughed for arable use (N.S.A.S. 11 1845) and "The Hill of Hatton is ploughed almost to its summit; on the north of the parish, where standing water, marsh, and morass were, corn fields now are" (N.S.A.S. 11 1845 p563). This cultivation of hill ground, Hatton Hill is 265m, must have removed many species which grew more widely at lower altitudes than today.

The local micro-climate was affected by the reduction in the amount of standing water. Of the Parish of Glamis near Forfar it was written: "The climate is now dry and early, over all the lower portions of the parish, the extensive drainage of the swamps and mosses which have taken place, of late years, having had a great effect on its improvement" (N.S.A.S. 11 1845 p 38). Similar ideas were expressed in another account from Garvock in Kincardineshire. "But the dark, cold, wet, and dreary days, which were formerly almost the constant portion of Garvock, have now in a good measure passed away. Its climate, indeed, is still, often cold and moist, but within the last forty, nay, within the last twenty, years, it has been wonderfully meliorated, by draining and the reclaiming of waste land" (N.S.A.S. 11 1845 p28).

An indication of either local changes in humidity, or perhaps an indication of small climatic changes, comes from old lists of the flora on Arthur's Seat in Edinburgh. Wallace (1925) compared a list of 115 species for Salisbury Crags, compiled in 1824, with his own list in 1924 when he found only 68 species. An old undated herbarium specimen of *Oreopteris limbosperma* from the Stueart collection, (collected on Salisbury Craigs early nineteenth century) (RBGE), probably relates to the earlier list. As species like *Montia fontana* were included in this list he suggested that the area may have become dryer. The sheep which then grazed the hill may have removed some species. He also thought that prevailing westerly winds from the city might have brought smoke which had a detrimental effect on the variety of species. A further recent discovery in Hunter's Bog behind Salisbury Crags (pers. comm. C.N. Page 1988) was a colony of *Ophioglossum vulgatum* which had not been recorded there before. The area had been used as a rifle range from 1859 but this was dismantled in 1961 and a new turf was laid to restore the area. Possibly *Ophioglossum* was introduced at this stage. Sheep-grazing ceased in 1977 but grazing from rabbits has continued. The level of grazing may account for the colony becoming more noticeable, or perhaps it has only recently colonised through spores.

In 1769 Pennant described riding towards Nairn through rich land which was intermixed with deep and black peat cuttings which demonstrated the nature of the land before clearance. This shows that many of the peat deposits had already been removed. Crookies Moss and Moss of Barmuckity near Elgin were almost completely removed for fuel (Peacock et al 1968). Fenton (1987) wrote that most Lowland peat has been used for burning and only flat fields remain where there was once a bog. On Mull (Bangerter et al 1978) it was suggested that peat cutting had contributed to the reduction in the abundance of *Osmunda regalis*. Certainly the general drainage schemes would have had an effect on the few stations where this remained on the east of the country and probably to a lesser extent in the west.

Heron in 1799 noted an abundance of peat around the town of Aberdeen. But the Loch of Aberdeen disappeared in 1838. The last of the peat mosses in Moss of Ferryfield near Aberdeen were reclaimed soon after 1850. Stocket Moor which had been botanically rich had been replaced by cultivated fields after 1880. Trail wrote of the few remaining habitats which were unsuitable for cultivation and had thereby survived. "The dry or rough ground and thickets on the slopes beside streams, as well as on parts of the moor formerly, had their peculiar species, some of which have become very infrequent, such as . . . *Equisetum sylvaticum*" (1923 p87).

The Dee had alpine plants which were not found by the Don but have now disappeared. Species like *Meum athamanticum, Oxyria digyna, Galium boreale* and *Trollius europeaus* were found. Many interesting plant species were known from old lists of this area before 1770, but they have now gone. Trail (1923) predicted that a new road would be built around the perimeter of the whole area, and that the eastern links would dry out leading to the extinction of *Botrychium lunaria*. A "carriage drive" was built, which has resulted in filling in hollows with rubbish from the town. Sewers were allowed to drain into the burns running across the area. A refuse dump now occupies the eastern fringes, and the former links are neatly cut grass which have been used as a race course and for golf. Professor Trail also wrote that although changes had been slowly taking place in cultivation and drainage from 1750 onwards, 1800 to 1900 had seen the most rapid changes affecting most particularly the moors and swamps.

One of the biggest peatmoss clearances took place around Blair Drummond Moss near Stirling (Cadell 1913). From six to twelve feet (1.8m to 3.6m) of peat was removed in reclaiming the area. The surface consisted of peatmoss and *Calluna* with deep pools in between. Work commenced in 1766 directed by Lord Kames. Plots were given to smallholders who paid no rent until the land was productive. As the clearances were displacing a lot of people from the Highlands there were many grateful for the opportunity. A deep channel was cut through the peat to the underlying clay. A stream was diverted through this and washed the peat away into the Forth. Fifty families settled there, digging holes through the peat to build houses which eventually emerged as the peat was removed from around them. The shores of the Forth Estuary were littered with peat as far as Borrowstouness (Bo'ness) and the fishing was severely affected. This method of clearance was banned in 1870 (Cadell 1913). Parts of the moss still remain and *Dryopteris carthusiana* continues to be found in the area as instanced by herbarium specimens from 1947,1953, 1966 and 1981 (RBGE and BDA).

An awareness of the loss of marsh plant species is reflected in the New Statistical Account from Arbuthnot in Kincardineshire. "The hand of agriculture has almost extirpated the plants of the marshes, *Trollius Europæus* (lucken gowan,) bur marygold, and *Anagallis tenella* " (N.S.A.S. 11 1845 p155). These plants were part of a community which in other places include such species as *Equisetum palustre, Selaginella selaginoides* and *Dryopteris carthusiana*.

Dryopteris carthusiana is one species which does not show a very dramatic decline in *Atlas* records but which seems from past and present floras to have declined markedly in overall abundance. The presence of the hybrid *Dryopteris x deweveri* indicates the existence of *D. carthusiana* at one time and marks the transition period in an area which is becoming dryer. *D. carthusiana* can no longer survive in dryer conditions but the hybrid is better adapted to intermediate conditions and can reproduce vegetatively for some time. But if the area is being drained, the hybrid will eventually also die out (Page 1982).

D. carthusiana has suffered from drainage schemes but also seems to have edaphic requirements which are not readily apparent. There are sites which appear to be suitable and yet a careful search does not reveal the expected species. In at least one area near Killiecrankie in Perthshire, this species was seen in 1981 and 1983 and yet is no longer visibly present. Although spreading by creeping rhizomes it may be a short-lived species depending on active erosion to maintain a reasonably open habitat suitable for new potential colonisation. It is a comparatively small fern, rarely higher than 50 cm, and may not be able to compete in very dense undergrowth. As a natural component of seral changes it would depend on new environments to provide a suitable niche. Older partially choked forestry ditches are a useful habitat in this connection, as seen in a colony growing near Kindrogan in Perthshire.

Lycopodiella inundata has been affected by drainage in areas to be planted as forest. In 1844 William Gawlee wrote on a herbarium specimen (BDG) from the Carse of Arderries "Two miles east of Fort George is a moor now planted with wood, which will in a few years, I fear make a radical reform in the Vegetable Kingdom of this locality". Webster (1978) recorded the demise of *Lycopodiella* from the Culbin sands. Earlier writers (Patton & Stewart 1914 and 1924) had recorded its presence in the dune slack but Webster last saw it in 1976 where it grew in seasonally inundated hollows, but is now probably extinct due to forestry drainage. It was also recorded at the end of the nineteenth century (Sonntag 1894) and in 1936 (Young) from Tentsmuir in Fife. Like Culbin, the area has been greatly altered by forestry and it is no longer recorded there.

4.3.5 The Reversion of Cultivated land and the Spread of *Pteridium*

After sheep had been introduced on a large scale there were fewer people living on the hills which meant that *Pteridium* was no longer cut and exploited. Sheep trample vegetation less than cattle do and do not provide any control against the spread of *Pteridium* (Mitchell 1973). Lamont specifically stated that "The Bracken has extended in living memory due to the burning of heather and having sheep instead of cattle on the hills" (1914 p 256).

Pteridium aquilinum subsp. *aquilinum* has greatly increased its area into land which had been laboriously drained and improved. The infield, around abandoned crofts and the lazybeds with better drainage, has in many places been overgrown by *Pteridium*. In 1949 Leigh looked at old croft land and wrote "Then the Laird removed the crofters to the hill above Glenuig and planted trees to give cover for pheasants. The marks of the old drains could still be seen in the woods and on the abandoned rigs bracken grew shoulder high " (Leigh 1974 p133).

To some extent in the depression between the two World Wars and also after the Second World War there was a reduction in the intensity of cultivation so that land which had been laboriously reclaimed has been allowed to revert. In the Parish of Kenmore, at the foot of Loch Tay, "bracken, thorns, brushwood and thistles" are quoted as the result (3rd S.A.S. 27 1979 p77).

Pteridium aquilinum survives burning when other vegetation is slow to recolonise although it cannot compete with *Ulex europaeus* (Fenton 1939). *Pteridium* can grow with especial success where woodland has been cleared but not actively managed subsequently. All the islands in Argyllshire studied by Jarvis and Duncan (1974) which had *Pteridium* have or had woodland. Some smaller islands had no *Pteridium* but had abundant *Dryopteris* instead, which implies that the presence of a fern may have been determined by its successful establishment many centuries ago (Jarvis and Duncan 1974).

Despite its abundance and ability to colonise new ground, *Pteridium* sporelings are not very frequently observed in the field. Their discovery was the subject of a note a contributor sent to the British Exchange Club in 1894 "I send these specimens in the belief that they are not common and will be acceptable to some of the members" (p463). It is significant that this record follows a very dry summer. Similarly H. Halcro-Johnston wrote on a fertile herbarium specimen collected in Orkney in 1933 in an exceptionally dry, early season "In ordinary seasons I have not found any plant in Orkney with sporangia developed". Conway (1957) found many plants produced spores after the hot summer in 1955 but found no sporelings in the field. Hot summers correlate to a limited extent with the production of spores although a series of poor summers can be followed by spore production in a comparatively better summer.

Pteridium aquilinum subsp. *aquilinum* seems to be the subspecies which most commonly produces spores. It may be best adapted to the intermediate conditions in this country for the *P. a. atlanticum* subspecies. will rarely have a long and mild enough season to develop spores, and *P. a. latiusculum* is also on the edge of its range. For the development of spores, an early season is necessary without damaging frosts, either early or later. The infrequency of sporing is supported by an examination of 55 Scottish herbarium specimens of which only 17 were fertile.

The most successful instances of *Pteridium* sporeling establishment were on bombed sites as observed in London. Conway (1953) suggested that the sterilisation was beneficial for successful growth. This would also apply in the case of muirburning. While sporelings are not frequently observed in the field, isoenzyme studies (Rumsey, Sheffield & Haufler 1991) show that large populations of *Pteridium* are composed of many separate clones, each of which must have originated from a different spore.

In the Parish of Kirkden near Forfar, the vegetation of uncultivated ground was listed in 1845 as "whins, broom, fern and heather" (N.S.A.S. 11 1845 p348). The fern is presumably *Pteridium*. Brown (1913) recorded *Pteridium* around Shotts on south-facing slopes, especially on dolerite outcrops and on ridges. Smith (1905) observed a zonation of *Pteridium* on the south side of the Ochils. The lowest ground was farmland, then Whin (*Ulex europeaus*) occurred up to 600ft (180m) and *Pteridium* continued up to between 1,200ft (360m) or 1,500 ft (450m), with summit pastures of *Nardus* and *Mollinia*. On the Sidlaws, Smith recorded *Pteridium* where trees had been cleared.

Once the accumulated vegetation of several thousand years has been removed it seems that the usual management practices do not necessarily encourage a species-rich alternative, even if the land is no longer intensively cultivated. A combination of over-grazing, or over-burning can allow the establishment of aggressive species like *Pteridium aquilinum* subsp. *aquilinum*, and other pteridophytes are less likely to succeed with such competition.

One species which has been recorded in association with *Pteridium* is *Ophioglossum vulgatum*. Duncan found it on the Island of Col "among bracken where it had not been grazed" (Duncan 1967 p483). It was found in Kintyre larger than nearby specimens and growing beneath *Pteridium* (Cunningham and Kenneth 1979) and also beneath *Pteridium* in

Inverness-shire (Hadley 1985). It was also observed among *Pteridium* on Rum. The *Pteridium* may well protect the *Ophioglossum* and discourage grazing in the area.

There are often localities in woodland for *Ophioglossum vulgatum*. Herbarium specimens (RBGE) are from Arniston Wood (1887), Dalmeny woods (1833) and Blair-Adam woods (1848). It grew in reasonably open, basic woodland which was presumably free from grazing. Balfour and Sadler (1871) give its distribution as both moist pastures and woods around Edinburgh, and Trail makes the same generalisation in Perthshire (1898). Hopkirk (1813) describes the species as rare near Glasgow but quotes a locality in pastures about Woodhall. The name suggests that there was originally a wood. Sadler (1863) found the plant near Bridge of Earn in Invermay woods. Johnston (1833) also found it in a wood near the Coldstream road in Berwickshire.

This suggests that *Ophioglossum* may originally have been a woodland plant but able to grow in the pasture which resulted from grazing in open woodland. The grazing would inhibit regeneration but the *Ophioglossum* could remain until the pasture was "improved". It is possible that *Ophioglossum* can return; Johnston (1833) described the plant from a field which was no longer cultivated. It is, however, very substantially reduced in Scotland compared with its former distribution (Jermy et al 1978). This trend it not so pronounced in the south of Britain where it has always been more frequent and suggests that other factors, possibly climatic, may have an influence on its distribution.

4.3.6 Herbicides

Herbicides are applied to the land in proportionately greater quantities than insecticides and their use has greatly increased since they were first introduced in the 1930s. The earliest dinitro compounds were very toxic to broadleaved plants and also to animals. In 1942 phenoxyacetic acids, hormone weed killers, were introduced and are still widely used. These herbicides drastically reduced the wild flowers which commonly grew in the crops. It was also used, more extensively formerly than currently, to spray road verges. This has affected pteridophytes as personal observations of browning fronds have shown. Herbicides using paraquat have been in use since the 1950s. It kills all green plants but deep rooted species can survive (Mellanby 1981). It is in such circumstances that *Equisetum arvense* has benefited. Formerly it was a weed of cultivated fields, "too common" Johnston described it (1829 p7), but modern methods of cultivation and improved drainage have reduced its nuisance value. Trail in the flora of the parish of Aberdeen described a reduction in all the *Equisetum* species due to "agriculture and drainage" (Trail 1923 p325).

Pteridium aquilinum subsp. *aquilinum* is probably the least popular pteridophyte and asulam can kill it (Mellanby 1981). Unfortunately asulam is not selective for *Pteridium* alone, and while it does not harm flowering plants, the prospect of widespread use of this herbicide, perhaps by spraying from the air, is not a very favourable prospect for other pteridophytes. While any area which has been cleared could hopefully be recolonised by pteridophytes from adjacent sporing plants, presumably the same applies to *Pteridium* and the same *Pteridium*-dominated association could grow again (Page 1982b). A greater probability is that the cleared ground would be "improved" so that the opportunity would not exist for natural associations to regenerate. Sympathetic management would be required if pteridophytes are to be part of the vegetation.

Another area in which herbicides are used is in the control of plants growing in ditches and waterways which must be kept open. While intended to affect only the plants, dead plant material can cause as much of problem with de-oxygenation as the after-effects of an algal bloom (Mellanby 1981). This can have wider-reaching effects than the immediate area to be cleared and would affect *Isoetes* in lochs which may be downstream.

4.4 The Impact of Grazing on Pteridophytes

4.4.1 Sheep and Cattle

Examination of exclosures among any kinds of vegetation show how heavily nearly all open countryside is grazed. The actual grazing species involved have changed during the past centuries for in the 1740s, sheep (*Ovis aries*) were introduced on a large scale instead of cattle (*Bos primigenius primigenius*) (Millman 1975). In the 1760s, the Cheviot and Linton sheep were introduced to the Highlands. While they spent the summer on the hills, it was necessary that they should over winter in the valleys. At the beginning of the nineteenth century the land was even more extensively cleared to use for sheep. Until 1764 there were many foxes (*Vulpes vulpes*) in the Highlands and this restricted the number of sheep (Anderson 1967) but with a reduction in the fox population, sheep farming was able to expand.

The traditional pattern which had been in use up until the eighteenth century involved taking the milk cattle to the hill for the summer months. The lowland pastures were not grazed during this time and flowering plants were able to set seed. With the introduction of sheep, this practice changed and many plant species were thus confined to inaccessible mountain ledges, the only habitat in which they could survive. Sheep are more selective grazers than cattle and graze fewer species more heavily. They also graze around the preferred species to give a mosaic of grazing. The result can be the removal of all the preferred species and the growth of ranker less palatable species which are not eaten. McNeil (1910) suggested that grazing could reduce the abundance of *Huperzia selago* as he saw plants lying uprooted.

Brien (1989) quotes Osgood Mackenzie's description of a glen near Loch Ewe which, in 1850, had never been grazed by sheep. He referred to the Primroses (*Primula vulgaris*), Bluebells (*Hyacinthoides non-scripta*), Honeysuckle (*Lonicera periclymenum*) and orchids and implied that they were no longer found like that elsewhere.

Cockburn, sailing north after a visit to Iona in 1840, remarked upon the wooded nature of even very small exposed islands. "A thousand small and exposed, but still oak-clad islands, and promontories, and bays, and knolls, and ravines, but especially islands which are most in the way of the spray and the wind, attest that, even though not planted in great masses, the whole of the Hebrides might be adorned and warmed by trees. It is sheep and poverty, not the ocean or the storm, that keep them hard and uniform." (Cockburn 1983 p50). Croal in 1873 noted a similar destruction when describing the Lammermuirs where he observed large areas of Birch trees gradually being reduced by the sheep through prevention of regeneration.

Most of the relict Oakwoods that Bunce examined in Wester Ross suffered from grazing, and regeneration of the Oak was not occurring. Only where the grazing was limited by steepness, as at Corrieshalloch were ferns especially noted to be abundant. Also, at Toscaig south of Applecross, where cattle grazed instead of sheep, regeneration of the trees did occur (Bunce 1969).

Woodland was deliberately burned in Strath Farrar to make better sheep pasture. Singer wrote in 1807 that the Highland woods were gradually disappearing to provide room for sheep. "To destroy the woods for the purpose of making room for sheep, is much the same kind of policy as it would be to destroy the buildings of a city, to make room for more inhabitants" (Anderson 1967 p136). Formerly cattle had been kept in the woods until January, but, without the cover of trees or bushes, a strong coarse grass was growing which was unsuitable for cattle. The trees were effective as a shelter belt, a protection against erosion and against leaching, which results in podsolization (Anderson 1967). Such mis-management made the habitat less profitable than it had been under a less intensive regime.

Cattle can have a positive influence on the number of the species found. Millman (1975) described the effects of the Great Glen Cattle Ranch around Fort William. He said that the cattle manured the ground while grazing, and the grassland was improving in consequence. An unusual source of food for cattle was revealed in an account by MacGillivray who described a use for *Equisetum fluviatile* which he saw at the densely overgrown Loch of Achlossan. "I was surprised to see people cutting the Equiseta, which the boatman said were for the horses to eat, but they are relished by them only in the green state " (MacGillivray 1855 p30). West (1904) also described cattle being fed *E. fluviatile* which had been specially cut for them from Loch Meiklie.

4.4.2 Deer and Grouse

The management of the moors to encourage Red Grouse (*Lagopus lagopus scoticus*) developed alongside deer (*Cervus elaphus*), but the success of the different sports varied according to the efficiency of the prevailing management schemes. The burning of *Calluna* to provide new young stems was conducted differently according to whether the management was for the benefit of sheep or grouse. To encourage grouse, small patches of heath were burnt with the provision of different aged stands in a small area. When the main provision was for sheep, much larger areas were burnt. The present deer population is far too high partly due to the traditional reluctance to shoot hinds. Apart from damage to crops there is not enough grazing for the deer and culling is urgently required.

In 1846 Cockburn wrote "This autumnal influx of sporting strangers is a very recent occurrence in Scotch economy" (Cockburn 1983 p193). In 1790 the old Statistical Account listed nine deer forests, in 1883 the Crofter's Commission recorded ninety-nine, in 1912 there were two hundred and three (Innes 1983). In 1895 the Black Wood of Rannoch was even fenced as a deer forest (Anderson 1967). Deer forest management was thought preferable to sheep as the deer ate less (Macvicar 1901).

Brien (1989) stated that the hill pasture was formerly much richer. Wolves and hunting by men had kept the Red Deer population low and there had been more trees on higher ground providing shelter for taller vegetation. Without the grazing pressure which the sheep brought to bear, the pastures supported more species which were less heavily grazed by cattle in the summer. While a smaller population of deer had been able to exist alongside the cattle, the introduction of the sheep greatly increased the grazing pressure and has led to the present excessively grazed landscape devoid of regeneration and with a reduced species diversity.

The arrival of the railways into the Highlands in 1864 (Millman 1975) stimulated the dairy and beef market so that the proportion of sheep was reduced. During the First World War more sheep were kept in preference to deer, but deer forests had become a very substantial part of the Highland economy (Innes 1983).

While pteridophytes are not very palatable, they can be eaten if there are inadequate supplies of vegetation for an excessively large population. I have observed heavily grazed *Dryopteris affinis* subspp. in various locations in Perthshire which were probably eaten by both Roe (*Capreolus capreolus*) and Red Deer. Other species seem to be less attractive but *Athyrium distentifolium* was described from Caenlochan as a species which had been "much disfigured through being eaten down by the deer" (Cowan 1911 p173). Britten (1860) found that sheep also ate *A. distentifolium*. Huntly (1979) described components of the grazed vegetation at Caenlochan as typical remnants of woodland with species like *Anemone nemorosa* and *Mercurialis perennis* found only on ledges which are protected from grazing. On a field excursion in 1990, no *Athyrium distentifolium* was found in Corrie Fee, although it was frequently recorded last century. Possibly the grazing has reduced its abundance. On Coll, Duncan (1967 p485) observed that *Osmunda regalis* was "stunted by grazing except on the islets or the more inaccessible places on the rocky shore".

An additional source of grazing pressure comes locally from goats (*Capra hircus*). Adam (1930) found that there were fewer plants of *Athyrium distentifolium* in Coire Ceanne Mor than expected and wrote "Another incident which may account for their apparent infrequency in that particular area, was the discovery of sixty head of goats, of comparatively recent introduction, browsing on precipitous ledges, where sheep and deer do not naturally venture" (Adam 1930 p249).

4.4.3 Geese

Large numbers of geese overwinter in this country and graze on grass. As they only eat grass which is already short they will not have a substantial effect on a habitat which is not otherwise grazed (Ogilvie 1978). As the majority of the geese are only in this country during the winter they cannot derive much benefit from young growing pteridophytes. However, 2,500 to 3,000 native Greylag Geese (*Anser anser*) remain in the north-west of Scotland and breed during the summer (Thom 1986). It is possible that they may eat some *Equisetum* during this period as Greylags further north have included *Equisetum* in their summer diet (Cramp et al 1977). In a study of the diet of the Barnacle Goose, (*Branta leucopsis*) in North Uist during January and February, Campbell (1936) found that 4% of the stomach contents were composed of *Equisetum palustre*. Presumably in the milder west coast climate the plant was still green.

In their summer breeding grounds many geese eat *Equisetum palustre*, *E. fluviatile* and especially *E. variegatum*. While actively growing, these species provide a high-protein food especially beneficial for geese which are about to lay eggs (Thomas and Prevett 1982). In a study of the Greenland White-fronted Goose (*Anser albifrons flavirostris*), goslings were found to select a diet composed of up to 50% of *E. variegatum* (Madsen and Fox 1979). Baur and Blotzheim (1979) found that the Pinkfoot goslings (*A. brachyrhynchus*) ate 80-100% of *E. variegatum*. Other geese which also eat *Equisetum* are the Canada Goose (*Branta canadensis*), Barnacle Goose, Lesser Snow Goose (*Anser c. caerulescens*) and Bean Goose (*A. fabalis*), (Cramp et al 1977).

While any nutritional benefit to the geese is of conservational interest, their consumption is not likely to constitute a threat to the survival of *Equisetum*. There may be a small benefit to the herbage in the local enrichment from goose droppings.

4.4.4 Rabbits

The Normans introduced rabbit (*Oryctolagus cuniculus*) farming into specially constructed warrens in England but not apparently on the same scale in Scotland. Anderson (1967) referred to rabbits in a warren at Callander, Stirlingshire, in 1458, and before this date, at Dirleton, Gullane and Aberlady in East Lothian. From the fifteenth century there was a trade in rabbit skins from Wick, Aberdeen, Edinburgh, Haddington and North Berwick implying that a substantial population of rabbits must have been maintained. By the seventeenth century Anderson (1967) refers to rabbits also on the coast near Dunrobin Castle in Sutherland, on Gigha off Kintyre, in Angus and near Girvan in Ayrshire. By the eighteenth century rabbits were in Orkney and Shetland. There was a warren at Old Luce in Galloway, two warrens in Ayrshire, an extensive one covered 280 acres (112 ha) at Kilconquar in Fife. They were recorded from many parishes, enjoying a success which was attributed to the lack of many predators (Anderson 1967). But by the middle of the nineteenth century the Kilconquar rabbits were being destroyed due to the lack of demand for skins.

Placed on islands in the Dee in the Parish of Banchory-Ternan in Kincardineshire they succeeded in reaching farmland by crossing the river when it was frozen (N.S.A.S. 11 1845). They became a nuisance agriculturally. Links like Gullane and Tentsmuir were widely colonised, but they also spread inland. Loss of habitat caused a decrease in their predators such as Polecats (*Putorius putorius*), Wildcats (*Felis sylvestris*), Pine Martins (*Martes martes*) and Buzzards (*Buteo buteo*), but the rabbits were finding a satisfactory habitat in new plantations. Anderson (1967) suggested the spread of the rabbit may have been a major factor in the decline of woods in the last stages of decay at the end of the nineteenth and beginning of the twentieth century. By 1890 expensive fencing was necessary. Voles (*Microtus agrestis*) and rats (*Rattus norvegicus*) were also increasing and providing similar problems with their destructiveness. It was recognised at the beginning of the twentieth century that both rabbits and hares (*Lepus europaeus*) were an increasing problem. Rabbits were destroyed as much as possible, but only myxomatosis had a profound effect although, even so, certain populations have gradually recovered (Anderson 1967).

Farrow (1917) observed that rabbits can nibble *Pteridium aquilinum* if very hungry but do not actually eat it. Instead they ate the *Calluna* nearby and this encouraged the preferential spread of the *Pteridium*. This was also observed by Fenton (1940) who found that grazed *Calluna* was replaced by grass which in turn was replaced by *Pteridium*.

The deciduous horsetails are not very often grazed but the evergreen ones seem to be more attractive. Tame rabbits have been observed to eat both *Equisetum variegatum* and *E. hyemale*. In the wild, observations have shown that *E. hyemale* is grazed more than *E. variegatum*. At Roslin Glen in Midlothian it is grazed by rabbits, near Schiehallion in Perthshire it is grazed by sheep and possibly also deer, while at Morrone near Braemar the deer have eaten the more exposed shoots. Even in the steep ravine at Reeky Linn in Angus, Gardiner (1843 p900) found that "*Equisetum hyemale*, which grows here abundantly, was all cropped" (most likely by rabbits).

Species like *Botrychium lunaria* grow among rabbit-grazed vegetation and are consequently often very small. Rackham (1986) described the sudden luxuriance of *Botrychium* in Breckland after the demise of the rabbits, but as taller grasses grew more successfully the *Botrychium* suffered from excessive shading. This is an instance of the way in which rabbits maintain a type of vegetation which would not otherwise exist.

Regeneration can be inhibited by rabbit nibbling. Trampling by sheep and cattle is useful in opening up the ground, but no regeneration can result if rabbits and other small animals eat the seeds or seedlings. After the myxomatosis of 1954 to 1956 more regeneration was observed (Anderson 1967). White, describing rabbit-free vegetation in Norfolk, said that *Polypodium vulgare* had spread markedly on old dunes, since the rabbits departed (White 1961).

4.5 The Effects of Woodland Exploitation and Newer Plantations on Pteridophytes

4.5.1 New Plantations and the Establishment of the Forestry Commission

In woodland which was planted during the eighteenth century many hardwoods were planted as well as Scots Pine (*Pinus sylvestris*), maintaining earlier planting traditions. Larch (*Larix decidua*) was first recorded in a list at the Physic Garden in Edinburgh in 1683 (Anderson 1967) but later the various Dukes of Atholl planted Larch around Dunkeld and Blair Atholl. The first 16 Larches were planted by the second Duke in 1738 but by 1826, more than fourteen million (14,096,719) Larches had been planted either in pure stands or intermixed with other species (Hunter 1883). As the European Larch was planted in increasing quantities, Scots Pine became second in popularity and Norway Spruce (*Picea abies*) third. Conifers are often planted as nurses for hardwoods. Towards the end of the nineteenth century, hardwoods were planted less, with the exception of Oak (*Quercus* spp.), and conifers became even more popular, especially with the introduction of more North American species. In 1910 Sitka Spruce (*Picea sitchensis*) was introduced and soon became widely planted. The Hybrid Larch (*Larix* x *eurolepis*) was discovered around 1897 at Dunkeld and was found more resistant to disease than the European Larch (Anderson 1967).

Travellers at the end of the eighteenth century described many new plantations which were deliberately planted to compensate for the general lack of woods. Pennant gave details of the plantations in the Bewley area, at Foules, Invergordon, Inveraray, around the Riven Leven and at Broxmouth (Pennant 1769). Heron at the end of the eighteenth century recorded that the Seaforth family annually planted many firs (*Pinus sylvestris*) at Castle Braan. He saw plantations at Gordon Castle, Banff, Blair Atholl, Kinnoul and Moncreiff, Edzell Castle, Blair Drummond, the Palace of Dalkeith, Annisfield near Dalkeith, Tyninghame, Dunglass, Channelkirk, Lauder Castle, Mellerstane, Gallashiels, Stobo and New Posso, Mid Calder, Caroline Park, Middleton House, Borthwick Castle, Arniston House, Barochan (Renfrew), Luce Bay and Drumlanrig (Dumfries) (Heron 1799).

After 1866 duty was removed on imported timber, Oak coppice ceased to be profitable, and the area occupied by woodland was reduced from 913,695 acres (365 478 ha) to 734,490 acres (293 769 ha) (Anderson 1967). There was a small-scale continuation of coppicing as the last Oak coppice was cut in 1912 for bark for tanning. This marked the end of a very ancient form of woodland management. Woods were no longer protected from stock, much of the Larch which had matured from the earlier planting was not replaced and land was used for grazing as it had been improved by the Larch. But towards the end of the nineteenth century there came the realisation that home timber supplies were not adequate. Extension of the railways also led to increased exploitation as wood was required for sleepers and timber wagons (Anderson 1967).

Prof. I.B Balfour in 1894 suggested that private forestry was not very satisfactory and that the state should act. The Forestry Commission was eventually established in 1919, with the initial policy of planting old coppice areas with conifers. It was thought that hardwoods would not grow well enough to be worth planting commercially. The First World War led to unusually heavy cutting of the existing mature woods. In the Second World War resources were more carefully managed although the Forestry Commission timber was not old enough to make a significant contribution.

Many large estates over the whole of the country were bought by the Forestry Commission. Glentress was the first in 1920. Land was also bought at Culbin in Morayshire in 1922, together with a large part of Tentsmuir and 4,073 ha (10,183 acres) in Dumfriesshire which later became the Forest of Ae. The Blair-Adam estate was acquired in 1926 and planted with conifers, although hardwoods had been suggested. Former deer forests were bought and a proportion was planted according to the nature of the ground. After 1955 less land was bought because private owners were planting more (Anderson 1967).

13% of Scotland is covered by woodland (Mather 1988). Of this, 90% is high forest and most of the rest is scrub. 54% belongs to the Forestry Commission but little new land is being acquired. Between 1947 and 1980 the area of woodland had increased by almost 80% but this is mainly through the planting of conifers. Up to the 1960s forests owned by private estates were planted to provide for agricultural or sporting uses as well. More recently land has been bought exclusively for commercial reasons. Since the last war the area of scrub has been much reduced, from 23% in 1947 to 7% in 1980, mainly by planting conifers into Birch scrub. Most of the more recent plantations have been on to areas of moorland, which has declined in area in consequence. 99% of Forestry Commission planting has been conifers and grant-aided woodland was composed of 95% conifers. But within other woodland which has been planted without grant aid, only 44% of conifers have been planted, as this woodland is more mixed. Most of the conifers growing in 1980 were less than forty years old with only 6% older than eighty years. Of the hardwoods on the other hand, 41% were planted in the nineteenth century, and only 30% since the Second War (Mather 1988). The rate of hardwood planting has been such that many old mature trees are not being replaced and the mature trees of the twenty-first century will have a smaller proportion of hardwoods than at the present.

A study by the Nature Conservancy Council (as it then was) compared the area of existing woodland in 1976 and 1977 with areas which were known to exist in a 1947 survey by the Forestry Commission (Bunce et al 1979). An overall reduction of 58% was estimated for the 30 year period although this was thought to be an over-estimate. It does nevertheless indicate that although new plantations are being established, they are not compensating for the loss of semi-natural woodland.

4.5.2 Woodland Habitats for Pteridophytes

Existing open woodland often does not have as wide a range of species as might be expected. One of the main reasons is grazing, usually from deer. Grazing removes the seedlings of trees which might have shaded *Pteridium aquilinum* and this allows it to grow more vigorously to the further detriment of other species. In the Oakwood at Dinnet in Aberdeenshire there is a small exclosure which has profuse growth in comparison with the surrounding area. *Cytisus scoparius* is conspicuous in the flora but is short-lived. After shading, *Pteridium*, it is itself later shaded out, and seedlings of *Quercus* can continue to grow naturally. A similar progression was also observed in an Oakwood near Killarney in Ireland which had been an exclosure for a longer period. *Pteridium* was a very minor component and other species like *Dryopteris dilatata* grew in an abundance which was not seen in the wood immediately outside the fence. Thus, restoration of the tree canopy permits other species like *Dryopteris* to grow in the shaded environment.

Brown (1913) described the pteridophytes growing in plantations near Shotts. Scots Pine had been planted at first but later plantations were mainly Spruce and Larch. Nothing grew in the very densest conifer plantation, but in the less dense areas *Athyrium filix-femina* and *Dryopteris dilatata* occurred. These two species were also mentioned by Webster (1968) in older plantations from the Culbin area.

Often it is not possible to plant an entire area owing to topographic irregularities, and these features can retain some natural vegetation within a sheltered woodland clearing. Such areas include rocky knolls with species which vary according to the base status. Acidic outcrops have *Polypodium vulgare*, *Dryopteris affinis* subspp., *D. dilatata*, *Asplenium trichomanes* subsp. *trichomanes* and *Athyrium filix-femina*. More basic outcrops can have *Polypodium interjectum*, *Polystichum aculeatum*, *Asplenium trichomanes* subsp.*quadrivalens* and *Dryopteris filix-mas*. Damp hollows which may not have been planted, or perhaps where the saplings have been unsuccessful, can have *Blechnum spicant*, *Oreopteris limbosperma* and *Dryopteris carthusiana*. All these species have been observed in various locations in Perthshire particularly as seen around Kindrogan Field Centre near Kirkmichael.

Although the densest parts of forestry plantations contain few species, rides and tracksides are habitats in themselves. *Lycopodium clavatum* has been recorded in forest rides by Webster (1978) in Moray, Nairn and

East Inverness. There is a herbarium specimen for 1883 from Methven Wood and also from a forest clearing in Blackcraig Forestry plantation in 1973, both in Perthshire. Near Dunkeld, *L. clavatum* was observed in 1990 growing on a bank beside a forest road. There appeared to be many separate plants laterally extending to more than 16m. Some of the plants grew on almost bare ground although there were a few grasses and mosses and a very little *Calluna*. Similar colonies were found in 1991 on the track-sides in a forest above Innerleithen, although there are no records of *L. clavatum* on moorland in the area.

Lycopodium annotinum is now generally found at higher altitudes but White (1898) recorded it in a few Lowland woods in Perthshire including Muirton Wood (1883 PM). There is also a herbarium specimen from "firwoods towards base of Lochnagar" (RBGE 1837). It certainly still grows in open although planted pinewood near Dunkeld. It has also been found in a more recent Sitka plantation north of Dunkeld. Given a suitable habitat it could still extend over this wider altitudinal range.

4.5.3 Forest Fires and their Influence on the Pteridophytes Present

Anderson (1967) referred to an account of an act in 1662 prohibiting burning within quarter of a mile of young trees. Glengarry Pine forest was accidently burned in 1740 during muirburning, but fortunately was allowed to regenerate without harmful grazing. In May 1765 a fire in the Black Wood of Rannoch was caused by careless muirburn nearby and a hundred trees were destroyed before it was controlled. There was a Strathspey fire in 1731. In Duack Valley at Abernethy in 1746, two and a half million trees were destroyed. Further fires occurred in 1770 at Glen Urquart and also in Strathspey in 1781 when there were two serious fires in succession in the Forest of Glentanar. Both the deep mosses and the hills for ten to twenty miles around were covered in flames, killing plants and cattle. The old trees survived, but not the young ones. 1826 was another dry summer with many fires especially in Aberdeenshire on "moss-grounds" (Anderson 1967).

These fires were similar in effect to muirburn but would affect a different range of species. In pinewoods there would be stands of *Pteridium aquilinum* most probably subsp. *aquilinum* but also subsp. *latiusculum*. Sykes and Horrill (1981) in a study of regeneration in a Caledonian Pinewood after fire found that dense *Pteridium* inhibited the regrowth of pine seedlings. Presumably the *Pteridium* was able to grow from rhizomes. Alternatively if there had been a good summer after the first season following the fire, the *Pteridium* was more likely to spore as it was no longer shaded. Spores landing on burnt surfaces have already been demonstrated to be more successful and this could account for some of the larger areas of *Pteridium* which occur in clearings in the forest. Regeneration of other species would only successfully occur where the *Pteridium* was initially less abundant.

4.5.4 Disappearing Remnants of Woodland

Anderson (1967) related the change from scrubby woodland at Kippen in Stirlingshire to cleared farmland over a fifty year period from 1752. The vegetation had formerly been old Oak with new young shoots, resembling former coppice which had been grazed and impoverished. As it was removed, it was typical of many of the last remnants of once extensive forests which were permanently lost. Coppiced woods were not protected against stock and were lost to further production. From Henderson's General Survey of Sutherland, Anderson (1967) described the natural decay of woods in Sutherland since 1789.

Woodlands at Lovat, Cromarty, Stobhall and Cargil were particularly mentioned by the Board of Commissioners of the Annexed estates as having suffered both from cutting wood and damage from stock following the Forty-five Rebellion (Smith 1982). An attempt was made to have closer control over timber cutting.

Pennant saw Birnam Wood in 1769 but it had gone by Heron's time(1799). While seeing the remnants of some forests, both Pennant and Heron also saw the beginning of plantations around the houses on big estates which have already been described. Pennant saw the local effects of woodland clearance in the deep glen with "brushwood" around Castle Campbell "for the forests that once covered the country are now entirely destroyed" (Pennant 1769 p71). He also saw the larger scale extraction as at Dalmore north of Braemar with what he described as the largest natural pines in Europe.

