THE EFFECT OF BRACKEN DISTRIBUTION ON MOORLAND VEGETATION AND SOILS

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by

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PREFACE

The cause of hill land improvement has seen many vicissitudes of fortune in the present century, reflecting basically the fluctuations in the profitability of livestock rearing on marginal land in this country. Whenever economic conditions are relatively favourable it is the better-drained uplands with mineral soils and usually some form of bent-fescue grassland which offer the best sites for reclamation. Since bracken infestation is a very widespread problem in this environment its eradication has been a standard component of reclamation schemes for many years. Despite this fact, little research has been done on the role of *Pteridium aquilinum* in the ecosystem and hence the ecological implications of eradication.

This thesis attempts to analyse the effect of bracken dominance on the ground vegetation and soils of semi-natural grasslands through field and laboratory investigations. In terms of academic interest it therefore offers a case study of the role of a dominant plant species in modifying a plant community and as a soil-forming factor. In practical terms it attempts to provide a more factual basis for the evaluation of the agricultural significance of bracken infestation and hence the desirability of eradication.

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ABSTRACT

Despite the existence of an extensive literature on the morphology, autecology, utilisation, and eradication of Pteridium aquilinum, relatively little research has been done on the Pteridium-grassland ecosystem of Scottish rough grazings. This study is a systematic and semi-quantitative investigation of the influence of Pteridium competition on its associated vegetation and soils, based on field and soil laboratory techniques.

It is postulated that the differential response of moorland species to varying degrees of bracken dominance and the modification of soil morphologica and chemical characteristics by the dominant plant species is partly responsible for the well-known association of Pteridium aquilinum with Festuca-Agrostis - brown forest soil ecosystems.

This hypothesis is tested in the field in three contrasting upland environments in Scotland. The influence of varying densities of bracken on three facets of the vegetation - soil association is examined: (1) the characteri particularly the biomass, of the ground vegetation as a whole (2) the species composition of the herb layer and (3) the morphological characteristics of the soil. The degree of dominance of bracken is defined in a semi-quantitative manner and correlated with indices of the vigour of the ground vegetation and its species composition. A classification of common dry moorland species, according to their response to Pteridium competition is produced.

The association of Pteridium aquilinum with soils of brown forest soil morphology is studied and the importance of the rhizome system in modifying the physical characteristics of the soil and the distribution of organic matter in

the profile demonstrated. The tendency of bracken to modify the morphological characteristics of podsolised soils is shown.

Subsequent laboratory analysis substantiates the morphological evidence of the relationship between Pteridium-dominated vegetation and soil type. By revealing the differences in nutrient status between bracken soils and podsolised heath soils and the seasonal variation in nutrient levels, the efficiency of Pteridium in cycling nutrients through the ecosystem is suggested. The ability of Pteridium to release phosphate from inorganic sources in the soil is demonstrated by laboratory experiment, anomalously high available phosphate levels in the subsoil of bracken soils having been revealed by routine analysis. Laboratory experiment also suggests that the modification of iron pans by Pteridium rhizomes may have a chemical as well as a physical component.

The evidence of Pteridium's influence on vegetation and soil characteristics allows preliminary comment to be made on the ecological significance of bracken eradication schemes.

CHAPTER I

INTRODUCTION

Pteridium aquilinum is the most common and persistent weed of hill pastures in Britain. Estimates based on the Agricultural Returns of 1957 (Hendry, 1958) gave the total area of bracken-infested rough grazings and permanent pasture in Scotland alone as 180,000 hectares. This success of *Pteridium aquilinum*, originally a component of the shrub stratum of deciduous woodland, in colonising and attaining dominance in the moorland environment is attributable partly to its morphological characteristics and partly to the history of human utilisation of the uplands.

The competitive vigour of *Pteridium* is largely a function of the height and density of the fronds which in one season's growth outstrip its moorland competitors to form an upper stratum of vegetation, the growing fronds and resultant litter of which determine the microenvironment of the other moorland plants. This vigorous aerial growth is supported by a well-developed network of underground rhizomes which provide the food reserves and which, under suitable environmental conditions, are capable of rapid elongation. Braid (1934) estimated that the rate of rhizome expansion in western Scotland is 60-90 cm per annum. In addition, the dominant sporophyte phase is extremely tolerant of the climatic and edaphic conditions prevalent on the better-drained and lower altitudinal areas of rough grazings especially on the western side of the country.

The inherent competitiveness of Pteridium aquilinum has been reinforced by recent human utilisation of rough grazings. When the uplands formed part of a basically subsistence rural economy in which small agricultural holdings carried a mixed stock of domestic animals, the nuisance aspect of Pteridium was less apparent. Indeed its value for human and animal bedding, thatching, fuel, and as a raw material for soap and glass production gave it the status of a resource, rather than a weed (see Mitchell, 1973). The harvesting of fronds for these purposes and the control effected by trampling cattle helped to check bracken vigour. The nineteenth century trends of rural depopulation, replacement of mixed farming small holdings by large-scale sheep farming or sporting estates, and the replacement of a subsistence by a commercial economy provided an economic environment in which Pteridium flourished. The end of bracken utilisation domestically, the ineffectiveness of sheep in controlling the fern, and the widespread practice of muirburn all contributed to the spread of bracken. Muirburn, particularly as practised by sheep farmers, favoured the fern with its potential for vegetative reproduction from protected underground shoots against those plants which rely on colonisation by seed.

No longer valued as a resource, the reduction in pasture productivity by bracken growth and the risk of bracken poisoning of livestock, became matters of concern in agricultural circles. In the last hundred years bracken eradication has become a central theme in all considerations of hill land improvement and reclamation, and increasingly sophisticated methods of mechanical and chemical control have been attempted. The limited success of these has resulted from the unfavourability of the economic climate for hill land reclamation over much of this period, as much as from the technical difficulties encountered. The latest weapon in the anti-*Pteridium* armoury is the relatively effective herbicide asulam, frequently administered from the air. Evidence of this preoccupation with bracken eradication is found in the vast literature in agricultural publications on bracken utilisation, life-history, autecology, toxic qualities, and eradication (see Chapter 2).

However, despite the large volume of research on *Pteridium aquilinum*, its synecology and, more specifically, the ecological implications of eradication is a relatively neglected field. The aim of the research project described in this thesis is to investigate the relationship between *Pteridium aquilinum* and its associated herb layer vegetation and the underlying soil. The association between *Pteridium* and a particular moorland community and soil type, namely *Festuca-Agrostis* grassland and brown forest soils is well-established. This relationship is usually expressed in terms of the preference of *Pteridium* in invading existing *Festuca-Agrostis* grassland and soils of the brown forest soil type, an approach encouraged perhaps by the occurrence of this vegetation - soil association without the *Pteridium* component. Botanists have been reluctant to confer the status of a separate community-type on *Pteridium*-dominated grassland. For instance McVean and Ratcliffe (1962, p.66), in their definitive work on the plant communities of the Scottish Highlands, state:

> The change from dwarf shrub heath to *Agrostis-Festuca* grassland has been accompanied in many places by the spread of bracken (*Pteridium aquilinum*). While this is partly a woodland relic it easily invades both species-rich and species-poor *Agrosto-Festucetum*

and produces communities which, although they have been described along with the birchwoods, may also be regarded as facies of the grasslands.

In this study the emphasis is on the modifying effect of the fern. Where it occurs, *Pteridium aquilinum* is the dominant organism in the moorland ecosystem, indeed forms the sole component of an upper stratum of vegetation. As the dominant it influences the microenvironment, particularly the light and moisture conditions, of associated herb layer species, which presumably vary in their reaction to the environmental conditions produced by frond canopy and litter. The hypothesis is put forward that *Pteridium*, by controlling the microenvironment, selects its associated species, variation in the specific composition of the herb layer with varying degrees of *Pteridium* dominance being postulated. Furthermore it is postulated that *Pteridium aquilinum*, as the vegetational dominant, plays a major role as a soil-forming factor influencing the morphological and chemical attributes of the underlying soil. This influence is exercised through the character of the litter it contributes and through the physical, and perhaps chemical, effects of its ramifying rhizome system. Any evidence of the contribution of *Pteridium* to the character of its associated vegetation - soil complex has obvious implications in terms of the ecological consequences of bracken eradication.

The breadth and complexity of the field of investigation means that this is, of necessity, merely a preliminary study. The aim of the research is to establish the extent to which *Pteridium aquilinum* influences the character of the ecosystem it dominates, rather than to explain the detailed mechanisms by which this influence is exerted. The emphasis is therefore on field investigation, in which variation in the character of vegetation and soils in the presence and absence of bracken, and under varying levels of bracken dominance, is systematically analysed. The soil field work is supplemented by laboratory analysis essentially aimed at providing a chemical description of the soils studied in the field.

Fortunately it is possible to find field situations in which the degree of dominance of Pteridium aquilinum can be isolated as the only major environmental variable. This occurs where boundaries exist between bracken-dominated communities and other moorland vegetation types without coincident change in environmental parameters such as soil parent material, surface drainage, slope, altitude, and aspect. For the purpose of this study these boundaries, which presumably reflect the competitive balance between species at a given point in time, possibly much influenced by human management, have been termed 'sociological boundaries', to distinguish them from habitat-controlled 'ecological boundaries'.

It would be theoretically possible to investigate the response of various plant species to Pteridium competition by artificial experimental plots and to examine the influence of Pteridium litter on soils by laboratory experiment, although it would be difficult to reproduce, in an acceptable period of time, the full competitive vigour of a well-established bracken stand. The selection of the field-study approach with subsidiary laboratory analysis of soils is justified as being most appropriate at this preliminary level of investigation. If it is established that Pteridium aquilinum does indeed modify actual ecosystems in the field, experimental investigation may be appropriate to the second stage of examination of the mechanisms involved. One of the aims of this study is indeed to define problems the elucidation of which may require the application of quite different research techniques and skills.

CHAPTER 2

REVIEW OF THE LITERATURE

Few species of wild plant can have achieved greater prominence in the botanical and agricultural literature of Britain, and other countries, than Pteridium aquilinum. The extent of this research interest is indicated by a review of the literature by Kenneth Braid (1959) in which he cites over one hundred references on one limited topic - bracken poisoning.

This popularity has two main causes. Firstly Pteridium aquilinum is the most cosmopolitan of all the Pteridophyta, representatives of its two subspecies and twelve varieties being found on all continents, apart from Antarctica, and ranging in latitude from the Tropics to the Arctic Circle. It is found in areas as far apart as the Guinea coast, the Himalayas, Newfoundland and Guatemala (Tryon, 1941). In addition it is in a unique position among the ferns of the British Isles, being the only member which attains prominence over extensive areas of vegetation, commonly achieving dominance in the shrub stratum of deciduous woodlands, and as the upper stratum of large areas of rough grazing.

While this position as an important component of the flora of many countries would probably have ensured its investigation by botanists, its study has undoubtedly been stimulated by the economic significance of the fern. Its position as a vigorous and poisonous week of pastures in the British Isles, New Zealand, and Western North America has guaranteed its study by agriculturalists. On other sites and among other varieties of the species, this weedy character has been much less obvious and indeed in various countries, at various periods, it has been regarded as a plant of economic value.

Initial research on the morphology and life cycle of Pteridium was carried out in the mid-19th century, the Germans Hofmeister (1862) and Klein (1884) being prominent, while Hooker (1861) demonstrated its global distribution. At this period also the spread of the fern in rough grazings in this country had stimulated the interest of agriculturalists in its control. For example as early as 1837 McTurk and Murray wrote essays on bracken control while the first instances of bracken poisoning in cattle were recorded in 1893 (see Stamp, 1947).

In reviewing the 20th century literature on Pteridium aquilinum it is perhaps useful to define two lines of research. The first of these consists of the applied aspects, encompassing control, uses, and toxic aspects of Pteridium. These facets received their first major stimulus in the First World War period when the British, faced with wartime shortages, were willing to explore the potentialities of any possibly useful native plant. At this time, 1917-19, people like Berry (1917) and Hendrick (1918, 1919) published results of the chemical analysis and potential feeding value of Pteridium. These workers were the early members of a school of bracken researchers which developed in Scotland, based particularly on the West of Scotland College of Agriculture. It is interesting that concurrently research was being published on similar themes in New Zealand.

This agriculturally oriented work continued throughout the Inter-War and

Second World War periods when research into control by various methods - mechanical, chemical, and biological - investigation of toxicity, chemical analysis, and possible uses produced an extensive literature on Pteridium aquilinum, published in the popular agricultural press as well as in academic journals. The West of Scotland College of Agriculture maintained its prominence in the field with Kenneth Braid in the forefront of the research. To some extent at least, effort along these lines has dwindled since 1950 with the exception of the continuing, and recently accelerated search for an effective herbicide, and the recent interest in the carcinogenic nature of bracken.

The other main line of research was the academic one although the two were never clearly differentiated since many researchers such as Braid, and later Conway, worked in a wide field encompassing both academic and applied aspects, the one stimulating the other.

Initially the investigation of Pteridium was part of an interest in the composition and ecology of British moorlands manifest in the first forty years of this century. Descriptive studies of moorland were undertaken by people like W.G. Smith, Fenton, and Stapleton, bracken receiving its share of attention. However in the 1940s a wave of literature on Pteridium aquilinum per se appeared. In addition to the early life histories a trickle of articles on narrow aspects of bracken morphology had appeared before 1940, but in the 1940s and 50s knowledge of the morphology and autecology increased enormously. Most prominent in this field was Elsie Conway working in Scotland, and Alex. Watt in the Breckland who between them produced some of the classical work on Pteridium, based on field and in the case of Conway, laboratory investigations. This basic research has been built on, both in this country and the United States, with specialised physiological and biochemical aspects receiving further attention.

The cinderella of bracken research has been its synecology, the study of the bracken community and ecosystem as a whole. This aspect has not developed with its autecology, morphology, and physiology, much of the present knowledge of the topic being based on the qualitative descriptive work of the pre-1940s era.

A review of this vast literature on many aspects of Pteridium is clearly outwith the scope of the present study. The more narrowly agricultural aspects of control, toxicity, and utilisation have therefore been omitted. This chapter deals with aspects which bear some relevance to the present topic namely physiology and morphology, chemical analysis, autecology, and synecology, the literature being considered under these headings.

I. PHYSIOLOGY AND MORPHOLOGY

In common with other Pteridophyta Pteridium aquilinum is characterised by a life-cycle with two distinct phases: the gametophyte (prothallus) phase which is sexually active takes the form of a very minute plant; the sporophyte phase is represented by the familiar plant with its aerial shoots or fronds borne on a network of underground shoots (rhizomes). While the rhizome is the most important part of the sporophyte, being the perennial food storage organ, early anatomical works tended to stress the more visually striking fronds.

Frond Structure and Reproduction

The main aspects of the anatomy of the frond and the life-history of the fern had been worked out by the beginning of the twentieth century, the Germans Hofmeister and Klein having been prominent nineteenth century researchers. At this early period anatomical research was closely associated with taxonomy, Hooker (1861) for instance describing the anatomy of his herbarium specimens.

Early botanical works such as Moore's "A Popular History of the British Ferns and their Allied Plants" (1851, pp. 164-165) described the anatomy of the frond as bipinnate (or tripinnate when very luxuriant) with pinnae in pairs. Moore described the inward rolling formation of rachis and pinnae and the manner in which the rachis unrolls with subsequent unrolling of each pair of pinnae as they are exposed. The situation of the sporangia (the spore-bearing organs) on the underside of the fertile frond was also known by Moore and the presence of a membranous covering called the indusium, on the sori. More detailed investigations of anatomical features were carried out in the early twentieth century, for instance the fact that frond structure varies according to light conditions being noted by Boodle (1904).

The relationship of the sporophyte and gametophyte phases was elucidated by Druery (1903). The sporangia on the frond of the sporophyte phase rupture on the drying and contraction of the marginal cells, thus dispersing the spores. If successful germination of the spores occurs they give rise to the gametophyte phase or prothallus. The prothallus develops both antheridia (male sexual organs) and archegonia (female sexual organs). The former contain small cells, spermatocytes, each of which gives rise to a male gamete, the spermatozoid. These spermatozoids escape when the mature antheridium ruptures and must move in water to come in contact with the ripe archegonium when fertilisation of the oosphere (female gamete) can take place. The sporophyte phase develops from this fertilised oosphere.

While the main aspects of the sexual life of Pteridium has thus been known for seventy years it has also been appreciated for many years that in British conditions sexual reproduction is of minor importance compared to vegetative reproduction by the rhizome. For instance Long and Fenton (1938) stated that the prothallus stage is rarely found in eastern Britain though commoner in the west, while Conway (1953a) stated that in twenty-five years of pre-Second World War research Braid found only six sites of sporeling development.

The general state of knowledge of the life-history of the fern by 1950 is well summarized in publications such as Long and Fenton (1938), Conway (1952), and Braid (1952). Research in the 1950's and 1960's was directed at filling in and quantifying the details of the picture. Conway (1952) estimated that 300 million spores per annum may be produced by one fertile frond. Later, in 1957, she published the results of a survey of spore production on sites in west Scotland from 1946-52. This showed that spore output is potentially very high, but that in fact fertility among fronds is highly variable in time and place. She quantified the frond anatomy, stating that fronds usually bear 13 to 20 pairs of pinnae, each of which has 30 to 35 pairs of secondary pinnae (pinnules). Vegetative development of the frond is at a maximum at the third pair of pinnae and the basal pair are normally sterile.

In the same article Conway related the variability of spore production to environmental conditions and the physiology of the plant. Sporangia development was shown to occur throughout the summer correlating with the maturing sequence of the frond. As each pinnae unfurls its soral tissues get a chance to mature. Main frond expansion in west Scotland was found to occur from late April to early June and these fronds have the best chance of producing mature sporangia. Late-emerging fronds were seldom fertile, possibly at least partly due to unfavourable weather conditions. Variation in spore production from year to year could be partly explained by weather conditions, frond destruction in late spring by frost, and wet weather in late summer inhibiting the drying of the sporangia necessary for spore dispersal, being crucial. Her hypothesis that variation in fertility might coincide with microenvironmental conditions will be considered later (see page 31).

More recent research into fertilisation in Pteridium has been undertaken by Wilkie (1954) who showed that while the occurrence of male and female organs on the same prothallus makes self-fertilisation possible and indeed fairly common, cross-fertilisation is in fact the norm. Further, Wilkie demonstrated that in some prothalli only antheridia develop and the plant is male.

Rhizome Morphology

Important though the frond is, it lives for only one season and the perennial part of the Pteridium plant is the rhizome system which acts both as underground storehouse of carbohydrates and the main organ for vegetative spread. References to the rhizome are found in the early life histories such as Moore (1851) and Klein (1884) while Tansley and Lulham (1904) described the vascular system of the underground shoots.

However the foundation of detailed knowledge of the structure and development of the rhizome was laid by workers such as Braid and Conway working in west Scotland from the 1930s to the 1950s, and Watt in the Breckland in the 1940s and 1950s. Watt (1940) stressed the significance of the underground system by describing bracken as a travelling geophyte in which the rear part of the rhizome dies away as the actively growing points advance.

Braid's studies in the 1930s demonstrated that the rhizomes run more or less horizontally in the soil, branching frequently to produce a complicated, dense network of shoots. Roots are borne along the whole rhizome while fronds are produced alternately along its length. He noted (1935) that the main, elongating rhizomes are deeper in the soil and bear few fronds, while the frond-bearing rhizomes occupy shallower regions. He also noted the occurrence of dormant buds which can give rise to new rhizomes and fronds if dormancy is broken.

Watt's (1940) investigation of rhizome structure verified these findings, in particular elucidating the distinction between frond-bearing and non-frond-bearing sections. He identified three types of rhizome shoot which he differentiated both in terms of the length of the internodes and frond-bearing capacity. The long shoots, of an average 30 to 40 cm internodal length, are deep-seated and frondless. Short shoots of 0.5 to 2 cm internodal length are the main frond-bearing rhizomes and grow upward from the main axis to occupy the upper soil zones, while non-frond bearing shoots of intermediate length were also identified.

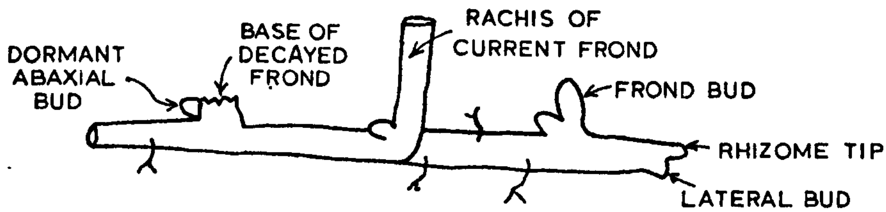
According to Watt, each short shoot produces on average one frond, and therefore one internode, per annum although two fronds are occasionally produced and dormancy is common. He considered that the apex of the short shoot differentiates into frond and rhizome around the end of June. The frond bud grows slowly until the following April when an acceleration of growth pushes it above the soil surface.

Watt's finding that frond bud differentiation occurs chiefly in summer is supported by Conway and Stephens' (1954) work in the west of Scotland. According to them, by the end of the growing season fifty percent of field rhizomes on their sites had a differentiated frond bud behind the stem apex. They summarized the situation at the end of the summer in diagrammatic form (Fig. 2.1).

Conway and Stephens were particularly interested in dormant buds as their basic concern was the reaction of the rhizome to frond cutting. The recovery ability of the plant is closely linked to the existence of the dormant frond buds which can be stimulated into development by damage to existing fronds. Like Watt they found that an excess of frond buds is a feature of *Pteridium*, while in addition they found dormant branch buds at the abaxial bases of the majority of the current year's fronds. These buds have the potential to develop into lateral rhizome branches but normally remain dormant as long as the fronds are active. Hence the ability of bracken to recover quickly after cutting, or any form of frond damage, is due to the stimulation of these

Fig. 2.1

STAGES OF DEVELOPMENT OF FRONDS & ABAXIAL BUDS IN THE APEX OF A RHIZOME



(from Conway, E. and Stephens, R., 1954, p.3).

dormant frond buds and lateral rhizomes. Indeed Conway and Stephens found that the first effect of frond cutting was an increase in the number of fronds which expanded the following season, an effect that had been noted by Smith (1928). This increase was at the expense of frond buds, for after 2 years of severe cutting the ratio of frond buds to expanded fronds was significantly reduced. In other words the plant was drawing on its reserves of dormant buds to maintain frond production. While this obviously weakens the plant, cessation of cutting was followed by a speedy restoration of the reserve of frond buds through the increased activity of the rhizome tips.

Watt's definition of frond-bearing and frondless rhizomes has been largely supported by later work in the north eastern United States by Webster and Steeves (1958), who studied rhizome structure in the variety 'latisculum'. They agreed that fronds are mainly confined to the slow-growing short shoots which form lateral branches on the vigorous, frondless, long shoot which forms the main axis of the plant. They questioned however the significance of Watt's intermediate shoots, identifying instead transitional shoots, similar in morphology to the long shoots but frond-bearing.

The rate of growth of Pteridium rhizome has been the subject of much interest by various writers because of its significance for the rate of spread of the weed over pasture. Results have varied widely according to local conditions. For instance Farrow (1941, p.216) measured the rate of expansion of a bracken patch on a dry, sandy soil on Breckland Heath from 1915 to 1941 and found it averaged 17 cm per annum. In the same area Watt (1954, p.118) found average growth rates of 43 cm per annum from 1936 to 1952. On the other hand, in the more favourable west Scotland conditions, Braid (1934a) described rates of growth of 2 to 3 ft. annually. An experiment by Braid and Conway (1943) in which sporelings were planted out in laboratory, non-competitive, conditions produced even faster rhizome growth rates of over 200 cm in seven months. Under these artificial conditions it was also shown that Pteridium is by no means limited to producing one frond per branch per season. Watt (1940) suggested that rate of growth is related to temperature, noting the distinct seasonality of rhizome growth in British conditions with growth at a very slow rate from October to May.

Research on the Pteridium rhizome has therefore thrown considerable light on the vigour and competitiveness of the plant, highlighting the problems of control. Pteridium is basically an underground plant, the rhizomes of which provide a reserve of carbohydrate which can only slowly be drained by attack on the aerial portions. Its supply of dormant buds and its potentially very high growth rate in favourable environmental conditions help to explain its success despite the attempts of man to control it.

This storehouse of carbohydrate in the rhizomes is replenished annually by the mature fronds in a process which has been further elucidated in recent years with the development of the technique of labelling substances with radioactive isotopes. Whittle (1964) using C^{14} labelled CO_2, traced the translocation of carbohydrates, showing that as the young frond expands each pair of pinnae goes through a sequence of stages. Early in the growing season carbohydrate is imported into the pinnae from the rhizome and from any expanded lower pinnae. While this import is still continuing export of carbohydrate is initiated to apical regions of the frond. In the third stage import ceases and export both up the rachis to apical pinnae and downward to the rest of the plant is the main function, until finally export upward ceases and movement is confined to downward transport to the rhizome. As in spore production, each pair of pinnae goes through this sequence in turn.

Morphology of Bracken Population

While earlier botanists had studied the morphology of individual fronds, detailed investigation of the structure of *Pteridium* communities was mainly the work of Watt. He followed his research on the structure of the rhizome with his classical work on the Breckland, in which he analysed the relationship between aerial and underground portions of individual plants and the variation in structure of bracken plants within a *Pteridium* population. Working on a number of sites, Watt (1940) identified four zones within the bracken stand differentiated mainly on the basis of frond height and density. These zones were defined as (1) the 'Advancing Margin': vanguard of scattered, short fronds increasing in density and size to complete canopy; (2) the 'Crest': zone of maximum frond height; (3) an area of relatively uniform fronds in terms of height and density, forming a complete canopy but shorter than in crest; and (4) the 'Hinterland': discontinuous bracken cover with fronds of irregular height and density in patches some of which form consecutive zones or rings with bare patch in centre. Of these zones, number three is not always clearly developed.

Investigation of this structural pattern indicated little correlation between frond height and environmental parameters within any one stand, and Watt deduced that the zonality of the bracken stand was a function of the morphology of the component bracken plants _per se_.

Watt found that a transect of the _Pteridium_ stand from stand margin into the hinterland revealed a continuous rhizome system through zones 1, 2, and 3 with the main rhizomes dying off at the limit of zone 3. In other words the _Pteridium_ plants on the margin of the bracken stand are characterised by three zones of frond development, this spatial variation being a function of the increasing age of the plant from the apex in zone 1 to the decaying end of the plant in zone 3. As the oldest part of the rhizome dies away, sections of the rhizome system break off to become independent plants in the hinterland zone, which therefore contains a population of bracken plants of mixed ages. Systematic examination by Watt (1943, 1945) revealed many contrasts in form between the marginal and hinterland plants.

The marginal plant (that is the rhizome system) is larger than the hinterland one and has a faster rate of growth. This more vigorous marginal plant therefore produces a greater number of new fronds per annum. Since competition between plants is less in the marginal area than in the hinterland, the form of the rhizomes differ, the relatively straight main axes of the marginal plants, parallel to each other and perpendicular to the advancing frond, contrasting with the rather tortuous layout of rhizomes in the hinterland.

In the marginal zones the mean depth of origin of the frond decreases across the advancing frond to the crest to increase again, but in irregular fashion, in Zone 3. Thus the marginal plant is characterised by zones, parallel to the advancing front, each of which is relatively uniform in terms of frond height and depth of origin of fronds but with increasing variation in frond height in Zone 3. In the hinterland, by contrast, variation in frond height and depth is the norm, a situation which Watt compared to forest structures, the marginal bracken plant corresponding to the homogenous structure of immature woodland, while the hinterland bracken situation corresponds to the heterogenous structure of mature forest where natural regeneration has produced an uneven-aged population.

Watt (1945) also studied variation in certain characteristics of the fronds, length of aerial petiole, length of total petiole (that is underground plus aerial sections), length of lamina, and the relative proportions of these components. In the marginal plant these dimensions alter from zone 1 to 3; the stout, deep-set fronds in zone 1 have short petioles and moderately long laminae with high lamina to petiole and lamina to total petiole ratios; the ratios of lamina to petiole and lamina to total petiole reach their minimum in the tall, shallow-seated fronds of the crest; in zone 3 the more slender fronds have still relatively low ratios but with the lamina relatively more developed than in the crest. In contrast all sections of the frond are shorter in the hinterland plant but the ratios of lamina to petiole and lamina to total petiole are significantly higher than in the marginal plant.

Thus there are significant differences in rhizome and frond structure and in the pattern of the frond population between the marginal and hinterland plants, as well as zonal variation in these characteristics between different age sections of the marginal plant.

The fact that the visual characteristics of the marginal plants clearly vary in a definable way according to the age of sections of the rhizome, led Watt (1945) to postulate that the irregular pattern of fronds in the hinterland might also reflect the age of the associated rhizomes. Identifiable groups of fronds within the hinterland were compared in terms of frond dimensions, vigour, density, depth of origin, as well as litter and associated species characteristics, with their counterparts in the marginal zones of known relative age. On this basis Watt recognised four age phases within the hinterland-pioneer, building, mature and degenerate which along with the grass-heath (no fronds) phase completes the cycle of bracken development. This hypothesis provides a possible key to the pattern of circles, rings, and arcs of fronds observed in the hinterland, the phases tending to be arranged in concentric circles with frequently a frondless patch in the centre. Watt estimated the whole cycle from grass-heath to degenerate phase lasted approximately one hundred years in the Breckland.

Subsequent research by Watt (1970, 1971) indicated that, in contrast to the rapidity with which the marginal plant could colonise fresh ground, the Pteridium plants in the hinterland are very slow to reinvade the grass-heath phase. This difference he attributed to the relative vigour of the two types of plant - the colonising shoots of the marginal plant are fed by a large, deep-set rhizome system encountering little competition. The hinterland plant, subject to fierce competition, is small with limited food reserves, and proportionately reduced litter production, and hence greater vulnerability to adverse climatic conditions for the litter protects the young shoots from frost and desiccation.

Hellum (1968), working in northern Lower Michigan, has followed up Watt's research in a different environment. He identified bracken plants with the characteristics of Watt's hinterland plants and, by using frond shape and relative size of frond parts, managed to identify bracken clones within the hinterland population.

II. CHEMICAL ANALYSIS

While botanists, particularly those with agricultural interests, were examining the morphology and physiology of Pteridium aquilinum, agricultural chemists were analysing its chemical composition. A large volume of work appeared on this topic, particularly between 1914 and 1950 when there was considerable concern in agricultural circles in Britain about the spread and control of bracken. During this period therefore the biochemical investigation of the fern had practical overtones, being directed mainly at finding an economic use for the weed, emphasis frequently being placed on the feeding value of rhizome and frond.

The first of these research programmes was initiated by the Ministry of Agriculture in 1918 when wartime conditions had strained feedstuff supplies. Hendrick (1919) published his findings on the feeding properties of the rhizome which had been used in the past for pig fodder and he found the average content of soluble carbohydrates over the summer season was comparable to potatoes but the protein content was roughly fifty per cent that of potatoes while the fibre content was much higher. However there was a significant seasonal variation, with both protein and carbohydrate levels at a minimum in mid-July and a maximum in April, a result which incidentally supports the former as the optimum time for frond cutting to control the weed. Hendrick's overall conclusion was that while the rhizomes offer an adequate subsistence diet the protein content is too low for fattening purposes.

Later analyses tended to concentrate on the fronds and stems, important work being done on these during the 1940s. Ferguson and Armitage (1944) analysed the fronds for a number of organic compounds over the length of the growing season. Crude protein levels were found to be fairly high in June (21 per cent oven-dried dry matter) but fell steadily through the growing season while the proportion of lignin increased. They found a high percentage of reducing sugars, mainly glucose and fructose, but their attempts to estimate digestibility by laboratory methods were unsuccessful.

These values for protein correspond closely to the results obtained by Smith and Fenton (1944) and those quoted by Tocher (1941) while Moon and Pal (1949), working however only on mature, fully unrolled fronds and basing their calculations on air-dried samples, obtained rather lower protein levels but with a similar seasonal distribution. The marked increase in crude fibre levels from early August found by Moon and Pal is in line with Ferguson and Armitage's results for lignin and cellulose. Moon and Pal also had some success in assessing digestibility by feeding trials, concluding that although late in the growing season the fronds are of little value, the nutritive value of young fronds in June is comparable to hay.

Most of these chemists did not restrict themselves to analysing the organic compounds in Pteridium but also investigated the mineral constituents of the ash, a point pertinent not only to the plant's nutritional value but to its possible utility as a manure.

In subsistence agricultural economics, such as Wales and the Scottish Highlands in the eighteenth century, bracken ash was used to make soap due to its apparently high potash content. Berry (1917) found that 50 per cent of the weight of ash of the young fronds consisted of potash but that this diminished rapidly through the growing season due to leaching and translocation to the rhizome.

Similarly high values for potassium were obtained by Smith and Fenton (1944) who found 45-47 per cent K_2O in the ash of fronds cut in June, decreasing to 32-35 per cent in September. They noted an inverse relationship between K_2O and SiO_2 concentrations in the ash, the latter increasing through the summer as potash declined.

Other workers in the 1940s to some extent challenged the theory that bracken fronds are particularly potash-rich. Ferguson and Armitage (1944) and Moon and Pal (1949) obtained reasonably comparable results of 2.8 - 3.8 per cent K_2O in fronds in June, expressed as percentage of total dry matter rather than ash. When these results are translated into the proportion of potassium in the ash Moon and Pal's values of 30-37 per cent in June and July are certainly somewhat lower than those obtained by earlier workers. Moon and Pal put the potash content of _Pteridium_ into perspective by pointing out that it is certainly lower than in good pasture grasses.

However it is perhaps more meaningful to compare bracken with moorland plants growing on similar soils rather than with improved pasture grasses. Hunter

(1953) in a detailed analysis of bracken fronds and rhizomes at various times in the season concluded that young bracken fronds have certainly a high potassium content compared to other moorland species and indeed exceed the values obtained by Thomas et al (1952), for eight grass species growing on agricultural soils.

The weight of evidence therefore supports the contention that young bracken fronds do have a relatively high potassium content but that this concentration declines rapidly through the growing season.

Seasonal variation is also found in the levels of other nutrients in the frond. Both Ferguson and Armitage (1944) and Moon and Pal (1949) found a decrease in phosphate concentrations from June to autumn, the latter pointing out that the level of P_2O_5 (0.9 per cent dry matter) in the young frond is relatively high. In contrast Moon and Pal found that the calcium concentration in the frond increased from June to September, a result substantiated by Hunter (1953). The latter was responsible for the most complete analysis of the mineral composition of Pteridium, examining both major and trace elements. He found trace nutrient contents relatively constant in the frond throughout the summer compared to the variation found in the major elements. The latter he explained in terms of the growth pattern of the fern. He found that the weight of the fronds increased until early August, thereafter translocation of material to the rhizome and later drying and senescence of the frond producing a decline in weight. Until August the absolute contents of nitrogen, potassium, magnesium, and sodium increased with expansion of the frond although, apart from sodium, their concentration expressed as percentage of dry matter was at a maximum in

May. Absolute calcium levels, on the other hand, increased until September, its relative importance also increasing throughout the growing season, a reflection of the relative immobility of calcium in the tissues, an explanation which seems to apply equally to the trace elements.

Less attention has been paid to the mineral content of the rhizome although both Ferguson and Armitage (1944) and Hunter (1953) investigated this aspect. Hunter found that the rhizomes had a lower concentration of nitrogen, phosphate, and potassium than the mature fronds, a similar content of calcium, and higher levels of magnesium and sodium.

This analytical work by agricultural chemists has produced a fairly comprehensive picture of the major organic and mineral constituents of Pteridium fronds, and to a lesser extent the rhizomes. As far as nutritional value is concerned there is evidence that in terms of the protein, potassium, and phosphate levels, the very young fronds in May and June have a nutritional value comparable to that of more conventional feeding stuffs. However there is general agreement that the concentration of potentially useful components declines quickly as the growing season advances. It is hardly surprising that there is some variation in detail in the results of different analysts since there is methodological variation in the types of fronds sampled and in the subsequent drying and analytical procedure. It is possible however that some of the variation in mineral content may be ascribable to soil differences, a point investigated by Hunter (1953) who analysed the soils from which these bracken samples were taken. He found some positive correlation between potassium, phosphorus, and calcium levels in plant and soil but in general the variation in level of plant constituents was considerably less than the range found in the soil.

Whatever the theoretical nutritional value of Pteridium as revealed by laboratory analysis, the actual utilisation of the frond for livestock feeding has been bedevilled by the danger of inducing bracken poisoning. An investigation of this condition in animals together with the search for an effective herbicide control led to more sophisticated investigations of the enzymotic constitution of Pteridium at Rothamsted Experimental Station in the 1950s. A detailed synopsis of this research is beyond the scope of the present study. Suffice to say that Kenten (1955, 1956, 1957, 1958) concentrated on the enzyme thiaminase, present in Pteridium and absent from many higher plants. Evans, Jones and Evans (1950) had established the occurrence in bracken of this enzyme capable of destroying thiamine. Since the symptoms of bracken poisoning are those of acute thiamine (Vitamin B_1) deficiency the occurrence of this enzyme is obviously significant.

III. AUTECOLOGY

The history of the study of the autecology of Pteridium aquilinum is as old as the investigation of the plant's morphology, although the earliest writers tended to restrict themselves to incidental references to the habitat preferences of the fern. For instance Moore (1851) mentioned that Pteridium avoids chalk lands and is susceptible to frost, while Druery (1903) commented on the vulnerability of the sporeling to frost.

It appears to have been recognised at an early period that in any investigation of the autecology of bracken the two phases, gametophyte and sporophyte, must be treated separately. Spore germination and the development of the prothallus and young sporeling require different habitat conditions from the mature plant, the latter having a much wider range of tolerance. It has been mentioned above that prothalli are rarely found in the field in Britain (see page 12), a fact which reflects the vulnerability of the young plant to unfavourable environmental conditions and the rare occurrence of the necessary combination of factors for sexual reproduction of the fern at least in this country.

It had been appreciated before 1920 that spore germination requires a moist environment; Farrow (1915) attributed the occurrence of prothalli in rabbit burrows in the Breckland to locally moist conditions. Jeffreys (1917) working on the Durham Coalmeasure Fells also pointed out that moist micro-environmental conditions at the base of Ulex and Calluna plants and in clay cracks provided a suitable site for spore germination.

White (1930) investigated the spread of bracken by spores and suggested the possible significance of another parameter by noting the occurrence of prothalli on burned-over areas which he suggested might be attributable to a sterilisation effect.

The rarity of sexual reproduction in Pteridium stimulated Elsie Conway to initiate her classical systematic studies of the autecology of bracken in the late 1940s. In an early article in 1949 she summarised the results of past research which had indicated that preferred sites for prothalli development were moist habitats, old walls and mortar heaps, and burned over areas. It had been observed that sites bombed during the Second World War had apparently provided the necessary combination of conditions for sporeling development which were so rarely found in the normal environment of the fern. At this initial stage in her research Conway isolated a number of relevant parameters. Although light conditions were not significant in spore germination, the rate of subsequent prothallus development increased with light. Moisture had been established as a limiting factor, and germination appeared to favour a medium pH from 6-7. She suggested that prothallus development could be impeded by micro-organisms such as algae, perhaps due to competition for nutrients. Temperature influenced germination which was at an optimum from 50-60°F, stopped above 95°F and was considerably retarded at temperatures approaching freezing point.

Later research by Conway (1953a) revealed additional dangers to sporeling survival in the field. Laboratory experiments showed that the young sporophyte was very susceptible to frost which appeared to increase its vulnerability to a fungal pathogen. Since spore dispersal occurs late in the summer in Scotland the young plants have little chance of successful establishment before the onset of winter. In addition spores and young sporophytes were found to have other enemies; a number of soil collembola species feed on the young plant and Conway found a disease of prothalli under two months old caused by a new species of Telachidium. These microbial enemies probably provide at least a partial explanation of the favourability of fire-sterilised sites.

In 1957 Conway published the results of her survey of spore production in West Scotland, some of the findings of which have been enumerated above, (see page 13). She discovered that the variability of fertility in bracken fronds partly reflected local environmental conditions. Shade appeared to be a limiting factor, fertility being reduced in woodlands, while shelter was also significant as wind damage to pinnae reduced spore production.

During the 1950s both Conway and Stephens (1957) and Schwabe (1951, 1953) investigated the mineral nutritional requirements of the prothallus generation. Schwabe (1951) tested spore germination and prothallus development under laboratory conditions in which one major nutrient was completely omitted from the growth medium. He found that phosphorus was the most critical nutrient for both germination and prothallus growth, followed by nitrogen. Absence of potash, sulphur, and magnesium caused a slighter but still noticeable check, while absence of calcium appeared to be immaterial.

Conway and Stephens' (1957) investigation of the effect of sporeling development of mineral nutrient levels gave rather different results. However they worked with a different range of nutrient levels, investigating the effect on sporeling establishment of varying, but relatively high, levels of different nutrients, concentrations being within the normal arable range. High levels of nitrogen and potassium were found to stimulate sporeling development markedly, with phosphorus less effective. Moreover high calcium levels also induced a positive response. Nutrition was found to have a morphological significance; bracken in the nutrient-deficient situation in which it is normally found in the field, usually produces one frond bud per axis tip by the end of the growing season. When nutrient supplies were increased to agricultural levels more frond buds and secondary rhizomes were initiated.

Thus Conway's work in particular had by the late 1950s produced a fairly comprehensive picture of the autecology of the prothallus phase. It had been discovered that environmental conditions influence spore production, as well as germination and prothallus establishment and growth. At this point in its life cycle Pteridium had been shown to have rather specific requirements of moisture, temperature, and soil pH, and to be vulnerable to a number of insect and microbial pests. This work had done much to explain the infrequency of sexual reproduction of Pteridium, especially in the drier and more frost-prone areas of eastern Britain. These environmental restrictions are however in marked contrast to the toughness and tolerance of the established sporophyte.

Naturally a component of acid woodlands, but also an embarrassing success on open moorland up to 600 metres, Pteridium aquilinum flourishes in a variety of environments.

Bracken's niche in the undergrowth of woodlands focused the attention of ecologists on its reaction to shading. Salisbury (1918, p.31) cited an estimate by Weisner (1907) that Pteridium has a minimum light requirement of 5 per cent maximum diffuse illumination. Salisbury's own research on oak-hornbeam woods of Hertfordshire, suggested that bracken typically occurred where the shrub layer was sparse; his light requirement for individual plant survival was similar to Weisner but he considered that vigorous communities were restricted to places where light values rose to at least 11 per cent exterior illumination in the 'shade-phase'. This suggestion that bracken cannot tolerate the deepest shade of dense woodland is substantiated by Braid's (1934) observation that beech and spruce suppress growth, oak distinctly curtails it, but bracken flourishes under larch. It has been mentioned above (see page 31), that Conway identified shading as a limiting factor on spore production. It would appear that Pteridium vigour is controlled by shading in its woodland habitat and that its success as a plant of open moorland is partly due to the removal of this limiting factor.

However, closely related to the question of shading is bracken's need for shelter. This is some evidence that the limiting factor of shading in the woodland setting is replaced by the limitation of exposure in the moorland environment. Braid (1934) mentioned the frond's susceptibility to wind damage, a point he developed in his article on bracken control in 1947. He observed unhealthy bracken with frond discolouration on sites in Ayrshire where funnels within the grassy ground vegetation had developed at the base of fronds. He attributed this phenomenon to wind damage of the vascular tissue at the junction of rhizome and frond, while wind damage to pinnae may allow fungal penetration and subsequent browning of the fronds. Conway's (1957) identification of wind damage to pinnae as a limiting factor in spore production appears to substantiate these findings.

The other relevant climatic control is frost, which is a hazard to both the young sporophyte and the frond of the established plant. Long and Fenton (1938) noted that frost kills young fronds but rarely affects rhizomes, while many writers have referred to the resilience of the bracken plant in sending up new fronds should the early emerging ones be damaged by spring frosts. In environments where severe winter and spring frosts are common this factor appears to exercise considerable control on the advance and retreat of bracken, an aspect studied in detail by Watt (1954) on the Breckland. He found that the margin of bracken stands in frost pockets fluctuated in extent from 1936 to 1952 but that, in contrast to neighbouring sites, no overall advance was achieved. The presence or absence of bracken litter influenced susceptibility to frost damage. When there was little frost, the fronds in the advancing front emerged first since there was no litter cover to retard soil heating. Conversely, the insulating effect of the litter gave the crest fronds the advantage when severe winter frosts occurred. The potential severity of frost damage is highlighted by Watt's observation (1954, p.118) that shoots were killed to a depth of 19.5 cm in the soil in the particularly severe frosts of 1940.

Later research by Watt (1956, 1967) indicated the influence of frost on the structure of the Pteridium stand. For instance ring formation, i.e. the development of patches of bare ground or stunted fronds within a bracken stand, was attributed (Watt, 1956) to frost damage of the shoots induced by litter removal by Man. This explained the occurrence of the most fully developed rings within the tallest stands of Pteridium, conditions favourable to the development of frost pockets. The incidence of spring frosts was also shown (Watt, 1967) to influence the development of senescence in a Pteridium stand. Young shoots are the first to send up fronds in spring. If these are damaged by frost, the older shoots are stimulated to frond production. Under these conditions the food reserves of the older shoots rather than the younger are replenished leading to an ageing population of shoots and senescence in the Pteridium stand.

The influence of the edaphic factor on Pteridium growth has been a subject of considerable controversy, soil depth, moisture content, pH, and nutrient status all being suggested as relevant parameters. Several writers including Gordon (1916) and Braid (1934) mentioned bracken's preference for deep soils but provided little supporting evidence. Watt (1964) provided more concrete evidence of the significance of soil depth by showing a significant correlation between various indices of Pteridium vigour and soil depth. Watt's suggestion that this effect may be related to soil water supply on the dry sandy soils of the Breckland raises the possibility that soil depth may be more significant where water supply may be a limiting factor due to climatic or edaphic conditions.

The fact that Pteridium aquilinum occurs at all on sand dunes in the Breckland highlights its tolerance of dry soil moisture conditions compared to most ferns, Salisbury (1944) also noting its occurrence on dry, alkaline sand dunes. Recent research has suggested possible morphological reasons for this tolerance. Tinklin and Bowling (1969) compared the water relations of Pteridium with Dryopteris filix-mas by correlating leaf water status with rates of atmospheric evaporation. In the case of Pteridium the curve was U-shaped, the initial fall in leaf-water content with increasing evaporation rates being arrested and then reversed as the relative water content actually rose at high evaporation rates. In Dryopteris filix-mas there was sustained dehydration of the leaf. They suggested that Pteridium controls water loss by transpiration by stomatal closure.

While tolerant of edaphic drought, Pteridium's dislike of waterlogged soils has long been appreciated. Indeed irrigation of hill pasture was a nineteenth century technique for bracken control (McTurk, 1837; Murray, 1837). Gordon (1916), Long and Fenton (1938), and Salisbury (1944) all mentioned Pteridium's dislike of excess soil moisture, while Braid (1934) described sites on which a bracken plant was pushing out rhizomes into a poorly drained area which could only be maintained at the expense of the parent plant. Subsequent drainage was observed to permit the plant to become self-supporting, while conversely on sites with a rising water table bracken plants were noticeably losing vigour.

At a later date Poel (1951) studied the relationship between Pteridium and soil waterlogging and was successful in halting the fronds by irrigation although the rhizomes were only slowly affected. He noted that the fern, although intolerant of stagnant, waterlogged conditions would tolerate excessive water provided it was adequately aerated, and concluded that oxygen deficiency rather than excessive water *per se* is the controlling limiting factor.

A more controversial aspect of the edaphic preferences of bracken is its pH range. The fern's avoidance of chalk soils led writers such as Long and Fenton (1938) and Salisbury (1944) to conclude that it cannot tolerate calcareous conditions. De Silva (1934) however considered that Pteridium has a rather wide range of tolerance of pH from 4.6 - 6.2, although it is usually found on soils devoid of $CaCO_3$ and low inexchangeable calcium. That bracken is not a true calcifuge is suggested by De Silva's observations that it is found associated with *Mercurialis perennis* on soils with moderate levels of exchangeable calcium, a result supported by the work of Hope Simpson (1938). The latter examined the flora of a Lower Greensand area which had been rendered calcareous by the addition of chalk for agricultural purposes. This soil had a pH of 7.4 and relatively high calcium levels, yet it supported bracken, albeit reduced in vigour and apparently, from visual evidence, suffering from a degree of lime chlorosis. It has been noted above (see page 31) that Conway and Stephen's (1957) research on sporeling establishment had shown a positive response to liming, again questioning the classification of the fern as a calcifuge.

However, although bracken may not be an obligate calcifuge, the weight of evidence suggests that it usually attains its greatest vigour on soils at the acid end of the scale but has a wide range of tolerance. Gordon's statement (1916, p.94) that it dislikes acid conditions is not substantiated by later evidence. Braid (1940, p.32) gave the pH range of bracken soils as 3.54 - 4.38. Poel (1951) suggested that the optimum pH was higher (around 5.5), while Hunter (1953) gave the pH of the A horizon of ten bracken soils as ranging from 3.6 - 6.2. These results are in line with those of Heath and Luckwell (1938) in their article on the rooting system of heath plants. Analytical data was given for different depths of a <u>Pteridium</u> - dominated soil, sampled monthly from November to February. The mean pH increased with depth, from 4.6 at 4 cm, to 5.4 at 15 cm, and 6.3 at 23 cm.

While many research workers have investigated the pH of bracken soils, few have undertaken detailed studies of the nutritional requirements of the sporophyte generation. One exception is Schwabe (1951, 1953) who followed up his investigation of the nutrient requirements of the prothallus with a study of the effect of phosphate, potassium, and nitrogen supplies on various indices of growth in the sporophyte. Bracken plants were grown in a range of concentrations of potash and phosphate solutions with a variety of cations as carriers. Schwabe found deficiency of phosphate, potash, and nitrogen all had extremely detrimental effects on plant growth with extreme nitrogen deficiency being particularly lethal. Despite the fact that high potassium levels are often found in *Pteridium* in nature, plants were in fact less affected by potash deficiencies than by equal reductions in phosphorus, suggesting that luxury absorption of potash may occur.

Thus the considerable amount of research conducted on the autecology of bracken has revealed a plant which in the prothallus generation of its life cycle has quite specific environmental requirements, in marked contrast to the wide range of tolerance exhibited by the mature sporophyte. Heavy shading, exposure, anaerobic soil conditions, and frost emerge as the main limiting factors to bracken vigour but both the global range of the fern and the variety of British environments in which it occurs, from oak woodlands and even sand dunes to moorland at over 500 metres,testify to the environmental tolerance of *Pteridium*.

IV. SYNECOLOGY

While the literature on the morphology and autecology of bracken is extensive, the literature on the bracken community and ecosystem is noticeably sparse. The work done has focused on the effectiveness of *Pteridium* as a competitor and on qualitative descriptions of bracken communities.

The earliest references to the effect of Pteridium on associated herb layer species are found in the ecological literature of the first quarter of the twentieth century. Jeffreys (1917), in his work on the Durham Coalmeasure Fells, noted that in areas where bracken was completely dominant Holcus mollis was the only vascular species to persist in the herb layer, while Deschampsia flexuosa, Calluna vulgaris, and Vaccinium myrtillus were found in open areas of the stand. He attributed this differential response to bracken dominance partly to resistance to shading, light intensity under Pteridium being estimated at 5 per cent light intensity outwith the fronds. He regarded this degree of shading as adequate reason for the exclusion of Calluna and Nardus stricta from areas of dense frond growth, the former being obliterated by light reduction to 10 per cent and the latter to 30 per cent. However he believed that the exclusion of Deschampsia flexuosa and Vaccinium could not be explained in these terms as they survived in association with heavy Calluna and Ulex europaeus growth which produced even heavier shading than the fern.

Jeffreys postulated that the heavy litter associated with bracken might have a more deleterious effect on the ground layer than the growing frond population. This litter effect he suggested might have three components: a shading effect estimated at 2.5 per cent external light intensity under heavy litter, even more severe than the frond effect; increased water content of the soil due to the reduction of evaporation by the litter mulch and postulated toxic substances released by the decaying litter. In isolating the effect of these three factors, Jeffreys postulated that the toxic effect would only be manifest after decomposition had started, while fresh litter would be equally effective shade-producers, testing this with experimental plots. He concluded that *Ulex* was halted by shading alone, which might also contribute to *Nardus* destruction, but he believed that the eradication of *Deschampsia flexuosa* and *Calluna vulgaris* was attributable to toxic effects, while *Holcus mollis* was resistant to both.

There appears to be some ambiguity within Jeffrey's work on the relative importance of shading and toxic substances in checking heather growth and Farrow (1917) challenged these conclusions. He estimated light reduction by dead fronds as 1.67 - 1.04 per cent exterior light intensity and suggested that light reduction alone would be sufficient to kill *Calluna*, without postulating toxic factors. He claimed in support of this that *Calluna* was killed before litter decomposition started, thus ruling out toxic effects.

Since that time the toxic substances hypothesis has gained little support, the main emphasis being placed on shading as the competitive weapon of *Pteridium aquilinum*.

Salisbury (1918) and Hopkinson (1927) both studied bracken as a component of woodland ecosystems. The former, in his work on the oak-hornbeam woods of Hertfordshire, estimated that *Pteridium* fronds reduced light intensity to 8 per cent external diffuse light intensity, a value which agrees approximately with the findings of both Jeffreys and Hopkinson. The latter, working on oakwoods in Nottinghamshire, estimated that 0.4 - 10 per cent light penetrated to the herb layer where bracken dominated the shrub layer. Where bracken was densest the ground vegetation was obliterated but thinning of the frond canopy allowed the invasion of *Holcus mollis*, *Deschampsia flexuosa*, and *Galium* hercynicum.

Hopkinson also examined bracken communities outside the woodland and found that where light intensity was over 2.4 per cent Deschampsia flexuosa dominated the herb layer, a finding at variance with Jeffreys' results. However he noted that light depression to less than 12.5 per cent appeared to prevent Deschampsia flowering. Like Jeffreys he emphasised the shading effect of the litter rather than the growing fronds as a limiting factor on the germination of Deschampsia, but in marked contrast to earlier workers suggested that conditions under the canopy were too dry for such germination rather than too moist. More recent research on the autecology of Deschampsia flexuosa is relevant to this argument. Hackett (1967, p.837) in his study of the nutrition of Deschampsia flexuosa suggested that the grass's growth in beech woods was inhibited by desiccation in the loose, deep beech litter, a situation which may have some analogy to the bracken community.

On moorland sites Pteridium is frequently in competition with Calluna vulgaris. It was recognised by students of moorland vegetation in the 1930s that the competitive situation on rough grazings would be influenced by Man's activities. For instance E.W. Fenton (1937) suggested that the replacement of sheep by cattle on Scottish hillsides had favoured the fern while heavy muirburn of Calluna was noted to have a similar effect, the rhizome system of Pteridium being less inhibited by burning than the growing points of heath plants.

D.A. Ratcliffe's (1959) work on the Carneddau describes similar responses to human activities on Welsh rough grazings, where heavy biotic pressure and burning led to degeneration of Callunetum and replacement by mixed communities in which bracken was prominent.

A more detailed investigation of competition between Calluna and Pteridium was made by Watt (1955) on a Breckland site. He described a situation in which the relative vigour of the two species was unrelated to environmental conditions but appeared rather to reflect the developmental stage of the communities which influenced the growth habit and size of the plants. Calluna was suppressed where Pteridium was advancing over a continuous front but the opening of the frond canopy in the hinterland of the Pteridium stand allowed the colonisation of heather from seed. A Calluna community of even-aged plants in the building phase was capable of suppressing bracken but where the Callunetum was uneven-aged or had been reduced in vigour by rabbit grazing or fire, bracken gained the ascendancy.

In addition to these studies of the competitiveness of Pteridium, qualitative descriptions have been made of the two communities in Britain in which bracken is an important component - the deciduous woodland, particularly the oakwood, and the grass moorland. On the face of it these two communities are so different structurally and ecologically that they might appear to bear little relationship to each other. However the literature suggests that there is in fact an interesting overlap in species composition between the two ecosystems. The account of Jeffrey's work on grasslands and Hopkinson's on oakwoods given above (see pages 39-41.) shows that Holcus mollis and Deschampsia flexuosa were prominent herb layer species in both situations. Holcus mollis was also cited as a common associate of Pteridium in the oak-hornbeam woods of Hertfordshire (Salisbury, 1918) although the other enumerated associates, Rubus fruticosus, Lonicera periclymenum, Teucrium scorodonia, Scilla nutans, and Anemone nemorosa are more restricted woodland species.

The relationship between the woodland and moorland ecosystems was set in its theoretical framework by Tansley (1939) in his classic work on the British Isles and their vegetation. He regarded bracken as a woodland species which has survived deforestation to become dominant in a moorland environment and in so doing has created a microenvironment in which other woodland species can persist. The moorland bracken community can be regarded as a relic community which at least in some cases still shows evidence of its woodland origin. In support of this approach Tansley quotes Pethybridge and Praeger (1905) who in their research on the Wicklow Mountains described bracken communities in early spring which had a luxuriant growth of woodland species such as Primula vulgaris, Endymion non-scriptus, Viola, and Ranunculus ficaria.

However these woodland species associated with bracken-dominated rough grazing are usually rather insignificant in terms of cover-abundance, the herb layer normally being dominated by species, such as Festuca ovina and Agrostis tenuis, which are widespread in moorland vegetation. Indeed moorland ecologists have commonly regarded Pteridium aquilinum as merely an invader of the bent-fescue community, rather than as a community-type or nodum in its own right. For instance, in Burnett's (1964) descriptive work on Scotland's vegetation, King and Nicholson state that species-poor Agrosto-Festucum is frequently invaded by Pteridium aquilinum which may result in the co-dominance of Holcus mollis or, with high fern density, in the complete elimination of the grass sward (Burnett, 1964, p.189).

Several other workers have described Pteridium moorland in various parts of the country. For instance Leach (1931) enumerated the common associates of bracken on the Longmydd. A few attempts have been made to describe the variation in herb layer composition with varying bracken density. Watt (1947), for instance, described the ground vegetation of his various 'phases' of the bracken community for a small number of samples. Predictably the smallest number of species was associated with the mature phase, while *Agrostis* species, *Luzula campestris*, *Rumex acetosella*, and several mosses were prominent in the pioneer, building, and degenerate phases.

Poel (1949) is perhaps the only worker who has attempted a detailed definition of different bracken associations on moorland sites on the basis of the degree of dominance of the fern. On his study area at Ballochraggan in Perthshire he recognized three bracken associations: 'pure' *Pteridium aquilinum*, *Pteridium-Holcusetum*, and *Pteridium Festuco-Agrostidetum*. The 'pure' *Pteridium* occurred where the density of fronds was sufficient to almost completely obliterate the herb layer although several species such as *Holcus mollis*, *Scilla nutans*, and *Anthoxanthum odoratum* occurred. A reduction in bracken cover by cutting resulted in a *Pteridium-Holcus mollis* nodum while further thinning of the fern canopy produced a *Pteridium-Festuco-Agrostidetum* nodum. A large number of species could occur in the latter community but with *Agrostis tenuis*, *Agrostis canina*, and *Festuca ovina* dominant.

The drawback of Poel's study is that there was no attempt to quantify the degree of dominance of *Pteridium* associated with these three community types. Like Watt, he recognized that the composition of the herb layer varies with variation in bracken cover but both produced basically qualitative descriptions of bracken stands in the course of investigations aimed primarily at other aspects of bracken communities.

An attempt has been made to quantify Pteridium cover and relate this to herb layer composition by Nicholson and Robertson (1958). In a study of the ecology of upland grazings in the Grampian foothills, which in fact concentrated mainly on Callunetum, four Pteridium communities were briefly described. Pteridium cover was estimated on a percentage basis while the relative importance of herb layer species was described in the Tansleyan terms - dominant, co-dominant etc. Where Pteridium cover was 80 per cent, Agrostis species, Deschampsia flexuosa and Galium hercynicum were the main species. At 100 per cent Pteridium cover Oxalis acetosella assumed dominance.

The prominence of Pteridium aquilinum on rough grazings in this country gives it an economic significance. The plant has been virtually universally condemned as a weed in agricultural circles, but only one study has investigated the possible contribution of bracken communities to the grazing potential on an area of extensively grazed mixed moorland. Hunter (1954) published the results of a laborious investigation of the seasonal variation in comparative grazing intensities by sheep of various sward types on an area of rough grazing. His general conclusion was that, while there are some preferred communities which support relatively high grazing intensities in comparison to others, there is a marked seasonal variation in grazing pattern, most moorland communities being utilised at some period of the year. The Pteridium community involved was the typical Pteridium-Festuca-Agrostis type with relatively open bracken. This was grazed throughout the year at an intensity greater than its share of the total acreage would suggest. However it tended to be neglected during the growing season of the frond when abundant grazing was available elsewhere, but when the fronds died back in September it provided a useful 'backend' bite on the accumulated summer growth. Grazing intensity fell to a minimum in January and February to rise again in the pre-frond emergence period in March and April. This result of course does not seriously challenge the view that bracken eradication would further increase the grazing value of the sward since Festuco-Agrostis stands without Pteridium were Hunter's most intensely grazed sward type.

The above summary shows that several ecologists have investigated bracken-dominated vegetation. On the other hand very little systematic work has been done on the dynamics of the bracken ecosystem or the plant's relationship to the underlying soil. One noteworthy exception is Carlisle, Brown and White's (1967) investigation of the contribution of a Pteridium understorey to nutrient cycling in an oak woodland. They examined the relative contribution of the tree and bracken strata to the nutrient supply at ground level, and showed that the bracken litter provided more than its share (as a proportion of weight) of phosphate and more especially potassium, but a relatively low percentage of calcium. Significant quantities of magnesium, potassium, and phosphate were also added as throughfall from the fronds and they concluded that Pteridium played an important role in nutrient cycling, particularly of potash, a result which accords with the chemical analysis of the fern. It must be borne in mind that this study is restricted to the aerial parts of the plant and the nutrient supply from fronds and petioles must constitute only a proportion of nutrients entering an ecosystem from the bracken plant, the perennial portions, analogous to the trunks of the oak trees, being underground.

This question of bracken as a source of nutrients was also touched upon by Nicholson (1964). Using G.G. Hunter's analytical data as a basis, he calculated the nutrient loss per acre involved in the cutting and removal of Pteridium fronds, a common practice when fronds were used for purposes such as bedding and thatching. Again the analogy is with the nutrient loss involved in harvesting timber. Nicholson postulated that bracken may play a positive role in maintaining soil fertility and that while the bracken community may be relatively worthless in terms of grazing value, in terms of long-term fertility maintenance it may be more valuable than the more highly regarded heather and bent-fescue communities. Unfortunately Nicholson offered no supporting evidence for this viewpoint.

Finally a specialised study has been made of the decomposition of bracken litter by Juliet Frankland (1966) who studied the sequence of decomposers on bracken petioles on six different sites. Decomposition was universally slow, fungi being the main organisms involved. The limiting factors in decomposition appeared to be the availability of nutrients, most of the readily-soluble nutrients having been lost before the litter stage was reached, and the physical state of the substrate.

This summary of synecological research emphasises that while bracken communities have been studied on many sites and general descriptions of the vegetation produced, this has been done as part of general vegetation surveys or incidental to a study of some other aspect of bracken. There has been little attempt at systematic investigation of the variations in species composition within bracken communities, or at evaluating the contribution of the fern to the structure and functioning of the ecosystems of which it is such a prominent component.

CHAPTER 3

FIELD METHODOLOGY

The aim of this research project, as defined in Chapter 1, is to investigate the influence of Pteridium aquilinum on the moorland ecosystem of which it is the dominant plant. Instead of regarding bracken as merely an invader of rough grazing communities, it is recognized that large areas of Scottish moorland support a two-tiered vegetational system in which the upper stratum is composed entirely of Pteridium aquilinum. This canopy of fronds necessarily modifies the microenvironment of the herb layer and influences the pedological processes in the underlying soil mantle. It is postulated that the degree of modification of the microenvironment depends on the height and density of bracken fronds, and is reflected in the vigour and species composition of the ground vegetation.

It has been pointed out above (see page 5) that there are a number of possible methodological approaches to the investigation of the effect of Pteridium aquilinum on a moorland ecosystem. The method selected in this case is a field and laboratory investigation of the vegetation and soil conditions found in association with bracken communities compared to those existing in adjacent moorland communities. This approach is made possible by the fact that, while in some cases bracken distribution is determined by the habitat preferences of the fern, a factor which for instance influences its altitudinal range, in other cases the margins of the stand do not coincide with changes in environmental conditions. Frequently Pteridium has failed to colonize all potentially suitable sites on an area of rough grazing and bracken stands are found juxtaposed against other freely drained grass or heath communities. In these cases it must be assumed that the community boundaries are dictated, not by habitat conditions, but by competition between the dominant species, competitive vigour being frequently influenced by human interference. As defined above (see page 5), these boundaries have been termed 'sociological' for the purposes of this study to distinguish them from habitat-controlled 'ecological' boundaries. In some cases where Pteridium is actively advancing or retreating sociological boundaries may be of a very temporary nature; in others a relatively stable competitive balance appears to have been reached, producing more or less stationary stand margins. Unfortunately in the absence of historical data on community boundaries it is frequently difficult to distinguish categorically between temporary and semi-permanent margins.

Thus in this study of the influence of Pteridium aquilinum on its associated vegetation and soils, the basic approach chosen is the field study of the effect of bracken on sites where vegetation is the only discernible macro-environmental variable. This approach focuses attention on vegetation and soil conditions across sociological boundaries of bracken stands and within stands of variable frond height and density.