Juniper bushes in a field are often the last remnants of former woodland (Fenton 1939). Juniper (*Juniperus communis*) grew in a field above Boghall experimental farm in the Pentlands, surrounded by encroaching *Ulex europaeus* with *Pteridium* present but not spreading, and *Nardus stricta*. These species suggest that formerly Boghall Glen was mostly *Calluna* with Juniper and *Vaccinium myrtillis*, and presumably some Birch or Pine as well (Fenton 1933). There are often small scattered remnants of Juniper trees in an area where grazing prohibits regeneration of seedlings. The mature Juniper association was very rich in the postglacial scene, and these remnants are a species-poor relic.

Other factors influencing woodland in particular are occasional catastrophic events associated with the weather. In a temperate climate, tropical extremes are not encountered, but from time to time exceptional winds or storms leave a strong impression on the countryside. The table in **Appendix 6** shows an assemblage of extremes in weather conditions gathered from a variety of sources. While one particular extreme can be expected from time to time, a combination of poor climatic conditions will make growing conditions very unsuitable. In November 1893 there was a very strong gale which Coates (1923) described as stripping the hillside in a particular locality in Perthshire. He described the subsequent disappearance of shade-loving fungi and found that the whole micro-climate of the hillside had changed. The gale followed a year which had had floods in February and a drought in the summer. In the following year, 1894, much the same pattern of floods, drought and gales was repeated, with the addition of a late frost in May. Mature pteridophytes which had grown in the shelter among trees would not respond well to such treatment and it might be expected that many would die. At the same time, such events do create new habitats which can be readily exploited by pteridophytes, especially with a sporebank extending up to at least 95 cm into the soil (Lindsay and Dyer 1990). When trees are blown over, the roots are often ripped, up exposing cavities which are damp and suitable for gametophyte growth. Unless the forest is cleared and converted to farmland, there should be every opportunity for a similar habitat to regenerate as saplings grow in the increased light and eventually provide the necessary shade again.

4.6 Summary of Pteridophyte Abundance

From the previous sections the general picture is one of very marked decline in pteridophytes. Over a period of more than two centuries the traditional farming pattern has been radically changed. This has brought about the complete removal of many former habitats in "wasteland" and marshes. This has affected species like the club-mosses and horsetails. *Dryopteris carthusiana* has been described in floras as common, when it is now usually infrequent. Montane species like *Dryopteris expansa, D. oreades* and *Athyrium distentifolium* have been restricted by grazing and although they still exist, they are no longer present in anything like their former abundance. Very little natural pasture remains which has not been "improved". The improvements have removed many habitats which were formerly occupied by *Ophioglossum* and *Botrychium*. *Pteridium aquilinum* is one of the few species which has markedly benefited by changes in farming practice, perhaps to the detriment of different potential habitats. On the other hand, habitats created by man do offer a suitable environment for many species, particularly those which like calcareous conditions, and these are discussed further in the next chapter.

Chapter 5

Pteridophytes in an Industrial and Urban Setting from the Eighteenth Century to the Present

5.1 Introduction

At the end of the eighteenth century there was a major change in the distribution of the population as the people became less involved with agriculture and moved towards the industry based around towns or villages. The earliest industries were centred around mills and were widely dispersed to take advantage of water power. With greater specialisation and the use of steam power these industries became localised near the source of fuel. Coal provided the main source of energy and its extraction was enormously increased over the second part of the nineteenth century and into the twentieth. Most of the Scottish collieries were in Lanarkshire and Ayrshire where other industries like smelting became able to exploit the ironstone. This chapter traces the historical development of industrial activities like mining and quarrying and the effect that these activities have had on pteridophytes.

Ambitious construction work was undertaken in the nineteenth century with the benefit of a large labour force. With the advanced technology of the twentieth century, even bigger reservoirs and dams have been built which have had substantial effects on whole river valleys as described in section **5.3.2**. The provision of improved transport has made such projects possible and the environs of both roads and railways provide habitats which are described in sections **5.4.2** and **5.4.1**.

Also contained within this chapter in section **5.5** is a brief review of the influence which collecting has had on the less common species of pteridophytes. Finally, the recreational use of the countryside accounts for an increasing area and may conflict with other interests. While large hunting forests may have existed in the past, they were only for the benefit of a few. The present larger more mobile population brings pressure on remote areas of a different kind to that which may have existed with traditional farming methods even though the land was then more densely populated. Pteridophytes are affected in common with all the other specialised plants and animals which occur in these sites.

5.2 The Use of Raw Materials

5.2.1 Smelting

The use of iron from Wester Ross was mentioned as early as 1529 (Anderson 1967). An enormous amount of industry was associated with obtaining charcoal for use in smelting. In 1610 the woods of Letterewe in Wester Ross around Loch Maree were cut for charcoal used to smelt iron obtained from local ore. There does not seem to have been any effort to manage the woodland and smelting ceased when the woods became "exhausted". By the end of the eighteenth century there were numerous small ironworks north of the Forth-Clyde line in areas of former natural wood. Anderson (1967) located 93 ironworks in 12 counties identified by the remains of slag-heaps. As the foundries were situated among slow growing mixed Oak and broadleaf forest, regeneration was not naturally very fast. With the later increase in sheep farming and the encroachment of stock into unfenced woodland the woods were left in a weak state unable to survive the repeated over-grazing of the sheep.

Some of the forfeited estates from both the 1715 and 1745 Risings were sold to speculative English companies like the York Buildings Company. They had a lease on the Abernethy Pine forest from 1728 and floated the largest timbers down the Spey. A blast furnace at Abernethy operated for nine years used and the local wood at a rate of 168 tons a week. This made further substantial inroads on the native pinewood.

Hundreds of people were employed in Bonawe Woods in Argyll from 1730 to 1875 cutting wood to make charcoal for iron smelting, using imported iron ore (Cadell 1913). Although the woods were coppiced they were cut too frequently for the growth to sustain a continuing supply (Anderson 1967). Cadell noted that the last of these charcoal furnaces was located at the mouth of the River Awe on the shores of Loch Etive. When smelting ceased the hills were cleared of woods. However, wall ferns benefited from the buildings which were left, as Cadell described the "fern-covered walls outside" the ruins that remained (1913 p149). The Carron Company bought or leased woods at Callander, Leny, Lowbank, Newred, Northwood and Tinnichside. Their earliest furnaces were in operation from 1760 (Cadell 1913). Charcoal was gradually succeeded by coke which occasioned the removal of the iron works from the Highlands to the Lowland coal-bearing areas.

At Leadhills where lead was mined and smelted Heron recorded the absence of trees or shrubs. There were enough sheep and black cows around the mines to prevent natural regeneration although some near the mines had died of lead poisoning (Heron 1799). Anderson (1967) refers to a 1609 report recording the felling of many trees around the Wanlockhead mines. There was criticism of a lack of fencing to encourage regeneration. In 1679 a dyke was built to protect the new growth. There were deep mines from 1680 and wood was used for smelting the lead until coal was introduced from 1710 (Anderson 1967). The lead mines closed in 1928, but the lead content in the soil derived from the abundant spoil-heaps in the village at Leadhills was still high enough to have killed hens (3rd S.A.S. 8 1960).

These incursions into the native broadleaved and pine-dominated woods contributed to the overall reduction of woodland habitats already described in Chapter 4.

5.2.2 Quarries

Quarries were opened for building materials, minerals and limestone for both agricultural and building purposes and are now mainly for roadstone, clay, sand and gravel.

There are slate quarries around Dunkeld, Aberfoyle and elsewhere along the outcrop of the rocks associated with the Highland Boundary Fault. Leach (1930) described the early stages of colonisation of screes which are equally applicable to tip heaps. *Racomitrium* and *Diplophyllum* are the first colonisers on to more acidic screes making cushions of moss and liverwort on which Leach suggests the *Cryptogramma crispa* spores can land. The decaying fronds of *Cryptogramma* build up humus until other ferns like *Blechnum spicant*, *Dryopteris filix-mas* and *Oreopteris limbosperma* can become established. With a sufficiently large accumulation, heath plants may colonise including *Calluna vulgaris*. The pteridophyte component can be reduced through time, but often too great an accumulation becomes unstable and slipping creates new areas for colonisation. *Pteridium aquilinum* and *Phegopteris connectilis* were quoted as species which could grow from stable areas through into less stable to contribute humus.

Asplenium adiantum-nigrum is a further species which is a frequent component of a slaty flora, growing both on the outcrops and waste-heaps especially around Dunkeld. *Diphasiastrum alpinum* can also be found on the spoil heaps at Aberfoyle with some *Huperzia selago*, all typical early colonists of such habitats.

Fluvioglacial features, and outwashes of sand and gravel, are quarried and can provide new habitats with well-drained marginal areas and pools which are ideal for colonies of *Equisetum*, ranging from *E. fluviatile* in the permanently wet areas, through *E. palustre* in marshy parts, to *E. arvense* in the dryer margins. Given this range of species within a small area it is not surprising that *E. x litorale* was found in a Cleish Hills gravel pit pond (Ballantyne 1985). The post-glacial features themselves can provide specialised habitats for uncommon floras.

Clay pits are a less common feature in Scotland than in the south of Britain, but there are ponds in several areas in the Lowlands such as those surviving at Doune in Perthshire, which occupy the quarried remains of former clay workings. Here the steep-sided pond margins have a luxuriant vegetative growth of *Pilularia globulifera*. This species almost seems to be dependent on man-made ponds and lochs to provide suitable uncolonised habitats. It cannot survive among closed vegetation and without a source of disturbance to maintain an open habitat it can be short-lived in some sites. Some of the records of its occurrence in the nineteenth century were in ponds created through industrial usage as at Philpstoun near Edinburgh in 1872 and near Winchburgh in 1867 (RBGE). Small brickworks were widespread and would have often been beside open clay pits.

Building materials are now transported further in larger lorries. Instead of smaller local quarries used as demand required, the trend is for a few very big quarries like the development at Glensanda in Morven which have a major impact on the environment and local landforms (Pollock 1988).

Smaller local quarries which were worked when occasion demanded, could provide the equivalent of slight erosion which provides new habitats for pteridophytes. This is comparable to the effect of small-scale peat workings with the opportunity for new colonisation on to an adjacent fresh surface.

Quarrying operations can affect the groundwaters and springlines. Johnston collected herbarium specimens in 1921 and 1922 of *Equisetum pratense* from the only colony he discovered in Orkney (RBGE). In 1925 and 1926 he added that he could not find any more specimens. He attributed their disappearance to the opening of two small flagstone quarries nearby which might have affected the drainage and groundwater without actually destroying the site.

Larger quarries can remove the very rocks upon which plants are growing. In 1919 the Botanical Society of Edinburgh sent a protest to the Town Council of Edinburgh as the rock on Blackford Hill was being quarried to an extent which threatened rare plants growing there (Grieve 1919). This account is especially interesting in view of the existence of a small colony of *Asplenium septentrionale* on the hill which was still recorded in 1972 (RBGE).

Abandoned quarries can provide new and more extensive rock faces for subsequent recolonisation compared with the original rock face. Limestone rocks have *Cystopteris fragilis, Asplenium ruta-muraria, A. adiantum-nigrum,* and *A. trichomanes* subsp. *quadrivalens* with *A. viride* at higher altitudes and in the west. Calcareous areas of accumulated soil within a quarry can be suitable for both *Ophioglossum vulgatum* as found at Cults in Fife (Young 1936) and *Botrychium lunaria* which Gardiner noted as unusually large specimens up to a foot (30 cm) high in old quarries at the Hill of Stracathro, Forfarshire (Gardiner 1848). Fallen debris is often colonised by larger ferns like *Dryopteris filix-mas*.while more acidic quarries have *D. affinis* subspp. and *D. dilatata* (Thompson 1807).

An unusual species was found in the nineteenth century at a limestone quarry near Aberdeen (Sim 1868) and a similar quarry near Aberfeldy (Balfour 1868). *Gymnocarpium robertianum* is only known from two locations in Scotland neither of which had been recorded at that time. Controversy surrounded both reports with suggestions particularly that the Aberdeen specimens at Scotston Moor had probably been "planted by someone interested in ferns" (Trail 1923 p324). While flourishing briefly at both localities, neither colonies persisted. Whether introduced or not, conditions are obviously not very appropriate for this species of more southern affinities. Interestingly one of the two present colonies is in a small gryke on limestone near Schiehallion from which it has not spread. The area is not very far from Aberfeldy and this colony may have provided a local source of spores, or possibly it too was introduced.

At Wanlockhead the old waste heaps from lead mining are still too toxic for many plants to grow except for *Equisetum palustre*. It was observed that this species was able to grow well without competition. On the hills the lines of the old wooden flues can still be seen by the lack of vegetation around them. *Botrychium lunaria* has been found at Leadhills (1902 RBGE) and (1916 BDG) demonstrating its ability to grow provided it has a calcareous environment. Ellis (pers. comm. 1991) found *Asplenium viride* growing in spoil from a lead mine near Tyndrum.

Several pteridophytes can grow on rocks which other plants find toxic. *Asplenium viride* flourishes with other calcicolous pteridophytes on the basic rocks in the abandoned debris of the mines at Strontian, from which the mineral Strontium derives its name. *Equisetum* species can grow in seeping groundwaters which may contain dissolved minerals which other plants cannot tolerate, but providing there are adequate supplies of silica the plants will grow successfully (Page 1988).

5.2.3 Coal

During the fifteenth century the demand for coal increased as wood supplies became less. The early mines were constructed on a small scale and did not go very deep due to drainage problems (NCB 1958). But by the end of the seventeenth century the seams near the surface had been worked out. The coalfields particularly in the west of Scotland at greater depth were beginning to be exploited and during the next century came the use of steam power to pump water. After the unsettled times at the beginning of the century there was a rapid improvement both in agriculture and industry. In 1760 the Carron Iron Company opened its first coal-coke furnace. From this time less wood was required for charcoal burning and eventually only the bark was required for tanning (NCB 1958).

After mining has ceased, subsidence can occur and in heavily mined areas ponds are created as well as deep holes or old shafts. These shafts are the equivalent to damp caves and *Phyllitis scolopendrium* was recorded from a mine air-shaft near Kirkcaldy (Young 1936). Subsidence can break drains and cause waterlogging of pasture which had been improved (3rd S.A.S. 8 1960). Such waterlogged land is not very suitable for many pteridophytes but *Equisetum palustre* could occur with *E. fluviatile* in standing pools.

Substantial land area is also lost through mining activities. "Throughout the past century there has been much destruction of land once available for agricultural purposes. This has come about chiefly as the result of surface disturbance from mineral workings and associated bings of refuse, which cover many acres" (3rd S.A.S. 8 1960). In the later stages of dereliction, the shrubs and eventually trees which grow in these abandoned sites offer shade to the larger woodland ferns. Coal, lime, ironstone and clay could all be mined opencast.

Often opencast holes have been utilised for town refuse so that such large areas are no longer lying derelict. In many parts of the country positive efforts at reclamation are now being pursued. (3rd S.A.S. 3 1953). The pit coal-washings went either into the sea or into smaller streams which in turn polluted larger rivers. This was resolved by using settling ponds.

Bellshill in Lanarkshire had 20 pits working at one time (3rd S.A.S. 8 1960) but the use of coal has fallen considerably. In 1950 coal accounted for 94.5% of all energy consumed but by 1978 this had fallen to 35.3%. Production has fallen also and now nearly all of the Scottish coal comes from opencast pits (Pollock 1988).

Opencast mining is carefully managed. The topsoil is stripped and put on one side with the subsoil in a separate place. The rock is blasted and removed to retrieve the coal. After extraction the subsoil is replaced, then the topsoil which is levelled on a similar slope to the original fields but at a slightly lower level. Although the finished appearance will be similar any vegetation present will be entirely disrupted. There is the possibility of species re-establishing from seed or spore banks in the topsoil but as the area will be cultivated they will have little opportunity to become established. Only if new hedges are planted will there be local strips with species like, *D. dilatata, D. affinis* subspp., *Athyrium filix-femina* and *Equisetum arvense* which would otherwise not be present at all.

5.2.4 Oil-shale

In 1851 James Young set up the first oil-shale refinery at Bathgate in West Lothian. Using first a form of coal, but later oil-shale, a large industry was eventually based in West Lothian to extract paraffin oil and wax. While at a maximum in the later decades of the nineteenth century, the shale was worked up until 1962. The whole area was dominated by shale bings, the reddened remains of the shale left after heating to extract the oil. Some of the bings have been removed but many remain and have been preserved for their wildlife interest. Corner (1966) examined 70 bings and found *Lycopodium clavatum* on five bings in Fife and Kinross and three in Lanarkshire and Stirlingshire. All were found on stable north or north-east facing slopes. Two of the bings also had *Huperzia selago* and *Diphasiastrum alpinum*. *Botrychium lunaria* (Page 1988) and *Osmunda regalis* (personal observation) have also been found on bings.

5.2.5 Mills

There was a considerable number of mills on suitable stretches of river. The Water of Leith flowing through Edinburgh had eighty mills on fourteen miles of water producing flour, barleymeal, paper, linen, tobacco, dressed cloth and water for distilling (Heron 1799). There were fifteen mills on the stream from Loch Turret to Crieff and forty mills on the ten miles of the River Leven leading from the Loch (Heron 1799).

With expansion, dependence on water-power became more difficult. When lochs and bogs were drained as part of the agricultural improvements, the speed of run-off was increased and the supply of water-power became less regular. Steam-mechanisation led to an increasing centralisation of industry away from the smaller local mills and the subsequent abandonment of many buildings throughout the country.

The remnants of this widespread industry seen both in the people's homes and the remains of mills with accompanying leats still form substantial features in the landscape. Damp, shaded walls with mortared stone are good habitats for many calcicolous ferns. The buildings which remain are often shaded by trees and very close to the water. At Cramond near Edinburgh the buildings of the old iron works mentioned by Heron (1799) have abundant *Cystopteris fragilis* and *Asplenium trichomanes* with some *A. ruta-muraria*. Further personal observations on old leats at Blairgowrie and near Ballinluig, both in Perthshire, have revealed luxuriant plants of *Polystichum aculeatum* which excel in these abandoned areas. In the south of Scotland *Phyllitis scolopendrium* also occurs in this habitat.

5.3 The Construction Industry

5.3.1 Hydro-electric

There are several large hydro-electric schemes in Scotland. In a scheme based around the Tay catchment area, construction started in 1927 on Rannoch power station and at Tummel Bridge in 1933 where work continued until 1942. There were further phases until 1964. Tunnels were dug to divert water from other catchment areas into the power stations. In 1950 at Loch Tummel the level was raised by 5.1m (17 feet) so that it is now 3.2km (two miles longer). The level of Loch Lyon was raised by 21m (70 feet). Lochan Breaclaich was raised by nearly 20m (66 feet) and a completely new loch was created in Glen Lednoch. Lochan na Lairige was enlarged with a conspicuous dam between Ben Lawers and Meall nan Tarmachan. New lochs were created like Dunalistair, Loch Errochty and Loch Faskally while Loch Giorra and Loch Daimh were dammed and combined. There are nine power stations on the River Tummel and tributaries alone and other rivers have similar complexes (3rd S.A.S. 27 1979). These new water bodies often have steep sides and are not very suitable for vegetation. Only in situations where the topography has provided gentle slopes at the waterside have interesting plant associations developed.

Pilularia globulifera is not generally very common in Scotland, but its appearance is often associated with abrupt alterations in the original water level as can occur with new reservoirs and lochs. The water level of Loch Tummel was raised in 1950 and *Pilularia* was recorded from 1965 when it had not previously been known in the Loch. It also occurs in deeper water offshore from the main colony. This seems to be the mode of growth which has been adopted in several sites. In 1960, when Jordieland Loch in Kirkcudbrightshire was drained for maintenance the shore was found to be abundantly covered with *Pilularia*. Loch Ken in the same area, which was formed by damming the river, was found under similar circumstances to have *Pilularia* growing on the former river-banks which had been inundated (Stewart 1988).

When new lochs are created the margins may be unsuitable for many species if the water-level fluctuates considerably. Lochan na Lairige near Ben Lawers has a wide range in water level and in these circumstances the commonest pteridophyte on the rocky shore is *Equisetum palustre.*

5.3.2 Reservoirs and Ponds

As small towns expanded and cities required ever-increasing water supplies, reservoirs have been built with increasing capacities. Edinburgh's water was piped in from Comiston springs from the end of the seventeenth century. Then reservoirs in the Pentland Hills were opened from 1820, and in the Moorfoots from 1870. Glasgow was supplied from Loch Katrine (Mackie 1962), with additional supplies from five other enlarged lochs, including Loch Venachar, where *Pilularia globulifera* has been recorded.

East Lothian's water supply comes from five reservoirs in the Lammermuir Hills built between 1882 and 1935 (3rd S.A.S. 3 1953). One of these, Hopes reservoir, which was built in 1935, has *Lycopodium clavatum* on the embankment of grass with mixed *Calluna-Vaccinium.* As the bank is mown, although perhaps only once a year, the *Lycopodium* plants presumably spread vegetatively. The mowing may also prevent competition and maintain the habitat. *L. clavatum* was also found in 1824 (Greville) near an old reservoir in the Pentlands near Edinburgh. Possibly the exposure of bare earth at both these sites provided an opportunity for the colonisation by the local flora with a pteridophyte typically among the pioneers. In the Pentlands, however, there is no longer any *L. clavatum* near Edinburgh, although apparently suitable habitats exist. This plant is affected by pollution and may have diminished in this area for that reason. This is further discussed in Chapter 7.

Temporary low levels in a reservoir can provide an expanse of mud ideal for the germination of *Equisetum* spores (Page 1967). Lake margins also offer suitable conditions for hybrids to occur as illustrated by the *Equisetum x litorale* in the North Esk reservoir. *Isoetes lacustris* and *I. echinospora* can be found in reservoirs unless there is an excessive range in water-levels. A certain amount of bottom scouring is necessary to maintain an open habitat for *Isoetes.* Pearsall (1917 & 1920) found that *Isoetes* in the Lake District grew at the opposite end of the lake from the inlet where silt was deposited. It was found in depths from 2-4m, a range which could be accommodated within some reservoirs. Levels of light were less important than the substrate which tended to be coarser and lower in potash than at the head of the lake. *Pilularia,* on the other hand, has a preference for the silty conditions such as are found around the head of suitable lakes.

Small artificial ponds, such as in curling ponds, also offer a suitable habitat for *Pilularia globulifera.* Herbarium specimens from the artificial curling pond at Moncreiffe were collected by F. B. White in 1874 and are held at Perth Museum. Three other ponds in Perthshire contained *Pilularia* and were also probably artificially made. There was the Laird's Loch above Red Myre; specimens collected 1874, an undated specimen from Rossie Priory, and a specimen collected near Murthly castle in 1889 (all PM). The "fishing ponds" in the Pentlands were also localities for *Pilularia* (1834 RBGE).

An old reservoir above Innerleithen has affected the adjacent vegetation through the decomposition of the concrete which has caused local enrichment. The acidic flora dominated by *Calluna vulgaris* has been replaced by grasses containing *Botrychium lunaria* which was presumably not there before and has been able to colonise as a suitable habitat has been created.

5.3.3 Buildings and City Habitats

Buildings and harbour walls near the sea can offer a suitable place for pteridophytes to grow. *Asplenium marinum* is recorded as herbarium specimens from Shipness Pier in Kintyre (RBGE 1899) and from Iona where it has been found on the "Nunnery " walls with *Asplenium viride* (RBGE both 1907). Even inside rebuilt sections of the Abbey, *A. marinum,* which was mentioned in this site by Newman (1844), has persisted growing from the old lime mortar within the newly pointed walls (pers. comm. A.F. Dyer 1990). Grieve (1880) also found this species on ruins in

Oronsay. *Asplenium adiantum-nigrum* can likewise be found growing on damp mortar near the sea, along with *Phyllitis scolopendrium* and *A. ruta-muraria*, most especially on the west coast.

Although the buildings in a city are often at a high density, many shady corners are incidentally created which are ideal for pteridophytes. *Equisetum arvense* can be found with its rhizomes growing around the bases of masonry. It squeezes through cracks between paving slabs and pushes through thin layers of asphalt. It often seems to be the prostrate sand-dune form, which may relate to the habitat before building took place, or possibly it was introduced in imported sand. It is also not uncommon among shrubs in municipal planting schemes. Cultivation of the soil, or possibly the use of weedkiller, suppresses other weed species but has little effect on the *E. arvense* which grows with far greater vigour than it would have otherwise done.

Figure 5.1 *Dryopteris filix-mas* growing on a basement wall in Edinburgh's New Town.

Damp basement walls, such as are found below Edinburgh's New Town houses, can offer sheltered areas which may rarely be reached by the sun.

Phyllitis scolopendrium may be found with *Dryopteris filix-mas* but the species are often ones which prefer more acidic substrates. The house walls are probably maintained more carefully than the basement retaining walls so that this mortar may be well-leached. This particularly applies in areas receiving additional water supplies from leaking gutters or faulty down-pipes. Their presence can be seen by mossy corners which may be occupied by *Dryopteris dilatata* and *Athyrium filix-femina* which are surprisingly common.

An unexpected species which is found in the juvenile form growing on mortar, is *Pteridium aquilinum*, proving as ubiquitous as always. It seems to be able to tolerate calcareous conditions while juvenile (Page 1988) but seldom continues to adulthood in such cases.

Repointed walls result in a poor habitat for fern establishment, but this does not necessarily remove this niche as previously established ferns like the *Asplenium marinum* on Iona can grow through the new mortar. In 1882 McAndrew lamented the destruction by repointing, of twelve plants of *Ceterach* on Kells churchyard wall, in the south west. *Asplenium ruta-muraria* is another species which has been observed growing through repointing and is often the only common species beside very busy roads. It can be found with old fronds encrusted with mud and dust. Its presence on the seaward side of a railway embankment in Edinburgh shows a tolerance of salt and shows that it can accept the salt it must receive splashed off the roads in winter. Page (1988) describes *A. ruta-muraria* from metal-mining areas implying a tolerance of heavy metals which explains the resilience of this species in what might have been a lead polluted environment. An example of this species' tenacity, faced with the less usual elements, may be found in in an old record of the fern in a manganese quarry near Laverock Braes not far from Aberdeen (Sim 1868).

Edwards (1982) provides an example of a pteridophyte being able to tolerate polluted conditions and to grow where other plants cannot succeed. He described the appearance and progress of *Dryopteris carthusiana* in an English woodland. Oil was accidently spilled in two places creating bare ground and young plants of *D. carthusiana* appeared at these places in 1972 and 1973. At the first locality the plants were fertile by 1974 and increased in abundance until 1978. From 1979 there was a marked decline and by 1981 there was one plant left which died as the other plants had, by decaying overwinter. A similar pattern was followed on the same time-scale at the other oil-spill one kilometre away. Interestingly, as the number of *D. carthusiana* plants declined, *D. dilatata* became established and eventually became the dominant species after the *D. carthusiana* had all disappeared. Possibly this implies that in a habitat which could be suitable for either species, *D. dilatata* is most likely to dominate at *D. carthusiana* 's expense. It is also possible that the presence of the oil had the effect of inhibiting the drainage making the habitat temporarily more suitable for the *D. carthusiana.*

5.4 Transport

5.4.1 Railways

Horse-drawn wagonways were first used in the eighteenth century to convey coal from the pits to the nearest existing transport. The first steam train in 1820 was designed merely to link to canals or existing roads. By 1830 independent passenger trains were constructed with the Glasgow to Edinburgh line completed in 1842. Major railway expansion occurred throughout the 1840s, partially assisted by the Board of Destitution. This Board was appointed to alleviate the effects of the 1840s potato famine and employed Highlanders to construct both roads and railways. The line to Inverness was open by 1863, Thurso by 1874, Oban in 1880, Fort William 1899 and Mallaig 1912. At the maximum use of railways nearly all of Scotland was within twenty miles of a railway line (Mackie 1962).

After this period of expansion the lines were gradually closed, especially in the 1950s and 1960s. Some lines have been used as roadways, others have been left unfenced and form little more than a raised mound crossing a field. Where the fencing is well maintained with both old and existing railways, an ungrazed strip of vegetation is created. On abandoned railway lines, shrubs and eventually trees have grown and illustrate the natural wooded vegetation which could exist given protection from grazing (Page 1988).

In some instances the presence of railway embankments changed the local drainage patterns and thus affected the local micro-climate and associated vegetation. In the Dornoch Firth a small bay was cut across changing the enclosed environment from saltmarsh to freshwater. Further north the upper end of Loch Fleet was truncated by a combined road and rail embankment called "The Mound" completed in 1884 (Hunter 1988). *Zostera marina* no longer grew at this end of the estuary thereafter and *Asplenium marinum,* which had been recorded in 1882 and 1889, was not present in 1972 (Kenworthy 1976).

Railway lines which are still in use have several species on the embankments which are usually unshaded and are maintained as such. The actual trackbed is kept clear of weeds with regular spraying but *Equisetum arvense* is often seen as it is the only plant which can survive in such conditions. It is even more conspicuous on the less-used sidings and margins of the ballast. In 1896 Scott-Elliot recorded *E. arvense* from the "cinders" on railway lines. *Equisetum sylvaticum* is found on the sides of railway lines in the north-west in particular (Page 1988) and was recorded in the Railway Flora of Teviotdale (Braithwaite 1975) in an especial abundance around Newcastleton. *E. fluviatile* and *E. palustre* were also seen in appropriate habitats in ditches and pools associated with the railway in Teviotdale. The intermediate habitat formed between the wet foot of the embankment and the dryer trackbed is ideal for the hybrid between *E. fluviatile* and *E. arvense,* and *E. x litorale* was recorded by Webster (1978) from an embankment near Kirkhill in north Aberdeenshire.

Similar conditions are suitable for *Dryopteris dilatata* on the embankment sides, with *D. carthusiana* lower on the embankment. Webster (1978) recorded both these species and also their hybrid *D. x deweveri* on the embankment beside the A9 near Slochd.

A few patches of *Lycopodium clavatum* and two plants of *Diphasiastrum alpinum* became established on cinder ballast in the old railway yards at Acreknowe in Teviotdale (Braithwaite 1975). Given a suitable habitat pteridophytes are often among the first colonists. But with progressive growth of vegetation, these species would not necessarily continue. At lower altitudes especially, it is an advantage for pteridophytes to have new habitats exposed from time to time. Laying new ballast on current railway lines can provide habitats, as the large quantities of *Dryopteris affinis* subsp. *borreri* demonstrate on the section of line between Perth and Inverness. *Polypodium vulgare* was found by Webster (1978) in similar circumstances near Slochd. Dyer (pers. comm. 1991) found *Asplenium adiantum-nigrum* on ballast at Goldielea near Dumfries. The scree conditions thus provided can supply a suitable damp environment for germinating spores which can become large plants before any further maintenance is carried out. The plants do not appear to suffer from the small consistent amount of pollution which must be present.

Botrychium lunaria was recorded as "abundant" on an old railway embankment crossing Dava Moor in the north-east Highlands. Although no longer in use, this embankment was presumably still not very overgrown. *Botrychium* was also "abundant" on the railway embankment between Drumochter and Newtonmore in 1954 (Webster 1978). As the latter is the main line still in use, its presence shows that protection from grazing may be of considerable benefit. *Ophioglossum vulgatum* was also found on an overgrown embankment near Braehead in Glasgow (Dickson 1991).

Some flooded sidings in Glasgow provided a habitat for *Oreopteris limbosperma* and *Osmunda regalis* with *Lycopodium clavatum* growing higher up the siding (Dickson 1991).

Both used and unused lines have exposures of rock faces in cuttings. These are typically damp and are frequently well covered with the commoner species of ferns. Braithwaite (1975) found *Athyrium filix-femina*, *Dryopteris dilatata* and *D. filix-mas* on both rock-cuttings and embankments. Dyer (pers. comm. 1991) found *Dryopteris affinis*, *Asplenium adiantum-nigrum*, *A. ruta-muraria* and *A. trichomanes* on rock cuttings near Goldilee. Larger ferns which grow on a rock face may have a limited life-span as they are governed by similar factors which restrict species growing on walls. There are often a large number of small young plants and only a few older ones. Given a series of wetter seasons the plants would grow well, but with the occasional exceptionally dry summer many plants would succumb, unless they were in particularly deep crevices. Their sites would then become available for recolonisation, aided by the humus from the previous colonists. An unusual species which has made use of a rock cutting is *Ceterach officinarum*, which Braithwaite (1975) found at Whitlaw.

Mortar in stonework on bridges, station buildings and tunnel mouths all contribute to a calcareous environment which is colonised by *Asplenium ruta-muraria* and *A. trichomanes* subsp. *quadrivalens* most commonly, with *Phyllitis scolopendrium* in the south and west as recorded by Braithwaite at the Station yards at Hawick. Duncan (1980) found *Cystopteris fragilis* in walls by the railway line at Auchterneed, Braithwaite (1975) found it uncommon on both rock cuttings and stonework and Webster (1978) recorded this species from below railway platforms. *Ceterach officinarum* grew in a recess in the station platform at Newcastleton until the station was demolished, but it is still found on a wall in Newcastleton. It also grows on the ramparts of a dismantled footbridge at Riccarton Junction in the same area (pers. comm. D. Ellis 1991). In 1901 Macvicar described *Asplenium ruta-muraria* on bridges "faced with lime" (Macvicar 1901) and demonstrated that such habitats were available to this species when the bridges were somewhat younger. This is also another example of the expanded habitat for *A. ruta-muraria* beyond its natural range.

Sparks from railways in the days of steam engines caused considerable damage in a dry season (Fenton 1939). In addition to burning trees the ground was cleared in the manner best suited to *Pteridium* which often occurs in large patches by the trackside. Page (1988) suggested that areas of *Pteridium* may mark the actual sites of former fires.

5.4.2 Roads and Bridges

Road verges and motorway embankments cover a considerable area in total. They provide complete cross-sections of the varying geology and soil types across the whole country.

In an increasingly managed landscape the line of the hedgerow and accompanying ditch is sometimes the only remaining habitat for pteridophytes. The more basic hedgerows usually have *Dryopteris filix-mas* while more acidic areas have *D. dilatata, D. affinis* subspp., *Blechnum spicant* and *Athyrium filix-femina*. *Equisetum* species can find a last refuge and *Equisetum arvense* is often abundant on roadsides. The shade below hedgerow trees can provide a suitable niche for *E. sylvaticum*, and *E palustre* occurs in the wetter ditches. Along several side roads in parts of Perthshire occasional colonies of *E. pratense* are found. As this species is especially associated with calcareous soil it is of particular interest where its spread from adjacent areas on to the roadside occurs. *E. pratense* has been found coated with dust from a limestone quarry, growing beside a long walled garden with an old crumbling wall, and on the road verge beside a substantial culverted stream with mortared stones and a small bridge. In these instances accidental calcareous enrichment has been to the benefit of an uncommon species.

Calcareous enrichment along the verge can also come from roads which have been made up with a final layer of limestone chippings (Page 1988). Limestone is usually very hard and often selected for this purpose. The limestone quarry on Tuloch Hill near Blair Atholl, for example, supplies roadstone for a wide area of Perthshire. Murray and Birks (1980) when recording *Botrychium lunaria* on Skye specifically mentioned its occurrence on roadside verges and it may be that its presence is associated with this type of basic surfacing material. It has also been found at the roadside east of Nethy Bridge (RBGE 1876) and on a grassy ridge by the road at Coylum Bridge (pers. comm. A. F. Dyer 1991).

Bridges over a river and wet retaining walls offer a damp micro-environment suitable for mortar-loving species. *Asplenium ruta-muraria* is most frequently found on old bridges with *A. adiantum-nigrum* and *Cystopteris fragilis*. *A. trichomanes* subsp. *quadrivalens* is less commonly found. In some areas of acidic rock, bridges are often the only basic habitat. Spillage of lime associated with the building of the bridge can also make the local area more basic. On Rum *Botrychium lunaria* was observed in the turf at the edge of the track over a bridge surrounded by acidic moorland and Webster (1978) found this species on an old bridge over the Tomlachin Burn in Glenferness.

Asplenium viride is not very commonly found on mortared walls but was seen on an old bridge built over a long-disused road near Blair Atholl in Perthshire. There is also a herbarium specimen from a bridge over the Moriston in Glenmoriston (RBGE 1975).

Drains and culverts constructed with mortar may be the only basic areas along a roadside. *Phyllitis scolopendrium* was observed below a grating in a drain beside a reservoir access road in the Pentland Hills and Webster (1978) described some young plants in a culvert in Reelig Glen.

Newly dug ditches can be suitable places for hybridisation of *Equisetum* species to occur. *Equisetum x litorale* is the commonest in eastern Scotland, but in the more favourable conditions for hybridisation in the west, *Equisetum x rothmaleri* and *Equisetum x dycei* have been found (Page 1982).

Such marginal habitats are often ungrazed, especially if stock are fenced in to keep them off the roads. The most serious threat to any species in these habitats comes from close cutting of the verges with mowing machines. Ferns can produce another flush of fronds but these do not have a long enough season to become fertile and the plant can only be progressively weakened. Deciduous species would not be affected by cutting near the end of the season as is practised with flowering plants after they have set seed.

Motorway embankments have provided extensive areas for colonisation. Although often planted with seed mixtures, trees and shrubs, pteridophytes readily establish extensive colonies. Perhaps the most frequently observed is *Equisetum arvense.* It is particularly noticeable growing in the "scree" created over Y-shaped drainage channels on the side of embankments. When growing among other vegetation it is especially conspicuous when the grasses change colour at the end of the summer but the *E. arvense* retains its characteristic shade of green until the first severe frosts.

Pteridium aquilinum loses little time in extending on to the top of well drained sunny embankments and extensive patches form. Usually it is the subsp. *aquilinum* with its typical tall, dense canopy. But near Aviemore there are colonies which are conspicuously different both in habit and colour and may be more closely connected with *Pteridium aquilinum* subsp. *latiusculum.* Unfortunately motorways do not provide opportunity to examine roadside specimens.

Extensive cuttings through rock faces for main roads are also not very accessible to examination. Some areas, such as the the northern approach to the Forth Road Bridge, the large interchange south of Perth and the A9 north of Calvine, have cut through substantial quantities of rock. As the rock surfaces weather and mature, colonisation by a variety of plants will inevitably take place and more pteridophytes can be expected. *Dryopteris affinis* subspp. have been observed on rock beside the "new" road which replaced the Glenfarg route south of Perth. *Polypodium vulgare* would also grow on acidic rocks while *P. interjectum* or even the less common *P. australe* may grow on more basic cuttings. Different sides of the road may eventually have diverse floras. *Polypodium* can occupy southern aspects but more species are likely to occur in more shaded situations. As the shade of overhanging trees become more extensive the larger species of fern will be able to establish.

5.4.3 Canals

Before steam power became widely used in the nineteenth century many canals were made. The Forth and Clyde Canal from Grangemouth to Bowling was completed in 1790, and the Union Canal extended it into Edinburgh in 1822 (Mackie 1962). Subsequently canals were built from Aberdeen to Inverurie and also Ardrishaig to Crinan making the Crinan Canal which linked with the Caledonian Canal through the Great Glen.

Carlingwark Lane from Carlingwark Loch in Galloway was cut to reduce the level of the loch to remove marl. The cut was deep enough for boats to enter from the River Dee by which route the marl was taken to the shores of Loch Ken. It was planned to extend the canal from the Loch to the Solway, but this was never carried out (I & K Whyte 1987).

It was also necessary to have reservoirs for canals. Hillend in Lanarkshire, was a new loch and Black and Lily Lochs were enlarged to serve this purpose (3rd S.A.S. 8 1960).

With the exception of the Caledonian and Crinan Canal most of the waterways have become fragmented and often overgrown. The construction of canals required bridges, aqueducts, locks and associated buildings with a large extent of bank, towpath and embankment. Lochs were specially constructed to provide additional water supplies to maintain levels. From the regularly maintained open waterways to the derelict overgrown pond-like remnants, a wide variety of habitats is provided.

Mortared habitats are occupied by the usual wall species, *Asplenium ruta-muraria* and *A.trichomanes* subsp. *quadrivalens*, with *Cystopteris fragilis* in the damper more shaded areas. In southern or western areas *Phyllitis scolopendrium* and *Polystichum aculeatum* may grow. Leached stonework contains many plants of *Athyrium filix-femina* (Page 1988).

In the water, stands of *Equisetum fluviatile* are often found, with *E. palustre* in shallower areas which have become choked and silted. The banks beside the tow path are often well shaded by adjacent shrubs and provide suitable habitats for the larger ferns ranging from *Dryopteris dilatata* and *D. affinis* subspp. in the more acidic areas to *D. filix-mas* where it is more basic. These areas are often protected from grazing animals. More open areas commonly have *Pteridium aquilinum* subsp. *aquilinum* and *Equisetum arvense,* especially on urban canal banks. Less usual species are *Equisetum sylvaticum* from the north-west and *Osmunda regalis* found on canal bank stonework in Glasgow (Dickson 1991).

Hennedy (1865) recorded *Lycopodium clavatum* from a canal bank in Paisley but added that it was probably now extinct. The *Lycopodium* would not be able to survive if the vegetation provided dense shade, as probably occurred through natural progression.

5.5 The Human Influence on Pteridophytes Through Collecting

In the eighteenth century roads, were built into the Highlands, and the country generally became a safer place to venture into. This encouraged travellers like Heron and Pennant to tour the Highlands and record their impressions. Botanists also began to extend their ranges and to record species. These excursions were not without difficulties. Professor J. H. Balfour described an early expedition to Sutherland with Professor Graham in 1825. "The excursion lasted for about five weeks. In those days these were no roads in the wild districts of Sutherland, such as Eddrachillis. Our baggage was conveyed on horses, and we had to make the best of our way through trackless moors. Moreover our accommodation was anything but good. Small shielings were often our only shelter, and we had to sleep on mud floors or on wooden chairs or tables" (Balfour 1864c).

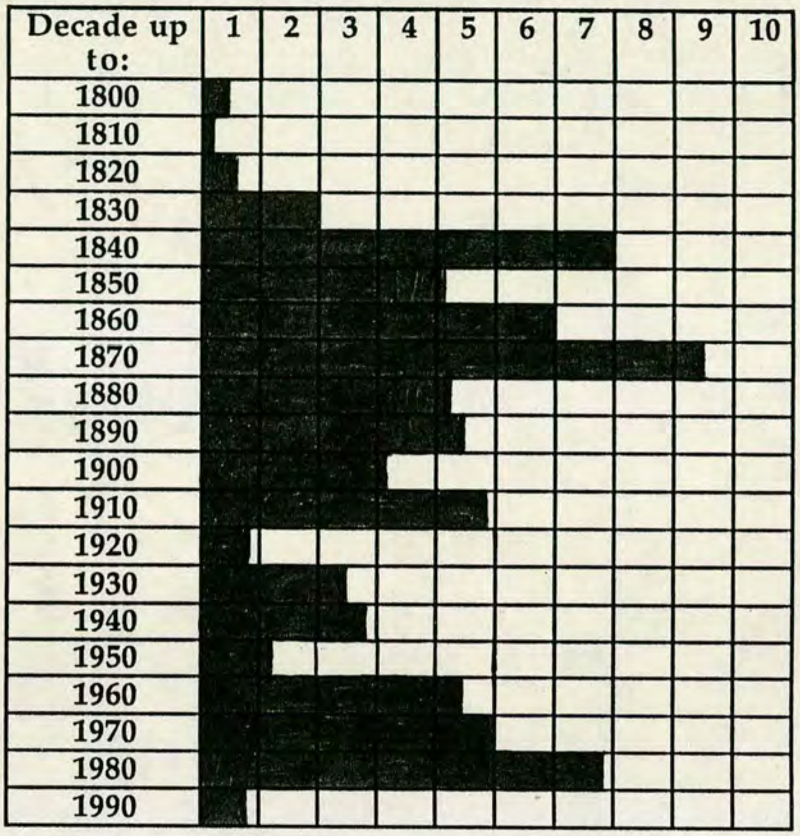
Later when the railways covered the country with a comprehensive network, many excursions were planned to begin and end at convenient stations.

In the following years many of the present-day well-known localities were visited, continuing earlier traditions which recognised the especial merits of mountains like Ben Lawers. Some classic localities seem to have been invariably visited for certain species. Loch Brandy in Glen Clova, for example, was the inevitable venue for *Isoetes lacustris*. This is not uncommon but must have been collected from this loch more than most species from one single locality. There are nineteen specimens from Loch Brandy out of the specimens in the collection at the RBG Edinburgh. These specimens span from 1823 to 1913. Fortunately this species is in no way endangered and still grows in the loch (pers. comm. J.G. Roger 1989). At least attention was channelled into one area leaving many other localities largely unvisited, which can be useful for some rare species.

An unfortunate feature of nearly all botanical excursions was the amount of plant material "gathered". The average numbers of pteridophytes collected each decade, and preserved as herbarium specimens at the RBG in Edinburgh, are shown in **Table 5.1**. There was an average of 73 sheets per species collected over the period altogether, but *Thelypteris palustris* (6 specimens in total), *Dryopteris cristata* (1 specimen), *Athyrium flexile* (9 specimens) and *Cystopteris dickieana* (1 specimen) were excluded.

It can be seen that there was a gradual rise in the number of specimens collected at the beginning of the nineteenth century with a peak around the time Professor J. H. Balfour was appointed to the chair of Botany at Edinburgh University in 1845. A further large number of specimens in the 1870s are accounted for by the interest in varieties. The early decades of the twentieth century were affected by the war years, with less activity between the wars also. The collection again increased into the 1980s only to diminish with pressure on space.

Table 5.1 Average number of dated sheets per decade collected for each pteridophyte in the Herbarium of the Royal Botanic Garden Edinburgh



While more recent collecting was mainly to provide voucher specimens for a national collection and for local records, the earlier specimens were often collected by private individuals who expected to have their own comprehensive selection. Various botanical exchange clubs existed where multiple sheets were collected and redistributed to members. The Watson Botanical Exchange Club experienced a problem recorded in the 1908-09 volume when the author wrote "It must be remembered that the club does not exist for the extinction of rarities, and that their attention is called to the remark at the commencement of the list of desiderata, that in gathering plants they are to take care they run no risk of destroying or appreciably diminishing a plant in any locality".

The Moffat area suffered very notably from collecting. When a railway line was extended to Moffat in 1848 the local population of *Woodsia ilvensis* came under very heavy pressure from collectors. Also, as the cultivation of ferns became popular, a worse problem was generated by "nurserymen" who took whole plants in quite excessive quantities. In Mitchell's accounts of the progressive extinction of the *Woodsia* at Moffat, he described the eventual decline to one known clump remaining in 1909. Since that time two colonies have re-established. Ratcliffe found 25 plants in 1954 and Rickard found another small colony in 1972 (Mitchell 1979). Recolonisation could have come from the remaining clump or perhaps another which had been overlooked, or possibly from spores which had remained viable and had met with favourable conditions which permitted germination.

The problem with species like *Woodsias* centres around the fact that such plants are effectively relict species on the southern edge of their range. Climatic factors alone can reduce their abundance and the impact of collectors can be enough to cause a final decline and disappearance. Mitchell (1979) described the effect of the 1977 drought in Wales on *Woodsia ilvensis* which grew in an exposed south-facing locality. Of six clumps only one survived while another damper colony nearby survived. Mitchell also refers to the effect on plants in Corrie Fee in Glen Clova which produced less fronds in the year following the 1976 drought. Personal observations at the same site during August in the drought of 1983, found that some plants had completely shed their fronds and only one clump remained visible. On a further visit in August 1990 only one clump was found but in a different place. As *W. ilvensis* prefers a high rainfall, a dryer climate would reduce the population. If a natural reduction is combined with wholesale removal of the plants, very little regeneration can be expected to occur.

The rarer specimens like *Cystopteris montana* and *C. dickieana* were eagerly sought after by nurserymen. *C. dickieana* is best known from one sea cave near Aberdeen, although it may exist in others along the nearby coast. Dickie reported in 1860 that it "is now completely extirpated from the little cave" (Dickie 1860 p229) but specimens continued to be collected from time to time. Trail in 1923 and Greenfield in 1951 described it as almost extinct. While collectors may have accounted for the earlier reduction in abundance, it seems that climatic factors also affected the fern's success as did occasional roof-falls (Marren 1984). These very local factors may have had as much, if not a greater, effect than collectors. The capacity to recolonise is regulated by the availability of spores and it would be interesting to know to what extent these came from surviving plants within the cave or from a spore bank.

No species were safe from collectors even if they were known to be difficult in cultivation as instanced in the following account by Sadler at Girpel Linn near Moffat. "We searched in vain for *Ophioglossum vulgatum* and *Botrychium lunaria* on the banks where we had seen them growing on a former occasion. I fear, however, that some sordid nursery man's collector has been in that neighbourhood, as well as in many others; hence the mysterious and rapid disappearance of not a few of our rarest gems from their wonted hiding places" (Sadler 1860 p130).

There are repeated references in the literature and annotated to herbarium specimens of the extent to which the rarer species were being over collected. Sadler (1863 p19) wrote of *Asplenium septentrionale* that "At one time it was abundant on the rocks in Queen's Park in Edinburgh but is now less so, being nearly eradicated by 'fern hunters' ". Fortunately the population has survived and can still be found in reasonable abundance. In Orkney, H.H. Johnston (1929) wrote of *Asplenium marinum* "I am not going to mention the name of the place where it grows as there are very few who know that it is there and it would soon be gone . . . In several of the well-known stations for this species in Orkney, the plants, unfortunately, have been almost exterminated. The same remark also applies to several other rare ferns in Orkney, which are now almost on the point of extinction".

Species like *Osmunda regalis* which were probably already under pressure from widespread drainage schemes have never fully recolonised the areas which they once occupied. Examination of the *Atlas of Ferns* (Jermy et al 1978) shows that most of the eastern records have not been confirmed recently. In 1833 Johnston wrote of the *Osmunda* in the East Borders "Small, as though the 'last remnants of its race' ". White in 1898 recorded its demise from Balquidder, the east end of Loch Tay and Culross. There are many references to the large-scale removal of the fern in the west. In 1865 Hennedy described *Osmunda* around Glasgow as "Frequent. Boggy places and woods. Rapidly disappearing due to collectors"(p125). In 1933, Lee wrote of the same area "Boggy woods, rare and rapidly disappearing. Formerly abundant in many parts of our area, now extinct in most of them "(p345).

5.6 Recreation

5.6.1 Ski-ing and Montane Activities

Montane vegetation, defined as that which occurs around and above 1,000 metres, varies according to slope and aspect. In the Cairngorms, for example, *Calluna* can extend up to 950 metres on exposed ridges. A moss heath with lichens and a large percentage of *Racomitrium* will cover summits below 1,150 metres. In the corries there can be more shelter and late snow lie gives a different vegetation. *Calluna* extends up to 800 metres with *Vaccinium* intermixed, continuing higher to associate with *Empetrum* heath and lichens. Summit areas can be very fragile with sparse vegetation, often mainly lichens and areas of open ground (McVean 1964). Among pteridophytes *Huperzia selago* is one of the few species which grows on barren, base-deficient mountain tops. It is sensitive to grazing as it grows only from the tips of its branches and if these are nibbled, Red Deer being the most likely grazers, then the plant dies (Headley and Callaghan 1990).

The very areas which are suitable for an extended ski-ing season are also vegetatively interesting with late snow lie and high-altitude types of vegetation. Lurcher's Gully is a recent example of an area which has aroused much dissent and controversy between conservationists and potential skiers. Ski-ing has been developed in this area since 1961 with the interesting effect that increased human access has discouraged the deer and lessened grazing pressure. Scots Pine, Juniper and other trees have regenerated up to the natural tree-line (Conroy 1987) and the acid flora is exceptionally well developed. Lurcher's Gully itself has abundant plants of *Lycopodium clavatum* and *L. annotinum* (pers. comm. A. Lavery 1991).

Recreational activities, especially ski-ing, can damage vegetation when the snow cover is thin. Once the plant cover is removed the shallow layer of soil or gravelly detritus can rapidly be eroded down to bare rock. Chairlifts have allowed increased access for people all the year round, resulting in extended erosion of paths (Bayfield 1974). This heavy erosion can be reduced by re-routing the paths away from the worst affected areas and seeding with fertiliser can give a vegetative cover. Heavy machinery, both for construction and maintenance, can crush the vegetation but it is now more commonly the practice to use helicopters to bring in new materials for building, which reduces the damage (Selman 1988).

5.6.2 Golf Courses

Golf courses occupy a considerable area. The well-maintained fairways and greens do not offer useful habitats, being very frequently mown and treated with fertiliser. The rough areas, which may be mown perhaps only annually to prevent the growth of scrub, contain more species. As golf courses are often located near the sea, usually on fixed dunes and links, their flora reflects that of the dune slack. The golf course at Gullane which is beside Aberlady Bay, grades from a well-maintained expanse of grass into very sandy areas grazed by rabbits. *Botrychium lunaria* grows there. As this species has been reported from links which now are occupied by golf courses, it may still exist in many rough areas. It has been found at Lundin Links (RBGE 1865), Monifieth Links (RBGE 1869), Burntisland (RBGE 1857), Prestwick and Troon Links (BDA 1853) and Aberdeen Links (BDA 1898). Records of this species found on other golf courses come from Lossiemouth (BDG 1907), Brora (RBGE 1961), Fortrose and Rosemarkie (Duncan 1980), the Nairn Dunbar course (Webster 1978) and from an inland golf course at Newtonmore (BDG 1914).

Another inconspicuous pteridophyte which can be found in damper flushed areas on golf courses is *Selaginella selaginoides*. It has been recorded in suitable places such as Gullane Links (RBGE 1812), (Martin 1934), Carnoustie (RBGE 1902) and Milngavie (Dickson 1991). *Ophioglossum vulgatum* would also be expected in what could be a very suitable environment. Dyer (pers. comm. 1991) found this species in rough grass, which is possibly never cut, near the fairway on Southerness golf course in Kirkcudbrightshire. It was also found on Whitecraigs Golf Course in Glasgow (Dickson 1991).

A ditch near Hopeman golf course near Inverness (Webster 1978) had *Lycopodiella inundata* which would probably benefit from small scale clearing operations to maintain the open habitat.

Too much attention to the fairways can, however, be unsuitable for some species. *Equisetum variegatum* was recorded from the sandy links near North Berwick (Keddie 1845), but when the area was examined in 1989 it was found to be species-poor and composed of neatly cut grass.

5.6.3 Fishing and Riverbanks

Fishing can have an indirect affect on pteridophytes. Riverbanks in the best salmon-fishing areas are carefully managed and maintained. Vegetation can be mown in a strip along the water's edge, but at the same time access for cattle or sheep may be restricted, resulting in very dense vegetation further up the bank. There is a locality given on a herbarium specimen in 1889 (RBGE) for *Equisetum hyemale* on the "bank of the Tay opposite the mouth of the river Isla". When this locality was visited exactly one hundred years later the bank was densely overgrown and the plant was not seen. An interesting aspect of the present vegetation was the large amount of *Impatiens glandulifera* which has spread since its introduction and provides part of a dense herbaceous layer which would not be suitable for any *Equisetum* species as they cannot survive such competition. Riverbanks are often occupied by introduced species which have been planted on large estates and then naturalised, as has occurred with *Petasites albus*. *Mimulus luteus* has also spread since it was introduced in 1812. It was first widely reported in Scotland in the 1840s (Watson 1841) and can form a very dense low cover. A small but widespread introduction is *Epilobium brunnescens* which occurs on streamsides and mountain flushes. These two species may reduce the available habitats and by rapid growth colonise newly eroded areas which are especially appropriate for the establishment of new pteridophyte colonies. At the opposite extreme in size is *Heracleum mantegazzianum* (Scott 1990), growing over three metres high, which can swamp all other vegetation. *Reynoutria japonica* has similar undesirable properties and forms dense thickets to the exclusion of everything else.

5.6.4 Coastal

The recreational use of beaches can have an unfortunate effect on the flora inhabiting the dunes. Excessive erosion along footpaths and in areas used for parking can open dune systems to the natural effects of the wind and make the whole system unstable. To counter this many local authorities have restricted access to beaches with controlled areas for parking and clearly defined footpaths. The use of buried matting or honey-comb concrete blocks has allowed vegetation to remain to bind the fragile surface while withstanding the effects of being driven over. Stout wooden paths prevent erosion on the the dunes themselves and channel the majority of people towards the beach.

Given the fortunate tendency of many people to use the facilities which are provided, the adjacent areas of dune slack can continue to be occupied by *Botrychium lunaria*, *Selaginella selaginoides* and *Equisetum variegatum*, which have all recently been observed within well-used country parks in East Lothian as at Aberlady and the John Muir Country Park.

5.7 The Colonisation of New Habitats

Most pteridophytes release minute spores often 40-50 microns in size which can be transported considerable distances by wind. This rapid transport has led to ferns being among the first species to colonise areas which have been covered by volcanic ash and lava. Page (1979) collated various authors' work on the number of species which colonised Krakatoa after nearly all the vegetation had been destroyed. After only three years there were 11 species of ferns on the island and 53 years later more than 60 ferns and fern-allies were found, showing how rapidly ferns can colonise a suitable habitat.

In other species, however the spores and dispersal mechanisms differ. *Equisetum* spores have a structure unlike other pteridophytes with the presence of four elaters which are initially coiled around the spore. When the spores are shed, the hygroscopic elaters expand in the drier atmosphere outside the sporangium and the spores are carried away on the wind (Sporne 1975) perhaps with extra buoyancy. Page has suggested (pers. comm.) that when the spores meet moist air rising perhaps from wet mud, the elaters contract and the spores comes to rest. This mechanism would also presumably operate over any water body, where this could lead to spores being washed up on a shoreline, especially if water levels are unusually low. It would also explain the colonisation of mud in a reservoir with low water which has already been referred to (Page 1967).

Huperzia selago is unusual among the British species because it produces bulbils at the tip of each shoot. These detach easily, wash down the hillside, and root. The tiny bulbils and mature plants can been found along the edges of sporadic rills and beside more permanent streams. The bulbils would be very easily blown around the hillside and whole detached plants can be found which shed bulbils as they tumble along. Spores are produced but have a low potential viability estimated by Headley and Callaghan (1990) as only 6.7 - 2.2%. This means remote areas can be colonised by occasional spores, but most plants probably have a vegetative origin.

Selaginella selaginoides has megaspores and microspores. The microspores are borne near the tip of the cone shoots and are merely released to the passing breezes as the sporangium splits. The megaspores occur in clusters of four in the axil of the leaf, or sporophyll, and are explosively released when they are ripe. The leaf which encloses the megasporangium curves downward with dryer conditions and eventually two of the megaspores are released by compression from the adjacent megaspores which also dehisce almost instantly, catapulted from the split megasporangium (Page 1989a). The spores can be propelled at least a metre and could also be washed down flushed areas. The abundantly produced microspores will be more generally distributed so that fertilisation can occur wherever both kinds of spores eventually germinate. This plant is typically found in permanently damp calcareous areas.

Isoetes and *Pilularia* also produce megaspores and microspores. In *Isoetes* the megaspores are produced earlier in the year, contained within sporangia within the base of the leaf, or quill. The microspores mature later nearer the centre of the corm-like plant (Sporne 1975). Both spores are released as the quills decay with the possibility of mega and microspores from the same plant being released over different time periods. *Pilularia* has round sporocarps a few millimetres across borne on the creeping rhizome. Internally these consist of four segments, the sori of which contain sporangia along a stalk. There are single megaspores in the sporangia at the base of the stalk and microspores within the remaining sporangia (Jermy and Camus 1991). The whole sporocarp splits into the four segments when ripe, and the spores are extruded into the water through a jelly-like mass.

The mechanism by which new colonies of these heterosporous pteridophytes arrive in a newly created body of water, has been the subject of some conjecture. Webster described the occurrence of *Pilularia globulifera* in Moray Nairn and East Inverness (1978) as a doubtful native in that region which had probably been introduced by waterfowl. As an example of direct interaction between ducks and a pteridophyte, Haggart (1915 p52) wrote about finding "the water's edge for some yards littered with a green, chives-like plant . . . The castaway plants of *Isoetes lacustris* I attributed to the hundreds of ducks I noticed diving and swimming beyond the Killin Pier, as plants were apparently being dislodged by them." This reference is especially interesting as *Pilularia globulifera* was found near the pier by the same writer in 1913. As an example of ducks actually eating *Isoetes*, Halcro-Johnston (1921) in Orkney wrote "My boatman informs me that in autumn large quantities of the leaves, which become detached from the plants, are washed up on the shore of Peerie Water, and that wild ducks greedily feed on them".

Two possible mechanisms for the dispersal of *Isoetes* and *Pilularia* can be suggested. Megaspores are less than a millimetre across and could easily be carried in mud on a duck's or goose's leg,together with the microspores. Wet vegetative fragments may cling to a duck's leg and thus be transported some distance, or larger pieces of *Pilularia* rhizome may be transported, tangled in a ring.

My own experiments with plants in cultivation have shown that disturbance of *Isoetes* quills allows the release of both kinds of spores and fertilisation occurs. The sprouting megaspores have been found floating on the surface of the water and tangled in water mosses at different levels in the water. Only the fertilised megaspores in contact with the basal substrate have developed further. *Pilularia* megaspores float on the surface but sink more readily when fertilised and the first green stem has emerged. These megaspores with a green shoot cling more easily than a megaspore on its own, although the jelly which is extruded from the sporocarps with the megaspores and microspores would perhaps aid attachment.

An alternative mode of internal transport is less easily demonstrated. Observations on the diet of the Greenland White-fronted Goose (*Anser albifrons flavirostris*) (Madsen and Fox 1979) have shown that food passes very rapidly through the alimentary canal averaging 0.75 to 1.5 hours. The uptake of nutrients is poor and the epidermis of the plants consumed is undigested. This suggests that the tough *Pilularia* sporocarp, and possibly even mega and microspores, could survive being eaten and subsequently deposited elsewhere.

It may be significant that some of the locations colonised at various times by *Pilularia* are also well-known sites for geese. Feral populations of Greylag (*Anser anser*) live on Loch Tummel in Perthshire and Loch Ken in Kirkcudbrightshire (Thom 1986) which are both *Pilularia* sites. There is an old record of *Pilularia* in 1933 (Ingram and Noltie 1981) from the Loch of Lintrathen which has very large wintering flocks particularly of Pink-footed Goose (*Anser brachyrhynchus*) and other migrating wildfowl as they return northwards. This certainly indicates a possible source of transport to appropriate areas.

The margin of the Loch of Lintrathen was examined in 1991 and is now well vegetated, mainly by *Littorella uniflora*, and no longer offers the open areas free from competition which *Pilularia* requires.

5.8 Summary

After the reduction in habitats brought about by changes in farming methods and more intensive cultivation, pteridophytes have been able to exploit new areas associated with current or past industrialisation. Provided there is not a complete reclamation of abandoned sites, many areas are available which have only become suitable for colonisation over the nineteenth and twentieth centuries. Overgrown shale bings, for example, have become recognised not only as pteridologically rich, but also as suitable habitats for a wide range of plants and animals. These areas offer naturally regenerated countryside often as islands in the middle of intensively managed areas. They are appreciated for their recreational value as well as for their flora and fauna.

A recurring problem with many pteridophytes is the fact that some species only survive in newly eroded habitats and depend on the creation of new sites to maintain their populations. As there is nowhere in the whole of the country which is not managed and affected by anthropogenic interference, the provision of a new habitat is usually a by-product of human activity. This has been seen especially in the production of calcareous habitats on walls. Many species' level of abundance can be clearly related to the management of grazing and the success of a species in a derelict site is often because of the exclusion of grazing animals. But this alone is not enough, and eventually with natural progression the habitat will change to become more densely vegetated and pioneer species which prefer open habitats will not be able to survive. To have a wide range of species some human interference may be both necessary and welcome.

Quite apart from changes associated with people, tundra species were more abundant 14,000 years ago and woodland species were more abundant at the height of the Boreal. It is natural that many of the earlier species have become less common. More recently small areas of moorland, which were formerly only found on exposed mountain tops, have been artificially extended and maintained through management as grouse moors. There are several pteridophytes associated with this moorland and their survival strategies are examined with particular reference to *Lycopodium clavatum* in Chapter 6.

Chapter 6

The Effects of Moorland Burning on Heathland Pteridophytes

6.1 The History of Muirburn

One current feature of land management which has had a significant effect on vegetation is the practice of muirburn. This might have an effect on pteridophyte success and survival as it has been a long established practice to burn the uncultivated vegetation on hill ground. As a result of carefully controlled burning, any grass present produces a new flush of growth and *Calluna vulgaris*, which otherwise becomes old and woody, produces fresh new shoots which are more productive for grazing. This form of management has been exercised primarily for the benefit of sheep, but also for grouse and deer.

The regulation of muirburn has long been a problem and the antiquity of the practice is indicated in a Scottish Act of Parliament of 1685 prohibiting burning after April 1. In 1773 the burning season was confined to within November 1 to April 10 (Anderson 1967). Cockburn remarked on the burning near Aviemore in April 1839, "There has been more burning of heather, all along, than I remember to have seen before. The fires on the distant hills were striking at night, but not so much as the long trailing streaks and the high curling of the smoke during the day" (Cockburn 1983 p 25). This suggested quite extensive areas were being burnt. The Hill Farming Act of 1946 gave the present burning dates for Scotland as October 1 to April 15 which could be extended to April 30 in a wet spring or May 15 on high ground above 500m (Tivy 1973). The initial need for legislation implies that there had previously been an excessive amount of careless burning. Some areas might have been burned for at least three hundred years and, assuming that the practice was common before 1685, probably much longer on a less regular basis.

It has been recognised that when *Calluna* grows continuously without being burnt it passes through four stages with increasing age (Gimingham 1970).

1) The pioneer phase, with young, green, separate plants growing from seed which may require up to 6 years to cover the ground thinly.

2) The building phase, when a woody frame of branches builds up to coalesce after 8-10 years from establishment.

3) The mature stage, commencing after 14-16 years from the initial establishment and lasting until around 25 years old, when the plants are more woody. The maximum height is reached and the canopy begins to thin in the centre of individual clumps.

4) The degenerate phase from 25 years, with a gap in the centre of each clump. The plants can live for up to 30 or 40 years.

This assumes that the plants are not layering and continuing to grow vegetatively. Layering occurs in many areas (Miles 1981) and can maintain a vigorous dense canopy for a longer period than would be expected in the typical cycle outlined above. Some genotypes of *Calluna* layer more readily than others, thus giving local variation.

It is important that burning is carefully managed if it is to achieve its purpose. A ten to fifteen year cycle of burning seems to be sufficient to maintain young green growth (Gimingham 1981). If the *Calluna* plants have grown too woody, too high a temperature is reached during burning and regeneration is poor. On the other hand, if the temperature is too low, the old thick stems are left unburnt. Ideally only the top parts of the stems are burnt so that the lower parts can produce new shoots. Under good conditions, a complete cover of *Calluna* can be vegetatively restored within two to three years. Stems older than 15 years are less likely to regenerate in this way, and new plants grow from seed which require up to six years to achieve a similar cover (Gimingham 1960).

It has been suggested that repeated muirburn leads to a progressive impoverishment of the heathland. Macvicar (1901 p28) wrote "We read of heather in the eighteenth century as high as a man's waist". Very tall

Calluna of this order can be seen today only in a very few places as in the partial shade below the Pines in the Black Wood of Rannoch. One indication of how our modern moorlands have changed from their original condition is given in an old story about an escaping Highlander hiding among the heath which had the added explanation "which was then very high" (Burt 1876 p3).

The carrying capacity of grazing for sheep may have declined by the end of 19th century. Innes (1983) thought that although it could not be conclusively proved, burning removes potassium in smoke; phosphates are leached out, and the irregular burning practised in the nineteenth century, especially with excessively high temperatures, may have led to high losses. Gimingham (1981) reported that phosphorus and nitrogen are washed out with overburning. If smaller areas are burnt, the run-off benefits the adjacent heath but a large area suffers loss into the hillside streams. Larger areas are burnt if intended for sheep grazing, but smaller blocks are burnt for grouse, as they require a range of *Calluna* stands of different ages for feeding and for shelter.

On good soil with frequent burning *Calluna* dies out and grass grows instead. When old stands are burned areas of heath retreat if sheep graze the new young shoots too soon. The author of the New Statistical Account describing the Parish of Balquhidder in 1845 wrote that forty or fifty years before, the hills were covered in *Calluna,* which had subsequently been replaced by grass. He mentioned that there were many more sheep than formerly (N.S.A.S. 10 1845). Unfortunately *Calluna* is not always replaced by nutritional grasses, but by *Nardus stricta* in over-grazed areas. The sheep do not eat *Nardus* (Fenton 1939) and this can lead to a deterioration in the pasture available. Macvicar wrote in 1901 that in living memory hills have changed from brown heather to green grass. He also thought that the less common species had diminished (Macvicar 1901). Gimingham (1981) found that there was a greater species diversity in the new growth with *Calluna* when small patches were burned, as there was a local source of seed for recolonisation to more readily take place.

Calluna growth is stronger on the dryer soils in the east of Scotland with generally more continental climatic conditions. The slightly milder climate of the 1930s did not favour its growth. With no winter snow lying on the ground, there was no protection from winds searing across the younger shoots on top. The higher winter temperatures would also make even worse the effects of such frosts as did occur (Fenton 1939).

From around five thousand years ago *Calluna vulgaris* enjoyed favourable conditions for spreading across moorland at the expense of trees (Pennington 1969). But increasingly over the last hundred years this habitat has suffered a decline. In 1925 Balfour wrote that the muirburning was left to inexperienced shepherds so that the *Calluna* was diminishing. Ratcliffe in 1958 described the vegetation in the Moffat Hills and said that *Arctostaphylos uva-ursi*, which is often associated with old stands of *Calluna*, had almost gone. He also said that the *Calluna* was much reduced to grassland and erosion was beginning to become apparent. Erosion occurs when the *Calluna* is burned so severely that bare patches of peat are exposed and eventually gullies can form (McVean and Lockie 1969). Meek in 1976 described the Border vegetation and attributed the reduction of *Calluna* to a combination of burning and grazing. The former Nature Conservancy Council used aerial photographs of different ages of the same area, and demonstrated a 25% decline of *Calluna* moorland in the Grampians over a thirty year period from the 1940s to the 1970s More than 60% of the *Calluna* moorland has been lost in Galloway over a similar time-span (Macdonald 1989). Forestry has accounted for the loss of substantial areas, but much of the loss has arisen from poor management of burning, often with subsequent overgrazing and the replacement of the heathland by unpalatable grasses.

6.2 Background to the Study Topic

6.2.1 *Lycopodium clavatum*

A continuous history of muirburn would probably influence the pteridophyte populations which characteristically inhabit heathland. Although all pteridophytes have been included, this study was conducted with particular reference to *Lycopodium clavatum* which can be found growing among *Calluna*. Just as the moorland is declining, so too is *Lycopodium clavatum* with an estimated loss of 28% of its squares over the whole of Britain since 1950, as recorded in the *Atlas of Ferns* (Jermy et al 1978). In Orkney, Sinclair described the existence of *L. clavatum* "in great quantity on the Round Hill until it was completely wiped out by a big fire several years ago" (Sinclair 1963 p39). He knew that regeneration could take some time from spores and revisited the site "many times", but with no success.

Its general decline could be attributed merely to the removal of its habitat as can often be demonstrated to be the case in lowland sites in England, but Page (1982) proposed that repeated muirburn may lead to a progressive diminishing of abundance within the *Calluna*.

This hypothesis has been tested on the slopes of Ben Vrackie which has a comparative abundance of *Lycopodium clavatum* and is managed by burning. The flora of adjacent areas has been examined together with information on the timing of burning over the last fifty years. The impact of burning has been assessed for all species present but with particular reference to pteridophytes, especially *Lycopodium clavatum.*

Lycopodium clavatum occurs in a wide range of habitats. It has been recorded on dune slack as in Morayshire (Patten and Stewart 1914) and Wigtonshire (Sutherland 1925). It is perhaps more commonly expected on upland moors where it is usually associated with *Calluna vulgaris* (Page 1982), but it can occur on grassy moors (Hadley 1985).

Specific literature references for this species seem to confirm the suspected trend of a reduction in abundance of the clubmoss. They imply a considerable abundance in the past. It is often described as "frequent" or "abundant", except in the west where the damper climate is not so suitable. Johnston in 1829 said that it was plentiful on all the moors in the south-east of Scotland and was used to wind around hats. The spores were used for dyeing. Queen Victoria was reputed to have used *Lycopodium* to "grace the Royal table" (Balfour 1854 p3) and as a wreath for her head. Gardiner (1848 p244) mentioned that it was "frequently manufactured into door-basses". Gardiner also described it as abundant on the Sidlaw Hills. Smith in 1905 described it as scattered or locally abundant in the Sidlaws which he compared favourably with the Ochils for being less cultivated. By 1985 Ballantyne wrote of its Kinross distribution as "Probably common in the past, but now only occasionally seen"(p90).

Lycopodium clavatum has an unusual life-cycle with an underground prothallus which depends on a mycorrhizal association for its nutrition (Sporne 1975). Sussman (1965) found that *L. clavatum* took 6-7 years to germinate. As laboratory experiments often use a sterile growing medium like agar, this may not be an accurate reflection of conditions in the field where germinating spores can derive nutrition from mycorrhizae during the prothallus stage and beyond. Possibly in natural conditions the whole process takes less time. Certainly Øllgaard (1985) found young sporophytes of various species including *L. clavatum* which must have grown from spores within only three years of a site becoming available, although Sussman suggested that as water extract from *L. clavatum* spores inhibited the germination of other fern spores, they may also have a self-inhibiting effect. With such slow germination of *Lycopodium clavatum* itself this hypothesis is difficult to test. A time delay is perhaps necessary while burial occurs which may account for the 6-7 year laboratory delay until the spores are at a suitable depth. The eventual prothallus is up to 6mm across and shaped like an inverted cone (Sporne 1975). As the prothallus remains at that stage for several years it is not clear what eventually precipitates maturity and fertilisation. In an area with local supplies of *Lycopodium* spores there must be an underground source of spores and gametophytes which have the potential to provide future sporophytes over a long period.

With an underground prothallus it might be thought most probable that self-fertilisation occurs. A study on populations of various species of *Lycopodium* in America, however, strongly suggests that cross-fertilisation usually occurs. When the mature sporophytes were used in an enzyme study using electrophoresis, low rates of self-fertilisation were found in both *L. clavatum* and *L. annotinum* (Soltis & Soltis 1988). Observation on individual young plants on Ben Vrackie showed that they often occurred in groups. Older colonies were difficult to disentangle to recognise individual plants. A few isolated plants were located at some distance from other plants and might be assumed to have resulted from self-fertilisation.

With such a long period necessary for the production of mature sporophytes, muirburn could occur just as the plants reach maturity and terminate the colony. In the light of this possibility, it was particularly interesting to observe an area which was burnt during the winter of 1990-91. This contained a large colony of *Lycopodium clavatum* which had been burnt, but was regenerating. This was also observed in the Cairngorms (pers. comm. A F Dyer 1990). In an attempt to assess the effect of burning and the long-term survival of *Lycopodium*, it was decided to examine a range of burnt sites and the associated vegetation.

6.2.2 Choice of Locality for Study

It was necessary to choose an accessible area known to have *Lycopodium clavatum*, a regular pattern of burning and a series of aerial photographs to give an indication of the frequency of previous burns. Ben Vrackie in Perthshire was selected, and five aerial photographs taken in 1946, 1959, 1965, 1976 and 1988 were obtained.

The study was conducted in two parts. The first, which is described in section **6.3**, was a general survey of the lower part of the area closely linked to the aerial photographs. Only the pteridophytes and flowering plants were recorded at this stage. The second part described in section **6.4** was designed to eliminate subjectivity and clarify the precise nature of the vegetation associated with *Lycopodium* and on the hill generally.

The whole study area on Ben Vrackie lies between 340m and 500m in altitude with a slope inclining to the south-east. The uppermost section includes steep slopes with some rocky outcrops, while the lower area crossed by the path has a more gentle gradient. There are a few very distinctive features which were selected to define the area for study (see **Figures 6.1** and **6.2**). The tumbled remains of a drystone dyke was used as a base-line on the south-east and east of the area. The wall acted as a useful reference point both on the ground and in aerial photographs and only the area to the west and north of the wall was studied. Part of the line of a fence and the course of a stream were used to limit the north-western boundaries. A footpath emerges from the wood in the south and runs approximately north for 420m before turning sharply to the north-east where it continues for 200m until it meets the ruined wall and the largest stream, continuing for a further 600m, crossing and re-crossing the line of the wall before the path goes beyond the study area. Some power lines cross the first straight section of the path about one third of the way to the sharp bend.

On the hillside above the first sharp bend there is a basic area with flushes and small streams which converge on the area above the bend and flow down the deep ditch on the west side of the straight section of the path. The largest stream flows across the centre of the study area from the north before it crosses the wall Before it crosses the path and wall it flows around a small island which has not been burned within the period covered by the aerial photographs. Another smaller stream has a conspicuous little valley and comes from the moor in the north to join the deep ditch only a short distance above the sharp bend. Most of the recently burnt patches can be identified on the 1988 aerial photograph except for a large area in the north-west which was burnt during the 1990-91 winter burning period, and is marked on **Figure 6.1**.