The selection of study sites and the choice of field data and method of collection are to a large extent dictated by the hypothesis and basic approach outlined above. Several requirements must be satisfied:

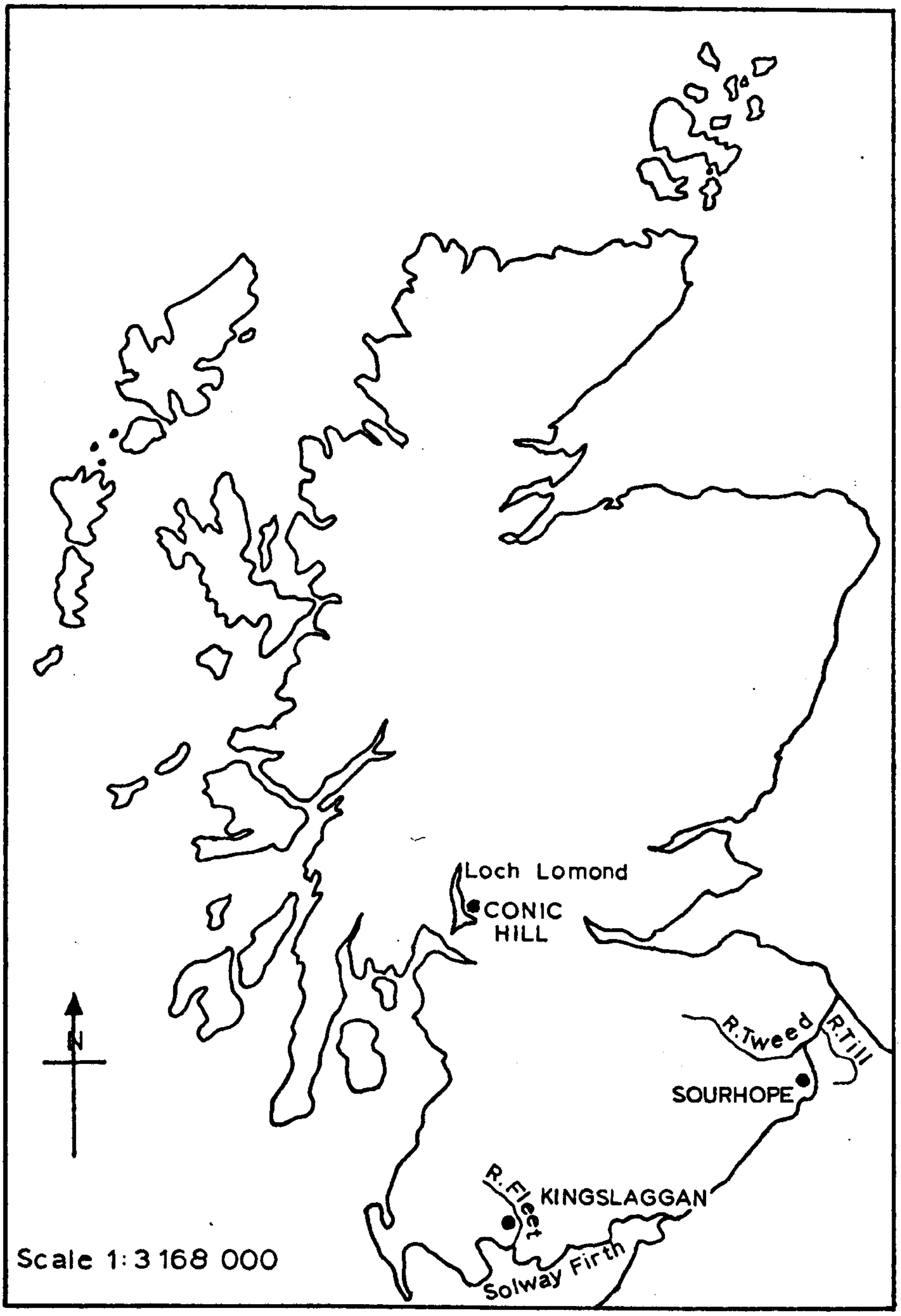
(1) It is obviously necessary to select sites supporting well developed bracken stands of variable density where bracken distribution is not solely controlled by habitat conditions. The study of the effect of bracken a propos of a variety of moorland communities, and in conditions producing a variable degree of fern vigour, necessitates the selection of sites offering a range of environmental conditions, particularly of macroclimate and geology.

(2) The nature of the topic demands the collection of a wide range of data at each site. Since interpretation of results is to be based on the tenet that bracken density and height are the only significant environmental variables, the visual evidence of sociological boundaries must be supported by the collection of evidence on other environmental parameters. Vegetational information required includes detailed, and preferably quantifiable, data on the degree of dominance of Pteridium aquilinum. To investigate the modification of the herb layer by bracken growth details of both total cover and biomass of the ground vegetation and of its species composition must be assembled. Finally the collection of soil data in the field is necessary.

1. SITE SELECTION

The time available permitted the investigation of three major sites. These were selected from different parts of the country, the western Southern Uplands, the edge of the Southwestern Grampians, and the Cheviots, to provide a range of macro-environmental conditions (Fig. 3.1). Differences in altitude and climate produce vegetational contrasts between the three sites, both in terms

Fig. 3.1. LOCATION OF SITES



of bracken vigour and of the species composition of associated and adjacent plant communities. The geological contrasts between the sites are particularly significant in their effect on the parent material from which the soils are derived.

Kingslaggan.

The first site, Kingslaggan, in the Galloway uplands, is located in the hills south of the Cairnsmore-of-Fleet massif. This area of rough grazing covers the slopes of two hills, Kenlum Hill and Doon Hill, to the east of the Skyre Burn which flows into the estuary of the River Fleet.

The climate of Kingslaggan is influenced, not only by its location in the temperate southwestern corner of Scotland, but by its proximity to the sea, the Solway Firth being only four miles distant. Thus of the three sites, Kingslaggan has the most temperate climate, and one well suited to vigorous bracken growth. Winters are relatively mild, with an average January temperature of 3.3°C while in summer temperatures averaging 14°C in July are similar to those on the other sites*. Frosts are normally restricted to the November and late April period but there is on average considerably less snow than in the Highland and Cheviot areas. In terms of rainfall amounts, Kingslaggan with 1143 mm annually is intermediate in character between the wet Grampians and drier Cheviot sites, with a well-defined winter maximum.

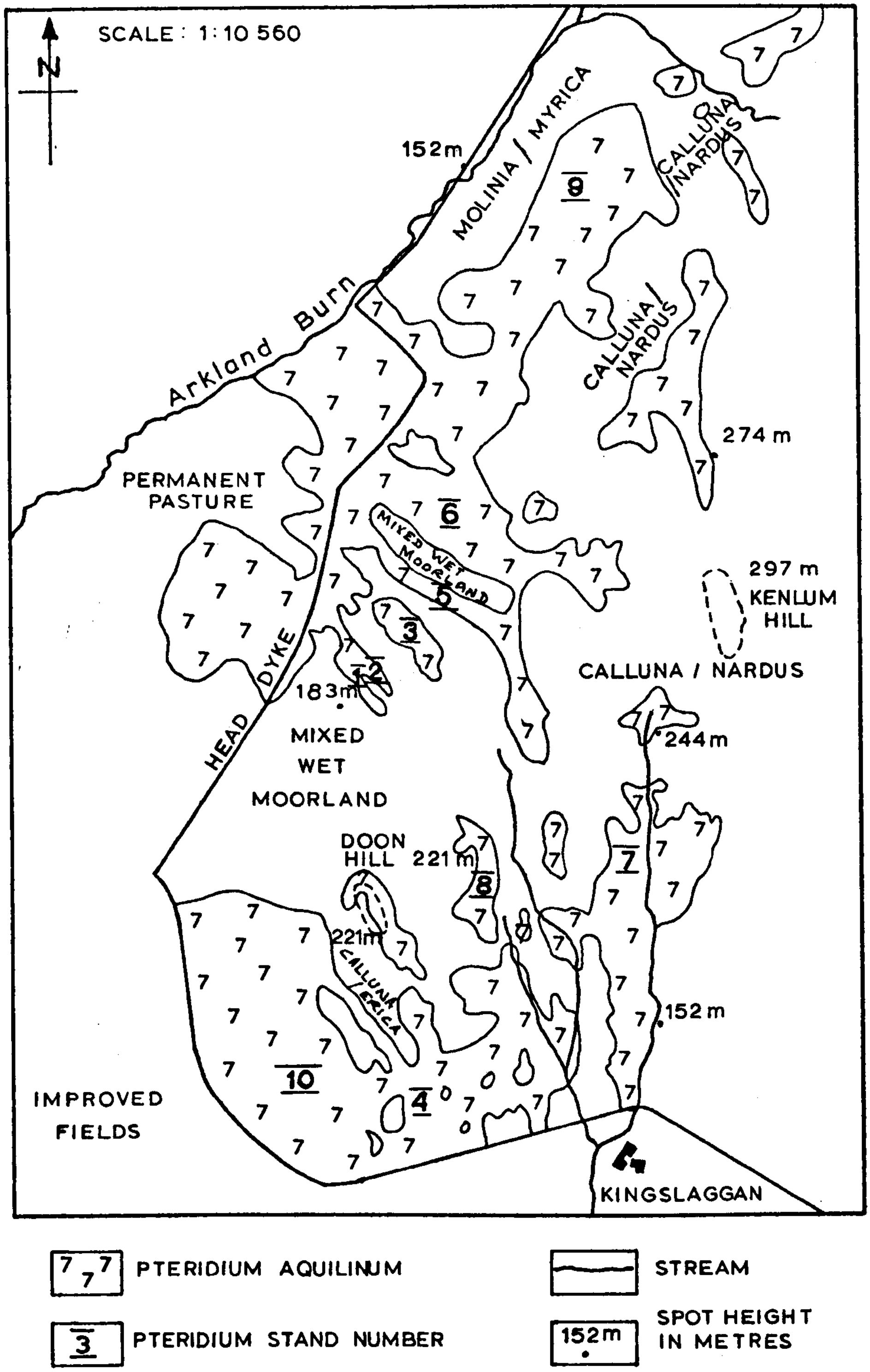
Although quite modest in altitude, rising to a maximum of 297 m, Kenlum and Doon Hills have the rather rough and rugged surface relief typical of the

*See 'Section Notes' at the end of this chapter. Throughout the thesis all notes are inserted at the end of the relevant chapter.

Galloway terrain. The bedrock of Silurian shale forms the parent material of much of the area. Where there is a till cover, derived mainly from shale but with some granitic components, it is thin resulting in a shallow soil mantle. The only exceptions are the deeper soils associated with colluvial material on parts of the lower slopes.

Investigations were concentrated on the southern and western sides of the hills, the lower slopes of which, up to 152 - 168 m, are enclosed into permanent and rotational pastures. The most vigorous bracken growth occurs at the level of the head dyke, the fern occupying some of the poorer permanent pasture below this level and invading the rough grazing above it, up to a normal maximum of approximately 214 m although sparse *Pteridium* is found almost to the summit of Kenlum Hill. (Fig. 3.2). In close juxtaposition with these *Pteridium* stands on the lower slopes is the mixed wet moorland commonly found on the Galloway uplands. No one species is consistently dominant in this wet moorland but in drier areas *Calluna vulgaris* and *Nardus stricta* are the main components with *Molinia caerulea*, *Erica tetralix*, and *Sphagnum* species becoming more significant on damper sites. Upslope from the main bracken stands a simpler *Calluna vulgaris-Nardus stricta* community takes over.

Significant differences exist between the western and southern slopes in terms of both detailed relief and vegetation. The western slope bordering the Arkland Burn has a relatively smooth surface relief, the most pronounced feature being a gently sloping bench occupied by *Pteridium* Stand 9 (see Fig. 3.2), the largest and most vigorous stand on the Kingslaggan site with fronds up to 130 cm. In general the distribution of bracken within this area is controlled


SCALE : 1:10 560
N
152m
MOLINIA / MYRICA
CALLUNA / NARDUS
9
Arkland Burn
CALLUNA / NARDUS
274 m
PERMANENT PASTURE
6
MIXED WET MOORLAND
5
3
2
297 m
KENLUM HILL
CALLUNA / NARDUS
183m
HEAD DYKE
244m
MIXED WET MOORLAND
DOON HILL 221m
8
7
221m
CALLUNA / ERICA
152m
10
4
IMPROVED FIELDS
KINGSLAGGAN
PTERIDIUM AQUILINUM
PTERIDIUM STAND NUMBER
STREAM
SPOT HEIGHT IN METRES

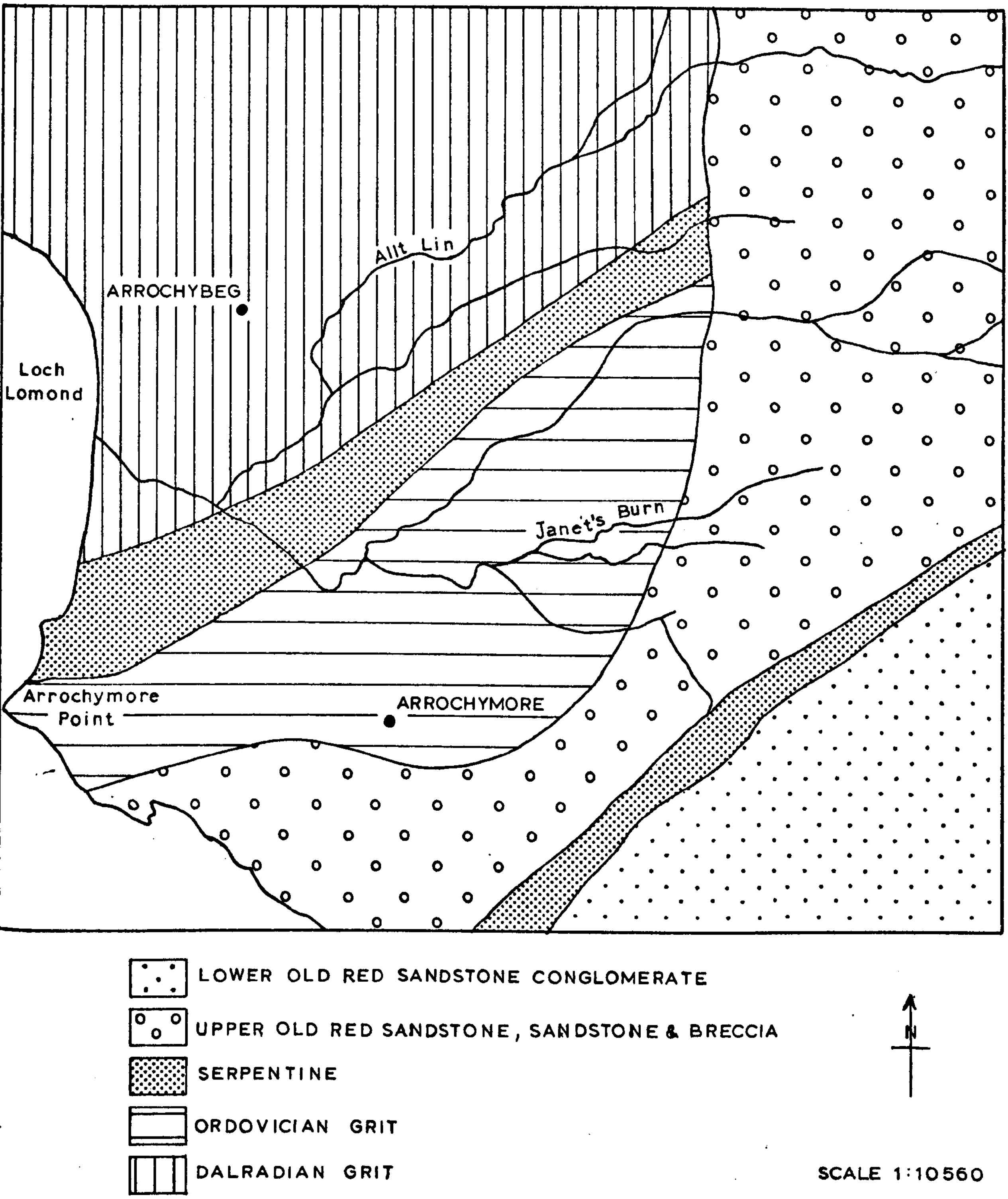
partly by relief and drainage, the upslope limit coinciding in places with breaks of slope and rocky outcrops while wet flushes and boggy valley floor situations are avoided by the fern. However in many instances the boundaries of the bracken stands occur on smooth slopes with no discontinuity in habitat conditions, providing several clear sociological boundaries for investigation.

On the southern slope relief is much more broken. The hillside is scored by small south-trending channels separated by steep-sided spurs and rocky knolls. The head dyke area and lower slopes of the channels form the nuclei of _Pteridium_ growth from which centres bracken fingers uphill along the channel sides to peter out on rocky knolls and ridges where _Calluna vulgaris-Erica cinerea_ and _Calluna vulgaris-Nardus stricta_ communities take over. In this rather hostile environment for bracken _Pteridium_ stand margins tend to be controlled by soil depth and fewer suitable sociological boundaries exist.

Conic Hill

The other western site occupies the northern slope of Conic Hill on the east side of Loch Lomond. The situation of Conic Hill on the line of the Highland Boundary Fault results in the complex geological pattern shown in Figure 3.3. The slopes of Conic Hill, above approximately 90 metres, are derived from rocks of Upper Old Red Sandstone age which also extend to the loch shore in the southern part of the area. Most of the bracken stands examined are underlain by this rock formation which lies unconformably on the Ordovician grits which occupy the lower slopes to the north. The Old Red

Fig. 3.3. CONIC HILL, GEOLOGY



(from Bassett, D.A., 1958).

Sandstone rocks are diverse both lithologically and structurally, coarse conglomerate strata with fairly large pebbles being interstratified with finer sandy layers. In addition to quartz and quartzite pebbles, schistose material occurs within the conglomerates.

The geological picture is further complicated by intrusions of serpentine associated with the Highland Boundary Fault and Serpentinite Fault, the more southerly one outcropping along the ridge Druim Nam Buraich. North of Arrochymore Point another broad fracture-zone contains serpentine rocks. (Anderson, 1946).

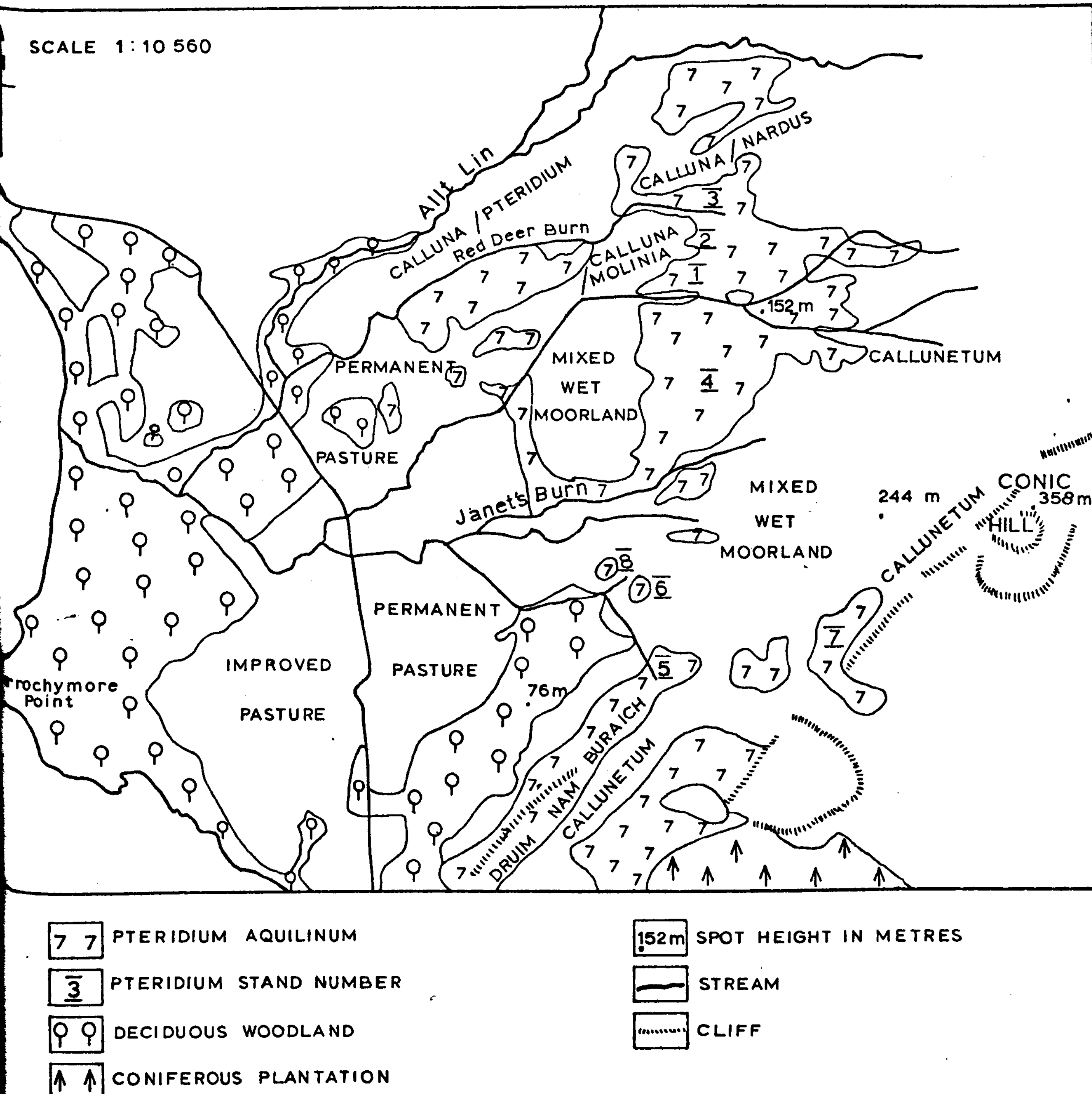
This complex geological situation obviously produces soil parent material which is more diverse than that found at Kingslaggan. While bedroch outcrops in many parts of the summit area and steep upper slopes of Conic Hill, the lower slopes have a till covering of varied lithological character, serpentine and the weathering products of the conglomerates and sandstones being found in varying proportions.

The climate of Loch Lomondside is broadly similar to that of Kingslaggan but modified by its more inland situation and proximity to a more extensive mountain mass. Thus while average temperatures (3.2°C in January and 13.8°C in July) are very similar to those found on the Galloway site, the greater severity of the winters is evidenced by the longer period of frosts which occur normally from mid-October to mid-May and in the greater frequency of snow. Rainfall totals within this mountainous area are also higher, approximately 1462 mm annually with, like Kingslaggan, a winter maximum.

The influence of geology can be seen in the relief of the Conic Hill area, the conglomerates of the upper slopes producing typically steep, and in places precipitous, slopes. The summit at 358 m has a distinctive humped appearance produced by a series of extremely steep-sided rounded bosses from which a series of ridges run in a south-westerly direction along the line of the Highland Boundary Fault. Below this level there is a sharp break of slope to a gently sloping broad surface into the edge of which deeply incised gullies have been cut by the upper reaches of a number of south-west flowing streams. From there the land falls more gently to the woodland and farmland of the loch shore.

It is evident from Figure 3.4 that the main zone of Pteridium growth occurs from 90 to 180 m on the edge of the broad surface below the upper ridges. Below this level woodland and pasture form the vegetation cover while the limited gradient between 180 and 240 m results in impeded drainage and a mixed wet moorland vegetation in which bracken only finds a foothold on isolated better drained knolls. The best habitat for bracken is on the sheltered slopes of the deep gullies from where the fern spreads to the crests of the intervening spurs. In these situations bracken stands have to compete with Calluna-dominated communities and many clear sociological boundaries exist between Calluna vulgaris, Nardus stricta and Calluna vulgaris-Molinia caerulea communities on the gully sides and ridges. The natural advantages of these slopes for bracken growth result in the most vigorous Pteridium of any of the sites examined - pure stands with fronds up to 140 cm in height. On the summit slopes bracken has a much more precarious foothold, but stands are found on the ridges and intervening channels up to the summit cliffs. The

. 3.4. CONIC HILL SITE



relative competitiveness of Calluna vulgaris and Pteridium on these slopes has been influenced by management practice; heavy burning has tended to tip the competitive balance in favour of bracken on certain sites as well as encouraging severe soil erosion.

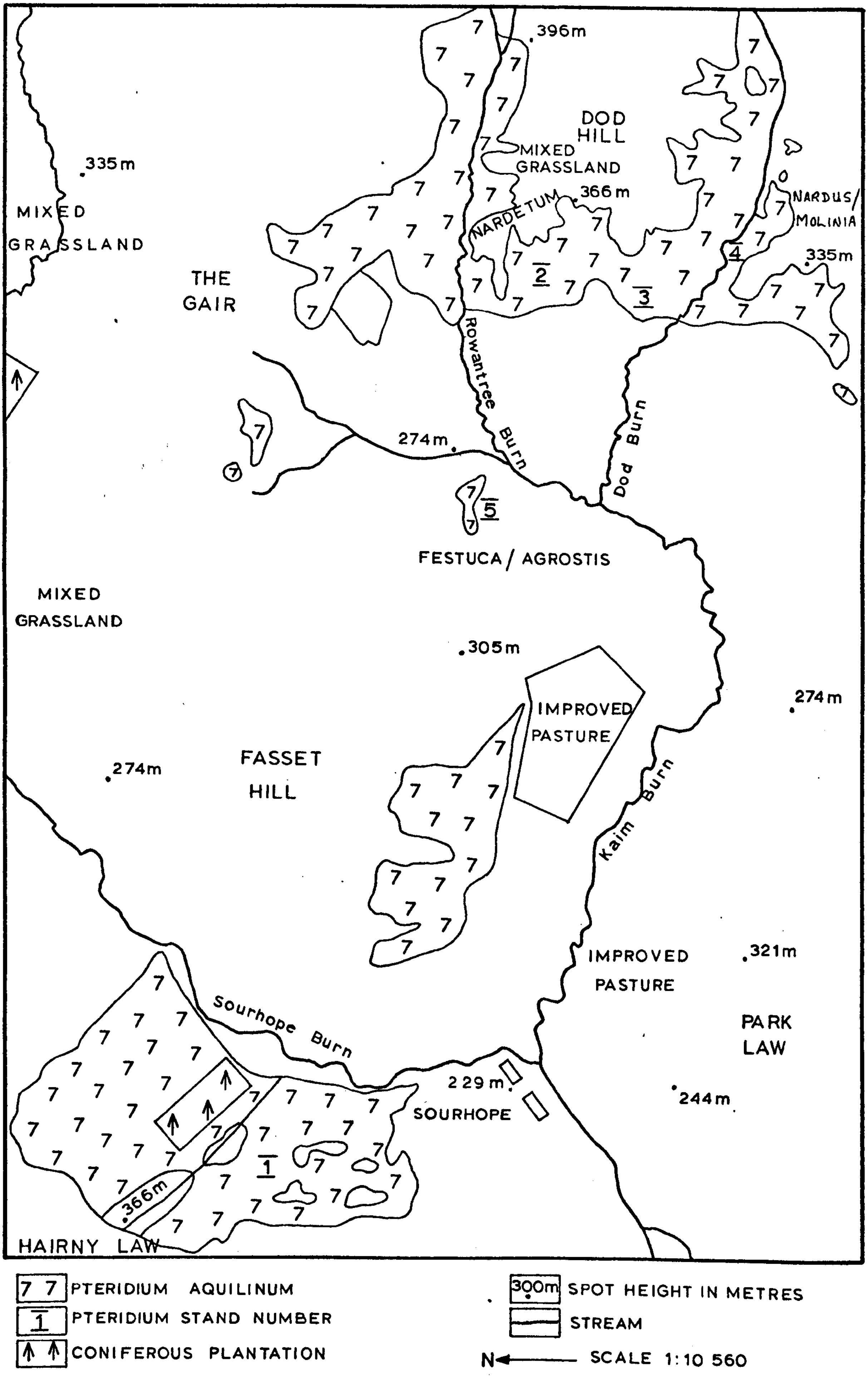
Sourhope

The third site was selected from the very different environment of the Eastern Borders. Sourhope, a Hill Farm Research Organization research station, is situated on the northern flanks of the Cheviot Hills, at the head of the Bowmont Water, a north flowing tributary of the Till.

The farm occupies a high-level basin, formed by the drainage basin of the Sourhope Burn and its tributaries, the perimeter of which is demarcated by the summits of Blackdean Curr (501 m), Black Hag (546 m), The Schil (602 m) and Park Law (321 m). In the centre of this basin between Sourhope Burn and its tributary, Kaim Burn, rises Fasset Hill (369 m). (Figure 3.5). Within this large unit investigations were concentrated on the lower slopes of the basin where the rough grazing consists of Festuca-Agrostis grassland with a varying proportion of Nardus stricta developed on brown forest soils. While Pteridium aquilinum is a locally prominent or dominant component of this grassland, it is noticeably less vigorous than on Conic Hill or Kingslaggan, probably mainly as a result of differences in climate and management practice.

Due to Sourhope's inland situation on the eastern side of Scotland it enjoys a less temperate climate than either of the western sites. This is

Fig. 3.5. SOURHOPE SITE



particularly evident in winter temperature conditions and in the rainfall regime, both of which are modified by the relatively elevated situation. Sourhope has the most severe winter temperatures of the three sites examined - the January mean temperature is only 2°C and although the normal period of frost risk is similar to Conic Hill, the greater severity of the winter is evidenced in the much more frequent occurrence of snow (snow falls on average on 25 days in the year on the low ground, compared to 12½ days at Kingslaggan and 20 days at Conic Hill).

Although altitude results in Sourhope experiencing a considerably higher rainfall than the nearby lowlands of the Tweed basin, the average annual rainfall of 1016 mm is well below the mean for the other sites and, typical of eastern locations, the winter maximum is less pronounced with a secondary peak occurring in July and August.

Research on the autecology of *Pteridium aquilinum* suggests that these climatic conditions are less conducive to vigorous growth than those prevailing in Galloway and the Western Grampians. In particular lower winter temperatures are likely to be significant, Watt having demonstrated that frost causes severe damage to shallow rhizomes and retards the advance of the bracken front. (Watt, 1954). It is worth noting in this context that bracken on Sourhope has a very shallow rhizome system (see page 197).

While the potential vigour of bracken in the area as a whole is probably mainly under the control of climatic factors, detailed distribution is influenced by drainage, altitude, human management, and possibly soil depth. *Pteridium* is found on lower slopes, avoiding more poorly drained valley bottoms and extending up to 365 - 400 m. This upper altitudinal limit is higher than on the other sites, a result partly of less rugged surface terrain at higher altitudes and partly of less exposed climatic conditions. Compared to Kingslaggan and Conic Hill, the Sourhope hill slopes, although frequently steep, are relatively smooth and lack the gully and spur formation which is found on a small scale at Kingslaggan and on a much more impressive scale on the lower slopes of Conic Hill. There is therefore a tendency for more continuous bracken stands with a more clearly defined altitudinal zonation to occur at Sourhope, rather than the discontinuous pattern of Pteridium and heath communities associated with broken surface terrain which is typical of large areas on the other sites.

It has been suggested in the past that bracken growth is related to soil depth. (Gordon, 1916). Since many of the Sourhope soils are skeletal, consisting of an extremely thin weathered mantle over the ubiquitous andesitic lavas of Lower Old Red Sandstone age, which form the bedrock, it seemed likely that soil depth would prove to be a controlling factor in bracken distribution. In practice, however, although in some areas, such as Fasset Hill, the extremely shallow soils appear to have reduced bracken vigour, permitting only stunted frond development, on other stands studied no consistent correlation was found between the occurrence of bracken and soil depth.

The choice of sites for detailed analysis at Sourhope was influenced by current management practice on the research farm. Areas, such as the Gair, which had been subjected to modification such as recent fertilizer application were avoided. The main area selected was the west-facing slope of Dod Hill, the smooth slopes of which provided an interesting pattern of bracken distribution with little obvious habitat control. Pteridium Stand 2 is particularly interesting as it has a well developed structure, consisting of advancing front, crest and hinterland phases as described by Watt (1940), yet according to local information, the stand margin has been relatively stationary for at least the last decade although there is no obvious reason for the failure of the fern to colonize the adjacent Nardetum. The other main area studied was the south-east facing slope of Hairny Law where again suitable sociological boundaries exist. This area is included in the experimental paddock grazing system at Sourhope but has been subject only to fencing and controlled grazing.

Thus the sites selected for this research project permit the investigation of the bracken ecosystem in three quite different environmental settings. On Conic Hill and Kingslaggan bracken is found in optimal climatic conditions, adjacent to heather moorland; the Sourhope environment is less amenable to vigorous bracken development and the neighbouring stands are mainly Festuca-Agrostis-Nardus communities. Relief and geology also differ widely from site to site with a range from the uniform geology and smooth terrain of Sourhope, to the complex geology and broken relief of the Highland Boundary Fault zone.

II. FIELD PROCEDURES

Basically the same methodology was used at each of the sites described above, the following sequence of procedural steps being employed:

(1) The starting point for the investigation at each site was a reconnaissance survey in which the distribution of Pteridium aquilinum over a large area was mapped. At Kingslaggan and Conic Hill 1:10560 Ordnance Survey maps were used as a basis for mapping; at Sourhope air photographs of reasonable quality were available and were used in conjunction with maps. This initial survey provided a general impression of the nature of the vegetation and the factors influencing bracken distribution. It thus facilitated the selection of bracken stands with sociological boundaries suitable for detailed study, the number chosen varying from site to site. As can be seen from Figures 3.2, 3.4 and 3.5 Kingslaggan and Conic Hill offered a larger number of suitable stands (10 and 8 respectively) than Sourhope where only 5 stands were examined, of which Stands 2, 3 and 4 were on contiguous areas of Dod Hill, a reflection of the complexity and inherent interest of this area.

(2) The initial step in the investigation of each stand was a field sketch - basically an extension of the reconnaissance survey on a more detailed scale. The boundaries of the Pteridium stand were noted more accurately, the variation in frond height and density within the stand observed, and a general description of the species composition of adjacent communities made. For instance at this stage the well-developed structure of the bracken communities at Dod Hill on Sourhope became apparent. The field sketch was therefore a necessary preliminary to the next stage of selecting quadrat sites for semi-quantitative investigation, as well as providing a sketch map of appropriate scale for the recording of quadrat locations.

(3) The selection of quadrat sites was done subjectively on the basis of two main

criteria. Differences in vegetation and soil conditions on either side of stand margins were obviously of particular significance, hence the concentration of quadrats across boundaries, particularly sociological ones. Secondly, since variation in the herb layer with varying bracken cover was of interest, quadrats were selected to provide a range of frond density and height. Care was taken to ensure that variation in frond height and density within quadrats was minimal. The number of quadrats per stand depended on the complexity and interest of vegetational conditions, all visually apparent variations being sampled. Obviously this type of subjective sampling does not permit statistically valid analysis to be undertaken of the character of each plant community. Had this been the object of the exercise a random or stratified sampling technique would have been necessary. However, since quadrat data was to be used, not as a basis for individual stand characterisation, but as a source of information about the modifying influence of Pteridium in a broad environmental setting, the subjective selection of samples to provide maximum diversity was deemed appropriate.
(4) The size of quadrat chosen was the 4 sq. m square, a size appropriate to the height of Pteridium aquilinum fronds. The 1 square metre quadrat, commonly used in moorland vegetation, is too small for this height of vegetation. Data was recorded on 6 x 4 inch record cards to facilitate subsequent sorting and analysis.

The data collected at each quadrat falls into three main categories (Table 3.1). Since much of the later interpretation would be based on the premise that degree of bracken dominance was the only major environmental variable, it was essential to record environmental parameters to check the subjective assessment of the existence of a sociological boundary between plant communities.

Environmental Parameters	Character of Pteridium aquilinum	Character of ground vegetation
Altitude	Frond cover	Cover total ground vegetation
Aspect		Height ground vegetation
Slope		Species list
Drainage Class	Frond numbers	Cover-abundance of each species
Microrelief (where Soil depth appropriate)	Frond height	
	Bracken litter cover	

Table 3.1. Quadrat data collected.

+	Occurring as a single individual with reduced vigour: no measurable cover.
1	Occurring as one or two individuals with normal vigour: no measurable cover.
2	Occurring as several individuals: no measurable cover.
3	Occurring as numerous individuals but with cover less than 4% of total area.
4	Cover 4 - 10% of total area
5	Cover 11 - 25% of total area
6	Cover 26 - 33% of total area
7	Cover 34 - 50% of total area
8	Cover 51 - 75% of total area
9	Cover 76 - 90% of total area
10	Cover 91 - 100% of total area

Table 3.2. Abundance-Vigour-Cover Scale of Domin, as modified by Dahl (Cain and Castro Manual of Vegetation Analysis, 1959).

Approximate altitude was recorded from the 1:10560 Ordnance Survey map, and aspect was measured using a Silva Ranger compass. Slope and surface drainage conditions were also recorded, the former using an abney level, while the drainage class was subjectively assessed using a range of categories from excessively to very poorly drained. In practice the autecological preferences of _Pteridium_ resulted in only the excessively to imperfectly drained categories normally being required. In addition to these parameters, which were consistently recorded, other environmental conditions were noted where appropriate, such as pronounced micro-relief features or evidence of obvious modification by domestic animals or humans. In situations where bracken vigour could possibly have been influenced by soil depth this was measured using a soil auger.

The second category of data collected concerned the character of the _Pteridium aquilinum_ fronds. The proposed correlation of herb layer and soil variations with bracken influence necessitated a quantitative assessment of degree of bracken dominance. For this purpose a visual assessment of frond cover expressed either as a percentage or by allocation to a cover-abundance class was inadequate although both these types of data were consistently recorded. A more precise measure of frond density was required and therefore the number of fronds on each quadrat were counted permitting the expression of dominance in terms of density of fronds per unit area. At an early stage in the research it became apparent that the influence of bracken depends on the height of frond, which influences the weight of litter produced, as much as an actual density of fronds. The height of fronds was obtained by measuring the mean height of the fronds in the canopy. Since quadrats had been selected to give as uniform height conditions as possible, the measurement of a few fronds per quadrat was normally sufficient for reasonably accurate assessment. Where the litter produced by the fronds of previous years had a measurable ground cover this was visually assessed and expressed in percentages.

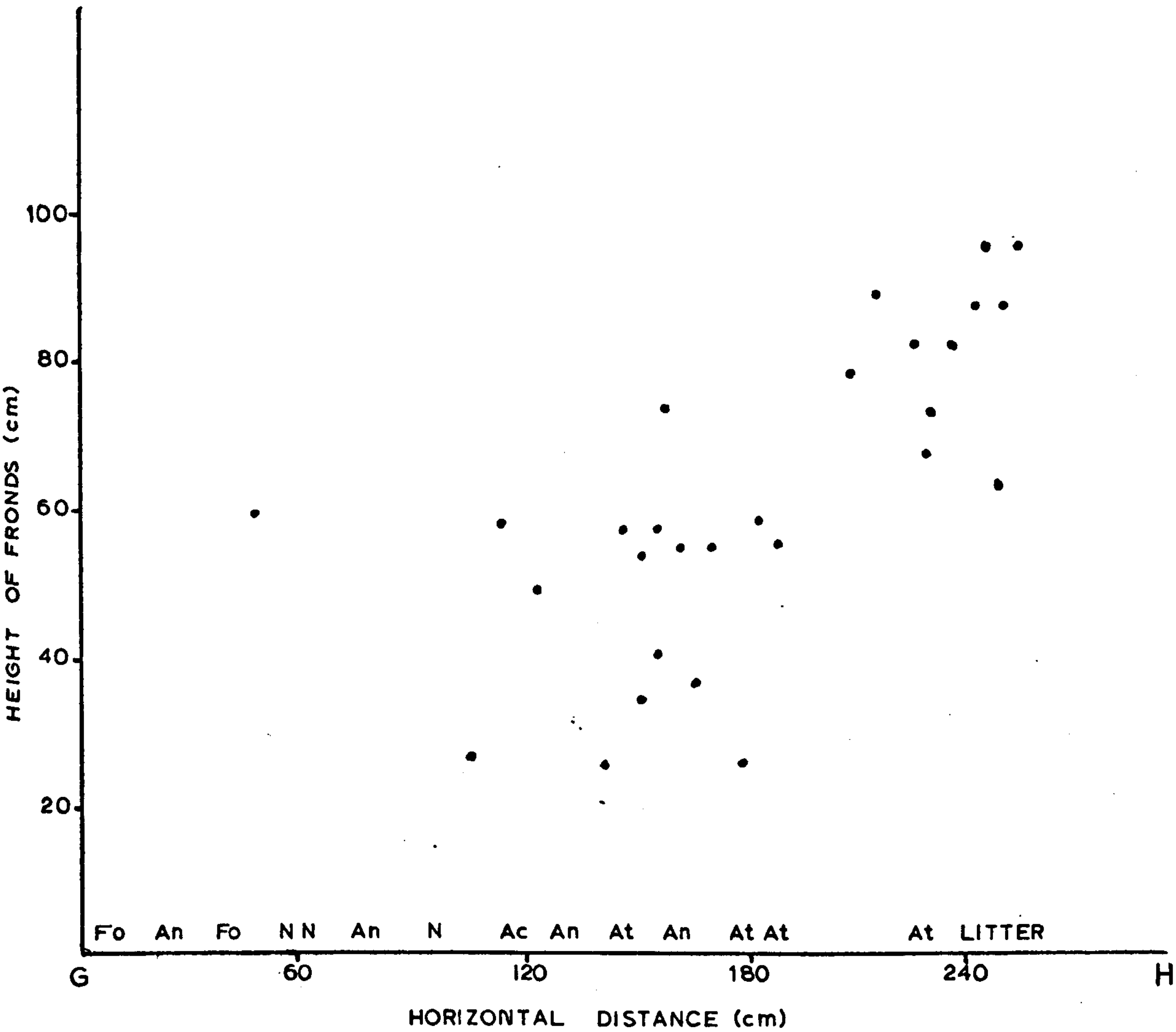
At the outset it had been assumed that one of the main ways in which Pteridium modifies the micro-environment of the ground vegetation is through the shade cast by the growing frond.[2] It therefore seemed desirable to obtain a direct measurement of the modification of light conditions by the canopy. An attempt was made to assess this using an ordinary camera light meter and comparing light readings on the surface of the canopy with those on the surface of the herb layer. Unfortunately this proved unsatisfactory and was eventually abandonned, the main problem being that the unavoidable disturbance of the canopy surrounding the quadrat in the course of field work distorted light readings obtained even in the centre of the quadrat.

The third category of quadrat data concerned the ground vegetation itself. Modification of the herb layer takes two forms - reduction of total cover and the modification of species composition. The former was assessed for each quadrat by allocating the ground vegetation as a whole to a cover-abundance class (supplemented by the bracken litter assessment) and by measuring the general height of the herb layer. Species composition was recorded by making a full species list of herb layer components, and ascribing each to a cover-abundance class. For the latter the 10-point Domin Scale as modified by Dahl was employed, as illustrated in Table 3.2 (page 68). In the assessment of cover-abundance it frequently proved very difficult to separate grasses of similar leaf type when these were not in flower, for instance the fine-leaved Deschampsia flexuosa and Festuca ovina. In these cases, rather than imply an accuracy which would be spurious, a combined cover-abundance rating was given plus a note on the apparent relative importance.

This full range of data which provided a more objective check on habitat conditions, a quantitative assessment of bracken dominance, and a semi-quantitative description of species composition, was recorded for 100 quadrats at each site, this number being the maximum possible in the time available.

(5) A supplementary method of monitoring vegetational change across community boundaries was also used. On stand margins variation in vegetation obviously occurs mainly in one direction. Therefore on occasions it seemed that a linear method of sampling would be more appropriate than an areal one, particularly where changes occurred across a narrow ecotone. In these situations line transects were sometimes used rather than square quadrats. The technique involved the placing of a length of cord, subdivided into 60 cm lengths and attached to a surveyor's pin, at right angles to the stand margin, that is along the axis of maximum vegetational variation. The data was recorded on a graph, as shown in Figure 3.6, each species in the ground vegetation actually touched by the cord being noted on the X axis, while the height of each bracken frond touched was recorded on the Y axis. While this method gives a good visual impression of stand margins, the data provided is less amenable to subsequent manipulation than quadrat data thus restricting its utility.

Fig. 3.6. EXAMPLE OF LINE TRANSECT
(TRANSECT G–H SOURHOPE)



Fo	FESTUCA OVINA
An	ANTHOXANTHUM ODORATUM
N	NARDUS STRICTA
Ac	AGROSTIS CANINA
At	AGROSTIS TENUIS

VERTICAL SCALE 1:10
HORIZONTAL SCALE 1:20

(6) An important aspect of the research was the investigation of the effect of _Pteridium aquilinum_ cover on the biomass of the associated ground vegetation. Clearly the type of data recorded for each quadrat on this subject, namely the cover-abundance category of the herb layer as a whole and its height, is inadequate. Normally the reduced vigour of the herb layer results in a general thinning of the ground vegetation and etoliation of the plants without much obvious reduction in ground cover. Only at a fairly advanced stage do measurable bare or litter-covered patches appear.

A more accurately quantifiable measure of biomass was obtained by cropping a sample area of vegetation in 25 per cent of the quadrats. A square 35 x 35 cm in the centre of the quadrat was cut. The size of square was determined empirically on the basis of practicality. The centre of each quadrat was chosen to reduce the subjective element of choice since ground cover conditions were seldom uniform throughout the quadrat, particularly where modification was relatively severe. Bracken fronds occurring within the 35 sq cm sample were also cut, the fronds and ground vegetation being placed in separate paper bags, polythene having proved unsuitable for storing moist plant matter.

The material collected was oven-dried for 24 hours at 85°C and weighed. Although the fronds present in the sample area were collected and weighed, this data was not used in analysis, since the sample area involved was much too small to provide reliable evidence of the importance of bracken of which ample other information had been collected for the quadrat as a whole.

(7) Finally, information on soil morphology was collected in the field. A

selection of vegetation quadrat sites (45 in total) were chosen subjectively as sites of soil pits, once more the emphasis being on stand margin situations with a few soil profiles from locations in the centre of Pteridium stands, for comparison. The technique used in soil profile description was the standard method of the Soil Survey of Great Britain as set out in its Field Handbook (1960). Environmental parameters were recorded and visible soil horizons defined. For each horizon moisture, colour (based on Munsell Colour Charts), texture, stoniness, structure, consistency, porosity, permeability, nature of organic matter, roots, and, where possible, soil fauna were recorded. Detailed information on the selection of soil profiles and examples of soil descriptions are given in Chapter 5.

Section Notes

1. Climatic data for this chapter is mainly taken from "The Climatological Atlas of the British Isles", H.M.S.O. 1952.

2. As research proceeded it became apparent that shade and interference by previous years' litter, in addition to that produced by the growing frond, is significant.

CHAPTER 4

VEGETATION ANALYSIS

The aim of the vegetation survey in this study is to elucidate the relationship between *Pteridium aquilinum* and its associated ground vegetation. In structure and species composition the bracken-dominated community frequently offers a marked contrast to neighbouring moorland communities. Its two-tiered structure and the severe reduction in the cover of ground plants associated with the heavy litter of dense frond growth are points of common observation. This impairment of pasture together with the toxic properties of bracken and its unpalatibility to domestic stock have led to its designation as one of the most noxious weeds of rough grazing.

The fact that a more open frond canopy is usually associated with a herb stratum in which grasses such as *Festuca ovina* and *Agrostis tenuis* are dominant is also a readily observable phenomenon. Of course as mentioned above (see page 3) similar *Pteridium*-free *Festuca-Agrostis* grassland is found on the better drained brown forest soils of Scottish rough grazings. However the *Pteridium* - *Festuca - Agrostis* assemblage is often found juxtaposed against a moorland community of completely contrasting species composition in which the species of the bent - fescue assemblage are either absent or of minor importance. One of the principal aims of the present analysis is to determine whether in such situations a causal relationship exists between the frond cover and the species composition of the ground vegetation. In other words does the co-existence of Pteridium and allied grasses merely reflect their similar habitat preferences or does the frond canopy encourage the fescue-bent assemblage either by providing a suitable microenvironment or by reducing the efficacy of competitors?

The techniques of field observation chosen to examine these relationships, namely the concentration of observations across sociological boundaries between vegetation types in which all macroenvironmental factors other than vegetation are constant, and the investigation of variations in ground vegetation within a bracken stand associated with varying density of fronds, have been described in the preceding chapter.

The relationship between bracken and its ground vegetation can be broken down into a number of constituent points on which the lay-out of this chapter is based. First the effect of Pteridium on the ground stratum as a whole is considered, the relevant attributes of the ground vegetation being its cover, biomass, and species richness. Secondly the major issue of the influence of Pteridium on the species composition of the ground layer is considered. This is divided into two sections. First an attempt is made to identify combinations of species associated with varying degrees of bracken dominance; in other words the definition of noda. Secondly, the response of individual species to bracken competition is examined permitting a classification of species on the basis of their response to Pteridium.

In considering the above points each of the three sites is examined independently, since there is to some extent a variation in results from one site to another, for instance in the response of herb layer species. This permits a comparison of the three sites and an identification of results which appear to have general validity compared to others in which local conditions, which influence the relative vigour of Pteridium and other species, are significant. As might be expected Sourhope with its markedly different environment, including vegetation types, produces results which are to some degree at variance with the western sites.

Finally, specific examples from each site are described to illustrate the points arising from the preceding general analysis, and to isolate bracken dominance from other possible environmental variables.

Any necessary discussion of the analytical techniques adopted is included in the appropriate section of the chapter.

I. MODIFICATION OF HERB STRATUM AS A WHOLE.

It is generally appreciated that bracken growth suppresses the ground vegetation. Where frond growth is vigorous the herb stratum is usually severely restricted by the competitive power of the fern, shading both by the current year's fronds and by the litter of previous years' growth, which tends to accumulate under dense and tall Pteridium, probably being significant factors. Reduced vigour of the herb layer is expressed in a reduction of its total cover with patches of bare ground and litter appearing, by a reduction in the biomass of the ground vegetation, and by the morphological modification of individual plants, weak etiolated specimens occurring.

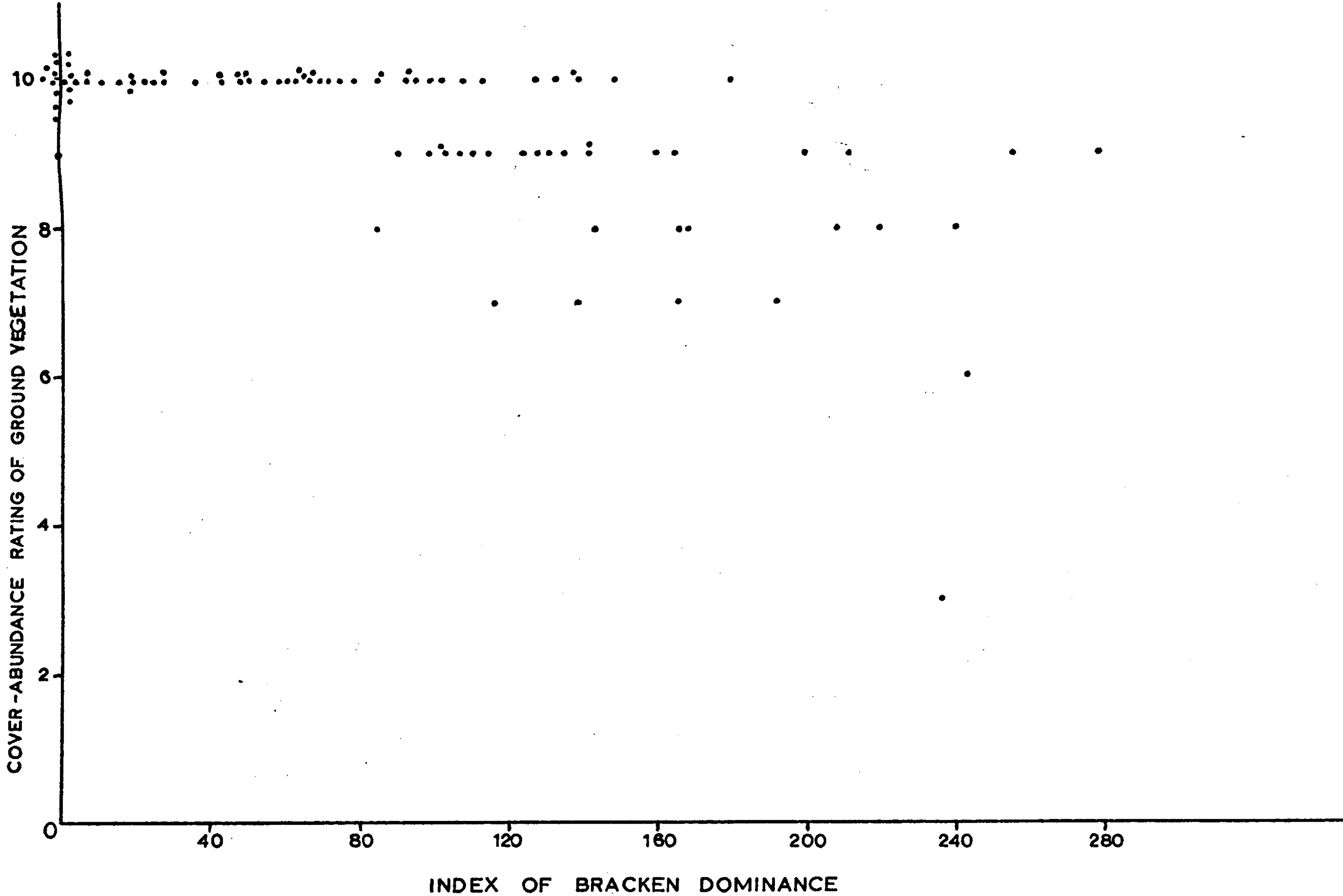
Cover of Ground Vegetation

In the field survey the total cover of ground vegetation was recorded for each quadrat by allocation to a cover-abundance class on the Domin scale (see Chapter 3, page 70). In the subsequent analysis these cover-abundance ratings have been related to a measure of the competitive vigour, or degree of dominance, of *Pteridium aquilinum*. Several attributes of the bracken fronds were recorded in the field survey to provide a quantitative measure of their competitive powers, namely the cover of the canopy expressed both as a cover-abundance rating and as percentage cover, the average height of the fronds, and the number of fronds per quadrat (see Chapter 3, pages 69-70). The greater accuracy and objectivity obtained by the direct measure of frond number and height has resulted in these being utilised, rather than the percentage cover or cover-abundance values, in this, and most of the following analyses. The significance of both density and height of fronds has been recognized by combining them into an Index of Bracken Dominance computed as follows:

$$\text{Index of Bracken Dominance (I.B.D.)} = \frac{\text{Total number of fronds} \times \text{mean height}}{100}$$

The cover-abundance rating of the ground vegetation has been plotted against the I.B.D. for each quadrat, as illustrated for Kingslaggan in Figure 4.1. These results have been summarized in histograms by calculating the median cover-abundance rating for each 20 unit range of I.B.D. i.e. the median cover-abundance rating where I.B.D. = 0-20, 21-40 etc. This same technique is used in many of the later analyses. To illustrate the method

Fig. 4.1. Effect of *Pteridium* competition on cover-abundance of ground vegetation. Kingslaggan.



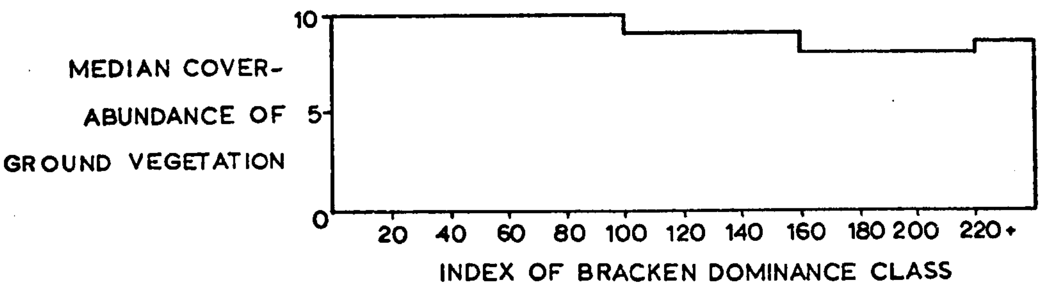
both the scatter diagram (Fig. 4.1) and the histogram derived from it (Fig. 4.2 (a)) for Kingslaggan have been included, but thereafter for the sake of conciseness the histograms alone are presented for most of the analyses.

It should be noted on the histograms that at the upper indice limits (i.e. where the index exceeds 200 or 220) the 20-unit range has been abandoned due to the paucity of samples and one median value calculated for all remaining quadrats. Despite this precaution a few distortions still occur on these histograms where a very small number of samples happen to fall within a particular 20-unit range. This is particularly noticeable in the later examination of individual species for which the same analytical technique is used. The number of sample quadrats in each 20-unit range for each site has been summarized in Table 4.1 to help the reader to identify those values of the bracken dominance index for which results may be distorted by the small number of samples.

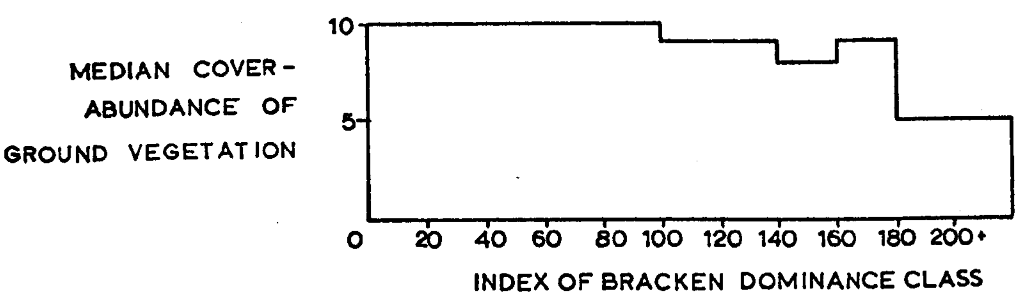
Examination of Figure 4.2 indicates that on each site the cover of ground vegetation is reduced at higher levels of bracken dominance. It also appears to be generally the case that relatively low levels of bracken have little or no effect on the ground cover. Instead there appears to be a critical bracken 'threshold' at which ground cover quite suddenly reacts to the competition of the fern. It is interesting to note that this point is I.B.D. = 100 on each site, although too much significance should not be attached to any precise value. When I.B.D. exceeds 100 the cover of ground vegetation is reduced on each site but to different degrees, the situation being summarized in Table 4.2.

Fig. 4.2. Summary of effect of Pteridium competition on cover abundance of ground vegetation.

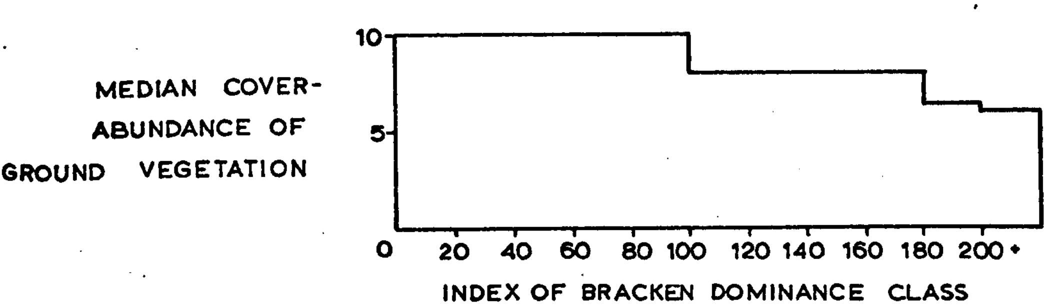
(a) KINGSLAGGAN



(b) CONIC HILL



(c) SOURHOPE



Range I.B.D.	Number of Sample Quadrats		
	Kingslaggan	Conic Hill	Sourhope
0-20	25	20	26
21-40	4*	9	9
41-60	11	4	13
61-80	8	12	12
81-100	9	10	11
101-120	9	9	7
121-140	9	12	7
141-160	5	6	7
161-180	5	5	2*
181-200	2*	9	2*
200+	3*(200-220)	3*	5
	5 (220+)		

Table 4.1. Distribution of Samples in I.B.D. Classes.

*I.B.D. classes for which paucity of samples may invalidate results.

Median c/a class ground vegetation cover	I.B.D. Kingslaggan	I.B.D. Conic Hill	I.B.D. Sourhope
10 (90-100%)	0-100	0-100	0-100
8-9(50-90%)	100+	100-180	100-180
7 or less (less 50%)	-	180+	180+

Table 4.2. Effect of Pteridium Competition on Cover of Ground Vegetation.

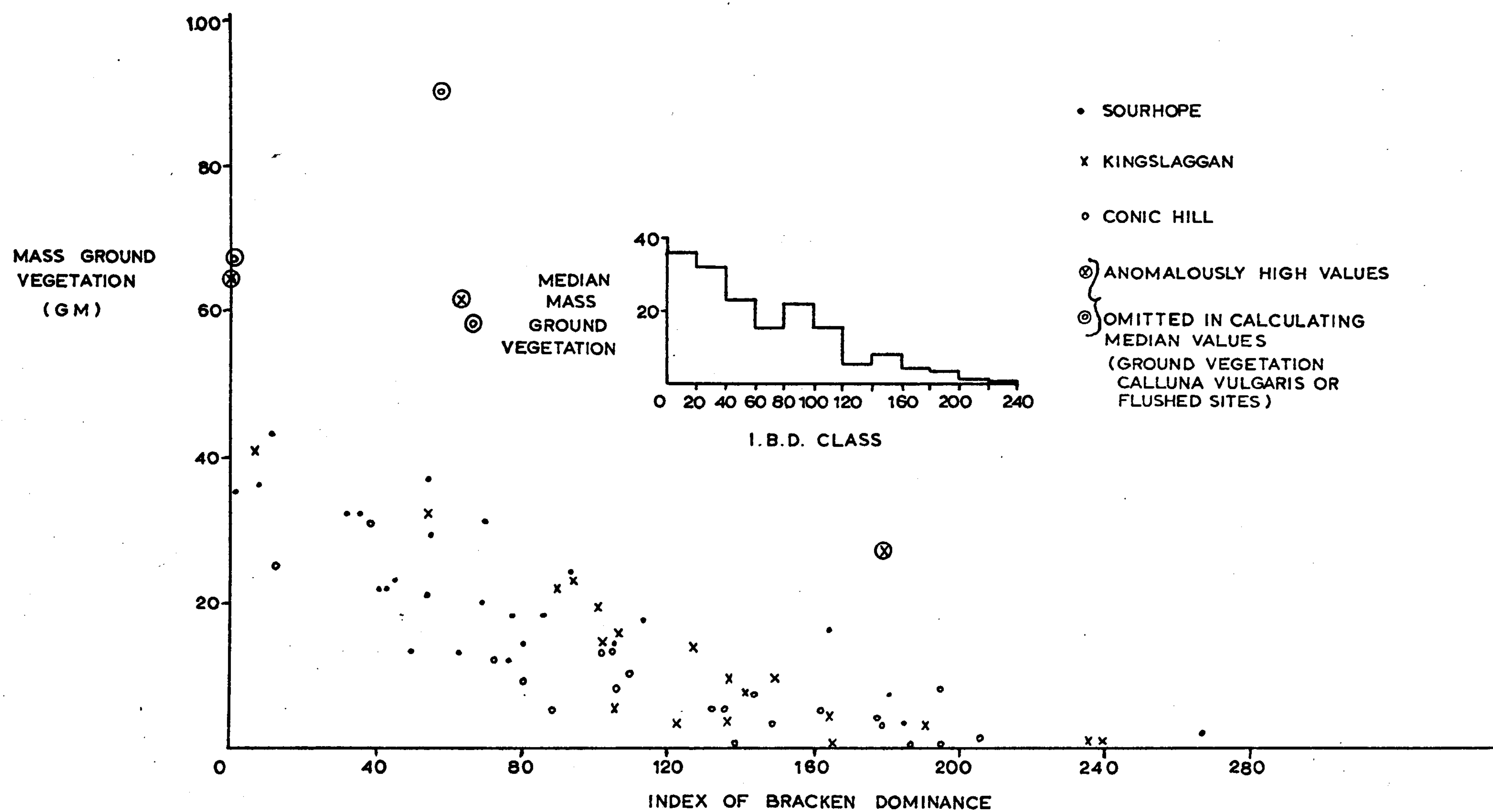
The reduction in ground cover is less severe at Kingslaggan than on the other two sites, the median value never falling below 50 per cent. At Conic Hill and Sourhope very dense, tall *Pteridium* does produce the severe suppression of the herb layer which one might expect, resulting in a situation analogous to the sparse vegetation or bare woodland floor found under the dense canopy of certain deciduous woodland species such as beech.

Biomass of Ground Vegetation

The method used to measure the biomass of the ground vegetation has been described in detail in Chapter 3 (see page 73). In twenty-five percent of the quadrats a sample area of ground vegetation was cut, dried and weighed. The analytical technique used is the same as for cover but because of the small number of quadrats involved the data from all three sites has been combined on one scatter diagram and inset histogram (see Fig. 4.3).

In interpreting this diagram two points must be borne in mind. The number of samples for each site is small and hence for individual sites the limitation of restricted data for certain index classes is particularly apparent, although the combined results provide a fairly comprehensive cover of values for index levels below 200. Secondly, anomalously high results are obtained for quadrats in which *Calluna* heath is the dominant ground vegetation or on flushed sites. If these anomalously high results are excluded the ground vegetation values for each site range from 30 to 40 gm biomass at the lowest levels of *Pteridium* competition to 0 gm at high levels.

Fig. 4.3. Effect of Pteridium competition on biomass of ground vegetation – all sites.



Even allowing for these sources of distortion there is clearly a considerable scatter of results with substantial variation in biomass values at any given level of bracken dominance, although certainly general trends can be discerned. This inconsistency is hardly surprising considering the variation in site conditions, grazing pressure, and time of sampling from one site to another and from one bracken stand to another within any one site. For instance, the values for Conic Hill tend to be relatively low, and for some unknown reason the Sourhope results are the least consistent.

The limitations of the data necessitate cautious interpretation. Nevertheless two points do emerge. The biomass of ground vegetation is inversely related to the level of competition from Pteridium. Unlike the values for cover of the herb layer, this inhibiting effect is apparent at even relatively low values of I.B.D. and the general trend is one of steady decrease in biomass with increasing bracken levels. This difference in response between cover and biomass values reflects the relative sensitivity of the two indices, the herb layer being reduced in density before any measurable reduction in cover occurs.

Secondly, the consistency of the results appears to vary with the Index of Bracken Dominance. There is a considerable scatter of results below the bracken dominance levels of 100-120, while above 120 there is very marked and consistent curtailment of the ground vegetation. This suggests that when a critical level of bracken density is attained its influence overrides all other variables, while at lower levels a considerable range of herb stratum densities can exist and other factors may be decisive in determining actual biomass levels.

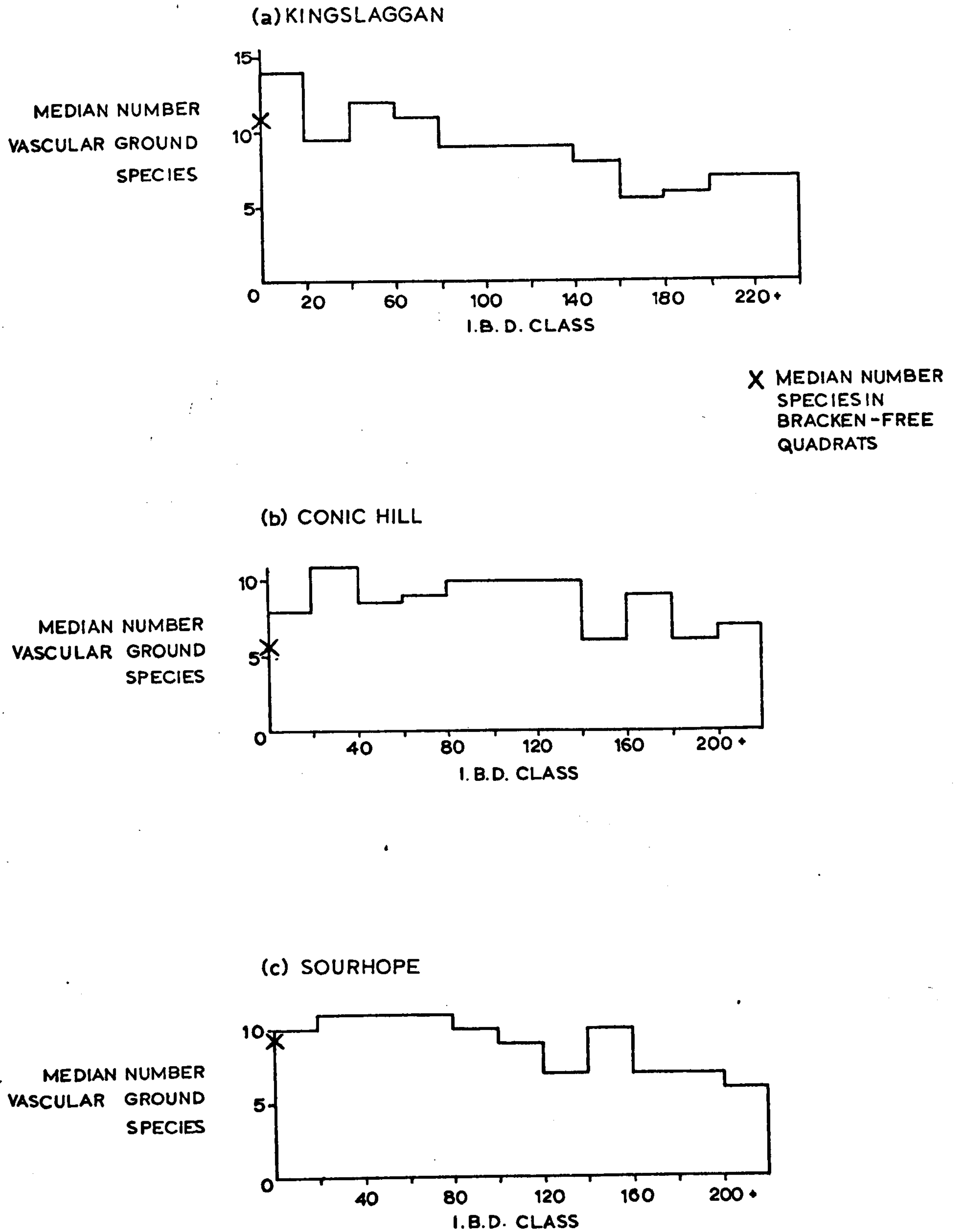
Species-Richness of Ground Vegetation

The third characteristic of the herb layer as a whole is its species richness. Clearly this attribute will be influenced by many factors such as nutrient status of the soil and grazing management so that inter-site and inter-stand variation is to be expected. Some correlation with bracken dominance was however anticipated as increasing frond density imposes microenvironmental conditions which presumably a decreasing number of ground species can tolerate.