Figure 6.2 Enlarged copy of part of the 1988 aerial photograph of Ben Vrackie

Scale 1 : 10,000

Figure 6.3.1

Copy of part of aerial photograph of Ben Vrackie 1946

Scale 1 : 10,000

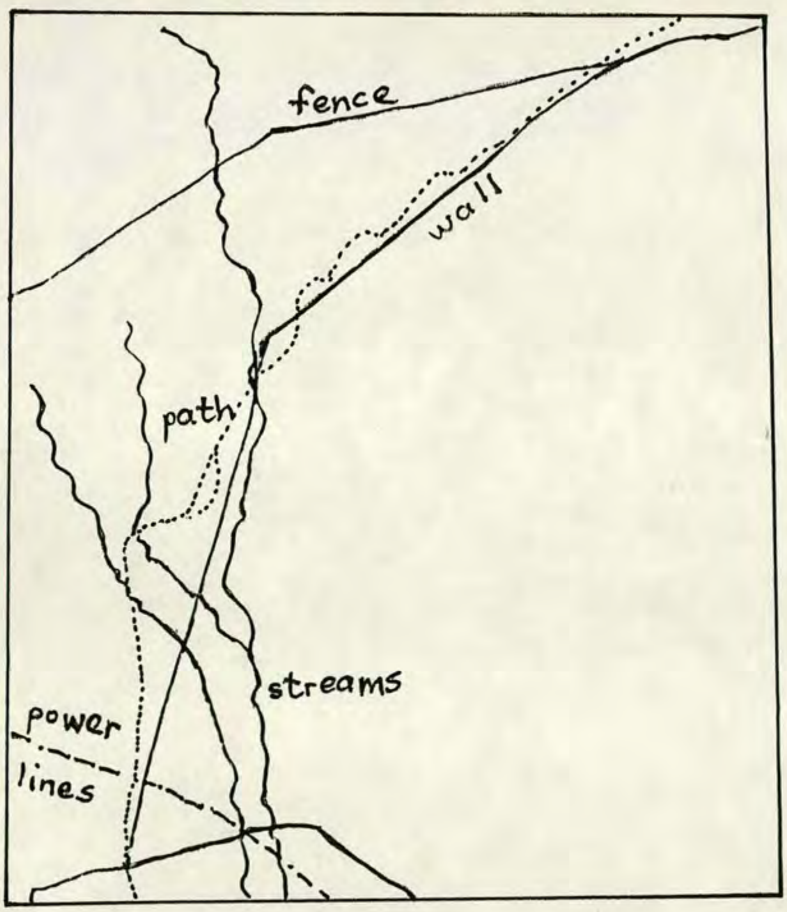


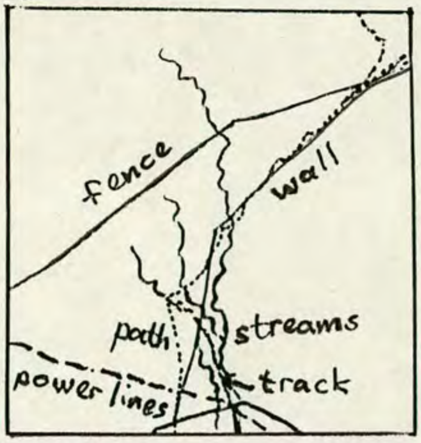
Figure 6.3.2

Map of main physical features on 1946 photograph

Figure 6.4.1

Part of 1965 aerial photograph

Figure 6.4.2

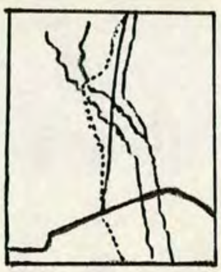


Map of main physical features

Scale 1 :25,000

Figure 6.5.1

Figure 6.5.2



Part of 1959 aerial photograph. Lower part of area only with a physical map

Scale 1 : 23.000

Figure 6.6.1

Figure 6.6.2

Part of 1976 aerial photograph with a physical map

Scale 1 : 58,000

6.3 The First Study

6.3.1 Materials and Methods

It was initially decided to select areas which had been burnt from zero to five times within the period covered by the five photographs. Three problems were encountered. Firstly, the only point which seemed to have been burnt on five occasions was within the lower part of the flushed area. Although this part has obviously been burnt recently and has younger *Calluna*, it also has patches of paler *Juncus* and grasses which could appear like burnt areas in an aerial photograph. It was felt that any information based on this area is not very reliable and no other area seemed to offer the coincidence of so many burns. Secondly, only small areas had been burnt before 1959 and these had mostly been burnt again since, so that areas which had only been burnt before 1959 were difficult to find. Thirdly, after the 1976 and prior to the 1988 photograph there was very little new burning so that only one area was selected with burning from this period. It was eventually decided that no more than three burning episodes could be identified at a given point with reasonable accuracy. It was found necessary to restrict the choice to areas which could be located by the proximity of a path, a bend of the stream, or perhaps at the corner of a recently burnt patch which was easily distinguished from the moor around it. The size of the area varied as it was often identified with the whole of a burnt area.

Several patches of *Lycopodium clavatum* were found in the course of the general investigation. The areas in which they were growing were included in the sixteen selected sites.

The sixteen sites were chosen to include:

1. Areas which had been burnt zero, one, two or three times.

2. Areas which were last burned before 1946, 1959, 1965, 1976 or 1988.

Table 6.1 Areas selected for species descriptions in the first study and identified on Figure 6.13

Times burnt	Dates burnt			
Zero	Oa	Ob	Oc	Od
Once	1a pre-1959	1b pre-1976	1c pre-1946	1d pre-1965
Twice	2a pre-1959, 1965	2b pre-1946, 1965	2c pre-1965, 1976	2d pre-1959, 1965
Thrice	3a pre-1959, 1965, 1976	3b pre-1946, 1965, 1988	3c pre-1946, 1959, 1976	3d pre-1946, 1959, 1965

For both pre-1946 and pre-1959 burning one area was examined which had not been burnt since, five areas were last burned before 1965, four after 1965 but before 1976, and one after 1976 but before 1988.

The aerial photographs used to compile the maps were all taken from different altitudes and at slightly different angles. Tracings were made of the burnt areas and basic features like the path and a wall were copied on to acetate sheets. As the photographs were all at different scales, an overhead projector was used to enlarge the information to a standard scale. Unfortunately some photographs were so small, (see photocopies of actual size in **Figures 6.3 - 6.6**), that the thickness of a line enlarged to an excessive amount of error. Also the different angles from which the photographs had been taken gave an accumulated distortion. Eventually a base map was prepared at the scale of 1 : 5,000 and the photographs were used for drawings of maps of the burnt patches using identifiable landmarks to position the affected areas (**Figures 6.7 - 6.11**). When complete the maps were superimposed and they give an indication of the frequency of burning over the whole area since 1946, and presumably several years before that date (**Figures 6.12**). It is possible that little burning took place after the beginning of the Second World War and that the burnt patches are therefore pre-1939. Similarly none of the maps may show burning from the exact year of the photograph. They simply indicate which areas were burnt between the dates of successive photographs

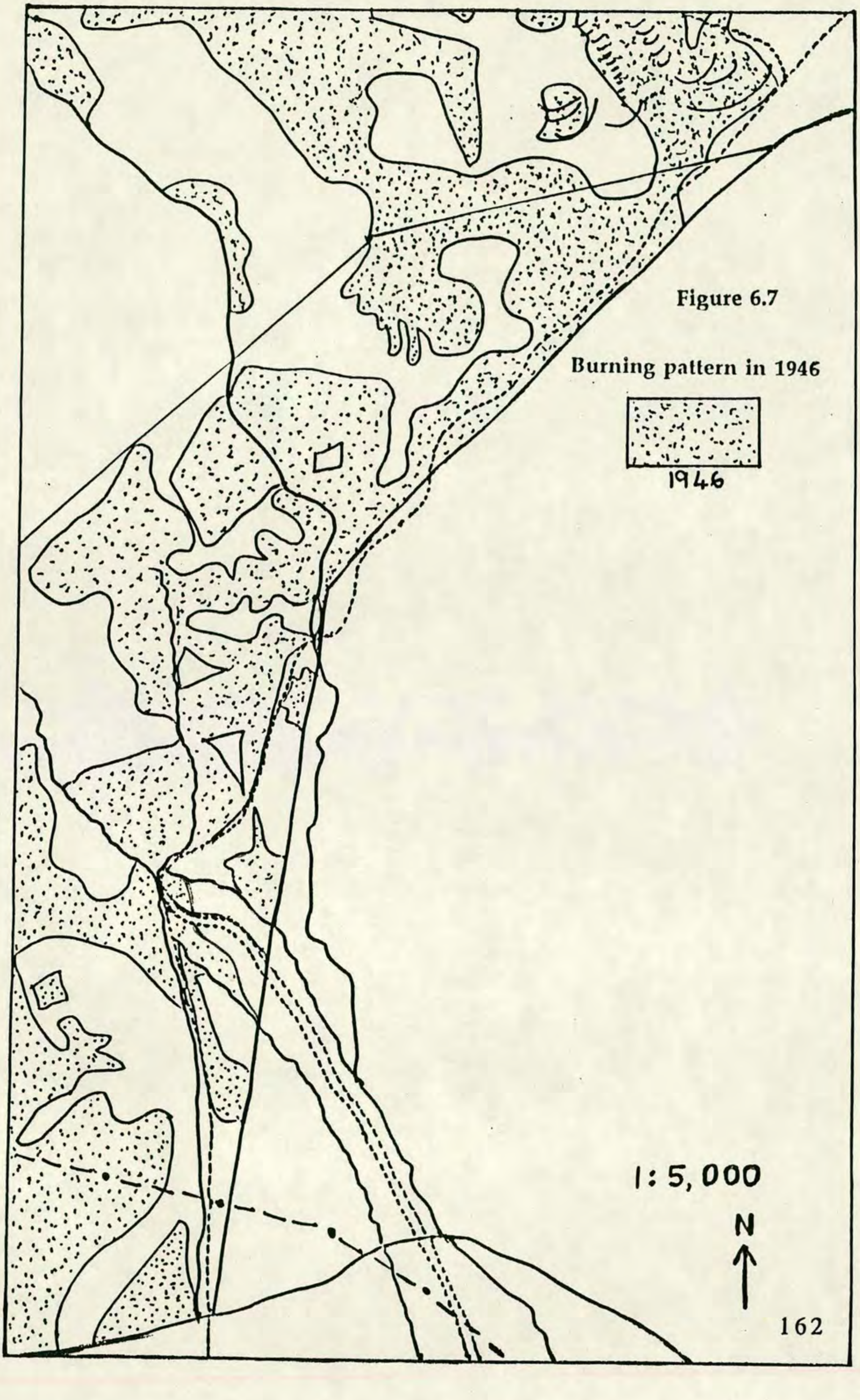


Figure 6.7

Burning pattern in 1946

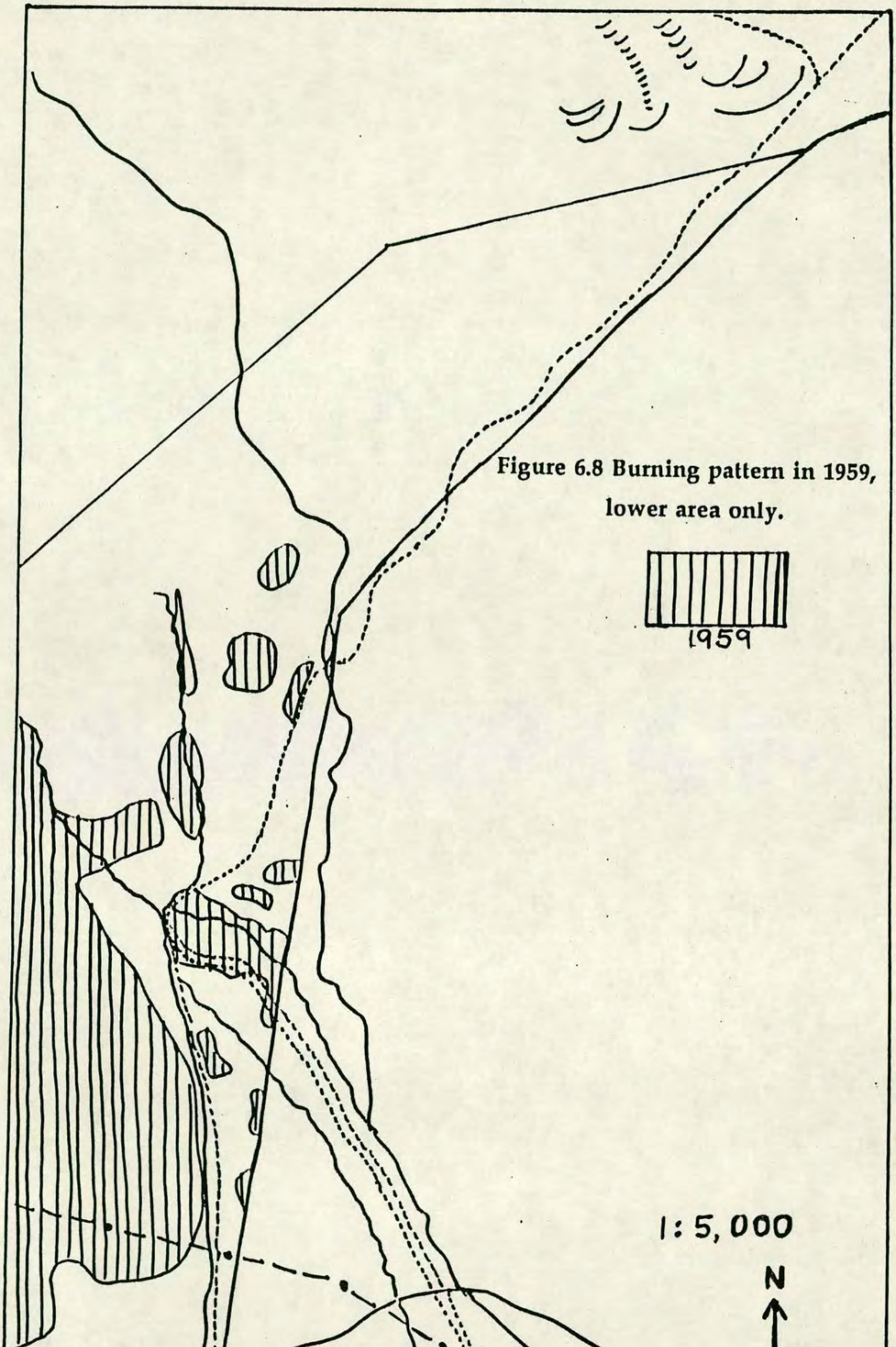


Figure 6.8 Burning pattern in 1959, lower area only.

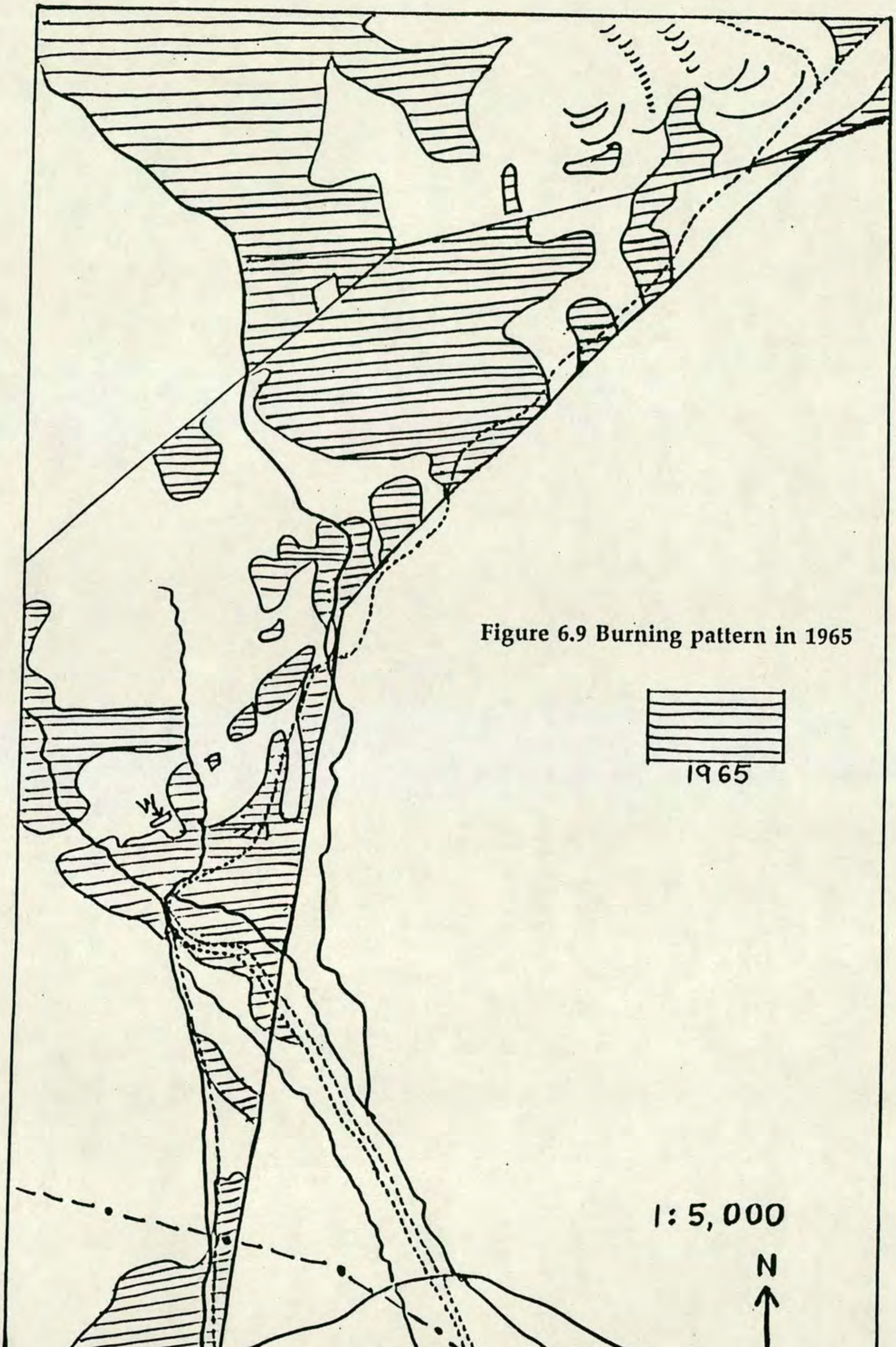


Figure 6.9 Burning pattern in 1965

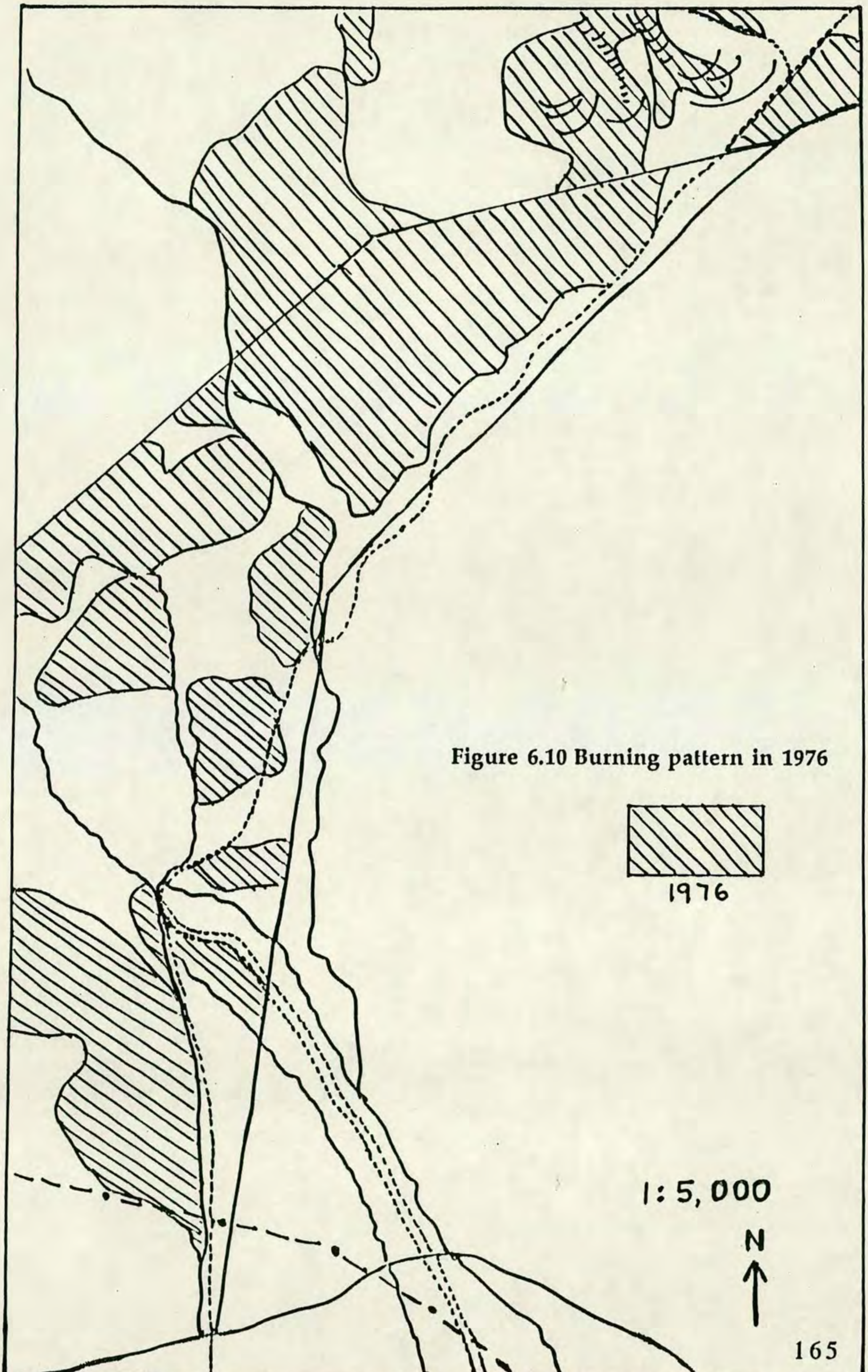


Figure 6.10 Burning pattern in 1976

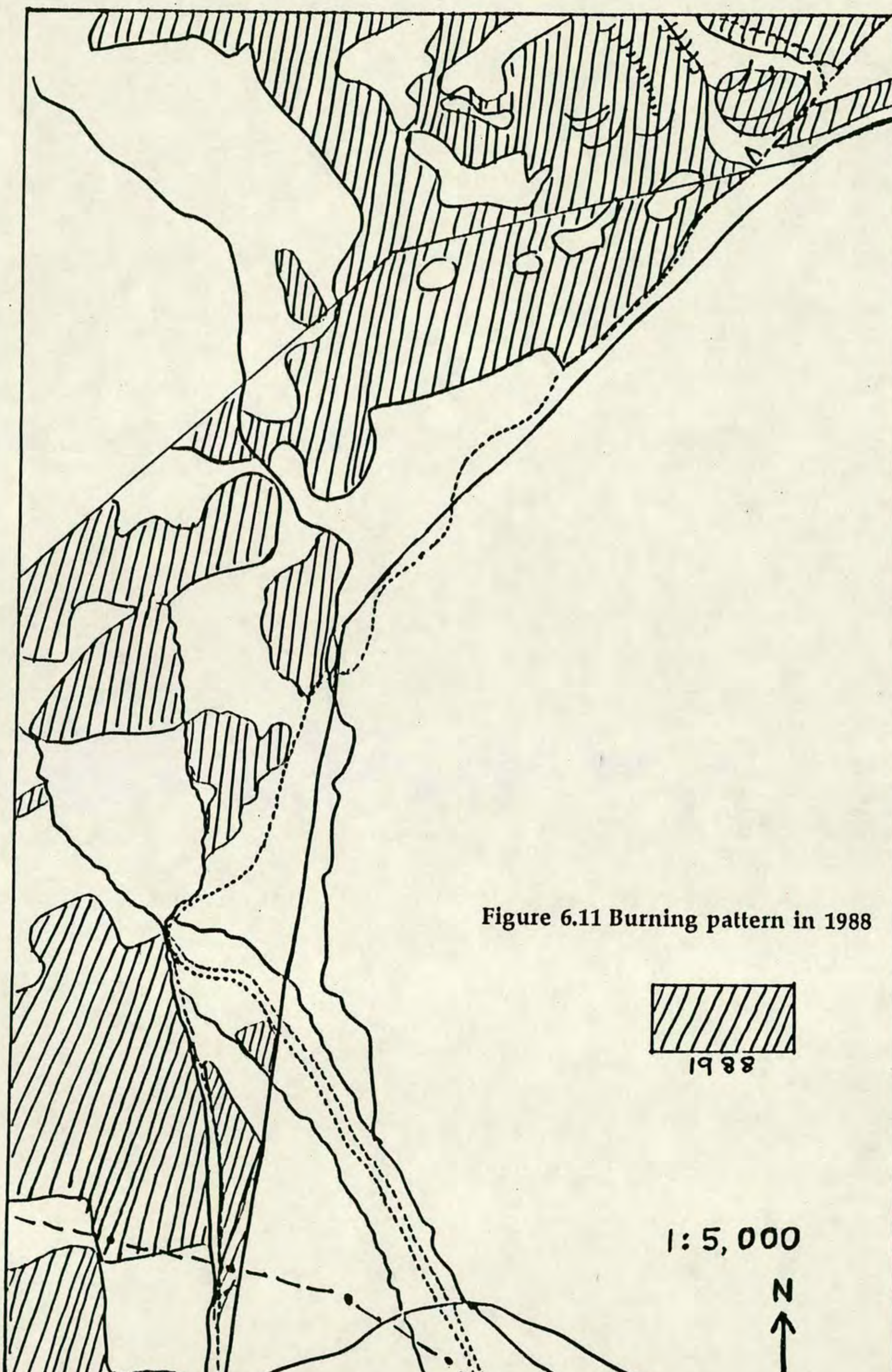


Figure 6.11 Burning pattern in 1988

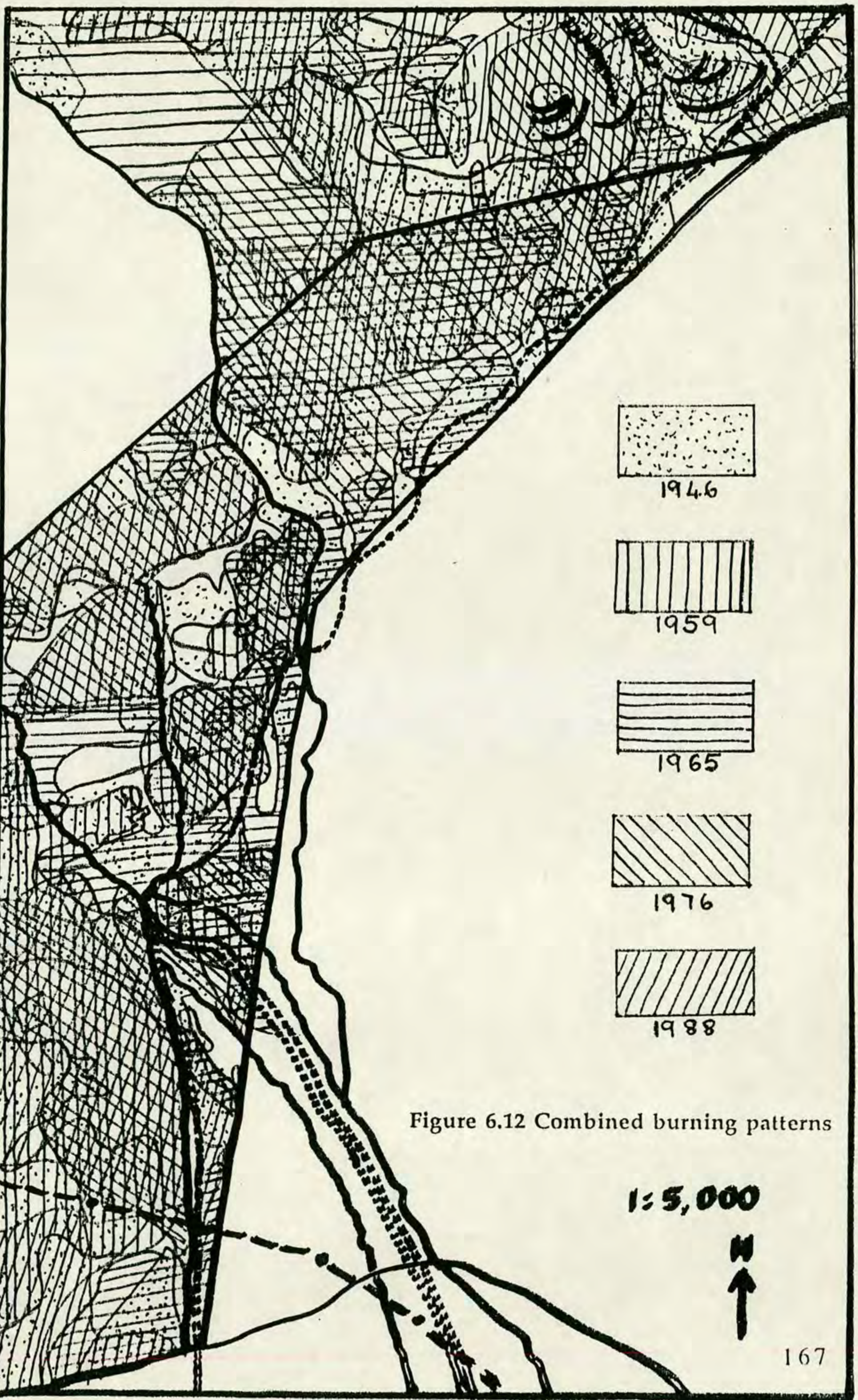


Figure 6.12 Combined burning patterns

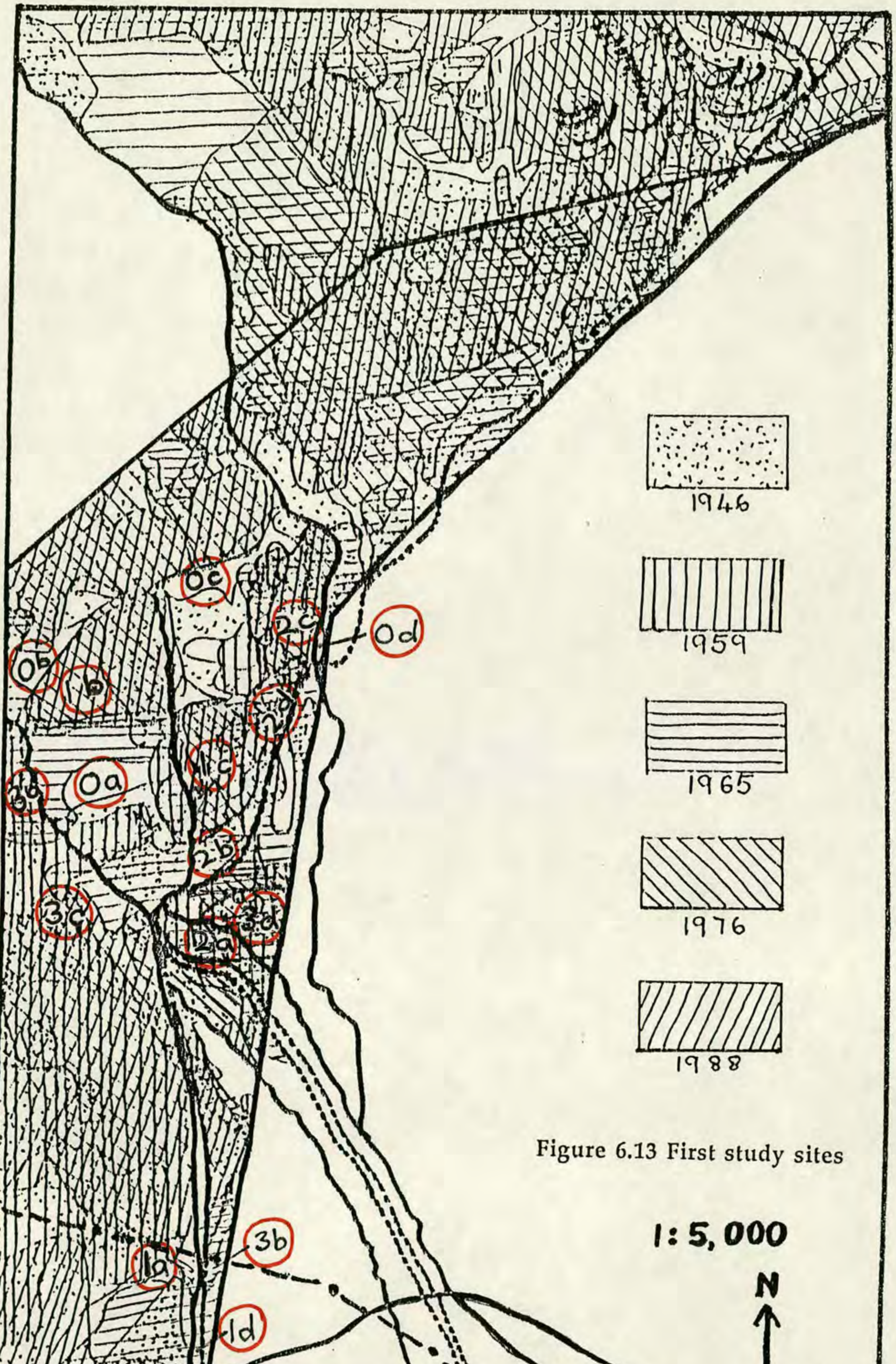


Figure 6.13 First study sites

The photographs used were all black and white. Old areas of *Calluna* are very dark in colour. Burnt patches are comparatively pale, often rectangular and usually have straight edges. Sometimes different shades of grey are seen indicating older and younger patches. Also it was found that many of the areas which were still pale grey on the 1988 photograph, in particular, had been burnt prior to the 1976 photograph and yet were still conspicuous. There were no patches in this first study area which have been burnt after the 1988 photograph was taken. From the dates based on counting the growth rings in *Calluna* stems, the most recent burning must have been soon after the 1976 photograph was taken.

Having made maps of burnt patches based on photographs, it is not necessarily very easy to interpret the maps in the field. Burnt patches photographed from above, become longer viewed on the side of a hill, especially when seen from below. Pale areas which are assumed to have been burnt quite recently can have surprisingly tall *Calluna*. But these patches can be caused by other factors such as dry areas, by vegetation other than burnt *Calluna* and expanses of rock. One area consistently appeared pale and looked as though it had been burnt five times. Examination in the field revealed an oval hollow consisting mainly of *Juncus* species which could have been a pond at one time. There are no large areas of standing water immediately within the study area, but water can look either completely white, or even completely black, depending on the direction of the light relative to the position of the aircraft at the time when the photograph was taken. The 1965 photograph shows a small pool in a marshy area (marked W on **Figure 6.9**). That year was exceptionally wet as this feature does not appear on any of the other photographs. Because of the difficulty of accurately differentiating between small areas of bog, or marks left by muirburn, the flushed area above the sharp bend in the path has not been included in the study.

For each area studied in detail, ten of the thickest available stems of *Calluna* were collected to check the estimated minimum ages of the burnt patches. The growth rings were counted using a x20 stereo microscope. It was found best to make an oblique cut across the stem with a very sharp knife. This made the rings appear wider than a straight cross-section. The rings are often not easily seen but sometimes can be more easily counted by holding the cut end at an angle when the light shines on the harder wood between the main annual growth. Sometimes several rings look a different colour giving the appearance of only one ring. The counts are more likely to be underestimates, rather than overestimates, of age but it was felt that a reasonable level of accuracy was achieved with this method. In an area with a high proportion of *Myrica* it was initially assumed that *Myrica* stems would have a similar age to the *Calluna,* but none of the *Myrica* stems were older than 13 years while the *Calluna* was as much as 30. Of the ten stems counted for each area, the very oldest stems were taken as an indication of the near maximum age of the stand although there could have been a delay in regeneration. In areas where layering has taken place over a long period the age of the stems will not reflect the maximum possible age, as the layered shoots perpetuate mature stems without allowing progress to the degenerate phase. All the ages for the stems counted are shown in **Appendix 2**.

After an area has been burned, *Erica cinerea* provides a far larger proportion of the new growth than *Calluna*. As the *Erica* flowers earlier than *Calluna,* the more recently burnt areas are conspicuous on the ground from a considerable distance in July and early August. As the heath becomes older the proportion of *Calluna* increases so that the *Erica* becomes a minor component. It is immediately apparent on looking at a rotationally burned landscape that the areas are of different ages. The vegetation looks darker as it becomes older and also becomes more uneven and hummocky. It becomes increasingly difficult to walk across and an indication of the age of a stand can be obtained in a simple traverse.

6.3.2 Results of First Study

Species lists for the following area are in **Appendix 3**. Of the four areas which have not been burned since before 1946, site **Oa** is situated high above the flushed area. There are many mounds between little rivulets covered in long, old bushes. Grazing has not permitted any trees to grow but the flora is varied. *Myrica* can locally form up to 70% of the vegetation with *Calluna* 20%, but the *Calluna* is generally more abundant to at least

90% on dryer mounds. The oldest *Calluna* stems are up to 30 years old and are layering, not following the degeneration model. *Erica cinerea* is frequent but not abundant. *Erica tetralix* grows on the lower damper margins of the mounds. *Blechnum spicant* is well represented together with *Oreopteris limbosperma*. On comparing the older areas of *Calluna* with the more recently burnt, the bright green *Oreopteris* fronds are conspicuous among the dark older growth in **Oa** and notably absent from the younger *Calluna*. *Dryopteris affinis* which is found here is not generally very common on the hill. It is usually found only in the shelter of substantial boulders or the ruined wall. *Selaginella selaginoides* found a suitable habitat in the open base-flushed areas. The other sites had vegetation too dense for *Selaginella*.

It would seem reasonable that old areas which had possibly not been burnt for fifty years would have had more time to be colonised by a greater number of species. But this did not necessarily seem to be so. **Oa** has a varied topography and the flush maintains open areas to provide habitats for smaller species. **Ob** is very conspicuous on the 1988 aerial photograph, but was difficult to locate on the ground. The adjacent regenerated pre-1965 burning was similar in height and had a slightly higher proportion of *Erica cinerea*, but there was no obvious break where the two areas joined. **Ob** proved to be on a smooth slope with a dense canopy containing surprisingly few species. There was little *Erica cinerea*, no pteridophytes at all, and apart from *Listera cordata* the other species were in the few open areas at the bases of old stems. Examination of the stems confirmed that the area was indeed old. The oldest dated from 1949 but all the *Calluna* was layering vigorously so that most of the stems sampled were younger.

Oc has a less dense canopy and is composed of large old bushes, some of which have died. The oldest dated specimen was at least 36 years old. As the area is on a small plateau, it is not well drained and has a good proportion of *Juncus*. The open gaps between clumps provide habitats for more species including the acid-loving *Athyrium filix-femina*, *Blechnum spicant* and *Oreopteris limbosperma*, with the addition of *Equisetum sylvaticum*.

Od is situated on a small mound in a generally unburnt little river-valley. The oldest *Calluna* stems are 30 years old and some are dying. The stream usually runs down one side of the rocky mound but has an overflow channel on the other side which almost makes the area an island. There is a large patch of *Lycopodium clavatum* measuring 20m by nearly 5m. The proximity of the stream maintains a damp environment but the actual substrate is well-drained. There are open gaps in the *Calluna* with its long bare stems exposed and the *Lycopodium* is sporing abundantly. There are the common ferns which might be expected, such as *Blechnum, Oreopteris* and *Dryopteris affinis* among the rocks.

Oa, Oc and **Od** are probably in areas which are too wet to be regularly burnt. They have a reasonable range of species as might be expected in areas which have not been burnt a long period, but they were all probably burnt at one time. **Ob** shows that merely being old does not imply a good range of species. It is of especial note that no *Pteridium* was found. Without the advantage of a burnt locality to colonise, it cannot compete with established heath.

Of the four areas selected for being burnt once, **1a** was burnt before 1959 and has the high percentage of *Calluna* observed in old stands. The remains of old watercourses run through the area, giving a varied surface. The oldest Calluna stem was 37 years and such old leggy stems leave many gaps for other species. The pteridophyte flora is restricted to *Blechnum* and *Oreopteris*. This is the first example of several instances where an apparently suitable habitat exists for *Lycopodium* but despite a careful search it could not be found.