As in the previous two investigations, the data on species richness was initially analysed in scatter diagrams, the histograms derived from these being presented in Figure 4.4. As anticipated the number of vascular ground layer species in Pteridium-free communities varies from site to site, ranging from a median value of 6 in the predominantly species-poor Callunetum of Conic Hill to 9 in the Sourhope grassland and 11 in the mixed heath of Kingslaggan. In each case the response to Pteridium is similar. At low Pteridium levels the ground flora is at least as rich as in the surrounding communities. Indeed there is a consistent tendency for light coverings of bracken to be associated with a larger number of herb layer species than the bracken-free moorland communities. For instance at Conic Hill Pteridium communities with I.B.D. levels below 140 usually have 8 to 11 vascular herb layer species compared to the median value of 6 for the Calluna-dominated heath.

However at each site a critical level of bracken is reached beyond which species numbers fall, usually below the level of outside communities.

Fig. 4.4. Effect of Pteridium competition on the species-richness of ground vegetation.



The critical index value varies from site to site but the general picture of a relatively varied flora at low bracken densities becoming depleted as the fern offers increasingly severe competition is consistent.

II. INFLUENCE OF PTERIDIUM AQUILINUM ON THE SPECIES COMPOSITION OF THE HERB LAYER - NODA IDENTIFICATION.

The field methods used in examining the modification of species composition of ground vegetation by varying densities of bracken have been described in Chapter 3 (see pages 69-71). The reader is reminded that within any one site the quadrats are all taken from imperfect to freely drained sites, on similar parent material and within a limited altitudinal range. The presentation of this field data has been attempted in two ways. On each site it is possible to classify the quadrat data into distinct assemblages of herb layer species using Poore's nodum table method (Poore, 1955). This definition of noda is useful in presenting a background picture of the vegetation types and in suggesting points worthy of more detailed investigation. This classificatory approach has however limited value for the analysis of specific variation within Pteridium stands where discrete noda are rarely well developed. In addition the cover-abundance rating for Pteridium used in noda identification is an insufficiently accurate measure of bracken dominance for detailed analysis of the influence of the fern. Detailed consideration has therefore been given to the response of individual species to bracken competition permitting a classification of moorland species according to their tolerance of Pteridium aquilinum.

In defining noda the cover-abundance rating of Pteridium aquilinum was used as the basic criterion in sorting quadrat data. This was supplemented at Conic Hill and Sourhope by the cover value of bracken litter which was sometimes a more meaningful indicator of the level of bracken interference. Nodum tables are presented in Appendix A.

Kingslaggan

On the Kingslaggan site three noda were identified.

(1) Heath Nodum (Table 1, Appendix A). All the bracken-free quadrats with free surface drainage can be allocated to one mixed heath nodum in which Calluna vulgaris is usually the dominant species. In addition to Calluna vulgaris, Nardus stricta, Vaccinium myrtillus and Potentilla erecta are constant species. [2] Of these constants only Nardus stricta is usually prominent in terms of cover, and on a few sites this grass takes over the dominance. Other locally prominent species are Scirpus caespitosus and Molinia caerulea, and if characterization of the heath vegetation had been an important aim it might have been necessary to extract Calluna-Scirpus and Calluna-Molinia noda. For present purposes the rather variable mixed heath vegetation can be allocated to one nodum.

(2) Pteridium aquilinum-Agrostis tenuis-Festuca ovina Nodum (Table 2, Appendix A). The vast majority of Pteridium quadrats can be grouped into a Pteridium - Agrostis - Festuca grassland nodum. Within this nodum the Pteridium cover-

abundance class ranges from 6 to 9 but the ground vegetation is of essentially similar type with Agrostis tenuis and Festuca ovina the dominant species. [3] In some quadrats Agrostis tenuis is absolutely dominant, but in many instances it shares dominance with Festuca ovina. It is however noteworthy that the balance between these two species appears to vary according to the cover of Pteridium aquilinum with Agrostis tenuis more clearly dominant at higher bracken densities. In addition to these two grasses, Anthoxanthum odoratum is constant and sometimes prominent, along with the forbs Potentilla erecta and Galium hercynicum.

This nodum is typical of Pteridium grassland and is a strikingly different type of vegetation from the Kingslaggan heath nodum, Potentilla erecta being the only common constant. The heath shrubs have been completely replaced by grasses and herbs yet, as will be demonstrated later, the two noda occupy adjacent sites with apparently identical independent habitat variables.

(3) Pteridium aquilinum-Agrostis tenuis nodum (Table 3, Appendix A). To clarify the influence of bracken density on the species composition of the ground vegetation quadrats with the highest Pteridium rating, cover-abundance class 10, have been extracted. It is questionable whether this would really be justified on a strict vegetation classification basis, as this 'nodum' is essentially a modified version of the Pteridium aquilinum - Agrostis - Festuca assemblage described above. The two have merely been separated as a tool in the investigation of bracken's influence. At this density of fronds all ground level species suffer diminution in cover value but Festuca ovina is more adversely affected than Agrostis tenuis. In most cases Agrostis is the

clear dominant in the herb stratum. Festuca ovina and Potentilla erecta lose their constant status, leaving only Agrostis tenuis, Galium hercynicum and Anthoxanthum odoratum.

One is therefore dealing at Kingslaggan with a fairly simple situation in which there are two distinct and separate freely drained vegetation types, one a mixed heath and the other a bracken grassland. Within the latter there appears to be a continuum of variation according to the density of bracken fronds but this will be examined more fully later.

Conic Hill

Three vegetation noda were also defined at Conic Hill.

(I) Heath nodum (Table 4, Appendix A). The heath nodum at Conic Hill is simpler than its Kingslaggan equivalent with Calluna vulgaris the undisputed dominant. Indeed in some cases it is almost pure Callunetum heath. Vaccinium myrtillus and Molinia caerulea are the other constant species, the latter being locally prominent in terms of cover-abundance.

(2) Pteridium aquilinum - Agrostis species - Festuca ovina nodum (Table 5, Appendix 4). The Pteridium grassland nodum in which the cover-abundance rating of Pteridium is usually between 7 and 9 is very similar to its Kingslaggan counterpart. The constant species are identical, namely Agrostis species (Agrostis canina occasionally appears in addition to the more common Agrostis tenuis), Festuca ovina, Anthoxanthum odoratum, Galium hercynicum and Potentilla erecta. The broad-leaved grasses are usually dominant with Festuca

ovina and sometimes Deschampsia flexuosa in a subordinate role.

(3) Pure Pteridium aquilinum nodum (Table 6, Appendix A). A pure Pteridium nodum of limited extent has been identified at Conic Hill. Although cover-abundance ratings for the fronds are high the definitive characteristic used was the cover of bracken litter which must exceed 50 per cent. In most cases the ground vegetation has been almost or totally eliminated and there are no constant ground species. Of the sporadically occurring herb layer species Deschampsia flexuosa is the most prominent.

Sourhope

The vegetation situation at Sourhope is quite different from Kingslaggan and Conic Hill. The bracken noda are juxtaposed, not against a completely contrasting heath community, but against a mixed acid grassland which is essentially similar to the ground layer of the Pteridium community. The differences between noda are therefore much less well defined than on the western sites.

(1) Mixed Acid Grassland Nodum (Table 7, Appendix A). Four hill grasses, Nardus stricta, Festuca ovina, Agrostis species, and Deschampsia flexuosa are constant components of this vegetation type but Nardus stricta is the clear dominant. This fact plus the minor role of the broad-leaved grasses in terms of cover-abundance distinguishes it from the mixed grassland associated with Pteridium at Kingslaggan and Conic Hill. Three other species are constant - Potentilla erecta, Galium hercynicum and Luzula multiflora.

(2) Pteridium aquilinum - Festuca ovina - Agrostis species nodum. (Table 8, Appendix 4). The mixed grassland associated with Pteridium at Sourhope is slightly different from the equivalent community at Kingslaggan and Conic Hill. The main constant species, Agrostis tenuis or canina (often the latter in this case), Festuca ovina and Anthoxanthum odoratum are the same but Deschampsia flexuosa is not only constant but frequently prominent. Unlike the other two sites, the fine-leaved grasses frequently take over dominance from the broad-leaved although the latter are more important than in the bracken-free mixed grassland. This nodum is also characterized by relative species richness and a large number of constant species, Potentilla erecta, Galium hercynicum, and Luzula multiflora joining the four grasses named above. In addition Poa pratensis is frequently present at lower bracken levels and Holcus lanatus is locally important.

This herb layer is obviously similar to the general mixed acid grassland nodum but the balance of species is different. The bents and fescue have displaced Nardus from its dominant position and the latter, if present at all, is of only minor importance. On the other hand the broad-leaved grasses have a greater cover than in the mixed grassland nodum.

(2a) Pteridium aquilinum - Nardus stricta Phase (Table 9, Appendix A). Within the general Pteridium grassland nodum it seemed appropriate to recognize a separate 'phase' in which Nardus is prominent. In the usual situation described above Nardus is absent or of little cover value, but on a relatively small number of sites, almost restricted to Pteridium Stand 2, Nardus stricta attains high cover values and is dominant or co-dominant with the other grasses.

In other respects the community is identical to the Pteridium aquilinum - Festuca ovina - Agrostis species nodum but the fact that this occurs in a discrete area justifies its definition as a separate 'phase'.

(3) Pure Pteridium aquilinum Nodum (Table 10, Appendix A). As at Conic Hill, a pure Pteridium nodum has been defined on the basis of over 50 per cent litter cover. In this case the ground layer, although severely restricted, is not obliterated and four species, Deschampsia flexuosa, Agrostis species, Galium hercynicum, and the moss Rhytidiadelphus are constant. The most important casualties from the usual Pteridium grassland are Festuca ovina and Potentilla erecta.

Noda description therefore indicates that on all sites Pteridium is usually associated with Agrostis - Festuca grassland and only slight variations in this nodum are found from one site to another. At Kingslaggan and Conic Hill this nodum is in complete contrast to the heath vegetation found on freely-drained bracken-free sites, while at Sourhope the bracken grassland community is a modified version of the general mixed acid grassland. At the highest levels of frond density a virtually pure Pteridium nodum occurs.

However even this relatively crude classification suggests that within the Pteridium noda there is a continuum of change in species composition associated with varying densities of bracken. For instance Festuca ovina, Agrostis tenuis and Deschampsia flexuosa appear to respond rather differently to Pteridium dominance. Indeed at Sourhope there is a continuum of vegetation from mixed acid grassland through Pteridium-Festuca-Agrostis grassland to pure Pteridium in which, as specific examples will show later, bracken dominance is the controlling variable.

The next step in analysis is therefore an examination of the response of individual species and their classification according to their tolerance of *Pteridium aquilinum*.

III. INFLUENCE OF PTERIDIUM AQUILINUM ON THE SPECIES COMPOSITION OF THE HERB LAYER - RESPONSE OF INDIVIDUAL SPECIES

The analysis of the response of individual species was tackled in a similar way to the analysis of the response of characteristics of the herb stratum as a whole to *Pteridium*. Scatter diagrams were constructed in which the cover-abundance class of the species under consideration was plotted against the Index of Bracken Dominance; in other words the species were ordinated against bracken dominance. Histograms were then employed to summarize the data from the scatter diagrams for 20 unit ranges of I.B.D. (see, for example, Fig. 4.5 and its derived histogram, Fig. 4.6 (a)). Two attributes of the ground layer species were extracted from the scatter diagrams, namely the median cover-abundance value and percentage of samples in which the species occurred for each 20 unit class of I.B.D. Taken in combination these two indices give a fairly comprehensive picture of the response of species to bracken competition.

In interpreting the histograms two descriptive terms have been employed which require definition. Examination of the histograms shows that for some species there are sharp breaks in the graphs of median cover-abundance and

Fig. 4.5. The effect of Pteridium competition on cover-abundance of Calluna vulgaris. Kingslaggan.

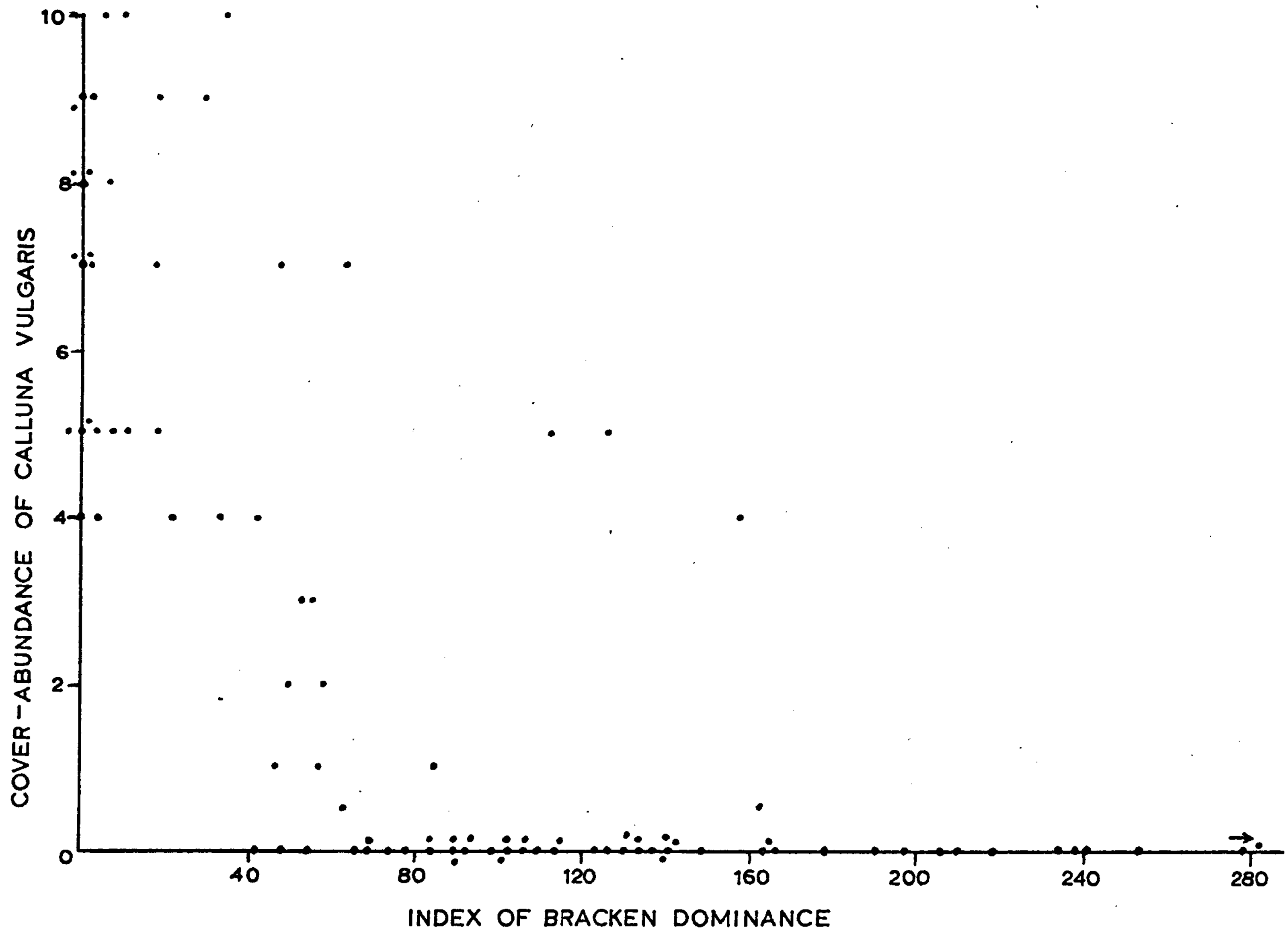
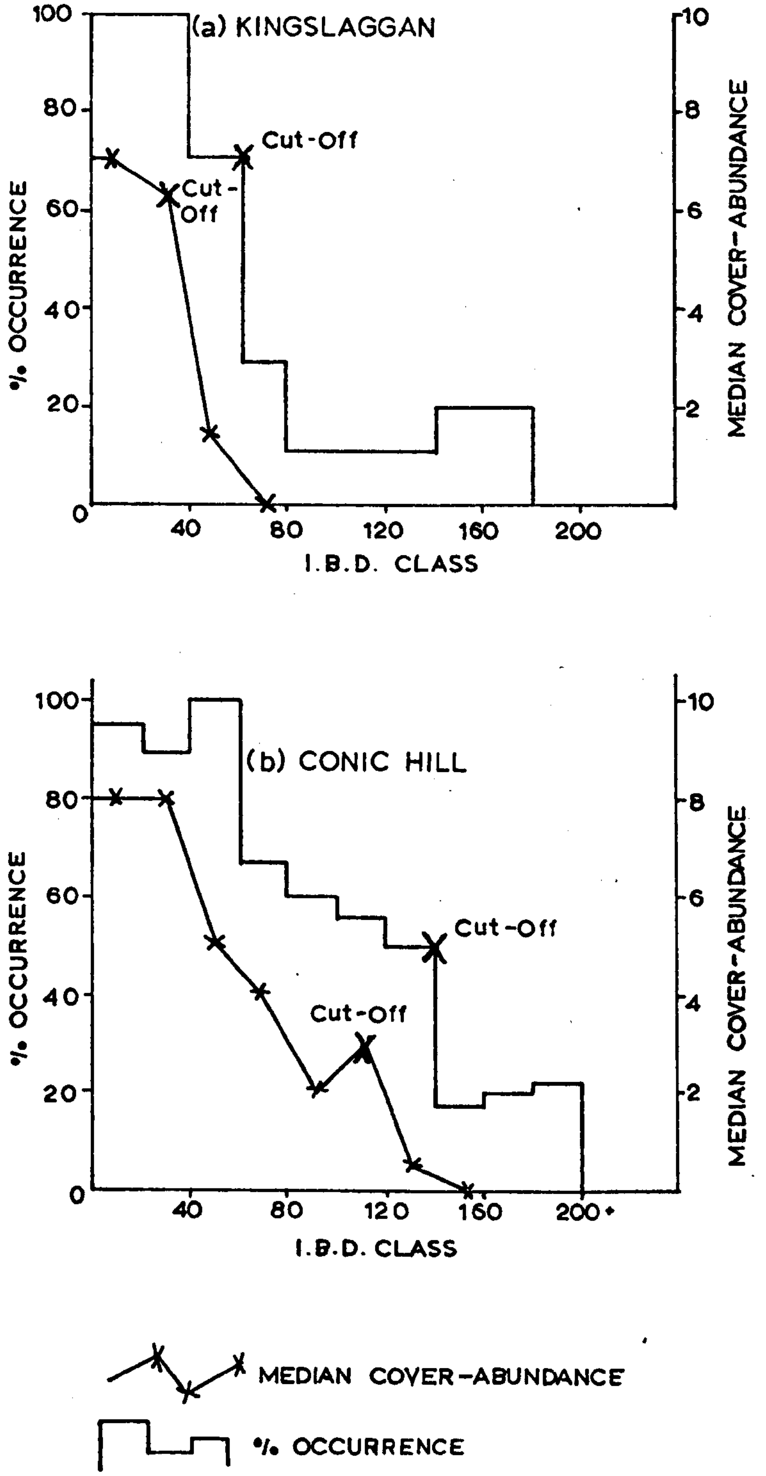


Fig. 4.6. Effect of Pteridium competition on Calluna vulgaris.



percentage occurrence although these critical bracken levels do not necessarily correspond exactly for each indice. These break points have been termed 'cut-off points' and with reference to percentage occurrence have been defined as the level above which occurrence is reduced by fifty per cent compared to the preceding index class. The cut-off value for median cover-abundance is defined as the level above which the species ceases to have any measurable cover, i.e. the cover-abundance falls to class 2 or lower.

The histograms for other species are characterized by relatively low cover-abundance and occurrence at low bracken levels with frequently a falling off at the highest level. For these the optimum range of I.B.D. has been defined.

In interpreting these histograms the reader is reminded of the possibility of anomalous results caused by a small number of samples falling within a few of the index categories and is referred to Table 4.1 (page 82). For example the Sourhope category of I.B.D. = 161-180 frequently gives anomalous results because only two quadrats fall within this range.

The main species are now classified according to their response to bracken competition, as illustrated in the histograms.

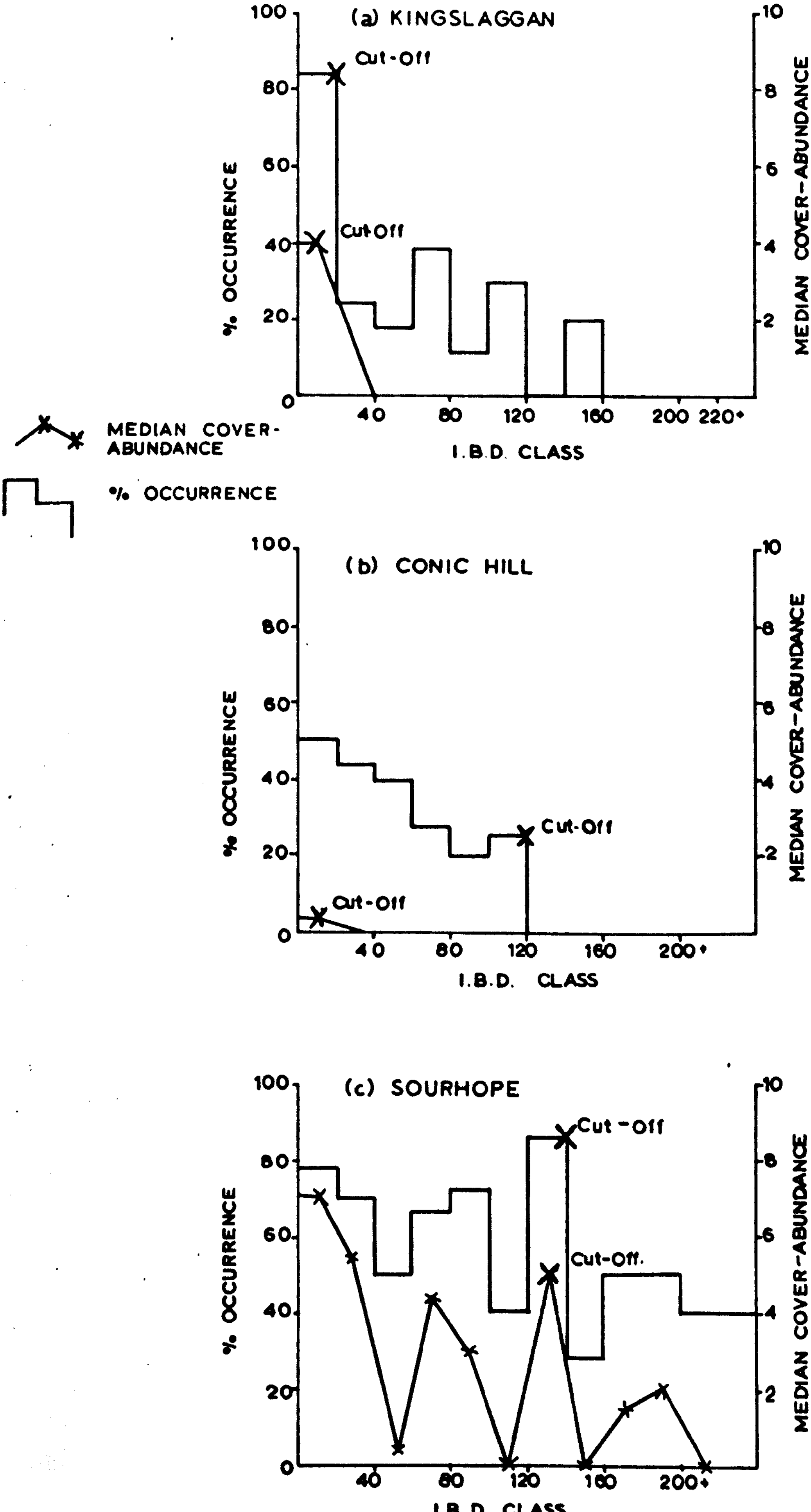
Intolerant Species

These are essentially heath nodum species which are adversely affected by competition from Pteridium aquilinum. They may persist at low levels of bracken interference but their histograms are characterized by critical cut-off points.

(1) Calluna vulgaris (Figs. 4.5 and 4.6, pages 97-98). The scatter diagram showing the relationship between the cover-abundance of Calluna vulgaris and degree of bracken dominance at Kingslaggan is included in Figure 4.5 as well as the histogram derived from it (Figure 4.6 (a)) to illustrate the method. There is no data from the Sourhope site where Calluna is an insignificant component of the vegetation.

This is a typical heath nodum species, prominent and often dominant in the heath vegetation of Conic Hill and Kingslaggan. The histograms are typical of intolerant species, the cover-abundance value of Calluna being adversely affected by even low levels of frond density, particularly at Kingslaggan, although it retains a high level of occurrence somewhat longer. As bracken density increases a cut-off point for occurrence is reached at I.B.D. = 60 at Kingslaggan and I.B.D. = 140 at Conic Hill. It is noteworthy that, although the trend of the histograms is the same on both sites, the absolute values involved are different, Calluna vulgaris apparently being more tolerant of medium levels of bracken at Conic Hill, a point which will be discussed later.

(2) Nardus stricta (Fig. 4.7). Nardus stricta is an interesting species as its ecological position and significance at Sourhope contrasts with that at the western sites. At Kingslaggan and Conic Hill it is a minor component of the heath nodum, and indeed it attains cover-abundance ratings greater than 3 on only two quadrats at Conic Hill. In these conditions it appears to be


(a) KINGSLAGGAN
Cut-Off
Cut-Off
% OCCURRENCE
MEDIAN COVER-ABUNDANCE
100
80
60
40
20
0
10
8
6
4
2
40
80
120
160
200
220+
I.B.D. CLASS
MEDIAN COVER-ABUNDANCE
% OCCURRENCE
(b) CONIC HILL
Cut-Off
Cut-Off
% OCCURRENCE
MEDIAN COVER-ABUNDANCE
100
80
60
40
20
0
10
8
6
4
2
40
80
120
160
200+
I.B.D. CLASS
(c) SOURHOPE
Cut-Off
Cut-Off.
% OCCURRENCE
MEDIAN COVER-ABUNDANCE
100
80
60
40
20
0
10
8
6
4
2
40
80
120
160
200+
I.B.D. CLASS

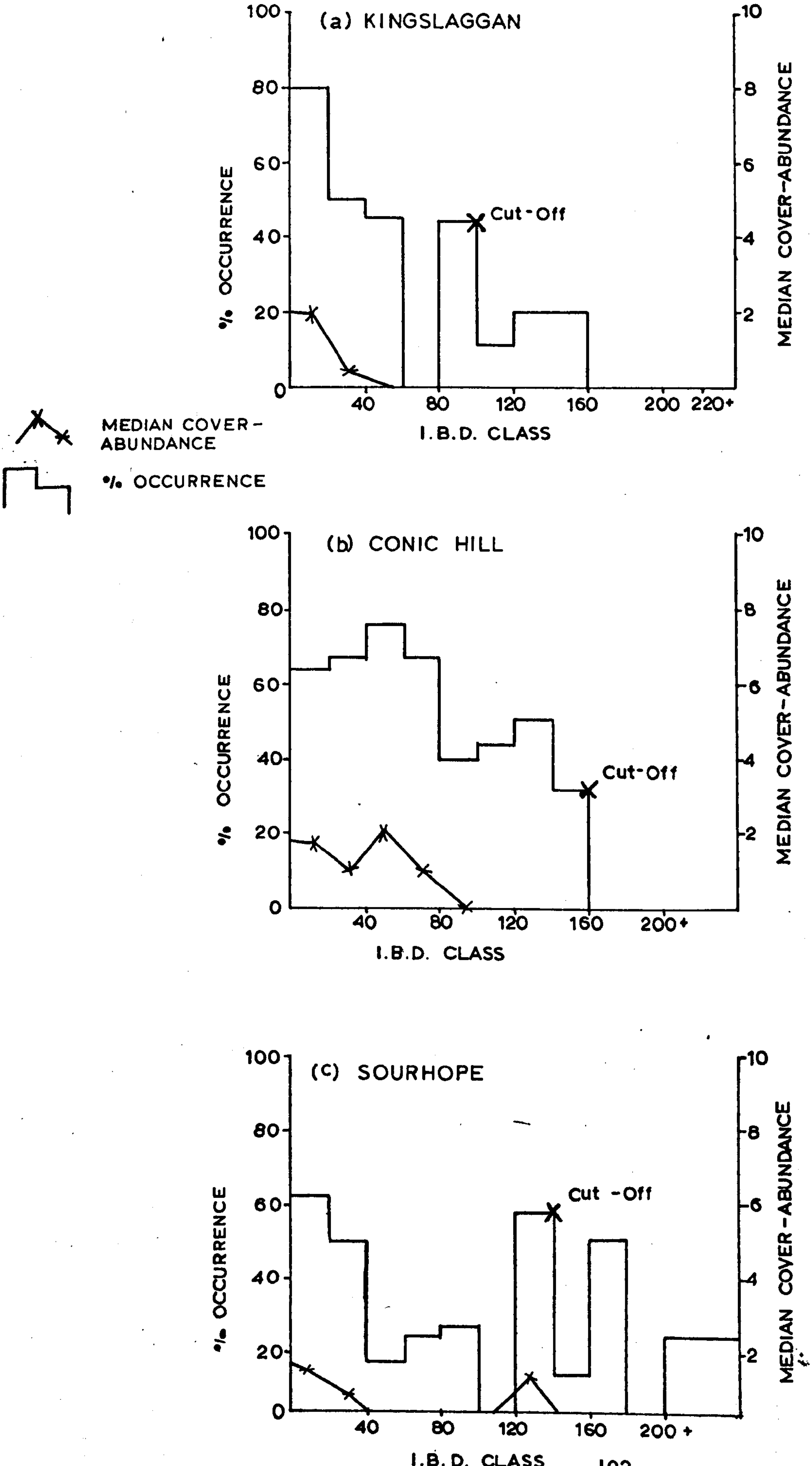
completely intolerant of bracken, its cover value under even light bracken cover being insignificant and it is completely obliterated when the I.B.D. exceeds 120.

At Sourhope, on the other hand, Nardus stricta is an important and often dominant component of the acid grassland nodum and its response to bracken is highly erratic. The histogram suggests that this species is adversely affected by bracken competition and certainly above I.B.D. = 140 occurrence is reduced to less than fifty per cent of the quadrats and its cover-abundance to insignificant levels. This is not a typical 'intolerant' histogram however and its most striking feature is the erratic behaviour of the cover-abundance values in particular, a fact which reflects the existence, as outlined above, of a Pteridium-Nardus 'phase' of restricted areal occurrence.

(3) Vaccinium myrtillus (Fig. 4.8). Vaccinium is only a minor component of the bracken-free nodum on all three sites, and its median cover-abundance rating nowhere exceeds 2. Both cover-abundance and occurrence are consistently adversely affected by bracken, although it persists longer as a frequent component of the ground layer at Conic Hill than elsewhere.

Tolerant Species

The tolerant species are those which are typical associates of Pteridium although in most cases there are limits to their tolerance. In other words, since they are more important members of the herb stratum in the Pteridium community than in the bracken-free noda, and since they often are adversely


(a) KINGSLAGGAN
% OCCURRENCE
MEDIAN COVER-ABUNDANCE
Cut-Off
I.B.D. CLASS
MEDIAN COVER-ABUNDANCE
% OCCURRENCE
(b) CONIC HILL
Cut-Off
(c) SOURHOPE
Cut -Off

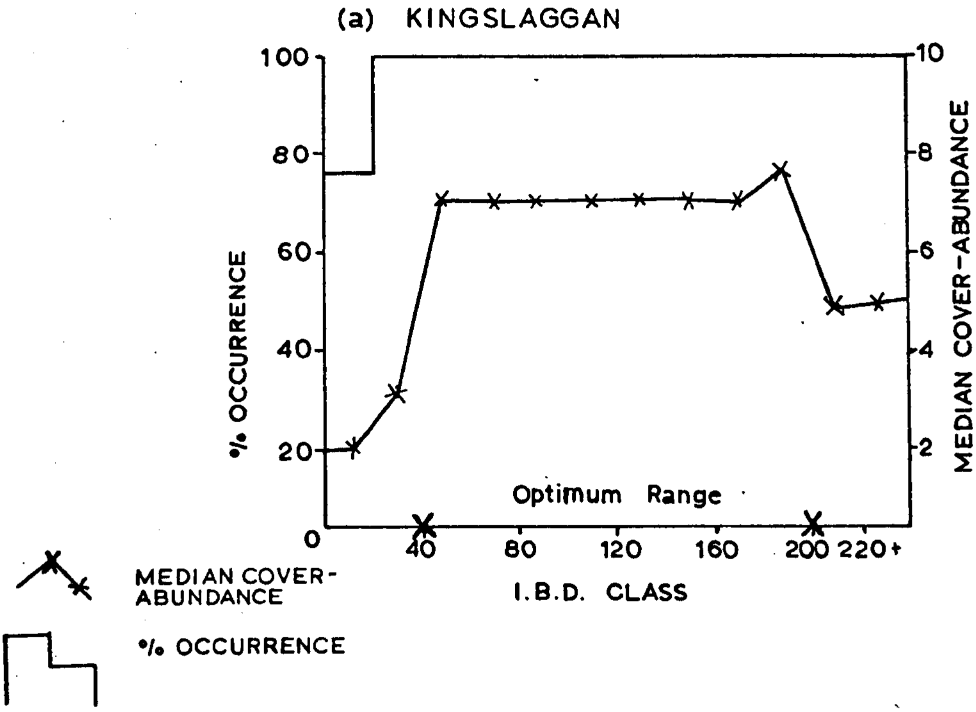
affected when bracken competition reaches a certain level, the histograms are characterized by an optimum range of the index of bracken dominance in which these species attain their maximum cover-abundance and, to a lesser extent, most consistent occurrence.

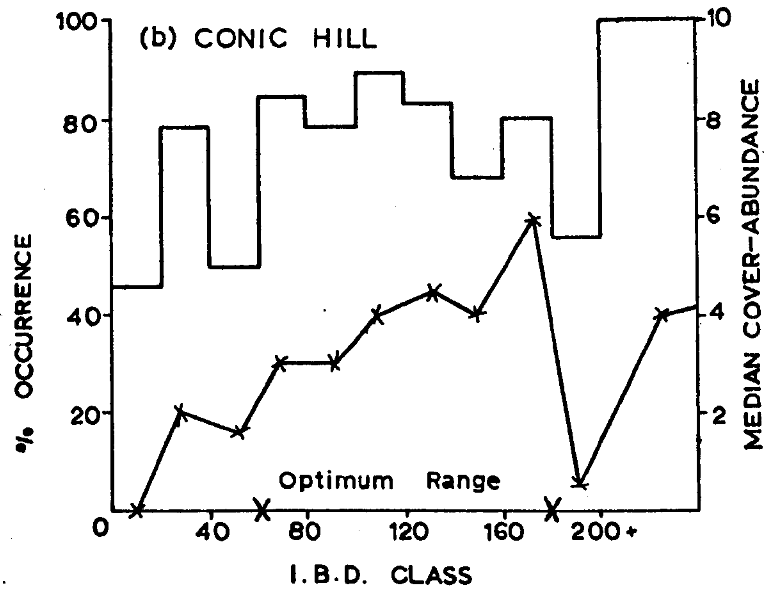
(1) Agrostis tenuis (Fig. 4.9). The nodum data has shown that Agrostis species, usually Agrostis tenuis, is typically the dominant or co-dominant ground species in the Pteridium grassland nodum. The histograms for this species therefore show a totally different pattern of response to Pteridium interference than the intolerant species dealt with above. For instance at Kingslaggan, Agrostis tenuis occurs in all samples with an I.B.D. exceeding 20, but the graph of median cover-abundance shows that its cover is restricted at the highest levels of bracken, so that an optimum range of I.B.D. = 40-200 emerges.

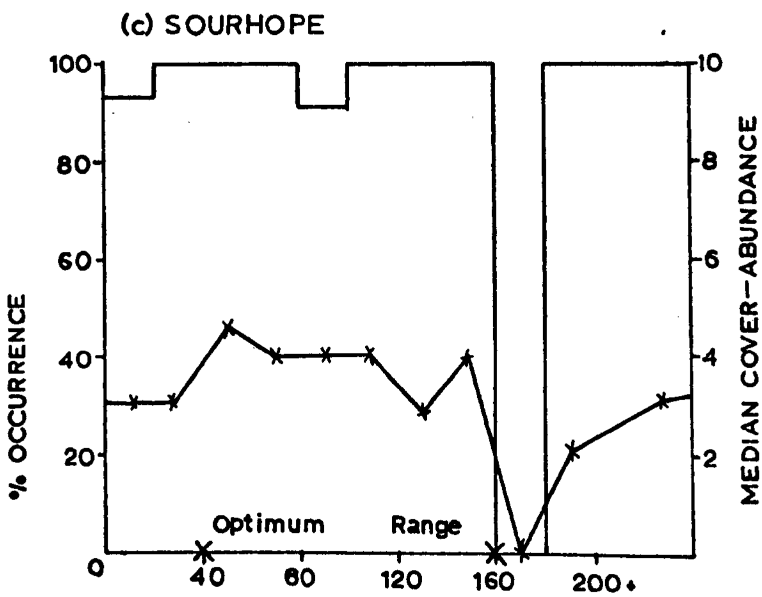
At Conic Hill the picture is similar although less simple - Agrostis tenuis occurs less consistently. No optimum range can be defined from the cover-abundance values but the occurrence data suggests most consistent occurrence between I.B.D. 60 to 180, values similar to those at Kingslaggan.

As usual the Sourhope situation is rather different since Agrostis species are a normal, although not a particularly important, component of the bracken-free nodum, occurring in 86 per cent of the samples. It is interesting to note however that even at Sourhope the cover-abundance values suggest that Agrostis attains its greatest cover at low to medium bracken cover, producing an optimum range very similar to the other sites.

(2) Festuca ovina (Fig. 4.10). The histograms for Kingslaggan and Conic Hill are rather similar to Agrostis tenuis but both sites substantiate the evidence


(a) KINGSLAGGAN
% OCCURRENCE
MEDIAN COVER-ABUNDANCE
Optimum Range
I.B.D. CLASS
0
20
40
60
80
100
2
4
6
8
10
40
80
120
160
200
220+
MEDIAN COVER-ABUNDANCE
% OCCURRENCE


(b) CONIC HILL
% OCCURRENCE
MEDIAN COVER-ABUNDANCE
Optimum Range
I.B.D. CLASS
0
20
40
60
80
100
2
4
6
8
10
40
80
120
160
200+


(c) SOURHOPE
% OCCURRENCE
MEDIAN COVER-ABUNDANCE
Optimum Range
I.B.D. CLASS
0
20
40
60
80
100
2
4
6
8
10
40
60
120
160
200+

from the nodum data that Festuca is suppressed to a greater extent than Agrostis at high bracken levels. Indeed at Conic Hill there is evidence of a cut-off in cover-abundance values at I.B.D. = 140. This adverse reaction of Festuca is even more clearly shown at Sourhope - Festuca ovina is an important component of the bracken-free nodum and retains its significance at low bracken levels, up to I.B.D. = 100. Beyond that it decreases to a cut-off point at I.B.D. = 160. Taken together the histograms of Agrostis species and Festuca ovina at Sourhope illustrate how Pteridium modifies the species composition of the bracken-free acid grassland nodum by the curtailment of some species and the relative favouring of others.

(3) Anthoxanthum odoratum (Fig. 4.11). As shown above, Anthoxanthum odoratum is the third grass species typically associated with bracken grassland, but although its occurrence is usually high, it never attains the dominant position of Agrostis or Festuca species. The histograms show however that it is a very good example of a tolerant species, for at all three sites it attains its maximum development under low to medium bracken cover. Indeed it is virtually absent from the heath nodum at Conic Hill and Kingslaggan. It is however subdued at high bracken densities and on all sites shows a well-defined optimum range.

(4) Poa pratensis (Fig. 4.12). This species is of minor importance and only at Sourhope. However it has been included because it is in the interesting position of being the only grass at Sourhope which is almost absent from the bracken-free nodum but occurs in the Pteridium herb layer. Although occurrence is erratic there is a suggestion from both occurrence and cover-

Fig. 4.10. Effect of Pteridium competition on Festuca ovina.

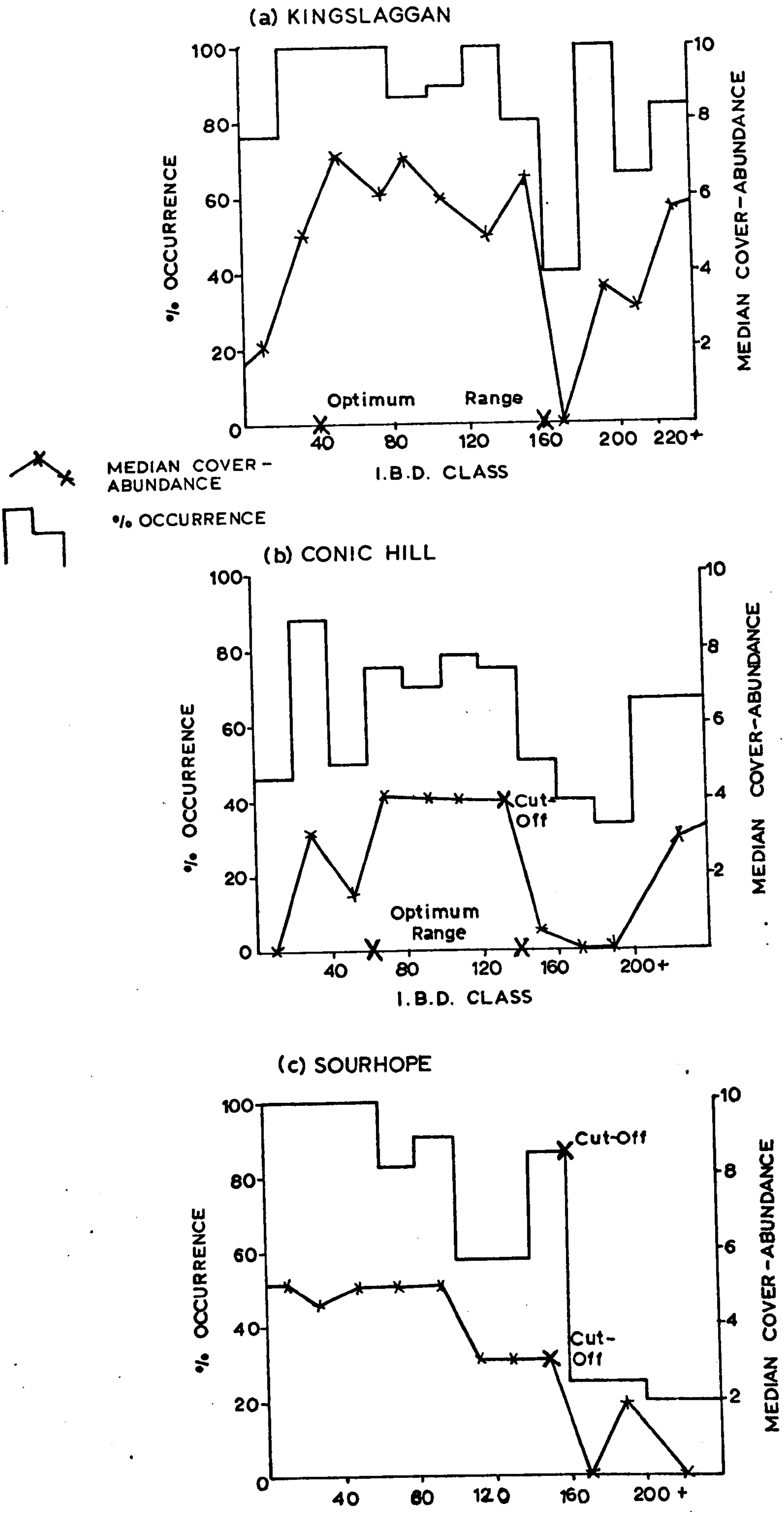


Fig. 4.11. Effect of Pteridium competition on Anthoxanthum odoratum.

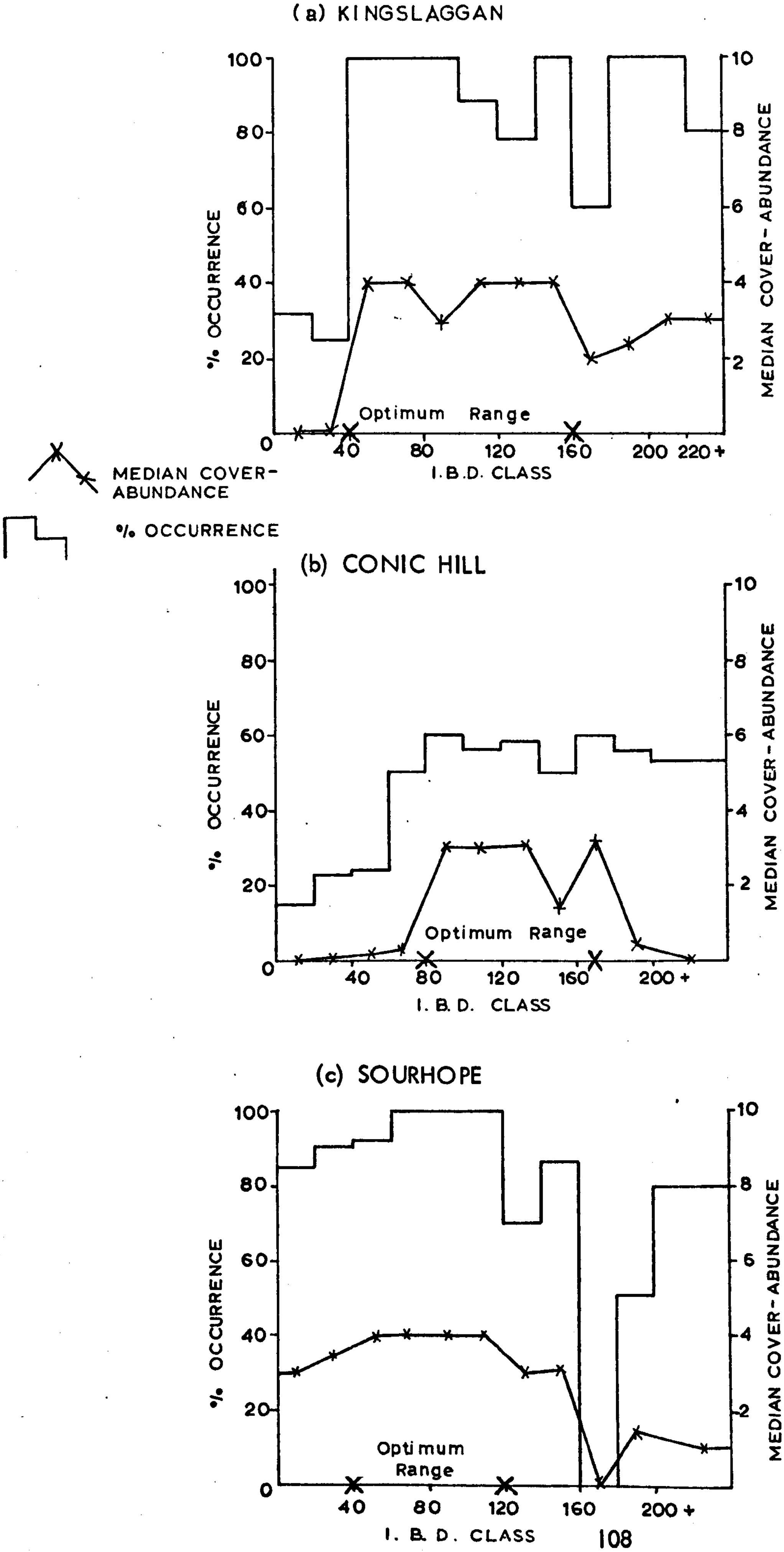
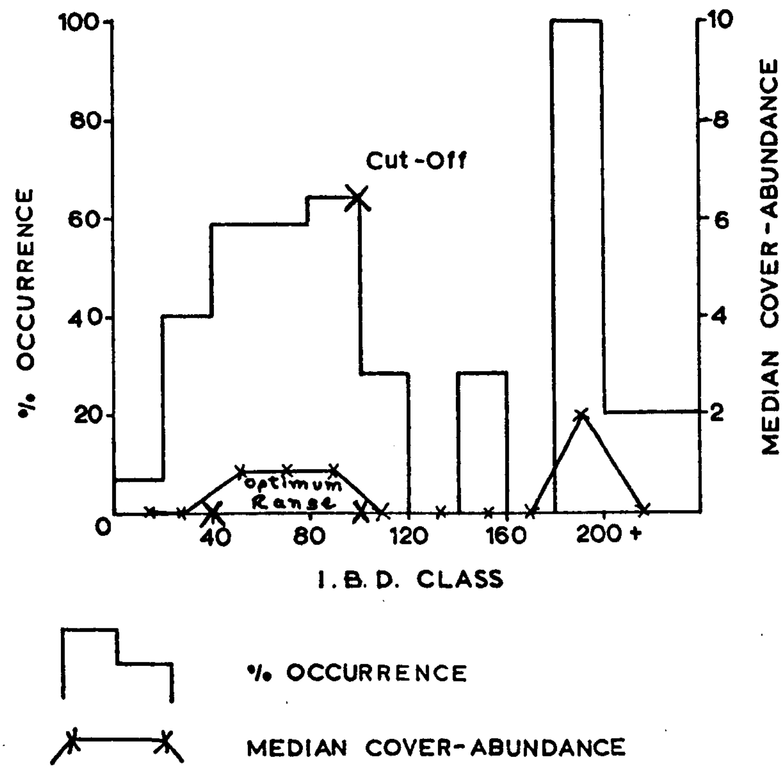


Fig. 4.12. Effect of Pteridium competition on Poa pratensis - Sourhope.



abundance values of a cut-off at the relatively low Pteridium level of I.B.D. = 100, so Poa pratensis is a species confined to low bracken levels on the Sourhope quadrats examined.

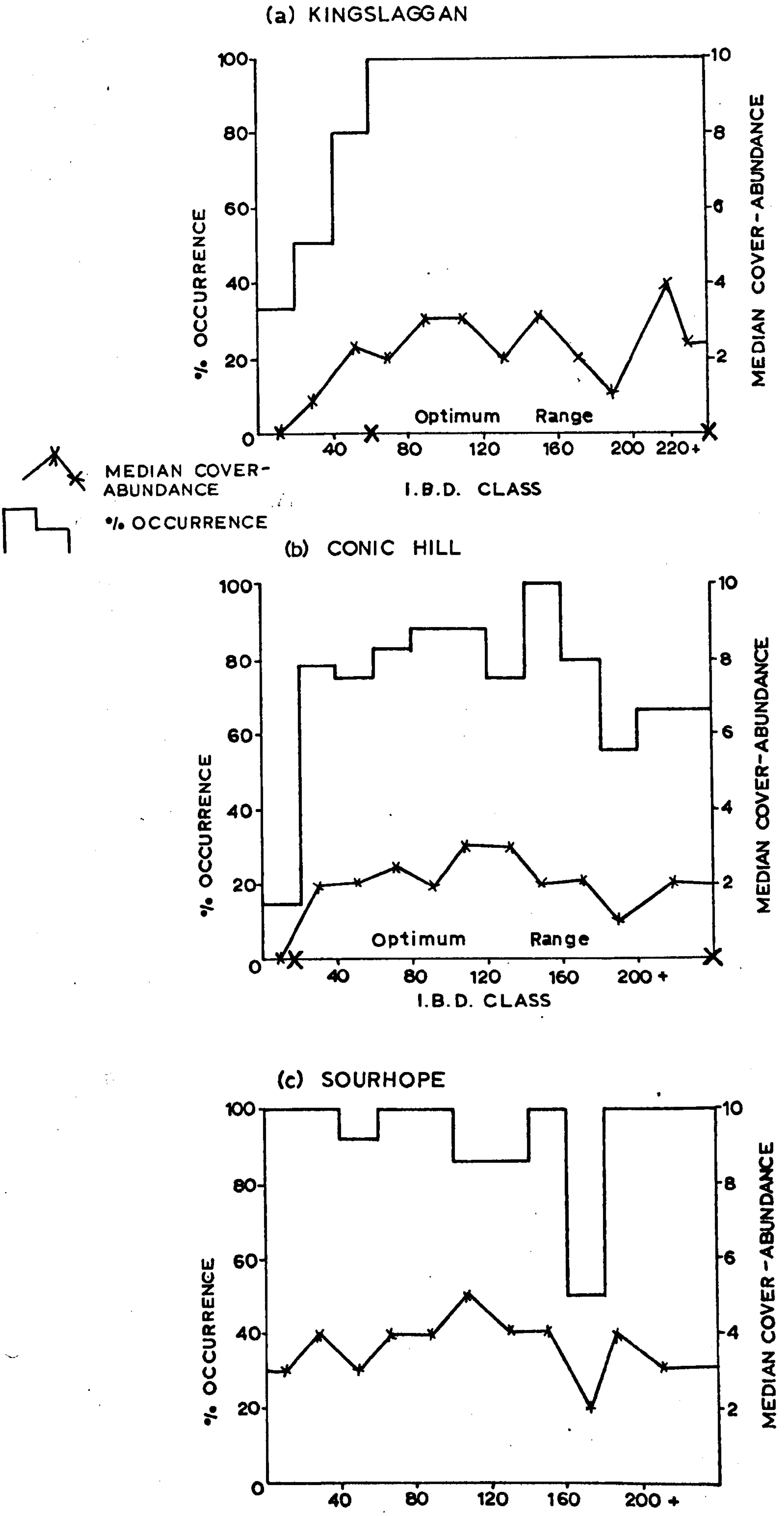
(5) Galium hercynicum (Fig. 4.13). This is the only herb which emerges as a significant 'tolerant' species and, while important in terms of consistency of occurrence, it seldom attains significant cover value. The histograms for Conic Hill and Kingslaggan show that Galium is undoubtedly a bracken community species on these sites, and one which tolerates very high levels of frond development. On neither site is there any cut-off point and indeed little evidence of reduced vigour at high bracken levels. It may be of course that any adverse effect on Galium performance is offset by reduced competition from the grasses which are less tolerant of fierce bracken competition.

Galium hercynicum cannot be classified as a 'tolerant' species in the Sourhope setting, since it is equally common on bracken-free and bracken-covered sites. In other words it shows little response to Pteridium levels and more properly belongs in the 'indifferent' category.

Indifferent Species

A few moorland species seem to be equally happy with or without bracken cover. They are common constituents of both bracken-covered and bracken-free rough grazing although they do differ in their response to high Pteridium levels.

Fig. 4.13. Effect of Pteridium competition on Galium hercynicum.



(1) Deschampsia flexuosa (Fig. 4.14). This species is more important at Sourhope than elsewhere. A fairly common component of the acid grassland nodum, it persists, apparently little affected, to the highest bracken levels. At Conic Hill and Kingslaggan it is of erratic occurrence seldom achieving significant cover at the latter. Nevertheless what evidence is available substantiates the Sourhope data that this is an extremely tolerant species and bracken density is not a controlling factor in its distribution.

(2) Potentilla erecta (Fig. 4.15). This herb is of almost ubiquitous occurrence, being a very common, though minor, component of heath and grassland communities. Although unaffected by low and medium frond densities, there is evidence from all sites that, unlike its common associate Galium hercynicum, it is adversely affected at high bracken levels.

This classification of herb layer species has revealed a general similarity in the response of species to bracken competition in three rather different moorland environments. The nature of the response is sufficiently uniform for consistent allocation of each species to the appropriate 'response category' - intolerant, tolerant and indifferent. Only in the cases of Nardus stricta and Galium hercynicum is there evidence of sufficient variation to question their classification, and as far as the latter is concerned the discrepancy results from the difference in the bracken-free nodum rather than any difference in the reaction of Galium hercynicum.

Nevertheless, there is some inter-site variation, if not in the nature of the response, at least in the level of bracken dominance which is significant. It would obviously be misleading to overemphasise absolute values which can

Fig. 4.14. Effect of Pteridium competition on Deschampsia flexuosa.

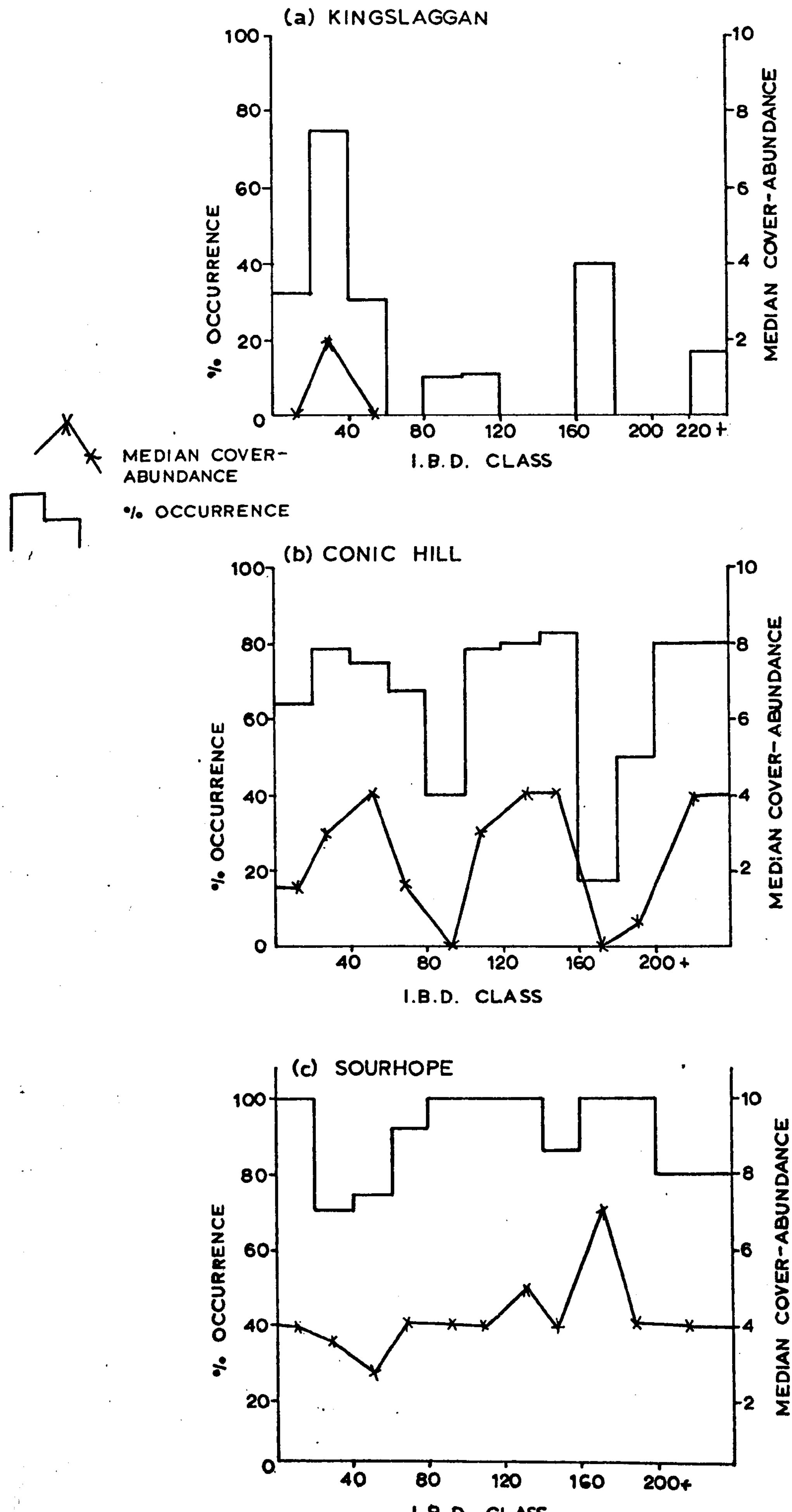
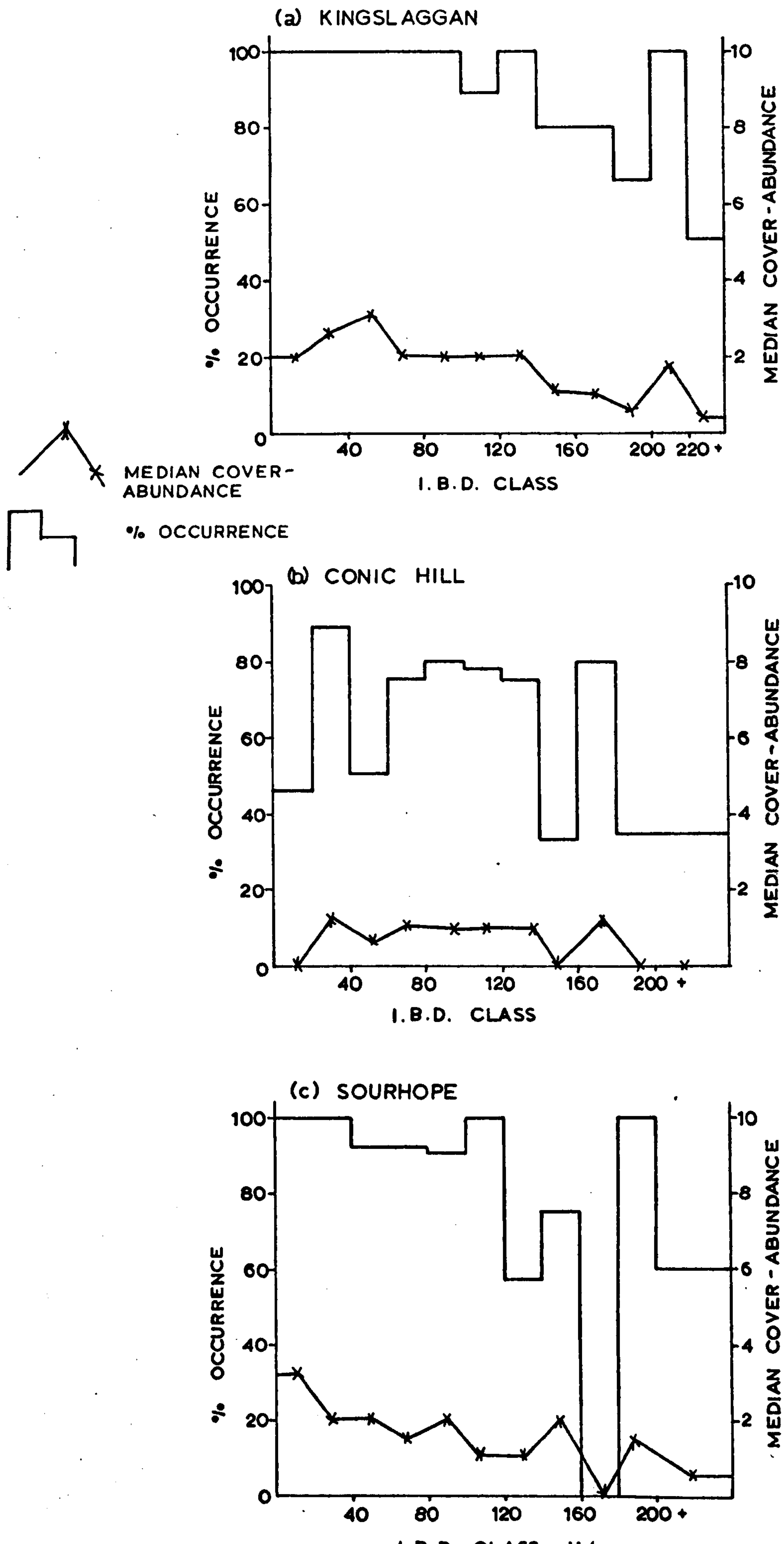


Fig. 4.15. Effect of Pteridium competition on Potentilla erecta.



only provide an indication of the tolerance of the species. However in some cases the crucial bracken level varies sufficiently to suggest that the tolerance of a particular species to bracken competition depends on other environmental factors and perhaps specifically on the ecological status of the species.

The response of species at each site is compared in Table 4.3. For most species the pattern of response is reasonably consistent. The anomalous situation of Festuca ovina at Sourhope is more apparent than real. Its tolerance of bracken is similar in all three sites but at Sourhope it is a prominent component of the bracken-free, as well as the Pteridium - grassland nodum.

More difficult to explain are the variations in response of Calluna vulgaris and Nardus stricta. As previously noted (see page 100) Calluna is apparently considerably more tolerant of Pteridium competition at Conic Hill than at Kingslaggan. The key to this may lie in the difference in the ecological status of the plant in the bracken-free noda at each site. At Conic Hill one is dealing with a heath nodum, a Callunetum, in which Calluna vulgaris is dominant, vigorous, and sometimes in virtually pure stands. At Kingslaggan Calluna is an important but less vigorous and less dominant member of a mixed heath moorland. This difference in vigour appears to influence the ability of the heath to withstand bracken competition.

The position of Nardus stricta is more complex. Highly intolerant at Kingslaggan and Conic Hill, it appears to be quite resistant to bracken

Species	occurrence cut-off point (I.B.D.)	cover-abundance cut-off point (I.B.D.)	optimum range (I.B.D.)
<u>Calluna vulgaris</u>			
Kingslaggan	60	40	-
Conic Hill	140	120	-
<u>Nardus stricta</u>			
Kingslaggan	20	20	-
Conic Hill	120	low values	-
Sourhope	140 (erratic)	140 (erratic)	-
<u>Vaccinium myrtillus</u>			
Kingslaggan	100	low values	
Conic Hill	160	low values	
Sourhope	140 (erratic)	low values	
<u>Agrostis tenuis</u>			
Kingslaggan	-	-	40-200
Conic Hill	-	180	60-180
Sourhope	-	-	40-160
<u>Festuca ovina</u>			
Kingslaggan	-	-	40-160
Conic Hill	-	140	60-140
Sourhope	160	160	-
<u>Anthoxanthum odoratum</u>			
Kingslaggan	-	-	40-160
Conic Hill	-	180	80-180
Sourhope	-	160	40-120
<u>Galium hercynicum</u>			
Kingslaggan	-	-	60- ∞
Conic Hill	-	-	20- ∞
Sourhope	-	-	-
<u>Poa pratensis</u>			
Sourhope	-	low values	40-100
<u>Deschampsia flexuosa</u>			
Kingslaggan	-	-	-
Conic Hill	-	-	-
Sourhope	-	-	-
<u>Potentilla erecta</u>			
Kingslaggan	-	low values	-
Conic Hill	180	low values	20-140
Sourhope	-	low values	-

Table 4.3. Comparison of species response to <u>Pteridium</u> competition at different sites.

competition on at least one stand at Sourhope. The relative vigour of the species again appears to hold the key, for on the western sites Nardus is only a very minor component of the bracken-free nodum while at the Sourhope site it is a vigorous and usually dominant species outside the bracken stands. Furthermore the relatively high cover of Nardus obtained at Pteridium Stand 2 at Sourhope is rather misleading. Field observation reveals that the hinterland of the Pteridium stand consists not of a continuous frond canopy with a Nardus ground cover, but patchy frond growth in which Pteridium and Nardus form a mosaic. Where Nardus plants are found under heavy bracken shade observation suggests that their vigour is reduced by curtailed flowering (Plate 4.1). A similar response has been noted for Deschampsia flexuosa growing in sub-optimal conditions by Hopkinson (1927). Elucidation of the complex interrelationship of Pteridium aquilinum and Nardus stricta on this site would require more prolonged investigation of the evolution of the mosaic pattern of vegetation which might clarify the response of the Nardus to frond competition.

The species-response data can also be used to identify species assemblages. This acts as a check on the nodum approach and provides an appropriate summary. The median cover-abundance values of the main ground vegetation species have been combined in Figure 4.16.

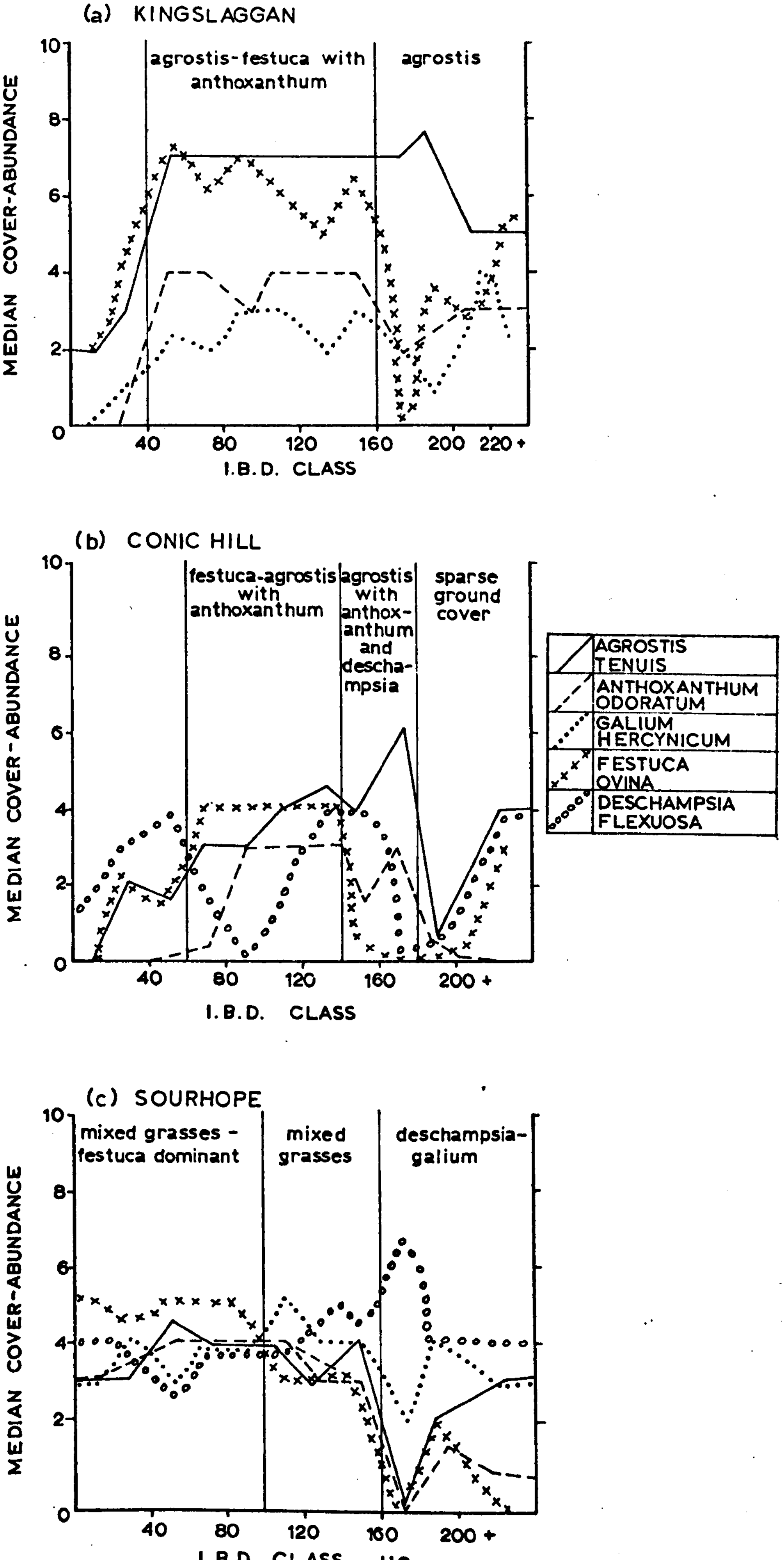
Two Pteridium-dominated assemblages have been identified at Kingslaggan - Agrostis-Festuca with Anthoxanthum odoratum where I.B.D. = 40-160, and Agrostis tenuis alone where the Index of Bracken Dominance exceeds 160.

Plate 4.1. Response of Nardus stricta to Pteridium competition.

Deschampsia flexuosa (Domin value 4) in flower, invading Nardus stricta tussock

tussock of Nardus stricta (Domin value 6); note dead tissue and lack of flowers

Sourhope Pteridium-Nardus Phase (Pteridium Stand 2, quadrat 25).



(a) KINGSLAGGAN
agrostis-festuca with anthoxanthum
agrostis
MEDIAN COVER-ABUNDANCE
I.B.D. CLASS
(b) CONIC HILL
festuca-agrostis with anthoxanthum
agrostis with anthoxanthum and deschampsia
sparse ground cover
AGROSTIS TENUIS
ANTHOXANTHUM ODORATUM
GALIUM HERCYNICUM
FESTUCA OVINA
DESCHAMPSIA FLEXUOSA
(c) SOURHOPE
mixed grasses - festuca dominant
mixed grasses
deschampsia-galium

These correspond closely to the noda identified. The apparent recovery of Festuca ovina and Anthoxanthum odoratum above I.B.D. = 200 is probably a distortion caused by the small number of samples.

At Conic Hill it is possible to identify three Pteridium assemblages - Festuca-Agrostis with Anthoxanthum at I.B.D. = 60-140; Agrostis tenuis with Anthoxanthum and Deschampsia at I.B.D. = 140-180; and pure Pteridium where the Index of Bracken dominance exceeds 180. The recovery of Agrostis tenuis and Deschampsia flexuosa above I.B.D. = 200 has been discounted as it is based on only three quadrats. Again this is in general accord with the nodum classification but the data based on the reaction of individual species permits a more detailed subdivision of the Pteridium - Agrostis - Festuca nodum.

The continuum of change at Sourhope is clearly shown in Figure 4.16. Where the Index of Bracken Dominance is less than 100 there is a mixed grass assemblage with Festuca ovina dominant; where I.B.D. = 100-160 Festuca loses its overall dominance and several species become co-dominant; above I.B.D. = 160 Deschampsia flexuosa assumes dominance but this really corresponds to the pure Pteridium nodum as the total ground cover is low.

IV. EXAMPLES OF FIELD SITUATIONS

The validity of the conclusions drawn from the above analyses depends on the tenet that Pteridium density is the sole macroenvironmental variable. For instance the conclusions drawn from the noda definition would be invalidated if it were found that each noda is associated with a different habitat.

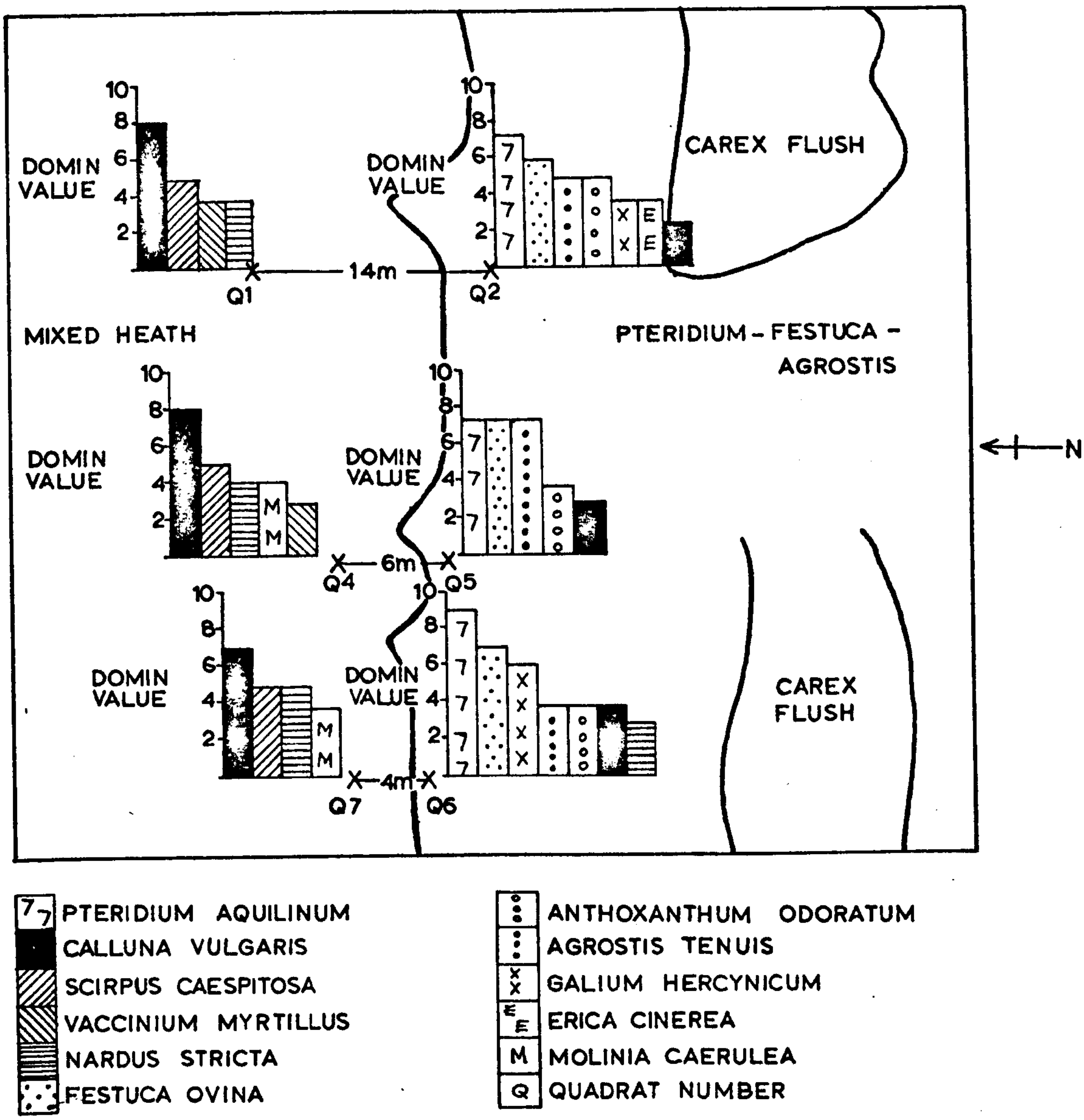
Similarly it might be argued that the reaction of individual species reflects, not their degree of tolerance of bracken competition, but their tolerance or otherwise of macroenvironmental conditions uniquely associated with the Pteridium communities. To establish the insignificance of other variables and to illustrate the general conclusions reached in the analyses, this chapter concludes with concrete examples of vegetation situations from each site.

Kingslaggan

(I) Pteridium Stand 5 (see Fig. 3.2, page 55). This stand occurs on the west-facing slope of Doon Hill between 185 and 207 m. Two distinct vegetation types occur on this slope, Pteridium-Festuca-Agrostis grassland and mixed heath moorland. The slope varies from 10° to 18° with a roughly terraced profile but the vegetation cuts across these slope elements so that there is no apparent change in physical environmental conditions corresponding to the vegetation change.

The field technique chosen at this site was the comparison of pairs of quadrats situated on either side of the vegetation boundary as illustrated in Figure 4.17. The bracken quadrats were selected close to the stand edge as the situation in the hinterland is complicated by the presence of Carex flushes. Recorded habitat conditions are identical for each pair of quadrats which, as the diagram shows, are only a few metres apart. The diagram highlights the abrupt change in species composition with a virtually complete change in the complement of species across the Pteridium margin. Calluna

Fig. 4.17. Kingslaggan Pteridium Stand 5.



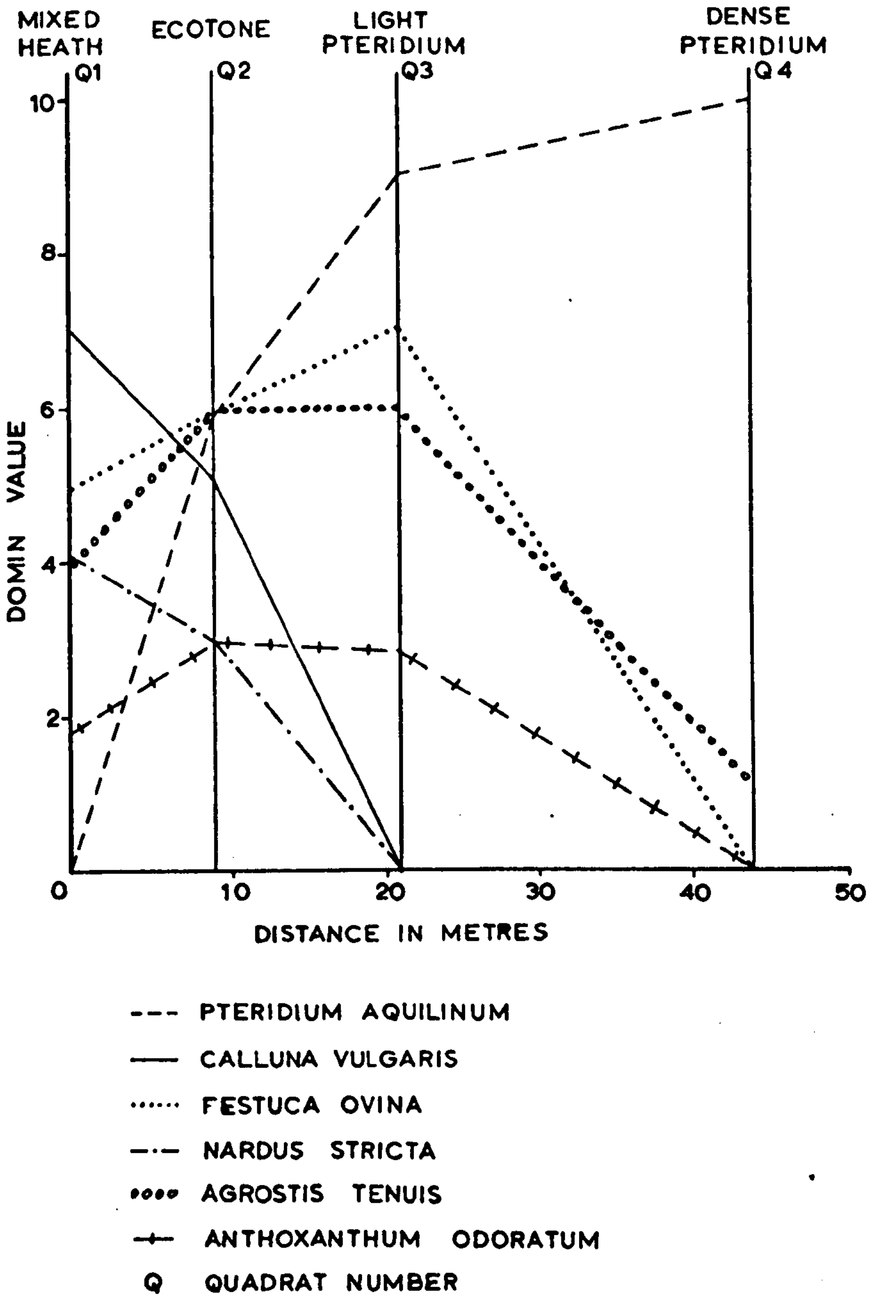
vulgaris indeed is found in every quadrat but reduced from the dominant species in the heath to a very minor component of the Pteridium stand. Conversely the grasses which dominate the ground vegetation under the bracken have no cover value in the heath nodum.

This site was also selected for detailed examination of soil type which is considered fully in Chapter 5 (see pages 161-169). The soil type varies in conjunction with vegetation from a peaty podsol under the mixed heath to a brown forest soil under the Pteridium, yet, apart from vegetation, soil-forming factors are constant. Two distinct vegetation-soil systems thus exist side by side on identical parent material and constant drainage regimes but on opposite sides of a sociological vegetation boundary.

(2) Pteridium Stand 9. Another good example of a sociological boundary occurs at Stand 9 situated on a bench at approximately 180 m on the north-west side of Kenlum Hill. This is a very extensive stand of vigorous bracken and the example chosen and illustrated in Figure 4.18 is from its northern extremity. Unlike the first example, the vegetation boundary is apparently currently changing as the Pteridium appears to be invading the Calluna-Nardus community which, at the time of the survey, had been recently burned (probably in the preceding season).

In this case quadrats were selected along a transect across the ecotone over a distance of approximately 50 metres. Figure 4.18 illustrates the change in species composition along this transect, each quadrat having been subjectively chosen to examine visually obvious changes in the character of

Fig. 4.18. Kingslaggan Pteridium Stand 9.



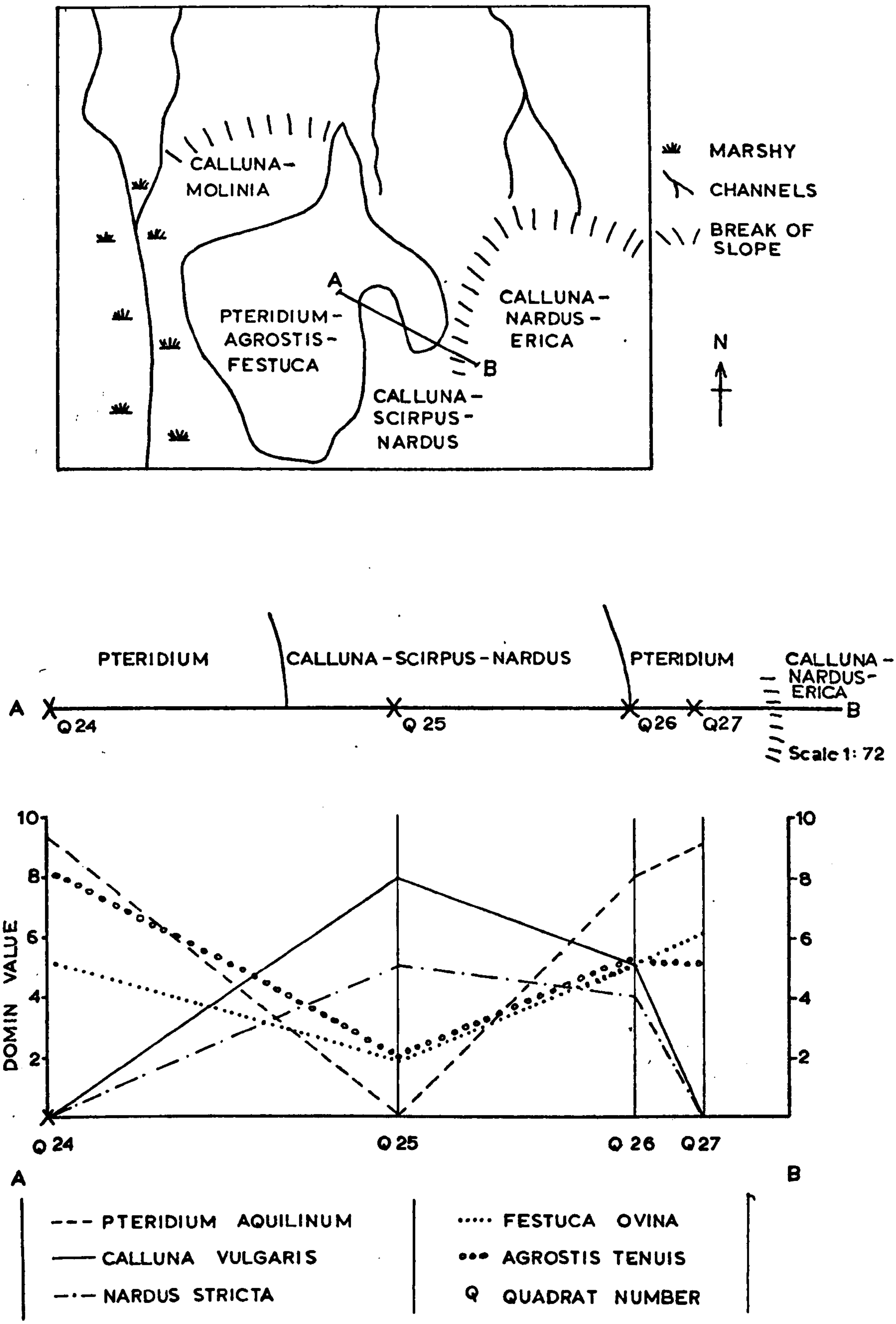
(Adapted from: Mitchell, J. in Tivy, J., 1973, page 105).

the vegetation. Ql is 6 metres within the heath stand, Q2 represents the ecotone with the greatest number of species, Q3 is relatively light Pteridium growth, while Q4 emphasises the suppression of herb stratum species under dense Pteridium. Within this 50 metre stretch is therefore found the full range of Kingslaggan noda described above.

(3) Pteridium Stand 3. Not all sites provide as straightforward examples of sociological boundaries as examples (1) and (2), and Stand 3 has been selected to illustrate a more complex situation. This is an isolated stand of bracken close to Pteridium Stand 5 described above. As Figure 4.19 illustrates, Pteridium distribution is partially controlled by habitat conditions, the western boundary coinciding with a marshy channel while a sharp break of slope on the east determines the change to a Calluna-Erica cinerea-Nardus community situated on a rocky knoll. However, in the south-east a spur of Pteridium is separated from the main stand by an area of mixed heath with no apparent habitat control. Transect A-B demonstrates the sharp and dramatic changes in vegetation type across a distance of approximately eight metres as the Pteridium-Agrostis-Festuca stand gives way to mixed moorland, succeeded by the Pteridium community spur. Since quadrats 24 to 27 are all freely drained and range in slope from 8 to 12° it is concluded that the presence or absence of Pteridium aquilinum and its associated soils determine the composition of the herb stratum.

These three examples from Kingslaggan provide concrete instances of sharp changes in vegetation types with no associated changes in altitude, aspect, slope or surface drainage. Heath and bracken with their associated

Fig. 4.19. Kingslaggan Pteridium Stand 3.



soil types form two distinct little ecosystems side by side, the occurrence and degree of dominance of Pteridium being the variable which apparently controls the species composition of the herb layer.

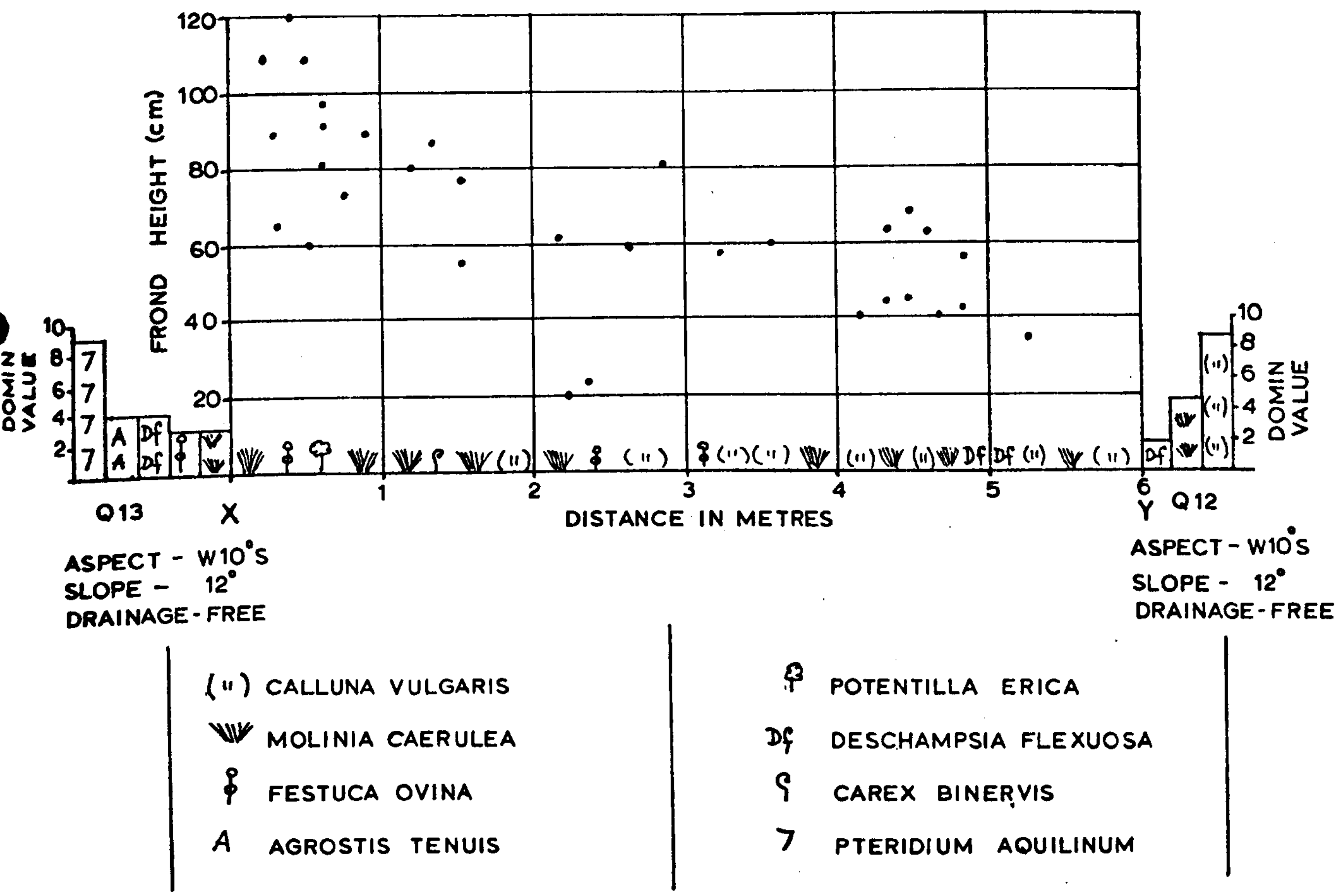
Conic Hill

(I) Pteridium Stand 3 (See Fig. 3.4, page 60). The lower slopes of Conic Hill are scored by deeply-incised gullies the sides of which are occupied by bracken which gives way to heath vegetation on the intervening ridges. Stand 3 is one of these extensive gully-side bracken stands, the example included here being taken from the ridge crest where a sociological boundary occurs between the Pteridium and Callunetum.

The ecotone between the two vegetation types is narrow, and the change in species composition was recorded using the line transect method described in Chapter 3 (see page 71). This method provides a complete record of the continuous variation in herb stratum species and in Pteridium frond numbers and height along the line.

The results are presented in Figure 4.20, the line transect data having been supplemented by quadrat data from each end of transect - Q13 within the Pteridium stand, Q12 in the Callunetum. As the diagram indicates, environmental conditions at the two quadrats are identical but the vegetation types are in marked contrast. Across the intervening ecotone (X to Y) there is a steady decrease in frond height and a more erratic decrease in density

Fig. 4.20. Conic Hill Pteridium Stand 3.

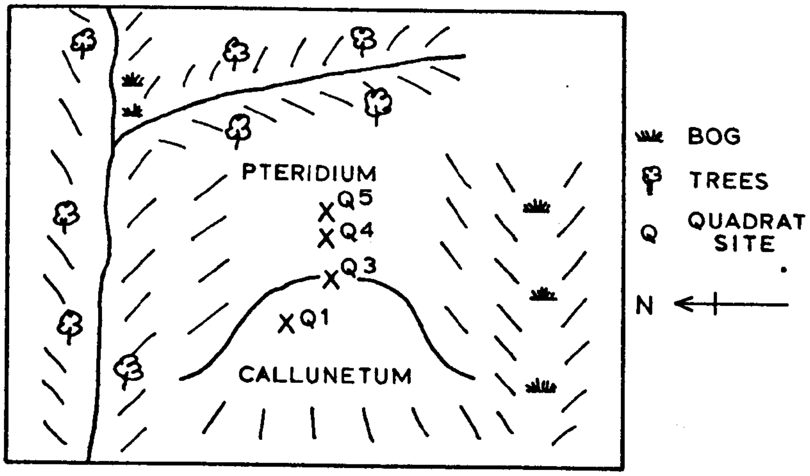


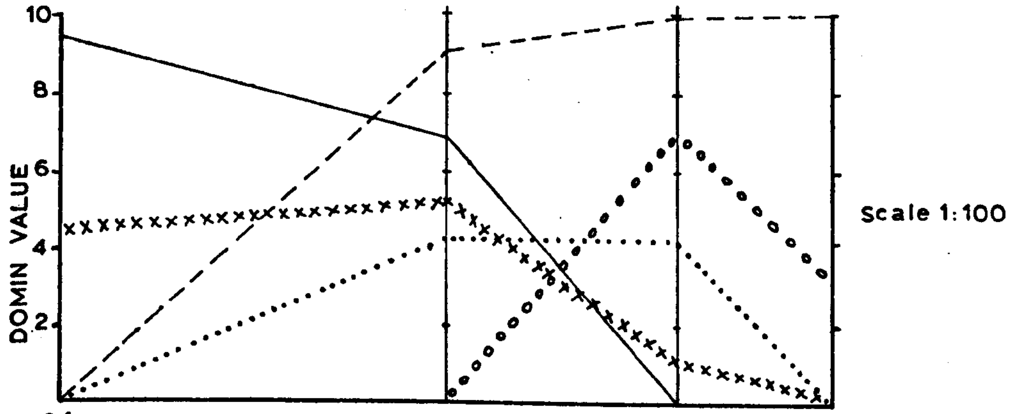
associated with which the ground flora gradually alters from _Pteridium-type_ to _Callunetum-type_. Figure 4.20 suggests that _Molinia_ is more persistent than _Calluna_ in the face of bracken competition.

(2) _Pteridium Stand 6_. The lower slopes of Conic Hill on the southern site are mainly poorly drained with isolated well-drained knolls occupied by _Pteridium_. Stand 6 is an example of one of these isolated bracken stands, bordered on three sides by marshy or tree-lined channels as shown in Figure 4.21. However on the western side of the knoll _Pteridium_ occupies the crest and upper slope giving way abruptly to _Callunetum_ on the lower slopes with no associated sudden environmental change. Although the heath occupies steeper slopes than the _Pteridium_ the difference in slope appears to be an inadequate explanation for the complete and abrupt change in species composition revealed in quadrats 1 to 5, particularly since, on other sites on Conic Hill, it is more usual to find the vegetation situation reversed with bracken on the steeper slopes and heath occupying the more gently-sloping ridge-top sites.

Like example (2) from Kingslaggan, this transect is an excellent example of change in ground vegetation across a sociological boundary with _Pteridium_ dominance the significant variable. It includes the complete range of vegetation noda described for Conic Hill (see pages 92-93) - _Callunetum_, _Pteridium - Agrostis_ grassland and pure Pteridium. Associated with this vegetation change is change in soil type from a peaty podsol with thin iron pan under the _Callunetum_ to brown forest soils under the _Pteridium_ with intermediate soil types in the ecotone. The soil data from this stand is presented in Chapter 5 pages 184-189, and taken together the vegetation and

Fig. 4.21. Conic Hill Pteridium Stand 6.





	Q1	Q3	Q4	Q5	
Aspect -	W 20° N	W 20° N	W 20° N	W 20° N	environmental parameters
Slope -	14°	8°	9°	7°	
Drainage -	Free	Imperfect	Imperfect	Imperfect	

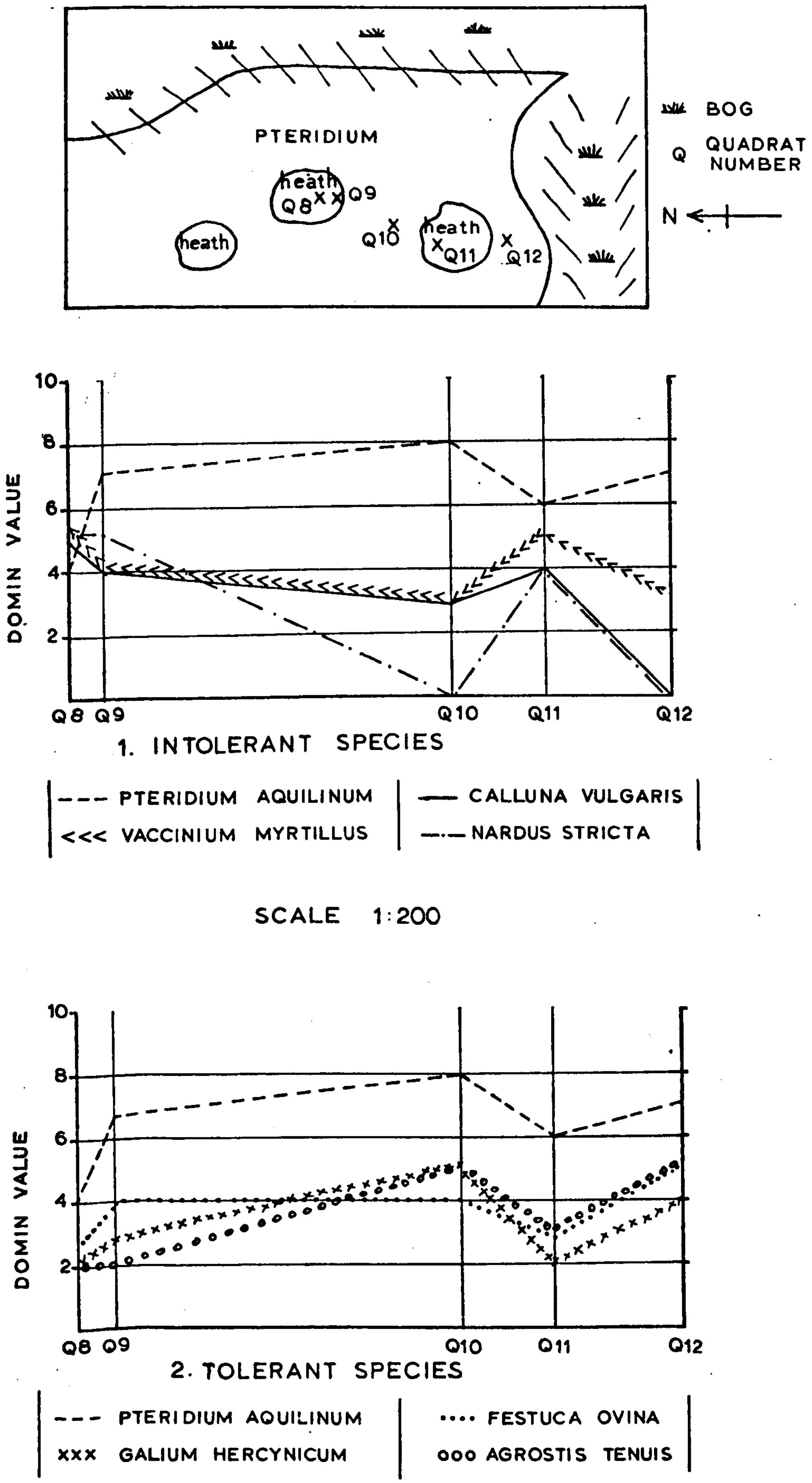
soil data present again a picture of two distinct ecosystems in which bracken dominance is the controlling variable.

It is noteworthy that Pteridium has been allocated to the same Domin class in quadrats 4 and 5 yet the degree of development of ground cover is quite different. In fact the density of fronds is almost identical in the two quadrats but the height of fronds and hence the index of bracken dominance is much greater in quadrat 5 (I.B.D. = 188 compared to 143 in quadrat 4). This emphasises the importance of frond height and hence weight of litter in determining the competitive power of the fern, and incidentally stresses the greater accuracy of the bracken dominance index as a measurement of competitiveness.

(3) Pteridium Stand 4. In most of the previous examples attention has been focused on sociological boundaries between vegetation stands. Stand 4 is included to illustrate the variation in ground vegetation which can occur within a Pteridium stand when frond density and height are variable. Like Stand 6, this stand occupies a better drained site within generally poorly drained mixed wet moorland, but, unlike Stand 6, Stand 4 is extensive and variable. Frond cover is uneven and within the stand there are 'islands' of heath vegetation coinciding with gaps in the frond canopy.

Figure 4.22 illustrates the nuances of change in the species composition of the herb stratum associated with these alternate pockets of heath and bracken. The distribution of the two vegetation types is independent of external environmental factors for all quadrats were regarded as imperfectly drained,

Fig. 4.22. Conic Hill Pteridium Stand 4.



are within a narrow range of slope from 6 to 10°, and occur on identical parent material. The two graphs provide a nice illustration of the contrasting response to bracken of the two categories of 'intolerant' heath species and 'tolerant' Pteridium community species which have been identified and described above (see pages 99-110). Clearly the cover values of the 'intolerant' species, in this case Calluna vulgaris, Nardus stricta and Vaccinium myrtillus are inversely related to Pteridium cover. The cover of the 'tolerant' species is correlated positively with bracken cover suggesting that in this case the relatively light frond cover is within the limits of tolerance of the species shown, that is the bracken dominance index does not exceed the upper limit of the 'optimum range' for Festuca ovina and Agrostis tenuis as described above (see Table 4.3, page 116). In fact the maximum value of the index of bracken dominance in the quadrats under consideration is 130, within the optimum range for both Festuca and Agrostis.

(4) Pteridium Stand 7. In the examples described so far sociological boundaries between heath and Pteridium stands have been abrupt and clearly defined. However competition between heath species and Pteridium does not always result in sharply delimited stands and broad ecotone zones between the two communities do exist, as Watt has described from the Breckland (Watt, 1955). An example of such a mixed vegetation zone occurs at Pteridium Stand 7 on the ridge immediately below the summit area of Conic Hill, which contrasts nicely with the sharp sociological boundaries between the vegetation types found nearby (see Plate 4.2).

Plate 4.2. Conic Hill _Pteridium_ Stand 7.

burned _Calluna_

sharp _Pteridium_-_Callunetum_ sociological boundary

mixed _Calluna_-_Pteridium_ zone (quadrats 9, 10, 16)

The quadrat data, depicted in Figure 4.23, taken from this zone shows the mixture of Pteridium and heath noda species which occurs, while the considerable areal extent of this zone may suggest a fairly even competitive balance between the mature Calluna vulgaris and Pteridium. Watt's study has shown that even-aged Callunetum in its building and mature phases can compete successfully with Pteridium. However, as in the Pteridium-Nardus phase at Sourhope, cover-abundance values sometimes fail to give the complete picture. There is visual evidence that, despite the high Domin values for Calluna vulgaris, the vigour of the heath shrub has been reduced by bracken competition which appears to be curtailing flowering, an effect already described for Nardus stricta at Sourhope (see page 117). In Plate 4.3 (a) which shows the ground vegetation of quadrat 16 the restricted flowering and prevalence of dead tissue of Calluna vulgaris are evident. The contrast in the number of Calluna flowers between the bracken-free and Pteridium-Calluna zone is equally apparent in Plate 4.3 (b).

It seems reasonable to postulate that in such a finely-balanced competitive situation the balance could easily be tipped by human activity in favour of one or other vegetation type. Evidence of this is found at the northern extremity of Stand 7 where the Callunetum had been destroyed by muirburn and replaced by a pioneer heath community. At the time of survey a dense canopy of short Pteridium fronds was found over the ground stratum of burned Calluna and mixed heath vegetation along the margin between the two stands (see Fig. 4.23 (b)). It seems probable that removal of Calluna competition has permitted more vigorous frond development and possibly bracken encroach-

Plate 4.3. Response of Calluna vulgaris to Pteridium competition.

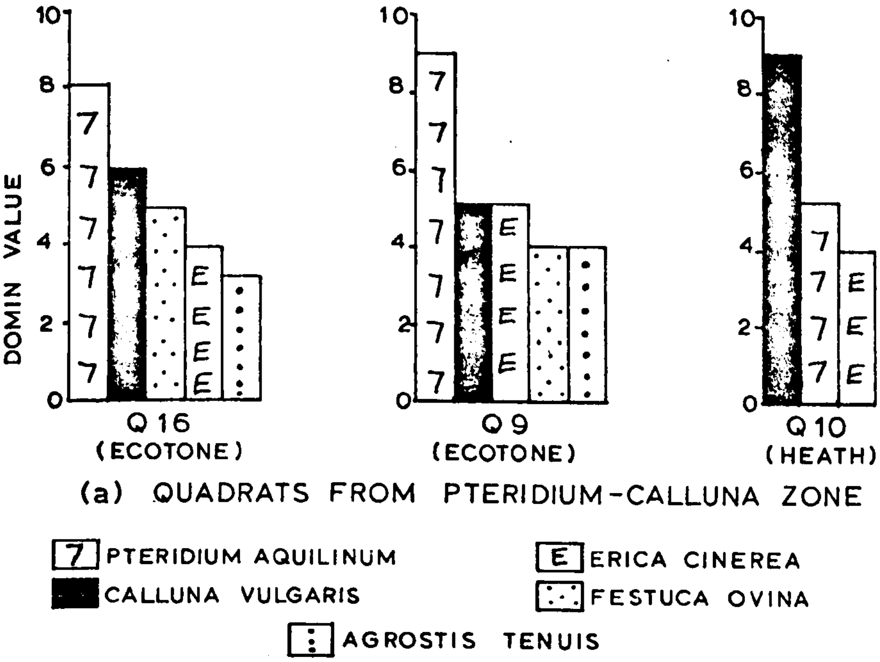
(a) Conic Hill Pteridium Stand 7, Quadrat 16 - Pteridium fronds removed.

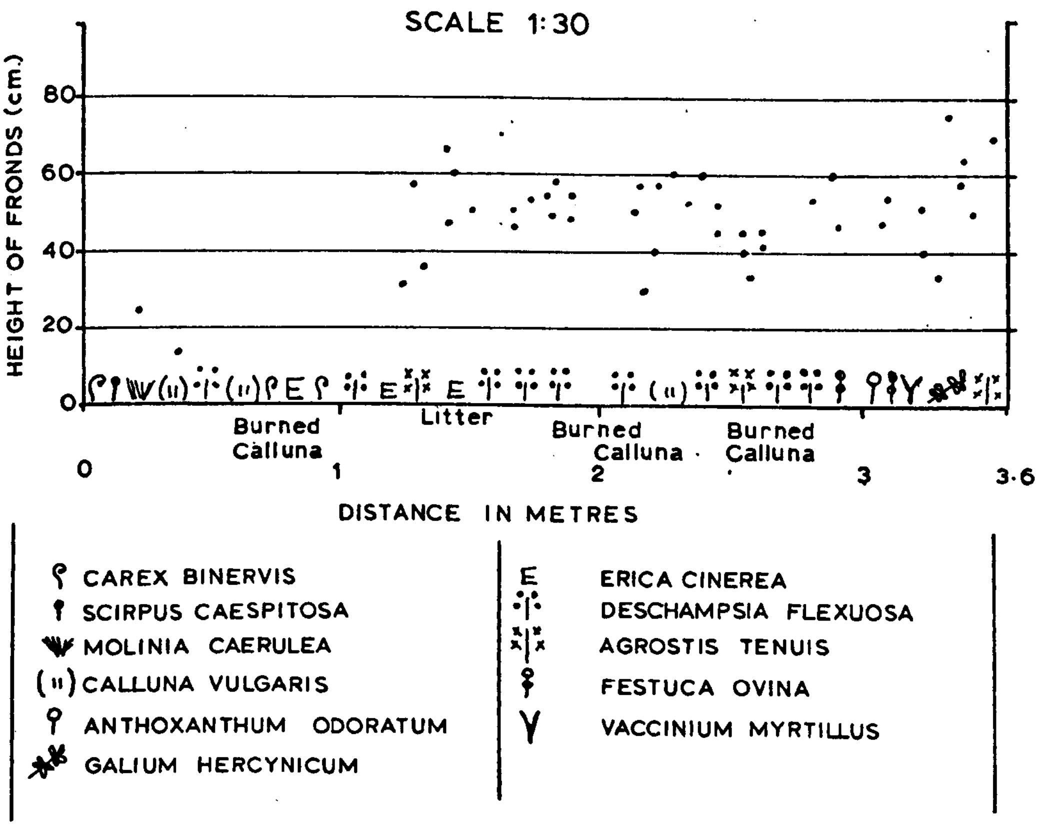
Callunetum

mixed Calluna - Pteridium zone

(b) Conic Hill Pteridium Stand 7

Fig. 4.23. Conic Hill Pteridium Stand 7.





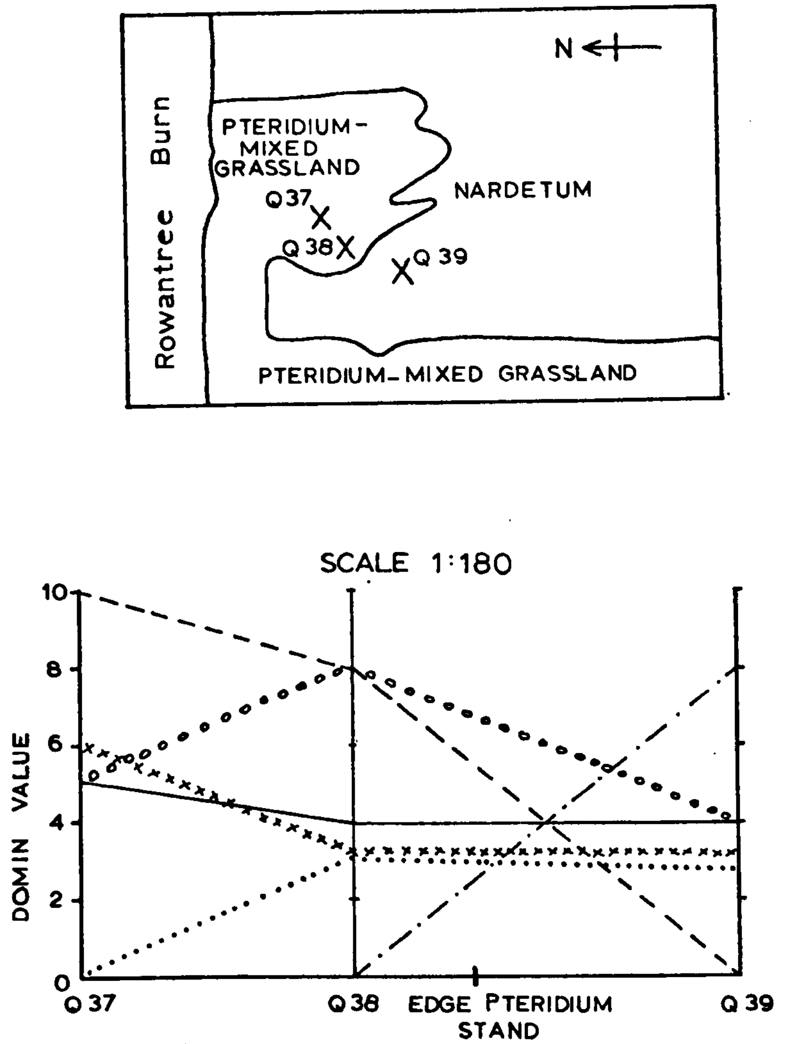
(b) TRANSECT ACROSS BURNED CALLUNETUM-PTERIDIUM BOUNDARY ment. The data on specific response presented in this study would suggest that this bracken encroachment should lead to a modification of the ground flora with the encouragement of Agrostis-Festuca grassland at the expense of heath. Unfortunately verification of this requires protracted study, outwith the time-span of the present project; the methodology used here provides only a 'still shot' of the situation at one point in time where the monitoring of an evolving situation would necessitate data collection over a number of years.

Sourhope

(I) Pteridium Stand 2 - northern extremity (see Fig. 3.5, page 62). Pteridium Stand 2 at Sourhope occupies the lower part of the west-facing slope of Dod Hill between approximately 300 and 400 m. Upslope the bracken gives way to the mixed acid grassland nodum, the boundary between the two vegetation types sometimes coinciding with a break of slope. However the boundary meanders and frequently coincides with no obvious change in physical environmental conditions, offering good examples of sociological boundaries which, according to local information, have been stationary for a considerable number of years.

The first example is a sequence of quadrats cutting across one of these sociological boundaries (see Fig. 4.24). Quadrat 39 is typical of the mixed acid grassland nodum, dominated by Nardus stricta, which is a common vegetation type on adequately drained sites in the Sourhope area. As Figure 4.24

Fig. 4.24. Sourhope. Pteridium Stand 2.(Northern extremity).



	Q 37	Q 38	Q 39
SLOPE -	12°	14°	14°
ASPECT-	N20°E	N 20° E	N 20° E
DRAINAGE CLASS -	FREE	FREE	FREE

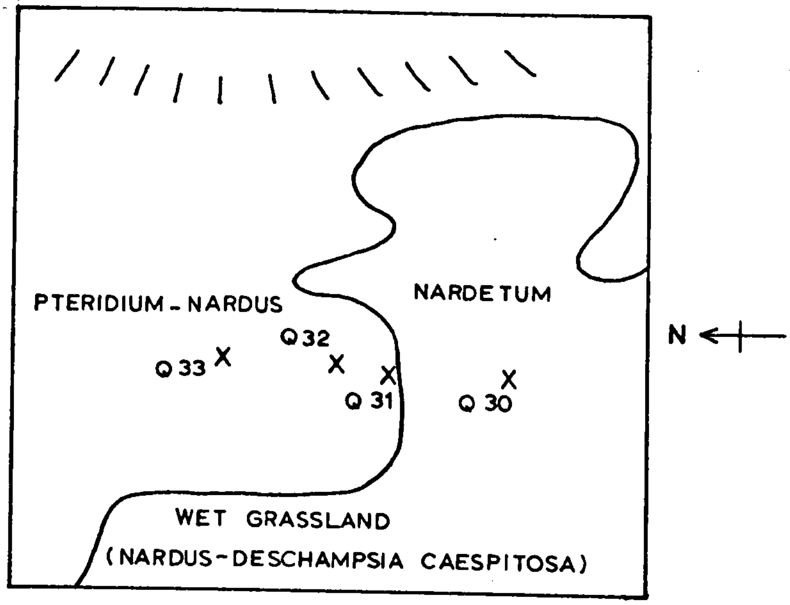
— — — PTERIDIUM AQUILINUM	•••• FESTUCA OVINA
••• AGROSTIS SPECIES	××× GALIUM HERCYNICUM
—— ANTHOXANTHUM ODORATUM	—·— NARDUS STRICTA

illustrates, the intrusion of Pteridium aquilinum alters the balance of species in this grassland, the Nardus stricta in this case disappearing and Agrostis species, Anthoxanthum odoratum and Galium hercynicum becoming of approximately equal importance. However the complete contrast in the ground vegetation across sociological boundaries which has been shown to be a feature of the Kingslaggan and Conic Hill sites is not found here; important species such as Anthoxanthum odoratum and Agrostis species do not alter much in cover-abundance from the bracken-covered to bracken-free areas. The response of Festuca ovina, which dies out as bracken dominance increases, should also be noted. At Kingslaggan and Conic Hill Festuca ovina is a prominent component of the Pteridium community, only succumbing to bracken competition at high frond densities, but its apparently greater vulnerability at Sourhope has already been noted above (see page 106).

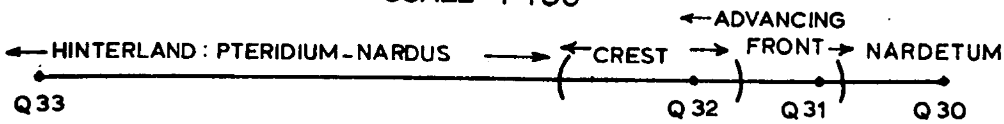
(2) Pteridium Stand 2 - Southern Extremity. The most widely occurring bracken community at Sourhope is the one described in example (1) - Pteridium-Agrostis with variable amounts of Festuca ovina and Anthoxanthum odoratum. However as already noted (see page 94), over a limited area Nardus stricta persists in conjunction with the Pteridium producing a Pteridium-Nardus 'phase', which this example has been chosen to illustrate (see Fig. 4.25).

The stand boundary is again a sociological one as the environmental data indicates. The fact that the Pteridium community ground vegetation is essentially merely a modified version of the bracken-free acid grassland is even more apparent here than in example (1). The Domin values of Agrostis

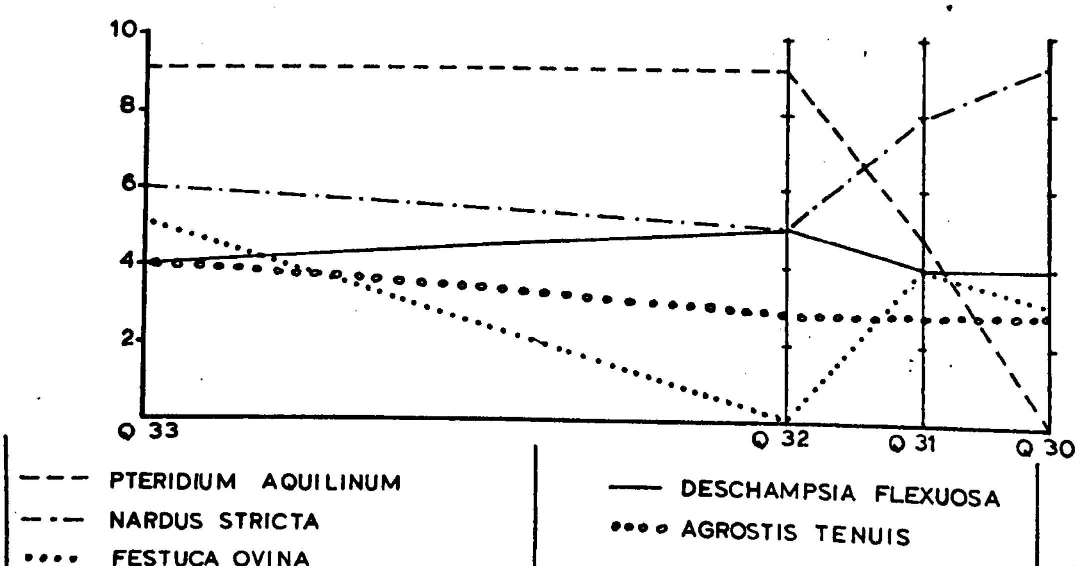
Fig. 4.25. Sourhope Pteridium Stand 2. (Southern extremity).



SCALE 1:180



	Q 33	Q 32	Q 31	Q 30
ALTITUDE	323 m	323m	323m	323m
ASPECT	W 10° N	W 10° N	W 10° N	W 10° N
SLOPE	11°	12°	13.5°	11°
DRAINAGE CLASS	FREE	FREE	FREE	FREE



tenuis and Deschampsia flexuosa scarcely alter along the transect, and while Nardus stricta is reduced in cover it still remains the dominant herb layer species. It should however be recalled that in this situation the vigour and specifically the flowering of the Nardus is apparently more adversely affected than the cover-abundance values suggest.

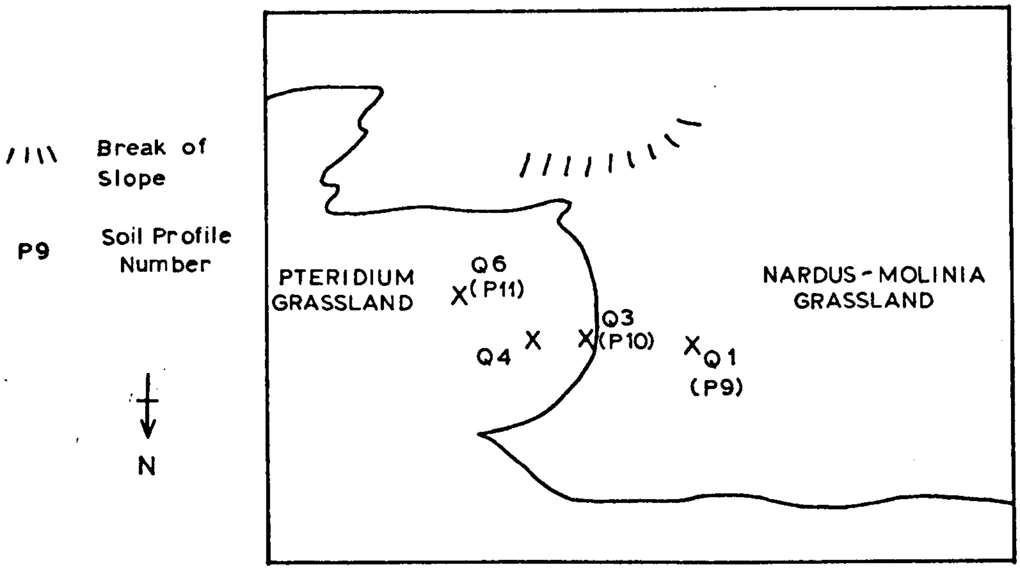
Another interesting feature of this example is the phase development within the bracken stand, each quadrat representing a 'phase' in Watt's terminology (Watt, 1940) - Q31 the advancing front, Q32 the crest, and Q33 the hinterland. The fact that the Pteridium attains its maximum vigour in the crest (Q32) is inadequately shown by the cover-abundance values but is revealed in the index of bracken dominance values - at Q32 the index value is 131 compared to 69 in the hinterland (Q33). This explains why the maximum depression of Nardus stricta and Festuca ovina values occurs at quadrat 32 - bracken is exercising its greatest competitive power close to the stand margin.

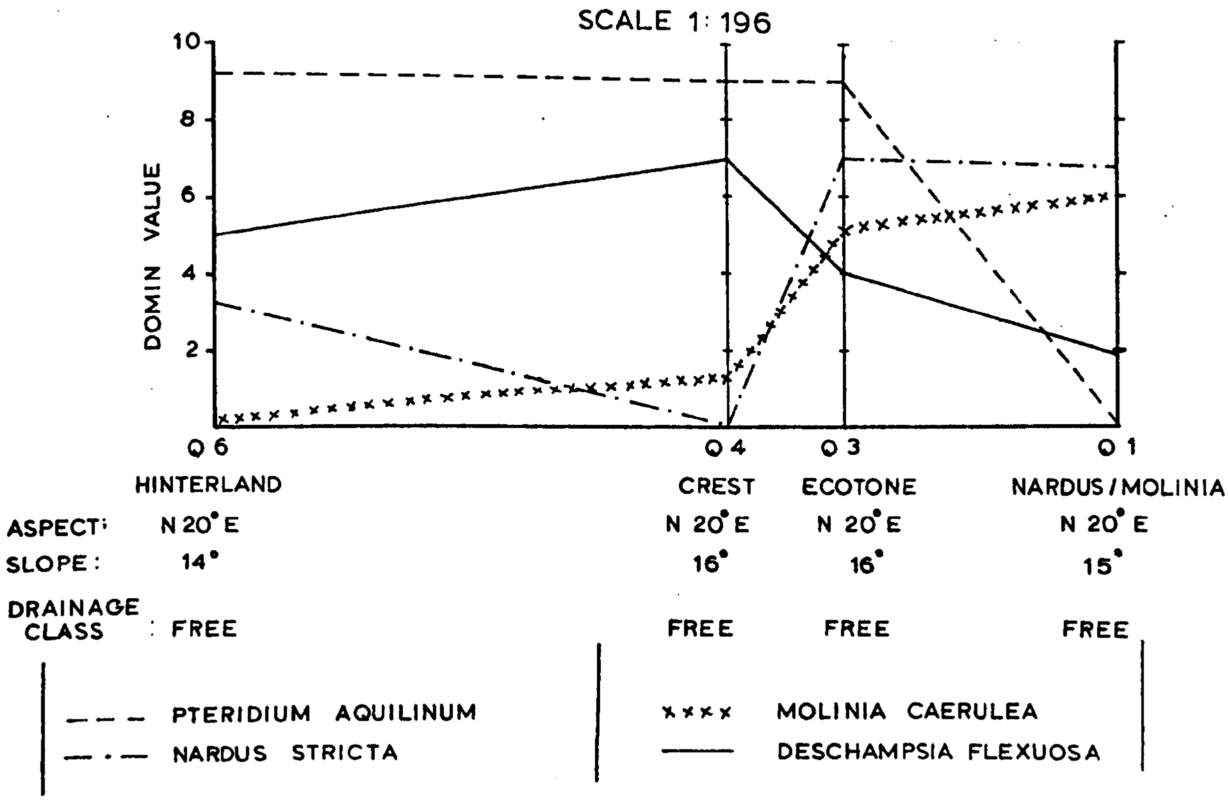
(3) Pteridium Stand 4. Molinia caerulea is not an important component of the vegetation on any of the sites examined in this project, hence there is insufficient data to determine its reaction to Pteridium aquilinum. At Conic Hill Pteridium Stand 3 competition between a Pteridium stand and Calluna-Molinia heath has been described and the fact that Molinia succumbs to bracken competition, though in that example less quickly than Calluna vulgaris, has been noted (see page 129).

Pteridium Stand 4 at Sourhope provides another example of Pteridium-Molinia competition. In this location, on the north-facing valley side of Dod Burn, a Pteridium stand is juxtaposed against an acid grassland stand in which Nardus and Molinia are co-dominant. Vegetation change across the sociological boundary between the two stands is illustrated in Figure 4.26. The apparent constant degree of dominance of Pteridium from quadrats 3 to 6 is somewhat illusionary. At quadrat 3, on the stand boundary, the Pteridium index of dominance is 89, rising to 164 in quadrat 4, and decreasing to 126 in quadrat 6. In other words, although Watt's phases are less clearly developed here than in Pteridium Stand 2, there is a suggestion of a 'crest' of bracken at quadrat 4. Both Nardus and Molinia succumb to this bracken competition in the crest although Nardus tends to recover a little in the more open bracken hinterland.

The reaction of Deschampsia flexuosa is also interesting. The dominant grass species in the bracken stand, its resistance to bracken competition is clear from the relatively high cover it attains under the vigorous bracken competition in quadrat 4, while it loses all cover value in the Nardus-Molinia quadrat. This might suggest that Deschampsia flexuosa finds the macroenvironment provided by the fern particularly favourable, whereas in fact the total evidence available has led to its classification as an 'indifferent' species (see page 112) which occurs, and is locally prominent, in both bracken-free and bracken communities. It seems more likely that the distribution of Deschampsia flexuosa in this example is related, not to the distribution of Pteridium directly, but to the competition from other herb stratum species, so that its prominence in the crest results from the reduced competition from other species such as Nardus, Molinia, Agrostis species and Anthoxanthum odoratum, the last two being prominent in quadrat 6, although

Fig. 4.26. Sourhope Pteridium Stand 4.





not included in Figure 4.26.

As in other locations, soil type as well as vegetation alters across this boundary at Stand 4. Quadrats 1, 3 and 6 are the sites of Profiles 9, 10 and 11 respectively described later in Chapter 5 (see pages 205-209). The Molinia-Nardus community is associated with a peaty podsol and the Pteridium community with a brown forest soil, the implications of which will be more fully considered in the next chapter.

V. CONCLUSIONS

In this chapter bracken communities have been described from three sites which offer a reasonably wide range in environmental conditions, as detailed in Chapter 3. Despite the variation in climate, altitude, surface relief and geology the bracken communities at Kingslaggan, Conic Hill and Sourhope are remarkably consistent in species composition. The herb stratum is a mixed acid grassland dominated by Agrostis species and Festuca ovina with Anthoxanthum odoratum, Deschampsia flexuosa and Galium hercynicum the most common minor constituents. However although Agrostis-Festuca grassland is the usual associate of Pteridium on the rough grazings studied it is well to remember that this type of grassland community often exists in the absence of Pteridium, as for example on Fasset Hill at Sourhope. Nevertheless, on the sites studied, the moorland community found on the freely drained sites outside the bracken cover is not usually Festuca-Agrostis grassland but, in the case of Kingslaggan and Conic Hill, a heath community totally different in species composition, and at Sourhope a Nardus stricta dominated mixed acid grassland. Evidence has been presented which indicates that the difference in species between these communities results from the different response of species to bracken competition and to the micro-climate and edaphic environment which Pteridium produces.

Although Agrostis-Festuca grassland is the usual associate of Pteridium, this vegetation type is not homogenous and internal variations correlated with variations in the level of bracken competition have been elucidated. Almost all species appear to be adversely affected by the most vigorous Pteridium growth resulting in pure Pteridium stands, the ground vegetation of which is severely restricted in biomass and cover. The characteristic associates of Pteridium have been shown to vary in their resistance to bracken competition with Agrostis species, Deschampsia flexuosa and Galium hercynicum the most resistant while Festuca ovina and Anthoxanthum odoratum are less tolerant. At the other extreme are the completely intolerant heath shrubs such as Calluna vulgaris and Vaccinium myrtillus.

While results from the three sites have been sufficiently consistent to permit the classification of species according to their response to Pteridium, the complex and dynamic nature of specific interaction must not be forgotten. Two points in particular must be borne in mind. The ground layer species are competing not only with Pteridium, but with each other. Therefore the apparent preference of certain species, such as Galium hercynicum, for high levels of bracken may reflect the reduced competition of other herb layer species, rather than any particular preference for the bracken environment.

Secondly, the interaction of species depends on their relative vigour which will vary from place to place and from time to time. In fact most species in this study have been quite consistent in their reaction to *Pteridium* from one site to another but there is evidence that the competitive powers of *Nardus stricta* and, to a lesser extent, *Calluna vulgaris* vary from one site to another.

Section Notes

1. This Index of Bracken Dominance is essentially the same as the Index of Production used by Watt (1956) as a measure of the amount of litter production by *Pteridium aquilinum*. Watt defined his Index of Production as the mean height of fronds multiplied by number of fronds based on an area of 10 square feet. The density component in this Index of Bracken Dominance is based on the quadrat area of 4 sq m. If it is desired to translate these indices into a more immediately recognizable form, the figure for frond number should be divided by four to give a standard measure of density in terms of numbers of fronds per square metre. For example if the average height of fronds in a stand is 100 cm, I.B.D. = 100 is equivalent to $\frac{100}{4}$ = 25 fronds per sq. m.; I.B.D. = 120 might represent $\frac{120}{4}$ = 30 fronds per sq. m. of average height 100 cm or $\frac{160}{4}$ = 40 fronds per sq. m. of average height 75 cms.

2. For the purposes of this study, a constant species is defined as one which occurs in 81-100 per cent of the constituent quadrats of a nodum. Since this research does not aim to classify stands of vegetation into community types, the same number of quadrats was not analysed for each stand of the nodum.

Thus the present use of the term 'constant' differs slightly from Braun Blanquet's usage in which exactly equivalent areas of stands were compared.

3. It will be noted in the nodum tables that the cover-abundance ratings of the broad-leaved grasses, Agrostis species and Anthoxanthum odoratum, have often been combined, as have the narrow-leaved Festuca ovina and Deschampsia flexuosa. This is due to the difficulty described above (see page 71) of separating these species in cover-abundance determination where they are of approximately equal importance and it was felt that generalisation was preferable to spurious accuracy.