1b was burnt prior to 1976 although it is still very clear on the 1988 aerial photograph. The high proportion of *Erica cinerea* suggests that the burn was comparatively recent but this is surprising as at least fourteen years have elapsed since the burn, and a higher percentage of *Calluna* could be expected. The vegetation is still very short and there are several bare patches covered in moss or lichen. The oldest stems appear to be twelve years old. The summers since the previous photograph was taken in 1965 were all average to very hot and dry (See **Appendix 4**). This means the burning may have been especially hot and destructive. Following this, the very fine dry summers of 1976 and 1977 might have slowed the regeneration and allowed the burnt areas to remain conspicuous for longer than usual. Although it is an open habitat with bare patches, the species are limited. One plant of *Blechnum* was seen. Presumably the *Anemone* and *Vaccinium vitis-idaea* survived underground and the other species which are generally common arrived by seed.

1c was burnt before 1946. *Erica cinerea* appears in higher proportion than in **1a** and **1d** in the large open gaps left by thick old stems. The oldest stem is only 32 years old and is layering. There is a good species diversity including various pteridophytes, most notably the uncommon *Equisetum pratense* at the only known station on the hillside. *E. sylvaticum* is also present but it has been found in other places on the hill. Presumably all *Equisetum* species can survive burning by means of deep underground rhizomes. A sloping site near water, with the added shelter of the stream-banks, is an appropriate habitat for many pteridophytes. It is interesting that two patches of *Lycopodium clavatum* here are associated with *Equisetum*, the first with a group of *Equisetum sylvaticum*, and the second with a stand of *E. pratense*. The lowest patch of *Lycopodium* is 3m square. The higher patch is 4.2m by 1.8m. The *Arctostaphylos uva-ursi* found here has not been found anywhere else in the area and might not withstand burning very successfully (Ratcliffe 1958), although it can regenerate from seed.

1d is in an area which was burnt before 1965. After the previous photograph was taken in 1959, the summers of 1959 and 1960 were above average warmth, but the next five summers were below average or average. As the hillside would have been permanently wet this may have helped to prevent too high a temperature of the winter burning and encouraged more rapid regeneration. The oldest stems are 24 years old and the canopy is well advanced and dense. This is reflected by the small proportion of *Erica cinerea* and the few species present. *Lycopodium clavatum* was found growing on a slope down to the small stream. The patch was only just over 1 metre by 90cm in size and looked like one young individual plant. Not surprisingly *Blechnum* is present. Another small patch of *Lycopodium* approximately 60cm square was found in deep dense *Calluna* not far away with a very limited range of species. *Listera cordata* was the only flowering plant. A dense sward of the mosses *Pleurozium schreberi* and *Hypnum jutlandicum* covered the ground.

Within the areas which have been burned twice, **2a** is composed of a close canopy of *Calluna* which is reflected in the lower number of species present. The oldest stems are 24 years old. As the area lies on the edge of a wet flush, it is very damp and the species include *Myrica* and *Drosera.*

2b was burnt at approximately the same time although the oldest stems are 21 years old and they are not all as tall as **2a** . They are also denser with less open centres. **2b** is on a wide, gently sloping bank above a stream and has a good range of pteridophytes. A small amount of *Pteridium* is thinly growing in from a large stand further up the slope. *Athyrium filix-femina* is present with the usual *Blechnum* and *Oreopteris.* The most abundant pteridophyte is *Lycopodium clavatum,* presumably many individual plants, 7m by 8m. There is another separate smaller patch 3m square.

2c is the most recently burned area in the twice burned group and has the characteristically high percentage of *Erica cinerea.* The oldest stems of *Calluna* were only nine years old, which, as in **1b,** implies a considerable delay in regeneration following burning, which must have been at least 14 years ago. Only one plant of *Blechnum* was seen, which is surprising as it has often been observed in areas which have been recently burnt. This implies a high temperature of burning or only a few plants present initially. Most interestingly there is a small area of *Lycopodium clavatum* 60 x 90cm very close to the large area described in **Od.** Old stems were traced leading from the little patch in **2c** towards the *Lycopodium*-covered hummock in **Oa**. There was a gap of 50cm along the bottom of the overflow channel where the stems could not be found. The new patch could have grown from spores, or vegetatively from a link which has been severed by floodwater. A few old *Calluna* stems still exist in the middle of the small patch of *Lycopodium.* These suggests that the burning may have been cooler at that point and that the *Lycopodium* may even have survived being burnt in the dampness of the watercourse, which marked the edge of the burnt area.

2d does not initially look very promising with few species. This is another area which was burnt before 1965 and is of an appropriate age to have a dense canopy. The oldest stems are 20 years old. However it does offer a well drained hummock and has a patch of *Lycopodium clavatum* 3m by 2.4 m.

3a is one of the areas which was severely burned before 1976 and has been burnt three times in total. There are bare patches with a sparse covering of moss and lichen between the evenly distributed cushions of *Erica cinerea* and *Calluna*. *Nardus stricta* is the only grass, *Juncus squarrosus* the only rush. The *Pteridium* at the lower edge would have survived unscathed below ground. There are many stems which are 8 years old which dates the beginning of regeneration.

3b offers a complete contrast. It is one of the most recently burnt areas within the study section. It is situated on the flat well-drained area between the first straight part of the path and the wall. The stems are up to 13 years old which suggests it was burnt very soon after the 1976 photograph. There is a substantial amount of *Erica tetralix*, rather less of *E. cinerea*, still less of *Calluna* but a variety of grasses, sedges and rushes so that there are no uncovered areas of ground. There is no sign of 20-year-old unburnt stems from the previous growth which would suggest underburning but the new growth is vastly more successful than after the pre-1976 burnings, so that it cannot have been as hot or as destructive. There is an area of *Lycopodium clavatum* 3m square. The clumps of mixed *Erica* and *Calluna* are uneven and the *Lycopodium* has alternately more open and closed areas to occupy.

3c was also last burnt after 1976 and before 1988 but is in a much wetter area with more bog plants and *Equisetum palustre*. The oldest stems are 8 or 9 years old except for one stem of 14 years which may have escaped burning. The dampness of the area may have influenced the burning temperature. **3d** is also in a wet area. It was last burnt before 1965 but such a wet area could not burn successfully. The oldest stems are up to 26 years old. It was still found to be very wet after the dry summers of 1989 and 1990. A sharp line is seen on the hill above it where the pre-1976 burning ends. The line is marked by a strong growth of *Pteridium* which presumably has made use of the lack of competition to grow more successfully. Within **3d** there is a good range of acid-loving pteridophytes growing with other species in a habitat which is probably more disturbed by grazing than by other factors.

6.3.3 Discussion on First Study

The presence of *Lycopodium clavatum* is largely determined by the existence of a suitable habitat. It is typically found on better-drained banks and mounds although it also occurred within the study area on flatter areas like the colony at **2b, 3b** and across the stream from **1d**. It was not found, nor would it be expected, in the marshy areas. The number of times an area has been burnt seemed to be less significant than the nature of the burn.

Table 6.2 The occurrence of *Lycopodium clavatum* showing the most recent possible date of burning

Date of aerial photograph	0	1946	1959	1965	1976	1988
	0d	1c		1d	2c	3b
				2b		
				2d		

Table 6.2 shows that it is not necessarily the oldest *Calluna* which offers a suitable habitat for *Lycopodium*. Of the sites which had not been burnt within the period covered by the photographs, **Oc** was too wet but **Ob** and **Oa** could have been suitable. The one pre-1946 area examined offered a good habitat and did have *Lycopodium*, but not large colonies. A large colony might be several small groups of plants or the result of vegetative spread over a wide area.

This preliminary study indicates that the *Lycopodium* grows in a variety of ages of *Calluna*, after a variety of burning patterns, and seems to occur anywhere on the hillside in a suitable habitat.

Figure 6.14 Photograph of an area near the top of the study site which shows different ages of burning. The sheep are grazing on a patch which was burnt several years ago (minimum of 5 years from ring counts) but which is not regenerating well. *Erica cinerea* is in bloom showing areas which have been burnt more recently as this species always has a higher percentage of cover in the early part of a succession.

6.4 The Second Study

The second study was carried out in order to extend the area of the survey to include very recently burnt areas and to assemble data suitable for use in an objective examination of *Lycopodium* occurrence. As the *Lycopodium* plants only seemed to occur sporadically on the hillside it was decided to compare the vegetation of randomly chosen quadrats, with that of other quadrats which were deliberately selected adjacent to clumps of *Lycopodium clavatum*.

6.4.1 Materials and Methods

A grid was drawn on a map to cover the whole of the study area with points located 50m apart. Those points in areas known to be very wet were excluded as unsuitable for *Lycopodium clavatum*. From 129 possible points (**Figure 6.15**), 40 were selected using random tables and these were named 1-40. A further 15 quadrats were selected to sample the vegetation beside *L. clavatum* plants (**Figure 6.16**). The forty quadrats on the grid were located by pacing along compass bearings using the wall as a base-line. The 15 *Lycopodium* quadrats were recorded either to the east or south of the main *Lycopodium* patch immediately beyond any growth of the plant itself. A one metre square quadrat was used four times at each location. Percentage coverage was estimated for *Calluna, Erica cinerea* and *E. tetralix*, grasses and sedges, bryophytes, bare ground and any vegetation which may be locally dominant like *Vaccinium myrtillus*. Species lists recording presence or absence were then compiled, together with information on the general height of the vegetation and the nature of the soil to a depth of 10cm. Ten stems were collected from each $4m^2$ quadrat for ring-counting. Of these the oldest was taken to indicate the likely minimum age, although a considerable amount of layering was observed. One much older stem was disregarded as a possible survivor from an earlier burn (**Appendix 5**). The fieldwork was carried out during July and August 1991.

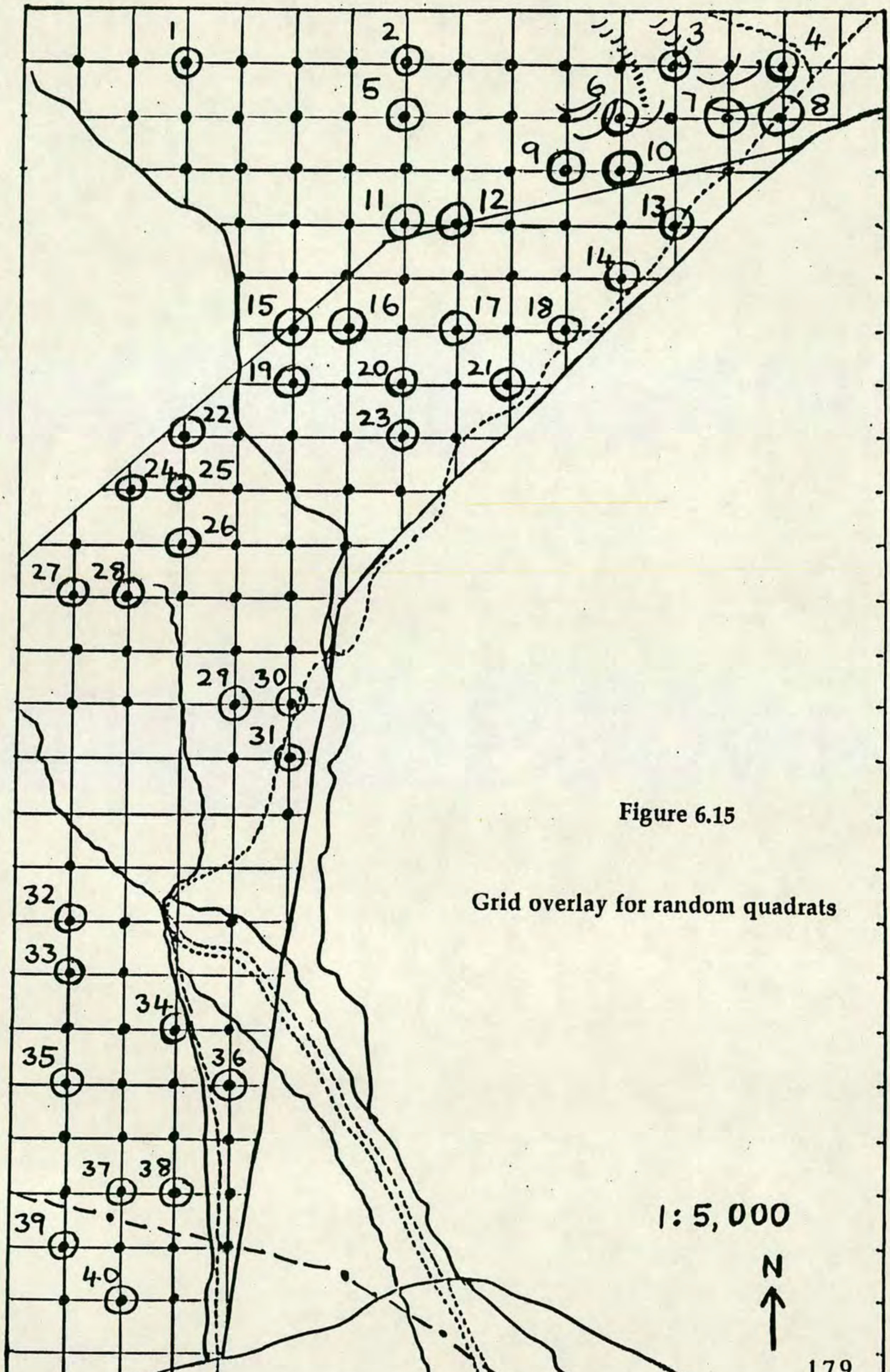


Figure 6.15

Grid overlay for random quadrats

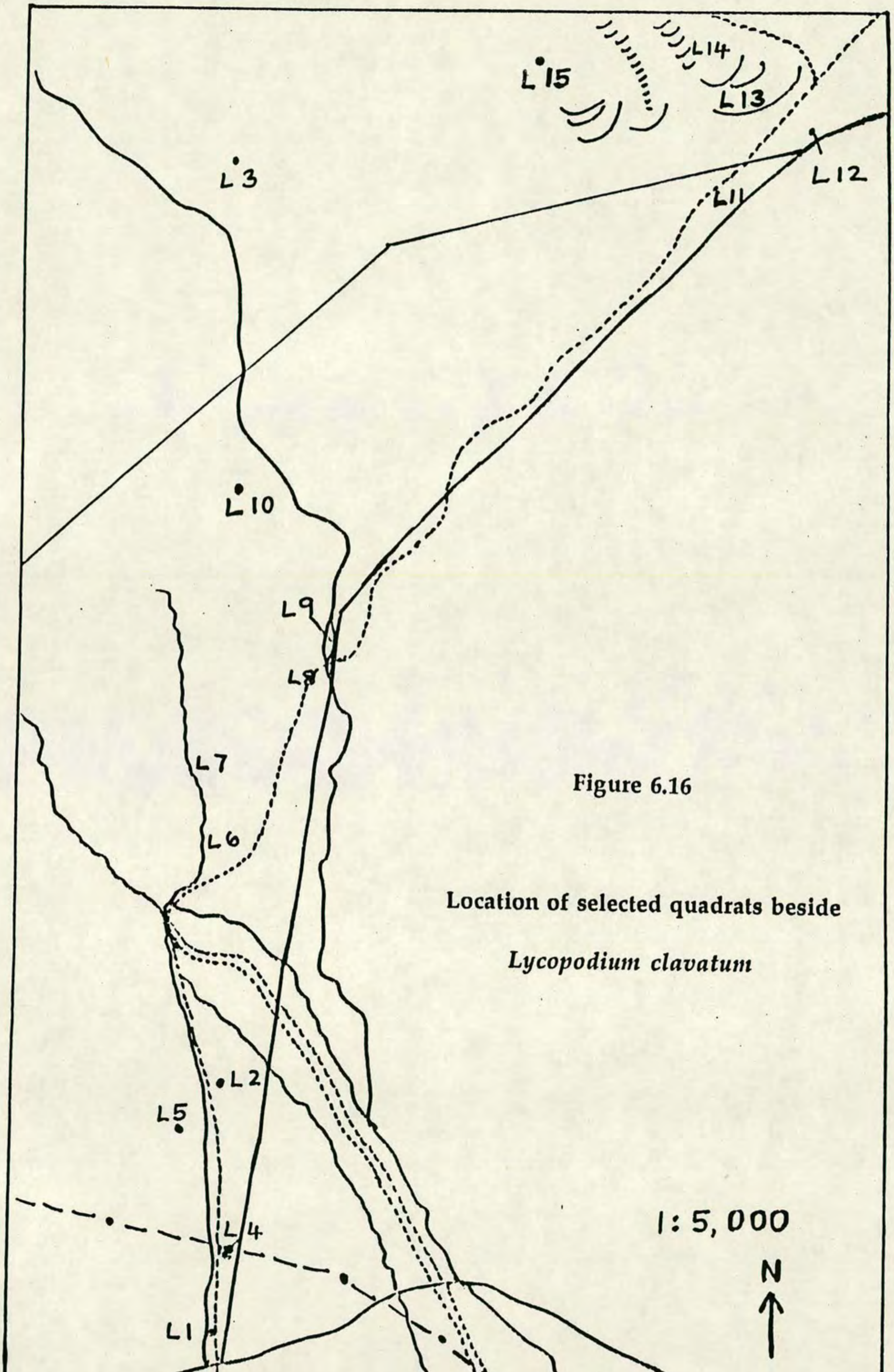


Figure 6.16

Location of selected quadrats beside

Lycopodium clavatum

6.4.2 The Results

The following tables show the species recorded for each $4m^2$ quadrat together with additional information on percentage cover and layering which varies within groups of quadrats.

Table 6.3 Species in random quadrats 1-10

Number of quadrat	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Oldest age of *Calluna* stems	33	32	11	16	27	34	5	9	11	23
Bare ground %			30				50	15	5	
Calluna vulgaris %	95	95	60	95	50	95	20	80	90	5
Erica cinerea %										
Erica tetralix %										10
Grasses and Sedges %					40		20			80
Mosses %	5	5	10	5	10	5	10	5	5	5
Layering	x	x			x	x				x
Pteridophytes										
Athyrium filix-femina					x					
Blechnum spicant	x									
Equisetum arvense										
Equisetum palustre										x
Equisetum pratense										
Oreopteris limbosperma										
Pteridium aquilinum										
Selaginella selaginoides										
Bryophytes										
Aulacomnium palustre										x
Campylopus introflexus			x							
Ceratodon purpureus										
Climacium dendroides										x
Dicranum scoparium		x	x					x	x	
Gymnocolea inflata										
Hylocomium splendens		x			x					
Hypnum jutlandicum	x	x		x	x			x		
Ptilidium ciliare									x	
Pleurozium schreberi	x	x				x				
Polytrichum commune					x					
Polytrichum piliferum							x			
Polytrichum juniperinum			x						x	
Pseudoscleropodium purum					x					x
Rhytidiadelphus loreus										
Rhytidiadelphus squarrosus	x	x			x	x				x
Sphagnum spp.										
Thuidium tamariscinum					x					x
Grasses										
Aira praecox							x			
Anthoxanthum odoratum					x					x
Briza media										
Deschampsia flexuosa										
Festuca vivipara									x	
Festuca ovina	x	x	x		x		x			x
Molinia caerulea										
Nardus stricta					x					x

Table 6.3 continued **Species in random quadrats 1-10**

	1	2	3	4	5	6	7	8	9	10
Sedges, Rushes										
Carex binervis										
Carex echinata										x
Carex panicea										x
Carex pilulifera									x	x
Carex pulicaris					x					x
Juncus conglomeratus					x	x				
Juncus effusus										
Juncus squarrosus					x					
Luzula multiflora		x	x	x	x		x		x	x
Trichophorum cespitosum										
Flowering plants										
Achillea millefolium										
Ajuga reptans										
Anemone nemorosa										
Antennaria dioica										
Betula seedling										
Calluna vulgaris	x	x	x	x	x	x	x	x	x	x
Campanula rotundifolia										
Cerastium fontanum										
Cirsium palustre										
Erica cinerea		x		x			x			
Erica tetralix										x
Euphrasia sp										x
Fragaria vesca										
Galium saxatile	x	x			x		x			x
Hypericum pulchrum										
Lathyrus montanus										
Listera cordata										
Lotus corniculatus										
Myrica gale										
Narthecium ossifragum	x									
Oxalis acetosella					x					
Polygala serpyllifolia					x					
Potentilla erecta	x	x			x					x
Rumex acetosella							x			
Salix aurita										
Sorbus seedling										
Succisa pratensis										
Taraxacum sp.										x
Trientalis europaea										
Vaccinium myrtillus						x		x	x	
Vaccinium vitis-idaea	x	x	x	x				x	x	
Veronica officinalis										
Viola palustris					x					x
Viola riviniana					x					
Total number of species	10	12	7	5	21	5	8	5	9	19

Table 6.4 Species recorded in random quadrats 11-20

Number of quadrat	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Oldest age of *Calluna* stems	33	20	18	10	8	5	20	11	38	27
Bare ground %					10	20				
Calluna vulgaris %	95	5	10	20	60	40	80	10	75	50
Erica cinerea %				20	20	30		5		
Erica tetralix %		25	5					30		
Grasses and Sedges %		20	80	60	10	10	5	50		20
Mosses %	5	50	5				15	5	25	30
Layering	x						x			
Pteridophytes										
Athyrium filix-femina										
Blechnum spicant										
Equisetum arvense										
Equisetum palustre		x								x
Equisetum pratense										
Oreopteris limbosperma										
Pteridium aquilinum										
Selaginella selaginoides										
Bryophytes										
Aulacomnium palustre										
Campylopus introflexus										
Ceratodon purpureus				x		x				
Climacium dendroides										
Dicranum scoparium					x					
Gymnocolea inflata										
Hylocomium splendens	x		x					x	x	
Hypnum jutlandicum	x			x	x	x	x	x	x	
Ptilidium ciliare										
Pleurozium schreberi	x							x	x	
Polytrichum commune									x	x
Polytrichum piliferum										
Polytrichum juniperinum				x		x				
Pseudoscleropodium purum										
Rhytidiadelphus loreus		x					x			
Rhytidiadelphus squarrosus			x	x				x		
Sphagnum spp.		x					x			x
Thuidium tamariscinum										
Grasses										
Aira praecox				x		x				
Anthoxanthum odoratum	x		x	x		x		x		
Briza media								x		
Deschampsia flexuosa										
Festuca vivipara				x						
Festuca ovina	x		x	x	x	x		x		
Molinia caerulea		x				x		x		
Nardus stricta			x	x						

Table 6.4 continued **Species recorded in random quadrats 11-20**

	11	12	13	14	15	16	17	18	19	20
Sedges, Rushes										
Carex binervis							x			
Carex echinata		x					x			x
Carex panicea										
Carex pilulifera				x		x				
Carex pulicaris										
Juncus conglomeratus										x
Juncus effusus										
Juncus squarrosus			x				x			
Luzula multiflora	x		x	x	x	x		x		
Trichophorum cespitosum							x			
Flowering plants										
Achillea millefolium										
Ajuga reptans										
Anemone nemorosa						x		x		x
Antennaria dioica										
Betula seedling										
Calluna vulgaris	x	x	x	x	x	x	x	x	x	x
Campanula rotundifolia				x		x		x		
Cerastium fontanum			x	x						
Cirsium palustre										
Erica cinerea				x	x	x		x	x	
Erica tetralix	x	x	x				x	x		x
Euphrasia sp				x				x		
Fragaria vesca										
Galium saxatile	x			x	x	x				
Hypericum pulchrum				x		x		x		
Lathyrus montanus										
Listera cordata								x	x	
Lotus corniculatus								x		
Myrica gale										
Narthecium ossifragum		x								
Oxalis acetosella			x							
Polygala serpyllifolia				x		x		x		
Potentilla erecta	x	x	x	x		x	x	x	x	x
Rumex acetosella										
Salix aurita										
Sorbus seedling										
Succisa pratensis		x		x						
Taraxacum sp.								x		
Trientalis europaea										
Vaccinium myrtillus									x	
Vaccinium vitis-idaea				x					x	
Veronica officinalis										
Viola palustris										
Viola riviniana	x		x							
Total number of species	11	10	13	22	7	17	10	21	10	9

Table 6.5 Species recorded in random quadrats 21-30

Number of quadrat	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
Oldest age of *Calluna* stems	24	7	26	32	20	13	14	13	15	16
Calluna vulgaris %	95	40	95	85	95	70	50	70	95	95
Mosses %	5		5	10	5	5	5	5	5	5
Erica cinerea %						5	20	10		
Bare ground %		10								
Grasses and Sedges %		50		5		20	25	15		
Layering	x		x							
Pteridophytes										
Athyrium filix-femina										
Blechnum spicant	x									
Equisetum arvense										
Equisetum palustre										
Equisetum pratense										
Oreopteris limbosperma										
Pteridium aquilinum									x	
Selaginella selaginoides										
Bryophytes										
Aulacomnium palustre										
Campylopus introflexus										
Ceratodon purpureus		x								
Climacium dendroides										
Dicranum scoparium		x			x	x	x	x		
Gymnocolea inflata										
Hylocomium splendens	x		x							
Hypnum jutlandicum	x	x			x	x	x	x	x	x
Ptilidium ciliare										
Pleurozium schreberi				x	x					x
Polytrichum commune										
Polytrichum piliferum										
Polytrichum juniperinum		x								
Pseudoscleropodium purum		x							x	
Rhytidiadelphus loreus										
Rhytidiadelphus squarrosus	x		x			x			x	
Sphagnum spp.										
Thuidium tamariscinum										x
Grasses										
Aira praecox		x								
Anthoxanthum odoratum						x	x	x		x
Briza media										
Deschampsia flexuosa		x					x			
Festuca vivipara										
Festuca ovina		x	x			x		x		x
Molinia caerulea	x									
Nardus stricta										x

Table 6.5 continued **Species recorded in random quadrats 21-30**

	21	22	23	24	25	26	27	28	29	30
Sedges, Rushes							x			x
Carex binervis	x									
Carex echinata										
Carex panicea										
Carex pilulifera						x				
Carex pulicaris										
Juncus conglomeratus	x									
Juncus effusus										
Juncus squarrosus										
Luzula multiflora	x	x		x				x	x	x
Trichophorum cespitosum										
Flowering plants										
Achillea millefolium										
Ajuga reptans				x						
Anemone nemorosa	x		x	x		x			x	x
Antennaria dioica										
Betula seedling										
Calluna vulgaris	x	x	x	x	x	x	x	x	x	x
Campanula rotundifolia										
Cerastium fontanum										
Cirsium palustre										
Erica cinerea	x	x	x		x	x	x	x	x	x
Erica tetralix	x									
Euphrasia sp										
Fragaria vesca			x	x						
Galium saxatile		x	x	x	x	x	x	x		
Hypericum pulchrum					x	x			x	x
Lathyrus montanus									x	x
Listera cordata	x		x	x	x				x	
Lotus corniculatus										x
Myrica gale										
Narthecium ossifragum										
Oxalis acetosella				x						
Polygala serpyllifolia		x				x	x			
Potentilla erecta	x		x	x		x		x	x	x
Rumex acetosella										
Salix aurita									x	
Sorbus seedling										
Succisa pratensis										
Taraxacum sp.									x	
Trientalis europaea										
Vaccinium myrtillus										
Vaccinium vitis-idaea		x			x	x	x			
Veronica officinalis							x	x		
Viola palustris										
Viola riviniana		x	x	x				x	x	x
Total number of species	14	15	11	11	9	14	11	10	15	16

Table 6.6 Species recorded in random quadrats 31-40

Number of quadrat	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
Oldest age of *Calluna* stems	29	16	19	19	13	18	33	20	10	6
Calluna vulgaris %	95	75	75	50	90	60	20	75		
Erica cinerea %			5					10		
Erica tetralix %				20					20	10
Grasses and Sedges %		5		10	5	30	60	10	70	30
Mosses %	5		15	20	5	10	20	5		
Myrica gale %									10	60
Salix aurita %		20								
Vaccinium vitis-idaea %			5							
Layering	x							x		
Pteridophytes										
Athyrium filix-femina										
Blechnum spicant				x		x		x	x	x
Equisetum arvense							x			
Equisetum palustre										
Equisetum pratense										
Oreopteris limbosperma									x	
Pteridium aquilinum										
Selaginella selaginoides				x						
Bryophytes										
Aulacomnium palustre							x	x		
Campylopus introflexus										
Ceratodon purpureus										
Climacium dendroides										
Dicranum scoparium			x			x				
Gymnocolea inflata										
Hylocomium splendens	x			x	x	x	x			x
Hypnum jutlandicum	x		x	x	x	x		x	x	x
Ptilidium ciliare										
Pleurozium schreberi					x	x	x	x	x	
Polytrichum commune				x		x		x		
Polytrichum piliferum										
Polytrichum juniperinum			x							
Pseudoscleropodium purum			x							
Rhytidiadelphus loreus		x					x	x		
Rhytidiadelphus squarrosus						x				
Sphagnum spp.				x			x	x	x	
Thuidium tamariscinum		x		x					x	
Grasses										
Aira praecox										
Anthoxanthum odoratum						x	x			
Briza media										
Deschampsia flexuosa										
Festuca vivipara										
Festuca ovina			x	x	x	x	x	x	x	x
Molinia caerulea					x	x	x			x
Nardus stricta		x		x			x		x	

Table 6.6 continued **Species recorded in random quadrats 31-40**

	31	32	33	34	35	36	37	38	39	40
Sedges, Rushes										
Carex binervis		x		x	x	x				x
Carex echinata							x			
Carex panicea									x	x
Carex pilulifera			x							x
Carex pulicaris									x	x
Juncus conglomeratus										
Juncus effusus										
Juncus squarrosus						x	x	x		
Luzula multiflora		x				x	x		x	
Trichophorum cespitosum								x		
Flowering plants										
Achillea millefolium	x									
Ajuga reptans										
Anemone nemorosa		x		x	x			x	x	x
Antennaria dioica										
Betula seedling		x								
Calluna vulgaris	x	x	x	x	x	x	x	x	x	x
Campanula rotundifolia										
Cerastium fontanum										
Cirsium palustre					x				x	
Erica cinerea	x	x	x		x	x		x		
Erica tetralix				x	x		x		x	x
Euphrasia sp						x				
Fragaria vesca										
Galium saxatile						x				x
Hypericum pulchrum				x	x	x				x
Lathyrus montanus		x		x	x					x
Listera cordata							x	x	x	
Lotus corniculatus										
Myrica gale									x	x
Narthecium ossifragum							x	x		
Oxalis acetosella						x	x			
Polygala serpyllifolia				x		x	x		x	
Potentilla erecta	x	x		x	x	x	x	x	x	x
Rumex acetosella										
Salix aurita		x								
Sorbus seedling		x			x					
Succisa pratensis				x				x		x
Taraxacum sp.				x					x	
Trientalis europaea				x			x			
Vaccinium myrtillus			x							
Vaccinium vitis-idaea			x							
Veronica officinalis										x
Viola palustris							x		x	
Viola riviniana		x		x	x	x				x
Total number of species	6	14	10	20	16	22	22	17	21	20

Table 6.7 Quadrats which were sampled near *Lycopodium clavatum* plants L1-L10

Number of quadrat	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
Oldest age of *Calluna* stems	24	13	0	14	15	21	33	19	31	9
Calluna vulgaris %	80	50		20	70	95	75	90	70	75
Mosses %	10	20		5	25	5	15	5	10	
Erica cinerea %	10	10					10	5		5
Bare ground %					5					
Erica tetralix %		10		70						
Grasses and Sedges %		10		5					20	20
Layering							x			
Pteridophytes										
Athyrium filix-femina										
Blechnum spicant				x		x	x		x	
Equisetum arvense										
Equisetum palustre										
Equisetum pratense							x			
Oreopteris limbosperma										
Pteridium aquilinum						x				
Selaginella selaginoides										
Bryophytes										
Aulacomnium palustre										
Campylopus introflexus										
Ceratodon purpureus										
Climacium dendroides										
Dicranum scoparium		x			x			x		
Gymnocolea inflata					x					
Hylocomium splendens	x					x	x		x	
Hypnum jutlandicum		x		x	x		x	x	x	x
Ptilidium ciliare										
Pleurozium schreberi	x	x				x	x	x	x	
Polytrichum commune				x					x	x
Polytrichum piliferum					x					
Polytrichum juniperinum		x								
Pseudoscleropodium purum										
Rhytidiadelphus loreus										
Rhytidiadelphus squarrosus						x		x		
Sphagnum spp.										
Thuidium tamariscinum						x				
Grasses										
Aira praecox										
Anthoxanthum odoratum				x					x	
Briza media										
Deschampsia flexuosa	x								x	
Festuca vivipara										
Festuca ovina	x	x	x	x				x	x	x
Molinia caerulea	x									x
Nardus stricta		x			x				x	

Table 6.7 continued **Quadrats which were sampled near *Lycopodium clavatum* plants L1-L10**

	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
Sedges, Rushes										
Carex binervis								x		x
Carex echinata										
Carex panicea									x	
Carex pilulifera										
Carex pulicaris										
Juncus conglomeratus										
Juncus effusus										
Juncus squarrosus										
Luzula multiflora	x	x		x				x	x	x
Trichophorum cespitosum				x						
Flowering plants										
Achillea millefolium										
Ajuga reptans										
Anemone nemorosa		x	x						x	
Antennaria dioica					x					
Betula seedling										
Calluna vulgaris	x	x		x	x	x	x	x	x	x
Campanula rotundifolia								x		
Cerastium fontanum										
Cirsium palustre										
Erica cinerea	x	x		x	x	x	x	x	x	x
Erica tetralix		x		x					x	
Euphrasia sp										
Fragaria vesca						x				
Galium saxatile		x						x	x	x
Hypericum pulchrum		x							x	
Lathyrus montanus		x						x	x	
Listera cordata	x	x	x	x		x	x	x	x	x
Lotus corniculatus								x		
Myrica gale										
Narthecium ossifragum										
Oxalis acetosella						x			x	
Polygala serpyllifolia		x								x
Potentilla erecta	x	x	x	x		x		x	x	
Rumex acetosella										
Salix aurita										
Sorbus seedling				x						
Succisa pratensis									x	
Taraxacum sp.						x				
Trientalis europaea										
Vaccinium myrtillus			x				x			
Vaccinium vitis-idaea							x			x
Veronica officinalis										
Viola palustris										
Viola riviniana							x		x	
Total number of species	10	17	5	13	8	13	11	15	23	12

Table 6.8 Quadrats which were sampled near *Lycopodium clavatum* plants L11-L15

Number of quadrat	L11	L12	L13	L14	L15
Oldest age of *Calluna* stems	12	25	5	5	11
Calluna vulgaris %	80	60	20	30	60
Mosses %	10	20	10	5	10
Bare ground %		10	40	5	5
Grasses and Sedges %	10	10	30	60	
Vaccinium myrtillus					25
Layering		x			
Pteridophytes					
Athyrium filix-femina					
Blechnum spicant					
Equisetum arvense					
Equisetum palustre					
Equisetum pratense					
Equisetum sylvaticum					
Oreopteris limbosperma					
Pteridium aquilinum					
Selaginella selaginoides					
Bryophytes					
Aulacomnium palustre					
Campylopus introflexus					
Ceratodon purpureus					
Climacium dendroides					
Dicranum scoparium	x		x	x	x
Gymnocolea inflata	x	x			
Hylocomium splendens	x				
Hypnum jutlandicum	x	x		x	x
Ptilidium ciliare	x	x		x	x
Pleurozium schreberi	x	x		x	
Polytrichum commune					
Polytrichum piliferum		x	x		
Polytrichum juniperinum			x	x	
Pseudoscleropodium purum					
Rhytidiadelphus loreus	x				
Rhytidiadelphus squarrosus					
Sphagnum spp.					
Thuidium tamariscinum					
Grasses					
Aira praecox			x	x	
Anthoxanthum odoratum					
Briza media					
Deschampsia flexuosa		x		x	
Festuca vivipara	x	x			
Festuca ovina		x	x		x
Molinia caerulea				x	
Nardus stricta	x				

Table 6.8 continued **Quadrats which were sampled near *Lycopodium clavatum* plants L11-L15**

	L11	L12	L13	L14	L15
Sedges, Rushes					
Carex binervis					
Carex echinata					
Carex panicea					
Carex pilulifera			x	x	
Carex pulicaris					
Juncus conglomeratus					
Juncus effusus					
Juncus squarrosus		x	x		
Luzula multiflora	x	x			
Trichophorum cespitosum					
Flowering plants					
Achillea millefolium					
Ajuga reptans					
Anemone nemorosa					
Betula seedling					
Calluna vulgaris	x	x	x	x	x
Campanula rotundifolia				x	
Cerastium fontanum					
Cirsium palustre					
Erica cinerea			x	x	x
Erica tetralix					
Euphrasia sp	x	x			
Fragaria vesca					
Galium saxatile	x			x	
Hypericum pulchrum					
Lathyrus montanus					
Listera cordata		x			
Lotus corniculatus					
Myrica gale					
Narthecium ossifragum					
Oxalis acetosella					
Polygala serpyllifolia				x	
Potentilla erecta				x	
Rumex acetosella			x		
Salix aurita					
Sorbus seedling					
Succisa pratensis					
Taraxacum sp.					
Trientalis europaea					
Vaccinium myrtillus	x	x		x	x
Vaccinium vitis-idaea	x	x	x	x	x
Veronica officinalis					
Viola palustris					
Viola riviniana					
Total number of species	15	15	11	17	8

6.4.3 Analysis of Data

The Twinspan computer program (Hill 1979) was used to analyse the frequency of species within quadrats. The data based on presence and absence of species were ordinated by reciprocal averaging which sorted the samples into groups with the most different communities at opposite extremes of the ordination. Each group which Twinspan isolates can be further subdivided a specified number of times. Division 1 split the quadrats into species which are more characteristic of wetter environments, contrasting with drier associations in Division 2. Subsequent subdivisions of Division 1 showed that the first four quadrats 12, 17, 20 and 38 in the ordination, were all similar with *Sphagnum, Equisetum palustre* and *Rhytidiadelphus loreus* more frequent than in other quadrats. A further group of five quadrats, 39, 5, 10, 13 and 17 also had marshy affinities but the species suggest perhaps slightly more basic flushing with species like *Carex pulicaris, Viola palustris* and *Climacium dendroides*. None of the *Lycopodium* quadrats were among these very wet communities but they were distributed among the two remaining major divisions which ranged from damp to drier associations.

Several species range across the damp end of the ordination spanning from the wettest groups up to the first major group division. *Erica tetralix* only occurs in this group together with most of the records for *Hylocomium splendens, Potentilla erecta, Listera cordata, Lathyrus montanus* and *Anemone nemorosa*. The drier communities in the second major group division do have several species in common with the first major group as *Calluna vulgaris, Hypnum jutlandicum* and *Erica cinerea* are found throughout. Within the second major group are species characteristic of more recently burnt ground, like *Aira praecox* and *Ceratodon purpureus*, but there are also other species which characteristically prefer drier habitats like *Polytrichum juniperinum, Carex pilulifera, Dicranum scoparium, Vaccinium vitis-idaea* and *Vaccinium myrtillus*. One clear division can be seen within the 2nd major group as most of the *Vaccinium myrtillus* is confined to this group.

From the distribution of the *Lycopodium clavatum* quadrats among all but the wettest areas, it appears that this species shows no especial preference for one particular association.