In the analysis of individual species' response to Pteridium it has been necessary to separate the species and where this had not been undertaken in the field it is assumed that they are of approximately equal cover, a reasonable assumption since it is relatively easy to allocate them to separate cover classes where one is clearly dominant.

In a few quadrats at Kingslaggan, one cover-abundance rating was given for the three main grasses - Agrostis tenuis, Anthoxanthum odoratum and Festuca ovina but this degree of generalisation soon proved unnecessary and was abandoned.

Kingslaggan Sample	Date of Collection	Conic Hill Sample	Date of Collection	Sourhope Sample	Date of Collection
Q24 S3	25/7/70	Q5 S1	30/8/70	Q15 S1	8/7/71
Q1 S4	26/7/70	Q6 S1	30/8/70	Q16 S1	8/7/71
Q4 S4	27/7/70	Q7 S1	30/8/70	Q19 S1	8/7/71
Q30 S3	29/7/70	Q9 S3	11/9/70	Q2 S2	10/7/71
Q4 S5	29/7/70	Q11 S3	11/9/70	Q4 S2	10/7/71
Q5 S5	29/7/70	Q15 S3	15/9/70	Q10 S2	10/7/71
Q1 S6	31/7/70	Q18 S3	16/9/70	Q14 S2	16/7/71
Q3 S6	3/7/70	Q19 S3	16/9/70	Q15 S2	16/7/71
Q1 S8	9/8/70	Q3 S4	19/9/70	Q17 S2	17/7/71
Q2 S8	10/8/70	Q5 S4	19/9/70	Q21 S2	18/7/71
Q3 S8	10/8/70	Q9 S4	21/9/70	Q22 S2	18/7/71
Q5 S8	10/8/70	Q10 S4	21/9/70	Q24 S2	18/7/71
Q6 S8	10/8/70	Q14 S4	23/9/70	Q27 S2	19/7/71
Q4 S9	11/8/70	Q18 S4	24/9/70	Q33 S2	20/7/71
Q5 S9	11/8/70	Q19 S4	24/9/70	Q36 S2	20/7/71
Q6 S9	11/8/70	Q5 S5	6/9/71	Q40 S2	1/8/71
Q7 S9	11/8/70	Q3 S6	6/9/71	Q1 S3	21/7/71
Q8 S9	21/8/70	Q4 S6	6/9/71	Q3 S3	21/7/71
Q9 S9	21/8/70	Q6 S6	6/9/71	Q4 S3	21/7/71
Q12 S9	21/8/70	Q7 S6	6/9/71	Q11 S3	27/7/71
Q13 S9	21/8/70	Q1 S7	7/9/71	Q4 S4	28/7/71
Q14 S9	21/8/70	Q2 S7	7/9/71	Q11 S4	28/7/71
Q15 S9	22/8/70	Q8 S7	8/9/71	Q14 S4	28/7/71
		Q10 S7	8/9/71	Q16 S4	29/7/71
		Q13 S7	9/9/71	Q17 S4	29/7/71
		Q2 S8	10/9/71	Q22 S4	29/7/71
		Q4 S8	10/9/71		

Date of Collection of Biomass Samples

The date of sampling is the only variable other than degree of bracken dominance which can readily be accurately described. The biomass of ground vegetation will vary seasonally, independent of the seasonal variation in bracken dominance (concurrent sampling of the ground vegetation and measurement of frond height and density renders the seasonal variation with bracken dominance irrelevant). Where grazing pressure is light, accumulation of plant material and therefore increase in biomass of ground vegetation, is to be anticipated. The complexity of the factors affecting biomass is demonstrated by the fact that there is little evidence that the autumn sampling at Conic Hill has resulted in relatively higher biomass values.

CHAPTER 5

SOIL PROFILE MORPHOLOGY

It is a well-known fact that Pteridium aquilinum is normally associated with soils with the morphological features of brown forest soils although Watt (1964) has described bracken growing on podsols on sand dunes in the Breckland. E. Wyllie Fenton (1956, page 106) in his description of the vegetation of the Jedburgh and Morebattle area, states:

> Peat is generally absent from the lower slopes and here on a moderately fertile mineral soil (brown forest soil) two main vegetation types occur. Acid grassland dominated either by Bent (Agrostis spp.) or Fescue (Festuca spp.) is characteristic of the valley slopes and stream sides.... Bracken (Pteridium aquilinum) is a common invader of these acid grasslands and has become dominant over many of the sheltered lower slopes.

The relationship between Pteridium and the underlying soil is usually explained in terms of the fern's dislike of acid peat (Long and Fenton, 1938) and its well-documented intolerance of poorly drained conditions (Poel, 1951), the latter inhibiting its development on gleys. It has also been suggested that bracken requires deep soils (Gordon, 1916) an opinion on which the research findings of this chapter cast doubt although extreme shallowness of profile may inhibit vigour. Watt (1964) working on the Breckland found a positive correlation between soil depth and several indices of Pteridium vigour, but this was in an area where rainfall is a limiting factor and Watt suggested that soil moisture deficit might be the controlling factor on his shallow soils.

Most commonly writers discussing the association of bracken with brown earths imply that this is a function of bracken's selective invasion of Agrostis-Festuca grassland, and while this is undoubtedly at least partially true, the alternative approach that bracken may itself help to produce a brown earth morphology in the underlying soil has been given little attention. One exception to this is I.A. Nicholson (1964) who, without offering an explanation for the phenomenon, suggested that bracken maintains or may improve soil conditions, noting that some bracken areas give high crop yields when ploughed.

In this chapter an account of the influence of Pteridium on soil profile morphology on the three sites described in Chapter 3 will be given. As in the case of the vegetation studies, observations were concentrated across sociological boundaries between different plant communities in an effort to eliminate other variable environmental factors which would influence profile development. Soils developed under varying densities and heights of bracken were also examined to investigate whether morphological characteristics vary according to the vigour of the fern and the consequent degree of development of a ground layer.

Throughout this study the terminology of the Scottish Soil Survey is employed in which brown forest soils of low base status are regarded as belonging to the Brown Earths major soil group. They are approximately equivalent to the brown podzolics of the U.S.A., a term which has also been used in England and Wales (Ball, 1966).

In this chapter each site will be considered in turn, in each case a brief summary of the general soil characteristics being followed by an account of the bracken soils and a comparison with those developed under other moorland communities. Only a selection of the profiles studied will be described in full in the text, a complete account of the remainder being given in Appendix B. The chapter will conclude with a summary of the findings from all three sites.

I. KINGSLAGGAN

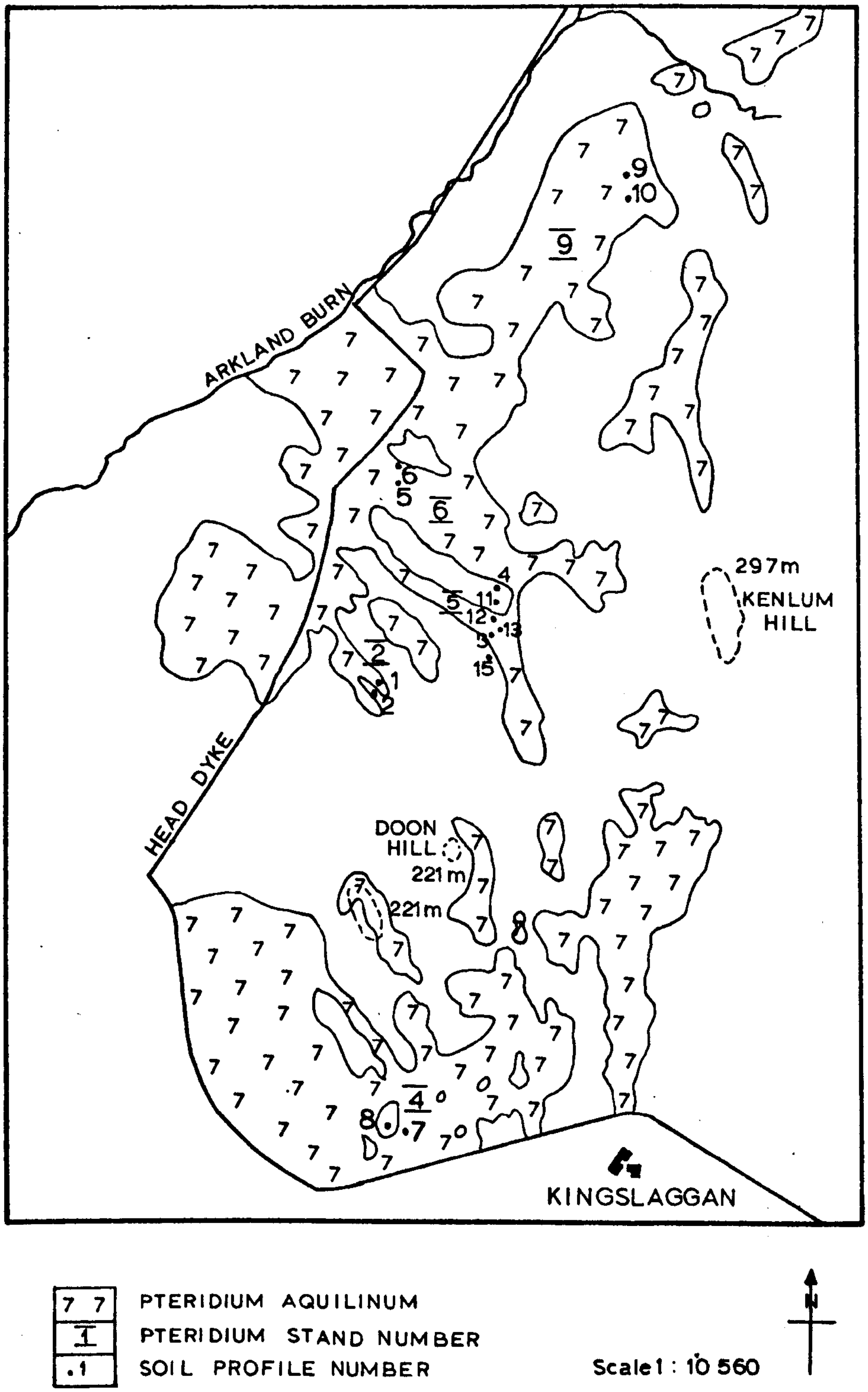
Fourteen soil profiles were described in detail together with several inspection pits. The distribution of profiles is shown in Figure 5.1. The pit sites were selected to give a range of aspect, slope, and drainage conditions within the limits set by the vegetational requirements.

Parent material is quite uniform consisting mainly of bedrock of Ordovician shale or a thin veneer of till derived mainly from shale with occasional granitic components. On some sites below breaks of slope pockets of colluvial material derived again from shale produce deeper profiles which differ texturally from the others having sandier Band C horizons with a lower stone content. On the whole, however, the mineralogical uniformity of parent material produces rather uniform B and C horizons characterized by yellowish brown coloration on freely drained sites and by a weakly developed platy structure derived from the shaly parent material.

Bracken Soils

Four soils developed under bracken of varying height and density were

Fig. 5.1. KINGSLAGGAN SOIL SITES



studied without particular reference to equivalent soils under contrasting vegetation. Two of these profiles, formed in very close proximity and under similar site conditions illustrate the characteristic features of bracken soils on Kingslaggan as well as suggesting some of the variations which are associated with varying degrees of bracken development.

Profiles 9 and 10 (see Fig. 5.2, page 154) were excavated near the northern limit of the study area on a bench at 188 m on the southern valley side of the Arkland Burn (Pteridium Stand 9).

DESCRIPTION OF KINGSLAGGAN PROFILE 9 (Plate 5.1)

Slope: 4^{o} Surface Drainage: imperfect. receiving site.

Aspect: $N40^{o}W$ Altitude: 188 m

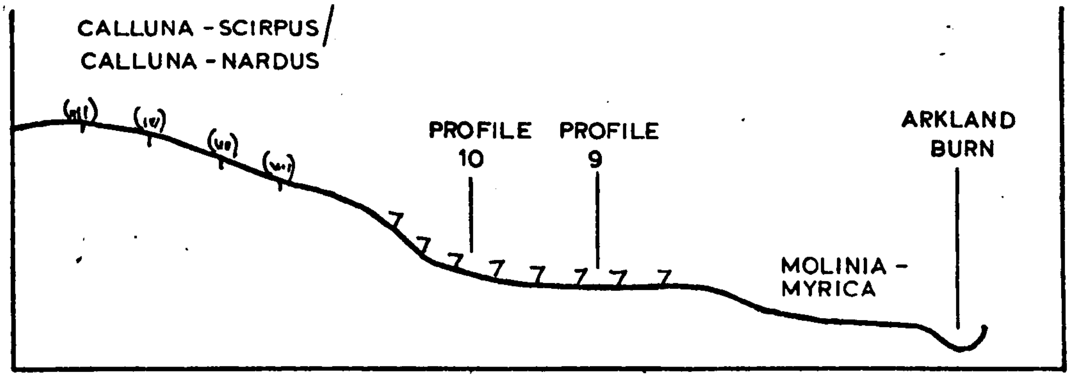
Vegetation: dense growth of tall Pteridium aquilinum (I.B.D. = 235) with 100% cover and 100% litter cover eliminating herb stratum.

Drainage Class: free Parent Material: Ordovician shale.

Horizon	Depth or thickness	
L	6 cm	Undecomposed bracken litter
H	6 cm	Black (5 YR 2/1) moder humus, few sand grains, few rhizomes. Narrow even change into
A_1	0 - 8 cm	Dark brown (10 YR 3/3) very humose loam, stony, weakly developed medium subangular blocky, friable, abundant medium fissures and pores, rapid permeability, gradual downward decrease in moder-type organic matter, extremely abundant rhizomes; merging into
B	8 - 32 cm	Dark brown (7.5 YR 4/4), loam, very stony, weakly developed fine subangular blocky, friable, common fine-medium fissures and pores, moderate permeability, common rhizomes to 31 cm; merging into

Fig. 5.2.

SITE OF KINGSLAGGAN PROFILES 9 & 10



7 7 PTERIDIUM AQUILINUM

CALLUNA VULGARIS

Plate 5.1. Kingslaggan Profile 9.

Kingslaggan Profile 9 (Pteridium soil).
Brown forest soil of low base status.

C	32+ cm	Dark yellowish brown (10 YR 4/4) sandy loam, extremely stony, weakly developed coarse platy, friable, common fine pores and fissures, moderate permeability.
Soil Type		Brown Forest Soil of low base status.

This soil illustrates several of the features typical of Kingslaggan bracken soils. The A horizon is a mixture of organic and mineral material, the organic matter content decreasing gradually toward the B horizon with no evidence of a leached A_2 horizon. The subangular blocky structure and friable consistence are also typical. Very good internal drainage, resulting from well developed pores and fissures, the latter apparently a consequence of the mechanical effect of the rhizomes is a constant feature of these soils. These features can clearly be seen in Plate 5.1.

The organic horizons developed in Profile 9 are not however typical of all bracken soils. The extremely vigorous bracken growth gives a fairly thick litter cover of the previous year's fronds, beneath which there is a reasonably developed organic horizon of well humified remains.

<u>DESCRIPTION OF KINGSLAGGAN PROFILE 10</u> (19 m from Profile 9)

Slope: 4^{o} Surface Drainage: imperfect. receiving site

Aspect: N40^{o}W Altitude: 188 m

Vegetation: <u>Pteridium aquilinum</u> shorter and less dense than Profile 9 (I.B.D. = 100.8) giving 80% cover. Well developed ground vegetation dominated by <u>Agrostic tenuis</u> (7)[2] with <u>Festuca ovina</u> (6), <u>Anthoxanthum odoratum</u> (4), various forbs.

Drainage Class: free Parent material: sandy colluvium derived from Ordovician shale.

Horizon	Depth or thickness	
L	1 cm	Dark brown turf. Sharp change to
A_1	0 - 14 cm	Very dark brown (10 YR 2/2) very humose loam, slightly stony, moderately developed fine subangular blocky, friable, common pores and fissures, moderate permeability, abundant rhizomes; organic matter decreasing gradually with depth; merging into
B	14 - 46 cm	Dark yellowish brown (10 YR 4/4) sandy loam, stony, weakly developed fine subangular blocky, firm, porosity and permeability as A_1, common rhizomes to 20 cms. Narrow change to
C	46+ cm	Light yellowish brown (10 YR 6/4) loamy sand, stony, weakly developed coarse platy, firm, few fine pores and fissures, moderate permeability
Soil Type		Brown Forest Soil of low base status.

This soil is very similar to the previous one sharing the physical characteristics of its mineral horizons. The reduction in porosity and increased firmness of consistence associated with reduced density and depth of rhizomes is noteworthy. The main contrast lies in the organic horizons for which the reduced vigour of the bracken and the well developed grass turf seems to be responsible. The litter layer has virtually disappeared and a true mull humus has replaced the moder humic horizon found under the pure bracken stand.

Two other bracken soils, Profiles 5 and 6, situated in Pteridium Stand 6, were examined, Profile 5 supporting a bracken cover similar to Profile 10 while on Profile 6 the bracken is further reduced in cover. These profiles, which are described in full in Appendix B (see pages 322-323) are morphologically very close to Profile 10 with similar mull humus development and absence of H horizons.

Bracken and Heath Soils

At three sites on Kingslaggan bracken soils were examined in conjunction with nearby soils developed under heath vegetation to ascertain the effect, if any, of *Pteridium* growth on soil morphology.

At Pteridium Stand 4 on the south-facing slope of Doon Hill upslope from the head dyke, Profiles 7 and 8 were excavated. This stand occupies one of a series of ridges separated by deep channels. The bracken is at its most vigorous on the lower slopes of the ridge, giving way on the crest to *Calluna vulgaris* and *Nardus stricta*-dominated heath with *Erica cinerea* on the rocky outcrops.

Profile 7 occurs under bracken on the channel side while Profile 8 is 16 m upslope where heather has taken over. Both are shallow, stony soils developed on Ordovician shale bedrock.

DESCRIPTION OF KINGSLAGGAN PROFILE 7

Slope: 25^{o}, terraced — Surface Drainage: free

Aspect: $E30^{o}S$ — Altitude: 165 m

Vegetation: tall, dense *Pteridium aquilinum* (I.B.D. = 238.7) gives 95% cover with 25% cover of bracken litter. Ground vegetation reduced in cover, *Festuca ovina* and *Agrostis tenuis* co-dominant (8) with *Anthoxanthum odoratum* (4).

Drainage Class: free-excessive Parent Material: Ordovician shale

Horizon	Depth or thickness	
L	2 cm	Bracken litter
H	4.5 cm	Very dark brown (10 YR 2/2) but colour varies, moder humus with some mineral matter, common rhizomes. Narrow change to
A_1	0 - 8 cm	Dark brown (10 YR 4/3) slightly humose loam, stony, moderately developed fine subangular blocky, friable, abundant medium fissures and fine pores, rapid permability, abundant rhizomes; merging into
A/C	8 - 28 cm	Dark brown (10 YR 4/3) loam, stones dominant, structureless, firm, porosity and permeability as A_1, organic content decreases gradually with depth, common rhizomes to 26 cms. Narrow change to
C	28+ cm	Dark yellowish brown (10 YR 4/4) loam, stones dominant, structureless, firm, common medium fissures, rapid permeability.
Soil Type		Shallow Brown Forest Soil of low base status.

This soil is very similar to Profile 9 developed under a similar stand of Pteridium. The moder humus horizon, lack of horizon differentiation, well developed fissures and rapid permeability, features typical of soils developed under heavy bracken, are all present. Note also the ability of rhizomes to penetrate a thin, extremely stony subsoil, where they act as agents of weathering, which throws doubt on the theory that bracken requires deep soils.

DESCRIPTION OF KINGSLAGGAN PROFILE 8

Slope: 18° terraced Surface Drainage: free

Aspect: E30°S Altitude: 165 m

Vegetation: degenerate *Calluna vulgaris* (9) with *Nardus stricta* (4) *Erica cinerea* (3), *Agrostis tenuis* (3), *Deschampsia flexuosa* (3).

Drainage Class: free Parent Material: Ordovician shale

Horizon	Depth or thickness	
L	3 cm	Brown *Calluna* litter
H	9.5 cm	Dark reddish brown (5 YR 2/2) mor. Sharp change to
A_2	0 - 6 cm	Dark grey (10 YR 4/1) humose loam, extremely stony, very weakly developed fine subangular blocky, firm, common fine-medium fissures and pores, moderate permeability, common fibrous and woody roots. Sharp, very irregular change to
Iron Pan		Discontinuous iron pan with organic matter deposition on its surface
B	6 - 14.5 cm	Dark brown (7.5 YR 3/2), slightly humose loam, extremely stony, physical features as A_2. Sharp, irregular change to
C	14.5+ cm	Dark reddish brown (5 YR 3/4) loam, colour suggesting iron illuviation, stones dominant, structureless, firm, common pores and fissures, moderate permeability
Soil Type		Shallow Peaty Podsol with iron pan.

Apart from vegetation, site characteristics are almost identical to Profile 7, yet soil morphology is quite different. Profile 8 has all the features of a moderately well developed podsol including a well developed mor humus horizon and an A_2 horizon with clear evidence of iron mobilisation. These differences can only be attributable to the contrast in vegetation cover.

Similar evidence of the difference between Calluna vulgaris and Pteridium aquilinum as agents of soil formation was found at Pteridium Stand 5. This stand of relatively open bracken which has been described in Chapter 4 (see pages 121-123), occurs at 200 m on the terraced west-facing slope of Doon Hill. Bracken growth is less vigorous than on the Kingslaggan sites already described and is best developed in the margin adjacent to the mixed moorland. Fern growth in the hinterland of the stand is restricted by impeded drainage which produces Carex-Nardus flushes. Between the flushes and the bracken stand a zone of large Calluna clumps and scattered Pteridium fronds occurs where the fern appears to be losing the competitive struggle.

A sequence of profiles was investigated to correspond to this zonation of vegetation as shown on Figure 5.3. The contrast in species composition of the vegetation across the sociological boundary has been described above (see Fig. 4.17, page 122). Profile 4 described here corresponds to Quadrat 1, and Profile 3 to Quadrat 2. Slope and aspect are constant and surface drainage is everywhere imperfect although, as will be seen below, internal drainage varies. The occurrence of pockets of sandy-gravelly colluvium gives some variation in soil depth and texture but the mineralogy of the parent material is uniform.

Profiles 4, 13 and 3 will be described in detail in the text, the descriptions of Profiles 11, 12 and 15 being inserted in Appendix B. The morphological characteristics of the sequence of profiles are summarized in Figure 5.4.

Fig.5.3 PROFILE SEQUENCE AT KINGSLAGGAN PTERIDIUM STAND 5.

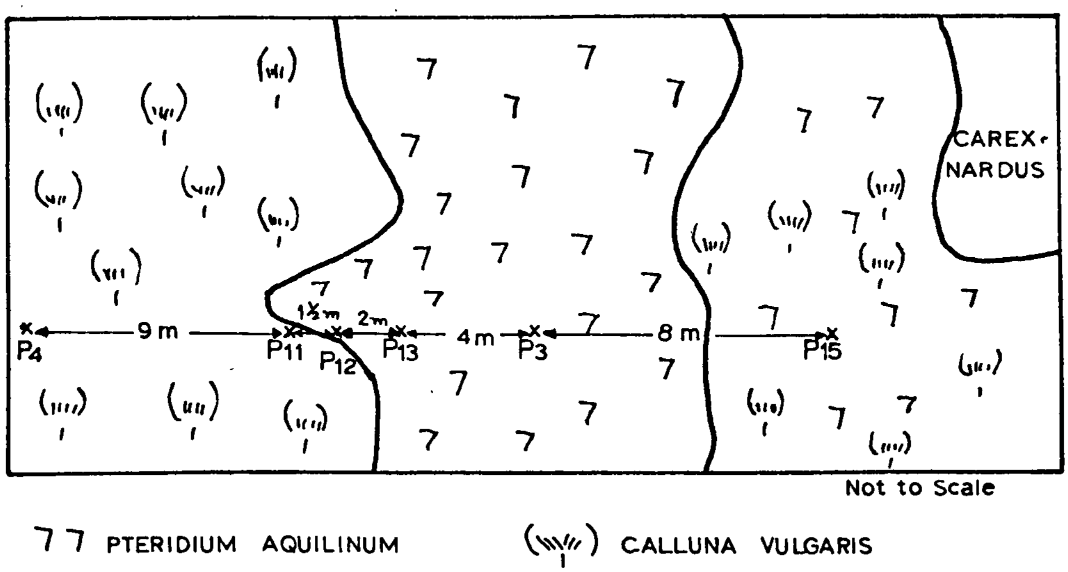
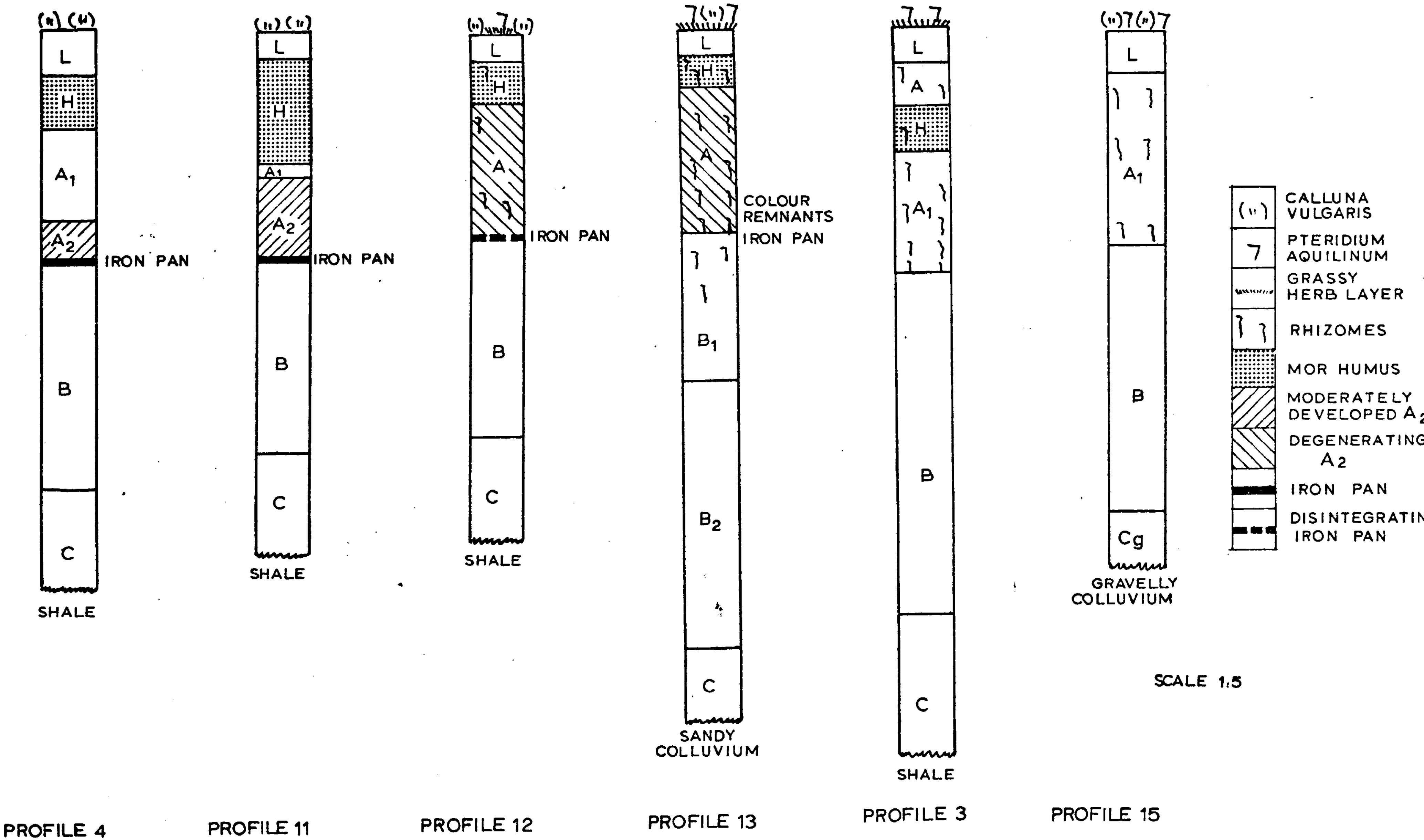


Fig. 5.4 PROFILE SEQUENCE AT KINGSLAGGAN PTERIDIUM STAND 5.



DESCRIPTION OF KINGSLAGGAN PROFILE 4

Slope: 10° concave Surface Drainage: imperfect

Aspect: due W Altitude: 208 m

Vegetation: Calluna vulgaris (8)-dominated heath with Scirpus caespitosus (5) Nardus stricta (4), Vaccinium myrtillus (4) and Festuca ovina (3) (Quadrat 1, Figure 4.17, page 122).

Drainage Class: free below iron pan Parent Material: till derived mainly from Ordovician shale

Horizon	Depth or thickness	
L	3.75 cm	Black litter
H	5 cm	Waterlogged black (10 YR 2/1) mor humus, abundant roots; merging into
A_1	0 - 9 cm	Waterlogged very dark greyish brown (10 YR 3/2) slightly humose loam, slightly stony, structureless, friable, rare fine pores, slow permeability, moderate organic matter content, abundant roots; merging into
A_2	9 - 13 cm	Very moist dark greyish brown (10 YR 4/2) sandy loam, stony, structureless, firm, few fine pores, moderate permeability, common roots. Sharp change to
Iron Pan	0.5 cm thick	Well defined, undulating, indurated iron pan with root mat on surface
B	13 - 34 cm	Yellowish brown (10 YR 5/8) loam, extremely stony, very weakly developed platy structure, firm, common fine-medium pores and fissures, moderate permeability; merging into
C	34+ cm	Dark brown (7.5 YR 4/4) stones dominant, structureless, very firm
Soil Type		Peaty Podsol with thin iron pan

This is quite a well-developed iron pan podsol although the apparently gradual change in organic matter content in the A horizons which produces an

A_1 and merging boundaries is not typical of this soil type.[3] The poorly developed structure, low porosity, underlying iron pan and overlying spongy humus combine to produce poor drainage conditions in the A horizons.

Compare this with Profile 13 which occurs just within the bracken stand.

DESCRIPTION OF KINGSLAGGAN PROFILE 13

Slope: 10° concave   Surface Drainage: imperfect

Aspect: due W   Altitude: 208 m

Vegetation: several fronds of Pteridium aquilinum with low cover value; ground vegetation Agrostis tenuis (d), Holcus lanatus (f), Calluna vulgaris (f), Festuca ovina (f).

Drainage class: free   Parent Material: colluvium derived from Ordovician shale.

Horizon	Depth or thickness	
L	2 cm	Grass turf and comminuted bracken litter
H	3 cm	Black (10 YR 2/1) mor humus with sand grains, common rhizomes. Sharp and irregular change to
A	0 - 14 cm	Mixed colour, dark greyish brown matrix (10 YR 4/2) with many faint dark yellowish brown (10 YR 3/4) stains and small ochreous mottles, the latter concentrated at the foot of the horizon, humose loam, slightly stony, moderately developed medium angular blocky, friable, few large pores and fissures, moderate permeability, common rhizomes. Ochreous zone at foot of horizon appears to be unindurated colour remnants of an iron pan. Narrow and very irregular change to
B_1	14 - 27 cm	Dark yellowish brown (10 YR 4/4) slightly humose silty loam, stony, weakly developed fine subangular blocky, friable, common fine-small pores and fissures, moderate permeability, few rhizomes to 20 cms;

		merging into
B_2	27 - 52 cm	Dark brown (7.5 YR 4/4) loam, stony, weakly developed fine angular blocky, firm, few fine pores and fissures, moderate permeability; merging into
C	52+ cm	Dark yellowish brown (10 YR 4/4) coarse sandy loam, stony, structureless, friable, moderate permeability.
Soil Type		Intermediate between Brown Forest Soil and Podsol with iron pan.

This soil is difficult to classify as the surface horizons are undergoing alteration. It is in some respects similar to the iron pan podsol, Profile 4, and the following comparative points should be noted:

(1) Both soils have mor humus horizons although Profile 13's is thinner.

(2) The matrix colour of the A horizon of Profile 13 resembles the A_2 in Profile 4 but within the former brown organic stains occur.

(3) The iron pan of Profile 4 is replaced in Profile 13 by a concentration of ochreous mottles through which rhizomes have penetrated to the B horizon.

Profiles 11 and 12, situated between Profiles 4 and 13, were examined (see Appendix B, pages 323-325 for full description).These help to illuminate the problem of the nature and cause of the soil modifications which appear to be occurring on this site (see Fig. 5.4, page 163).

Profile 11 which occurs under Callunetum right on the edge of the bracken stand and is free of bracken fronds has a well developed mor humus layer, clearly differentiated A_1 and A_2 horizons, and a continuous indurated iron pan.

Profile 12 which contains some rhizomes and in which both Calluna vulgaris and Agrostis tenuis are prominent in the ground vegetation, has an A horizon similar to the A_1 in Profile 4 but no A_2. The rhizomes reach the foot of this A horizon but do not go through the underlying iron pan which is thin and discontinuous in comparison to those found under the purely heath vegetation.

This sequence suggests that the bracken rhizomes invading the iron pan podsols are responsible for the modification of the A horizons and the disintegration of the iron pan, a hypothesis which is supported by study of the remaining profiles in the sequence, 3 and 15.

DESCRIPTION OF KINGSLAGGAN PROFILE 3

Slope: 8° concave   Surface Drainage: imperfect

Aspect: due W   Altitude: 208 m

Vegetation: dominated by 50% cover of short Pteridium aquilinum (I.B.D. = 85.2), too thin to curtail development of a complete ground cover dominated by Festuca ovina (6), Agrostis tenuis (5), Anthoxanthum odoratum (5) with Erica cinerea (4), Galium hercynicum (4), Calluna vulgaris (3), Potentilla erecta (3), Luzula campestris (3). (Quadrat 2, Fig. 4.17, page 122).

Drainage Class: free   Parent Material: till derived from Ordovician shale

Horizon	Depth or thickness	
L	2.5 cm	Turf
A	0 - 4.5 cm	Dark brown (10 YR 3/3) organic-mineral mixture with lense of mineral matter at the foot, loam, abundant roots and occasional rhizomes. Narrow change to
fossil H	4.5 - 8.75 cm	Black (10 YR 2/1) mor humus apparently fossil, numerous sand grains, abundant rhizomes. Narrow undulating change to

A_1	8.75 - 19 cm	Dark brown (10 YR 4/3) humose sandy loam, slightly stony, weakly developed fine subangular blocky, friable, common fine pores, moderate permeability, common rhizomes; merging into
B	19 - 52 cm	Dark yellowish brown (10 YR 4/4) loam, very stony, weakly developed thick platy, firm, few fine fissures and pores, moderate permeability; merging into
C	52+ cm	Dark yellowish brown (10 YR 4/4) loam, extremely stony, structureless, very firm, few pores, moderate permeability.
Soil Type		Brown Forest Soil of low base status.

In this soil the iron pan is completely absent and there is no sign of an A_2. The only suggestion of podsolisation is the anomalous mor humus layer which is sandwiched between an overlying lense of mineral material and an underlying A_1. It would seem that there must have been some surface disturbance to produce this horizon sequence although none is apparent at the present time and the slope is too gentle for soil creep. Certainly the mor humus is divorced from the surface litter and, since it cannot be actively forming at present, has been defined as a fossil feature.

The final profile in the sequence, 15, is sited in the Calluna-Pteridium hinterland under a clump of Calluna vulgaris (see Appendix B, page 325). Although only a few weak fronds occur on its surface the upper soil is full of rhizomes suggesting that this soil must have supported a more vigorous growth of bracken in the past and that Calluna is in fact actively invading this site. Two other soils were examined under heather clumps with similar results. A clue to the lack of success of Pteridium in this zone lies in the markedly poorer subsoil drainage, the C horizons being distinctly gleyed.

The abundance of rhizomes however makes Profile 15 a definite bracken soil and it is in fact, except for the Cg, a beautifully developed brown forest soil. The mor humus horizon iron pan, and A_2 are completely absent and instead there is a friable, well fissured A_1 with a mull humus.

Pteridium Stand 5 thus offers a sequence of vegetation from Calluna heath through various ecotone situations to bracken-dominated grassland and finally a hinterland undergoing Calluna invasion. The bracken appears to have made advances on one front but is being overtaken by heather on the other. This sequence is paralleled by the soils, the range of which is summarized in Figure 5.4. The further into the bracken stand one progresses, the greater the change from the well-developed iron pan podsol of the Calluna heath.

The final two profiles at Kingslaggan, 1 and 2, are described in Appendix B (pages 320-322). Profile 1, developed under bracken, is a slightly gleyed brown forest soil, while Profile 2 under a nearby Calluna-Nardus community is intermediate between a brown forest soil and an iron podsol having incipient A_2 development and a zone of iron illuviation.

Summary

The Kingslaggan site provides an area of mineralogically uniform parent material which leads to the development of rather similar subsoils on its well-drained sites. Yet there is considerable variation in the character of its surface soils which can be ascribed to the modifying effect of vegetation.

The influence of Pteridium aquilinum can be summarized as follows:

(I) The rhizomes modify the physical conditions of the soil, presumably by a purely mechanical mechanism. Wherever they are found the friable consistence and well-developed pore and fissure space produce free internal drainage with often a marked increase in firmness of consistence and reduction in porosity either below the depth of rhizome penetration within a given profile, or in comparison to soils under heath vegetation.

(2) Bracken does not produce a thick spongy peaty layer but, depending on its density and on the development of a grass turf, it may form a thin humic horizon. Where there is a continuous grass stratum this seems to disappear.

(3) Bracken is closely associated with brown forest soils which show little or no evidence of podsolisation. Indeed the invasion of bracken appears to modify the morphological features of podsols. Evidence has been presented that iron pans are disintegrated and the penetration of rhizomes into A_2 horizons modifies at least their visible characteristics.

II. CONIC HILL

Soil development on Conic Hill is under the influence of soil-forming factors which are rather different from those operating on Kingslaggan. In particular the more complex geology provides parent material which differs in lithology, physical characteristics, and variability from that on the Galloway site.

The variation in parent material results from the juxtaposition of Ordovician grits, Upper Old Red Sandstone sandstones and conglomerates, and intrusive ridges of serpentine (see Figure 3.3, page 57). In addition there is diversity within the Old Red Sandstone strata, layers of coarse conglomerate with large pebbles being interstratified with finer sandstone strata. The conglomerate contains schistose material as well as the dominant quartz and quartzite.

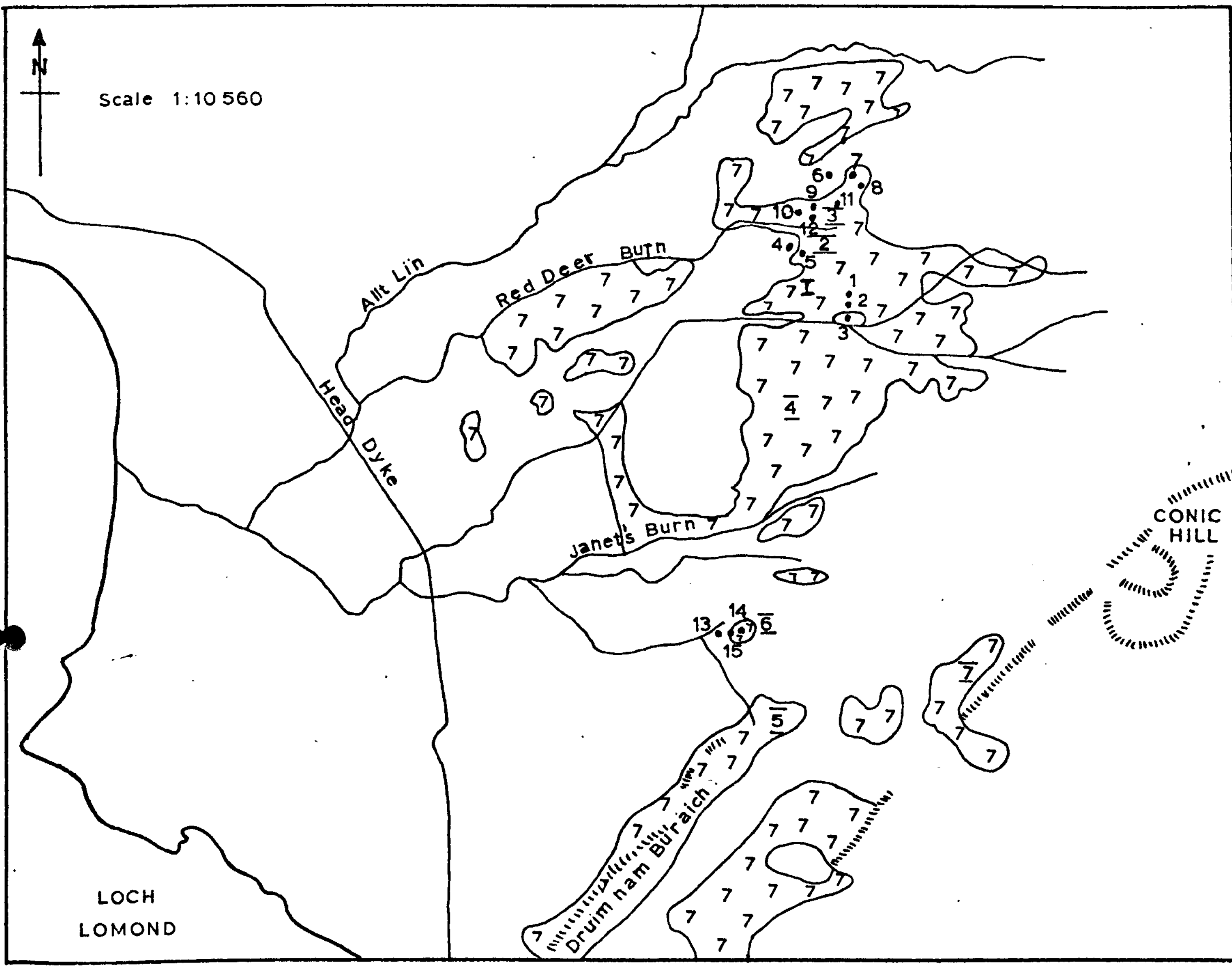
Most of the soils studied are derived from till in which serpentine and the weathering products of sandstones and conglomerates are both present. This produces mainly reddish brown B and C horizons, with in some cases a mosaic of reds and yellows. On freely drained sites this mottling reflects diversity of lithology not gleying conditions. The mineral horizons also differ from the Kingslaggan soils in their physical attributes. Very weakly developed sub-angular blocky structure is common and the subsoils are almost all friable and fairly porous thus masking any modification along those lines by rhizomes. Despite the steep slopes on which many of the Conic soils are developed, the profiles are generally deeper and less stony than on the Galloway site.

As noted above (see page 59), the most vigorous stands of Pteridium are found on the sheltered steep-sided gullies which dissect the lower slopes of the hill. Most of the fifteen soils studied in detail are located on those gully sides or on the intervening spurs, the distribution being shown in Figure 5.5.

Bracken Soils.

Because of the interesting comparisons between bracken and heather soils on Conic, most of the soils under Pteridium were studied in relation to nearby Calluna soils. Two profiles, 8 and 11, can however be taken as representative of soils under well-established bracken. Both are situated under the very vigorous

Fig. 5.5. CONIC HILL SOIL SITES



7 7 PTERIDIUM AQUILINUM $\overline{2}$ PTERIDIUM STAND NUMBER

• 1 SOIL PROFILE NUMBER

growth of Pteridium Stand 3 which spreads from the steeply sloping gully sides of Red Deer Burn on to the crest of the ridge north of the valley, Profile 8 being sited on the ridge top and Profile 11 on the upper slope of the gully. Both are developed on deep till but the lithology of the parent materials differs, Profile 11 having a markedly higher serpentine content.

DESCRIPTION OF CONIC PROFILE 8

Slope: 19° Surface Drainage: free

Aspect: due W Altitude: 150 m

Vegetation: tall *Pteridium aquilinum* giving 100% cover with incomplete ground cover of *Deschampsia flexuosa* (a), *Galium hercynicum* (a), *Agrostis tenuis* (f).

Drainage Class: free Parent Material: till derived mainly from Old Red Sandstone sandstone

Horizon	Depth or thickness	
L	2 cm	Grass turf
H	5 cm	Black (10 YR 2/1) moder humus with considerable mineral component, occasional rhizomes; merging into
A	0 - 8.5 cm	Reddish grey (5 YR 5/2) with brown organic staining, very humose loam, slightly stony mainly quartz, very weakly developed fine subangular blocky, slightly sticky, few fine pores and large fissures, moderate permeability, abundant rhizomes. Narrow and irregular change to
B	8.5 - 54.5 cm	Yellowish red (5 YR 4/6) loam, slightly stony mainly sandstone, moderately developed angular blocky, friable, common fine pores, moderate permeability, no rhizomes; merging into

C	54.5+ cm	Reddish brown (2.5 YR 4/4) sandy loam, stony, weakly developed medium platy, friable, few fine pores, moderate permeability.
Soil Type		Brown Forest Soil of low base status.

DESCRIPTION OF CONIC PROFILE II

Slope: 33° slightly terraced   Surface Drainage: free

Aspect: due S   Altitude: 150 m

Vegetation: pure stand of tall Pteridium aquilinum with 100% cover which has completely obliterated ground layer.

Drainage Class: free   Parent Material: till derived from Old Red Sandstone sandstone and serpentine.

Horizon	Depth or thickness	
L	18 cm	Bracken litter
H	2 cm	Discontinuous very dark brown (10 YR 2/2) moder with some mineral content. Narrow irregular change to
A	0 - 10.5 cm	Very dark greyish brown (10 YR 3/2) slightly humose loam, slightly stony mainly serpentine, moderately developed medium subangular blocky, very friable, common fine pores and fissures, moderate permeability, common rhizomes; merging into
B	10.5 - 65 cm	Reddish brown (5 YR 4/4) with darker organic staining, loam, stony sandstone and serpentine, very weakly developed crumb, friable, porosity and permeability as A, common rhizomes to 75 cms; merging into
C	65+ cm	Mottled reddish brown (5 YR 4/4) and light olive brown (2.5 Y 5/4) due to mixed lithology, stony, sandy loam, structureless, firm, moderate permeability
Soil Type		Brown Forest Soil of low base status

Despite the parent material differences these are rather similar soils of broadly brown earth type. However Profile 8 has features which may suggest some degree of podsolisation. Like the Kingslaggan soils developed under heavy bracken, organic H horizons occur but in Profile 11 this horizon is much less developed than in Profile 8. The A horizons also differ, the paler grey coloration of Profile 8 suggesting some development of A_2 characteristics although this is modified by brown organic staining. Profile 11 has a more classic A_1. It should be noted in relation to this, that the rhizomes of Profile 11 penetrate to much greater depth, the decomposing rhizomes producing patchy organic stains in the B horizon while the rhizomes are restricted to the A horizon of Profile 8. This correlation of rhizome depth and degree of development of brown forest soil characteristics will be shown to be a feature of Conic soils.

Bracken and Heather Moorland Soils

Pteridium Stand 3, in the centre of which Profiles 8 and 11 described above were excavated, also provided interesting data from the sociological boundaries on the ridge crest and on the western edge of the stand.

Profiles 6 and 7, described in detail in Appendix B (see pages 331-332), were studied on the ridge top which coincides with the easternmost extension of a serpentine outcrop, overlain by a thin veneer of till containing both serpentine and conglomerate residues. The surface of the ridge which slopes rather steeply to the west is dominated in its lower section by *Calluna-Molinia* heath which gives way upslope to the bracken community without any discernible change in habitat conditions.

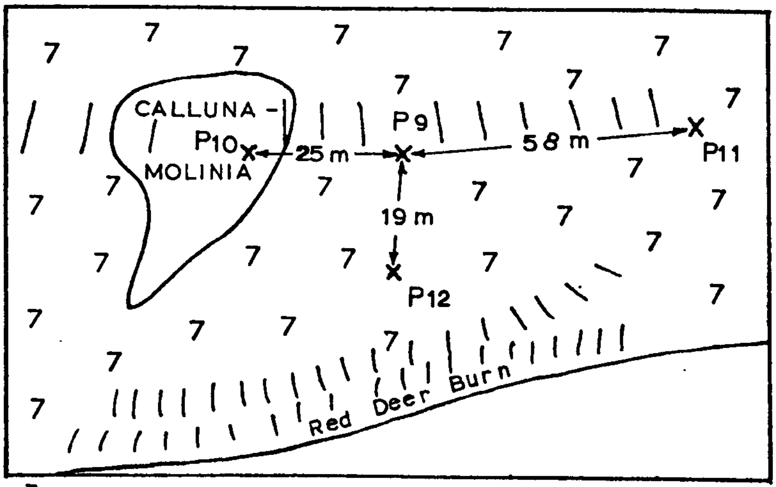
Profile 6 in the Calluna-Molinia stand is a well-defined though shallow podsol in which the C horizon consists of weathered serpentine while the B is derived from till. It is characterised by sharply defined horizons with typical podsol features - a thick mor humus, well defined grey A_2, and an organic illuvial B horizon. The last is a feature of podsols studied in the Conic area.

In marked contrast is Profile 7 situated a few metres within the bracken stand about 20 m upslope from Profile 6. Although this soil still has a fairly thick humus layer, the higher mineral content results in this being designated of moder type. Otherwise it has normal brown forest soil features - the grey brown A_2 of Profile 6 is replaced by a dark reddish brown A, with a high humus content, and the organic illuvial B is absent. These two profiles illustrate the contrast in degree of podsolisation under different vegetation types already noted at Kingslaggan.

On the south facing side of the Red Deer Burn valley the dense bracken found at Profile 11 thins out to the west where an open area of Calluna-Molinia heath with only scattered fronds occurs. Soil investigations were made along the slope at this point as shown in Figure 5.6. Profiles 9, 10, and 12 on this site are all developed from a uniform till derived from conglomerate and serpentine.

Profile 10, a peaty gleyed podsol, in the Calluna-Molinia stand is described in Appendix B (see page 332). Despite the 22° slope this soil is poorly drained with a uniformly pale C horizon and mottled gleyed A_2g and B_2g. The increase in gleying down profile and the fact that Profile 9 also has a gleyed C horizon suggests that despite the apparently unlikely location, ground water must be responsible for the impeded drainage. In addition however the thick root mat

Fig.5.6 LOCATION OF PROFILES AT CONIC HILL PTERIDIUM STAND NUMBER 3.



7 PTERIDIUM AQUILINUM

/ | \ SLOPE

and spongy mor humus horizon of Profile 10 restricts internal drainage in comparison to the looser, more porous surface material of Profile 9. This was demonstrated when both soils were examined following very heavy rain the previous night. The wetting front had reached only 49 cm in Profile 10 compared to 85 cm in Profile 9. This highlights the contrast in internal drainage characteristics between bracken and heath soils.

While the very pale grey coloration of the A_2g in Profile 10 can be ascribed partly to reducing conditions, in other respects also this profile has podsol characteristics. There is again a zone of organic matter illuviation at the top of the B, iron concretions in the same zone indicating iron mobilisation.

When Profile 9 was investigated it was anticipated that this soil under dense Pteridium would lack this podsol morphology. The results were surprising.

DESCRIPTION OF CONIC PROFILE 9

Slope: 26°

Surface Drainage: imperfect, slightly receiving site on edge of shallow channel

Aspect: S20°W

Altitude: 150 m

Vegetation: pure stand of tall Pteridium aquilinum (I.B.D. = 193.1) giving 100% frond and 100% litter cover.

Drainage Class: imperfect

Parent Material: till derived from Old Red Sandstone conglomerate and serpentine.

Horizon	Depth or thickness	
L	33.5 cm	Bracken litter
H	6.5 cm	Black (5 YR 2/1) mor humus with small percentage of quartz sand, abundant rhizomes concentrated at foot. Narrow change to

A_2	0 - 14 cm	Greyish brown (10 YR 5/2) with dark brown (7.5 YR 4/2) organic stains, slightly humose loamy sand, stony quartz, serpentine, and sandstone, weakly developed medium subangular blocky, friable, common fine pores and fissures, no rhizomes. Narrow irregular change to
B_1		Discontinuous horizon of illuviated organic matter, very firm, somewhat indurated. Narrow irregular change to
B_2	14 - 30 cm	Reddish brown (5 YR 4/4) matrix with more ochreous mottles and darker brown organic stains, loam, slightly stony, quartz and sandstone, moderately developed medium angular blocky, physical features same as A_2; merging into
C_g	30+ cms	Grey brown (10 YR 5/2) matrix with ochreous mottles, loam, stony sandstone and serpentine, structureless, slightly sticky, slow permeability.
Soil Type		Iron Podsol with gleyed C horizon.

This podsol with its characteristic mor humus, leached A_2 and organic matter translocation appeared to cast doubt on the theory that podsolisation does not occur under bracken. The only slight deviation from the typical podsol features is the patches of higher organic matter content within the A_2.

Investigations were carried further by a reconnaissance soil survey further downslope within the Pteridium stand which revealed that the degree of development of the mor humus and A_2 horizons varies considerably in an apparently random manner. Profile 12 was investigated in detail to examine this phenomenon.

DESCRIPTION OF CONIC PROFILE 12 (Plate 5.2, page 182)

Slope: 30° with small terracette   Surface Drainage: free

Aspect: S35°W   Altitude: 150 m

Vegetation: pure stand of Pteridium aquilinum identical to Profile 9

Drainage Class: free   Parent Material: till derived from Old Red Sandstone conglomerate and serpentine.

Horizon	Depth or thickness	
L	10 cm	Bracken litter
H	6.5 cm (ranging 3.5-9.5 cm)	Variable thickness, very dark brown (10 YR 2/2) mor with small percentage of sand grains, few rhizomes. Sharp - narrow irregular change to
A	0 - 8.5 cm (ranging 3.5-14.5 cm)	Variable thickness and colour, dark greyish brown (10 YR 4/2) sandy loam patches mixed with dark brown (10 YR 3/3) humose loam, slightly stony, weakly developed medium subangular blocky, very friable, abundant medium-large fissures, moderate permeability, abundant rhizomes varying in depth and density - lowest density and depth where soil grey. Sharp - narrow - merging irregular change to
B_1	8.5 - 27 cm	Variable thickness, very mottled, dark yellowish brown (10 YR 3/4) dominant with very dark brown (10 YR 2/2) organic matter concentration at top and small yellowish brown (10 YR 5/4) mottles, slightly stony quartz and serpentine, weakly developed fine subangular blocky, friable, few pores and medium-large fissures, moderate permeability, rhizomes vary in depth - below grey section of A no rhizomes elsewhere common to 23 cm; merging and irregular change to
B_2	27 - 39.5 cm	Discontinuous, brown (7.5 YR 5/4) with ochreous mottles and organic stains, loamy sand, stony, quartz and serpentine, structureless, firm, few small pores and fissures, slow permeability, rare rhizomes; this lense appears to be inherited from

		parent material; merging into
B_3	39.5 - 80 cm	Yellowish red (5 YR 4/6) loam, stony mainly serpentine, very weakly developed fine subangular blocky, firm, few fine pores and fissures, no rhizomes; merging into
C	80+ cm	Reddish brown (5 YR 5/4) with ochreous mottles, sandy loam, extremely stony quartz and serpentine, structureless, firm, few pores.
Soil Type		Degraded Podsol

This profile developed under virtually identical site conditions to Profile 9 presents important contrasts which appear to be related to depth of rhizome penetration. Perhaps the most striking features of this profile are its horizontal variability and extremely confused and irregular horizon boundaries. It is very difficult to give horizon depths or even to match the horizon sequence from one section of the profile to another. The situation is best summarized in terms of two profiles in the surface soil which can be identified on Plate 5.2.

(1) One section is characterised by relatively sharp horizon boundaries and a low density of rhizomes which do not penetrate below the A horizon (maximum depth 18 cm). The A horizon is dark greyish brown, somewhat darker than the A_2 of Profile 9, and is underlain by the remnants of an organic illuvial B. This sequence is very similar to that found in Profile 9.

(2) The other section with merging horizon boundaries has a high concentration of rhizomes which penetrate to 40 cm into the B_2. The A horizon is dark brown and humose while there is no clear illuvial horizon. In the B horizon there are patches of darker organic matter staining apparently

Plate 5.2. Profile Modification by Rhizomes.

Conic Hill Profile 12 Degraded podsol.

associated with decomposing rhizomes.

In this case the morphological evidence of podsolisation appears to be inversely correlated with the depth and concentration of rhizomes. When rhizomes are confined to the surface horizons, as in Profile 9, the horizon sequence associated with podsolisation may be found at greater depth but the penetration of rhizomes into the mineral soil leads to a modification of at least the visual characteristics of the soil, the addition of organic matter to the A_2 possibly being an important aspect of modification. This hypothesis would help to explain the variation in degree of development of mor humic and A_2 horizons on this slope in general, although the reason for the variation in rhizome penetration is obscure. There is no clear cut evidence either of the vegetation history of the site although it appears plausible that better developed podsols possibly formed under heath vegetation were formerly more widespread and have been modified by bracken invasion.

A similar situation is found on the spur south of Red Deer Burn on the crest of which there is a good sociological boundary between Pteridium Stand 2 and Calluna-Molinia heath. Profile 4 was investigated under heath and Profile 5 under tall dense bracken just 3 m from the edge of the stand. These soils are described in detail in Appendix B (see pages 329-330).

Profile 4 is a well-developed podsol with a thick mor humus horizon and a thick pale A_2 underlain by illuviated organic matter. Subsoil conditions are similar in Profile 5 but the rhizomes which reach the top of the A_2 have considerably modified the surface soil. In place of the mor humus there is a mixed organic and mineral layer which is reminiscent of an A_1. The underlying

A_2 is darker with a higher organic matter content than its equivalent in Profile 4 and its upper and lower boundaries have become confused and irregular.

Another opportunity to investigate the contrast between heather and bracken soils was provided at Pteridium Stand 6 which has been described in Chapter 4 (see pages 129–131). This site is on the gently sloping area below the southern serpentine ridge. The generally poor drainage produces a mixed wet moorland vegetation but raised hummocks of till provide locally dry sites suitable for bracken. On one of these hummocks heather dominates the lower slopes bordered by a sociological boundary with the bracken of the upper slopes. Three soils were investigated - Profile 13 in the heath stand (corresponding to Quadrat 1, see Fig. 4.21 page 130), Profile 14 within the bracken stand (Quadrat 5), and Profile 15 near the edge of the bracken stand (Quadrat 4). Derived from till containing conglomerate and serpentine, these soils demonstrate a nice sequence of features.

DESCRIPTION OF CONIC PROFILE 13 (Plate 5.3 (a), page 186)

Slope: 14° convex Surface Drainage: free

Aspect: W20°N Altitude: 90 m

Vegetation: Callunetum, Calluna vulgaris (9), Molinia caerulia (4), Erica tetralix (3) (Quadrat 1, Figure 4.21, page 130)

Drainage Class: free Parent Material: till derived from Old Red Sandstone conglomerate and serpentine

Horizon	Depth or thickness	
F	4 cm	Partially humified heather and grass remains
H	2.5 cm	Black (5 YR 2/1) mor humus, one dead rhizome. Sharp change to
A_2	0 - 5.5 cm	Greyish brown (10 YR 5/2) with darker organic stains (7.5 YR 5/2) sandy clay loam, stony serpentine and quartz, very weakly developed fine platy, firm, few fine pores and fissures, slow permeability, root mat at base. Sharp change to
B_1	5.5 - 6 cm	Incipient iron pan with iron and organic matter concentration
B_2	6 - 11 cm	Light brown (7.5 YR 6/4) sandy loam, stony quartz and serpentine, weakly developed medium angular, friable, few fine pores and fissures, moderate permeability; merging into
B_3	11 - 28 cm	Yellowish red (5 YR 4/8) clay loam, slightly stony mainly serpentine, weakly developed fine subangular blocky, consistence and porosity as B_2, one dead rhizome; merging into
C	28+ cm	Reddish brown (5 YR 5/3) loam, very stony mainly serpentine, moderately developed thick platy, firm, rare fine pores, slow permeability.
Soil Type		Shallow Iron Podsol with incipient iron pan.

This is a well developed, although shallow, podsol and investigations showed that the iron pan is better developed in other parts of the *Calluna* stand. The presence of rare dead rhizomes suggests that invasion by occasional bracken plants has met with little success.

Plate 5.3 Conic Hill Profiles 13 and 14.

Callunetum

thick F and H horizons

grey A_2, sharp horizon boundaries

incipient iron pan

(a) Conic Hill Profile 13
(Callunetum soil)
Iron pan podsol

bracken litter, no H horizon

deep A_1, merging boundaries, even rhizome distribution

(b) Conic Hill Profile 14
(Pteridium soil)
Brown forest soil of low base status

DESCRIPTION OF CONIC PROFILE 15

Slope: 8° convex   Surface Drainage: free

Aspect: W20°N   Altitude: 90 m

Vegetation: on edge of Pteridium stand with tall Pteridium aquilinum giving 100% cover (I.B.D. = 142.6) and 25% litter cover. Ground vegetation dominated by Agrostis canina and Anthoxanthum odoratum (8) Deschampsia flexuosa (4), Oxalis acetosella (3), Galium hercynicum (3) with Vaccinium myrtillus and Calluna vulgaris present. (Quadrat 4, Fig. 4.21, page 130).

Drainage Class: free   Parent Material: till derived from Old Red Sandstone conglomerate and serpentine.

Horizon	Depth or thickness	
L	3 cm	Bracken litter and grass turf
H	3 cm	Black (5 YR 2/1) mor humus of very variable thickness, common rhizomes. Narrow and irregular change to
A_1	0 - 6 cm	Very dark grey (5 YR 3/1) humose loam, slightly stony, weakly developed fine crumb, friable, common fine-medium fissures, moderate permeability, common but unevenly distributed rhizomes; merging and irregular change to
A_2	6 - 13 cm (range 11 - 15 cm)	Discontinuous and variably developed dark reddish grey (5 YR 4/2) with ochreous mottles at foot apparently iron pan remnants, slightly humose loam, slightly stony quartz and serpentine, very weakly developed fine subangular blocky, friable, few fine pores and fissures, moderate permeability. Sharp irregular change to
B	13 - 25 cm	Yellowish red (5 YR 4/6) loam stony quartz and serpentine, physical characteristics as A_2. Narrow and undulating change to
C	25+ cm	Variable colour due to mixed lithology pinkish grey (5 YR 6/2) with light grey (5 YR 7/1) and ochreous mottles, loamy sand, extremely stony quartz and serpentine in weathered sandstone matrix, structureless,

firm, rare pores.

Soil Type — Shallow Degraded Podsol.

This soil retains some podsol features, such as the mor humus layer, but in a modified form. Unlike Profile 13 there is an A_1 and the A_2 has a higher organic content. The indurated iron and organic matter illuvial horizon has been replaced by the colour remnants of an iron pan. The latter is reminiscent of Kingslaggan Profile 13 (page 165) while the irregular and variable horizon boundaries are similar to Conic Profile 12 (page 180).

<u>DESCRIPTION OF CONIC PROFILE 14</u> (Plate 5.3(b), page 186)

Slope: 7° convex — Surface Drainage: free, slightly shedding

Aspect: W20°N — Altitude: 90 m

Vegetation: 9 m inside bracken stand and dominated by tall *Pteridium aquilinum* (I.B.D. = 187.96) giving 100% of cover and 85% litter cover with ground vegetation reduced to sparse cover of *Agrostis tenuis* (4), *Anthoxanthum odoratum* (4) and *Oxalis acetosella* (4). (Quadrat 5, Figure 4.21, page 130).

Drainage Class: free — Parent Material: till derived from Old Red Sandstone conglomerate and serpentine

Horizon	Depth or thickness	
L	2 cm	Bracken litter
A_1	0 - 11 cm	Very dark greyish brown (10 YR 3/2) with rare faint ochreous mottles, humose loam, slightly stony quartz and serpentine, moderately developed fine subangular blocky, friable, common fine-medium fissures, moderate permeability, mull humus, common evenly distributed rhizomes: merging into

A/B	11 - 21 cm	Dark brown (7.5 YR 4/4) humose loam, slightly stony quartz and serpentine, weakly developed fine crumb, very friable, numerous fine pores and fissures, moderate permeability, common evenly distributed rhizomes; merging into
B	21 - 36 cm	Yellowish red (5 YR 5/8) loam, stony serpentine and quartz, very weakly developed fine subangular blocky, physical features as A/B, common rhizomes to 34 cms. Narrow change to
C	36+ cm	Reddish brown (5 YR 5/3) with ochreous and green mottles due to mixed lithology, loamy sand, extremely stony serpentine and weathered sandstone, structureless, firm, rare pores and fissures.
Soil Type		Brown Forest soil of low base status.

This is perhaps the best example of a brown earth investigated on the Conic site. There is no H horizon and the organic matter content of mull type decreases gradually down the profile. The lack of horizon differentiation can be seen clearly in Plate 5.3(b).

This sequence from podsol - degraded podsol - brown forest soil correlated with the vegetational sequence from Callunetum - ecotone - Pteridium stand emphasises again the extent to which bracken can contribute to the brown forest soil morphology of the underlying soil.

Further evidence is provided by Profiles 1, 2, and 3 which are described in detail in Appendix B (pages 326-329). They straddle a sociological boundary in Pteridium Stand I and represent bracken hinterland, ecotone and Calluna heath situations. The usual sequence from brown forest soil to podsol with organic illuvial B with an intermediate soil in the ecotone is found.

Summary

Conic Hill provides an opportunity to compare soils under vigorous bracken with nearby _Callunetum_ and _Calluna-Molinia_ soils. The results are similar to these from Kingslaggan, Profiles 13-15 and 1-3 producing sequences from brown forest soil to podsol very similar to those on the Galloway site. Profiles 13, 14, and 15 provide further morphological evidence of the disintegration of iron pans by rhizomes.

However there are some notable differences between the two sites:

(1) There are fewer really classic brown forest soils at Conic Hill, Profiles 14 and 11 being the best examples. Most of the Conic bracken soils have at least a thin H horizon which tends however to have a noticeable mineral content. This difference can possibly be ascribed to the very vigorous frond growth which on all soils examined severely limits grass turf development, a situation which was seen on Kingslaggan to favour the development of thin humic horizons.

(2) Since almost all subsoils on Conic are friable and porous, the physical effect of rhizomes is less noticeable although they are still associated with good fissure development.

(3) There are instances on Conic of bracken being underlain by podsols, such as Profile 9. The fact that rhizomes in this instance were restricted to the H horizon led to the investigation of soil modification with rhizome penetration. This resulted in the establishment of the fact that while shallow rhizomes can be underlain by a soil with podsol morphology, deeper penetration of rhizomes produces horizon modification. Boundaries become merging and irregular and the

A_2 takes on A_1 characteristics probably due to the addition of organic matter.

These results are summarized in Figure 5.7 which illustrates the relationship between depth of rhizome penetration and depth of A_1. The positive correlation between the two variables is clear, the correlation coefficient being +0.65, the probability of obtaining such a value by chance being $<$ 1%. While this is a convenient way of summarizing the relationship it should be stressed that it only provides a partial picture. Rhizome concentration and distribution, as well as depth, are significant factors while the original assessment of whether a horizon should be designated A_1 is necessarily subjective.

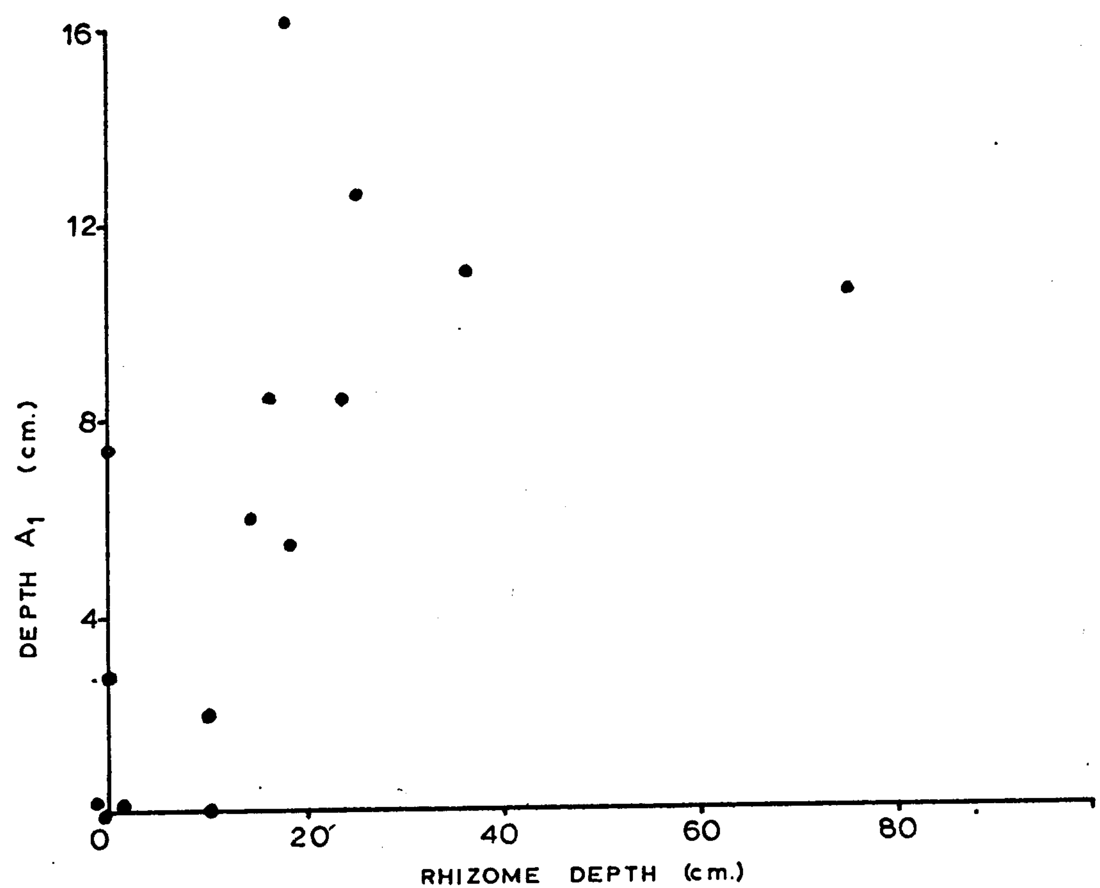
It was impossible in the time available to establish conclusively whether the spatial sequences described also represent temporal sequences i.e. whether well-developed podsols have indeed been modified by the influence of bracken colonisation. Investigation of this point would require knowledge of the vegetational history of the site.

III. SOURHOPE

The Sourhope environment provides a contrast to both Kingslaggan and Conic Hill in soil-forming factors. The characteristics of climate, parent material and vegetation described on pages 61-64 result in soils with rather different morphological features from those already described.

The thirteen soils examined on Sourhope are all situated on the western slopes of Dod Hill, a selection justified by the interesting and complex vegetation and soil pattern of this area. The macro-relief is a convex-concave slope with

Fig. 5.7. RELATIONSHIP BETWEEN DEPTH RHIZOME PENETRATION & DEGREE OF DEVELOPMENT OF A_1 HORIZONS ON CONIC HILL SITE.



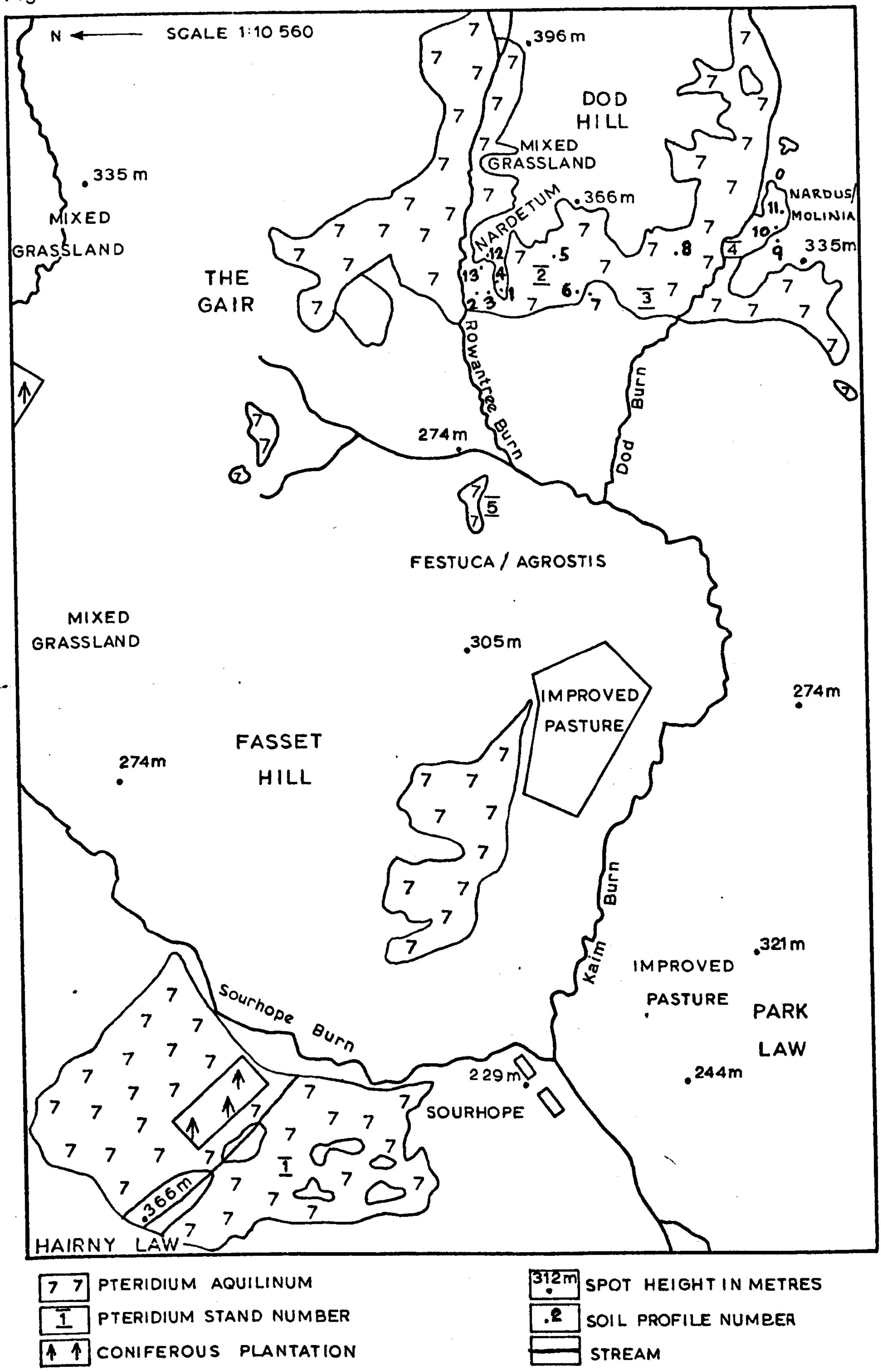
the bracken and selected soils concentrated on the lower concave section (see Fig. 5.8). Within the discontinuous bracken stand there are enclaves of Nardetum producing clear sociological boundaries between the two communities.

The parent material is in every case derived from andesitic lavas of Lower Old Red Sandstone age, the associated soils belonging to the Sourhope Association and mainly to the Sourhope and Cowie series (Muir, 1956). Some soils are developed directly on bedrock, others on a thin till cover but there is general lithological uniformity. The only exception to this is in Profiles 9-11 where two different basalts are present (see pages 205-209). The uniform parent material results in similar B and C horizons. They are usually reddish brown (5 YR 4/4) or yellowish red (5 YR 4/8), extremely stony with only a weakly developed angular blocky structure. They are also characterised by a consistence which although friable to the fingers is very resistant to the spade, a phenomenon possibly resulting from the stoniness of the mineral soil.

Bracken Soils

Bracken growth on Sourhope is less vigorous than on Kingslaggan or Conic Hill with really tall, dense fronds only occurring along the stand margins - the 'crest' described by Watt (1940, p.403). In the hinterland of the stands the fronds tend to be short with an open canopy which gives relatively low indices of bracken dominance. There is therefore little opportunity to compare soils under different densities of bracken in situations which can be assumed to be reasonably stable.

Fig.5.8 SOURHOPE SITE - Soils



The bracken soils are all very similar, Profile 5 providing a typical example. This soil was excavated in the centre of Pteridium Stand 2 on a concave section below the break of slope.

DESCRIPTION OF SOURHOPE PROFILE 5 (see Plate 5.4)

Slope: 12° convex–concave   Surface Drainage: free

Aspect: W10°N   Altitude: 315 m

Vegetation: dense short *Pteridium aquilinum* (I.B.D. = 113.4) with 80% cover and 20% litter cover. Ground vegetation dominated by *Festuca ovina* and *Deschampsia flexuosa* (7) with *Agrostis canina* and *Anthoxanthum odoratum* (4), *Holcus lanatus* (4) and *Galium hercynicum* (5)

Drainage Class: free   Parent Material: Lower Old Red Sandstone andesitic lava – bedrock

Horizon	Depth or thickness	
L	2.5 cm	Turf and bracken litter
H	2.5 cm	Black (7.5 YR 2/0) humus with few mineral particles, common rhizomes. Sharp change to
A_1	0 – 25 cm	Dark reddish brown (5 YR 3/4) slightly humose loam, stony, weakly developed fine subangular blocky, friable, abundant medium-large fissures, rapid permeability, abundant evenly distributed rhizomes to 20 cm; merging into
C	25+ cms	Yellowish red (5 YR 4/8) with faint reddish brown (5 YR 4/3) mottles, stones dominant, structureless, extremely firm, common fissures, moderate permeability.
Soil Type		Skeletal soil with brown forest soil characteristics.

Plate 5.4. Sourhope Profile 5.

very thin, indistinct organic horizons

deep A_1 with merging lower boundary; rhizomes restricted to A_1

weathered lava bedrock

Sourhope Profile 5 (Pteridium soil)
Skeletal soil with brown forest soil characteristics.

Apart from its shallowness and lack of a weathered B horizon, this soil is typical of the bracken soils described on the other sites. The thin organic horizon underlain by a well-developed A_1 can be seen clearly in Plate 5.4. The friable consistence, well developed pore space, and subangular blocky structure are all physical attributes well documented for other bracken soils.

Three other soils, Profiles 2, 6, and 8 were examined under bracken on other parts of Dod Hill. They are described in detail in Appendix B (pages 334-337).These soils are essentially very similar to Profile 5 differing only in their greater depth and fuller development of B horizons due to the existence of a till cover lithologically similar to the lava bedrock. They all have thin H horizons and lack any morphological evidence of podsolisation while the influence of rhizomes on physical conditions is very evident especially in Profile 2.

A noticeable feature of the Sourhope soils is the restriction of rhizome penetration to the surface horizons. In only one soil do the rhizomes reach below 17 cm. This exclusion of rhizomes from the Band C horizons was at first thought to be attributable to the mechanical resistance offered by the stony, firm mineral soil. Watt (1971) attributes the shallowness of rhizomes at Blaxhall Heath to the compaction of the underlying soil, yet at Kingslaggan and Conic Hill rhizomes were seen to penetrate indurated soil horizons. Subsequent laboratory analysis described below (see page 253) suggests that there may be chemical reasons for rhizome shallowness.

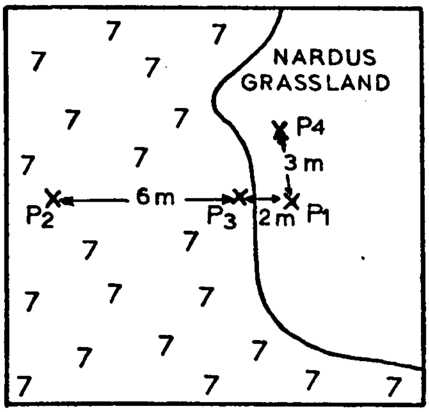
Bracken and Nardetum Soils

Although some Sourhope soils exhibit features associated with podsolisation, well developed podsols are absent. Even under mor humus horizons A_2 development is minimal and there is little morphological evidence of organic matter or sesquioxide mobilisation. The base-rich parent material may well be an important factor in this while the occurrence of Nardetum rather than Calluna-dominated heath may be significant. The result is that the contrasts between bracken and other well drained moorland soils are less marked than on Kingslaggan and Conic Hill. For example Profile 7 (see Appendix B page 335 is sited in the Nardus stand under similar habitat conditions to Profile 6 yet the differences between the soils are only marginal. The only significant points of contrast are a deep F horizon in Profile 7 produced by the very thick, tough root-stocks of Nardus and firm consistence and lower porosity of the surface soil.

However in other locations the contrasts are better developed and similar in kind to those described elsewhere. For example Profiles 1, 3 and 4 were examined across the clear sociological boundary at the northern section of Pteridium Stand 2 (see Fig. 5.9).

Profile 3 was examined on the edge of the bracken stand among the tall fronds which form the crest.

Fig. 5.9. LOCATION OF PROFILES AT SOURHOPE PTERIDIUM STAND 2.



DESCRIPTION OF SOURHOPE PROFILE 3

Slope: 12° convex-concave Surface Drainage: imperfect

Aspect: W36°N Altitude: 300 m

Vegetation: tall, dense Pteridium aquilinum (I.B.D. = 156.8) producing 75% cover and 70% litter cover. The very thin ground layer contains Deschampsia flexuosa (4), Festuca ovina (4), Agrostis canina (4), Nardus stricta (4), Galium hercynicum (4)

Drainage Class: free Parent Material: till derived from andesitic lavas of Old Red Sandstone age.

Horizon	Depth or thickness	
L	2 cm	Bracken litter
F	3 cm	Dark yellowish brown (10 YR 3/4) comminuted litter
H	2 cm	Black (7.5 YR 2/0) humus with little mineral content, abundant rhizomes concentrated at foot. Sharp change to
A_1	0 - 14.5 cm	Dark brown (7.5 YR 3/2) slightly humose loam, very stony, weakly developed very fine subangular blocky, firm especially in lower section, common fine fissures, moderate permeability, common rhizomes restricted to upper section; merging into
B	14.5 - 55 cm	Reddish brown (5 YR 4/4) sandy loam, very stony, structure as A_1, friable to fingers but resistant to spade, few fine pores, moderate permeability; merging into
C	55+ cm	Reddish brown (5 YR 4/4), stones dominant, structureless, very firm, moderate permeability.
Soil Type		Brown Forest Soil of low base status.

This is a standard bracken soil although the F horizon is unusually well developed. There is no evidence of podsolisation either in the form of a bleached A_2 or an illuvial B horizon.

Profile I was examined a few metres away in the *Nardus*-dominated grassland.

DESCRIPTION OF SOURHOPE PROFILE I

Slope: 12° convex-concave   Surface Drainage: imperfect

Aspect: W36°N   Altitude: 300 m

Vegetation: *Nardus stricta* (8) dominant with *Deschampsia flexuosa* (4) and *Festuca ovina* (4), *Anthoxanthum odoratum* (4), *Potentilla erecta* (3) and *Agrostis canina* (3).

Drainage Class: free   Parent Material: till derived from andesitic lava

Horizon	Depth or thickness	
L	1 cm	Turf with thick *Nardus* root-stocks
F	2 cm	More humified *Nardus* remains
H	2 cm	Black (10 YR 2/1) humus containing no mineral component. Sharp change to
A	0 - 18 cm	Dark brown (7.5 YR 4/2) with tendency to grey immediately below H, slightly humose loam, very stony, weakly developed fine subangular blocky, firm and very resistant to spade, common medium fissures, moderate permeability; merging into
B_1 (or A/B)	18 - 23 cm	Dark brown (7.5 YR 3/2) (darker than A), slightly humose loam, physical characteristics same as A; merging into
B_2	23 - 59 cm	Reddish brown (5 YR 4/4) loam, very stony, weakly developed fine angular blocky, friable to fingers but resistant to spade, common fine pores and medium fissures, moderate permeability; merging into

C	59 - 73 cm	Reddish brown (5 YR 4/4), stones dominant, structureless.
Soil Type		Brown Forest Soil of low base status.

This soil is very similar to Profile 3 and has been assigned to the same classificatory type. However it has unusual features such as the horizon designated B_1 which differs from the overlying A in its darker colour suggesting a higher organic content. Subsequent laboratory analysis (see page 248) however gave similar organic carbon contents. This throws doubt on the validity of the B_1 designation with its connotation of organic matter illuviation. Pertinent to this may be the grey coloration noted at the surface of the A. It is weakly developed and, rather than appearing as an identifiable horizon, occurs as a grey band at the foot of the individual peds immediately below the organic H horizon. Further light was thrown on this situation by the examination of Profile 4 just 3 metres away.

Profile 4 is situated in the 'advancing front' of the bracken where, except for the presence of two fronds, the vegetation is identical to that on Profile 1. Discussion with people with a long association with Sourhope had revealed that the bracken margin is very stable and Profile 4 was examined mainly in an attempt to discover the reason for <u>Pteridium's</u> failure to successfully invade the site. Examination of the rhizome system invading the <u>Nardetum</u> revealed that it consisted of only one main rhizome lying on the surface of the mineral soil at a depth of only 1.5 cm. It rotted away at the end and had failed to produce any lateral branches. It is difficult to see any visible soil reason for the lack of vigour of the plant. Mechanical barriers such as stoniness inhibiting rhizome penetration and the very thick Nardus turf restricting frond emergence may be significant but as suggested above (see page 197) chemical factors cannot be ruled out.

DESCRIPTION OF SOURHOPE PROFILE 4

Slope: 12° convex-concave   Surface Drainage: imperfect

Aspect: W36°N   Altitude: 300 m

Vegetation: *Nardus stricta* (d), *Festuca ovina* (a), *Deschampsia flexuosa* (c), *Agrostis tenuis* (a), *Anthoxanthum odoratum* (f) with 2 short fronds of *Pteridium aquilinum*

Drainage Class: free   Parent Material: till derived from andesitic lavas.

Horizon	Depth or thickness	
L	3.5 cm	Thick, compact turf of Nardus root-stocks
F	2 cm	Comminuted Nardus litter and root-stocks
H	2.5 cm	Black (7.5 YR 2/0) humus, little mineral matter. Sharp change to
A_2	0 - 5 cm	Dark reddish grey (5 YR 4/2) loam, extremely stony, weakly developed fine subangular blocky, friable to fingers but resistant to spade, numerous medium pores and fissures, moderate permeability, few rhizomes to 1.5 cm; merging and irregular change to
A/B	5 - 16 cm	Dark yellowish brown (10 YR 3/4) slightly humose loam, very stony, physical characteristics same as A_2. Narrow and irregular change to
B	16 - 52 cm	Dark brown (7.5 YR 3/4) loam, very stony, weakly developed fine angular blocky, friable, few small pores, moderate permeability; merging into

C	52+ cm	Reddish brown (5 YR 4/4), stones dominant, structureless.
Soil Type		Incipient Podsol.

This soil differs from Profile I in the degree of development of the organic horizons and particularly in the thickness of the L horizon which consists of compact, tough Nardus root-stocks. The most interesting feature however is the relatively thin but quite distinct grey A_2 which overlies a thicker, darker, more humose horizon designated a transitional A/B. This is a situation reminiscent of Profile I but in this case horizon development is more advanced. The relative thicknesses of the horizons seems significant. Rather than regarding the lower horizon as an illuvial B, its thickness suggests it is a normal A_1 in the upper section of which a leached or gleyed A_2 is developing. (In this situation it would be more appropriate to use the A_e and A_o terminology of the English Soil Survey). Gleying is probably a contributory factor, the thick fibrous organic horizons acting as a sponge.

The contrast between Profiles I, 3 and 4 are certainly less striking than those found on Kingslaggan and Conic Hill, yet there is evidence that differences in the organic horizons under Pteridium and Nardetum are associated with differences in the development of the underlying mineral soil.

The uphill margin of Pteridium Stand 2 provides more evidence of the contrast in surface organic horizon between bracken and Nardus soils. Two profiles 12 and 13, examined there are described in detail in Appendix B (pages 338-340) and illustrated in Plate 5.5. Both soils are skeletal. They differ in their subsoil conditions with internal variation occurring in the till from which Profile 13, the bracken soil, is derived. An indurated, weakly cemented till overlies a much more friable one.

The most interesting contrast lies however in the organic horizons and the internal water regime. The Nardus soil has the thick, tough L and F horizons typical of this community. Compare Plate 5.5(b) where a thinner, looser L and F are underlain by a discontinuous H horizon. This has its effect on drainage. Examined on the same day, the surface layers of Profile 12 were wet, moisture decreasing down profile, while the reverse was true under Pteridium. This retention of moisture by the spongy organic horizons may contribute to the gleying of the underlying mineral soil in the Nardus profiles, as suggested for Profile 4.

The final soil sequence examined on Sourhope is located south of Dod Burn on the north-facing valley side. Pteridium Stand 4, described in the previous chapter (see pages 142-145), covers the lower slopes and is juxtaposed against a grassland community in which Molinia caerulea is almost co-dominant with Nardus. The soils examined, Profiles 9, 10, 11 form a sequence across the sociological boundary on the western edge of the bracken stand, corresponding to Quadrats 1, 3 and 6 respectively (see Figure 4.26, page 144).

Profile 9 is situated 6 m within the grassland community, Profile 10 on the bracken margin where the ground vegetation is still dominated by Nardus and Molinia, and Profile 11, under a dense clump of fronds. The situation is complicated by variation in parent material, the till from which Profiles 9 and 11 are derived containing two distinct basalts, the usual pink one plus a greenish grey basalt which outcrops at the top of the slope.

Plate 5.5 Sourhope Profiles 12 and 13

Nardetum

thick, compact L and F horizons

thin but clear H horizon

(a) Sourhope Profile 12
(Nardetum soil)
Skeletal soil with incipient podsol features

bracken litter

thin, irregular organic horizons

rhizomes restricted to A horizon

indurated till

friable till

(b) Sourhope Profile 13
(Pteridium soil)
Skeletal soil with brown forest soil features

DESCRIPTION OF SOURHOPE PROFILE 9

Slope: 15° Surface Drainage: free

Aspect: N20°E Altitude: 315 m

Vegetation: Nardus stricta (7); Molinia caerulea (6), Polytrichum commune (4), Vaccinium myrtillus (3), Festuca ovina (3) (Quadrat I).

Drainage Class: free Parent Material: till derived from two lavas of Old Red Sandstone age.

Horizon	Depth or thickness	
L	3 cm	Thick Nardus root-stocks and moss litter, wet.
F	3 cm	More decomposed litter, wet
H	2.5 cm	Wet, black (7.5 YR 2/0) raw humus with no mineral component. Sharp change to
A_2	0 - 11 cm	Wet, very dark greyish brown (10 YR 3/2) with streaks of black organic matter, slightly humose loam, stony, weakly developed very fine subangular blocky, friable, common fine pores and fissures, moderate permeability. Narrow, undulating change to
B	11 - 31 cm	Very moist, dark brown (7.5 YR 4/4) loam, very stony, very weakly developed fine crumb, friable, common medium fissures, moderate permeability; merging into
C	31+ cm	Very moist, dark brown (7.5 YR 4/4) gritty loam, extremely stony with 2 basalts present, structureless; firm to spade, few pores or fissures, slow permeability.
Soil Type		Peaty podsol - weakly developed.

This is a weakly developed, shallow peaty podsol with thick organic layers but the A horizon contains a considerable quantity of organic matter and is not particularly bleached.

Profile 10, on the edge of the bracken stand with a cover of only short fronds is described in full in Appendix B (page 337). It is a very similar soil to Profile 9, with even thicker organic horizons in which a deep H is a marked feature resulting presumably from the Nardus-Molinia ground vegetation. The A horizon is variable in colour with some bleached patches while other sections with higher organic content are brown to dark brown.

DESCRIPTION OF SOURHOPE PROFILE II

Slope: 14^{o} Surface Drainage: free

Aspect: $N20^{o}E$ Altitude: 315 m

Vegetation: dense Pteridium aquilinum (I.B.D. = 126.36) giving 85% cover and 25% litter cover, markedly reducing ground vegetation of (6) Agrostis tenuis and Anthoxanthum odoratum (4), Deschampsia flexuosa, Holcus lanatus (4), various mosses (4), Nardus stricta (3) Oxalis acetosella (3). (Quadrat 6).

Drainage Class: free Parent Material: thin till containing 2 basalts on weathered andesitic lava bedrock.

Horizon	Depth or thickness	
L	I cm	Turf, very moist
F	1.5 cm	Very moist, comminuted bracken litter
H	2 cm	Wet, discontinuous black (5 YR 2/1) moder with low mineral content abundant rhizomes. Sharp change to
A	0 - 20.5 cm	Moist, very dark brown (10 YR 2/2) with occasional dark grey (10 YR 4/1) patches reminiscent of A_2 remnant, humose loam, very stony, medium crumb, friable, abundant large fissures, rapid permeability, common rhizomes evenly distributed to 15 cm; merging into

B	20.5 - 33.5 cm	Moist, dark brown (7.5 YR 4/4) loam, extremely stony, very weakly developed fine angular blocky, firm few large fissures, moderate permeability; merging into
C	33.5+ cm	Weathered lavas
Soil Type		Shallow Brown Forest Soil of low base status.

The main difference between Profile II and the Nardus-Molinia soils is again the shallower organic layers with minimal H development of the former. The A horizon has a higher humus content more evenly mixed with the mineral components than in Profile 9.

Summary

Sourhope offered an opportunity to study bracken soils on a site on which Pteridium growth is less vigorous than on the western sites, and where the contrasting vegetation is dominated by Nardus stricta, not Calluna vulgaris. The results reinforce the findings from Kingslaggan and Conic Hill to the extent that bracken is associated with soils of brown forest soil morphology and friable and porous physical conditions.

On the other hand the poor development of podsols under any community resulted in less marked contrasts between the bracken and other freely drained moorland soils. However two main points of contrast emerge:

(I) There is clear evidence of the difference in organic layers between the two communities. The *Nardus* soils are characterised by very thick, compact layers of partially decomposed litter in which the thick root-stocks of *Nardus* are located. Under bracken the thinner organic horizons are composed of loose, partially decomposed comminuted litter and thin black humus of moder type. These surface differences produce contrasts in the internal drainage of the profiles.

(2) Although well developed bleached A_2 horizons are absent from the *Nardus* soils, there are several examples of rather pale A horizons with signs of gleying, particularly immediately below the H horizon. This grey coloration may be due to incipient podsolisation but gleying under the spongy layers seem a likely contributory factor. The bracken A horizons are typical A_1s.

Field investigations of the Sourhope soils posed questions which could only be illuminated by laboratory analysis:

(I) Is there any difference in chemical characteristics between the A horizons under *Pteridium* and *Nardetum*?

(2) Is there any chemical reason for the failure of bracken rhizomes to penetrate the Band C horizons?

IV. CONCLUSIONS

Considerable evidence has been presented of the effect of bracken on soil morphology. The three sites offered contrasting soil environments and differing degrees and types of podsolisation associated with different moorland communities. Kingslaggan has iron pan podsols, on Conic Hill the podsols are characterised by organic illuvial B horizons, while at Sourhope podsolisation is at a rudimentary stage.

Yet on all sites Pteridium aquilinum was found associated with porous, friable brown forest soils in situations where, under otherwise identical habitat conditions, varying degrees of podsolisation existed under Calluna or Nardus communities. The inescapable conclusion is that while Callunetum and, to a lesser extent, Nardetum favour podsolisation, bracken normally produces brown forest soil morphology. The hypothesis that Pteridium merely invades existing brown forest soils cannot be supported.

The relationship between bracken communities and the underlying soil has been carried further by the evidence submitted from Conic Hill and Kingslaggan that the fern and its associated ground vegetation is capable of reversing the podsolisation process. Sequences ranging from well developed podsols under heath, through various intermediate soil types, to brown forest soils under bracken, have been described. The ameliorating action of Pteridium clearly appears to depend on rhizome depth and density, the only example of a well-developed podsol under bracken, Profile 9 Conic Hill, being associated with shallow rhizomes which had failed to penetrate the mineral soil.

At this stage the mechanism by which bracken ameliorates soil conditions is not clear. It is possible however to analyse the morphological manifestations of its influence. Since rhizome depth appears crucial these underground stems must alter the character of the mineral soil into which they penetrate:

(1) Rhizomes are clearly capable of disintegrating iron pans.

(2) The movement of rhizomes through H and A_2 horizons seems to confuse

and irregularise horizon boundaries with a darkening of the grey A_2. This may simply be due to the addition of organic matter by rhizome decomposition to horizons which under Calluna vulgaris are normally below the level of main root concentration. In a typical podsol under Calluna the plant roots are heavily concentrated in the organic horizons while in a well developed bracken soil rhizome penetration is well into the A and B mineral layers.
(3) Both rhizomes and bracken litter certainly modify internal drainage conditions. The typically thick and compact organic horizons of Callunetum and Nardetum which retain moisture, are replaced by loose organic debris and a thin layer of humified remains under bracken with a very porous underlying mineral soil. The rapid drainage associated with the Pteridium community precludes the gleying of the surface soil which is frequently associated with leached A_2 development and iron mobilisation in podsols in cool temperate moist climates (Crampton, 1963).

The above points can be inferred from the morphological evidence. The extent to which morphological modifications are associated with chemical alterations will be examined in the succeeding chapter. Soils from each site have been selected for laboratory analysis. From Kingslaggan, Profile 9 was selected as an example of a brown forest soil developed under vigorous Pteridium, while Profiles 3 and 4 were analysed as examples of equivalent bracken and heather soils. From Conic Hill the bracken podsol, Profile 9, and the modified podsol, Profile 12, were selected to ascertain whether the morphological modifications apparently resulting from rhizome penetration are paralleled by chemical changes. Conic Hill Profiles 13, 14 and 15 were analysed to provide an example of soil sequence associated with vegetational variation. Finally the chemical differences between Nardus and bracken soils at Sourhope were investigated using Sourhope Profiles 1, 3, and 5.

Both the morphological and chemical examinations can only elucidate the situation at one point in time. Soil sequences associated with vegetational change have been described but in the absence of information about the vegetational history of the site, it is difficult to ascertain whether these also represent temporal sequences. Only a long term project investigating the modification of a moorland soil by Pteridium invasion would perhaps provide categorical proof of the morphological modification of a podsol toward a brown forest soil by Pteridium's influence.

Section Notes

1. Index of Bracken Dominance, defined on page 78.

2. Where soil profiles coincide with vegetation quadrats, vegetation data includes Domin values in brackets. Otherwise the vegetational notation of the Scottish Soil Survey - (a) abundant, (f) frequent, (d) dominant, is used.

3. The laboratory analysis, presented on page 225 , indicates that this gradual change in organic matter content is more apparent than real.

CHAPTER 6

SOIL CHEMICAL ANALYSIS

The morphological characteristics of the soils examined at Kingslaggan, Conic Hill, and Sourhope have been described in Chapter 5, where the desirability of extending the examination of a selection of these soils to their chemical properties was pointed out. The purpose of this laboratory work is basically twofold - to investigate the extent to which morphological similarities and contrasts between profiles are matched by chemical similarities and contrasts, and to see whether chemical data will provide any clues to the causes of morphological variation. There is also the possibility that chemical differences which have no visible morphological manifestation will be revealed.

A propos the correlation between morphological and chemical properties there are two main issues:

(1) Vegetation dominated by *Pteridium aquilinum* has apparently imparted relatively uniform brown forest soil morphological characteristics to soils developed under the influence of otherwise variable soil-forming factors. Do these bracken soils also share similar chemical attributes?

(2) Comparison of bracken soils with those developed under communities in which *Calluna vulgaris* is a prominent component and with *Nardus stricta* - dominated communities has consistently revealed less morphological evidence of

podsolisation under the Pteridium community. Will chemical analysis verify these contrasts?

The explanation of morphological variation obviously poses a more difficult and complex problem. It has been postulated in Chapter 5 that certain of the features of bracken soils may be attributable to the physical characteristics of bracken litter and rhizome system (see page 212) but the possibility of vegetation-induced chemical characteristics cannot be ignored. The hypothesis which forms the starting point for these laboratory investigations is that vegetation influences the chemical aspects of pedological processes partly through its effect on nutrient cycling within the soil mantle. This influence is thought to operate mainly in two ways. The efficiency of plants in utilising the nutrient reserves of the soil depends on the volume of soil tapped by their rooting system. Plants with different rooting characteristics are therefore likely to extract and return, in the form of dying roots, nutrients from different horizons. Secondly since plants vary in their nutrient requirements and hence in the chemical composition of their litter, they will differ in the quantity and proportions of various nutrients which they extract and return to the soil. A particular species may be effective in keeping certain elements in circulation through the plant-soil ecosystem thus decelerating their loss by leaching. For instance it was anticipated that the well-documented high potassium content of bracken tissues (see pages 25-26) would result in relatively large quantities of this element being extracted and returned to the soil.

Chemical investigations are therefore concentrated on nutrient levels and distribution within the profile of the soils examined. It is appreciated that other aspects of the chemical, and particularly biochemical, attributes of a litter are likely to be crucial to an understanding of the vegetation's effect on pedological processes. For instance workers such as Bloomfield (1953, 1954, 1955, 1957) and Coulson et al (1960, 1964) have demonstrated the significance of the quantity and type of polyphenols in plant and litter on pedological processes. These more sophisticated biochemical investigations are outside the scope of the present study.

The organisation of the material in this chapter reflects the course of development of the laboratory investigations. The techniques and results of the initial routine soil analysis are presented first. These gave rise to queries about seasonal variation in nutrient levels which are dealt with next. Finally the results of two experiments designed to examine further the specific questions of phosphate levels and iron solution, which had arisen from basic laboratory and field investigations, are presented.

1. TECHNIQUES USED IN ROUTINE LABORATORY ANALYSIS

Apart from the samples taken in March and April for the investigation of seasonal variation in nutrient content, all soil samples were collected during the growing season of the *Pteridium aquilinum* fronds from June to September. Where two or more profiles were to be directly compared, care was taken to sample the soils at the same time.

Samples were air dried in a drying-oven at 32°C and sieved through a 2 mm round hole sieve. For each determination results were duplicated, where necessary analysis being repeated until good duplicates were obtained.

The results presented in the tables are therefore the mean of identical or closely similar values. The only exceptions to this are the nitrogen determinations (see below page 218), and some of the cation exchange capacity measurements in which duplication was found to be so close and the method so time-consuming, that some samples were analysed only once.

The methods chosen for the routine chemical analysis are all standard techniques such as are used in the testing of agricultural soils and in some cases by the Scottish Soil Survey.

Organic carbon content was determined by the Walkley and Black (1934) wet combustion method using standard potassium dichromate solution. This involves the oxidation of the carbon by $K_2Cr_2O_7$ and the measurement of the reduced dichromate by back-titration with ferrous iron. This technique produces 77 per cent oxidation of the organic carbon, a factor used in the calculation of total carbon content.

Total nitrogen was measured by the Kjeldahl method. This technique involves the oxidation of organic matter to CO_2 and H_2O by digestion in excess sulphuric acid. The nitrogen present is liberated as ammonia which is fixed by the excess acid as ammonium sulphate. After digestion the solution is made alkaline by the addition of 50% Na OH and the ammonia distilled off and collected in a known amount of standard HCl. The excess acid which has not been required for ammonia neutralisation is measured by back-titration with standard NaOH, and from this the nitrogen content of the sample can be calculated.

This technique presented many difficulties in obtaining total release of the nitrogen. This produced problems in obtaining duplicated and therefore reproducable results. For this reason not all the soil samples were tested for nitrogen and the results presented must be regarded with caution.

pH was determined in the laboratory on a bench meter using a 1:2.5 soil:water ratio.

Cation exchange capacity was measured by the saturation of the exchange complex by potassium ions. The soluble salts are first removed from the soil with ethanol and then the exchange complex saturated with potassium ions supplied by potassium acetate solution buffered at pH 7. After the removal of excess potassium with ethanol, the potassium adsorbed is replaced by ammonium supplied by ammonium acetate solution buffered at pH 7 and the solution containing displaced potassium collected. Determination of K^+ by flame photometry gives a measure of the soil's total cation exchange capacity. In this procedure the washing of the soil with the various solutions is frequently done by leaching but problems arose due to contamination of the samples by the silica sand which had to be added to aid leaching. Therefore the alternative procedure of centrifuge washing, in which samples are well shaken in the solutions, centrifuged, and the supernatant removed, was adopted (see Jackson, 1962, pp. 57-58). This proved to be entirely satisfactory.

A very similar method was used in the determination of exchangeable cations, NH_4OAc being used in extraction. Removal of soluble salts with ethanol was followed by the displacement of exchangeable cations by ammonium. The centrifuge technique was again preferred to leaching. The K^+ and Na^+ content of the supernatant collected was measured by flame photometry, while Ca^{++} and Mg^{++} were determined by atomic absorption spectro-photometry.

'Readily available' phosphorus and potassium are widely equated with the amounts of the elements which are extracted by certain acids, notably citric acid and acetic acid. In this project 1% citric acid was preferred to acetic acid because the large quantity extracted by the former (frequently including more phosphate than would normally be available to plants) seemed more suited to the Kingslaggan and Conic Hill soils, which were expected to give low P and K readings. This treatment is less suited to the Sourhope soils with their high phosphate levels but was maintained there for the sake of comparability.

After extraction with citric acid, potassium was determined by flame photometry. Phosphorus was determined using King's (1932) molybdenum blue method in perchloric acid 60% W/V system. This technique is based on the complexing of the phosphorus with molybdenum which is then reduced to a lower valence state of blue colour allowing colorimetric determination of the phosphorus content.

Finally total phosphorus content was measured by digesting the sample with perchloric acid 60% W/V and then measuring phosphorus contents by King's method as used in the citric-soluble phosphate determination.

II. RESULTS OF ROUTINE CHEMICAL ANALYSIS

Kingslaggan Soils

Profiles 3, 4 and 9 were selected from Kingslaggan for laboratory analysis.

It will be recalled that Kingslaggan Profile 9 was selected as an example of a soil developed under vigorous bracken, without reference to any nearby heath soil. Morphologically it is a typical bracken brown forest soil of low base status with merging horizons and no visible signs of podsolisation. As noted above (see page 156) the H is well developed for a bracken soil, a feature which appears to be associated with the very vigorous Pteridium growth and complete lack of ground vegetation. Its morphological features are summarized below, while the full profile description is given on page 153 .

SUMMARIZED DESCRIPTION OF KINGSLAGGAN PROFILE 9

Vegetation: tall, dense Pteridium aquilinum with no ground vegetation

Horizons

Surface Organic	relatively thick litter and moder humus horizon
A	dark brown very humose A_1 with abundant rhizomes, no A_2; merging boundaries
B	dark brown, very stony loam with rhizomes in upper section
C	dark yellowish brown, extremely stony sandy loam derived from Ordovician shale
Soil Type	Brown Forest Soil of low base status.

It seems appropriate to use this typical bracken soil as the starting point for the laboratory analysis, the data from which is summarized in Table 6.1.

The carbon percentages of the H and A horizons are characteristic of the mixed organic and mineral surface horizons found in brown forest soils. Indeed

Horizon	Carbon %	Nitrogen %	C/N Ratio	milliequivalents/100gm oven-dry soil								mg/100g oven-dry soil		
				pH	CEC	Ca^{++}	Mg^{++}	K^+	Na^+	TEB	% base saturation	citric soluble K	citric soluble P	Total P
1/2 (L/H)	13.34	0.52	26	3.7	37.60	1.82	0.92	0.58	0.25	3.57	9.5	12.28	6.67	108.66
3 (A_1)	8.10	0.44	19	4.0	29.16	0.59	0.44	0.39	0.14	1.56	5.3	8.57	2.66	85.73
4 (B)	2.95	0.17	16	4.7	19.48	0.36	0.06	0.11	0.15	0.68	3.5	2.71	2.83	59.27
5 (C)	1.58	0.12	13	4.6	14.77	0.25	0.02	0.06	0.11	0.44	3.0	2.01	5.40	67.64

Table 6.1. Routine Analysis Kingslaggan Profile 9 (Bracken Soil).

2 (A)	7.90	No data	-	4.2	29.62	0.62	0.34	0.36	0.16	1.48	5.0	8.41	0.91	75.52
3 (fossil H)	16.03	0.89	18	4.4	45.71	1.07	0.70	0.84	0.35	2.96	6.5	19.55	4.56	118.30
4 (A)	6.04	0.44	14	4.6	23.14	0.55	0.24	0.28	0.17	1.24	5.4	5.79	0.53	50.54
5 (B)	3.58	0.24	14	4.75	23.49	0.31	0.10	0.14	0.18	0.73	3.1	2.90	1.46	67.20
6 (C)	1.90	0.12	16	4.5	14.32	0.32	0.05	0.09	0.17	0.63	4.4	2.31	8.19	43.27

Table 6.2. Routine Analysis Kingslaggan Profile 3 (Bracken Soil).

the relatively low value of 13.4 per cent for the L/H horizon suggests a much higher mineral content than was morphologically apparent and seems to justify the designation of the organic constituent as moder rather than mor. The C/N ratios of 26 and 19 in the surface horizons approximate to the range for oligotrophic moder (15–25) given by Duchaufour (1965, p.136).

The low base status of Profile 9 is very obvious from the chemical data. The pH values are unexpectedly low, a phenomenon which was found to be a constant feature of bracken soils. Percentage base saturation values are also indicative of an acid, nutrient-deficient soil. The distribution of exchangeable nutrients within the profile is however interesting. C horizon levels are consistently low, suggesting a rather base-deficient parent material, and there is a steady decline in values down through the profile. The decrease from the L/H to A_1 horizons, which one would expect with declining organic content, is not particularly dramatic and there is no evidence of a severely leached A horizon.

Citric-soluble phosphate and potassium levels show the same decline down profile with decreasing organic content, except for the relatively high available phosphate in the C horizon, a feature which will be discussed at greater length in connection with other soils.

The analysis of Kingslaggan Profile 9 is therefore in keeping with what might be expected in a brown forest soil of low base status, developed under moorland vegetation on relatively base-deficient parent material. Its characteristics will be discussed further in relation to the other two Kingslaggan soils.

Profiles 3 and 4 were chosen as contrasting bracken and heath soils from the soil sequence at <u>Pteridium</u> Stand 5 (for full morphological descriptions see pages 164 and 167).

SUMMARISED DESCRIPTIONS OF KINGSLAGGAN PROFILES 3 and 4.

	Kingslaggan Profile 3	Kingslaggan Profile 4
Vegetation:	*Pteridium aquilinum* with grass understorey	Heath dominated by *Calluna vulgaris*
Horizons		
Surface Organic	grass turf with fossil mor humus between two A horizons.	thick mor humus
A	dark brown humose A_1, friable with rhizomes to 19 cm	both A_1 and A_2, latter dark greyish brown sandy loam, structureless, firm
B	dark yellowish brown loam	iron pan underlain by yellowish brown loam
C	dark yellowish brown, extremely stony, weathered till derived mainly from shale	dark brown, stones dominant, weathered till derived mainly from shale
Soil Type	Brown Forest Soil of low base status	Peaty Podsol with iron pan

Profile 3 (see Table 6.2 page 221) is chemically, as well as morphologically, similar to Profile 9, except for the unusual feature of the fossil H horizon. The chemical data from this H horizon verifies its mor-like character. Its organic carbon content is twice as high as the overlying mixed organic-mineral layer, and its high cation exchange capacity and relatively high nutrient levels provide further evidence of its mor humic properties. Interesting although this horizon is in terms of its pedological history, its separation from the turf by Horizon 2 suggests it has little relevance to current soil-forming processes.

Horizons 2 and 4 are similar in every respect and in terms of both organic and nutrient content are comparable to the A_1 of Kingslaggan Profile 9.

In contrast to Profiles 3 and 9, Profile 4, the data for which is presented in Table 6.3, has many chemical features associated with podsolisation. Like the brown forest soil, it is highly acid and base deficient but it differs strikingly in the distribution of its organic matter and nutrients within the profile. The great bulk of the nutrients in Profile 4 are concentrated in its surface mor humus layer with its high organic carbon content of over 34 per cent. This horizon has much higher exchangeable cation and available potassium and phosphate levels than any horizon in Profile 3. However below this zone there is a dramatic drop in nutrients content, the A_1 providing something of a transition to the highly leached A_2. The relatively gradual decrease in nutrient content down profile of Profile 3 (complicated by the fossil mor layer) is replaced by a situation in which most of the available nutrients are packed into the decaying organic horizon and the leached A_2 has available nutrients levels similar to, and in the case of exchangeable calcium lower than, the B.

It should be noted that nitrogen readings were obtained for only one horizon of Profile 4, the H, the C/N ratio of which is similar to those found in Profile 3 and lower than the surface horizons of Profile 9. The experimental difficulties mentioned above (see page 217) casts doubt on the authenticity of this result which is unfortunate as some workers have regarded the C/N ratio as a definitive characteristic of various types of humus.

Horizon	carbon %	nitrogen %	C/N ratio	pH	milliequivalents/100 gm oven-dry soil CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	% base satn.	mg/100g oven-dry soil citric soluble K	citric soluble P	Total P
2 (H)	34.50	2.04	17	4.15	82.65	1.76	2.19	2.33	0.66	6.94	8.4	23.32	7.98	135.17
3 (A_1)	7.73	no data	-	4.33	23.81	0.36	0.40	0.77	0.13	1.66	7.0	7.51	1.29	46.85
4 (A_2)	4.83	no data	-	4.1	26.53	0.18	0.20	0.13	0.06	0.57	2.1	5.33	0.26	43.88
5 (B)	3.43	no data	-	4.5	21.02	0.30	0.13	0.06	0.09	0.58	2.8	2.67	0	43.75
7 (C)	4.44	no data	-	4.55	31.15	0.22	0.15	0.07	0.08	0.52	1.7	4.31	0.57	59.92

Table 6.3. Routine Analysis Kingslaggan Profile 4 (Heather Moorland Soil).

The contrasts between Profiles 3 and 4 are summarized in Table 6.4. In this analysis equivalent horizons from each profile have been compared using the values for Profile 4 as base level. Several significant points emerge:

(1) Comparison of the A of Profile 3 with the A_2 of Profile 4 emphasises the highly leached nature of the latter. In particular, exchangeable Ca^{++}, Na^{+} and K^{+} and available phosphate levels are two to three times higher in the bracken soil.

(2) There is however a marked variation in the scale of difference found between individual nutrients in the two profiles. Exchangeable magnesium levels are rather similar and in fact are usually lower in Profile 3. Of greater interest perhaps is the unexpected result that citric-soluble potassium levels are similar where it had been anticipated that the high potash content of Pteridium tissues would produce relatively high levels of this element in the soil. On the other hand calcium levels are much higher in the A horizon of Profile 3.

(3) Available phosphate levels offer a very interesting contrast, despite the fact that total phosphate values are similar in the two soils. The available phosphate in Profile 4 is virtually all concentrated in the mor humus layer. In the Band C horizons it falls to trace levels whereas in the bracken soil there is a steep rise in available phosphate in the C horizon to 8.19 mg/100 mg oven-dry soil, a phenomenon which was found, although not quite so dramatically, in Profile 9. This unanticipated and interesting development obviously warranted further investigation.

Comparison of the data from Kingslaggan Profile 9 and Profile 4 provides similar results (see Table 6.5). Calcium levels are much higher in the A horizon of Profile 9. Calcium values are even equal in the surface organic horizons

Horizons Compared	carbon %	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	Citric-soluble K	Citric-soluble P	Total P
2(A) Prof.3 3(A_1)Prof.4	103	124	172	85	47	123	89	112	71	161
4(A) Prof.3 4(A_2)Prof.4	127	87	306	120	215	243	218	109	204	115
5(B) Prof.3 6(B) Prof.4	100	112	103	76	233	200	126	109	$\propto$	154
6(C) Prof.3 7(C) Prof.4	42	46	146	33	129	213	121	54	1437	72

<u>Table 6.4. Comparison of Equivalent Horizons of Kingslaggan Profiles 3 and 4</u>

In each case value for Profile 4 = 100.

Horizons Compared	Carbon %	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	Citric-soluble K	Citric-soluble P	Total P
2(H) Profile 4 1/2(F/H) Profile 9	39	45	103	42	24	37	51	53	84	81
$3(A_1)$Profile 4 $3(A_1)$Profile 9	107	122	164	110	51	107	94	116	204	182
$4(A_2)$Profile 4 $3(A_1)$Profile 9	166	110	328	220	303	233	274	164	1000	196
6(B)Profile 4 4(B)Profile 9	80	93	120	46	185	167	117	106	$\propto$	133
7(C)Profile 4 5(C)Profile 9	36	48	114	13	100	139	85	48	909	113

Table 6.5. Comparison of Equivalent Horizons of Kingslaggan Profiles 4 and 9.

In each case value for Profile 4 = 100.

whereas the much lower organic matter content of the L/H horizon of the bracken soil understandably results in much lower concentrations of all other nutrients than in the mor humus horizon of Profile 4. Apart from the organic layers, the available phosphate levels of the brown forest soil are far in excess of those in the podsol but once more the difference in potash is not to the degree, or even in some cases in the direction, anticipated.

In summary the differences in nutrient and organic matter distribution between the Kingslaggan bracken and heath soils reinforces the morphological evidence of differing degrees of podsolisation. On the question of nutrient levels, despite the low pHs of the bracken soils, exchangeable calcium and in the subsoil phosphate levels are higher under *Pteridium*, while the anomalous situation regarding potassium is interesting.

Conic Hill Soils

Profiles 13, 14 and 15, the sequence of soils at *Pteridium* Stand 6 were selected for laboratory analysis. Profile 14, from the centre of the bracken stand, is a brown forest soil of low base status, Profile 13 from the *Calluna*-dominated stand is a podsol, while Profile 15 from the ecotone between the two stands is intermediate in character. A summary of the morphological characteristics of these soils is given below (see pages 184-189) for full profile descriptions).

SUMMARIZED DESCRIPTION OF CONIC HILL PROFILES 13 AND 14

	Conic Hill Profile 13	Conic Hill Profile 14
Vegetation:	heath dominated by *Calluna vulgaris*	almost pure stand of *Pteridium aquilinum*
Horizons		
Surface Organic	mor humus	bracken litter with no H horizon
A	greyish brown A_2; sandy clay loam, fine platy structure	very dark greyish brown A_1, humose loam, common rhizomes; merging boundaries
B	incipient iron pan underlain by light brown sandy loam B_2; yellowish red B_3	yellowish red loam, common rhizomes
C	reddish brown weathered till containing sandstone and serpentine	reddish brown weathered till containing sandstone and serpentine
Soil Type	Iron Podsol with incipient iron pan	Brown Forest Soil of low base status

SUMMARIZED DESCRIPTION OF CONIC HILL PROFILE 15

Vegetation:	ecotone vegetation dominated by *Pteridium aquilinum* with grass understorey
Horizons	
Surface Organic	bracken litter underlain by mor humus of variable thickness, common rhizomes
A	very dark grey A_1, humose loam; discontinuous dark reddish grey A_2 with ochreous matter at foot; rhizomes restricted to A_1
B	yellowish red loam
C	variable colour, weathered till derived from sandstone and serpentine
Soil Type	Degraded Podsol.

The analytical data from Profile 14 (see Table 6.6) presents a picture broadly similar to the Kingslaggan bracken soils. The lack of a discrete humic horizon and the organic carbon levels of the A_1, are indicative of a surface soil with mixed organic and mineral composition, while the C/N ratio of 18 for the A_1 falls within the moder range.

Like the Kingslaggan brown forest soils, Profile 14 is highly acid and base deficient with exchangeable magnesium and potassium levels similar to those found on the Galloway site. There is apparently a complete absence of sodium but the calcium levels are even higher than at Kingslaggan. Once more the phosphate distribution is interesting with a very high concentration of available phosphate in the C horizon.

The heather soil, Profile 13 (Table 6.7) presents a nice contrast in degree of podsolisation giving an analysis very similar to Kingslaggan Profile 4. The distribution of organic carbon and cation exchange capacity stresses the mor humus character of the H horizon, reinforced by the wider C/N ratio. The bulk of the available nutrients are again packed into this zone which, for instance, has over six times the exchangeable magnesium content of the underlying A_2. This A horizon is strongly leached and there appears to be some accumulation of exchangeable calcium in the B.

Table 6.8 shows that Profile 15, intermediate in morphological characteristics, is also chemically transitional. The high carbon and nutrient content of the H horizon is similar to the situation in Profile 13 but the C/N ratio has narrowed. Moreover, unlike Profile 13, there is a mixed organic-mineral horizon, A_1 which provides a transition to the more leached A_2.

Horizon	carbon %	nitrogen %	C/N ratio	pH	milliequivalents/100g oven-dry soil CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	% base saturation	mg/100g oven-dry soil citric-soluble K	cit. sol. P	Total P
$2(A_1)$	10.05	0.56	18	3.8	24.58	2.42	0.26	0.37	0	3.05	12.4	8.88	2.43	106.76
3(A/B)	5.64	no data	-	4.1	23.91	1.13	0.17	0.26	0	1.56	6.5	5.36	0.65	76.57
4(B)	2.81	no data	-	4.4	no data	0.9	0.06	0.08	0	1.04	-	1.86	0.65	23.62
5(C)	0.31	no data	-	4.4	3.05	0.74	0.03	0.07	0	0.84	27.5	1.24	16.47	44.31

Table 6.6. Routine Analysis Conic Hill Profile 14. (Bracken Soil).

Horizon	Carbon %	Nitrogen %	C/N ratio	pH	milliequivalents/100g oven-dry soil CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	% base saturation	mg/100g oven-dry soil citric soluble K	citric sol. P	Tota P
1/2 (F/H)	48.48	1.73	28	3.5	79.92	3.2	1.99	1.65	0.67	7.51	9.4	38.71	2.77	94.72
3 (A_2)	7.44	no data	-	3.65	17.0	0.63	0.31	0.27	0.15	1.36	8.0	7.09	0.53	19.01
5 (B_2)	3.05	no data	-	4.15	15.06	0.69	0.12	0.09	0.11	1.01	6.7	2.69	0	23.80
6 (B_3)	3.04	no data	-	4.55	12.99	0.94	0.11	0.09	0.09	1.23	9.5	2.46	0	34.25
7 (C)	0.37	no data	-	4.5	9.97	0.41	0.05	0.07	0	0.52	5.2	2.03	2.04	31.80

Table 6.7. Routine Analysis Conic Hill Profile 13 (Heather moorland soil).

Horizon	Carbon %	Nitrogen %	C/N ratio	pH	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	% base saturation	citric-soluble K	citric-soluble P	Total P
					milliequivalents/100g oven-dry soil							mg/100g oven-dry soil		
2(H)	36.59	2.01	18	3.85	74.68	7.86	1.26	1.65	0.28	11.05	14.8	27.40	3.92	130.54
$3(A_1)$	10.55	no data	-	3.75	29.24	1.08	0.33	0.60	0.08	2.09	6.8	12.62	0.79	61.68
$4(A_2)$	6.01	no data	-	4.15	22.08	1.08	0.10	0.22	0	1.4	6.3	3.40	1.40	56.08
5(B)	4.57	no data	-	4.4	20.78	0.64	0.05	0.11	0	0.8	3.8	2.40	0	47.74
6(C)	0.59	no data	-	4.55	3.44	0.31	0.05	0.03	0	0.39	11.3	1.22	9.08	31.68

Table 6.8. Routine Analysis Conic Hill Profile 15 (Ecotone Soil).

The summary of these contrasts presented in Table 6.9 illuminates a situation closely analagous to the Kingslaggan soils. The following points are stressed:

(1) The comparison of the A_2 of Profile 13 with the A_1 horizons of Profile 14 and 15 highlights the leached nature of the former. Apart from sodium, and to a lesser extent magnesium, the bracken soils have a considerably higher nutrient content.

(2) Calcium again emerges as the exchangeable cation which is relatively most abundant in the surface horizons of the bracken soils, giving values at least 70 per cent higher than the heather soil, even when the A_2 of Profile 15 and the A/B of Profile 14 are compared to Profile 13's A_2.

(3) Levels of available potassium are once more unexpected. Only in the A_1 horizons do the bracken soils exceed the heather one in levels of citric-soluble potash.

(4) The greatest discrepancy however again occurs in the levels of available phosphate. Total phosphorus values in the subsoils provide no evidence of differences in the phosphate levels of the parent material. Yet in the heather soil available phosphate is absent from the B horizons and at a low level in the C, whereas in Profile 14, although it drops in the B horizon, it rises to a high level in the C. Profile 15 is intermediate in character. With the exception of the B horizon of Profile 15, available phosphate levels are from 1½ to 8 times higher in the bracken soils than in the podsol.

Conic Hill Profiles 9 and 12 were also analysed. Profile 9 is the soil found under shallow rooting but dense bracken at _Pteridium_ Stand 3, while

Horizons Compared	Carbon %	Nitrogen %	CEC	Ca++	Mg^{++}	K^{+}	Na^{+}	TEB	Citric-soluble K	Citric-soluble P	Total P
1/2 (F/H) Profile 13 2(H) Profile 15	75	116	94	246	63	100	42	146	71	142	138
3(A_2)Profile 13 3(A_1)Profile 15 2(A_1)Profile 14	141/135	no data	172/ 145	171/ 387	106/ 74	222/ 137	53/ 0	154/ 224	178/ 125	149/ 459	325/ 562
3(A_2)Profile 13 4(A_2)Profile 15 3(A_2/B)Profile 14	81/ 77	no data	130/ 141	171/ 179	32/ 55	81/ 96	0/0	103/ 115	48/ 76	264/ 123	295/ 403
5(B_2)Profile 13 5(B) Profile 15 4(B) Profile 14	153/ 93	no data	no data	93/ 130	42/ 50	122/ 89	0/0	79/ 103	89/ 69	0/∞	201/ 99
6(B_3)Profile 13 5(B) Profile 15 4(B) Profile 14	153/ 93	no data	170/ no data	68/ 96	45/ 55	122/ 89	0/0	65/ 84	98/ 75	0/∞	139/ 69
7(C)Profile 13 6(C)Profile 15 5(C)Profile 14	162/81	no data	34/ 31	76/ 180	100/ 60	43/ 100	0/0	75/ 162	60/ 61	445/ 807	99/ 139

Table 6.9. Comparison of Equivalent Horizons of Conic Hill Profiles 13, 14 and 15. In each case value for Profile 13 = 100; value for Profile 15 given first.

Profile 12 is the nearby complex soil undergoing modification by rhizomes which have penetrated to very variable depths (see pages 178-181 for full profile descriptions). It has been postulated that the penetration of rhizomes in one section of Profile 12 is responsible for the observed modification of the A_2, disappearance of an organic illuvial B, and general blurring of horizon boundaries. It is now possible to ascertain whether these morphological alterations have been accompanied by chemical changes, the samples from Profile 12 having been taken from the section with higher rhizome concentration and deeper penetration.

SUMMARIZED DESCRIPTION OF CONIC HILL PROFILES 9 AND 12

	Conic Hill Profile 9	Conic Hill Profile 12
Vegetation:	pure stand of *Pteridium aquilinum*	pure stand of *Pteridium aquilinum*
Horizons		
Surface Organic	thick litter and mor humus; abundant rhizomes	thick litter, variable mor humus horizon; few rhizomes
A	thick well-developed greyish brown A_2; no rhizomes	very variable, dark brown humose loam coinciding with maximum rhizome concentration
B	organic illuvial B underlain by mottled reddish brown B_2	organic illuvial B_1 (absent from area of rhizome concentration); yellowish red B_3 (sampled)
C	gleyed grey brown with ochreous mottles, derived from till containing conglomerate and serpentine	reddish brown, derived from till containing conglomerate and serpentine
Soil Type	Iron Podsol with gleyed C.	Degraded Podsol.

The chemical data in Table 6.10 indicates that Profile 9 has the classic analysis for a well-developed podsol. Almost the entire store of available nutrients is concentrated in the mor humus horizon. The organic carbon content of the humus horizon is 34 per cent dropping to 2 per cent in the underlying mineral soil; there is virtually no mixing of organic matter and mineral particles in the surface soil. Organic matter translocation is verified by the rise in organic carbon content in the B. The bracken rhizomes are living on the decomposition products in the organic layer and the underlying mineral soil is almost barren of nutrients.

Compare the results from Profile 12, presented in Table 6.11. Although equally acid in reaction, the difference in organic matter and nutrient levels of the H and A horizons is much less dramatic. The analysis Table 6.12 stresses the nutritive contrast between the two A horizons, nutrient levels being $1\frac{1}{2}$ to $11\frac{1}{2}$ times higher in Profile 12, the contrast in available phosphate and calcium being again the most marked. In examining these figures, however, it must be borne in mind that the A_2 of Profile 9 is so deficient that despite these enormous discrepancies Profile 12 is still highly base-unsaturated.

Comparison of the C horizons of the two soils underlines the similarity of the parent materials as there is little significant difference in exchangeable cation and total phosphate levels, apart from an anomalously high value for exchangeable potash in Profile 12. It is clear that the penetration of rhizomes in Profile 12 has profoundly modified the chemical as well as the morphological properties of the A horizon, possibly mainly through the addition of organic debris. Finally the difference in distribution of available phosphate must be

Horizon	Carbon %	Nitrogen %	C/N ratio	pH	milliequivalents/100g oven-dry soil CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	% base satur-ation	mg/100g oven-dry soil citric-soluble K	citric-soluble P	Total P
2(H)	53.80	1.64	21	3.5	95.40	3.81	1.96	1.08	0.30	7.15	7.5	22.99	7.67	73.42
$3(A_2)$	1.77	no data	-	3.75	10.03	0.05	0.11	0.10	0.04	0.30	3.0	1.92	0.25	12.95
$5(B_2)$	2.30	no data	-	4.5	21.56	0.05	0.12	0.10	0.07	0.34	1.6	1.85	0	25.47
6(C)	1.40	no data	-	4.65	10.69	0.17	0.09	0.08	0.05	0.39	3.6	1.80	0.96	22.11

Table 6.10. Routine Analysis Conic Hill Profile 9 (Bracken Soil).

					milliequivalents/100g oven-dry soil							mg/100g oven-dry soil		
Horizon	Carbon %	Nitrogen %	C/N ratio	pH	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	% base saturation	citric-soluble K	citric-soluble P	Total P
1 (H)	17.95	1.17	14	3.65	52.81	2.48	1.69	1.02	0.22	5.41	10.2	19.19	1.64	51.56
2 (A)	5.05	no data	-	3.9	24.02	0.57	0.37	0.23	0.07	1.24	5.2	7.07	1.61	24.89
6 (B_3)	2.68	no data	-	4.5	18.40	0.25	0.11	0	0.03	0.39	2.1	2.90	1.58	28.69
7 (C)	0.61	no data	-	4.6	4.93	0.13	0.06	0.40	0.04	0.63	12.8	1.64	6.61	24.02

Table 6.11. Routine Analysis Conic Hill Profile 12 (Bracken Soil).

Horizons Compared	Carbon %	Nitrogen %	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	citric-soluble K	citric-soluble P	Total P
2(H) Profile 9 1(H) Profile 12	53	71	55	65	86	94	73	76	83	21	70
$3(A_2)$ Profile 9 2(A) Profile 12	281	no data	239	1140	336	230	175	413	368	644	191
$5(B_2)$ Profile 9 $6(B_3)$ Profile 12	116	no data	85	500	91	0	43	110	157	$\propto$	113
6(C) Profile 9 7(C) Profile 12	44	no data	46	76	67	500	80	162	91	689	109

Table 6.12. Comparison of Equivalent Horizons of Conic Hill Profiles 9 and 12. In each case value for Profile 9 = 100.

stressed. Virtually all the phosphate available to plants is concentrated in the H horizon of Profile 9, where it presumably has an organic origin, while the C horizon of Profile 12 has a relatively high content of this element.

The analytical results from the Conic soils substantiate to a considerable extent the findings from Kingslaggan. They reinforce the morphological evidence of the difference in pedological processes between bracken and heather soils. Bracken, by inhabiting a greater volume of soil, gives a more even distribution of nutrients in the surface soil, while under podsolised conditions the plant roots live on the products of their own decomposition in the surface organic layers. Calcium and phosphate again emerge as the two elements in greater supply in the bracken mineral horizons, the distribution of the latter being particularly fascinating. Conversely, available potassium levels are once more surprisingly low in the bracken soils.

Sourhope Soils

Three soils from the Sourhope site, Profiles 1, 3 and 5 were analysed in the laboratory. Profile 5, which was excavated in the hinterland of Pteridium Stand 2 under short bracken with a grass turf, was selected as an example of a bracken soil; Profiles 1 and 3 are sited across a sociological boundary of Pteridium Stand 2 (for full profile descriptions see pages 195 and 200-202).

The morphological characteristics of Profile 5, a shallow skeletal soil, are summarized below.

SUMMARIZED DESCRIPTION OF SOURHOPE PROFILE 5

Vegetation:	dense, short Pteridium aquilinum with grass understorey
Horizons	
Surface Organic	thin black moder humus overlain by bracken litter in various stages of decomposition
A	well developed, dark reddish brown, slightly humose A_1 with abundant rhizomes in upper two-thirds
C	yellowish-red weathered andesitic lava
Soil Type	Skeletal Soil.

The main morphological difference between this soil and the Kingslaggan and Conic Hill bracken soils is the absence of a weathered B horizon.

The analytical data presented in Table 6.13 suggests that there are also other differences. The organic surface horizon of this Sourhope soil is more clearly defined than those found in bracken soils elsewhere. For instance this soil can be compared to Kingslaggan Profile 9 (see Table 6.1, page 221) since both profiles were selected as examples of soils developed in the hinterland of bracken stands and therefore presumably under the influence of Pteridium-dominated vegetation for a considerable length of time. The H horizon of the Sourhope soil has a much higher organic carbon content and consequently the contrast in nutrient levels between the H and A horizons is greater than in the Kingslaggan soil. This evidence suggests that the organic matter of Sourhope Profile 5 has mor characteristics, but the thinness of the H horizon (only 2.5 cms) indicates that mor humus development is limited.

The other striking contrast between this soil and those described earlier is in the phosphate levels. Total phosphorus content is far in excess of anything

Horizon	Carbon %	pH	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	% base saturation	citric-soluble K	citric-soluble P	Total P
			milliequivalents/100g oven-dry soil							mg/100 g oven-dry soil		
2/3 (H)	28.24	4.15	54.82	2.65	2.34	1.49	0.39	6.87	12.5	27.95	12.0	138.59
4 (A)	8.07	4.05	42.12	0.40	0.31	0.45	0.16	1.32	3.1	9.33	1.66	121.53
5 (C)	2.02	4.7	22.52	0.24	0.07	0.54	0.06	0.91	4.0	3.67	73.02	194.57

Table 6.13. Routine Analysis Sourhope Profile 5 (Bracken Soil).

described above - 195 mg/100 g oven-dry soil in the C horizon, compared to levels of approximately 60 mg/100g oven-dry soil in the Kingslaggan soils and 20-40 mg/100g at Conic Hill. This difference in scale is also found in levels of citric-soluble phosphate. Sourhope Profile 5 has 73 mg/100g oven-dry soil of citric-soluble phosphate in its C horizon, whereas 16.5 mg/100g oven-dry soil is the highest level found in mineral soils from the other sites. This suggests parent material-controlled contrasts, a suggestion reinforced by data from the other Sourhope soils.