Table 6.9 Showing spread of quadrats as determined by indicator species
(Quadrat number read vertically)

	1 - 40 are random quadrats *Lycopodium* quadrats are 41-55 marked *			
	1st major group			2nd major group
Species	1123 2708	30113 95037	** ** *** 22440134411234442333 4 34361911418152899026 40	* * * * *** * 11251222500500035245 5004 46645278037394835551 2267
Sphagnum spp.	1111	1___1	__________________1_	_______________________
Carex echinata	111_	__1_1	____________________	_______________________
Trichophorum ce	___1	_____	_______1____________	_______________________
Equisetum palussf	1_1_	__1__	____________________	_______________________
Narthecium ossi	1__1	____1	____1_______________	_______________________
Aulacomnium pal	1___	__1_1	____________________	_______________________
Erica tetralix	111_	1_111	_______1111_1_1__111	_______________________
Rhytidiadelphus l	11_1	____1	____________________	___________________1___
Carex panicea	____	1_1__	____________________	_______________________
Carex pulicaris	____	111__	___________________1	_______________________
Viola palustris	____	111_1	____________________	_______________________
Climaceum dendr	____	__1__	____________________	_______________________
Athyrium filix-f	____	_1___	____________________	_______________________
Equisetum arvens	____	____1	____________________	_______________________
Oreopteris limbo	____	1____	____________________	_______________________
Trientalis europea	____	____1	__________________1_	_______________________
Thuidium tamaris	____	111__	___1___________11_1_	_______________________
Polytrichum com	__11	_1___	_____1__1__1__1___1_	________1______________
Oxalis acetosella	____	_1_11	_1_1_______1__1_____	_______________________
Hylocomium sple	____	_1_11	1_1_111_1111__1__111	__________________1_1_1
Potentilla erecta	1111	11111	11111111111111111111	1111___1_____________1_
Taraxacum spp.	____	1_1__	___1_____1____1___1_	_______________________
Achillea millefoli	____	_____	_____1______________	_______________________
Ajuga reptans	____	_____	_1__________________	_______________________
Fragaria vesca	____	_____	11_1________________	_______________________
Selaginella selagin	____	_____	__________________1_	_______________________
Betula seedling	____	_____	________________1___	_______________________
Briza media	____	_____	_________1__________	_______________________
Pteridium aquilin	____	_____	___1___________1____	_______________________
Salix aurita	____	_____	_______________1_1__	_______________________
Sorbus seedling	____	_____	_______1________11__	_______________________
Lotus corniculata	____	_____	_________1__1__1____	_______________________
Lathyrus montanu	____	_____	____________11111111	______________________1
Succisa pratensis	1__1	_____	______________1___11	1______________________
Carex binervis	_1__	_____	__________11_1_11111	________1______________

Table 6.9 continued **Showing spread of quadrats as determined by indicator species**

	1 - 40 are random quadrats *Lycopodium* quadrats are 41-55 marked *			
	1st major group			2nd major group
Species	1123 2708	30113 95037	** ** *** 2244013441123444233334 3436191141815289902640	* * * * *** * 1125122250050003524550 04 466452780373948355512267
Anemone nemor	__11	1____	111_______11_1_1111111	_11______________________
Viola riviniana	____	_1_1_	11_______1__1__1111111	_____1_1_______________1
Listera cordata	___1	1___1	1111_1_11_11-1111_____	________1________1__1___
Blechnum spicant	___1	1____	___11___1__11__1____11	_______________________1
Rhytidiadelphus s	____	_111_	1__11_____111_1_1_____	1_1__________________11_
Nardus stricta	____	11111	_______________1_1_11_1_	1_______________11____
Anththoxanthum	____	_1111	_________111_1__1_1____	111___11_______________
Festuca ovina	___1	11111	1_1_1__1111_1111_1_111	111_11_11111___11___11__
Luzula multiflora	____	11111	_1_____111111111_11___	11__11_1111_11_____111__
Erica cinerea	___1	_____	1__1_1111_1111111111__	111111111__1_1_11111__1_
Campanula rotun	____	_____	__________1___1_______	11_1____________________
Veronica officin	____	_____	_____________________1	______11________________
Ceratodon purpur	____	_____	______________________	11___1__________________
Aira praecox	____	_____	______________________	11_1_1_____11___________
Polytrichum junip	____	_____	_______________1_______	11_1_1___1_11__1________
Carex pilulifera	____	__1__	_____________________1	1111________11__1_______
Dicranum scopar	____	_____	_____________111_______	__111111_1_11_111111_1__
Polytrichum pilife	____	_____	______________________	__________11_______1_1___
Vaccinium vitis-id	____	_____	____11________________	1_11_11_11_1111111_111_1
Ptilidium ciliare	____	_____	______________________	___1________1___1__11___
Festuca vivipara	____	_____	______________________	1___________1______11___
Vaccinium myrtill	____	_____	__1__1________________	___1________1_111__11_11
Campylopus intro	____	_____	______________________	_________1______________
Rumex acetocella	____	_____	______________________	__________11____________
Gymnocolea infl	____	_____	______________________	_________________111___
Equisetum praten	____	_____	______________________	_______________________1
Antennaria dioica	____	_____	______________________	__________________1_____
Juncus conglom	__1_	_1___	___________1__________	______________________1__
Pleurozium schreb	___1	1___1	_1_111_1_11_1111_1_1__	___1_______________1_11111
Juncus squarrosus	_1_1	_1_11	_____________1___1_____	___________1_________1___
Hylocomium sple	____	_1_11	1__1_111_1111__1___111	____________________1_1_1
Hypericum pulch	____	_____	__________1_11_111_111	111______________1______
Festuca ovina	___1	11111	1_1_1__1111_1111_1_111	111_11_11111___11___11__
Cirsium palustre	____	1____	___________________1__	__________1_____________
Pseudoscleropod p	____	_11__	________________1______	_____1_________1________
Molinea caerulea	1___	____1	_______1__111_______1_1	_1_1__1_1_______________
Polygala serpyli	____	11__1	__________1_11______1_	1111_11_1_______________
Euphrasia spp	____	__1__	__________1_1_________	1__________________11___
Hypnum jutlandi	_1_1	11___	____111_1111111111_111	111111111____111111111_1
Calluna vulgaris	1111	11111	11_11111111111111111111	111111111111111111111111
Cerastium fontan	____	___1_	______________________	1_______________________
Deschampsia flex	____	_____	_______1_________1______	___1_1_11____________1___
Galium saxatile	____	_11__	11__1____1__1111_____1	111111111_1_________1_1_1__

As the *Lycopodium* seemed able to grow successfully in a variety of communities these data were examined in an attempt to find a relationship between the percentage shrub cover and the presence of *Lycopodium*.

Table 6.10 Percentage shrub cover, number of species, age of *Calluna* and the presence of *Lycopodium*

% Shrub Cover	00	10	15	15	20	20	20	30	30	40	40	45	50	50	50	60	60	60
Quadrat name	43	40	10	13	53	37	39	07	54	12	22	14	18	20	19	05	03	55
* *Lycopodium*	*				*				*									*
Number of Spp.	05	20	21	13	11	22	21	08	17	10	15	22	21	09	10	21	07	08
Age of Calluna	00	06	23	18	05	33	10	05	05	20	07	10	11	27	27	27	11	11

% Shrub Cover	70	70	70	70	70	70	70	75	75	75	80	80	80	80	80	80	80	85	85
Quadrat name	36	52	49	16	42	27	34	32	26	45	08	51	28	17	50	15	33	38	47
**Lycopodium*		*	*		*					*		*			*				*
Number of Spp.	22	15	23	17	17	11	21	10	14	08	05	15	11	10	12	07	10	17	11
Age of Calluna	18	25	31	05	13	14	19	16	13	15	09	12	13	20	09	08	19	20	33

% Shrub Cover	85	90	90	90	90	90	95	95	95	95	95	95	95	95	95	95	95	95
Quadrat name	24	44	09	35	41	04	29	06	46	31	48	30	23	11	25	21	02	01
* *Lycopodium*		*			*				*		*							
Number of Spp.	11	13	09	16	10	05	15	05	13	06	15	16	11	11	09	14	12	10
Age of *Calluna*	32	14	11	13	24	16	15	34	21	29	19	16	26	33	20	24	32	33

Once again the *Lycopodium* was found to be distributed among all ages of *Calluna* and in a variety of densities of vegetation. The total number of species present did not show a very marked variation according to the shrub coverage, although all the quadrats with more than 20 species are found in cover densities of 70% or less. The cover density may be less because the stand is younger, or very old with open crowns, or possibly growing in a wetter area so that the *Calluna* grows less well and other species are also found.

These results suggest that on this particular hillside at the present time *Lycopodium clavatum* is not being eliminated by burning. One example already referred to had been burnt, possibly by a relatively cool burn, and was regenerating vegetatively. While the temperature of burning may not always permit this to occur, this does demonstrate that survival is possible in some instances. It is difficult to determine whether small plants in a recently burnt area have grown from surviving shoots or arisen from an underground gametophyte, although one small plant on the upper hillside had a very small nodular structure which may have been the remains of the prothallus.

An indication of the age of a plant can be gained from measurements of annual growth. These measurements shown in **Table 6.11** indicate that *Lycopodium clavatum* grows at least 5cm a year and possibly up to 20cm, with 12.4 cm per year as an overall average growth rate at these Perthshire localities. Using this value, it is possible to estimate how long a colony has taken to grow to its present dimensions. Assuming growth is equal in both directions from a central point, by dividing the length of a patch by two and then by 12.4 cm an approximate age is reached.

Table 6.11 Annual growth measurements of *Lycopodium clavatum* taken from a variety of locations in Perthshire (cm)

Location	1990	1989	1988	1987	1986	1985
Schiehallion			5	8	12	12
Schiehallion			10	8	10	10
Ben Vrackie			13	19	18	20
Glen Derby	15	10	14	12	13	10
Glen Derby	17	16	20	18	15	15
Glen Derby	12	11	13	14		
Ben Vrackie	9	11	12	15	10	9
Ben Vrackie	8	12	8	12	11	11
Ben Vrackie	11	13	11	10	11	9
Ben Vrackie	10	14	8	10	12	13
Average	11.7	12.4	13.3	12.6	12.4	12.1

The oldest *Calluna* or *Erica* stems within the **3b** *Lycopodium* patch are 13 years old. **3b** is 3 metres across so the amount of growth has possibly been produced within about 12 years. The similarity in these ages suggests that the *Lycopodium* appeared either very soon after burning or grew from existing vegetative remnants. This method of estimating the age of a patch of *Lycopodium* is only suitable for small patches which emanate from an obvious central point. With larger patches several plants may be involved and the origin of the plants is not clear.

Table 6.12 Estimated ages of small patches of *Lycopodium clavatum* in the study area

Name of Area	1ca	1cb	1da	1db	2b	2c	2d	3b
Age of oldest stem	32	32	24	24	21	10	20	13
Minimum time since last burn in years	44	44	25	25	25	14	25	2
Length of Lycopodium patch	3m.	4.2m	2.4m	0.6m	3m	0.9m	2.7m	3m
Average estimated age in years	12	16.9	9.5	2.5	12	3.6	10.8	12

Where there are two separate patches of *Lycopodium* within an area they are labelled a and b.

6.5 Discussion

3b is the only patch of *Lycopodium* which shows a close similarity in dates between the age of a patch and the age of the *Calluna* stand, possibly implying regrowth immediately after burning. All the other small patches appear to be younger than the *Calluna* stand and may have established from gametophytes in the interval since the area was last burnt.

These results indicate that *Lycopodium* can spread vegetatively after a burn and also by spores. It has also been observed growing out of older areas of *Calluna* into younger. Within this particular matrix of muirburn *Lycopodium* is able to survive in any density of cover. Its occurrence elsewhere on woodland rides indicates that it can tolerate moderate shade.

In Michigan in North America, Bruce and Beitel (1979) found nearly 500 gametophytes of various *Lycopodium* species including *L. clavatum* in an open pine plantation. The parent plants were some distance away. They found that many sporophytes were produced by the gametophytes but they often died away. The suggestion was that conditions were more suitable for the production of young sporophytes but not for their continued growth. In natural woodland, the amount of shade fluctuates as gaps open and close again. *Lycopodium* is well adapted to fill an appropriate role in this succession with mature sporophytes in the more open areas, and gametophytes producing young sporophytes over a period of time elsewhere. Should the conditions be suitable, the young sporophytes can develop into mature plants which produce sporing cones.

Øllgaard (1985) discovered a colony of mixed *Lycopodium* species in a disused gravel pit in Denmark. Within three years, the first sporelings had appeared, an unusually quick development perhaps assisted by the damp environment with a high water-table. The species involved were *Lycopodium clavatum, Lycopodiella inundata, Huperzia selago* and *Diphasiastrum alpinum.* The last named species had not been recorded in Denmark for twenty years and the nearest source of spores for the other species was at least 20km away. This implies that if a suitable site for gametophytes appears, then the spores are sufficiently well dispersed to attempt colonisation. In this site taller vegetation was beginning to shade the earlier colonists and Øllgaard thought that they would not survive the competion, except for *L. clavatum* which was spreading to higher drier ground, more typical of its usual habitat.

A *Calluna* canopy at its densest does not seem to provide excessive shade for *Lycopodium clavatum.* However, a thriving colony observed over a decade among a maturing conifer plantation at Faskally in Perthshire eventually died out altogether as the branches of the nearest Beech (*Fagus sylvatica*) spread overhead (**Figure 6.17**). It may be that the amount of shade on a managed moorland never exceeds that of open woodland and the rotational burning maintains this habitat, as the natural succession never proceeds any further, and that this is beneficial for *Lycopodium clavatum.*

Figure 6.17 ***Lycopodium clavatum*** **growing beneath** ***Fagus sylvatica*** **in Faskally Forest, Perthshire.** Photograph taken in 1983.

In the study area on Ben Vrackie there is enough *Lycopodium clavatum* in varying sizes of patches and differing ages of *Calluna* to suggest that this species has good immediate prospects of surviving in this area. Outside the quadrats and study area several plants of *Diphasiastrum alpinum* were also found in different ages of rotational burning together with two small patches of the uncommon *Lycopodium annotinum*. Other areas in Perthshire where *Lycopodium* plants can frequently be found, are in the Ben Lawers range and near Schiehallion. All these areas overlie either metamorphosed limestone or calcareous schists which give some flushing to *Calluna* moorland. The soil on Ben Vrackie was very rarely observed to be deep peat. There is usually a thin layer of silty peat over a sandy subsoil with frequent mole-hills. After a very wet period the sandy material was observed washed out of burrows. This must help to give a certain amount of mixing of the soil, a beneficial effect which was observed by Miles (1981). Jermy and Camus (1991) associate the distribution of *L. clavatum* with "a trace of base salts"(p7). This may explain the association of *Lycopodium clavatum* with these more basic areas and its especial success on Ben Vrackie.

6.6 The Current Status of *Lycopodium clavatum*

Lycopodium clavatum has a wide distribution over a substantial part of Scotland, especially the uplands. The squares where the plant has formerly been recorded, but is no longer found, can often be correlated with lowland land-use changes. Other large areas where it has not been recorded, can be identified with the wetter acidic rocks in the extreme north-west in Sutherland and the Outer Hebrides, the flatter agricultural land of Caithness, north-east Aberdeenshire and the south of Scotland.

Despite the apparent frequency of this species in the Atlas, and the observed ability of *Lycopodium clavatum* in some circumstances to survive within a burning regime, field observations around Scotland still do not suggest that this species is as frequent as the old floras seemed to imply. Casual observations over a period of ten years from 1980 to 1990 on the slopes of Schiehallion suggest that two large areas had less extensive amounts of *Lycopodium* species at the end of that period than had been noted before, although the *Calluna* has regenerated successfully. Perhaps a more strictly conducted burning regime would be less amenable to sporophyte development. If the ground does become progressively leached as large areas are burnt and hillwash removes nutrients, the habitat may progressively become less suitable. Øllgaard's Danish study has demonstrated the wide dispersal of spores, while the gametophytes in Michigan indicate that potential sporophytes may be widely distributed although not usually observed, and perhaps never developing into mature plants. There is little question that *Lycopodium* can colonise suitable areas, but inexplicably it is not as frequent as might be expected. This area offers further scope for research although the slow germination and development rate of *Lycopodium* gametophytes presents a problem. There is, however, a limit to the explanations of change in range which can be attributed to land-use changes. Another possible factor is pollution, especially in acidification of a *Lycopodium* habitat which requires a small amounts of bases and could be a major factor in the present rate of success of *Lycopodium clavatum*. The final chapter examines the effect which pollution might have, the wider consequences of global warming, and the impact this could have on the survival of pteridophytes in general.

Chapter 7

The Future

7.1 Introduction

All industrial activities have affected the environment on an unprecedented scale. Developing from the small local industry with a very moderate impact in the immediate environment, the scale of human activity is now such that no part of the globe is free from pollution. Future management of land and the implications this may have for the continuing existence of pteridophytes, might be decided by a range of factors such as those derived from European Community directives which are discussed in section **7.2.1**, the implications of the set-aside scheme examined in section **7.2.2**, and deliberate attempts to manage the countryside through reserves and national parks explored in section **7.2.3**.

In the discussion on possible sources of pollution in section **7.3.1**, use is made especially of the Scottish Development Department's publication of a symposium on Acidification in Scotland held in 1988. A joint publication by the World Meteorological Organisation with the United Nations Environmental programme comprising the Intergovernmental Panel on Climatic Change produced in 1990 was used for the basis of suggestions for the possible greenhouse effect on pteridophytes described in section **7.3.2**.

Finally a general view is taken in section **7.4** of pteridophytes in Scotland and their prospects in the immediate future assuming the climate and land management remain substantially the same.

7.2. Changing Land Use

7.2.1 The Influence of the EC

With improved methods and productivity more food is being produced than is required within the EC. The use of "intervention" prices has ensured that a crop can be sold at a reasonable price, regardless of demand. To control this, quotas were introduced to reduce the surplus. Setting artificial prices affected organisation within the farms. When barley commanded a good "intervention" price it was not available cheaply for cattle feed, so fewer cattle were kept (Mather 1988). The nature and variety of livestock on the hill can have a marked effect on the native vegetation. If more pasture is required for cattle, then marginal land might be drained and improved, thus reducing the area of unimproved pasture with a wider range of species. On the other hand, cattle graze hill ground in a way different from sheep and their heavier trampling can have a useful effect in retarding the spread of *Pteridium*.

The introduction of the set-aside scheme might, however, have the greatest long-term effect on vegetation, where farmers are encouraged not to cultivate all their land and are compensated for loss of remuneration from crops.

7.2.2 The Set-aside Scheme

In the *Guidance on Set-aside* (DAFS 1988), suggestions are made for the selection of suitable areas for the scheme. Some land has limitations through soil which is suffering from erosion, or is perhaps too acidic, or lacking in trace elements, badly drained or too shallow to be usefully cultivated. Such areas can support an appropriate natural vegetation, but would never have been very suitable for agriculture in the first place. Other land has become badly infested with diseases or persistent weeds, which cannot be easily treated, and would benefit from a long fallow period. A further category is land on exposed or north-facing slopes, especially at high altitudes, which cannot be easily cultivated.

Better quality land could be specially selected to enhance existing features, especially in the lowlands. Suggested areas are adjacent to ponds, and in naturally wet land which is liable to flooding. By suggesting that the environs of ponds, rivers and woods are taken out of cultivation, there is opportunity for the vegetation which might still exist associated with these specialised habitats, or even be present in seed or spore banks, to extend into a larger range.

Suggestions that land is not cultivated in order to make available space for recreation and access to monuments all contribute to a reduction in the use of weedkillers and the opportunity for a wider diversity of species. While the set-aside scheme intends to reduce productivity of cereals and livestock, there is the deliberate intention of using the land made available to benefit wildlife. This would be especially fostered in the concept of leaving at least fifteen metre strips around the margins of existing fields which could be sown with slow-growing grasses. A three metre margin of cut grass is recommended next to the actual crop-growing area, but the rest of the strip may be allowed to develop into scrub. Such strips would contribute a considerable amount of new habitat for both the flora and fauna and help to compensate for the previous losses of habitat to cultivation. The importance of hedges is emphasised, with an encouragement to cut less frequently and allow trees to grow above the line of the hedge. This would provide a habitat which is more like a narrow strip of woodland, inhabited by ferns, and less like the present closely trimmed hedges close-mown at the base.

It is required that the land should be set-aside for at least five years in minimum blocks of one hectare (2.5 acres). A plant cover is specified as bare soil is not allowed under the scheme. Grass or other crops can be deliberately sown to control the resulting cover, but this must not be harvested and no fertilisers should be applied. Various methods are recommended to counteract the aggressive weed species which might result. Natural regeneration might be dominated for a few years by species which have remained from previous crops. Without the spraying programme normally employed, these could become heavily infested with disease to the detriment of crops in the adjacent fields. To maintain low vegetation, at least annual cutting is advised, but after seed has been allowed to set, and all nesting has finished for the season. With exceptionally persistent weeds like thistles, docks and ragwort, it may be permissible to use herbicides.

The possibility that the land might be out of production for only five years might be less helpful for pteridophyte establishment than for the annual weeds which have been steadily diminishing through the use of increasingly effective weedkillers. But planting of hardwoods to provide permanent wooded areas should begin to provide woodland habitats and seems likely to be the most positive benefit to pteridophytes to come from this scheme. If better land in the lowlands is to be taken out of production then hardwoods will grow well and help to balance the abundance of conifers more suited to the uplands. As the saplings grow the ranker weeds will be shaded out and the larger woodland ferns like *Dryopteris dilatata, D. filix-mas, D. affinis* subspp. and *Athyrium filix-femina* can fill the appropriate niches with *Dryopteris carthusiana* in the damper habitats. As the essence of set-aside is not to use the land for grazing this gives a far greater potential for colonisation by species which are so often nibbled out of existence only to be succeeded by aggressive species like *Pteridium.* Saplings also should be able to regenerate naturally. Rabbits, however seem to be currently growing in numbers and will have a continued influence.

One habitat which is unlikely to be restored is the unimproved meadow. Once a particular environment which has existed for hundreds of years has been destroyed it cannot be reconstructed in a few years. The lush growth of weeds in a set-aside field shows how much fertiliser still remains and it would be some years before this ceases to have an effect. Even if *Ophioglossum* or *Botrychium* attempted to colonise, a time-lapse is necessary for establishment, and if a field was only taken out of production for five years these species would not continue to survive if the field was ploughed again at the end of this period. The practice of mowing annually would be beneficial in maintaining meadowland and preventing further succession into scrubby woodland. A more favourable habitat would be provided in areas intended for occasional recreational use adjacent perhaps to historic buildings. Heavily worn parking areas would not be very productive, but field edges and less-used areas could well be colonised by *Botrychium* or *Ophioglossum.* In any grassland it is important that mowing should be late in the season after seed has set on flowering plants and after *Botrychium* and *Ophioglossum* have died down.

7.2.3 Nature Reserves

Any area which has been set aside as a reserve is a possible habitat for pteridophytes. The preservation of a particular habitat for one group of organisms does not exclude others which must usually be included as part of the whole. The sea-birds which nest on the Bass Rock, for example, provide nutrients for *Asplenium marinum* which also enjoys this habitat and unusually luxuriant fronds result. The major problem which occurs in the management of reserves usually derives from a severe imbalance if one species exists at the expense of all others. This usually only occurs because natural controls cannot operate.

Two of the best known examples of disproportionate influences derive from an excessive amount of *Pteridium aquilinum* and far too high a population of Red Deer. The two problems are closely related. Since the last wolf in Scotland was killed around 1740 (Harting 1880) the only natural predator has been man. Since the beginning of the nineteenth century deer have been preserved and since this time natural regeneration of many of the great Pine forests has been inhibited as seedlings are grazed (Watson 1991). As deer stalkers prefer to shoot mature stags, an unequal proportion of hinds are left to produce more progeny and a substantial cull has long been necessary. This is both to allow vegetation to regenerate and also to prevent massive mortalities of deer in a severe winter.

The increase in *Pteridium* has been encouraged by the grazing of shrubs which would have shaded the Bracken and restricted its growth. Also as the deer sought out any kind of vegetation all other ferns were nibbled or shaded by unpalatable *Pteridium*. Fencing is expensive and has limited success and a certain amount of grazing is both natural and desirable. Grazing is used with the appropriate animals on a variety of types of reserve. Controlled grazing by cattle was found to be an effective method of managing the light grazing required to maintain Woodwalton Fen nature reserve in Huntingdonshire as the cattle selectively removed coarse grasses (Mellanby 1981). Sheep can also have a beneficial effect as instanced by the loss of *Ophioglossum vulgatum* in Orkney when sheep no longer grazed in a particular area near the sea, and coarse grasses appeared instead (Spence 1914). Conversely, carefully controlled grazing increased the numbers of *Primula scotica* plants on the Hill of White Hamars Reserve (Paterson 1991a).

Some reserves are Sites of Special Scientific Interest (SSSI) which were designated by the former Nature Conservancy Council and are managed by negotiated agreements with owners of the estates, or are areas which are under the control of Regional Local Authorities. Many small localised habitats encompassing a wide range of types are owned by societies which have a specialised interest, but which nevertheless encourage a full spectrum of wildlife. In Scotland, the Scottish Wildlife Trust has a large number of reserves as does the Royal Society for the Protection of Birds. The Forestry Commission is actively encouraging more access and has areas for public use which are not purely commercial. These reserve are surveyed in relation to the local climate, the species present and the general landscape. On the basis of this information management plans are prepared.

Any area which has been designated as a reserve must be actively managed, while allowing for recreational access and taking any necessary steps to counter erosion. With mature woodland a constant succession should fill gaps left by old trees, but only if regeneration can take place. Following the introduction of alien species it may be decided to remove mature stands of *Fagus sylvatica* to allow *Quercus* to grow instead or *Acer* seedlings might be deemed undesirable. The present combination of environmental factors is so far removed from the "natural" conditions which might have prevailed thousands of years ago, that it is necessary to be clear about precisely what kind of vegetation is required.

One particular phase of a sere might be the requirement. An area which has been a hay meadow for many years must be cut regularly to prevent the eventual establishment of trees. This can be achieved mechanically or by carefully planned grazing. The Grey Hill Grasslands in Ayrshire is an SWT Reserve which has been grazed for hundreds of years (Reynolds 1990). It is on unimproved species-rich grassland on serpentinite. The nearby Standard Farm also owned by the SWT has pasture land untouched by chemical sprays or artificial fertilisers, with meadows containing orchids and *Botrychium lunaria* (Paterson 1991b). The former area will continue to be grazed by sheep and the latter must be managed in a similar way to foster the species encouraged by grazing cattle and ponies.

Moorland which has been grazed and burnt would eventually become covered in trees if preserved without management. There are some areas of moorland like the Muir of Dinnet which has well developed communities of a distinctive types with *Pyrola media, Arctostaphylos uva-ursi* and *Genista anglica* (Gimingham 1964). In these circumstances a regular burning regime is necessary to maintain the particular association.

Local drainage can be a problem in managing a small area. The water table can be lowered by activities round about with inevitable effects on the specialised vegetation which the reserve is most likely intended to preserve. Activities further upstream may reduce the flow of water as when headwaters are diverted for hydro-electric purposes. Pollution can take the form of noxious substances or perhaps fertiliser-based enrichment which is inappropriate for the existing vegetation.

7.3 Pollution

7.3.1 Atmospheric Pollution and Acid Rain

Pollution can occur directly through effluent released into rivers and ultimately the sea, or indirectly from gases and particles which combine in the atmosphere. Primary gaseous pollutants are sulphur dioxide (SO_2), nitric oxide (NO), nitrogen dioxide (NO_2), hydrocarbons, ammonia (NH_3) and carbon dioxide (CO_2). Secondary pollutants give rise to nitrogen dioxide (NO_2) from the oxidation of nitric oxide (NO), ozone (O_3) and other photochemical oxidants derived from reactions with sunlight in the lower atmosphere. Particles of fuel ash and metals are also in the atmosphere and precipitates can form sulphuric acid (H_2SO_4), nitric acid (HNO_3) and ammonia (Derwent 1989).

These pollutants can be deposited dry on vegetation, from acid rain containing sulphur and nitrogen, or from fog or cloud droplets. Areas nearest to the source of pollution are most affected by gases while further away the pollutants are secondary in the form of modified gases or precipitates. The amount of air pollution in Scotland is determined by the direction of the prevailing winds. Westerly winds from the Atlantic ocean bring clean air, while winds from the continent contain impurities (Fowler and Irwin 1989). The general pattern is of cleaner air in the north and west, which receives relatively little pollution compared with the rest of Europe, and higher pollution in the south and east of Scotland.

Acid rain, which falls on basic soil is neutralised before eventually seeping into waterways. In areas which are naturally acidic this cannot happen. Many areas of Scotland have been becoming increasingly acidic over the last ten thousand years. Some soils naturally replenish their mineral content as rocks decompose but in granite areas, for example, decomposition of the rock to provide minerals is slower than the effect of leaching. These are the areas which are most affected by the additional acidity of acid rain as the soils and peat are especially vulnerable. Wilson et al (1989) estimated that more than 25% of the soils in Scotland have a low pH naturally, but have become even more acidic through addition from acid rain. A further 36% which was not naturally so acidic is in danger of becoming more acidic and not being able to neutralise the additional acidity, while another 36% is sufficiently basic to counter the effects of acidity in the immediate future.

Samples of peat collected between 1978 and 1982 reflected the typical pollution pattern of low additional acidity in the north and north-west with more acidified peat in the south-west of Scotland, the south-west Highlands and the Cairngorms. The type of landform most affected by the acidification is upland or montane with bog or *Calluna* moorland vegetation (Wilson et al 1989).

Eighteen lochs throughout Scotland were investigated to assess the degree of acidification. Using the fossil diatom assemblages present in sample cores, comparisons of acidity were made between 1800 and the mid 1980s.

Nearly all lochs had become at least slightly more acidic, only those in the least polluted north-west being unaffected. Lochs with basic water can maintain a higher pH despite some acidic input (Battarbee 1989). If the pH of water in streams and lochs falls below 5.6 then both fish and plant life are affected. Beyond the Great Glen such low pH values are mainly natural in origin in peaty pools, but further south the water is increasingly acidified, especially the south-west in Galloway with large plantations of conifers. In these lochs there can be a pH between 4 and 5, no fish are present and plant life is considerable reduced (Harriman 1989).

Forestry does not adversely influence the acidity in less polluted areas but where the air pollution is already high the trees can increase the level of acidity. Conifers with a large surface area of evergreen needles provide a greater area for evaporation than low vegetation on the ground. The leaves act as filters to trap pollutants in mist or cloud and increase the acidity of the water which eventually reaches the ground. Whitehead (1989) estimated that evapotranspiration from upland forests is twice the amount which would occur with grassland. This gives an increase of 14% in the chloride, nitrate and especially sulphate which are filtered out by the leaves. Nitrogen can be used by the plants, but in central Germany it appears that excessive amounts are deposited, in which case a surplus may enter the streams and cause blooms of growth. This is not yet a problem in Scotland (Miller 1989).

Monitoring demonstrates that the levels of acidity and sulphate in rain have declined by approximately 50% since the 1970s (Harriman 1989). Two lochs in Galloway showed a slight increase in pH between 1978-79 and 1984-86, although the levels were still too low for a full range of species to grow successfully. When the water is very acidic, aluminium, copper, lead and zinc are more soluble but precipitate with phosphate, removing the phosphate from the water column. Only plants rooted in the sediment then have access to the essential phosphate, eliminating those which can grow floating in the water (Morrison 1989).

Evidence from the south of Scandinavia and the Netherlands showed the replacement of *Littorella uniflora, Lobelia dortmanna* and *Isoetes lacustris* with *Juncus bulbosus, Sphagnum auriculatum* and *S. cuspidatum* under these more acidic conditions. In Galloway, *Sphagnum* growth at some loch margins has been attributed to increasing acidification, especially in areas which have more concentrated pollution filtered from the atmosphere by forestry plantations. *Isoetes* has not been observed to decline (Lee et al 1989).

In Holland, *Calluna* heath has become grassland with *Molinia caerulea* and *Deschampsia flexuosa,* possibly due to high levels of ammonia entering the atmosphere from intensive stock-rearing which provided high levels of nitrogen. Nitrogen enrichment can encourage more vigorous species like *Chamerion angustifolium* which has increased in the south of Sweden. As many less common species grow in sites which are nitrogen deficient, they lose this advantage if this niche is removed with artificial nitrification (Lee et al 1989).

Increasing sulphur dioxide levels in the Netherlands were correlated with a decline in species which included *Lycopodium clavatum* and *Polypodium vulgatum* (Lee et al 1989). Blanket bogs on the Pennines in England no longer have the *Sphagnum* species and *Racomitrium lanuginosum* which were once present. Their absence is attributed to past levels of sulphur dioxide and although such levels are not present today many species have not re-established. Lee et al (1989) also explained the absence from these areas of *Juniperus* and *Lycopodium* due to the high levels of sulphur dioxide. In 1872 Glasgow had levels of pollution as high as had been measured in Manchester near the Pennines and it has been suggested that similar effects would have been observed downwind of the prevailing westerly winds from Glasgow (Lee et al 1989). Certainly, Brown (1913) wrote that *Calluna* was reputed to have been killed in the south-east of the Shotts area due to the smoke and fumes from iron-stone burning.

Bryophytes and lichens are often studied as indicators of pollution. They are especially sensitive to chemicals in the rain or mist as they have little alternative source of nutrient. The moss *Racomitrium lanuginosum* can be the main component in montane heath containing species such as *Diphasiastrum alpinum,* observed on Ben Lawers. *Racomitrium* is declining in area in the south of Scotland which also has high levels of pollution. The same association further north does not seem to have been affected yet, although the rate of *Racomitrium* growth is being affected by increased levels of nitrogen. *Calluna* can grow more vigorously with high levels of nitrogen, but is then more frost-sensitive (Lee et al 1989). This could well affect a range of species and lead to their decline.

Another area in which pollutants can be concentrated is within snow beds. Meltwaters have been found to contain especially high levels of nitrate and sulphate with a pH as low as 3.2 (Lee et al 1989). Some pteridophytes like *Athyrium distentifolium*, *A. flexile* and *Cryptogramma crispa* rely on winter snow for protection. If they are affected by the nitrogen, possibly with excessive growth too early in the season, they may not be able to recover if attempts at new growth are made too frequently.

Pteridophyte rhizomes are usually in contact with a medium which provides some nutrients. The filmy ferns are perhaps the most vulnerable as they usually grow on wet rock faces. In this connection it is interesting that Ratcliffe recorded the loss of two colonies of *Hymenophyllum tunbrigense* and one colony of *Trichomanes speciosum* in Cumbria and Dumfries after the particularly hard winter of 1962-63. He wrote that other more vigorous colonies survived but these had already been made marginal by "human forestry modification " (Ratcliffe 1984 p76). This may have been due to removal of shade. Alternatively, it might have been because of more forestry, giving increased frost-sensitivity, due to more nutrients and acid rain filtered out by the trees.

An essential part of the homosporous pteridophyte life-cycle is the gametophyte stage with the liverwort-like prothallus. Like bryophytes, the prothallus is dependent on a damp environment to sustain life and effect fertilisation. It may be that mature sporophytes can survive but new young ones are inhibited, or perhaps merely less successful, due to acidic precipitation. Other gametophytes like *Lycopodium*, *Ophioglossum* and *Botrychium* depend on a mycorrhizal association for their nutrition. In this connection, Last (1991), described research into the root tip growth of *Pseudotsuga menziesii* growing in a polluted part of the Netherlands. The plants were less vigorous and had less mycorrhizae within the roots. This may indicate another factor in the inhibition of gametophytes and affect their success. It indicates an area for future research

Pteridium aquilinum has little difficulty in spreading vegetatively but the young plants seem to prefer a slightly more basic substrate initially as shown by their success on burnt moorland, bombed sites in London after the Second World War (Page 1982) and city basements. If the level of acidity in the atmosphere did affect prothallus success with species in general, this may help to explain why some apparently suitable habitats have not been colonised.

Although the levels of pollution have declined there is still an unacceptably high levels of pollution in the atmosphere. Whitehead (1989) estimated that a reduction of 50% is necessary to prevent further acidification, as only a slow recovery rate is possible. Also, in areas which have high level of pollution, forestry plantations compound the problem and he recommends that further planting in these areas is not advisable.

7.3.2 The Greenhouse Effect and Changing Climate

The atmosphere around the Earth has a natural greenhouse effect to contain heat. Short-wave radiation from the Sun passes through the atmosphere almost unimpeded and about a third is reflected back into space, while the remaining two thirds are absorbed by the sea, ice, land, plants and atmosphere, thus warming the surface of the Earth. This warm surface emits infra-red long-wave radiation which is partly absorbed into the atmosphere and also re-emitted by trace gases in the atmosphere. The greenhouse gases in the atmosphere ensure that the Earth is warmer than it would have been if the long-wave radiation was lost back into space, as occurs on other planets with no atmosphere. The most important greenhouse gases are water vapour, carbon dioxide, methane, nitrous oxide and ozone. Aerosols, as can naturally occur from volcanic eruptions, also reflect radiation away and absorb radiation, leading to cooling of the atmosphere. Natural variations in the proportions of carbon dioxide and methane correlate with variations in temperature.

These can be calculated from ice cores indicating temperatures over the last 160,000 years. There are also other factors involved in changing climates and natural changes can be expected regardless of human activity. What does seem to be increasingly apparent is that anthropogenic changes are having an additional warming effect over and above natural variation (Watson et al 1990).

Human activities have increased the CO_2 concentration in the atmosphere by 26% since the Industrial Revolution, which commenced in approximately 1800. Methane has more than doubled and N_2O has increased by 8%. Since the 1930s, chlorofluorocarbons (CFCs) have been introduced for use as aerosol propellants, refrigerants, solvents and foam-blowing agents. CFCs reduce the ozone in the lower stratosphere which is necessary for absorbing harmful ultra-violet radiation (Watson et al 1990).

In calculating possible changes many variables have to be considered. The increase in CO_2 may be compensated for by other natural factors, as the precise responses of the polar ice-sheets are difficult to determine. Increased precipitation could lead to greater accumulations of ice in polar regions which would reduce higher sea-levels. However, using the best information available, some predictions have been made and these are used as a basis for discussion of the possible effects these might have on pteridophytes:

1) Higher Temperatures.

It is predicted that if no changes are made to the present rate of increase in concentration of these gases there will be global warming. Temperatures might be on average up to 1.8°C higher by 2030. It has been estimated that an increase of 0.3 - 0.6°C has already occurred between 1900 and 1990. Even if measures are taken to restrict or even stop the emission of these gases, the temperature will still continue to rise for some time (Watson et al 1990).

2) Higher Sea Level

A rise in temperature will affect the sea level. Assuming no change in the present rate of emissions, a rise of 20 cm might be expected between 1990 and 2030. A 3 to 10 cm rise per decade will continue through the twenty-first century (Watson et al 1990).

3) Changes in Precipitation

Precipitation patterns will change. Some parts of the world will be more liable to flooding while drought prevails in previously fertile regions. Predictions for the south of Europe are for a wetter winter, but dryer summer. Storms might be more frequent although there is less agreement on this (Watson et al 1990).

A limited impression of the effects such changes could have is gained by making comparisons with recent changes in climate, such as has occurred on a large scale during the last 10,000 years, and on a smaller scale with a warmer period as was experienced from 800 to 1200 AD. Direct comparisons cannot be extended very far, as the reasons for warming were not exactly the same, but the vegetation might react to a warmer phase in a similar way.

An experiment with higher levels of atmospheric CO_2 encouraged better growth in plants, which produced proportionately larger roots, more branches, flowers and fruit. Mycorrhizal relations were also improved so that plants grew more strongly in nutrient-deficient soil (Melillo et al 1990).

An experiment was carried out in a boreal forest of Black Spruce (*Picea mariana*) in Alaska over three summers. Soil-warming cables raised the temperature 9°C higher. Growth was increased and organic matter in the soil decayed to release nutrients. This, incidentally, could add considerably to the amount of carbon entering the atmosphere. If the site become more nutrient-rich conifers would be replaced by deciduous trees so that the nature of the forest would change (Melillo et al 1990).

Migration of species would occur as different ranges become available under new climatic conditions, bringing together the appropriate climate, altitude and substrate. But very small relict populations might be lost from one area where conditions become unsuitable, before colonising a new area, especially if human land-use does not offer an appropriate habitat. Other species could, of course, have more success than previously (Melillo et al 1990). Such changes have occurred in the past, and will continue to occur in the future. Not all the plants in a community can be expected to migrate at similar rates so that new communities may be found.

There is some uncertainty in the proposed climatic changes surrounding the expected amount of precipitation. While drier summers are predicted for southern Europe (Watson et al 1990), it might be that the position of Britain continues to ensure generally more oceanic conditions than in Europe as a whole. Drier seasons would affect many species of ferns as they mostly require a damp environment for reproduction. Some species like *Botrychium lunaria* do not appear during an unusually dry season. Haggart wrote of *Botrychium lunaria* at Keltney in Perthshire that it "did not show this last year (1914) nor did I find it on Ben Lawers, as is usual on the rock ledges, no doubt owing to the very dry weather of the summers of the years 1913, 1914 " (Haggart 1915 p48). These two years were both unusually dry (see **Appendix 4**). In the Flora of East Ross-shire, Duncan (1980) described *Botrychium* as frequent but erratic in its appearance. This might mean a series of dry summers would lead to the virtual extinction of this species.

With a warmer climate, and dry summers, species which now only occur in the extreme south-west of Britain might extend their ranges further north. These include *Isoetes histrix, Ophioglossum lusitanicum* and *Anogramma leptophylla.* These species complete their growth overwinter and are adapted to survive dry summer conditions. Two other species which can cope with dry summers are *Polypodium australe* which can lose fronds during a dry summer, and *Ceterach officinarum* which will curl up to conserve moisture and also re-hydrate after desiccation.

An incidental hazard associated with dry conditions is the possibility of an increase in accidental fires. This could be a decisive factor in the survival of species which might survive light burning in average conditions (Gimingham 1949), but could not survive higher temperatures. *Pteridium aquilinum* subsp. *aquilinum* with deep rhizomes would probably be able to survive in generally dryer conditions. This leads to the possibility of a major expansion of *Pteridium* which would probably also spore more frequently. Species which grow in permanently damp and humid conditions would not be expected to survive, especially those like the filmy ferns which grow on the surface of damp rocks. All the western species would suffer and be restricted to the few areas which are permanently damp throughout the summer.

But if the climate became increasingly Atlantic in character, which means a higher rate of precipitation over the whole year and a general increase in temperature, western species would be expected to spread eastwards. These include *Osmunda regalis*, *Hymenophyllum wilsonii*, *H. tunbrigense*, *Trichomanes speciosum*, *Asplenium billotii*, *A. marinum*, *Dryopteris affinis* subspp. and *D. aemula* (Page 1988) which all require acidic conditions. *Asplenium trichomanes* subsp. *trichomanes* is found more commonly on damp acidic rock in the west. *Asplenium billotii*'s current Scottish distribution is only in Kintyre (Cunningham and Kenneth 1979) and the north west (Jermy et al 1978) where it is very uncommon.

Adiantum capillus-veneris and *Asplenium onopteris* are only found in the south-west of Britain or Ireland and require calcareous substrates. A warmer but still damp climate may allow these three species to extend north and eastwards provided a calcareous habitat is available. *Polystichum setiferum*, of the three British species of the genus, will tolerate more neutral conditions provided it has adequate rainfall and winter temperatures are not too low. Like *Phyllitis scolopendrium* it a southern and western species and can be expected to grow further north and east as temperature increases.

An increasingly wet climate might substantially reduce the range of some species which depend on a continental climate and would suffer from a damp winter. Species which are already uncommon might disappear from Scotland altogether. *Dryopteris cristata* has not been recorded since 1945, *Thelypteris palustris* now has very few localities in Scotland, *Gymnocarpium robertianum* is also very rare and like *Asplenium septentrionale* has never been common in recent centuries. *Ophioglossum vulgatum* also has a continental distribution and might decline.

Similarly arctic-alpine species, which in some cases are very much at the limit of their range and exist only in small populations, can be expected to decline and possibly disappear altogether with an increase in temperature. Their montane habitats would become suitable for taller, less specialised plants, and the competition would probably prove too great. These species have already had their range reduced by climatic variation and survive now in small enclaves, often dependent on winter snow cover to provide additional protection. *Diphasiastrum alpinum, Cryptogramma crispa, Athyrium distentifolium, A. flexile, Cystopteris montana, Woodsia ilvensis, W. alpina, Polystichum lonchitis, Dryopteris expansa, Lycopodium annotinum, Asplenium viride* and *Equisetum pratense* all come into this category (Page 1988).

Selaginella selaginoides, in common with *Equisetum variegatum,* grows on mountains and near sea level. *Equisetum variegatum* has evolved different ecotypes with an erect montane form and a prostrate coastal variety, but the montane form would possibly not survive. *Selaginella selaginoides* would still be found at lower altitudes, especially in dune slacks, and would appreciate a warmer climate providing there is adequate precipitation. A higher sea level would affect the fresh-water table in sand dune systems, but a similar flora would presumably be found relative to the new sea level. The area may be substantially reduced as many of the present coastal links and dunes are on former raised beaches and only occur at a low altitude above sea level.

Species like *Asplenium marinum* and *A. adiantum-nigrum* which grow near the sea on cliffs could adapt to higher sea levels, by growing higher up the cliff, provided the plants are within reach of sea-spray. *Cystopteris dickieana* grows in a very restricted area in an unidentified number of sea caves. It probably already represents the last remnants of a larger distribution. If sea level was to rise, the sea caves would be inundated and migration to suitable higher caves might not occur.

With unpredictable climatic changes there are pteridophytes which are adapted to benefit from either increasingly wet or dry conditions. Either extreme might lead to the loss of some species but bring an extension of others which are presently not common, repeating the pattern of the last 14,000 years.

7.4 The Current Status of Pteridophytes in Scotland and Their Prospects for the Future

There is no doubt that among the former pteridophyte flora there were several species which are now only seen in Scotland in a few relict sites, or surviving as hybrids to indicate the former presence of a parent. As pteridophytes are so often associated with damp areas, drainage must be one of the major factors in the decline of species like *Dryopteris cristata, Thelypteris palustris, Pilularia globulifera* and to a lesser extent *Dryopteris carthusiana*. Their demise might have been the result of natural changes in climate, but for montane species like *Woodsia*, human activity in the form of collecting and providing conditions of intense grazing might have been enough to create the difference between an uncommon species and one which has a doubtful future.

Nevertheless, the components of any vegetative association are never static and a climax vegetation can rarely be reached. All habitats throughout the whole country suffer constant interference by man and new species soon arrive to fill available niches, whether it be a new motorway embankment or a spoil heap. Many of the commoner pteridophytes thrive on disturbance in fulfilling their pioneer role. *Equisetum arvense*, for example, is especially successful although it is usually only these commoner species which are most prevalent.

Hybrids which occur in intermediate conditions such as between *Dryopteris carthusiana* and *D. dilatata* offer the potential for new species. The present super-abundance of *Pteridium aquilinum* subsp. *aquilinum* may have been the result of a fertile hybrid which was favourably encouraged by the clearances effected by early man on his first agricultural ventures. *Polystichum aculeatum,* derived from *P. setiferum* and *P. lonchitis,* has become a separate species by doubling its chromosomes and often occurs in man-made basic environments in Scotland. *Polypodium interjectum,* derived from *P. australe* and *P. vulgare,* is another example of a fern which has greatly exploited the man-made habitat of vast expanses of mortared walls throughout suitable parts of the country.

As over-production within the EC has become the result of increased efficiency and plant-breeding, less land in the future will be used for intensive cultivation. This releases the pressure to bring new areas into cultivation and reverses the trend which began when the first land was tilled. During the improvements which began in the eighteenth century non-productive "waste-land" was not appreciated. The current emphasis is on restoring old habitats, encouraging regeneration of the Pine forests before it is too late, and permitting many more "wild" areas than has been the case in the recent past.

While towns have spread into the surrounding countryside and agricultural land has been lost, there is a greater awareness of deliberately creating green areas both for recreation and wildlife as well. Addiewell Bing near West Calder in West Lothian is now a Scottish Wildlife Trust Reserve enhanced by planting with additional native trees. Such an area could so easily have been levelled and grassed over. Fortunately the management of once derelict areas within an urban setting can allow for more varied vegetation, and it is to be hoped that new landscaping plans are not at the expense of the existing vegetation.

Areas which once were dominated by heavy industry no longer have the same local levels of pollution often associated with large amounts of coal-burning, whatever the global problems may be. This has helped the inner-city environment and may have contributed to the appearance of *Lycopodium clavatum* in and near Glasgow. It was found in a disused power station and also on a steep bank facing north-west below the Necropolis, a cemetery (Steven & Dickson 1986). Colonisation of these areas, and others far removed from local sources of spores, emphasises that if the correct habitat is available a variety of species will become established.

Some species which are very infrequent in Scotland are much commoner further north or south. Given that they would still exist somewhere, it might be thought that the loss of a few species from one small area of the northern hemisphere is not significant. But the species which we have now, are most probably the result of thousands of years of genetic isolation. Although they do not merit full species, or even subspecies status, they are nevertheless unique populations, adapted to local conditions and soils, which cannot be exactly matched by plants imported from other countries should they be lost. An example of this kind of introduction is seen in the Red Kite (*Milvus milvus*) and the Sea Eagle (*Haliaeetus albicilla*). It was found necessary to re-introduce these species from other countries because of the complete extinction of the local genotype.

Wilcock in 1990 suggested that it might be necessary to establish botanical sanctuaries for specific plants, possibly making use of Botanic Gardens. At the end of 1991 this has been initiated in the Scottish Rare Plants Project, jointly funded by the Royal Botanic Garden in Edinburgh and the Nature Conservancy Council for Scotland. It is intended to monitor a range of species including pteridophytes and flowering plants. *Trichomanes speciosum*, which is now only found in a very few Scottish localities, is one of the species to be studied (pers. comm. P Lusby 1991). It is intended to establish seed and spore-banks for rare Scottish plants from appropriate provenances. It may also be necessary to cultivate species to maintain live plants ex-situ in the hope of re-establishing them in a restored habitat.

While large climatic changes due to natural causes could eliminate some species, it seems more probable that their demise would be brought about by human agency, especially as any climatic changes might well be precipitated by anthropogenic activity. Throughout geological time, pteridophytes have survived successive extinctions and they will doubtless survive now, although possibly in a reduced and changed form. While many species seem to be able to find a suitable habitat within human environs, careful monitoring and selective management might be the only way to ensure that the less common pteridophytes do not gradually diminish and possibly disappear from Scotland altogether.

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Appendix 1

Authorities for Scientific Names

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Names of pteridophytes taken from Page (1982 & 1989b) with authorities and common names

Lycopodiaceae

Lycopodium annotinum L.	Interrupted Clubmoss
L. clavatum L.	Stag's-horn Clubmoss
Lycopodiella inundata (L.) Holub	Marsh Clubmoss
Huperzia selago (L.) Bernh. ex Schrank & Mart	Fir Clubmoss
Diphasiastrum alpinum (L.) Holub	Alpine Clubmoss

Selaginellaceae

Selaginella selaginoides (L.) Link	Lesser Clubmoss

Isoetaceae

Isoetes lacustris L.	Common Quillwort
I. echinospora Durieu	Spring Quillwort
I. histrix Bory	Land Quillwort

Equisetaceae

Equisetum hyemale L.	Dutch Rush
E. x trachyodon A.Br. (*E. hyemale x E. variegatum*)	Mackay's Horsetail
E. variegatum Schleicher ex Weber & Mohr	Variegated Horsetail
E. fluviatile L.	Water Horsetail
E x dycei C.N.Page (*E. fluviatile x E. palustre*)	Hebridean Horsetail
E. arvense L.	Common Horsetail
E. x litorale Kuhlew. ex Rupr. (*E. fluviatile x E. arvense*)	Shore Horsetail
E. pratense Ehrh.	Shade Horsetail

Equisetum x rothmaleri C.N.Page (*E.palustre x E. arvense*)	Ditch Horsetail
E. sylvaticum L.	Wood Horsetail
E. palustre L.	Marsh Horsetail
E. telmateia Ehrh.	Great Horsetail

Ophioglossaceae

Botrychium lunaria (L.) Swartz	Moonwort
Ophioglossum vulgatum L.	Common Adder's-tongue
O. azoricum C. Presl	Small Adder's-tongue
O. lusitanicum L.	Least Adder's-tongue

Osmundaceae

Osmunda regalis L.	Royal Fern

Adiantaceae

Cryptogramma crispa (L.) Hook	Parsley Fern
Anogramma leptophylla (L.) Link	Jersey Fern
Adiantum capillus-veneris L.	Maidenhair Fern

Hymenophyllaceae

Hymenophyllum tunbrigense(L.) Sm.	Tunbridge Filmy-fern
H. wilsonii Hook.	Wilson's Filmy-fern
Trichomanes speciosum Willd.	Killarney Fern

Polypodiaceae

Polypodium vulgare L.	Common Polypody
P. interjectum Shivas	Western Polypody
P. australe Fée	Southern Polypody

Hypolepidaceae

Pteridium aquilinum (L.) Kuhn	Common Bracken
Pteridium aquilinum (L.) Kuhn subsp. *latiusculum* (Desv) C.N. Page *comb et stat nov*	Northern Bracken
Pteridium aquilinum (L.) Kuhn subsp. *atlanticum* C.N. Page *subsp nov*	Western Bracken

Thelypteridaceae

Thelypteris palustris Schott	Marsh Fern
Phegopteris connectilis (Michx) Watt	Beech Fern
Oreopteris limbosperma (All.) Holub.	Lemon-scented Fern

Aspleniaceae

Phyllitis scolopendrium (L.) Newm.	Hart's-tongue Fern
Asplenium adiantum-nigrum L.	Black Spleenwort
A. billotii F.W.Schultz	Lanceolate Spleenwort
A. septentrionale (L.) Hoffm.	Forked Spleenwort
Asplenium ruta-muraria L.	Wall Rue
A. marinum L.	Sea Spleenwort
A. viride Huds	Green Spleenwort
A. trichomanes. L. subsp. *quadrivalens*	Common Maidenhair Spleenwort
A. t. L. subsp. *trichomanes* D.E.Meyer emend. Lovis	Delicate Maidenhair Spleenwort
Ceterach officinarum D.C.	Rusty-back Fern

Athyriaceae

Athyrium filix-femina (L.) Roth.	Lady-fern
A. distentifolium Tausch ex Opiz	Alpine Lady-fern
A. flexile (Newm.) Druce	Flexile Lady-fern
Gymnocarpium dryopteris (L.) Newm.	Oak Fern

G. robertianum (Hoffm) Newm	Limestone Oak-fern
Cystopteris fragilis (L.) Bernh.	Brittle Bladder-fern
C. dickieana Sim	Dickie's Fern
C. montana (Lam) Desv.	Mountain Bladder-fern
Woodsia ilvensis (L.) R.Br.	Oblong Woodsia
W. alpina (Bolton) S.F.Gray	Alpine Woodsia

Aspidiaceae

Polystichum lonchitis (L.) Roth.	Holly Fern
P. aculeatum (L.) Roth.	Hard Shield-fern
P. setiferum (Forsk) Woynar	Soft Shield-fern
Dryopteris oreades Fomin	Mountain Male-fern
D. filix-mas (L.) Schott	Male-fern
D. affinis subspecies (Lowe) Fras-Jenk.	Golden-scaled Male-ferns
D. aemula (Ait) Kuntze	Hay-scented Buckler-fern
D. cristata (L.) A.Gray	Fen Buckler-fern
D. carthusiana (Vill) H.P.Fuchs	Narrow Buckler-fern
D. dilatata (Hoffm) A.Gray	Broad Buckler-fern
D. x deweveri (Jansen) Jansen and Wachter (*D. carthusiana x D. dilatata*)	Hybrid Narrow Buckler-fern
D. expansa (C.Presl) Fras-Jenk &Jermy	Northern Buckler-fern

Blechnaceae

Blechnum spicant (L.) Roth	Hard Fern

Marsilleaceae

Pilularia globulifera L.	Pillwort

Appendix 2

Ages of *Calluna* stems from the selected areas on Ben Vrackie

0a	22	21	27	17	21	28	30	26	28	19
0b	41	30	20	28	19	19	24	16	24	31
0c	36	19	25	32	21	16	21	26	25	24
0d	14	15	14	28	24	9	17	18	30	23
1a	26	32	35	21	33	34	27	25	37	30
1b	9	8	10	11	9	12	7	9	7	12
1c	29	20	22	25	24	32	26	14	12	22
1d	12	19	15	12	18	17	20	21	12	24
2a	15	21	20	17	20	20	24	18	24	23
2b	18	13	11	10	14	10	17	17	9	21
2c	8	7	5	7	7	8	6	5	8	5
2d	9	18	12	18	12	14	12	9	19	18
3a	8	8	7	8	8	8	8	8	5	5
3b	13	12	9	7	9	7	6	8	11	7
3c	8	8	7	8	8	9	9	5	9	14
3d	13	14	20	20	19	26	18	21	17	26

Appendix 3

Species Found in Selected Areas During the First Study

Table 1 Species Found in Areas which had Not Been Burnt

Symbols ● = Abundant ■ = Frequent ▲ = Occasional ✚ = Local

	0a	0b	0c	0d
Oldest date of *Calluna* stems	1960	1949	1954	1960
Calluna vulgaris	90%	95%	80%	75%
Erica cinerea	■	▲	▲	■
Grasses and Sedges	■	✚	10%	■
Athyrium filix-femina			■	
Blechnum spicant	■		■	▲
Dryopteris affinis	▲			▲
E. sylvaticum			▲	
Lycopodium clavatum				●
Oreopteris limbosperma	■		■	▲
Selaginella selaginoides	■			
Alchemilla vulgaris			▲	▲
Anemone nemorosa			▲	▲
Campanula rotundifolia		▲	▲	
Cirsium palustre	▲			▲
Drosera rotundifolia	▲			▲
Erica tetralix	▲		■	
Filipendula ulmaria	▲			
Fragaria vesca			▲	
Galium verum		▲		
Galium saxatile	▲	▲	▲	
Hypericum pulchrum		▲		▲
Lathyrus montanus	▲		▲	▲
Listera cordata		▲		
Lysimachia nemorum			▲	▲
Myrica gale	10%			
Narthecium ossifragum	▲			
Oxalis acetosella	▲		▲	▲
Pinguicula vulgaris	▲			
Polygala serpyllifolia	▲			
Potentilla erecta	▲	▲	▲	▲
Rhinanthus minor			▲	
Salix aurita				▲
S. caprea				▲
Saxifraga azoides	▲			▲
Succisa pratensis	▲			▲
Sorbus seedling		▲		
Vaccinium. vitis -idaea				▲
Veronica officinalis			▲	▲
Viola riviniana	▲	▲	▲	
Total number of species	22	11	20	22

Table 2 Species Found in Areas which had Been Burnt Once

Symbols ● = Abundant ■ = Frequent ▲ = Occasional ✚ =Local

Species	1c pre-1946	1a pre-1959	1d pre-1965	1b pre-1976
Date of oldest *Calluna* stems	1958	1953	1966	1978
Calluna vulgaris	70%	80%	75%	40%
Erica cinerea	10%	▲	▲	40%
Grasses and Sedges	▲	▲	✚	▲
Blechnum spicant	▲	▲	▲	✚
E. sylvaticum	■			
E. pratense	■			
Lycopodium clavatum	■		✚	
Oreopteris limbosperma		▲		
Pteridium aquilinum	▲			
Ajuga reptans	▲			
Anemone nemorosa		▲		▲
Arctostaphylos uva-ursi	▲			
Betula seedling				▲
Campanula rotundifolia	▲	▲		▲
Digitalis purpurea	▲			
Erica tetralix		▲		▲
Galium saxatile		▲		
Hypericum pulchrum	▲	▲	▲	
Listera cordata	▲		▲	
Lotus corniculatus			▲	▲
Potentilla erecta		▲	▲	
Rhinanthus minor		✚		
Sorbus seedling		▲		
Succisa pratensis		▲	▲	
Vaccinium myrtillus	▲			
V. vitis -idaea	▲			▲
Veronica officinalis	▲	▲		▲
Viola riviniana	▲	▲	▲	▲
Total number of species	17	16	11	12

Table 3 Species Found in Areas which had Been Burnt Two Times

Symbols ● = Abundant ■ = Frequent ▲ = Occasional ✚ =Local

Species	2a	2b	2c	2d
	pre-1959 1965	pre-1946 1965	pre-1946 1976	pre-1959 1965
Date of oldest *Calluna* stem	1965	1969	1980	1970
Calluna vulgaris	80%	95%	40%	90%
Erica cinerea	▲	▲	40%	▲
Grasses and Sedges	5%	▲	10%	▲
Athyrium filix-femina		✚		
Blechnum spicant	▲	▲	✚	▲
Lycopodium clavatum		●	✚	▲
Oreopteris limbosperma	▲	▲		
Pteridium aquilinum		▲		
Anemone nemorosa			▲	
Betula seedling			✚	
Campanula rotundifolia	▲	▲	▲	▲
Drosera rotundifolia	▲			
Erica tetralix	▲	▲		
Galium verum		▲		
G. saxatile	▲		▲	
Hieracium sp			▲	
Hypericum pulchrum	▲			▲
Lathyrus montanus		▲	▲	
Listera cordata		▲		
Lotus corniculatus		▲	▲	▲
Myrica gale	●			
Pinguicula vulgaris	▲			
Potentilla erecta	▲	▲	▲	▲
Taraxacum sp		▲		
Viola riviniana	▲	▲	▲	▲
Total number of species	13	17	14	10

Table 4 Species Found in Areas which had Been Burnt Three Times

Symbols ● = Abundant ■ = Frequent ▲ = Occasional ✚ = Local

Species	**3a**	**3b**	**3c**	**3d**
	pre-1959 1965 1976	pre-1946 1965 1988	pre 1946 1959 1988	pre 1946 1959 1965
Dates of oldest *Calluna* stem	1982	1977	1976	1964
Calluna vulgaris	40%	10%	30%	■
Erica cinerea	40%	20%	30%	■
Grasses and Sedges	▲	20%	10%	50%
Athyrium filix-femina				▲
Blechnum spicant		▲		▲
Dryopteris affinis		▲		
Equisetum palustre			▲	▲
E. sylvaticum				▲
Lycopodium clavatum		▲		
Oreopteris limbosperma			▲	▲
Pteridium aquilinum	▲			
Ajuga reptans			▲	▲
Anemone nemorosa		▲		
Betula seedling		▲		
Campanula rotundifolia	▲	▲		
Cirsium palustre			▲	▲
Digitalis purpurea		▲		
Drosera rotundifolia			▲	▲
Erica tetralix	▲	30%	■	●
Galium saxatile	▲			
Hypericum pulchrum		▲		▲
Lathyrus montanus				▲
Listera cordata		▲		▲
Lotus corniculatus	▲	▲		
Myrica gale			■	●
Narthecium ossifragum			■	▲
Pedicularis palustris			▲	▲
Pinguicula vulgaris				▲
Polygala serpyllifolia			▲	
Potentilla erecta		▲	▲	▲
Prunella vulgaris			▲	
Succisa pratensis				▲
Sorbus seedling		▲	✚	
Taraxacum sp			▲	
Trientalis europaea				▲
Vaccinium myrtillus		▲		
Viola riviniana			▲	▲
Total number of species	8	17	18	23

Appendix 4

An index of Scottish summers taken from Blair (1980) including notes on own data

Blair used a formula to combine temperature, sunshine and rainfall measurements to give an index value. These values were then divided into five quintiles indicating the following conditions:

1 = A very cold dull and wet summer
2 = Cooler and wetter than average
3 = An average summer with average rainfall and sunshine
4 = Warmer and dryer than average
5 = * Very warm sunny and dry

Year	Value	Year	Value	Year	Value	Year	Value
		1890	1	1900	2	1910	2
1881	1	1891	3	1901	5 *	1911	5 *
1882	2	1892	1	1902	1	1912	1
1883	2	1893	5 *	1903	2	1913	4
1884	4	1894	2	1904	5 *	1914	5 *
1885	4	1895	2	1905	5 *	1915	4
1886	4	1896	1	1906	4	1916	2
1887	5 *	1897	4	1907	1	1917	4
1888	1	1898	4	1908	3	1918	3
1889	3	1899	5 *	1909	3	1919	4
1920	3	1930	3	1940	4	1950	4
1921	5 *	1931	1	1941	3	1951	3
1922	1	1932	4	1942	2	1952	3
1923	2	1933	5 *	1943	2	1953	3
1924	1	1934	4	1944	4	1954	1
1925	5 *	1935	4	1945	4	1955	5 *
1926	5 *	1936	5 *	1946	1	1956	1
1927	2	1937	3	1947	5 *	1957	2
1928	1	1938	2	1948	1	1958	2
1929	2	1939	5 *	1949	5 *	1959	4

Year	Value	Year	Value				Year	Kind	Edin
1960	4	1970	3	Own	data		1980	4	4
1961	1	1971	3		Kind	Edin	1981	4	3
1962	2	1972	3				1982	4	3
1963	1	1973	4	1973	4	4	1983	5*	5*
1964	2	1974	3	1974	3	3	1984	5*	5*
1965	1	1975	5*	1975	5*	5*	1985	1	1
1966	3	1976	5*	1976	5*	5*	1986	4	2
1967	3	1977	5*	1977	4	2	1987	3	2
1968	3	1978	2	1978	4	2	1988	2	2
1969	5 *			1979	3	4	1989	4	4

Blair's weather index was calculated up to 1978 and a further decade was added from local information. It was calculated separately for Edinburgh and Kindrogan Field Study Centre which is near Ben Vrackie. Rainfall and temperature measurements were provided by the Meteorological Office in Edinburgh and the recording station at Kindrogan. Daily measurements for the three summer months of June, July and August were averaged for each year, and then all the measurements were divided into five approximately equal bands numbered from 1 to 5. 5 represented high temperatures and low rainfall. The two values for temperature and rainfall were then averaged for each year. The original quintiles included hours of sunshine but this information was not available from Kindrogan.

There is sometimes quite a large difference between the values in Edinburgh and Perthshire, as might be expected between geographically different areas. Blair's quintiles was calculated from measurements covering the whole of Scotland. Usually the most extreme years are similar and correspond reasonably well to the Blair values where they overlap.

Appendix 5

Table 1 showing ring counts on 10 stems collected within quadrats 1-40 for the second study

Quadrat	1	2	3	4	5	6	7	8	9	10
1	33	24	15	15	32	24	15	21	20	18
2	29	32	22	26	20	24	20	19	29	30
3	11	7	8	9	7	6	6	6	8	7
4	10	12	16	10	16	21	10	11	16	12
5	15	16	17	25	20	15	19	16	19	27
6	29	18	15	34	17	13	18	18	26	22
7	5	4	4	3	3	4	3	2	3	3
8	8	6	6	8	8	8	6	9	9	8
9	11	10	8	11	9	8	7	8	6	7
10	14	15	22	20	19	23	17	13	12	21
11	28	28	27	16	19	33	30	22	24	18
12	12	18	9	15	18	18	17	10	20	10
13	10	17	18	10	12	16	9	8	8	11
14	9	8	10	10	10	10	9	10	7	9
15	7	7	7	8	7	7	7	6	6	6
16	4	5	3	2	5	2	3	2	2	3
17	20	20	19	13	15	20	17	22	20	18
18	10	8	9	11	10	11	11	6	7	11
19	25	28	25	38	30	24	27	18	28	30
20	24	20	15	27	18	19	21	20	25	20
21	20	16	21	24	21	19	22	21	21	20
22	5	5	6	6	4	7	7	5	6	4
23	17	26	10	13	17	21	20	16	11	11
24	24	19	25	24	25	30	32	25	18	31
25	6	16	20	10	15	18	12	18	18	20
26	8	12	11	8	11	10	8	13	4	7
27	14	9	10	11	8	11	7	6	8	14
28	13	10	12	9	13	10	10	13	12	10
29	8	11	10	10	9	11	11	11	11	15
30	14	15	15	10	12	11	12	10	16	11
31	17	30	25	16	23	29	16	13	19	23
32	15	11	12	16	15	10	11	8	13	11
33	11	9	19	11	10	9	12	9	12	10
34	18	18	19	15	16	17	19	14	15	16
35	6	9	11	10	11	10	10	13	8	7
36	12	16	11	12	10	16	12	18	10	10
37	17	27	22	18	16	20	33	17	22	25
38	20	13	9	10	10	15	11	12	9	10
39	6	8	10	4	5	5	6	7	7	4
40	5	5	6	5	4	6	6	6	11	4

Table 2 showing ring counts on 10 stems collected within quadrats L1-L15 for the second study

Quadrat	1	2	3	4	5	6	7	8	9	10
L1	18	12	19	15	12	17	20	21	12	24
L2	13	12	9	7	9	6	8	11	7	7
L2	0	0	0	0	0	0	0	0	0	0
L4	8	8	12	9	7	10	8	13	10	14
L5	13	15	12	11	9	15	9	11	12	10
L6	18	13	11	14	10	10	17	17	9	21
L7	26	29	20	22	25	33	27	27	15	13
L8	19	13	19	13	15	13	15	10	13	19
L9	15	16	15	29	25	10	18	19	31	24
L10	7	7	8	9	7	9	7	6	8	7
L11	8	10	9	12	10	8	12	9	8	8
L12	18	23	25	24	17	20	16	23	12	18
L13	5	4	4	3	3	4	3	2	3	3
L14	5	4	4	3	3	4	3	2	3	3
L15	11	9	8	9	7	6	6	6	8	7

Appendix 6

Table showing extreme weather conditions in Scotland

Location	Floods	Frost	Drought	Gales	Early Spring	Bad Harvests	Snow
Dornoch				1605			
General				March 1625			
General		1604-1605					
General					1652		
General				1658			
General		March 1665					
General		Sept. 1665					
Cromarty				Dec 1674			
Central Scot.		July 1684					
Central Scot		Oct 1684					
General				Dec 1679			
General						1690s	
General					1700s		
General				Nov 1703			
Europe		1709-1710					
Europe		Sept 1709					Oct 1709
Central Scot		1715					
Central Scot		1739					
Local				1739			
General						1740	
North-west				1737			
General				1745			
General				1748			
South-west				1756			
General						1757	
General				1763			
General				1764			
General		1769					
General				1773			
General	1775						
General				Jan 1781			
General		1782					
General		1783					
General				1786			
General				1790			
North-west				1791			
General		1794-1795					1794-1795
South-west				Jan 1796			
Aberdeensh				Dec 1799			
Ballater	Aug 1799						
Sutherland				Dec 1806			
General		1807					
General					1809		
River Dee	1812						
General	1814	1813-1814					
General		1816-1817				1816-1817	
General			Sept. Oct. 1817				
General		Sept 1818					
General			1825				
General			1826	1826			
General			1827				1827
Morayshire	1829						

Location	Floods	Frost	Drought	Gales	Early Spring	Bad Harvests	Snow
West				1835			
General		1836					
General		1837					
General		1838		1838 x 2	1838 but late frost		
General				1839			
South west			1842				
South east	1846						
Perthshire	Oct. 1847			Apr 1847			
General						1849 Wet summer	
General		May. 1850					
Tweed		Aut 1853					
General		1860-1861		Oct. 1860			
General			1865				
North				1865			
General	1868			Jan. 1868			
General				Spring 1874			
General		1878-1879		Dec. 1879			
Perthshire		1880-1881		Oct 1881			
General				Jan. 1882			
Perthshire				March.1883			
General				1884			
General			1887 Hot dry				
General		1891	1891				
Galloway				1892			
General	Feb. 1893		Summer 1893	Nov 1893			
Perthshire		1894-1895					
General	Feb. 1894	May 1894	1894	1894			
General			1896				
Edinburgh			1902				
Perthshire	Jan. 1903						
East coast				1903			
General			1911	1911			
General				1912			
Perthshire	May and Aug. 1913		1913				
General				1915			
Edinburgh	1916						
General		Spring 1919					
General				1932			
South east	1948						
General				Dec. 1949			
General				Dec. 1951			
General				Jan. 1953			
East coast	1953						
General				1957			

The conditions indicated at a given locality might have covered the whole of Scotland, not merely the areas indicated.

Sources: Adams (1980), Anderson (1967), Brien (1989), Caird (1980), Coates (1923), Hunter (1883), Miller, (1887), Lamb (1966), Parry (1980), Smith (1982,) and Whyte (1980).

DID THE DANES SHARPEN THEIR SWORDS AT EMBO?

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An unusual colony of *Equisetum hyemale* (Dutch Rush) was discovered by R.E.C. Ferreira growing in an uncommon habitat on calcareous sand-dunes near the village of Embo in Sutherland in the north-east of Scotland. The shoots throughout this colony are more slender and prostrate than the typical British form which is much thicker and more upright. This decumbent form is unusual and seems to be a genetically adapted sand dune ecotype. It is not known from anywhere else in Britain other than at this site. Page (1988: 118-119) noted the resemblence of plants at this site alone to Danish material which grows in similar habitats in Denmark.

While Denmark is georgraphically not very far away, the distance is perhaps too far to expect floating fragments of *E. hyemale* to survive. Experiments by Page and Barker (1985) showed that fragments could survive for up to three days in sea water and still grow thereafter. Evergreen horsetails in particular do grow very readily from vegetative fragments, but it also seems possible that this could be an ancient introduction. A reference by Thomas Pennant in his Tour of Scotland in 1769, opens an interesting line of speculation as to its introduction. He referred to a battle at Embo in 1259 between the Earl of Sutherland and the Danes (p. 168). During this period there were, of course, repeated attacks by Vikings, including the Danes, all round the coast, but especially in the north and west. This particular battle came near the end of a long series of raids in the immediate area which allows for many possible introductions. This, therefore, raises the possibility that the plant could have been thus introduced directly by this route from Denmark.

But why, one might ask, would the Danes want to carry quantities of *E. hyemale?* It has several uses. During the Middle Ages the Dutch Rush was imported from Holland for use in scouring and polishing (Page 1988:24). It was used like sandpaper and one can perhaps envisage that it was used for the necessary restoration of blades which had suffered from a damp sea-journey. Discarded fragments thrown overboard could easily survive long enough to be washed ashore and take root. As Embo is on the east coast it is perhaps helpful to imagine that the *E. hyemale* may have been freshly gathered shortly before leaving Denmark and had not been in transit long enough to have lost the ability to grow. This may account for its absence from the west where there are other suitable habitats.

A further possible use of this horsetail arises from an account in the appendix of Pennant's travels (p339) where the writer said that the invading Danes were all "cut to pieces". Another use of horsetails was for staunching wounds. *Equisetum arvense* was the usual species used for this purpose but *E. hyemale* may have been pressed into service especially at a battle site such as Embo. We will probably never know exactly how the plant was introduced. We can imagine some of the Danes escaping, without their leader who was killed, scattering fragments of *E.hyemale* as they fled. Or perhaps they were all killed and only their boat was left to rot among the sand-dunes while *E. hyemale* made itself at home? Perhaps there had been an occasion when a raiding party had buried their own casualties. It may have been thought appropriate to leave the slain with a supply of *E. hyemale* to polish their swords in the after-life, thus planting it for posterity. The colony grows quite near to the present village. If there had been an earlier settlement it may be that some of the Danes had colonised the area and deliberately planted the species.

Without a detailed genetic comparison a more precise link between this anomalous colony and Denmark cannot be absolutely proven. But there does seem to be a high possibility that the plant may have been introduced by Danish Vikings. By any of the above means the shoots took root and established a colony which has survived for seven

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or eight hundred years. Any human Danish influence became incorporated into the local community, but this horsetail population seems to have retained its distinctive features.

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Pteridophytes as Indicators of Landscape Changes in the British Isles in the Last Hundred Years

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Introduction

The pteridophyte flora of the British Isles, like that of its flowering plants (e.g. Walters, 1984), is small in comparison with that of Europe as a whole. But as with the bryophytes of these islands (Ratcliffe, 1968), it contains many unusually Atlantic elements within a European context, setting a theatrical stage into which more local species as well as an unusually large number of hybrids (Jermy *et al.*, 1978; Page, 1982b) have become important players within a European context.

The ways in which the major features of our overall landscape and vegetation have been influenced by man in Britain and Ireland, both before and during the past century, have been extensively studied (e.g. Hoskins, 1970; Godwin, 1975; Mitchell, 1976; Webb, 1983; Dimbleby, 1978, 1984; Rackham, 1980, 1986; Ratcliffe 1984). These studies provide a particularly valuable background against which to set an interpretation of the ways in which the pteridophytes have responded, in our insular environment, to the general habitat changes resulting (Page, 1988).

Within the last century, the changes which have affected the landscapes of the British Isles, and thereby influenced the habitats available to pteridophytes, have been many and various. Those discussed here are some of the more major of these, whose influences have been felt widely in these islands, and which have served either to destroy or modify previous pteridophyte habitats, or to gain a suite of new ones.

Even in a flora so small as that of these islands, however, there is, among the pteridophytes, a considerable but scarcely-appreciated potential indicator value to many specific facets of environmental change, the study of which provides a valuable scientific basis for integration into broader aspects of conservational issues and towards the formulation of future management plans for many of the environments and locations around us.

Changes in forest extent and type

A steady reduction in the amount of natural forest cover in the British Isles has proceeded ever since man first set foot in these islands, but perhaps never more rapidly than in the period under consideration. This increasing rate of loss of remaining natural and semi-natural forest areas through the last century has continued to extensively reduce the original habitats for many woodland ferns, not only by direct removal of tree cover, but also by drainage of the majority of areas of originally naturally wet woodland. Today, some of the best remaining semi-natural woodland habitats for pteridophytes persist especially along steep stream and river ravines, while flatter areas of wet woodland have severely diminished, of which the modern scarcity of narrow buckler fern (*Dryopteris carthusiana*) provides a particularly vivid indicator.

In contrast to the original diversity of native forest vegetation, within the modern uplands and on poorer soils at low altitude, extensive forestry plantations, typically of conifers such as Sitka spruce, have provided a new standardised forest of the 20th century. In these, trees are treated as crops, and are typically clear-felled on a rotational basis of about 40 years, from whence the cycle begins again. Few native plants either tolerate this cycle or successfully compete with the high and even-aged density with which the spruce is artificially set. The resulting occurrence of pteridophytes in these communities is seldom little more than the limited success of a few of the commoner woodland ferns along marginal ditches and rides, or the persistence of streamside communities along ravines, where a break in the dense and monotonous tree canopy allows necessary extra light.