The morphological characteristics of Sourhope Profiles 1 and 3 are summarized below. It will be recalled that these soils are only a few yards apart, Profile 1 under _Nardetum_ and Profile 3 in the crest of _Pteridium_ Stand 2 (see pages 198-202).

SUMMARIZED DESCRIPTION OF SOURHOPE PROFILES 1 AND 3

	Sourhope Profile 1	Sourhope Profile 3
Vegetation:	_Nardus stricta_-dominated grassland	tall, dense _Pteridium aquilinum_ with very thin grass cover
Horizons		
Surface organic	thick turf of _Nardus_ root-stocks	thin moder humus overlain by bracken litter, abundant rhizomes
A	dark brown, slightly humose A_1 with grey mottles in upper part	dark brown, slightly humose A_1 with common rhizomes in upper section
B	dark brown horizon of doubtful origin underlain by reddish brown loam	reddish brown sandy loam
C	reddish brown weathered till derived from andesitic lavas	reddish brown weathered till derived from andesitic lavas
Soil Type	Brown Forest Soil of low base status.	Brown Forest Soil of low base status.

The analytical results from Profile 3 presented in Table 6.14, are similar to those given for Profile 5. Once more there is a clearly defined organic H horizon in which most of the available nutrients are concentrated. However in this case there is a nitrogen reading available which gives a C/N ratio of 16, well within the moder range. Thus, while these Sourhope bracken soils have humic layers which are in some respects more mor-like than those found on Kingslaggan and Conic Hill, the C/N ratio of Profile 3 supports the moder designation which was based on visible characteristics.

This question of the nature of the humus in the Sourhope bracken soils is further illuminated by a comparison of Profiles 3 and 1 (see tables 6.14, 6.15, 6.16). The organic carbon levels of the H and A horizons are quite similar yet the cation exchange capacity values in Profile 3, the bracken soil, are much higher. The CEC of the H horizon of Profile 3 is three times higher than that of the H horizon of Profile 1, although the difference in organic carbon percentage is only 7 per cent. In other soils examined there has been a close correlation between organic carbon and CEC levels. Duchaufour (1965, p.131) suggests that differences in cation exchange capacity are significant in terms of the degree of humification and hence the activity of the humus:

> La valeur T (CEC rapportée en % de la matière organique, est un tres bon critère pour apprécier indirectement le degré d'humification, la nateur des complexes humiques formés; elle est d'autant plus élevée que la matière organique est plus humifiée. Cette valeur traduit la "qualite" de l'humus.

On this basis it would appear that although the extent of mixing of organic and mineral components in the surface of the bracken soil is limited,

Horizon	Carbon %	Nitrogen %	C/N ratio	pH	milliequivalents/100g oven-dry soil CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	% base saturation	mg/100g oven-dry soil citric-soluble K	citric-soluble P	Total P
2/3 (L/H)	35.93	2.28	16	4.2	185.08	6.14	2.24	1.09	0.42	9.89	5.3	38.48	25.98	172.62
4 (A_1)	4.65	no data	-	4.3	78.27	0.33	0.20	0.15	0.09	0.77	1.0	5.02	8.11	163.29
5 (B)	1.86	no data	-	4.5	22.59	0.31	0.03	0.06	0.06	0.46	2.0	3.53	63.84	222.18
6 (C)	1.50	no data	-	4.65	15.57	0.18	0.06	0	0.01	0.25	0.6	3.13	114.23	239.92

Table 6.14. Routine Analysis Sourhope Profile 3 (Bracken Soil)

				milliequivalents/100 g oven-dry soil							mg/100 g oven-dry soil		
Horizon	Carbon %	Nitrogen %	pH	CEC	Ca^{++}	Mg^{+}	K^{+}	Na^{+}	TEB	% base saturation	citric-soluble K	citric-soluble P	Total P
3 (H)	28.91	no data	4.8	58.41	1.39	2.25	2.27	0.45	6.36	10.9	71.38	26.05	220.51
4 (A)	5.52	no data	4.4	23.34	0.14	0.18	0.23	0.05	0.60	2.6	6.95	3.06	140.13
5 (A/B)	4.07	no data	4.55	20.90	0.23	0.10	0.10	0.09	0.52	2.5	2.65	37.08	241.64
6 (B)	1.49	no data	4.65	15.27	0.41	0.05	0.06	0.07	0.59	3.8	2.42	82.11	281.81
7 (C)	0.81	no data	4.75	11.91	0.15	0.06	0	0.05	0.26	2.2	2.71	92.42	192.45

Table 6.15. Routine Analysis - Sourhope Profile 1. (Mixed - acid grassland soil).

Horizons Compared	Carbon %	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	TEB	citric-soluble K	citric-soluble P	Total P
3(H) Profile 1 2/3(L/H) Profile 3	124	317	442	100	48	93	156	54	100	78
4(A) Profile 1 4(A) Profile 3	85	335	236	111	65	180	128	72	265	117
6(B) Profile 1 5(B) Profile 3	128	148	76	60	100	86	78	146	77	79
7(C) Profile 1 6(C) Profile 3	185	131	120	100	100	20	96	115	124	125

Table 6.16. Comparison of Equivalent Horizons of Sourhope Profiles 1 and 3.

In each case value for Profile 1 = 100.

the humus is more humified and undergoing more rapid alteration than the organic remains of the nearby Nardetum. Investigations in soil biology and biochemistry would be necessary to elucidate this point further.

Tables 6.14, 6.15 and 6.16 demonstrate that Sourhope Profiles 1 and 3 are quite similar chemically, as indeed they are morphologically. It will be recalled that there was some doubt about the origin of Horizon 5 in Profile 1 (see page 202). Morphological evidence suggested that it could be regarded as either an organic illuvial B horizon, or as a transitional A/B zone. The chemical evidence available favours the latter explanation as the postulated higher organic content suggested by the darker coloration of Horizon 5 is not substantiated by the organic carbon figures. Other values also tend to be intermediate between the A_1 and B.

Despite the similarities in chemical characteristics particularly in the subsoil, the laboratory analysis does indicate some interesting divergencies in conditions in the surface soil. Apart from the cation exchange capacity values already discussed, these contrasts are similar to those noted on the other sites. Although the H and A horizons are similar in total nutrient content, both soils being acid and nutrient-deficient, exchangeable calcium levels are much higher in the bracken soil. The distribution of calcium within the profile also varies, the relative values of the A and B horizons of Profile 1 suggesting translocation of this element. Once more the available potassium contents are unexpectedly lower in the topsoil of the bracken soil.

In some respects the results are similar to those already discussed with reference to the other sites. However at Sourhope, the contrast in available phosphate levels which was such a prominent feature of the Kingslaggan and

Conic Hill soils is absent. Only in the A horizon is there a markedly higher value for the bracken soil, while it was in the subsoil that the difference was most noticeable elsewhere. This discrepancy in results is possibly due to the quite different phosphate situation which exists in these Sourhope soils.

It has been noted above that the total phosphorus and available phosphate levels of Sourhope Profile 5 are extremely high compared to the western sites. These very high values are repeated in Profiles 1 and 3, except for the A horizons. Very high phosphorus values of this type are associated with basic igneous rocks, Scottish Soil Survey data for the Sourhope area giving similar phosphorus levels on the andesitic lavas. For instance in one profile analysed from the Sourhope series the total phosphorus content is 166 mg/100g oven-dry soil in the A horizon, and 190 mg/100g oven-dry soil in the B_3 (Muir 1956, p.129). Similar results have been obtained in other parts of Scotland. The Darleith series is developed on porphyritic basalts and trachy-basalts in the Kilmarnock area and the Soil Survey Memoir for that district gives the total phosphorus content of one Darleith profile as 264 mg/100g oven-dry soil in the A and 238 mg/100g oven-dry soil in the B_2 (Mitchell and Jarvis, 1956, p.179).

Unfortunately a difference in the method of extraction of available phosphate (the Soil Survey uses acetic acid) precludes comparison of the Sourhope results with Scottish Soil Survey data. However H.J. Fullerton (1972, p.714) working on the Dunlop series, an imperfectly drained brown forest soil in the Darleith association, found 31.4 mg/100g oven-dry soil of available phosphate in the C horizon using the citric-soluble technique. Although this is not nearly as high as some of the levels found in these Sourhope soils, it is much higher than the values obtained from Kingslaggan and Conic Hill.

Thus on Sourhope one is dealing with soils derived from basic igneous rocks in which both total phosphorus and available phosphate levels are typically high. It is possible that at these levels any vegetation-induced effect of raising the concentration of available phosphate is masked, in comparison to phosphate-deficient environments such as Kingslaggan and Conic Hill.

This question of phosphate levels has further implications. Soils derived from basic igneous rocks are characterised by high levels of non-crystalline alumino-silicates (allophanic material), for example the Bowden and Trusham soils described by Loveland and Bullock (1976). Workers such as Ho Hsu (1965) and Williams, Scott and McDonald (1958), the latter working on soils from north-east Scotland, have shown that much of the phosphate sorption capacity of acid soils in particular is associated with aluminium compounds. This means that in the subsoil of the Sourhope profiles there is likely to be a situation in which large quantities of phosphate are attached to allophanic material. The effect of treatment with citric acid is to break this bond, releasing both phosphate and aluminium thus accounting for the high available phosphate readings obtained. This postulated high allophanic content was verified by H.J. Fullerton who tested the allophane content of Sourhope Profile 3 using the Fieldes & Perrott (1966) NaF reaction test. 50 ml satured NaF solution was added to 1 g air-dry soil and the rise in pH with time recorded. The underlying principle in this procedure is that addition of NaF to a soil with a high content of allophanic material results in the complexing of aluminium by the fluoride thus releasing OH^- ions, a reaction which is monitored by rising pH values. The results of the test are given in Table 6.17, the rapid rise in pH to approximately 11, verifying the existence of high allophanic concentrations, particularly in the B and C horizons.

An interesting incidental point to note is that these high results for allophane content may have implications in terms of the unusual rooting characteristics of bracken on the Sourhope soils. In Chapter 5 (see page 197) it was noted that on all the bracken soils examined on Sourhope the rhizomes were shallow and restricted to the A horizons. No satisfactory explanation could be found in the field for this limited penetration of the rhizomes. However this phenomenon appears similar to the situation encountered by the Forestry Commission on basalts on various sites where they have been faced with a problem of shallow rooting of trees. One possible explanation proposed is that shallow rooting may result from chemical inhibition of roots by high aluminium levels in the subsoil (Fullerton, 1972, pp. 347 and 741; and personal communication). It would appear possible that Pteridium aquilinum on Sourhope may be facing similar problems. However at this stage the restriction of rooting by high allophane concentrations can only be postulated as a hypothesis to explain the distribution of rhizomes in the Sourhope soils, a hypothesis which requires further investigation.

Summary

As pointed out in the introduction to this chapter, the routine analysis

Horizon 4(A)		Horizon 5(B)		Horizon 6(C)	
Time (min.)	pH	Time (min.)	pH	Time (min.)	pH
0.0	7.1	0.0	7.1	0.0	7.1
0.25	9.9	0.25	9.6	0.25	10.0
0.5	10.2	0.5	10.2	0.5	10.5
1.0	10.5	1.0	11.1	1.0	10.6
2.0	10.65	2.0	11.3	2.0	11.1
4.0	10.8	5.0	11.5	3.0	11.25
9.0	10.9	9.0	11.55	5.0	11.35
				10.0	11.4

Table 6.17. Allophane Test by NaF Reaction. Sourhope Profile 3.

was undertaken to examine the following questions:

(1) Do the bracken soils which are morphologically similar have similar chemical properties?

(2) Is the morphological evidence of differing degrees of podsolisation between bracken soils and other well-drained moorland soils substantiated by chemical evidence?

(3) Are there any chemical differences between the soils, particularly in nutrient content and distribution, which have no obvious morphological manifestation?

The results of the routine analysis will be summarized in terms of these three questions.

(1) Properties of bracken soils. Despite differences in other aspects of the soils' environments the brown forest soils developed under *Pteridium aquilinum* are chemically very similar, particularly those from Kingslaggan and Conic Hill. They are highly acid and nutrient-deficient, the pH of the surface horizons falling to 4.2 or lower, a degree of acidity which, it may be added, was lower than expected. The level of available nutrients is low, the percentage base saturation never rising above 15 per cent.

Laboratory analysis has substantiated the morphological evidence that bracken is not associated with peat or mor humus development. On Kingslaggan and Conic Hill the surface horizons have mixed organic and mineral composition as evidenced by relatively low organic carbon content. Although the difficulties in duplicating results for nitrogen values must lead one to treat C/N ratios with discretion, where available they reinforce the classification of humus-type as moder. Despite the high organic carbon contents found in the surface horizons at Sourhope, the CEC levels there also suggest that there is relatively active humus formation.

The distribution of organic matter and available nutrients within the profile are similar for the Kingslaggan and Conic Hill bracken soils and typical of brown forest soils. There is a fairly steady decline down profile with no dramatic drop from the H to A horizon and no evidence of illuviation of material in the B. On the Sourhope site the better development of the H produces a more marked contrast between organic carbon and nutrient levels of the H and A horizons.

(2) Degree of podsolisation. Laboratory analysis has clearly substantiated the morphological evidence of differing degrees of podsolisation between the bracken soils and those developed under other well-drained moorland communities. There are much greater contrasts in chemical properties between soils a few yards apart separated by sociological vegetation boundaries than exist between bracken soils from different parts of the country.

The most obvious differences lie in nutrient content and distribution within the topsoil. In contrast to the mixed organic-mineral horizons in the surface soil and gradual fall in nutrient content down profile of the bracken soils, the Calluna-dominated soils have mor humus layers with over 30 per cent organic carbon contents in which the great bulk of the available soil nutrients are concentrated. Comparison of the underlying A horizons with those developed under bracken has highlighted the highly leached nature of the former and in some cases there is chemical evidence of illuviation of organic matter or exchangeable bases in the B horizons of the podsols. The influence of bracken rhizomes in modifying the properties of the surface soil is very clearly demonstrated by comparison of the A horizons of Conic Hill Profiles 9 and 12 (see Table 6.12, page 241).

(3) "Invisible" chemical contrasts. While laboratory analysis has largely reinforced the morphological evidence of soil properties, it has also revealed unforeseen contrasts in the level of individual nutrients. These differences are summarized in Figures 6.1, 6.2, and 6.3. Exchangeable calcium levels are consistently higher in the surface horizons of bracken soils. In contrast, exchangeable and citric-soluble potassium levels are lower than expected, Figure 6.2 showing that, while there is a tendency for the citric-soluble potassium contents of the A horizons of bracken soils to be higher than in other soils examined, the distinction is not particularly well-defined. Since this result is the reverse of what was expected, it will be examined in greater detail in the next section.

The third point revealed by the chemical data is the contrast in available phosphate levels, at least on sites where this nutrient is in short supply. Not only are levels of available phosphate consistently higher in the mineral horizons of the bracken soil, but the peculiar distribution with dramatic increases in phosphate in the C horizons justifies the further investigations which are described in a later section. The marked discrepancy between available phosphate levels in the C horizons of bracken and heath soils on Kingslaggan and Conic Hill is illustrated in Figure 6.3.

III. SEASONAL VARIATION IN NUTRIENT LEVELS IN BRACKEN SOILS

One of the unexpected results of the routine analysis is the failure of

FIG 6.1 Exchangeable Ca^{++} levels in A horizons.

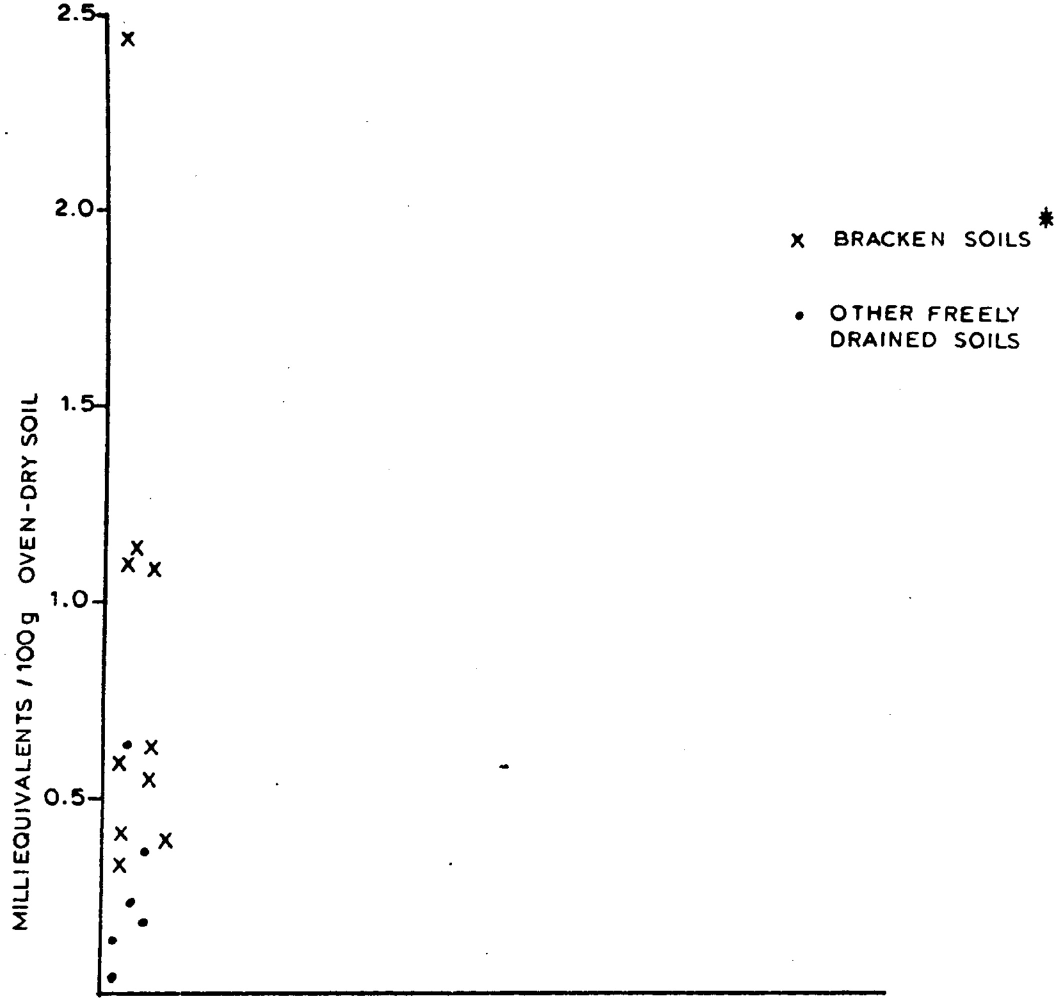
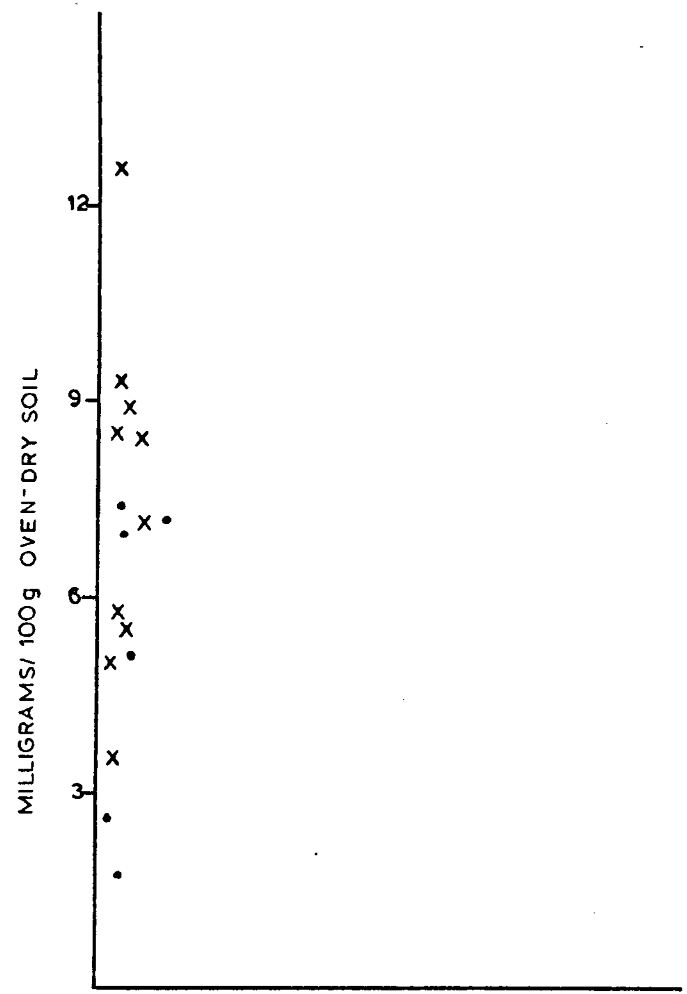
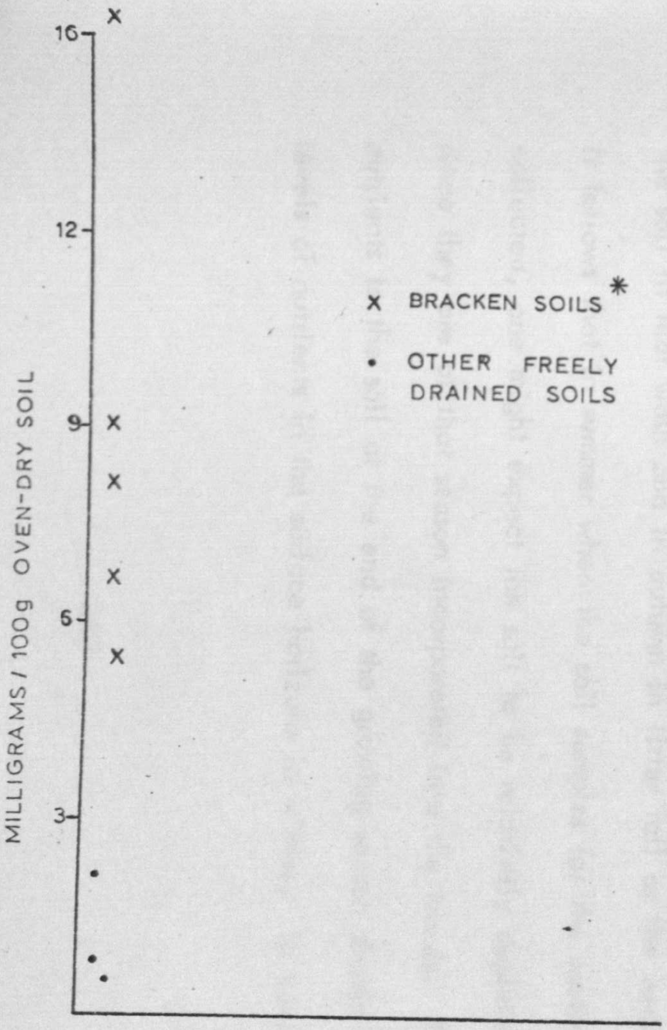
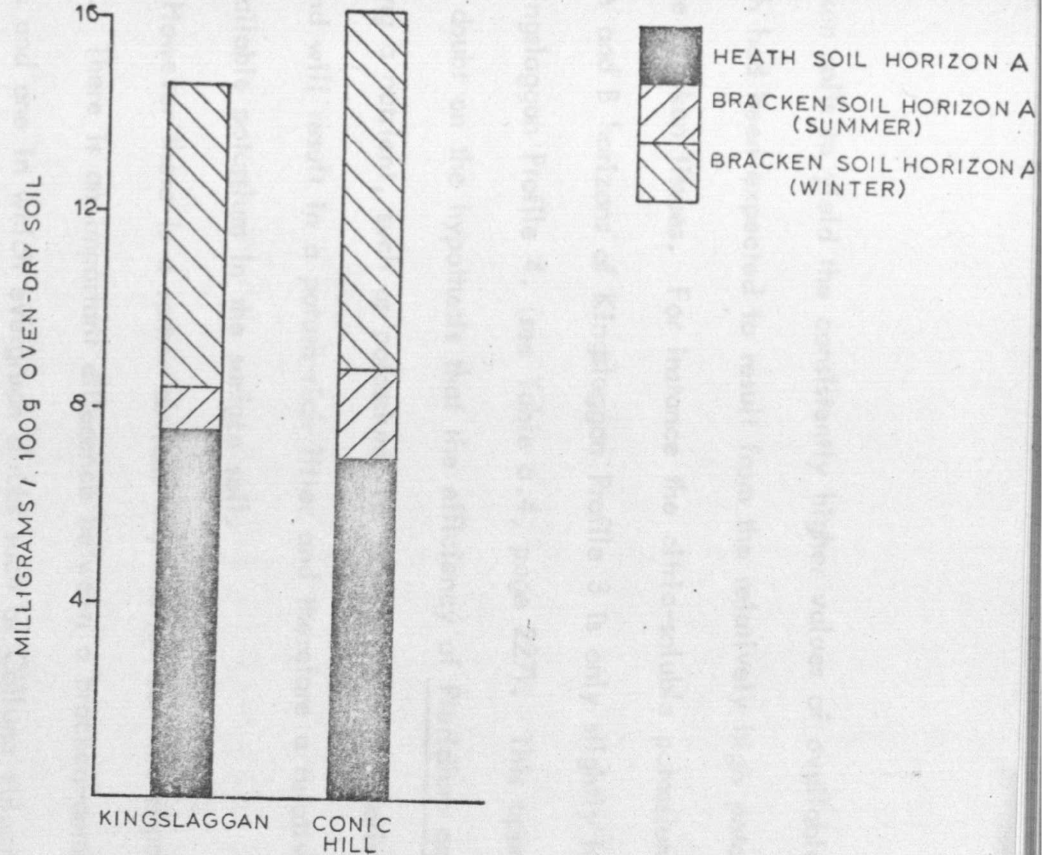


FIG 6.2 Citric-soluble potassium levels in A horizons.



*For purposes of this analysis 'bracken soils' are defined as those in which rhizomes penetrate mineral soil.





*For the purposes of this analysis 'bracken soils' are defined as those in which rhizomes penetrate mineral soil.

bracken soils to yield the consistently higher values of available potassium which had been expected to result from the relatively high potash content of the bracken tissues. For instance the citric-soluble potassium content of the A and B horizons of Kingslaggan Profile 3 is only slightly higher than in Kingslaggan Profile 4. (see Table 6.4, page 227). This appears to cast some doubt on the hypothesis that the efficiency of Pteridium aquilinum in cycling a nutrient, such as potassium, for which it has a relatively high demand will result in a potash-rich litter and therefore a relatively high level of available potassium in the surface soil.

However there is a rather obvious explanation for this apparently anomalous result. There is an important difference between a bracken-dominated ecosystem and one in which evergreen shrubs such as Calluna vulgaris and Vaccinium myrtillus are the main components of the vegetation. The deciduous habit of Pteridium results in a marked seasonal variation in the distribution of nutrients within the ecosystem as a whole. During the growing season a large proportion of the available nutrients can be expected to be locked in the living tissues of the bracken plants. Some of these nutrients are transferred to the rhizome in the latter part of the growing season, but the remainder are returned to the soil in leaf wash and in autumn in litter fall as the aerial tissues die. It follows that in summer when the soil samples for the routine analysis were collected, one might expect the soil to be relatively depleted of some nutrients since they are at that season incorporated into the fronds. The return of nutrients to the soil at the end of the growing season should result in higher levels of nutrients in the surface horizons in winter. In contrast the evergreen nature of Calluna-dominated vegetation results in the return of nutrients to the soil throughout the year, and hence a less marked seasonal variation in soil nutrient status.

To test this hypothesis two bracken soils, Kingslaggan Profile 3 and Conic Hill Profile 14, were sampled outside the growing season. The Kingslaggan soil was sampled in early April before frond emergence had started and the Conic Hill soil in March.

The chemical data for the A and B horizons of Kingslaggan Profile 3 (winter phase) is presented in Table 6.18 and compared to the summer phase and Kingslaggan Profile 4 (summer phase) in Tables 6.19 and 6.20. These show that the winter phase has a substantially higher content of available potassium than the summer phase. This is particularly marked for citric-soluble potassium levels which are 70-130 per cent higher in winter. Comparison of the winter phase with Profile 4, the heath soil, shows a marked accentuation of the tendency for the bracken soil to have higher potassium levels. While the summer phase had very similar potash levels in the A and B horizons to the heath soil, potash levels in the winter phase of the brown forest soil are 2-2½ times greater than in the summer phase of the podsol.

Unfortunately experimental error restricted the data available for exchangeable calcium in the winter phase to one horizon. However exchangeable magnesium levels are also higher in winter resulting in a reversal of the tendency for the bracken soil to have similar or lower levels of magnesium than the podsol. Available phosphate levels are also higher in the topsoil in winter presumably due to the return of nutrients in decaying litter.

Horizon	pH	milliequiv./100g oven-dry soil			mg/100 oven-dry soil	
		Ca^{++}	Mg^{++}	K^{+}	Citric-soluble K	Citric-soluble P
2(A)	4.7	0.51	0.58	0.50	14.47	1.60
4(A)	4.7	no data	0.23	0.34	10.23	1.28
5(B)	4.85	no data	0.16	0.22	6.80	1.47

Table 6.18. Analysis of Kingslaggan Profile 3 (winter phase)

Horizon	Ca^{++}	Mg^{++}	K^{+}	citric-soluble K	citric-soluble P
2(A)	82	171	139	172	176
4(A)	no data	96	121	177	242
5(B)	no data	160	157	235	100

Table 6.19. Comparison of Kingslaggan Profile 3 (winter phase) and Kingslaggan Profile 3 (summer phase).
Value for (summer phase) = 100.

Horizons Compared	Ca^{++}	Mg^{++}	K^{+}	Citric-soluble K	Citric soluble P
2(A) Profile 3 3(A_1) Profile 4	142	145	65	192	124
4(A) Profile 3 4(A_2) Profile 4	no data	115	262	192	492
5(B) Profile 3 6(B) Profile 4	no data	123	367	255	∝

Table 6.20. Comparison of equivalent horizons of Kingslaggan Profile 3 (winter phase) and Kingslaggan Profile 4 (summer phase).
Value for Kingslaggan Profile 4 (summer) = 100.

Examination of the results from Conic Profile 14 reveals a similar picture of seasonal variation (see Tables 6.21, 6.22, 6.23). In this case the A_1 has higher concentrations of every nutrient in winter than in summer, a difference which is particularly marked for citric-soluble potassium and for magnesium. For calcium, magnesium, and citric-soluble potassium the A/B shows a similar but much less marked trend. To verify that these increased nutrient levels do not merely reflect higher organic matter content in winter, the organic carbon content of Horizon A_1 of Conic Hill Profile 14 (winter phase) was measured - at 8.5 per cent it is in fact lower than the summer value.

Table 6.23 compares the situation in the winter phase of Conic Profile 14 with the summer phase of Conic Profile 13. In winter the higher potash content of the A horizon of the bracken soil is much more marked than in summer. The higher calcium content of the bracken soil is accentuated even further and the tendency for lower magnesium levels is reversed.

This necessarily brief examination of seasonal variation in bracken soils emphasises the need to look at the ecosystem as a whole. It is obvious that the relatively low values obtained for available potash in the soil in summer are due to the incorporation of much of the potassium in the vegetational part of the ecosystem at that season. In winter the A horizons of both soils examined have citric-soluble potassium levels which would be regarded as satisfactory for agricultural purposes[2], the extent of the seasonal variation being illustrated in Figure 6.4 (page 259).

This result is in line with the findings of Carlisle, Brown and White (1967) who examined nutrient cycling in a sessile oak woodland with a bracken under-

Horizon	Carbon %	pH	milliequivalents/100g oven-dry soil Ca^{++}	Mg^{++}	K^{+}	mg/100g oven-dry soil Citric-soluble K	Citric-soluble P
2(A_1)	8.5	4.35	3.61	0.89	0.45	16.13	3.34
3(A/B)		4.5	1.36	0.23	0.20	8.10	0.52

Table 6.21. Analysis of Conic Hill Profile 14 (winter phase).

Horizon	Ca^{++}	Mg^{++}	K^{+}	citric-soluble K	citric-soluble P
2(A_1)	149	342	122	182	137
3(A/B)	120	135	77	151	80

Table 6.22. Comparison of Conic Hill Profile 14 (winter phase) and Conic Hill Profile 14 (summer phase). Value for (summer phase) = 100.

Horizons Compared	Ca^{++}	Mg^{++}	K^{+}	Citric-soluble K	Citric-soluble P
3(A_2) Profile 13	573	287	167	227	630
2(A_1) Profile 14					
3(A_2) Profile 13					
3(A/B) Profile 14	216	74	74	114	98

Table 6.23. Comparison of Equivalent Horizons of Conic Hill Profile 13 (summer phase) and Conic Hill Profile 14 (winter phase). Value for Conic Hill Profile 13 = 100.

storey. They found that Pteridium aquilinum played an important role, particularly in the potassium cycle. For instance although bracken only supplied 22 per cent of the total weight of litter, it accounted for 31 per cent of the litter's potash content. When the leaf leachate source of nutrients was also taken into account the result was similar - bracken was supplying almost one-third of the total potassium returned to the soil by all components of the ecosystem.

It is interesting that the other nutrient which is clearly available in much larger quantities in winter is magnesium, an element which the routine analysis had suggested was in relatively short supply in bracken soils.

Apart from elucidating the potassium problem, this study emphasises the efficiency of nutrient cycling in the bracken ecosystem. It is noteworthy that by early spring there has apparently been sufficient mineralisation of the previous autumn's litter to considerably augment the available nutrient reserves of the soil.

IV. MOBILISATION OF PHOSPHORUS BY PTERIDIUM AQUILINUM

The routine chemical analysis of Kingslaggan and Conic Hill soils has revealed interesting anomalies in the available phosphate levels of bracken soils. It will be recalled that on these sites citric-soluble phosphate levels are markedly higher in the mineral soil under Pteridium aquilinum than in the podsols developed under the other vegetation communities studied. While the contrast in available phosphate levels is apparent to a slight degree in the B horizon, the most dramatic contrasts are found in the C horizons.

It is common to find a slight ~~use~~ rise in available phosphate concentrations from the B to C horizons of podsolised soils and indeed this phenomenon is evident in the podsols described which have developed under heath vegetation. The B horizons of the podsols examined contain no measurable citric-soluble phosphate while in the C horizons small amounts of up to 2 mg/100g of oven-dry soil have been recorded. However in the bracken soils the concentrations of phosphate in the C horizon are on quite a different scale, ranging from 5-16 mg/100g oven-dry soil, values which at the upper end would place them in the 'satisfactory' category for available phosphate for cultivation. This phenomenon of relatively high phosphate values under bracken has been recorded by other workers. Smith and Fenton (1944) while studying the composition of bracken fronds from Boghall Glen, examined the underlying soil and noted that available P_2O_5 levels were very good for that type of acid moorland soil.

These results raise two queries. Why are the bracken soils higher in phosphate and why is it so unevenly distributed within the profile?

Since care has been taken to eliminate site differences other than vegetation from the soil sequences examined, it appears that the contrast in phosphate levels must be a function of vegetational differences. Moreover similarity in total phosphorus contents precludes the possibility that parent material variation can be the controlling factor. Thus the possibility arises that either exudates or decomposition products of the bracken rhizome may be capable of releasing phosphate from inorganic sources in the soil. Inorganic compounds rather than organic ones have been selected as the most likely phosphate source due to the distribution of the nutrient within the profile. The possibility that organically derived phosphate may also be mobilized cannot however be ruled out. Since, as we have already noted, iron and particularly aluminium compounds are the main inorganic form in which phosphates are found in acid Scottish soils, these would appear to be the most likely source of phosphate.

The interesting distribution of phosphate within the profiles also requires explanation. The highest concentrations are found in the C horizons below the level of rhizome penetration in each case, while the A and B horizons in which the rhizomes are concentrated are relatively depleted of phosphate. The most likely explanation is that in those horizons the phosphate is mobilized but is quickly absorbed into the plant. This hypothesis requires that bracken makes reasonably heavy demands on the available phosphate reserves.

Various workers have estimated the phosphorus content of both rhizomes and fronds of Pteridium aquilinum, with broadly similar results. For instance Ferguson and Armitage (1944) estimated that fronds contain 0.13 - 1 per cent P_2O_5 calculated on a dry matter basis, while the equivalent value given by Moon and Pal (1949) is 0.3 - 0.89 per cent. This compares with a P_2O_5 content of the edible parts of Calluna vulgaris of 0.23 - 0.5 per cent dry matter according to Thomas et alia (1945), while the same workers found that pasture grasses from plots at Cockle Park contained 0.5 - 1.14 per cent P_2O_5 (on dry-matter basis) according to the fertilizer treatment, the lowest value of 0.5 per cent being for an untreated plot. The wide range of phosphate contents given for bracken is due to seasonal variation, frond samples for analysis having been collected at different times of year. The period of maximum phosphate concentration is the early part of the growing season when Moon and Pal (1949) regarded it as comparable to pasture grass. The weight of evidence therefore suggests that Pteridium has a fairly high concentration of phosphate in its fronds at least in early summer,[3] and under vigorous fern growth this would obviously entail a considerable drain on available phosphate reserves in the accessible horizons of the soil.

There are two possible explanations for the maximum phosphate levels occurring in the C horizons - either phosphate mobilised in the upper horizons is leached into the C, or the organic compounds responsible for the mobilisation are leached downward into the C where they react to release phosphate from inorganic sources. Since phosphorus is regarded as relatively immobile in soils, the latter explanation appears the more likely.

It was decided to test this hypothesis that bracken rhizomes may be capable of mobilising phosphate from inorganic sources, by setting up a leaching experiment in the laboratory (see Mitchell, 1973).

Design of leaching experiment

The action of *Pteridium aquilinum* on inorganic phosphorus compounds was compared with that of deionised water, roots of *Calluna vulgaris*, and mor humus from a podsol developed under *Calluna vulgaris* - dominated vegetation. These materials were blended with an inorganic phosphate compound and acid-washed silica sand, to aid leaching, and placed in leaching tubes. Since the organic constituents contained phosphate, allowance was made for this by establishing control columns containing no inorganic source of phosphorus.

A total of eight leaching columns were set up with the following contents:

Column 1	14.353g air-dried ground rhizomes of <u>Pteridium aquilinum</u> blended with 5.272g ground mineral phosphate and an approximately equal volume of sand.
Control Column 1	10.348g air-dried ground rhizomes of <u>Pteridium aquilinum</u> blended with sand
Column 2	10.184g ground mineral phosphate plus sand
Column 3	8.163g air-dried mor humus blended with 4.184g ground mineral phosphate plus sand
Control Column 3	5.017g air-dried mor humus blended with sand
Column 4	6.67g air-dried ground roots of <u>Calluna vulgaris</u> blended with 4.601g ground mineral phosphate plus sand
Control Column 4	6.919g air-dried ground roots of <u>Calluna vulgaris</u> plus sand
Column 5	6.547g air-dried ground rhizomes of <u>Pteridium aquilinum</u> blended with 9.296g air-dried soil from C horizon of Sourhope Profile 3, plus sand

In each case these columns were leached for six days with 250 ml deionised water in a cold room at 3°C and the leachate collected.

Two 10 ml aliquots were taken from each leachate. The first was filtered through Whatman No.1 Filter paper to remove any solid phosphate which might have leached from the tubes, and the filtrate tested for phosphorus using King's (1932) molybdenum blue method in perchloric acid 60% W/V system. The second aliquot was also filtered, treated with 15 ml perchloric acid 60% W/V, and the solution digested to clarity on a sand bath, thus removing any organic molecules with which phosphorus might be associated. The phosphorus content was then again estimated by King's method.

These measurements gave the amount of phosphate which had leached from the columns but the possibility existed that some of the mobilised phosphate might have been re-adsorbed on the column constituents. To obtain an estimate of this amount, the contents of each column were removed and thoroughly washed through a 0.3 mm sieve to remove the coarser material. The washings were centrifuged and the clear supernatant collected. This supernatant then received exactly the same treatment as the leachate, one aliquot being digested, the other only filtered.

Results of experiment

The results of these experiments are presented in Tables 6.24 and 6.25, Table 6.24 giving the results for the filtered aliquots and Table 6.25 for the filtered and digested samples. The relative results are similar but the digested aliquots gave higher phosphate values.

These results verify that extracts of Pteridium aquilinum rhizomes can mobilize inorganic phosphorus. The result from Column 2, where deionised water alone was used, indicates that the organic material is the only active agent in the other columns. By comparison Calluna vulgaris roots release only a trace of phosphorus and, despite the lower pH of the extractant, the mor humus is much less effective than the rhizomes. In a field situation the mor humus would be even less efficient relative to the bracken since profile morphology would

Sample	pH extractant	Total P content (mg) leachate + washings	P extracted from plant matter (mg) Control Columns	P extracted from inorganic source (mg)	P extracted mg/g inorganic source
C1 (*Pteridium* + g.m.p.)*	5.3	4.69	1.58	3.11	0.59
C2 (g.m.p. alone)	6.0	0	-	0	0
C3 (mor + g.m.p.)	4.2	4.0	2.69	1.31	0.31
C4 (*Calluna* + g.m.p)	5.3	1.4	1.4	0	0
C5 (*Pteridium* + soil)	5.3	1.31	0.72	0.59	0.06

Table 6.24. Results of leaching experiment a) filtered aliquots.

*C - column: g.m.p. - ground mineral phosphate

Sample	pH extractant	Total P content (mg) leachate + washings	P extracted from plant matter (mg) Control Columns	P extracted from inorganic source (mg)	P extracted mg/g inorganic source
C1 (*Pteridium* + g.m.p.)	5.3	5.31	1.29	4.02	0.76
C2 (g.m.p. alone)	6.0	0	-	0	0
C3 (mor + g.m.p.)	4.2	5.78	3.92	1.86	0.44
C4 (*Calluna* + g.m.p)	5.3	2.09	2.00	0.09	0.02
C5 (*Pteridium* + soil)	5.3	1.80	0.59	1.21	0.13

Table 6.25. Results of leaching experiment b) filtered and digested aliquots.

ensure that the mor humus was in contact with relatively little mineral matter compared to the ramifying network of bracken rhizomes. The ability of the rhizomes to extract some phosphorus from the C horizon of the Sourhope soil is particularly interesting, because of its direct relevance to the routine soil analysis. If the results are translated into the terms used in the routine analysis, 13 mg/100g oven-dried soil of available phosphate have been released from the Sourhope soil. This is an indication of the effectiveness of the rhizomes as an extractant where aluminium and iron compounds of phosphate are presumably the chief source, compared to the situation with ground mineral phosphate, less relevant to acid soils, in which calcium compounds are dominant.

This ability of Pteridium to supply itself with phosphate from the mineral reserves of the soil is significant both from the point of view of plant nutrition and pedological processes.

The levels of phosphate concentration in the fern's tissues have been discussed above, most of the evidence suggesting that bracken has a fairly high phosphate content relative to other moorland plants, at least in early summer. The importance of phosphorus to the nutrition of Pteridium has also been demonstrated by W.W. Schwabe (1951, 1953) who investigated the nutritional requirements of both the prothallus and sporophyte phases. He found that phosphorus was the most essential nutrient for spore germination and prothallus development, phosphate deficiency being more detrimental than shortage of either nitrogen or potassium. Of greater relevance to the nutrition of bracken stands in Scotland is his observation that phosphate deficiency has also serious effects on sporophyte vigour. The total dry weight of the plant, leaf area per plant, and size of leaf are severely reduced by phosphate deficiency. He concluded that phosphorus is as vital to vigorous sporophyte growth as nitrogen, although plants could survive for at least one growing season in a phosphate-starved environment. It is also at least, if not more, essential than potash.

This evidence suggests that the ability of bracken to mobilise phosphate may well be crucial to the maintenance of vigorous stands on phosphate-deficient sites.

The question of phosphate availability has also fascinating implications from the point of view of pedological processes. Coulson, Davies, and Lewis (1960), in their study of polyphenols in plant, humus and soil, found that plants on sites with mor humus formation had a higher and more diverse content of simple polyphenols than plants from mull-forming sites. These simple polyphenols were shown to be efficient tanning agents of protein, a process which Handley (1954) had suggested was responsible for the resistance to decomposition of protein on mor sites. In a later study Coulson et alia (1964) showed that plants cultivated in a medium deficient in nitrogen and phosphorus had a high content of simple polyphenols. They concluded that soils deficient in nitrogen and phosphate produce plants with high levels of simple polyphenols in their leaves. These polyphenols then react, in the prevailing acid conditions, with plant protein to form complexes resistant to decomposition, thus encouraging mor humus formation. These simple polyphenols have also been shown by Bloomfield (1957) to be effective agents in the reduction and complexing of Fe^{+++} ions, thus contributing to eluviation of iron and podsolisation of the soil.

Thus nitrogen and phosphate deficiency, mor humus formation, and podsolisation are closely related phenomena.

Given the causal relationship of these phenomena, the mobilisation of phosphate by Pteridium aquilinum suggests a possible mechanism for the retardation and reversal of the podsolisation process under bracken. It may be that bracken reduces the tendency to iron mobilisation by activating the phosphate reserves of the soil thus inhibiting the development of the simple polyphenols.

Obviously substantiation of this hypothesis would require biochemical investigations into the quantity and type of polyphenols found in Pteridium fronds. However one pointer is offered by Coulson et alia (1964) who applied polyphenols extracted from bracken to gelatin. In the case of other plants from mor sites this treatment resulted in gelatin precipitation due to the formation of gelatin-tannin complexes, but the bracken extracts failed to precipitate the gelatin. Instead a colloidal suspension was formed. The writers offered no comment on this phenomenon, but it suggests that bracken extracts are poor tanning agents and therefore unlikely to contribute to mor formation.

V. IRON PAN SOLUTION

In Chapter 5 field evidence of the modification of iron pans by Pteridium aquilinum was presented (see pages 161-169). The ability of rhizomes to disintegrate iron pans was attributed to the mechanical pressure of the shoots, but the possibility that chemical reaction may also be involved cannot be excluded. To investigate the possibility that exudates or decomposition products of the rhizomes may contribute to pan disintegration by solution, a leaching experiment was designed in the laboratory.

Experiment Design

Particles of iron pan from a Conic Hill podsol were mixed with ground air-dried Pteridium aquilinum rhizomes and placed in a leaching tube. A control column containing only rhizomes was also established to allow for the iron derived from the organic matter, together with a column containing only iron pan fragments.

The contents of the columns were as follows:

Column 1	2.861g iron pan particles plus 1.178g air-dried ground rhizomes of Pteridium aquilinum.
Control Column 1	1.257g air-dried ground rhizomes of Pteridium aquilinum.
Column 2	2.867g iron pan particles

These columns were leached with 250 ml deionised water over a period of 10 weeks in a cold room at 3°C and the leachate collected. At the end of this period a microbial growth had developed on Column 1. This was removed by treatment with 10 ml H_2O_2 and boiling to clarity.

One 10 ml aliquot was then taken from each leachate and filtered through Whatman No.1 Filter paper. The filtrate was tested for total iron content by the Shapiro and Brannoch method (see Hounslow and Moore, 1966) of reducing the ferrous iron with 0.1% orthophenanthroline solution buffered at pH 4.5, and measuring the absorbance of the orange ferrous orthophenanthroline complex at 506 mμ.

Results of experiment

The results of this experiment are presented in Table 6.26. While the deionised water alone had no effect on the iron pan fragments, the bracken rhizomes were quite effective in dissolving out iron. In a field situation this chemical action of the rhizomes would be continued over a period of years and would obviously be a powerful agent in the disintegration of the iron pan. Thus iron pan modification by bracken, while it may be partly mechanically controlled, has been shown to have an element of chemical action also.

This ability of a plant extract to mobilise iron is not however unique to Pteridium aquilinum. Indeed it could be argued that this characteristic would favour podsolisation, as has been discussed above with reference to the effect of simple polyphenols in the reduction and complexing of Fe^{+++} ions (see pages 273-274). Bloomfield (1953, 1954) however showed that the ability of plant extracts to mobilise iron is not necessarily closely correlated with the species' association with podsolised soils. In a study of the effect of leaf extracts from twenty to thirty species, he found all were capable of iron mobilisation yet some of these species were podsol-forming, others, such as ash, were not. The ability of Pteridium to dissolve iron pans may result from its rooting characteristics placing the rhizome in close contact with the iron pan, rather than from any unusual chemical property.

Sample	pH extractant	Total Fe content (mg) leachate	Fe extracted from plant matter (mg) Control Columns	Fe extracted from iron pan (mg)	Fe extracted (mg/g) iron pan
C1*(*Pteridium* + iron pan)	6.7	9.38	1.17	8.21	2.87
C2 (iron pan alone)	6.25	0	-	0	0

Table 6.26. Results of iron pan solution experiment.

*C - column.

VI. CONCLUSIONS

The laboratory investigations, the results of which have been described in this chapter, have confirmed that Pteridium aquilinum does indeed affect the chemical properties of the soil in which it grows. Although bracken soils have been shown to be acid and nutrient-deficient, consistent and significant differences in the levels of certain nutrients, namely calcium, potassium, and phosphate have been found between bracken and other dry moorland soils. Although the mechanics of the action of the fern have not been examined in this project, it seems likely that the relatively high levels of available calcium and, in winter, of available potash reflect the relative efficiency of bracken in cycling these nutrients, the extraction of nutrients from the mineral soil during the growing season and their return through the fairly rapid mineralisation of the litter ensuring that these elements are kept in circulation within the ecosystem. In contrast under heath vegetation the shallow rooting plants extract nutrients from the decaying mor humus layer, while the underlying mineral horizons become highly leached.

In the case of phosphate, the action of Pteridium has been shown to be more complex as the relatively high levels of available phosphate apparently originate, not only from organic matter mineralisation, but by extraction by the rhizomes directly from mineral sources in the soil, an ability which Calluna vulgaris roots at least have been shown to lack.

This question of the nutrient status of bracken soils is significant both from the vegetational and pedological points of view.

It is interesting to reflect on the effects on associated species of the chemical conditions engendered in the soil by Pteridium growth. This question can be examined in relation to the nutritional requirements of the subordinate species, although it must be borne in mind that in a semi-natural ecosystem the relative abundance of species is influenced at least as much by competition as by range of tolerance to edaphic or other environmental parameters.

It is clear that any herb or grass species which is to flourish in association with bracken must be tolerant of extremely acid conditions in the topsoil. In fact the common associates of bracken, Agrostis species, Festuca ovina, Anthoxanthum odoratum, and Deschampsia flexuosa are all tolerant of acid conditions, Deschampsia flexuosa in particular being strongly calcifuge (see Rogers and King, 1972; Grime and Hodgson in Rorison, 1969). A more complex issue is the supply of individual nutrients to the other plants in a bracken community. While the fern is efficient in keeping certain elements in circulation, its rather heavy demands on these during the growing season may result in other plants experiencing shortage. As far as the nutrition of the understorey is concerned, seasonal availability of nutrients must be as important as absolute quantity. For instance available potash and to a lesser extent magnesium have been shown to be in as short supply in summer in bracken soils as in nearby podsols. It may be significant that Agrostis tenuis and Anthoxanthum odoratum have been shown by fertilizer trial plots at Rothamsted to be tolerant of potassium deficiency (see Thurston in Rorison, 1969). On the other hand, these trials show that Anthoxanthum responds to phosphate which may be significant in the present context.

The pedological significance of Pteridium growth has been indicated at various stages throughout this chapter and the situation can now be summarized. The soils associated with bracken have been shown to display at least the simpler chemical, as well as the morphological, attributes of acid brown forest soils of low base status. It has been shown that the penetration of rhizomes into the mineral horizons of a podsol modifies its podsolised characteristics by replacing the mor humus and A_2 horizons with a topsoil in which humus and organic matter are mixed and by disintegrating iron pans. Nevertheless it is possible that some degree of podsolisation exists in bracken soils, a fact which could only be established by the investigation of more specialised indices of podsolisation, such as sesquioxide ratios or the ratios of iron extracted by different techniques. Loveland and Bullock (1976) have shown that the ratios of pyrophosphate-extractable iron (Fep) and oxalate-extractable iron (Feo) to dithionite-extractable iron (Fed) are useful indices in differentiating between brown podzolic soils and brown earths. In this context the work of Jarvis (1974; Jarvis and Duncan, 1976) is noteworthy. Working on soils in the Conic Hill area he found that the leaching of sesquioxides, as expressed in the vertical distribution of iron and aluminium in the profile, and hence the stage of podsolisation was distinctly more advanced under heather than under bracken.

The present study has suggested several possible mechanisms by which Pteridium may retard the podsolisation process.

(1) The way in which bracken rhizomes decay through a large volume of soil must be at least partly responsible for the mixing of organic and mineral constituents in the topsoil. It is probable however that more complex biochemical

and biological differences exist between Pteridium litter and that of mor-forming species.

(2) The experimental evidence of iron solution by rhizome extracts explains the observed disintegration of iron pans by bracken.

(3) Pteridium aquilinum has been shown to extract phosphate from inorganic compounds. The relationship between soil phosphate deficiency and the production of the type of polyphenols associated with mor humus development and iron and aluminium mobilisation suggests that this may be a significant factor in the limitation of podsolisation. The demonstrated ability of bracken extracts to mobilise phosphate from the Sourhope soil may not be unrelated to its power of dissolving iron since the inorganic phosphate of acid soils is often associated with iron and aluminium compounds. Obviously the chemical interaction of bracken extracts and inorganic constituents of the soil is extremely complex and the present study can only attempt to identify a few attributes of the fern which may be relevant to its observed relationship to the podsolisation process in soils.

Section Notes

1. For strict comparison it would have been preferable to analyse the heather soil in winter also, although the evergreen habit of its vegetation would suggest limited seasonal variation. Time did not permit this extension of the work.

2. 12-20 mg/100g oven-dry soil is regarded as the satisfactory range for agricultural soils.

3. It should be noted that Hunter (1953) disagrees with this, regarding the phosphorus content of bracken as comparable to other moorland plants. Nevertheless given the total mass of plant matter involved, even a fairly low concentration in the tissues would entail a considerable absolute mass of phosphorus.

CHAPTER 7

CONCLUSIONS

This research project began with the hypothesis that the association of Pteridium aquilinum with a particular moorland ecosystem might reflect the modifying influence of bracken on the ground vegetation and soils, as much as the tendency for the fern to invade established Agrostis-Festuca-brown forest soil ecosystems. Pteridium might be regarded as an active agent in the development of the ecosystem rather than an incidental and agriculturally undesirable intruder. The testing of this hypothesis involved two main lines of enquiry:

(1) The influence of the dominant Pteridium aquilinum on the vigour and species composition of the associated herb layer was investigated. While earlier writers such as Poel (1949), Watt (1947), and Nicholson and Robertson (1958), have briefly described variations in the ground vegetation with varying bracken density, no previous attempt has been made to quantify the relevant attributes of the herb stratum and to relate these to a measurable index of bracken dominance

(2) Variations in the morphological and selected chemical attributes of the soil were related to the presence and influence of Pteridium aquilinum.

I. SUMMARY OF RESULTS

(1) The main relevant ground vegetation species have been classified on the basis of their tolerance of competition from Pteridium aquilinum. While specific reaction has been found to vary to some extent from one environment to another, the main points of the classifications are valid for all the sites examined.

The 'intolerant' category contains the shrub species Calluna vulgaris and Vaccinium myrtillus and the grass Nardus stricta. Low levels of Pteridium dominance (Index of Bracken Dominance = 80 or less) are usually sufficient to severely restrict or eliminate these species. The grasses Agrostis tenuis, Anthoxanthum odoratum, and Festuca ovina and the herb Galium hercynicum belong to the category of 'tolerant' species. These species are only adversely affected by relatively high levels of bracken dominance (Index of Bracken Dominance = 160 or more) and are usually more prominent in the Pteridium-dominated community than in other nearly freely-drained plant communities. A few relatively minor species such as Potentilla erecta and Deschampsia flexuosa have been classified as 'indifferent'.

The association of Pteridium aquilinum with Agrostis-Festuca grassland therefore reflects the tolerance of these species, as compared particularly to the heath shrubs to bracken competition. Pteridium selects its associates rather than merely finding congenial the environmental conditions prevalent in pre-existing Agrostis-Festuca grassland.

(2) Within the 'tolerant' group of species varying degrees of tolerance to Pteridium competition have been demonstrated. Agrostis tenuis, Galium hercynicum and Deschampsia flexuosa are consistently more tolerant and therefore persist to

higher levels of Pteridium dominance than Festuca ovina or Anthoxanthum odoratum. At the highest levels of bracken (Index of Bracken Dominance = 200 or more) all species are severely curtailed. Hence a continuum of species assemblages from Pteridium - Agrostis - Festuca through Pteridium - Agrostis - (Galium) to pure Pteridium can often be identified.

(3) While individual highly tolerant species may survive to levels of bracken dominance exceeding 200, the vigour of the ground vegetation, as measured in cover and biomass, is severely curtailed before this stage. When the Index of Bracken Dominance exceeds 80-100 bracken competition appears to be responsible for a progressive reduction in the cover and biomass of the herb layer.

(4) The significance of Pteridium aquilinum as a soil-forming factor has been established, a greater similarity in morphological and chemical characteristics having been revealed between bracken soils from different parts of the country than between heath and bracken soils developed under uniform site conditions only a few metres apart.

Considerable evidence has been produced of the association of Pteridium with brown forest soils of low base status. These 'bracken brown earths' are characterised by loose litter, thin humic horizons usually of the moder type, mixed organic and mineral surface horizons with a gradual decrease in organic matter content and nutrient levels with depth. Horizons merge into each other and morphological and chemical data reveal little evidence of the development of nutrient or iron-depleted A_2 horizons with concomitant illuvial B horizons. This is in marked contrast to the clear evidence of podsolisation found under other nearby vegetation types. The only exception to this was found at Conic Hill where podsolic features were found beneath extremely shallow rooted bracken.

The physical characteristics of bracken soils are also distinctive - friable, porous, and well-fissured the bracken soils are internally well-drained so that evidence of gleying is absent from the surface horizons, in contrast to the contribution which gleying appears to make to the development of nearby peaty podsols.

(5) Evidence has been presented which suggests that Pteridium, far from merely invading pre-existing brown forest soils, is capable of modifying at least some of the podsolic characteristics of soils which it colonises. Modified and degraded podsols have been described from ecotone and bracken margin situations, field and experimental evidence of the disintegration of iron pans by rhizomes has been presented, and the correlation of podsolic horizon modification with depth of rhizome penetration has been shown.

(6) The nutrient status of bracken soils has been described - they are extremely acid and nutrient-deficient. On the other hand they tend to have higher nutrient levels, particularly exchangeable calcium and available phosphate, than the podsolised soils with which they have been compared. Experimental evidence has suggested that the anomalously high available phosphate levels of the C horizons of bracken soils is at least partly due to the ability of Pteridium to mobilise phosphate from inorganic sources, the possible relevance of this to the curtailment of podsolisation having been discussed.

The more even distribution of nutrients within bracken soils than in their more podsolised neighbours, and the marked seasonal variation in nutrient levels, especially potash, suggest more effective cycling of nutrients through the ecosystem by the deep-rooted fern than occurs under shallow-rooted heath vegetation.

II. LIMITATIONS OF RESEARCH AND POSSIBLE FURTHER LINES OF DEVELOPMENT

(1) In the case of both vegetation and soil work, inferences concerning the dynamic aspects of *Pteridium's* influence have been drawn from research carried out at one point in time. For instance it has been implied that the sequence in species composition of ground vegetation and soil characteristics found across bracken-heath ecotones are indicative of the changes which might be anticipated when *Pteridium* invades a heath moorland-podsol ecosystem. To test the validity of such conclusions the modifications produced by colonising bracken should ideally be studied over a period of years. Alternatively in the case of vegetation modification a field experiment could be designed in which changes in the character of the ground vegetation consequent on the artificial removal of bracken fronds could be monitored.

(2) A point of detail which might reward more protracted research is the relationship between *Pteridium aquilinum* and *Nardus stricta* on the east side of the country. Apparently more tolerant of *Pteridium* competition than in the west, a more detailed study of the evolution of the type of *Pteridium-Nardus* community found at Sourhope could be instructive.

(3) On the whole this research effort has been descriptive and only limited explanation of the phenomena has been attempted. In many cases the examination of the mechanisms of *Pteridium's* influence would require the application of

other types of research techniques and skills.

For instance no attempt has been made to examine the mechanism by which Pteridium influences the ground vegetation by assessing the relative importance of such factors as shading, modification of moisture conditions, exposure, and edaphic conditions. However, since the height of fronds appears to be as significant as their density, it is probable that the conditions imposed by the dead litter are as important as those produced by the growing fronds. Further the importance of extraneous environmental parameters should probably not be overemphasised since interspecific competition between species of ground vegetation may be equally important. For example the vigour of species such as Agrostis tenuis in the Pteridium environment may well result from the elimination of powerful competitors such as Calluna vulgaris rather than any particular preference for the conditions imposed by Pteridium.

(4) In examining the relationship between Pteridium growth and podsolisation simple morphological and chemical indicators of podsolisation have been employed. It is possible that podsolisation has progressed further in these 'bracken brown earths' than the research techniques used here have revealed. As noted above (see page 280) some investigation of sesquioxide ratios in bracken soils has been attempted (Jarvis, 1974; Jarvis and Duncan, 1976) and further research along these lines might be rewarding.

(5) The question of the seasonal distribution of nutrients in bracken soils is interesting and has only been touched on here. A comparison of the seasonal distribution of nutrients between the bracken ecosystem and other moorland ecosystems would be most worthwhile.

(6) There is scope for further examination of the modifying influence of *Pteridium* on the chemical characteristics of the soil, and particularly its relationship to the podsolisation process, by the application of biological and biochemical research. Investigation of the biological and biochemical characteristics of bracken litter and particularly the quantity and nature of the polyphenols in *Pteridium* is necessary to test the hypothesis which has been offered that *Pteridium's* ability to mobilise phosphate may inhibit podsolisation by affecting the type of polyphenols produced in the plant.

III. PRACTICAL IMPLICATIONS

Bracken infestation has for many years been regarded as one of the main obstacles to raising the productivity of rough grazings in this country. *Pteridium* has been virtually universally condemned in agricultural circles because of its toxic properties, particularly for cattle, and because it depresses the yield of the associated sward. *Agrostis-Festuca* grassland is generally regarded as the most agriculturally-desirable of the common semi-natural plant communities on our rough grazings, the grazing potential of which has been seriously restricted by its association with *Pteridium*. The eradication of bracken has therefore been advocated in hill land improvement schemes, numerous mechanical and chemical eradication techniques having been tried. The majority of these have met with limited application and success due to the economic and technical difficulties encountered.

(i) Probably the most technically successful method involves the ploughing up of the affected pasture, fertiliser application, and reseeding with improved species and strains of grasses. The drawbacks to this are obviously the expense involved, the problem of access with machinery, and the question of permanently maintaining the improved pasture which is likely to require regular fertiliser inputs. For these reasons only a small percentage of bracken-infested pasture involved has been regarded as suitable for this treatment.

(2) Less drastic mechanical treatments such as repeated cutting and bruising have been widely used in the past. While these control bracken growth they tend to have fallen into disrepute because of the high labour, and therefore cost, input.

(3) Numerous herbicides have been tested such as MCPA, aminotriazole, Picloram, and 4-CPA. These have suffered from drawbacks such as inconsistency of performance, harmful effects on desirable plant species, and relatively fast _Pteridium_ regrowth. The latest chemical to join this armoury is asulam which has produced quite promising results. Martin, Williams, and Raymond (1972) working in west Scotland have found 98 per cent reduction in _Pteridium_ fronds in the first year after spraying, with 81-96 per cent reduction in the second season. The results of McKelvie and Scragg (1973) from north Scotland, admittedly on limited data, are somewhat less encouraging, 90 per cent control in the first season being reduced to 70 per cent in the second year and 50 per cent in the third.

However while the problem of re-establishment of _Pteridium_ over a number of years may not yet be overcome, asulam does have a number of advantages compared to other herbicides. It has proved consistently effective over a wide range of conditions, it does not produce persistent residues, and most of the useful associated species are apparently little affected although _Agrostis tenuis_ appears to be an exception (Soper, 1972). In addition two other recent developments may encourage the more widespread adoption of bracken control by asulam than has occurred with other methods. The first is the development of aerial application techniques which help to resolve the problems of labour inputs and accessibility. Second there is some evidence that the long-term economic prospects for hill farming, especially the sheep industry, are better than they have been for many years. In a situation of higher profitability hill farmers may well be prepared to invest in hill land improvement even if this involves fairly regular applications of a herbicide.

There therefore now exists a situation in which technical and economic conditions may lead to more widespread bracken eradication schemes. The results of this research project suggest that this may have the following ecological implications:

(i) It has been demonstrated that at high levels of bracken dominance the effect on the cover and biomass of the ground vegetation is very severe. Where the vigour of Pteridium has been sufficient to obliterate the grass sward, the land is obviously agriculturally useless and bracken eradication and reseeding is the only way to remedy the situation. Marked and consistent suppression of the biomass of the grass sward has been shown to occur where the Index of Bracken Dominance exceeds approximately 120. To put this into more generally understandable terms, this level would coincide with an average frond height of 100 cm and a density of 30 fronds per square meter. In taller bracken a lower density of fronds would produce a similar effect.

On the other hand when the Index of Bracken Dominance falls below approximately 80 (for example fronds 100 cm tall at a density of less than 20 per square metre) the cover of ground vegetation appears to be unaffected (see Table 4.2, page 83), and the biomass varies widely (see Figure 4.3, page 85). The biomass shows little correlation with the level of bracken dominance and presumably other factors are decisive in determining the productivity of the ground vegetation.

On this evidence there is no justification in embarking on a bracken eradication programme where the frond cover is light in the expectation that it will enhance the productivity of the existing ground vegetation.

(2) The active role of Pteridium aquilinum in at least maintaining, and probably developing, the desirable Agrostis-Festuca brown forest soil ecosystem has been demonstrated. Even at low levels of bracken (below the Index of Bracken Dominance level of 80 discussed above) useful grass species tend to have taken over from the less desirable heath vegetation (see Table 4.3, page 116, and Figure 4.16, page 119). The underlying rationale of many bracken eradication schemes appears to be that the fern can be eradicated without any alteration occurring in the species composition of the herb layer or, in the longer term, in the soil characteristics. The evidence of this thesis suggests that this is untenable. There is every reason to conclude that the removal of competition from the dominant Pteridium, without the application of other treatment, will result in a gradual alteration in the balance of species in the herb layer. In particular in situations where strongly competitive species such as Calluna vulgaris, Vaccinium myrtillus and Nardus stricta are available to colonise, the removal of the Pteridium is likely to tip the competitive balance very much in their favour. The evolution of a heath shrub vegetation is likely to produce

concomitant soil changes which, according to the evidence of this thesis, will be in the direction of long-term reduction in soil fertility.

It must be concluded that bracken eradication should not be regarded as a desirable end in itself in every ecological situation. Each case must be examined on its own merits. Clearly the replacement of heavy bracken growth by a pastorally useful sward is agriculturally desirable if economically feasible. The case for removing a light frond cover needs more careful evaluation. At the lowest levels of bracken it seems pointless unless it is to be replaced by a sown improved pasture sward. In intermediate cases the benefits accruing from eradication must be weighed against the costs of maintaining the new system which may well be influenced by the character of the surrounding vegetation. It must be accepted that a management programme involving regular financial input, possibly in the form of fencing and fertiliser input, may well be necessary if the *Agrostis-Festuca*-brown forest soil ecosystem is to be maintained without its bracken component.

APPENDIX A

NODUM TABLES

TABLE I. KINGSLAGGAN HEATH NODUM

Species	Q1* (S1)	Q2 (S1)	Q4 (S1)	Q9 (S1)	Q12 (S1)	Q21 (S2)	Q22 (S2)	Q25 (S3)	Q29 (S3)	Q1 (S4)	Q9 (S4)	Q1 (S5)	Q4 (S5)	Q7 (S5)	Q11 (S5)	Q4 (S6)	Q10 (S6)	Q2 (S7)	Q4 (S8)	Q1 (S9)
Pteridium aquilinum	-	-	-	-	+	-	-	-	-	-	3	-	-	-	-	5	4	4	-	+
Agrostis tenuis	-	-	+	2	2	1	-	2	-	3	3	2	1	-	-	1	3	2	1	4
Anthoxanthum odoratum	-	-	-	-	-	-	-	-	-	+	1	-	-	-	-	-	2	-	-	2
Deschampsia flexuosa	1	3	3	1	-	-	2	-	-	3	1	-	-	-	-	-	-	-	-	-
Festuca ovina	-	-	1	2	1	-	-	2	-	1	4	3	2	-	1	2	4	2	2	5
Molinia caerulea	5	3	5	5	1	5	5	3	6	-	-	-	4	4	6	-	-	-	-	-
<u>Nardus stricta</u>	4	7	5	6	8	6	2	5	4	4	4	4	4	5	4	-	-	-	4	4
Sieglingia decumbens	-	+	-	-	1	-	-	-	-	-	3	-	-	-	-	-	1	1	-	1
Carex binervis	-	1	-	1	2	-	+	2	1	+	3	2	1	-	1	-	3	1	-	3
Carex nigra	-	-	-	-	-	2	-	-	-	-	2	2	-	-	1	-	-	-	-	-
Carex Panicea	-	+	-	-	-	-	-	1	+	-	-	-	-	-	+	-	-	-	1	-
Carex pilulifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Juncus squarrosus	-	-	-	2	+	1	-	-	-	-	-	-	-	-	1	-	-	-	+	-

TABLE 1 - CONTD.

Species	Q1* (S1)	Q2 (S1)	Q4 (S1)	Q9 (S1)	Q12 (S1)	Q21 (S2)	Q22 (S3)	Q25 (S3)	Q29 (S3)	Q1 (S4)	Q9 (S4)	Q1 (S5)	Q4 (S5)	Q7 (S5)	Q11 (S5)	Q4 (S6)	Q10 (S6)	Q2 (S7)	Q4 (S8)	Q1 (S9)
Scirpus caespitosus	4	4	3	3	2	4	-	3	3	-	-	5	5	5	5	-	-	2	4	2
<u>Calluna vulgaris</u>	6	4	5	6	5	5	9	8	7	9	5	8	8	7	7	10	8	10	9	7
Erica cinerea	-	-	-	-	2	+	1	2	3	3	3	1	1	-	3	3	4	1	+	3
Erica tetralix	1	1	-	1	-	1	2	-	+	-	-	-	+	3	2	-	-	-	2	-
Galium hercynicum	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	1	-	-	-
Polygala serpyllifolia	-	-	-	-	+	+	-	-	-	-	1	-	-	-	+	-	3	-	-	+
<u>Potentilla erecta</u>	2	2	1	2	2	2	2	2	2	1	5	2	1	2	2	2	-	2	1	3
<u>Vaccinium myrtillus</u>	3	2	2	2	2	2	1	2	2	2	2	4	3	2	2	-	2	-	-	-
Pleurozium schreberi	-	-	-	-	-	+	-	+	-	+	-	-	-	-	-	+	+	-	+	-
Polytrichum commune	-	-	-	-	-	-	-	-	+	-	+	+	-	-	+	-	-	-	-	-

In all nodum tables: *Q - quadrat number
(S) - <u>Pteridium</u> stand number

Constant species underlined.

For key to tables see Table 3.2, page 68.

TABLE 2. KINGSLAGGAN PTERIDIUM AQUILINUM-AGROSTIS TENUIS-FESTUCA OVINA NODUM

Species	Q3 (S1)	Q5 (S1)	Q6 (S1)	Q7 (S1)	Q8 (S1)	Q10 (S1)	Q11 (S1)	Q14 (S2)	Q15 (S2)	Q16 (S2)	Q17 (S2)	Q20 (S2)	Q23 (S3)	Q24 (S3)	Q27 (S3)	Q30 (S3)	Q3 (S4)	Q5 (S4)	Q6 (S4)	Q10 (S4)
Pteridium aquilinum	8	3	8	9	8	9	7	8	9	8	7	8	9	9	9	9	8	8	8	8
Agrostis tenuis													6	8	5	7	4	1	7	7
Anthoxanthum odoratum	9	9	9	8	9	9	9	9	9	8	10	9	4	3	3	2	1	-	1	2
Festuca ovina													6	5	6	4	8		7	
Deschampsia flexuosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	8	3	7
Holcus lanatus	-	-	-	-	-	-	-	-	-	-	1	-	2	1	-	3	-	-	-	-
Nardus stricta	2	+	1	-	1	-	+	-	2	-	-	-	-	-	-	-	1	-	-	-
Poa pratensis	-	-	-	-	-	-	-	-	-	-	-	+	+	1	-	+	-	-	-	-
Sieglingia decumbens	3	3	3	+	3	-	3	2	1	2	-	2	-	-	-	-	3	3	1	+
Carex binervis	2	1	-	1	-	+	-	+	1	+	1	+	-	-	-	-	2	2	2	1
Carex pilulifera	+	-	-	-	-	-	-	-	-	+	1	-	-	-	-	-	-	-	-	-

TABLE 2 CONTD.

Species	Q2 (S5)	Q3 (S5)	Q5 (S5)	Q6 (S5)	Q8 (S5)	Q2 (S6)	Q5 (S6)	Q6 (S6)	Q8 (S6)	Q9 (S6)	Q1 (S7)	Q3 (S7)	Q2 (S8)
Pteridium aquilinum	7	9	7	9	9	8	9	9	9	8	9	9	9
Agrostis tenuis	5	7	7	4	7	7	7	7	7	7	7	6	8
Anthoxanthum odoratum	5	5	4	4	4	5	4	4	3	4	3	3	3
Festuca ovina	6	7	7	7	7	7	8	7	7	7	6	7	-
Deschampsia flexuosa	-	-	-	-	-	-	-	-	-	-	-	-	-
Holcus lanatus	-	-	-	-	3	-	-	-	2	-	-	-	-
Nardus stricta	-	-	-	3	-	-	-	-	-	-	-	-	-
Poa pratensis	-	1	-	-	-	-	-	-	-	-	-	-	4
Sieglingia decumbens	+	-	+	-	-	+	-	-	+	+	1	1	-
Carex binervis	-	-	1	2	-	-	-	-	-	-	-	1	-
Carex pilulifera	-	-	-	-	+	-	-	-	3	3	-	-	-

TABLE 2 CONTD.

Species	Q3 (S1)	Q5 (S1)	Q6 (S1)	Q7 (S1)	Q8 (S1)	Q10 (S1)	Q11 (S1)	Q14 (S2)	Q15 (S2)	Q16 (S2)	Q17 (S2)	Q20 (S2)	Q23 (S3)	Q24 (S3)	Q27 (S3)	Q30 (S3)	Q3 (S4)	Q5 (S4)	Q6 (S4)	Q10 (S4)
Luzula species	+	+	-	+	-	+	2	+	+	+	+	+	-	+	-	1	1	-	1	1
Achillea millefolium	-	-	-	1	1	-	1	-	-	1	+	-	-	-	-	-	-	-	-	-
<u>Calluna vulgaris</u>	-	4	4	5	+	-	2	2	-	3	1	-	-	-	-	-	-	4	-	-
Erica cinerea	-	2	1	1	+	-	1	-	-	-	-	-	-	-	-	-	1	1	3	-
<u>Galium hercynicum</u>	2	2	1	1	2	2	2	3	3	4	2	2	2	3	5	1	3	3	3	3
Oxalis acetosella	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	3	-	-	-	-
<u>Potentilla erecta</u>	2	3	3	3	3	2	3	3	2	4	2	4	3	+	3	1	3	3	3	2
Rumex acetosella	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Trifolium repens	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	2	-	-	-	-
Vaccinium myrtillus	-	2	+	1	-	-	-	-	-	-	+	1	-	-	-	-	2	2	2	2
Viola ssp.	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Pleurozium schreberi	-	-	-	+	-	-	+	-	-	+	+	-	-	-	-	-	+	-	-	-

TABLE 2 CONTD.

Species	Q2 (S5)	Q3 (S5)	Q5 (S5)	Q6 (S5)	Q8 (S5)	Q2 (S6)	Q5 (S6)	Q6 (S6)	Q8 (S6)	Q9 (S6)	Q1 (S7)	Q3 (S7)	Q2 (S8)
Luzula species	3	1	1	2	+	-	1	2	1	-	-	+	-
Achillea millefolium	-	-	+	-	-	1	-	-	-	2	-	-	-
Calluna vulgaris	3	-	3	4	-	-	-	-	-	1	-	-	-
Erica cinerea	4	-	1	1	-	+	-	-	-	+	-	1	-
<u>Galium hercynicum</u>	4	3	3	6	2	2	2	2	2	2	4	4	3
Oxalis acetosella	-	-	-	-	1	2	-	-	2	1	-	-	-
<u>Potentilla erecta</u>	3	3	3	4	3	2	1	2	2	2	2	2	-
Rumex acetosella	-	2	-	-	1	-	-	-	-	-	-	-	-
Trifolium repens	-	-	-	-	-	-	+	-	3	3	-	-	-
Vaccinium myrtillus	+	-	1	2	-	-	-	-	-	-	1	-	-
Viola ssp.	-	-	-	-	1	2	+	-	+	-	-	-	1
Pleurozium schreberi	-	-	-	+	-	-	-	-	-	-	-	-	-

TABLE 2 CONTD.

Species	Q3 (S8)	Q5 (S8)	Q3 (S9)	Q5 (S9)	Q6 (S9)	Q8 (S9)	Q9 (S9)	Q11 (S9)	Q12 (S9)	Q13 (S9)	Q15 (S9)	Q3 (S10)	Q4 (S10)	Q5 (S10)	Q6 (S10)
Pteridium aquilinum	9	8	9	9	9	9	9	9	9	9	8	9	7	9	9
Agrostis tenuis	8	8	6	7	10	5	8	5	8	8	7	7	8	8	7
Anthoxanthum odoratum	4	3	3	4	-	-	3	2	-	-	4	4	5	4	5
Festuca ovina	4	-	7	6	1	1	5	7	5	-	7	4	4	4	5
Deschampsia flexuosa	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holcus lanatus	-	-	-	-	-	-	-	-	-	-	4	-	4	-	3
Nardus stricta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Poa pratensis	-	-	-	-	-	1	1	+	-	-	1	-	-	1	3
Sieglingia decumbens	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex binervis	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Carex pilulifera	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

TABLE 2 CONTD.

Species	Q3 (S8)	Q5 (S8)	Q3 (S9)	Q5 (S9)	Q6 (S9)	Q8 (S9)	Q9 (S9)	Q11 (S9)	Q12 (S9)	Q13 (S9)	Q15 (S9)	Q3 (S10)	Q4 (S10)	Q5 (S10)	Q6 (S10)
Luzula species	-	-	1	1	-	+	+	1	1	1	-	1	+	-	2
Achillea millefolium	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Calluna vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Erica cinerea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Galium hercynicum</u>	3	5	4	2	2	3	2	3	2	1	1	3	3	3	3
Oxalis acetosella	-	-	-	1	-	4	4	-	1	-	2	-	-	-	-
<u>Potentilla erecta</u>	2	1	2	2	1	+	1	2	2	1	1	1	1	+	1
Rumex acetosella	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Trifolium repens	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Vaccinium myrtillus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Viola species	-	1	-	-	-	1	-	-	-	3	1	+	-	-	-
Pleurozium schreberi	+	-	+	-	-	-	-	3	-	-	-	-	-	-	-

TABLE 3 KINGSLAGGAN PTERIDIUM AQUILINUM-AGROSTIS TENUIS NODUM

Species	Q19 (S2)	Q28 (S3)	Q4 (S4)	Q7 (S4)	Q8 (S4)	Q9 (S5)	Q1 (S6)	Q4 (S7)	Q1 (S8)	Q6 (S8)	Q4 (S9)	Q7 (S9)	Q14 (S9)	Q16 (S9)	Q1 (S10)	Q2 (S10)
Pteridium aquilinum	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Agrostis tenuis	6	7	6	5	7	6	8	7	7	5	1	7	7	7	5	5
Anthoxanthum odoratum	5	3	4	4	4	3	4	4	-	2	-	-	3	1	3	4
Deschampsia flexuosa	-	-	+	+	3	-	-	6	-	-	-	-	-	-	-	-
Festuca ovina	6	6	6	6	-	6	6	-	-	-	-	3	5	-	3	1
Holcus lanatus	2	-	-	-	-	4	-	-	-	-	-	-	4	3	5	4
Poa pratensis	-	1	-	-	-	-	-	-	-	-	-	-	-	-	4	1
Sieglingia decumbens	-	-	-	3	-	-	-	1	-	-	-	-	-	-	-	-
Carex binervis	-	-	-	2	-	-	1	-	1	1	1	-	3	-	-	-
Luzula species	1	+	-	2	-	-	1	-	-	-	+	+	-	-	+	-
Achillea millefolium	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-

TABLE 3 CONTD.

Species	Q19 (S2)	Q28 (S3)	Q4 (S4)	Q7 (S4)	Q8 (S4)	Q9 (S5)	Q1 (S6)	Q4 (S7)	Q1 (S8)	Q6 (S8)	Q4 (S9)	Q7 (S9)	Q14 (S9)	Q16 (S9)	Q1 (S10)	Q2 (S10)
Calluna vulgaris	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Erica cinerea	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Galium hercynicum	2	3	2	3	2	4	2	3	4	5	1	1	2	3	1	2
Oxalis acetosella	4	3	-	-	-	4	3	-	-	1	-	-	3	-	-	-
Potentilla erecta	2	-	2	2	1	1	2	1	-	-	-	1	1	+	-	-
Rumex acetosella	-	-	-	-	-	2	1	-	-	-	-	-	1	-	1	+
Trifolium repens	3	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-
Vaccinium myrtillus	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Viola species	1	-	-	-	-	-	1	-	+	+	-	-	-	-	-	-
Brachythecium velutinum	-	3	-	-	+	+	+	-	-	-	3	+	+	3	3	3
Polytrichum juniperinum	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-

TABLE 4 CONIC HILL HEATH NODUM

Species	Q1 (S1)	Q11 (S1)	Q13 (S1)	Q1 (S2)	Q5 (S2)	Q4 (S3)	Q12 (S3)	Q14 (S3)	Q17 (S3)	Q8 (S4)	Q1 (S6)	Q9 (S6)	Q5 (S7)	Q10 (S7)	Q12 (S7)	Q4 (S8)
Pteridium aquilinum	3	4	3	-	-	4	-	-	-	4	-	4	+	5	3	-
Agrostis tenuis	-	2	-	-	-	-	-	-	-	2	-	-	-	+	-	1
Deschampsia flexuosa	-	+	3	1	-	3	2	3	3	3	-	-	3	2	3	2
Festuca ovina	-	2	-	-	-	-	-	-	-	3	-	-	-	-	4	3
<u>Molinia caerulea</u>	5	3	5	5	1	-	5	5	3	4	4	5	-	-	1	4
Nardus stricta	1	3	+	3	-	-	-	+	4	5	-	-	-	-	3	3
Sieglingia decumbens	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Carex binervis	-	1	-	-	-	-	-	-	-	4	-	-	-	-	-	+
Juncus squarrosus	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	+
Scirpus caespitosus	3	4	1	-	-	-	1	-	3	-	-	-	-	-	+	-

TABLE 4 CONTD.

Species	Q1 (S1)	Q11 (S1)	Q13 (S1)	Q1 (S2)	Q5 (S2)	Q4 (S3)	Q12 (S3)	Q14 (S3)	Q17 (S3)	Q8 (S4)	Q1 (S6)	Q9 (S6)	Q5 (S7)	Q10 (S7)	Q12 (S7)	Q4 (S8)
Calluna vulgaris	8	8	7	8	8	8	9	9	8	5	9	9	9	9	5	9
Erica cinerea	1	4	3	-	3	4	-	-	-	-	+	+	+	4	1	1
Erica tetralix	3	-	4	-	1	-	-	-	-	-	3	-	-	-	+	-
Galium hercynicum	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
Potentilla erecta	-	1	-	1	-	-	+	-	-	3	-	-	-	-	1	1
Vaccinium myrtillus	-	5	4	2	4	3	1	1	2	5	1	2	2	-	-	2
Hypnum cupressiforme	-		+	-	-		-	-	-	-	-		3		-	-
Pleurozium schreberi	3	3	3	3	-	4	-	-	-	3	+	3	-	3	-	-
Polytrichum species	-		5	+	+		3	3	4	-	+	-	-	-	-	-
Sphagnum species	-	-	-	-	5		-	-	-	-	-	-	-	-	-	-

TABLE 5 PTERIDIUM AQUILINUM-AGROSTIS SPECIES-FESTUCA OVINA NODUM

Species	Q7 (S1)	Q8 (S1)	Q9 (S1)	Q10 (S1)	Q12 (S1)	Q14 (S1)	Q15 (S1)	Q1 (S3)	Q2 (S3)	Q5 (S3)	Q11 (S3)	Q15 (S3)	Q16 (S3)	Q18 (S3)	Q19 (S3)	Q20 (S3)	Q21 (S3)	Q2 (S4)	Q3 (S4)	Q4 (S4)
Pteridium aquilinum	8	7	8	9	8	8	7	7	7	6	7	8	8	8	7	5	8	8	8	7
Agrostis species	8	8	8	7	+	1	3	3	4	4	9	5	5	5	8	3	5	7	7	7
Anthoxanthum odoratum	-				-	-	3	3	3	3	3	1	3	4	3	3	4	4		
Deschampsia flexuosa	-	-	-	-	5	6	8	-	5	-	-	5	6	5	3	1	4	-	-	-
Festuca ovina	-	4	-	-				8		4	-		3		-	8		3	3	-
Holcus lanatus	-	-	3	3	-	-	-	3	-	-	-	-	-	-	3	-	-	7	4	3
Molinia caerulea	+	-	-	-	1	2	-	-	-	-	-	3	3	1	-	2	-	-	-	-
Poa pratensis	-	4	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3	3
Carex species	-	-	-	-	+	1	+	+	1	-	-	1	1	-	-	-	+	-	-	-
Luzula species	1	-	+	-	-	-	-	3	-	-	-	-	-	-	-	3	-	2	1	3
Calluna vulgaris	-	-	-	-	3	4	-	-	1	-	+	1	+	-	-	4	-	-	-	-
Cerastium Lolosteoides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 5 CONTD.

Species	Q5 (S4)	Q6 (S4)	Q10 (S4)	Q12 (S4)	Q14 (S4)	Q16 (S4)	Q18 (S4)	Q19 (S4)	Q3 (S5)	Q4 (S5)	Q5 (S5)	Q8 (S5)	Q4 (S6)	Q1 (S7)	Q2 (S7)	Q7 (S7)	Q13 (S7)	Q3 (S8)
<u>Pteridium aquilinum</u>	7	8	8	7	8	8	8	5	7	8	10	9	10	9	5	9	8	8
<u>Agrostis species</u>	6	7	5	5	7	4	5	6	5	5	7	8	8	5	5	7	9	8
<u>Anthoxanthum odoratum</u>			-	4	-	+	3											
Deschampsia flexuosa	+	-	5	5	-	4	5	6	-	3	-	2	4	3	+	3	-	-
Festuca ovina	6	4			-				6		-	4	1	6	5	4	4	4
Holcus lanatus	3	3	-	-	4	4	3	+	4	-	3	-	-	-	-	-	-	-
Molinia caerulea	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	4
Poa pratensis	3	4	1	-	4	-	+	-	-	1	4	1	-	-	-	-	-	-
Carex species	1	-	1	-	-	-	-	1	1	1	-	-	1	-	-	1	1	-
Luzula species	2	3	3	-	1	2	2	3	+	-	-	+	1	1	3	-	2	1
Calluna vulgaris	-	-	3	-	-	-	-	-	3	-	-	+	-	4	3	3	-	3
Cerastium Lolosteoides	2	+	-	-	-	-	-	-	-	-	1	-	+	-	-	-	+	-

TABLE 5 CONTD.

Species	Q7 (S1)	Q8 (S1)	Q9 (S1)	Q10 (S1)	Q12 (S1)	Q14 (S1)	Q15 (S1)	Q1 (S3)	Q2 (S3)	Q5 (S3)	Q11 (S3)	Q15 (S3)	Q16 (S3)	Q18 (S3)	Q19 (S3)	Q20 (S3)	Q21 (S3)	Q2 (S4)	Q3 (S4)	Q4 (S4)
Erica cinerea	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Galium hercynicum</u>	3	4	3	1	1	-	1	4	2	5	2	3	4	3	3	3	7	3	3	4
Oxalis acetosella	-	3	5	4	-	-	-	3	4	4	-	1	-	-	-	-	-	2	4	3
<u>Potentilla erecta</u>	-	-	-	+	1	1	1	1	1	1	1	-	+	-	1	3	2	2	1	1
Rumex acetosella	-	-	1	-	-	-	-	-	-	1	-	-	-	-	1	1	1	1	-	-
Vaccinium myrtillus	-	-	-	-	5	5	-	-	3	-	-	-	-	-	-	-	-	-	-	-
Brachythecium velutinum	4	3	3	3	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleurozium schreberi	1	3	-	-	3	4		3		5	-	-	-		-	3	-	-	-	-
Polytrichum species	-	-	-	-	+			3	6	-	-	+	-	3	+	+	3	-	-	-
Rhytidiadelphus squarrosus	-	-	-	-	-	-	-	+	+	3	-	+	4	3	3	-	4	3	3	5

TABLE 5 CONTD.

Species	Q5 (S4)	Q6 (S4)	Q10 (S4)	Q12 (S4)	Q14 (S4)	Q16 (S4)	Q18 (S4)	Q19 (S4)	Q3 (S5)	Q4 (S5)	Q5 (S5)	Q8 (S5)	Q4 (S6)	Q1 (S7)	Q2 (S7)	Q7 (S7)	Q13 (S7)	Q3 (S8)
Erica cinerea	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	4	-	-
Galium hercynicum	4	5	5	4	2	2	4	3	4	3	2	3	3	5	7	3	2	4
Oxalis acetosella	3	2	-	-	5	4	3	1	-	-	5	1	3	-	-	-	-	1
Potentilla erecta	2	1	1	2	1	1	1	1	2	1	1	-	-	2	2	2	2	2
Rumex acetosella	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Vaccinium myrtillus	+	-	3	2	-	-	-	+	-	-	-	-	2	2	-	-	-	2
Brachythecium velutinum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleurozium schreberi	3	+		3	-	3					-	3	3	-	-		-	+
Polytrichum species	-	-	3	-	-	7	4	4	4	6	+	3	+	-	-	3	-	-
Rhytidiadelphus squarrosus	3	+	3	3	+	3	3	3	3	3	+	+	-	-	-	+	-	-

TABLE 6 CONIC HILL PURE PTERIDIUM AQUILINUM NODUM

Species	Q2 (S1)	Q3 (S1)	Q4 (S1)	Q5 (S1)	Q6 (S1)	Q2 (S2)	Q3 (S2)	Q9 (S3)	Q10 (S3)	Q13 (S3)	Q5 (S6)	Q3 (S7)
Pteridium aquilinum	10	10	9	8	8	9	9	9	9	9	10	9
Agrostis tenuis	-	+	-	-	-	-	-	-	-	4	3	+
Anthoxanthum odoratum	-	-	-	-	-	-	-	-	-	-	3	3
Deschampsia flexuosa	5	1	4	7	-	-	3	-	-	4	-	1
Festuca ovina	-	-	-	-	-	-	-	-	-	3	-	1
Molinia caerulea	-	-	4	-	-	-	-	1	-	3	-	-
Carex binervis	-	-	-	-	-	-	-	-	-	-	+	3
Luzula species	+	-	-	-	-	-	-	-	-	-	-	+
Calluna vulgaris	-	-	-	-	-	-	+	1	-	-	-	-
Galium hercynicum	-	-	1	-	-	-	1	-	-	2	2	3
Oxalis acetosella	-	3	-	-	-	3	5	-	-	+	4	-
Potentilla erecta	-	-	-	-	-	-	-	-	-	1	+	-
Vaccinium myrtillus	-	-	-	+	-	-	1	-	-	-	-	-
Pleurozium schreberi	-	-	-	-	-	-		-	-	-	-	-
Polytrichum species	-	-	-	-	-	-	5	1	-	+	-	-
Rhytidiadelphus squarrosus	-	-	-	-	-	4		+	-	+	+	3
Litter	9	10	9	8	10	9	8	10	10	8	9	9

<u>TABLE 7 SOURHOPE MIXED ACID GRASSLAND NODUM</u>

Species	Q3 (S1)	Q5 (S1)	Q6 (S1)	Q8 (S1)	Q1 (S2)	Q8 (S2)	Q23 (S2)	Q30 (S2)	Q34 (S2)	Q39 (S2)	Q1 (S3)	Q9 (S4)	Q12 (S4)	Q13 (S4)	Q17 (S4)	Q18 (S4)	Q1 (S5)
Pteridium aquilinum	1	5	+	-	-	-	-	-	-	+	1	+	-	5	4	1	-
<u>Agrostis canina</u>	3	1	2	2	3	3	3	3	-	4	3	8	4	3	3	3	-
Agrostis tenuis	-	-	-	-				-	-	-	-	-	-	-			-
Anthoxanthum odoratum	-	-	-	-	4	3	+	3	+	4	3	8	4	3	3	3	3
<u>Deschampsia flexuosa</u>	4	4	3	4	4	4	3	4	3	3	1	4	3	3	4	4	5
<u>Festuca ovina</u>	5	5	4	5	4	4	3	3	2	3	6	3	3	3	5	4	5
Festuca rubra	-				-	-	-	-	-	-	-	-	-	-	-	-	-
Molinia caerulea	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Nardus stricta</u>	8	8	8	8	8	8	8	9	9	8	6	7	6	8	7	7	6
Carex species	-	+	-	-	2	1	+	-	-	1	1	1	-	+	-	-	1
<u>Luzula multiflora</u>	+	1	+	+	3	2	1	-	3	+	-	+	-	3	2	2	2
<u>Galium hercynicum</u>	3	3	3	3	2	3	3	3	2	3	4	4	5	2	4	5	2

TABLE 7 CONTD.

Species	Q3 (S1)	Q5 (S1)	Q6 (S1)	Q8 (S1)	Q1 (S2)	Q8 (S2)	Q23 (S2)	Q30 (S2)	Q34 (S2)	Q39 (S2)	Q1 (S3)	Q9 (S4)	Q12 (S4)	Q13 (S4)	Q17 (S4)	Q18 (S4)	Q1 (S5)
Potentilla erecta	2	3	4	3	3	4	3	2	2	3	3	2	3	3	3	3	5
Vaccinium myrtillus	1	2	2	-	2	2	4	2	2	1	-	-	-	+	-	2	3
Pleurozium schreberi	+	+	-	-	-	-	-	-	3	+	-	-	-	+	-	-	-
Polytrichum commune	-	-	-	-	-	-	-	-	4	3	-	4	4	-	-	-	-
Rytidiadelphus squarrosus	-	+	-	-	+	+	3	-	-	+	+	-	-	-	-	-	-

TABLE 8 SOURHOPE PTERIDIUM AQUILINUM-FESTUCA OVINA-AGROSTIS SPECIES NODUM

Species	Q1 (S1)	Q2 (S1)	Q4 (S1)	Q7 (S1)	Q11 (S1)	Q15 (S1)	Q17 (S1)	Q19 (S1)	Q21 (S1)	Q4 (S2)	Q6 (S2)	Q17 (S2)	Q21 (S2)	Q24 (S2)	Q26 (S2)	Q27 (S2)	Q28 (S2)	Q37 (S2)	Q38 (S2)	Q40 (S2)
Pteridium aquilinum	8	7	8	8	8	8	5	6	6	7	8	8	8	9	8	9	9	9	8	8
Agrostis canina	5	2	4	4	3	5	6	5	-	-	3	-	-	-	-	3	-	5	-	6
Agrostis tenuis	-	-						-	7	4	-	4	3	4	4		3		8	-
Anthoxanthum odoratum	4	3	3	4	4	5	4	4	5	3	3	4	3	4	5	3	3	5	4	6
Deschampsia caespitosa	-	-	-	-	-	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Deschampsia flexuosa	4	4	6	6	7	5	5	3	-	5	3	-	5	5	5	6	4	3	1	1
Festuca ovina	6	8	7	7	7	5	4	8	5	7	5	7	5	7	5	5	6	-	3	5
Festuca rubra	-	-			-	-	-			-	-	-	-	-	-	-	-	-	-	-
Holcus lanatus	-	-	-	-	-	-	-	-	-	4	6	3	4	-	1	4	5	4	-	3
Nardus stricta	+	3	3	4	-	-	-	-	-	3	-	1	4	-	4	-	-	-	-	-
Poa pratensis	4	2	2	3	1	-	6	4	5	1	2	4	3	1	3	-	2	1	-	-
Carex species	-	-	+	+	1	2	-	2	1	-	+	1	-	+	-	-	-	-	-	1

TABLE 8 CONTD.

Species	Q41 (S2)	Q4 (S3)	Q5 (S3)	Q6 (S3)	Q7 (S3)	Q8 (S3)	Q9 (S3)	Q11 (S3)	Q12 (S3)	Q13 (S3)	Q5 (S4)	Q6 (S4)	Q7 (S4)	Q8 (S4)	Q15 (S4)	Q20 (S4)	Q22 (S4)	Q3 (S5)	Q4 (S5)
Pteridium aquilinum	9	9	9	9	8	8	9	8	9	8	9	9	8	9	8	9	8	6	6
Agrostis canina	-			-	-	-	-		-	3	5			-	-	4	5	5	-
Agrostis tenuis	4	4	3	4	5	4	3	3	4	-	-	3	5	4	5	-	-	-	5
Anthoxanthum odoratum	4	4		-	5	4	3	3	4	3	5	3	5	4	5	4	5	5	5
Deschampsia caespitosa	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	4	+	1
Deschampsia flexuosa	5	3	4	-	5	3	5	5	5	4	4	5	4	4	3	4	-	4	4
Festuca ovina	5	8	4	-	5	5	5	-	3	3	-	-	-	+	7	4	5	4	5
Festuca rubra	-	-	-	-	-		-	-		-	-	-	-	-	-	-	-	-	
Holcus lanatus	3	-	4	7	4	-	-	8	6	7	4	4	4	3	2	-	3	-	2
Nardus stricta	-	3	4	-	-	3	3	-	-	-	-	3	-	-	1	4	-	-	4
Poa pratensis	-	2	1	4	1	3	-	3	-	-	-	-	1	-	1	-	2	-	2
Carex species	-	-	-	-	+	-	+	-	1	2	-	-	-	-	1	+	-	-	+

TABLE 8 CONTD.

Species	Q1 (S1)	Q2 (S1)	Q4 (S1)	Q7 (S1)	Q11 (S1)	Q15 (S1)	Q17 (S1)	Q19 (S1)	Q21 (S1)	Q4 (S2)	Q6 (S2)	Q17 (S2)	Q21 (S2)	Q24 (S2)	Q26 (S2)	Q27 (S2)	Q28 (S2)	Q37 (S2)	Q38 (S2)	Q40 (S2)
Luzula multiflora	3	1	1	1	1	-	1	1	+	2	2	2	3	2	3	2	1	1	-	1
Campanula rotundifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Conopodium majus	-	-	-	-	-	-	-	+	+	+	-	+	-	-	1	-	-	+	-	-
Galium hercynicum	3	4	4	3	3	3	4	2	2	3	5	-	4	3	4	5	4	6	3	4
Oxalis acetosella	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3	-
Potentilla erecta	1	+	2	2	2	2	1	1	1	1	+	1	2	2	3	2	2	2	1	2
Rumex acetosella	-	-	-	-	-	-	+	-	-	-	-	-	1	-	+	-	-	-	-	-
Vaccinium myrtillus	-	-	-	-	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
Viola species	-	-	-	-	+	-	-	1	1	-	-	-	-	1	-	-	2	-	-	-
Eurhynchium praelongum	-	-	-	-	-	+	-	-	-	+	+	-	-	-	-	-	-	+	-	-
Rhytidiadelphus squarrosus	2	3	-	+	+	+	+	-	-	+	+	+	-	-	-	3	+	+	+	+

TABLE 8 CONTD.

Species	Q41 (S2)	Q4 (S3)	Q5 (S3)	Q6 (S3)	Q7 (S3)	Q8 (S3)	Q9 (S3)	Q11 (S3)	Q12 (S3)	Q13 (S3)	Q5 (S4)	Q6 (S4)	Q7 (S4)	Q8 (S4)	Q15 (S4)	Q20 (S4)	Q22 (S4)	Q3 (S5)	Q4 (S5)
<u>Luzula multiflora</u>	2	2	+	-	1	1	3	-	1	1	1	-	4	1	2	-	+	+	1
Campanula rotundifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	2	-	-
Conopodium majus	+	+	-	-	-	+	-	-	-	-	-	-	-	-	+	-	+	-	-
<u>Galium hercynicum</u>	6	4	4	3	4	6	4	4	3	4	-	-	4	5	3	5	6	6	4
Oxalis acetosella	-	-	-	-	-	-	-	-	-	-	3	3	2	2	-	-	-	-	-
<u>Potentilla erecta</u>	2	3	2	-	3	2	3	1	2	1	1	-	1	-	3	1	2	1	2
Rumex acetosella	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Vaccinium myrtillus	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Viola species	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eurhynchium praelongum	-	-	-	-	-	-	+	-	-	-	+	-	+	-	-	-	-	-	-
Rhytidiadelphus squarrosus	-	+	+	3	-	-	+	+	-	-	5	5	3	3	-	-	-	-	+

TABLE 9 SOURHOPE PTERIDIUM AQUILINUM-NARDUS STRICTA PHASE

Species	Q10 (S2)	Q11 (S2)	Q12 (S2)	Q15 (S2)	Q16 (S2)	Q19 (S2)	Q20 (S2)	Q25 (S2)	Q29 (S2)	Q32 (S2)	Q33 (S2)	Q36 (S2)	Q3 (S3)	Q16 (S4)
Pteridium aquilinum	8	8	9	8	8	8	10	8	9	9	9	8	9	8
Agrostis canina		1	1				3		-			-	-	
Agrostis tenuis	3	-	-	3	4	3	-	3	3	3	4	5	4	6
Anthoxanthum odoratum	3	-	-	-	4	3	3	3	3	3	4	5	4	6
Deschampsia flexuosa	5	4	5	5	4	5	5	4	5	5	4	3	5	3
Festuca ovina	5	3	3	3	6	5	4	3	4	-	5	4	-	4
Holcus lanatus	-	-	-	-	-	4	3	4	-	-	-	4	-	-
Nardus stricta	5	7	7	8	5	6	6	6	5	5	6	6	5	5
Poa pratensis	-	-	-	-	1	+	-	-	-	-	-	-	-	-
Carex species	+	-	-	-	-	-	-	-	-	-	+	-	1	1
Luzula species	1	1	1	1	2	2	3	-	2	-	-	4	-	2
Galium hercynicum	4	4	4	4	3	4	4	4	4	5	4	3	5	4
Potentilla erecta	1	-	1	2	3	3	2	2	2	1	2	2	1	2
Vaccinium myrtillus	1	1	3	1	-	-	1	-	2	-	-	-	-	-
Eurhynchium praelongum	-		+	-	3	+	+	-	-		-	-	-	-
Rhytidiadelphus squarrosus	-	3	3	+	-	-	-	+	+	3	3	+	3	-

<u>TABLE 10 SOURHOPE PURE PTERIDIUM AQUILINUM NODUM</u>

Species	Q13 (S1)	Q16 (S1)	Q3 (S2)	Q5 (S2)	Q9 (S2)	Q22 (S2)	Q35 (S2)	Q21 (S4)	Q2 (S5)
<u>Pteridium aquilinum</u>	9	9	8	9	9	10	10	8	10
<u>Agrostis canina</u>	-	-	4	-	-	3	3	3	3
<u>Agrostis tenuis</u>	5	1	-	4	2		-	-	-
Anthoxanthum odoratum	4	-	3	3	1		+	-	3
<u>Deschampsia flexuosa</u>	3	3	4	5	4	4	4	1	4
Festuca ovina	1	-	4	-	3	-	-	-	-
Molinia caerulea	-	-	-	-	-	-	-	3	-
Nardus stricta	-	-	4	-	-	-	+	-	+
Poa pratensis	-	4	-	-	-	-	-	-	-
Carex species	+	1	1	-	+	-	-	-	1
Luzula species	+	-	2	+	+	-	-	-	1
<u>Galium hercynicum</u>	4	4	4	3	3	4	3	1	3
Oxalis acetosella	-	-	-	-	-	-	1	3	-
Potentilla erecta	2	1	1	-	1	+	-	-	1
Vaccinium myrtillus	-	-	-	-	1	-	-	-	-
Viola species	1	1	-	-	-	-	-	-	-
<u>Rhytidiadelphus squarrosus</u>	3	+	3	3	3	6	4	5	-
Litter	8	9	8	8	9	7	8	8	9

APPENDIX B

SOIL PROFILE DESCRIPTIONS

DESCRIPTION OF KINGSLAGGAN PROFILE I

Slope: $8\frac{1}{2}^{\circ}$ Surface Drainage: imperfect

Aspect: NW Altitude: 185 m

Vegetation: short, dense Pteridium aquilinum (I.B.D. = 110.5) with 90% cover. Ground vegetation dominated by Agrostis tenuis and Festuca ovina (9) with Anthoxanthum odoratum (4), Galium hercynicum (3)

Drainage Class: imperfect Parent Material: till derived from Ordovician shale and granite

Horizon	Depth or thickness	
L	3 cm	Grass turf
H	3 cm	Very dark greyish brown (10 YR 3/2) humus with small percentage of mineral matter, abundant rhizomes; merging into
A	0 - 9 cm	Dark brown (10 YR 3/3) humose loam, fine granular, considerable quantity moder organic matter, common rhizomes. Narrow, undulating change to
B	9 - 34 cm	Dark brown (10 YR 4/3) loam, stony, granite and shale, moderately developed medium subangular blocky, firm, common fine fissures and medium pores, moderate permeability, common rhizomes. Sharp, undulating change to

Cg	34+ cm	Light yellowish brown (10 YR 6/4) with ochreous mottles concentrated on old root channels, sandy loam, extremely stony, fine subangular blocky, slightly sticky, few fine pores and fissures, slow permeability.
Soil Type		Slightly gleyed Brown Forest Soil of low base status.

DESCRIPTION OF KINGSLAGGAN PROFILE 2

Slope: 8° Surface Drainage: imperfect

Aspect: NNW Altitude: 185 m

Vegetation: Nardus stricta (6), Molinia caerulea (5), Calluna vulgaris (5), Scirpus caespitosus (4)

Drainage Class: imperfect Parent Material: till derived from Ordovician shale and granite

Horizon	Depth or thickness	
L	5 cm	Calluna and Nardus litter
H	4 cm	Very dark brown (10 YR 2/2) mor humus with few quartz grains. Narrow, undulating change to
A	0 - 5 cm	Very dark greyish brown (10 YR 3/2), sandy loam, stony mainly granite, weakly developed medium subangular blocky, slightly sticky, few pores, slow permeability, fairly low organic matter content. Narrow, irregular change to
B_1	5 - 11 cm	Very dark greyish brown (10 YR 3/2) with discontinuous indurated ochreous mottles or iron deposition at variable depth. Narrow, irregular change to
B_2	11 - 41 cm	Strong brown (7.5 YR 5/6) sandy loam, stony, granite and shale, moderately developed medium angular blocky, slightly sticky, common, fine pores and fissures, moderate permeability, iron deposition at foot. Narrow, undulating change to

C	41+ cm	Dark yellowish brown (10 YR 4/4) sandy loam, extremely stony, structure and porosity same as B_2, firm, iron deposition mainly on stones.
Soil Type		Weakly developed Iron Podsol.

DESCRIPTION OF KINGSLAGGAN PROFILE 5

Slope: 21° convex–concave   Surface Drainage: free

Aspect: W20°N   Altitude: 185 m

Vegetation: Tall *Pteridium aquilinum* (I.B.D. = 129.3) giving 90% cover but with complete ground cover of *Agrostis tenuis* (8), *Festuca ovina* (6), *Anthoxanthum odoratum* (4), *Oxalis acetosella* (3) with various forbs.

Drainage Class: imperfect   Parent Material: Ordovician shale

Horizon	Depth or thickness	
L	2.5 cm	Grass turf
A_1	0 - 7.5 cm	Very dark greyish brown (10 YR 3/2) very humose loam, slightly stony, weakly developed coarse granular, friable, common medium - large fissures and medium pores, rapid permeability, high content of mull organic matter, earthworms, common rhizomes; merging into
B	7.5 - 40 cm	Dark yellowish brown (10 YR 4/4) with darker organic staining, loam, very stony, moderately developed fine subangular blocky, friable, abundant medium-large fissures, rapid permeability, common rhizomes to 35 cm; merging into
Cg	40+ cm	Light olive brown (2.5 YR 5/4) with ochreous mottles, loam, extremely stony, structureless firm, common fine pores and fissures, moderate permeability.
Soil Type		Slightly gleyed Brown Forest Soil.

DESCRIPTION OF KINGSLAGGAN PROFILE 6

Slope: 18° Surface Drainage: free

Aspect: due W Altitude: 185 m

Vegetation: ecotone, thin cover (40%) Pteridium aquilinum (I.B.D. = 63.3) with ground vegetation of Calluna vulgaris (7), Agrostis tenuis (6), Festuca ovina (5), Anthoxanthum odoratum (4), Erica cinerea (3), Potentilla erecta (3)

Drainage Class: free Parent Material: colluvium derived from Ordovician shale

Horizon	Depth or thickness	
L	2.5 cm	Turf
A_1	0 - 9 cm	Very dark greyish brown (10 YR 3/2) very humose loam, slightly stony, weakly developed medium granular, friable, common fine pores and fissures, moderate permeability, high content of mull organic matter, few rhizomes; merging into
B	9 - 50 cm	Dark yellowish brown (10 YR 4/4) with darker organic stains, loam, stony, weakly developed medium subangular blocky, friable, porosity higher in upper section, moderate permeability, few rhizomes to 30 cm. Narrow change to
C	50+ cm	Yellowish brown (10 YR 5/4) loamy sand, stony, structureless, firm, few fine pores and fissures, moderate permeability.
Soil Type		Brown Forest Soil of low base status.

DESCRIPTION OF KINGSLAGGAN PROFILE 11

Slope: 10° concave Surface Drainage: imperfect

Aspect: due W Altitude: 208 m

Vegetation: Calluna vulgaris (8), Vaccinium myrtillus (4), Agrostis tenuis (3), Festuca ovina (3), Carex binervis (3).

Drainage Class: free		Parent Material: till derived mainly from Ordovician shale.

Horizon	Depth or thickness	
H	12 cm	Black (5 YR 2/1) mor humus with few quartz grains, one rhizome; merging into
A_1	0 - 1.5 cm	Dark brown (10 YR 3/3) discontinuous predominantly mineral horizon; remains 1 dead rhizome. Narrow change to
A_2	1.5 - 9 cm	Dark greyish brown (10 YR 4/2) humose loam, slightly stony. Sharp, undulating change to clear, continuous indurated iron pan.
Iron Pan		
B	9 - 30 cm	Dark yellowish brown (10 YR 4/4) loam, very stony; merging into
C	30+ cm	Dark yellowish brown (10 YR 4/4), stones dominant.
Soil Type		Peaty Podsol with iron pan.

DESCRIPTION OF KINGSLAGGAN PROFILE 12

Slope: 10° concave	Surface Drainage: imperfect
Aspect: due W	Altitude: 208 m

Vegetation: Calluna vulgaris (d) with Agrostis tenuis (a), Galium hercynicum (o) Carex binervis (o), Erica cinerea (o). One frond of Pteridium aquilinum

Drainage Class: free	Parent Material: Ordovician shale

Horizon	Depth or thickness	
L	2 cm	Turf
H	4 cm	Black (10 YR 2/1) mor humus with few quartz grains, few rhizomes. Sharp irregular change to

A	0 - 11.5 cm	Very dark greyish brown (10 YR 3/2) humose loam with distinct ochreous mottles and black organic staining, humose loam, stony, moderately developed medium subangular blocky, firm, few medium pores and fissures, moderate permeability, few rhizomes. Sharp undulating change to thin and discontinuous iron pan
Iron Pan		
B	11.5 - 31.5 cm	Yellowish brown (10 YR 5/8) with dark yellowish brown mottles (10 YR 4/4) loam, very stony, very weakly developed platy, friable, few fine pores and fissures, moderate permeability, no rhizomes; merging into
C	31.5+ cm	Yellowish brown (10 YR 5/8), stones dominant.
Soil Type		Weakly developed Podsol with iron pan.

DESCRIPTION OF KINGSLAGGAN PROFILE 15

Slope: 10° concave

Surface Drainage: imperfect

Aspect: due W

Altitude: 208 m

Vegetation: clump of mature *Calluna vulgaris* in centre of which several weak, short fronds of *Pteridium aquilinum*, *Agrostis tenuis* (o), *Oxalis acetosella* (o).

Drainage Class: imperfect

Parent Material: gravelly colluvium derived from Ordovician shale.

Horizon	Depth or thickness	
L	3.5 cm	not a real litter layer; differentiated from A by root concentration.
A_1	0 - 16 cm	Very dark greyish brown (10 YR 3/2) very humose loam, slightly stony, weakly developed fine subangular blocky, friable, abundant fine - large pores and fissures, moderate permeability, high content of mull organic matter, abundant rhizomes: merging into

B	16 - 41 cm	Yellowish brown (10 YR 5/4) with darker organic staining (gradual decrease in organic matter content down profile), sandy loam, moderately developed medium subangular blocky, friable, few fine pores and fissures, moderate permeability, no rhizomes; merging into
Cg	41+ cm	Light brownish grey (2.5 Y 6/2) with distinct common fine mottles, loamy sand extremely stony, structureless, very firm, rare pores, slow permeability.
Soil Type		Slightly gleyed Brown Forest Soil of low base status.

DESCRIPTION OF CONIC HILL PROFILE I

Slope: 8° slightly convex

Surface Drainage: imperfect

Aspect: S30°W

Altitude: 154 m

Vegetation: relatively open *Pteridium aquilinum* with ground vegetation of *Agrostis tenuis* (a), *Anthoxanthum odoratum* (a), *Holcus lanatus* (a), *Oxalis acetosella* (a), *Juncus effusus* (f), *Endymion non-scriptus* (f)

Drainage Class: free

Parent Material: Old Red Sandstone conglomerate

Horizon	Depth or thickness	
L	1 cm	Bracken litter
H	1.5 cm	Thin dark brown moder humus and sand; merging into
A_1	0 - 16.5 cm	Reddish brown (5 YR 4/4) with darker organic matter (5 YR 3/2) patches, slightly humose loam, slightly stony, moderately developed medium subangular blocky, very friable, abundant medium fissures and fine pores, rapid permeability, abundant rhizomes. Narrow change to

B_1	16.5 - 41 cm	Very variable colour due to mixed lithology pinkish grey (5 YR 6/2), yellowish red (5 YR 4/6), loamy sand, very weakly developed medium subangular blocky, very firm, few fine fissures, moderate permeability, no rhizomes, the characteristics of this horizon appear to be derived from parent material; merging into
B_2	41 - 95 cm	Yellowish red (5 YR 5/6) loam, slightly stony, structure as B_1, very friable, few fine pores, moderate permeability; merging into
C	95+ cm	Reddish brown (5 YR 5/3) gravelly loam.
Soil Type		Brown Forest Soil of low base status.

DESCRIPTION OF CONIC HILL PROFILE 2

Slope: 5° — Surface Drainage: imperfect

Aspect: S30°W — Altitude: 154 m

Vegetation: short, dense *Pteridium aquilinum* with very sparse ground cover of *Deschampsia flexuosa* (f), *Molinia caerulea* (o), *Endymion non-scriptus* (o)

Drainage Class: imperfect — Parent Material: Old Red Sandstone conglomerate

Horizon	Depth or thickness	
L	2.5 cm	Bracken litter
H	7.5 cm	Black (5 YR 2/1) mor humus with few quartz grains, rhizomes concentrated at foot; merging into
A_1		Very thin transitional dark brown horizon containing concentration of rhizomes.
A_2	0 - 10 cm	Dark reddish grey (5 YR 4/2) humose loam, stony, structureless, friable, few fine pores, moderate permeability, occasional rhizomes. Narrow undulating change to

B	10 - 45 cm	Mixed reddish brown (5 YR 4/4) and reddish yellow (7.5 YR 6/6) loam, stony, very weakly developed coarse subangular blocky, friable, common fine fissures and pores, moderate permeability, no rhizomes; merging into
Cg	45+ cm	Reddish brown (5 YR 5/3) with ochreous and grey mottles, loamy sand, very stony, structure as B, non-sticky, few fine pores.

Soil Type: Slightly gleyed Iron Podsol.

DESCRIPTION OF CONIC HILL PROFILE 3

Slope: 9^{o}

Surface Drainage: free

Aspect: S30^{o}W

Altitude: 154 m

Vegetation: *Calluna vulgaris* (d), *Molinia caerulea* (a), *Erica tetralix* (o), *Erica cinerea* (o), 1 frond of *Pteridium aquilinum*

Drainage Class: free

Parent Material: Old Red Sandstone conglomerate

Horizon	Depth or thickness	
L	4 cm	Turf
H	6 cm	Black (5 YR 2/1) mor humus with few sand grains. Narrow change to
A_2	0 - 5 cm	Reddish grey (5 YR 5/2) with darker organic stains, slightly humose loam, stony, weakly developed platy, friable, few fine fissures and pores, moderate permeability. Sharp undulating change to
B_1	5 - 7.5 cm	Thin horizon of organic matter and iron illuviation
B_2	7.5 - 61 cm	Yellowish red (5 YR 4/8) loam, stony, weakly developed fine subangular blocky, very friable, common fine pores, moderate permeability; merging into

C	61+ cm	Reddish brown (5 YR 5/4) sandy loam, structureless, weathered conglomerate.
Soil Type		Peaty Podsol with incipient iron pan.

DESCRIPTION OF CONIC HILL PROFILE 4

Slope: 11° — Surface Drainage: imperfect

Aspect: W20°N — Altitude: 154 m

Vegetation: Calluna vulgaris (8), Molinia caerulea (5), Nardus stricta (3), Pleurozium screberi (3)

Drainage Class: free — Parent Material: Old Red Sandstone conglomerate

Horizon	Depth or thickness	
L	2.5 cm	Turf
H	7.5 cm	Very dark brown (10 YR 2/2) mor humus. Narrow change to
A_2	0 - 10 cm	Pinkish grey (7.5 YR 6/2) loamy sand, stony, structureless, very friable, common very fine pores and fissures, low organic content, moderate permeability. Narrow change to
B_1	10 - 23 cm	Mixed in colour, dark brown (7.5 YR 3/2) with grey in upper horizon, ochreous lower horizon, humose sandy loam, weakly developed medium subangular blocky, friable, common fine pores and fissures, moderate permeability, zone of organic matter and iron illuviation; merging into
B_2	23 - 35 cm	Yellowish red (5 YR 4/6) with darker organic staining, sandy loam, stony, structure and porosity as B_1; merging into
C	35+ cm	Reddish brown (5 YR 4/3) sandy loam, stony, structureless, firm, few small pores, slow permeability
Soil Type		Iron Podsol with organic illuvial B.

DESCRIPTION OF CONIC HILL PROFILE 5

Slope: 11°

Surface Drainage: free

Aspect: W5°N

Altitude: 154 m

Vegetation: dense, tall *Pteridium aquilinum* (I.B.D. = 173.6) giving 80% cover and virtually obliterating ground vegetation; litter cover 90%

Drainage Class: free

Parent Material: Old Red Sandstone conglomerate

Horizon	Depth or thickness	
L	12.5 cm	Very variable thickness of bracken litter
A_1	0 - 6 cm	Very dark grey (5 YR 3/1) very humose mixed moder organic and mineral matter, weakly developed fine subangular blocky, very friable, abundant fine pores, rapid permeability, abundant rhizomes; merging into
A_2	6 - 13 cm	Colour variable from dark grey (5 YR 4/1) at top to reddish brown (10 YR 5/3) at lower margin, loamy sand, slightly stony, structureless, firm, few fine pores, moderate permeability, few rhizomes at top, contains distinct but discontinuous band of organic matter at variable depth within horizon. Narrow, irregular change to
B	13 - 40 cm	Yellowish red (5 YR 4/8) loam, slightly stony, very weakly developed crumb, friable, common fine pores and fissures, moderate permeability; merging into
C	40+ cm	Reddish brown (2.5 YR 4/4) loamy sand, stony, structureless, very firm, rare pores and fissures, moderate permeability.
Soil Type		Weakly developed (degraded) Iron Podsol.

DESCRIPTION OF CONIC HILL PROFILE 6

Slope: 17° terraced

Surface Drainage: free

Aspect: W5°N

Altitude: 154 m

Vegetation: Calluna vulgaris (d), Molinia caerulea (co – d), Deschampsia flexuosa (f), Scirpus caespitosus (f), Vaccinium myrtillus (o), Juncus squarrosus (o).

Drainage Class: free

Parent Material: till derived from serpentine and conglomerate on bedrock of serpentine.

Horizon	Depth or thickness	
F	3.5 cm	Dark reddish brown (5 YR 2/2) partially decomposed organic matter
H	6.5 cm	Dark reddish brown (5 YR 2/2) mor humus with occasional sand grains. Sharp change to
A_1	0 - 2.5 cm	Variable in thickness mosaic of dark brown (7.5 YR 3/2) and grey, very humose, transitional between H and A_2. Narrow change to
A_2	2.5 - 7.5 cm	Greyish brown (10 YR 5/2) sandy loam, stony mainly quartz, moderately developed platy, friable, common fine fissures, rapid permeability. Sharp change to
B_1	7.5 - 10 cm	Discontinuous zone of dark reddish brown (5 YR 2/2) organic matter illuviation.
B_2	10 - 33 cm	Reddish brown (5 YR 5/4) dominant but rather mixed in colour due to mixed lithology, sandy loam, very stony olivine and sandstone, very weakly developed fine angular blocky, friable, common fine pores and fissures, moderate permeability; merging into
C	33+ cm	Reddish brown (5 YR 5/3) sand, stones dominant, weathered serpentine.

Soil Type: Iron Podsol with organic illuvial B.

DESCRIPTION OF CONIC HILL PROFILE 7

Slope: 15°　　Surface Drainage: free

Aspect: W5°N　　Altitude: 154 m

Vegetation: complete canopy of *Pteridium aquilinum* of medium height with discontinuous ground layer of *Agrostis canina* (f), *Deschampsia flexuosa* (f), *Anthoxanthum odoratum* (o), *Potentilla erecta* (o).

Drainage Class: free　　Parent Material: till derived from serpentine and conglomerate on serpentine bedrock.

Horizon	Depth or thickness	
L	3.5 cm	Bracken litter
H	6.5 cm	Dark reddish brown (5 YR 2/2) humus with considerable mineral component, extremely abundant rhizomes; merging into
A_1	0 - 13 cm	Dark reddish brown (5 YR 3/3) humose loam, slightly stony, fine subangular blocky, very friable, abundant fine - medium pores and fissures, rapid permeability, high organic content, common rhizomes; merging into
B	13 - 33 cm	Yellowish red (5 YR 4/8) loam, stony mainly serpentine, weakly developed fine angular blocky, common fine pores and fissures, moderate permeability, no rhizomes; merging into
C	33+ cm	Reddish brown (2.5 YR 5/4), sandy loam, extremely stony, sandstone and serpentine, structureless, very firm.

Soil Type　　Brown Forest Soil of low base status.

DESCRIPTION OF CONIC HILL PROFILE 10

Slope: 22° terraced　　Surface Drainage: imperfect

Aspect: S20°W　　Altitude: 146 m

Vegetation: few short fronds of Pteridium aquilinum (I.B.D. = 2.97) with no cover value; ground vegetation of Calluna vulgaris (7), Molinia caerulea (7), Nardus stricta (4), Scirpus caespitosus (3), Erica tetralix (3).

Drainage Class: poor

Parent Material: till derived from Old Red Sandstone conglomerate and serpentine

Horizon	Depth or thickness	
L	2 cm	Turf
H	4 cm	Waterlogged black (5 YR 2/1) mor with no mineral component. Narrow, irregular change to
A_1	0 - 7.5 cm	Dark greyish brown (10 YR 4/2) mixed organic and mineral layer, stony quartz and sandstone, very weakly developed fine subangular blocky, firm, common fine pores, moderate permeability; merging into
A_2g	7.5 - 18.5 cm	Pale brown (10 YR 6/3) with common distinct ochreous mottles, sandy loam, stony, weakly developed fine subangular blocky, very firm, porosity and permeability as A_1; merging to sharp change to
B_1	18.5 - 22 cm	Discontinuous dark brown (7.5 YR 3/2) organic illuvial B horizon. Narrow and irregular change to
B_2g	22 - 59 cm	Matrix reddish grey (5 YR 5/2) with prominent ochreous mottles (5 YR 5/8), sandy loam, very stony sandstone and serpentine, structure as A_2g, slightly sticky, abundant medium fissures and pores, rapid permeability; merging into
Cg	59+ cm	Light reddish brown (5 YR 6/4), sandy loam, stony, structureless, slightly sticky, slow permeability.

Soil Type: Gleyed Podsol.

DESCRIPTION OF SOURHOPE PROFILE 2

Slope: 10° convex-concave

Surface Drainage: imperfect, slightly receiving

Aspect: W36°N

Altitude: 308 m

Vegetation: short Pteridium aquilinum (I.B.D. = 45.45) with 40% cover; complete ground cover of Festuca ovina and Deschampsia flexuosa (8), Holcus lanatus (4), Agrostis tenuis (4), Nardus stricta (3), Galium hercynicum (3), Anthoxanthum odoratum (3)

Drainage Class: free

Parent Material: till derived from andesitic lavas

Horizon	Depth or thickness	
L	1.5 cm	Grass turf
H	2 cm	Black (7.5 YR 2/2) moder humus. Sharp change to
A	0 - 10 cm	Dark brown (7.5 YR 4/2) humose loam, stony, weakly developed fine subangular blocky, friable, abundant medium pores, rapid permeability, abundant rhizomes; merging into
A/B	10 - 21 cm	Dark brown (7.5 YR 4/2) slightly humose loam, very stony, structure as A, friable to fingers but resistant to spade, common fine fissures, moderate permeability, no rhizomes; merging into
B	21 - 75 cm	Dark brown (7.5 YR 4/4) loam, extremely stony, weakly developed very fine angular blocky, friable to fingers, porosity and permeability as A/B; merging into
C	75+ cm	Reddish brown (5 YR 4/4) predominantly stony, structureless, moderate permeability
Soil Type		Brown Forest Soil of low base status.

DESCRIPTION OF SOURHOPE PROFILE 6

Slope: 12° convex-concave

Surface Drainage: free

Aspect: W10°N

Altitude: 308 m

Vegetation: rather tall, dense Pteridium aquilinum (I.B.D. = 131.2) giving 85% cover and 25% litter cover. Ground vegetation of Nardus stricta (5), Deschampsia flexuosa (5), Galium hercynicum (5), Agrostis canina, Anthoxanthum odoratum (3), Mosses (3)

Drainage Class: free

Parent Material: till derived from andesitic lavas

Horizon	Depth or thickness	
L	2 cm	Bracken litter
F	2 cm	Comminuted partially decomposed litter
H	3 cm	Black (7.5 YR/N2) moder humus of variable thickness almost disappearing in places, few mineral particles, common rhizomes. Sharp, irregular change to
A_1	0 - 12 cm	Dark reddish brown (5 YR 3/4) slightly humose loam, very stony, weakly developed fine angular, blocky, friable to fingers but resistant to spade. Abundant medium fissures and pores, rapid permeability, common rhizomes to 8 cm; merging into
B	12 - 25 cm	Yellowish red (5 YR 4/8) loam, very stony, structure and consistence as A_1, common small pores and fissures, moderate permeability; merging into
C	25+ cm	Yellowish red (5 YR 4/8) stones dominant, structureless, very firm, few fine fissures, moderate permeability.
Soil Type		Shallow Brown Forest Soil of low base status.

DESCRIPTION OF SOURHOPE PROFILE 7

Slope: 11°

Surface Drainage: free

Aspect: W10°N

Altitude: 308 m

Vegetation: Nardus stricta (9), Deschampsia flexuosa (4), Festuca ovina (3), Anthoxanthum odoratum and Agrostis canina (3), Galium hercynicum (3).

Drainage Class: free | Parent Material: till derived from andesitic lavas

Horizon	Depth or thickness	
L	1.5 cm	*Nardus* rootstocks
F	4.5 cm (variable)	Comminuted litter and *Nardus* root-stock
H	1.5 cm (variable)	Black (5 YR 2/1) moder humus. Sharp, irregular change to
A_1	0 - 5 cm (variable)	Reddish brown (5 YR 4/3) with darker organic staining, slightly humose loam, very stony, weakly developed fine sub-angular blocky, firm, common fine-medium pores and fissures, moderate permeability; merging into
B	5 - 45 cm	Yellowish red (5 YR 4/8) sandy loam, very stony, structure as A_1, friable to fingers, porosity and permeability as A_1; merging into
C	45+ cm	Yellowish red (5 YR 4/8), extremely stony, gritty till, structureless, rare fine pores, moderate permeability.
Soil Type		Brown Forest Soil of low base status.

DESCRIPTION OF SOURHOPE PROFILE 8

Slope: 9° convex-concave | Surface Drainage: imperfect, slightly receiving

Aspect: due W | Altitude: 308 m

Vegetation: very dense, relatively short *Pteridium aquilinum* (I.B.D. = 201.4) giving 80% cover and 25% litter cover. Slightly flushed ground vegetation of *Holcus lanatus* (7), *Poa pratensis* (4), *Agrostis tenuis* (4), *Galium hercynicum* (3).

Drainage Class: free | Parent Material: till derived from andesitic lavas.

Horizon	Depth or thickness	
L	1.5 cm	Bracken litter and grass turf
F	1.5 cm	More decomposed litter
H	0.5 cm	Discontinuous thin very dark grey (5 YR 3/1) moder humus. Sharp change to
A_1	0 - 15 cm	Dark reddish brown (5 YR 3/4) slightly humose clay loam, stony, weakly developed fine crumb, friable, abundant medium-large fissures and fine-medium pores, rapid permeability, common rhizomes; merging into
A/C	15 - 35 cm	Yellowish red (5 YR 4/8) loam, very stony, very weakly developed fine subangular blocky, friable, common fine-medium fissures, moderate permeability, few rhizomes to 20 cm; merging into
C	35+ cm	Yellowish red (5 YR 4/8) loam, extremely stony, structureless, friable to fingers, few fine and large pores, moderate permeability.
Soil Type		Skeletal Soil with brown forest soil characteristics.

DESCRIPTION OF SOURHOPE PROFILE 10

Slope: 16° — Surface Drainage: free

Aspect: N20°E — Altitude: 323 m

Vegetation: short Pteridium aquilinum (I.B.D. = 88.92) giving 80% cover and 10% litter cover. Ground vegetation of Nardus stricta (7), Molinia caerulea (5), Deschampsia flexuosa (4)

Drainage Class: free — Parent Material: till derived from andesitic lavas

Horizon	Depth or thickness	
L	2.5 cm (variable)	Bracken litter and Nardus root-stocks
F	9 cm (variable)	Very variable in thickness comminuted and partially decomposed litter
H	11 cm	Black (5 YR 2/1) at top and reddish brown (5 YR 2/2) near foot, mor humus with very little mineral content, common rhizomes to 10 cm. Narrow and irregular change to
A	0 - 10 cm	Variable colour dark brown (7.5 YR 3/2) or brown (7.5 YR 4/2) depending on organic content, loam, stony, weakly developed fine subangular blocky, firm, few fine fissures and pores, moderate permeability, no rhizomes. Narrow undulating change to
B	10 - 21 cm	Dark reddish brown (5 YR 3/4) loam, very stony, weakly developed fine angular blocky, friable, few medium fissures and few pores, moderate permeability; merging into
C	21+ cm	Dark reddish brown (5 YR 3/4) predominantly stones gritty till, structureless, firm, few medium pores, moderate permeability.

Soil Type: Weakly developed Peaty Podsol.

DESCRIPTION OF SOURHOPE PROFILE 12

Slope: 12^{o} — Surface Drainage: free

Aspect: W20^{o}N — Altitude: 323 m

Vegetation: Nardus stricta (9), Polytrichum commune (4), Deschampsia flexuosa (3), Luzula pilosa (3), Pleurozium screberi (3)

Drainage Class: free — Parent Material: till derived from andesitic lava

Horizon	Depth or thickness	
L	3.5 cm	wet, Nardus root-stocks

F	6.5 cm	Wet, comminuted litter
H	4 cm	Wet, black (5 YR 2/1) mor humus with little mineral content. Sharp, undulating change to
A	0 - 15 cm	Very moist dark brown (10 YR 3/3) slightly humose loam, very stony, weakly developed very fine subangular blocky, firm, common fine fissures, moderate permeability; merging into
C	15+ cm	Moist yellowish red (5 YR 4/6) with less ochreous mottles (5 YR 4/3) due to lithological variation, extremely stony gritty till, very weakly developed fine angular blocky, friable to fingers but very firm to spade, rare fissures, slow permeability.

Soil Type — Skeletal Soil.

DESCRIPTION OF SOURHOPE PROFILE 13

Slope: 15° — Surface Drainage: free

Aspect: W20°N — Altitude: 323m

Vegetation: very dense Pteridium aquilinum (I.B.D. = 279.72) giving 90% cover and 70% litter cover. Sparse ground vegetation of Deschampsia flexuosa (4), Agrostis canina (3), Galium hercynicum (3)

Drainage Class: free — Parent Material: till derived from andesitic lavas

Horizon	Depth or thickness	
L	2.5 cm	Moist, bracken litter
F	1.5 cm	Very moist, partially decomposed litter
H	1 cm	Moist very thin black (5 YR 2/1) moder humus, abundant rhizomes. Sharp change to
A	0 - 10 cm	Moist, dark brown (7.5 YR 3/2) slightly humose loam, stony, weakly developed fine subangular blocky, friable, abundant medium-large pores and fissures, rapid permeability,

		common rhizomes to 8 cm; merging into
C_1	10 - 31 cm	Moist, reddish brown (5 YR 4/4) gritty loam, extremely stony, structureless, extremely firm, weakly cemented, rare fine fissures, slow permeability; merging into
C_2	31+ cm	Very moist, reddish brown (5 YR 4/4) predominantly stones, structureless, friable, common medium-large pores, moderate permeability.
Soil Type		Skeletal Soil.

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