In most cases, such forests have been responsible for loss rather than gain of pteridophyte biodiversity, especially for those species of natural wet heathlands. A particular pteridophyte indicator of such losses may well be marsh clubmoss (*Lycopodiella inundata*), which has almost certainly suffered from afforestation extending over its sites. In 1844 William Gawlee wrote on a herbarium specimen of this species (Glasgow University Botany Department) from the Carse of Arderries: *'Two miles east of Fort George is a moor now planted with wood, which will in a few years, I fear, make a radical reform in the Vegetable Kingdom of this locality'.* Webster (1978) recorded the similar demise of *Lycopodiella* from the Culbin sands. Earlier writers (Patton & Stewart, 1914, 1924) had recorded its presence in the dune slack areas but Webster saw it last in 1976 where it grew in seasonally inundated hollows, which had become more shaded and drier with tree upgrowth and forestry drainage.

Where rocks emerge in forests, small enclaves of existing sun-loving ferns are especially threatened by rapid tree upgrowth from dense conifer planting. There are also at least two sites in Scotland and one in Devon, for example, in which forked spleenwort (*Asplenium septentrionale*) is critically diminishing (in two of them already extinguished) through forestry planting (of Douglas fir in both Scottish sites, and Sitka spruce in Devon). In each of these cases, greater sensitivity to the existence of such already rare and localised species in initial forestry planting could well have saved them, at the expense, at each site, of only a handful of trees.

From the pteridophyte point of view, a conservationally more sensitive forest management policy for Britain would certainly be in not only awareness when planting of existing rare native species, but also of the overall progressive future construction of alternative forest types altogether. Conservationally infinitely more valuable would be ones of intermixed broadleaf and evergreen communities with wide planting-spaces and uneven-aged structures (mimicking the natural form of the majority of northern hemisphere forests of high latitudes), managing these forests on a principle of permanency of tree-cover, high contained and edge-effect habitat diversity, and sustained yield of more mature and more unusual timbers. In comparison with existing plantation tree-farms, such alternative forests have already successfully long existed, in limited extent, in the much more enlightened woodland plantings policy of many larger estates. Pteridophyte study in these habitats by the authors shows that, even when well-established and although artificial, such forest types do more typically come to contain a relatively rich assemblage of native fern species, including those of wetter habitats. They can also include more unusual elements, providing forest refuges for horsetails (notably wood horsetail, *Equisetum sylvaticum* [from Perthshire to Hampshire], but also shade horsetail, *E. pratense* in northern sites), as well as even for clubmosses (notably stag's-horn clubmoss, *Lycopodium clavatum* and alpine clubmoss, *Diphasiastrum alpinum,* in northern and western Britain) and interrupted clubmoss, *Lycopodium annotinum,* in at least one policy plantation pinewood in Perthshire. In these woodlands, the presence of woodland ferns, woodland horsetails and clubmosses, as well as the overall diversity of woodland flowering plants, mammals, insects and birds, provides particularly good indicators of the conservational value and status and potential for restoration of such managed woodland vegetation, in comparison with present nationally widespread tree-farm forests, from which conversion to such vegetation is yet possible.

Wetland drainage, losses of ponds, and changes in reservoir and lake-surface levels

The changes which have been wrought this century to wetland areas and standing waters of all kinds seem to be enormous, and have widely affected the few pteridophyte species associated with such habitats.

Wetland drainage

Drainage of natural wetland areas has occurred in lower-lying districts of the British landscape, either for gain of agricultural land or for peat extraction or for both, and has certainly widely affected some wetland pteridophyte frequency through wholesale destruction of entire habitats. Although the beginnings of this drainage long pre-date the last hundred years, nevertheless throughout this century demand for land and availability of appropriate machinery has enabled the process to continue with rapidly increasing momentum. Especially pteridologically affected have been species-rich fenlands in regions of Britain as far apart as south-western Scotland, Yorkshire, East Anglia, and the Somerset levels, and the rates of resulting losses of especially royal fern (*Osmunda regalis*), fen buckler-fern (*Dryopteris cristata*) and marsh fern (*Thelypteris palustris*) provide particularly apt pteridological indicators.

Ponds, reservoirs and lake-level changes

At the smaller end of the scale, ponds of all sizes have disappeared from farmland all over Britain, especially in post-1945 years, the speed of such processes probably stimulated by available agricultural grant-assistance. The pond losses have been ones largely of lowland Britain, with a relatively rapid loss of many muddy marginal habitats and consequent loss of the marginal plant species (as well as animal populations) dependent upon them. In some areas, however, notably in the Tertiary deposits of south and south-east England, new areas of water have also been created by flooding of former gravel extraction workings.

At the larger end of the scale, numerous old lake and former stream valleys have disappeared under new reservoir schemes, often destroying a whole diversity of pteridophyte stream-valley habitats beneath them. The new water levels, with initially often steep and rocky shorelines, by comparison are usually rather sterile pteridophyte sites, which have often only now scarcely begun to carve their own new habitats. The changes of the natural lake levels of the central Scottish Highlands by Scottish hydro-electric schemes of this century provide particularly vivid examples of quantifiable change. In 1950 at Loch Tummel, Perthshire, the level was raised by 17 feet (5.1 m), making its extent two miles (3.2 km) longer. The level of Loch Lyon was raised by 70 feet (21 m). Lochan Breaclaich was raised by 66 feet (nearly 20 m) and a completely new loch was created in Glen Lednoch. Lochan na Lairige was enlarged with a conspicuous dam between Ben Lawers and Meal nan Tarmachan. New lochs were created like Dunalistair, Loch Errochty and Loch Faskally while Loch Giorra and Loch Daimh were dammed and combined. There are nine power stations on the River Tummel and tributaries alone and other rivers have similar complexes (Taylor, 1979). In contrast to ponds, such reservoir changes are ones that largely (though not exclusively) change habitats of upland Britain, and similar examples can be found in the Pennines, central Wales and south-west England.

All of these changes have had both negative and positive effects on pteridophytes, with some of the losses partly offset by changes in range of other aquatic pteridophytes, including the horsetails and quillworts. Around larger bodies of water especially, the horsetails (*Equisetum* spp.) and their hybrids provide particularly useful indicators of change. Temporary low levels in a reservoir can provide sites for the germination of *Equisetum* spores (Page, 1967), and the occurrence of different shoreline hybrid horsetails can provide good pteridophyte indicators of different degrees and periodicity of shoreline disturbance. Quillworts (*Isoetes* spp., notably *I. echinospora*) may have increased their overall range, perhaps carried as spores to new reservoirs on the feathers of migrating water fowl (Page, 1982a). But for many such landscape modifications, a particularly sensitive pteridophyte indicator of change seems to be the pillwort, *Pilularia globulifera*.

In the last hundred years in the lowlands, *Pilularia globulifera* has widely disappeared, surviving mainly only in districts where ponds have persisted more widely, such as in the Hampshire basin. The species also seems to have shown particularly wide-range changes in Scotland, disappearing in many smaller ponds but appearing in some of the newer water areas created, where its appearance is often associated with the steady re-accumulation of new lakehead silt habitats resulting from abrupt alterations in the original water level around new reservoirs and lochs. The water level of Loch Tummel, for example, was raised in 1950, and *Pilularia* was recorded from the new lakehead habitats evolving in 1965 (and has persisted since), when it had not previously been known in the loch. It also occurs in deeper water off-shore from the main colony. This seems to be the mode of growth which has been adopted in several of the deeper lochs, while in naturally shallower ones, it has sometimes formed more extensive carpets. In Kirkcudbrightshire, for example, when Jordieland Loch was drained for maintenance in 1960, the shore was found to be abundantly covered with *Pilularia*. Loch Ken in the same area, which was formed by damming the river, was found under similar circumstances to have *Pilularia* growing on the former river banks which had been inundated (Stewart, 1988).

Agricultural landscape changes

Throughout the period under consideration, there has been a very general tendency for a landscape change from smaller, more diversified farms, to fewer, larger, more intensive ones, widely across Britain (less so in Ireland), and this trend has been increasingly heightened in the post Second World War period through to today. Some of the most obvious of these changes are in the widespread losses of ponds (see above) and the similar losses of woodland and hedgerow habitats (the latter themselves miniature remnant woodland environments) and their marginal zones, which have accompanied these changes (e.g. Clapham, 1953; Hooper, 1970, 1974). Other less obvious ways in which pteridophytes have been influenced by steady agricultural intensification have been through ploughing of old pastureland and water-meadow sites; in subtle changes in grazing regimes which have had particularly profound effects on pteridophyte survival; and in the practice of moorland burning ('muirburn' in Scotland). Because of the large area of the land surface of Britain devoted to agriculture (78% in 1978, Poore, 1985:191), these processes have often had particularly widespread effects on the diminishing survival of an exceptional range of pteridophyte communities, while the effect of grazing regimes and moorland burning both spread well beyond that of land classified as agricultural.

Losses of old pasture

According to Poore (1985), of the 78% of Britain's land surface devoted to agriculture, 48% is grassland. The pteridological importance in these islands of the turf of old, semi-natural pasture grasslands is that, in appropriate sites, these are the most ideal (and over large areas, almost the exclusive) habitats for the success of especially adder's tongue (*Ophioglossum vulgatum*) and moonwort (*Botrychium lunaria*). Both of these ancient ferns seem to have been widely known as regular and sometimes abundant members of grassland communities in the lowlands of Medieval England (Page, 1988), and both of these plants have certainly widely disappeared from many of their former sites.

Ophioglossum vulgatum still survives, however, in undisturbed sites, and its present habitats are probably mostly those which have persisted over a very long period of human history in these islands. It is especially typical of old, level, low-lying, unploughed, moist, grassy meadows, developed over deep, often heavy and usually markedly basic soils, and of old, moist, water-meadows and pastures in the rural lowlands of central and southern England, which have evolved a good species diversity. It is a species of the slight hollows which fill with rain, and it can consequently sometimes be characteristic of the damper, greener turf of the furrows in old ridge-and-furrow pasture. By contrast, *Botrychium lunaria* is a less gregarious species than adder's tongue, seldom forming such dense or numerous colonies, and occurring more often as rather more scattered individuals throughout lightly-grazed, grassland turf. In both genera, the materials supplied by the mycorrhizal fungal associates are probably largely derived from the steady soil breakdown of dead organic material deriving from many of the other plants in the neighbouring grassland sward, perhaps especially the grasses. Such steady states of dynamic equilibrium are probably built up only gradually over long periods of time, but can be rapidly destroyed by sudden external disturbance.

Both *Ophioglossum* and *Botrychium* are consequently particularly easily killed in agricultural grassland by break-up of their colonial structure, and typically catastrophically so by sudden ploughing, herbicide treatment and re-seeding of old meadow and pasture grasslands, although these species, and especially Ophioglossum, seem able to persist through slower, more natural, grassland changes. To judge from 19th century flora narratives and herbarium specimens, very much of this loss, of which these two plants are probably among the most sensitive indicators, has occurred mainly through the last century.

Intensity of grazing pressures

Increasing intensity of agricultural grazing pressures has also heavily influenced the distributions of many pteridophytes, in a considerable range of habitats. This includes not only the more managed grazing by cows and sheep, but also that of fluctuating rabbit populations and, in appropriate (especially upland) areas, that of increasing populations of deer. None of these animals are new, of course, but over the last century, the factor which has changed is, in most cases, one of degree (e.g. Hunter, 1962).

Many pteridophytes appear to provide especially sensitive and hence valuable indicators of such short- and long-term intensity of grazing pressures, occasionally in positive but more usually in negative ways, which can be especially seen in habitats which are marginal to lowland agriculture, and thereby act as important refuges for pteridophyte diversity. For although ferns may not seem to be very palatable, their susceptibility in spring when flushing tender, succulent croziers for the whole season's fronds is especially great. Such times coincide with a season when other forage may be at a premium.

Further, the evergreen ferns and the evergreen horsetails (notably dutch rush, *Equisetum hyemale*, but also variegated horsetail, *E. variegatum*) appear to be grazed heavily in winter when other vegetation is also scarce. Our observations show that in captivity, rabbits, for example, can eagerly seek and totally consume the shoots of *E. hyemale* and *E. variegatum*) in winter, to a degree which suggests that these might be important items of their diet when available in the field. Field evidence indicates that *E. hyemale* is also consumed out of existence by cattle grazing, wherever such stock has the opportunity to eat it (Page, 1988), and presumably so also, in more upland areas, by the much more omnivorous deer. Much of the halving of the abundance of *E. hyemale* in Britain in the last hundred years, especially throughout agricultural counties (see Jermy *et al.*, 1978:14), we attribute largely to exposure to increasing pressure of grazing of all sorts. Personal observations have also shown that water fowl may browse horsetails, notably water horsetail (*E. fluviatile*) in the nesting season, and recent evidence from ornithological research has also come to the fore that independently suggests that horsetails form an important source of food for migrating geese, these birds obtaining an energy-important fatty acid (linoleic acid) essential during migration flights, as well as a valuable source of protein, from these ancient plants (Thomas & George, 1975; Thomas & Prevett, 1982; Fox, pers. comm. 1990).

In the field, effects of grazing are always insidious, and hence the absence of a plant through grazing pressure is clearly difficult to prove. Such grazing pressures over the last century have almost certainly had especially widespread long-term effects on our native woodlands (e.g. Morgan, 1936; Peterken, 1974; Perring, 1974; Rackham, 1976; 1986), as well as upland vegetation (e.g. Tansley, 1939, 1949; Pearsall, 1950; Raven

& Walters, 1956; McVean & Ratcliffe, 1962; Gimmingham, 1964; King & Nicholson, 1964; Ratcliffe, 1977; Sydes & Miller, 1988; Mardon, 1990), and especially on the pteridophyte species within each of these major vegetation units. Many specific examples of recovery in pteridophyte abundance with sudden reversal in grazing regimes do, however, exist, which certainly show direct cause-and-effect linkages - in the case of rabbit-grazing, especially following the abrupt and widespread decimation of rabbit populations in the late 1950s through the outbreak of myxomatosis (Thomas, 1963).

Especially in coastal and other unploughed lowland vegetation, all three species of native *Ophioglossum* provide examples of good pteridophyte indicators of grazing regimes. In these cases, under low grazing pressure, all may be helped to succeed by removal of competing upgrowth. A particular case in point here is the loss of sites for *Ophioglossum lusitanicum* in the Channel Islands (McClintock, 1975) through the alternative upgrowth of invading gorse. Further Rackham (1986) described the brief luxuriance of *Botrychium* in Breckland after the demise of the rabbits, but as taller grasses grew more successfully the *Botrychium* suffered from excessive shading. Further, in a study of rabbit-free vegetation in Norfolk, White (1961) reported that *Polypodium vulgare* had spread markedly on old dunes since the rabbits departed. Personal observations have shown too, in the presence of grazing on the Kirkudbrightshire coast, that this latter species flourishes especially on the mounds created by active nests of ants, which appear if disturbed, and it seems possible that the plant here gains a grazing defence against herbivore depredations by its associations with such sites. These are instances of probably much more widespread phenomena in which, in some habitats, light grazing pressure may maintain a critical ecological balance, whereas in others any grazing may be harmful, and clearly much more research is yet needed.

In more upland and inland woodland areas too, high differential susceptibility of different pteridophytes to different grazing pressures, appears to exist. There is extremely little literature on this, but we believe it to be an extremely profound and widespread phenomenon, in which the potential indicator value of pteridophytes has been little appreciated. Independent observations by both authors in Highland Scotland, but especially in Perthshire, for example, have shown that such upland species as *Dryopteris affinis* can be especially heavily and extensively grazed in some seasons, probably by both roe and red deer. Other species seem to be less attractive, but *Athyrium distentifolium* [var. *distentifolium* Ed.] appears to be another extremely grazing-susceptible species. It has previously, for example, also been described (from Caenlochan) as a fern which had been *'much disfigured through being eaten down by the deer'* (Cowan, 1911:173), and personal observations suggest that this can be so in many of its sites. As well, *Oreopteris* and *Polystichum* are particularly frequently browsed by deer, the latter especially throughout the winter months. Such grazing factors are probably extremely important ones in limiting surviving populations especially to grazing-inaccessible ledges or under boulders (especially all upland *Athyrium*) and to deep holes in block scree (especially both upland species of *Polystichum*) (Ratcliffe, 1977; Page, 1988).

In other native woodland habitats, personal observations also suggest widespread changes in pteridophyte vegetation to have taken place especially in the last century as a result of grazing pressures of larger herbivores, and that this is true of different animal pressures in many types of woodland and forest (*cf.* also Peterken, 1981). In native pinewood vegetation, for example, in many areas of Speyside, where deer grazing is especially heavy, almost all ferns (except bracken) are notably absent over large areas in which appropriate habitats are manifold, and these areas appear to coincide with ones where winter grazing of large populations of deer is especially heavy. Experimental grazing-exclosure areas show how both fern regeneration (as well as that of pine and often juniper) is held constantly in check by such grazing pressure. Once excluded, all these plants recover. In native oak woodland vegetation too, personal observations show a similar picture. In south-west Irish oak wood vegetation known to be one in which atlantic species of pteridophytes can potentially thrive in particular abundance (e.g. Kelly, 1981), personal observations show that today, apart from bracken, there is a surprising dearth of common woodland ferns through substantial areas of these woods. Within limited grazing-exclosure sites established for experimental purposes, however, there is by contrast vigorous regeneration of those ferns which are largely absent in the grazed areas. These include especially hard fern (*Blechnum spicant*), hay-scented buckler-fern (*Dryopteris aemula*) and woodland lady-fern (*Athyrium filix-femina*). Where grazing is excluded, furthermore, there develops also a good natural suppression of invading bracken by seedling tree upgrowth. Almost certainly, a similar general suppression of fern growth is today apparent, but scarcely appreciated, in many of our woodlands, including especially virtually all of our Royal Forests, with consequent spread of bracken and steady depletion of their pteridophyte biodiversity.

Indeed, bracken, *Pteridium aquilinum*, has spread extensively in all types of marginal land extensively in the last century, almost certainly largely as a result of grazing and supplemented through a combination of this with moorland burning (Watt, 1955; Burnett, 1964; Page, 1972). Bracken appears to be a unique indicator of such pressures in our island climate (Page, 1972, 1989, 1990b), while the density and extent of bracken is itself ultimately inclement to the success of most other pteridophyte species in competition with it. Much of the grazing pressure in this case is that of sheep.

Sheep have played an important role in British agriculture since the Middle Ages, when they were widely kept in lowland England. Large scale upland sheep farming probably began in the Pennines in the 12th century, spreading gradually to other areas, and reaching the Scottish Highlands in the late 18th century (Coppock, 1968, 1971). In Britain as a whole, sheep populations probably reached a peak about the 1870s; thereafter they declined somewhat in England (Hart, 1956). In Scotland, increasing populations of sheep in the 18th and 19th centuries, however, largely displaced cattle (Watson, 1932; Fraser-Darling, 1955), and agricultural observations suggest that it has been mainly over the last century that upland pastures have become heavily invaded by bracken, with sheep grazings even in the early part of this century not uncommonly becoming halved in extent in 40 years (Long & Fenton, 1938).

Similarly in Wales, areas of bracken have been estimated to have doubled in 30 years, with, in Britain as a whole, a loss rate of agricultural land to bracken of 10,360 ha per year (Taylor, 1980, 1985). Such reduction in pasture size has almost everywhere resulted in the even heavier grazing pressure of the same number of sheep (Coppock, 1964, 1971) on the progressively smaller bracken-free areas remaining - a vicious circle of events that has probably contributed increasingly in the last century, to the momentum of bracken's further spread (Page, 1982a, 1986).

Moorland burning

The intensity and extent of upland moorland burning through the last century, for the management of upland deer and grouse shootings, has certainly enhanced this rate of bracken spread, while also serving to remove other pteridophytes which are characteristically associated with old unburned heather moorland. These include especially widespread and often total losses of virtually all the clubmoss species (but notably stag's-horn clubmoss (*Lycopodium clavatum*) and fir clubmoss (*Huperzia selago*)) from areas which are burned on the most regular cycle. This subject, which has no previous literature, is under current conservational study in Edinburgh, and will be the subject of a future report.

Thus these agricultural changes of the last century, and especially those of more recent years, have, as a whole, probably had a more far-reaching effect on diminishing pteridophyte survival in these islands through a greater range of original habitats, than have most other factors added together. Unlike those considered below, the intensity of modern agriculture has further ensured that its processes have themselves added virtually no new habitats of pteridological importance to our landscape. Perhaps opportunity now exists, under the present policies of 'set-aside' and dual-use agricultural land, to begin to redress, if even on a local scale, some of the more profound of the last century's changes.

Landscapes of mineral extraction

The geological composition of the British Isles is extraordinarily diverse, with rocks which not only include some of every known geological era, but also ones of a wide variety of sedimentary, metamorphic and volcanic origins. Between them, these include rocks of acidic, neutral, basic and ultrabasic character. This diverse matrix beneath our feet has ensured an equal diversity of mineral content, and wherever any of these have been perceived as being of value to man, then attempts to extract these minerals have been made, usually resulting in much unwanted rock and low grade ore becoming dumped at the surface around its site of extraction.

With progressive metalliferous mining demise and disuse in the period of the last hundred years, many of these new and often novel habitats within the landscape have become available for plant colonisation. Although superficially inclement to plant life, pteridophytes have usually been among the chief pioneers of these newly-created landscapes, tolerating edaphic conditions seldom accepted well by flowering plant competition, with different groups of pteridophytes acting as potential indicators of the underlying toxic mineral conditions and their current state of degradation.

Landscapes of coal and shale extraction

One of the most widespread traditional mineral extraction industries in Britain has been that of coal. The coal extraction industry in Britain has had a very long history, in some areas, such as in the Forest of Dean in west Gloucestershire, stretching back to Roman times. The modern, great, grey pit heaps associated with the more mechanised aspects of coal extraction, however, which occur through many of our industrial landscapes, are largely a phenomenon subsequent to the industrial revolution, and although some may still be in a phase of active addition, many have become derelict during the last century. In addition to these, very similar shale bings, usually pink in colour, are associated with the paraffin extraction industry in such areas as the central lowlands of Scotland, and these were also accumulated mainly in the 19th century to become largely disused thereafter.

These types of landscape have formed habitats which are very different in their edaphic aspects from most natural sites. The coal pit heaps of the debris and seat-earths from around the main productive coal seams typically include thin coal fragments associated with shales, mudstones, ironstones, sandstones, grits, fireclays and sometimes thin-bedded limestones. The shale bings consist mainly of numerous, approximately coin-sized flakes of roasted shale rock, the organic component of which has largely been removed in the extraction processing. Many may contain other mineral contaminants, especially quantities of sulphur in pit heaps. For years after their deposition, some of the more organic-rich heaps emit heat through a process of slow internal combustion.

Tolerant especially of both coal and shale mine debris are usually colonising clubmosses and horsetails, which are now known from a number of widely separated sites (Page, 1988). Clubmoss records from such sites include especially stag's-horn clubmoss (*Lycopodium clavatum*), fir clubmoss (*Huperzia selago*) and occasionally alpine clubmoss (*Diphasiastrum alpinum*), and in one recently recorded site in the East Shropshire Coalfields, for example, abandoned in the mid 1960s and at an altitude of only about 370 m, all three species occur together (Box & Cossons, 1988). The presence of these species would appear to say something about age of the surface since abandonment of tipping, but being both mycotrophic and dependent largely on incoming rainwater supplies, perhaps may also be indicative of a certain improving status of air cleanliness, about which they may be valuable indicators. The horsetails are, by contrast, almost totally groundwater-dependent, and are good indicators of the presence in the tip of the simultaneous availability of a mixture of bases and available silica (the proportions needing further research, and varying with the species and perhaps ecotypes) and sometimes also of heavy metals, which are accumulated in the plants in analysable quantities. All the species are probably valuable for this purpose. Usually in the driest and most well-drained spots, even on steep slopes, common horsetail (*Equisetum arvense*) has often become the most extensive pteridophyte component of older coal-tip surfaces. The water horsetail (*E. fluviatile*) and its hybrids and the marsh horsetail (*Equisetum palustre*) grow in the edaphically similar but moister sites (Page, 1988, 1990a). On these sites, the value of these extremely long lived plants in promoting the eventual vegetation of their surfaces seems also to have been generally little appreciated.

Landscapes of slate extraction

In other regions, notably in North and south-west Wales, the English Lake District and southern Scotland, the extensive debris of former slate mines has also been added in sometimes great extent to the local landscape of these regions. All of these substrates are generally siliceous and acidic ones, sometimes with local basic enclaves, and may contain extensive mineral contaminants.

The pteridophytes which have widely colonised old slate mine tailings, as these have become progressively abandoned throughout the last hundred years and earlier, include especially: parsley fern (*Cryptogramma crispa*), hard fern (*Blechnum spicant*), woodland lady-fern (*Athyrium filix-femina*), broad buckler-fern (*Dryopteris dilatata*), yellow golden-scaled male-fern (*D. affinis* subsp. *affinis*); and, in slightly more neutral habitats, also: common male-fern (*D. filix-mas*), common golden-scaled male-fern (*D. affinis* subsp. *borreri*), and black spleenwort (*Asplenium adiantum-nigrum*). Sometimes common polypody (*Polypodium vulgare*) and, especially in western districts, western polypody (*P. interjectum*) are present, and colonies of woodland oak-fern (*Gymnocarpium dryopteris*) and beech fern (*Phegopteris connectilis*) sometimes occur in sheltered pockets where there is an accumulation of humus amongst loose rock debris. Where dampness, humidity and shade increase hard fern (*Blechnum spicant*) and woodland lady-fern (*Athyrium filix-femina*) may become very characteristic in clefts and cracks of cool rock faces around the mouths of mine-tunnel entrances to former subterranean faces, where dripping or emerging water slowly trickles from innumerable springs, the seepage paths below them often marked by stains of minerals and local growths of mineral-tolerant algae. On the shallower edges of pools below, it is not uncommon to find bright green stands of horsetails - especially water horsetail (*Equisetum fluviatile*) in the water, marsh horsetail (*E. palustre*) near the margins, and common horsetail (*E. arvense*) in the debris of the drier parts of the quarry floor.

As with coal and shale mine debris, the presence of these pteridophytes on slate mine debris would appear to say much about age of the surface since abandonment of tipping, while as with those of metalliferous mineral-extraction mines (below), the intimacy of the root proximity of these pioneer pteridophytes to the bare rock surfaces undoubtably suggests a high tolerance and likely valuable specific indicator value of different species for the mineral content of the underlying rock type, about which much research is yet needed.

Landscapes of metalliferous mineral extraction

Metalliferous minerals have been very widely extracted in Britain, especially in such regions as Cornwall (especially tin and copper), North Wales (especially copper) and the Pennines and southern uplands of Scotland (especially lead and zinc), with occasional remote mines in other areas such as at Strontian in Ardnamurchan, western Scotland, whose mines produced (and gave rise to the elemental name) strontium. The waste rock dumped around these mines almost always included appreciably remaining quantities of the metals being extracted (either as native metals or as complex ores, especially as sulphides), as well as other generally toxic mineral contaminants, typically including arsenic compounds.

Unlike the rock of slate mine debris, the rock of metal-bearing lodes often also includes many base-yielding veins, and hence where exposed, also frequently (though not always) forms habitats for those basicolous and usually calcicolous pteridophyte species which are tolerant of the mineral excesses of the individual substrate. Typical pteridophyte communities include a blend of non-rupestral and rupestral species in unusual combination. Of the normally non-rupestral species which have adapted to such sites, common male-fern (*Dryopteris filix-mas*) occurs quite widely, often accompanied by hard shield-fern (*Polystichum aculeatum*) and sometimes abundant brittle bladder-fern (*Cystopteris fragilis*). Populations of woodland lady-fern (*Athyrium filix-femina*) may be very common, and this species, plus common horsetail (*Equisetum arvense*) appear to be, in west Cornwall, among the few plants able to tolerate the very highly toxic slurry deposits generated in old tin-mine settling ponds. In southern Scotland, and perhaps elsewhere, marsh horsetail (*E. palustre*) may vigorously colonise and sometimes dominate the tailings of old lead-mine workings. Of the rupestral species which have immigrated into such sites, it is, however, the spleenworts (*Asplenium*) which dominate most old metal-mining areas in these islands. In the more basic sites, wall-rue (*Asplenium ruta-muraria*) and common maidenhair-spleenwort (*A. trichomanes* subsp. *quadrivalens*) are again the two most usual species, with green spleenwort (*A. viride* [= *A. trichomanes-ramosum* Ed.]) joining them and sometimes becoming exceptionally abundant (notably so, for example, on strontium mine tailings). In what are probably the less basic sites, the composition of the flora usually shifts towards a different trio of spleenworts, the sites sometimes becoming dominated by black spleenwort (*Asplenium adiantum-nigrum*), accompanied by more scattered delicate maidenhair-spleenwort (*A. trichomanes* subsp. *trichomanes*) and especially the highly local forked spleenwort (*A. septentrionale*). Habitats of this type are notable in the lead and copper mine sites of North Wales, where sometimes these species become so abundant that they spread to form the vegetation on adjacent drystone walls of the local rock, where they are often joined by rusty-back fern (*Ceterach officinarum*) in many areas of former metal ore mining.

There is much interest today in the colonisation of areas of industrial wasteland in Britain (e.g. Gemmel, 1977). Regrettably, there is also a tendency to group all such areas of former mining with these, and thus to fill and flatten all such pteridologically interesting sites, in the name of landscape improvement. The high specific indicator value of different pteridophyte species for the mineral content of the underlying rock type, and the research needed on this, indicated above, applies especially to those which thrive in these sites, about which very much yet remains to be learned (Page, 1978, 1979a,b). Treating each on its own merit, what could be a better argument for the careful conservation for their botanical value for future research, of some of the more pteridologically important of these old mine sites ?

Landscapes of railways and their environs

Railways have gradually come to form a myriad of new habitats which have become colonised by plants. They have somewhat inherited this position from the much earlier canals (e.g. see Busby, 1976; Page, 1988), and, like the canals and the old mine sites (above), have usually substantially added to, rather than subtracted from, the diversity of pteridological habitats in our landscape in a little more than the last hundred years.

With the invention of the steam railway locomotive in the early part of the 19th century, the great age of railways began. Stimulated by the railway's ability to transport raw materials and finished products more quickly than could the canals, the development of the railway system to most parts of Britain proceeded particularly rapidly. By 1843 there were already 2,000 miles (3,200 km) of line, and by 1845, 5,000 miles (8,000 km) had been laid (Turner, 1982).

The nature of the terrain being crossed and the desire to create only wide curves and level or only shallow trackbed gradients largely determined the types and complexity of the civil engineering constructions needed to traverse our complex terrain. Britain's rolling landscape is seldom level, and where lines entered territory such as south-west England, Wales or Scotland, and crossed the 'grain' of the landscape, innumerable civil engineering constructions were sometimes needed. These included bridges, viaducts, embankments, cuttings and tunnels. The Great Western Railway, for example, the longest-lived of the once-numerous individual railway companies in Britain, from its inception in the early 19th century to its absorption into British Railways in 1947, built no less than twelve thousand bridges and one thousand six hundred stations along about 3,600 miles (*c.* 5,760 km) of track, which eventually included not only main lines, but also over 150 more minor, and mostly rural, branch lines (Thomas, 1981). Today, about 65% of this system still remains in active use, with the remainder, and especially many of the rural branch lines and their stations and yards, disused since the mid 1950s or early 1960s. With track lifted, these have subsequently fallen into various states of disuse and dereliction, and where not destroyed, have offered new opportunities for plant colonisation (Sargent, 1984; Page, 1988).

In addition to the more major construction works, the railways too, like the canals, brought with them a wide range of brick and stone-built structures, as well as the ballasted trackbeds themselves. Water for locomotives was needed at stations and drainage needed in tunnels and cuttings.

Either side of the track itself, within the fenced perimeter of each line in an area that can usefully be called the 'railway corridor', exist strips of varying width, which have also become vegetated. The original construction of the railways was usually carefully engineered to re-use the materials quarried from cuttings to construct adjacent embankments. Cuttings and embankments are thus usually approximately equally numerous, and the rock substrate of embankments usually has an affinity with the native geology of the locality. Under long conditions of relatively minimal management compared with both the trackbed itself and with much of the modern countryside around them, and free from grazing by larger animals, a wide range of semi-natural vegetation has usually become established on both embankments and cuttings, with even the tops of the most exposed embankments irrigated by water from passing trains.

The landscape changes which the railways brought were thus more fundamental and far-reaching than that of any previous transport system. In their early stages of construction, considerable scars were undoubtedly created in the landscape. Gradually these softened as bare surfaces became vegetated. Over the course of 120 or more years of use, most lines, and especially the smaller rural branch lines, came to blend closely into the countryside around them. During this period, few of the original railway structures were replaced, and most of the older of those which survive today are thus seldom less than a century in age. Many of the constructions created have provided excellent habitats for a variety of plants as well as animal life and where track lengths have been abandoned, recolonisation by plant life has reached a new stage of progression.

The trackbed was always one of the most important and hence assiduously-maintained of all the physical aspects of the railway. Ballasted trackbeds are usually of hard rock such as hornfels or granite. On minor tracks and sidings, less detailed attention from weedkilling trains enabled many plants to often continue to hold their own, and with the abandonment of substantial areas of rural branchlines, the whole trackbed has often reverted at a surprising speed to a covering of plants.

The most extensive trackbed ballast pteridophyte present during the active use of many railway lines, especially in minor sidings, beneath buffers and in railway yards, has come to be common horsetail (*Equisetum arvense*). The moist interstices of the trackbed ballast itself also provides particularly suitable habitats for the success of fern gametophytes, and in high-rainfall districts, ferns have consequently proved to be amongst the early pioneers of such sites. The most frequent arrivals in these sites have been male-fern (*Dryopteris filix-mas*), broad buckler-fern (*D. dilatata*), common golden-scaled male-fern (*D. affinis* subsp. *borreri*) and woodland lady-fern (*Athyrium filix-femina*). On more exposed lengths of trackbed, such as on embankments, black spleenwort (*Asplenium adiantum-nigrum*) occurs in some western districts, whilst adder's tongue (*Ophioglossum vulgatum*) and moonwort (*Botrychium lunaria*) have occasionally also established - both the latter probably greatly benefiting from the lack of disturbance or grazing of these sites.

Embankment sides provide especially well-drained habitats, down the slopes of which the edaphic mosaic has often become diversified, and this diversity is often maintained by regular tipping of spent trackbed ballast, creating scree-like patches with a rubble-like or cindery surface. Where embankment tops are edged with stone or mortared brick retaining courses below the ballast fringe, and where shrub or tree growth is absent, ferns such as wall-rue (*Asplenium ruta-muraria*), maidenhair spleenwort (*A. trichomanes* subsp. *quadrivalens* and perhaps subsp. *trichomanes*) and black spleenwort (*A. adiantum-nigrum*) have often widely colonised. In cutting interiors, the environment becomes generally more sheltered than on embankments and edaphically more moist, and in upland areas in particular, bare rock areas, including those of basic strata, are often directly exposed. A great number of widespread ferns have come to occur in these sites, while railway-inhabiting ferns are not solely confined to species of purely local origin, and the intriguing railway distribution of maidenhair fern (*Adiantum capillus-veneris*), Font-Quer's horsetail (*Equisetum* x *font-queri*) and limestone oak-fern (*Gymnocarpium robertianum*) suggests a high value of these species as indicators of important bio-historic aspects of the railway corridor habitat in relation to more general pteridophyte dispersal (Page, 1988).

The railway corridor has thus acted as both a refuge from changing conditions around it, and as a potential corridor along which pteridophytes sometimes meet new opportunities for unusual dispersal, along features which have themselves become integral to the broader landscape of these islands.

Conclusions

The above account summarises some of the more widespread habitat changes that have occurred in our landscape over the last century, and the ways in which ferns and fern allies have responded. Overall, the greatest changes which have occurred, in terms of land area affected, have thus certainly been those of agriculture (70% of land in Britain), followed by forestry (7% of land). It is a sad irony that it is these two sources of landscape change which the above analysis shows have generally eliminated the most and added the least to the persistence of the original pteridophyte biodiversity in the last century, while much of this destruction (especially that through agriculture) has occurred with ever-increasing intensity in the post Second World War period.

The analysis also shows that other types of land use have, however, added to our landscape habitat diversity for wild species and have thereby maintained old or created new sites, albeit on a very much more localised scale, in which pteridophytes have responded, often as pioneer species, to the availability of these habitats.

In terms of the pteridophyte biodiversity which has survived the last century's revolutionary landscape changes, this account only touches on the many special aspects of their ecology which can be learned from this, through sporophyte, gametophyte and spore stages. The indicator value and general biology of the species typically encountered

(Page, 1978, 1979a,b; Dyer & Page, 1985), the dynamic processes of adaptation and natural selection influencing them (*sensu* Turesson, 1922; Turrill, 1948), the special combinations of biological strategies which have enabled each of them to succeed (*cf.* Clapham, 1956; Southwood, 1977; Grime, 1977, 1984a,b, 1986; Grime & Mowforth, 1983). The plant community as a working mechanism, with the pattern and processes of change of its populations in time (*sensu* Watt, 1947; Harper, 1982), are all fields which are, as yet, scarcely researched. These factors are of special interest within an island flora (*cf.* MacArthur & Wilson, 1967), and for some of these, aspects of field research of animal communities can provide important and sometimes stimulating analogies (e.g. Elton, 1968). For the future exploration of many of these aspects, further dedicated coupled field and laboratory studies will certainly be paramount (e.g. Steers, 1964).

Today, towards the close of the 20th century, the creation of other new habitats in our ever-changing landscape is still taking place. There are the derelict areas in many inner cities with landscapes increasingly dominated by the residue of former heavy industry. There are continuing changes in wetlands and in agricultural and forestry enterprises, influenced by changing philosophy and practice. There are the short-lived changes which occurred in bomb-sites in London during and after the Second World War, which temporarily dramatically added to inner city pteridophyte diversity in a way which none would wish to recur. There is the appearance too of other grassland areas free from major grazing which have developed this century on airfields and along our motorway network as well as from earlier origins on and around golf courses - these, plus the almost all pervasive effect of pollution, both of groundwater and atmosphere, and changes in response to potentially shifting climatic parameters (e.g. Lamb, 1985) - will have to be studies for the future.

If there are any general deductions to be made from these changes for pteridophytes in the British Isles, they are these. That the continuing process of landscape change around us steadily (and sometimes dramatically) changes pteridophyte habitats, and that while many old ones are lost, we should not ignore the fact that there is also a plus side on several occasions, where new opportunities for pteridophyte exploitation are unwittingly created by man. Many of the habitats discussed here remain still in a state of dynamic change in time, and, as pteridologists, we have to be aware of these changes, and from them very much remains to be learned. In conservation terms, we must treat each situation on its own merit, to resist, where possible the worst, but to preserve some of each of the best of these changes, and continue to observe and learn from them as integral parts of our evolving island landscape, into the 21st century.

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Note: the English names for pteridophytes used by Page are not widely accepted. They have been left unamended to enable the reader to correlate this text with his books *The Ferns of Britain and Ireland* (1982) and *Ferns. Their habitats in the British and Irish Landscapes* (1988). Ed.

Chris Page omits only molecular science from the spectrum of his interest in gymnosperms (especially conifers) and pteridophytes (especially Equisetum). *An author and occasional broadcaster who has travelled widely in the British Isles, Australasia, the eastern Pacific and North America, he enjoys applying his knowledge to conservation, ecological changes and the development of arboreta in the British Isles.*